## SHARKS, BATOIDS AND CHIMAERAS OF THE NORTH ATLANTIC



# SHARKS, BATOIDS AND CHIMAERAS OF THE NORTH ATLANTIC 

## by

David A. Ebert
Pacific Shark Research Center
Moss Landing Marine Laboratories
Moss Landing, California
United States of America
and

Matthias F. W. Stehmann ICHTHYS
Ichthyological Research Laboratory and Consultant
Hildesheimer Weg 13
22459 Hamburg, Germany

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This catalogue represents a comprehensive and updated treatment of the identification, taxonomy, distribution, biology and ecology of the sharks, rays, skates and chimaeras of the North Atlantic, FAO Areas 21 and 27. In both areas, cartilaginous fishes are caught by both target and non-target fisheries and are subject to an extremely high fishing pressure. Most species are vulnerable to overfishing because of their specific biological characteristics such as slow growth, late maturity, low reproductive potential and thus low capacity for population recovery. Such characteristics limit their capacity to recover from overfishing and it is thus essential to implement an effective framework for the management of fisheries on sharks, batoids and chimaeras. In the North Atlantic the European Community, United States of America and Canada have adopted Plans of Action for the Conservation and Management of Sharks that set down measures for the sustainable management of the fisheries concerned. The plans include recommendations to improve species-specific monitoring of catch and landings of cartilaginous fishes.

Towards this direction, this catalogue is aimed at facilitating the species specific identification of cartilaginous fishes occurring in the North Atlantic by scientists, fishery officers and observers and the interested public.

Programme manager: Johanne Fischer (FAO, Rome)
Editorial assistance: Edoardo Mostarda (FAO, Rome)
Scientific illustrator: Emanuela D'Antoni (FAO, Rome)
Digitization of distribution maps: Fabio Carocci (FAO, Rome)
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#### Abstract

This volume is a comprehensive, fully illustrated Catalogue of the Sharks, Batoid Fishes, and Chimaeras of the North Atlantic, encompassing FAO Fishing Areas 21 and 27. The present volume includes 11 orders, 32 families, 66 genera, and 148 species of cartilaginous fishes occurring in the North Atlantic. The Catalogue includes a section on standard measurements for a shark, batoid, and chimaera, with associated terms. It provides accounts for all orders, families, and genera and all keys to taxa are fully illustrated. Information under each species account includes: valid modern names and original citation of the species; synonyms; the English, French, and Spanish FAO names for the species; a lateral view for sharks and chimaeras, dorsal and often also ventral view for batoids, and often other useful illustrations; field marks; diagnostic features; distribution, including a GIS map; habitat; biology; size; interest to fisheries and human impact; local names when available; a remarks sections; and literature. The volume is fully indexed and also includes sections on terminology and measurements including an extensive glossary, a list of species by FAO Statistical Areas, and a dedicated bibliography.


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## 1. INTRODUCTION

Sharks, and their relatives the batoids and chimaeras, collectively comprising the Class Chondrichthyes or cartilaginous fishes are among one the most successful groups of fishes (Compagno, 1973; Nelson, 2006) having penetrated most marine ecosystems. This includes continental and insular shelf waters from the intertidal out to a depth of 200 m , and into the deepsea as well as oceanic and pelagic forms. In some areas, some species have even penetrated into and occupy estuarine and freshwater river ecosystems. Recent reviews on the biodiversity and distribution of chondrichthyans in various ecosystems has shown that tropical marine ecosystems have the highest diversity, followed by deepsea and temperate ecosystems, and with the epipelagic and freshwater ecosystems having a lower diversity of species (Ebert and Winton, 2010; Kyne and Simpfendorfer, 2010; Rosa et al. 2010; Stevens, 2010; White and Sommerville, 2010). Worldwide there are at least 1200 known living and valid species of sharks, batoids, and chimaeroids comprising 13 orders, 58 to 60 families, and 192 genera, with additional species requiring description (Nelson, 2006; Ebert and Winton, 2010; D.A. Ebert, pers. database, 12 October 2011). These include over 500 species of sharks, over 650 species of batoids, or flat sharks, (orders Torpediniformes, Pristiformes, Rajiformes, and Myliobatiformes), and at least 50 species of ghost sharks, silver sharks, elephant fish, chimaeras or ratfish (order Chimaeriformes).

This catalogue covers all the described species of living sharks, batoids, and chimaeras found in the North Atlantic, FAO Areas 21 and 27 (Fig. 1). The catalogue is intended to be a comprehensive review of the shark-like fishes of the North Atlantic in a form accessible to fisheries workers as well as researchers on shark systematics, biodiversity, distribution, and general biology. It also caters to other researchers that need comparative information on sharks, and their relatives, and to people who encounter sharks during the course of work or play in the sea, or in freshwater, and the general public. It includes species of major, moderate, minor, and minimal importance to fisheries as well as those of doubtful or potential use to fisheries. It also covers those species that have a research, recreational, educational, and aesthetic importance, as well as those species that occasionally bite and threaten people in the water and the far more numerous species that are 'bitten' and threatened by people through exploitation and habitat modification.

The species specific information on the biology, conservation status, distribution, habitat, fisheries, and systematics of North Atlantic Ocean chondrichthyans was compiled from primary literature sources including, but not limited to, Bigelow and Schroeder (1948, 1953), Hureau and Monod (eds., 1973), Whitehead et al. (1984), Scott and Scott (1988), Branstetter, Burgess, and McEachran in Collette and Klein-MacPhee (2002), Moore et al. (2003), and Hartel et al. (2008). Regional FAO catalogues and identification guides for the Eastern Central Atlantic (FAO Area 34) and Western Central Atlantic (FAO Area 31), as well as the Mediterranean and Black Sea (FAO Area 37) were also helpful in rounding the species checklists from
these adjacent areas. Several grey literature and electronic sources were also of invaluable help, these included, but were not limited to, the California Academy of Sciences Catalogue of Fishes (http://www.calacademy.org/research/ ichthyology/catalog/fishcatsearch.html); European Union (EU), FAO (http://www.fao.org/fi/default. asp), ICES Working Group of Elasmobranch Fishes (www.ices.dk), IUCN Shark Specialist Group (http://www.iucnredlist.org), NOAA Fisheries, and Mar-Eco reports. A comprehensive bibliography of the literature, including primary, grey, and electronic sources is provided at the end of this volume.

Biogeography of Region. The North Atlantic region includes two major FAO Fishing Areas, the Eastern North Atlantic (Area 27) and the Western North Atlantic (Area 21). The Eastern North Atlantic region extends essentially from the North Pole to about $36^{\circ} \mathrm{N}$ in the central Atlantic, and is bounded from the east coast of Greenland and along the $40^{\circ} \mathrm{W}$ meridian southward to where it intersects at $36^{\circ} \mathrm{N}$ and to the east Area 27 is bounded in the eastern Barents Sea at about $68^{\circ} 30^{\circ} E$ and by continental western Europe. The Western North Atlantic extends from eastern Greenland westwards to the Arctic waters of northern Canada at $120^{\circ} \mathrm{W}$, and from northern Arctic waters at about $78^{\circ} 10^{\prime} \mathrm{N}$ southwards to about Cape Hatteras at $35^{\circ} \mathrm{N}$. The North Atlantic encompasses no less than 14 Large Marine Ecosystems, nine in the Eastern North Atlantic and five in the Western North Atlantic. This includes the East Greenland Shelf, Norwegian Sea, Barents Sea, Iceland Shelf, Faroe Plateau, North Sea, Baltic Sea, Celtic Biscay Shelf, and Iberian Coastal large marine ecosystems in the Eastern North Atlantic (Area 27), and in the Western North Atlantic (Area 21) this includes the Northeast US Continental Shelf, Scotian Shelf, Newfoundland-Labrador Shelf, Hudson Bay, and West Greenland Shelf large marine ecosystems (Fig. 1 - Map of the North Atlantic FAO Areas 21 and 27).

The North Atlantic region is essentially a cold temperate regime that extends from the Arctic Circle southwards to warmer temperate boundaries at about $36^{\circ} \mathrm{N}$ (Area 27) and $35^{\circ} \mathrm{N}$ (Area 21) latitude. In the Boreal mid-Atlantic the east flowing Gulf Stream becomes the North Atlantic Current, which forms the upper portion of the North Atlantic Gyre, a clockwise rotating ocean gyre. The main North Atlantic Current flows east towards the British Isles where it branches into two major divisions, with the North Atlantic current continuing southward and a separate major branch flowing northwards to become the Norwegian Current (Briggs, 1995). The Norwegian Current branch carries relatively warm, saline water of Gulf Stream origin into the seas off the western coast of Europe (Briggs, 1995) and as a result, the border of the warm and cold-temperate regions occurs farther north than in the western North Atlantic. In the Western North Atlantic, the Florida Current becomes the Gulf Stream at about Cape Hatteras ( $35^{\circ} \mathrm{N}$ ), North Carolina, USA, and continues flowing northwards, off the continental shelf and over deeper water, but veers back into shallower water over the Grand Banks, southeast of Newfoundland. The cold Labrador Current flows southward between the Gulf Stream and the coast, extending cold-temperate
conditions farther south than they occur in the eastern North Atlantic (Briggs, 1995). As a result, the environment along the western North American coastline transitions rapidly from warm-temperate to polar regimes, completing the shift within $20^{\circ}$ of latitude (Barnes and Hughes, 1982).

Classification and systematic arrangement used here. The higher classification of these fishes includes the class Chondrichthyes that is divided into two major groups, each with a long and separate, pre-Devonian history, the chimaeroids, Holocephali (with a single living order Chimaeriformes), and the sharks and batoids proper, with the surviving group Neoselachii divided into two cohorts, the Selachii (sharks) and the Batoidea (rays and skates) and includes all of the modern living species. The Selachii is further divided into two superorders, the Squalomorphii and Galeomorphii. The superorder Squalomorphii includes the orders Hexanchiformes, Squaliformes, Squatiniformes, and Pristiophoriformes, while the superorder Galeomorphii includes the Heterodontiformes, Orectolobiformes, Lamniformes, and Carcharhiniformes. The cohort Batoidea recognizes four orders, Torpediniformes, Pristiformes, Rajiformes, and Myliobatiformes. The ordinal classification of the shark-like fishes largely follows the arrangement of Compagno (2001, 2005), Ebert and Compagno (In press), and Ebert (In preparation) with some modifications in recognizing eight orders and 34 families. The higher classification of batoid fishes and the assignment of various families to suborders or orders are not yet fully clarified. Nelson (2006) provided a table reflecting different concepts and comparing his own classification of the previous $3^{\text {rd }}$ edition (Nelson, 1994) with those of Compagno (1999) with six orders and 21 families, by McEachran and Aschliman (2004) with four orders and 14 families, and finally his own concept of the $4^{\text {th }}$ edition (Nelson, 2006) with four orders and 17 families. Three more families, as compared to McEachran and Aschliman (2004), in the latter concept concern a new family Potamotrygonidae of South American freshwater stingrays and the preservation of the families Rhinidae and Rhynchobatidae. The classification used here follows Nelson (2006) with the exception of adding an $18^{\text {th }}$ family, Arhynchobatidae (Fowler 1934), resurrected by Compagno (1999, 2005), but without explanation. Recently, Naylor et al. (2012) and Aschliman et al. (2012) revisited the validity of this family using clasper morphology and molecular analysis and concluded that this family is valid, and is a sister group to the family Rajidae. The higher classification of chimaeras follows Didier $(1995,2004)$ and Didier, Kemper, and Ebert (2012). The relationship of the sharks to the batoids is still unresolved, with recent classifications suggesting that the batoids are either sister to the modern shark orders Pristiophoriformes and Squatiniformes, and share a common ancestry with the Squaliformes (e.g. the Hypnosqualean hypothesis), or follow traditional dichotomy of all modern sharks and batoids. The two hypothesis breaks down largely between traditional morphologist (Compagno, 1973, 1977, 1999, 2001, 2005; Shirai, 1992a, 1996; de Carvalho, 1996) and newer molecular evidence (Douady et al., 2003; Naylor et al., 2005; G. Naylor, pers. comm.).

The following classification to order is based on the above discussion on higher ordinal classifications (* starred orders are covered in this volume):

Class Chondrichthyes (cartilaginous fishes)
Subclass Holocephali (chimaeras and fossil relatives) Order Chimaeriformes (chimaeras or silver sharks)*
Subclass Neoselachii (modern sharks and batoids)
Cohort Selachii (modern sharks)
Superorder Squalomorphii (squalomorph sharks)
Order Hexanchiformes (cow and frilled sharks)* Order Squaliformes (dogfish sharks)* Order Squatiniformes (angel sharks)* Order Pristiophoriformes (sawsharks) Superorder Galeomorphii (galeomorph sharks) Order Heterodontiformes (bullhead sharks) Order Lamniformes (mackerel sharks)* Order Orectolobiformes (carpet sharks)* Order Carcharhiniformes (ground sharks)*
Cohort Batoidea (batoids) Order Torpediniformes (electric rays)* Order Pristiformes (sawfishes)* Order Rajiformes (skates and guitarfishes)* Order Myliobatiformes (stingrays)*

North Atlantic Biodiversity. The North Atlantic has a moderately diverse chondrichthyan fauna with 11 orders, 32 families, 66 genera, and at least 148 species being represented (Table 1). The most specious group of chondrichthyans in the North Atlantic are the skates (Rajiformes), which has at least 41 species, represented. This is followed by the Carcharhiniformes with 36 species and the Squaliformes with 30 species. Of these totals, the Eastern North Atlantic has a higher diversity in terms of families ( $n=32$ ), genera ( $n=63$ ), and number of species ( $\mathrm{n}=127$ ) in comparison to the Western North Atlantic that has 20 families, 50 genera, and 83 species. The number of batoids represented in the Eastern North Atlantic is more than double that of the Western North Atlantic, 49 species versus 23 , respectively.

| North Atlantic <br> (Tot.) | Sharks | Batoids | Chimaeras | Tot. |
| :---: | :---: | :---: | :---: | :---: |
| Orders | 6 | 4 | 1 | 11 |
| Families | 22 | 8 | 2 | 32 |
| Genera | 42 | 20 | 4 | 66 |
| Species | 84 | 56 | 8 | 148 |
| North Atlantic |  |  |  |  |
| (Area 21) |  |  |  |  |
| Orders | 6 | 4 | 1 | 11 |
| Families | 20 | 7 | 2 | 29 |
| Genera | 32 | 14 | 4 | 50 |
| Species | 54 | 23 | 6 | 83 |
| North Atlantic |  |  |  |  |
| (Area 27) |  |  |  |  |
| Orders | 6 | 4 | 1 | 11 |
| Families | 22 | 8 | 2 | 32 |
| Genera | 39 | 20 | 4 | 63 |
| Species | 70 | 49 | 8 | 127 |

Table 1 - The families, genera, and species represented within the North Atlantic (total for Areas 21 and 27), Eastern North Atlantic (Area 27), and Western North Atlantic (Area 21).

### 1.1 Plan of the Catalogue

The format for this catalogue follows that of the FAO Catalogue of Sharks of the World (Compagno, 2001; Ebert and Compagno, In press; Ebert, In preparation), orders as the highest taxonomic group dealt with here, followed by family, genus, and species accounts. A key to the families and genera, where appropriate is also included.

Order Accounts include the valid modern form of the order name with author and year; the original citation of the order name with its author, year, reference and pagination; the number of recognized families in the North Atlantic; common order Synonyms mainly from the North Atlantic region with the name, author, year, and pagination; the FAO order Vernacular Names in English, French and Spanish; Field Marks and Diagnostic Features of members of the order; an account of the natural history of the order under separate sections covering Distribution, Habitat and Biology; a section on Interest to Fisheries and Human Impact, a synopsis of the human issues affecting shark families; Local Names when available; a Remarks section mostly with systematic comments; and a Key to North Atlantic Families, when orders have more than one family.

Family Accounts include the valid modern form of the family name with author and year; the original citation of the family name with its author, year, reference and pagination; the valid type genus with author and date; the number of recognized North Atlantic genera in the family; family Synonyms with names mostly associated with the North Atlantic region and with the name, author, year, and pagination; the FAO family Vernacular Names in English, French and Spanish; Field Marks and Diagnostic Features of members of the family; an account of the natural history of the family under separate sections covering Distribution, Habitat and Biology; a section on Interest to Fisheries and Human Impact, a synopsis of the human issues affecting shark families; Local Names when available; a Remarks section mostly with systematic comments; a Literature section covering references to the entire family; and a Key to North Atlantic Genera, when families have more than one genus.

Generic Accounts include the valid modern form of the genus name with author and year; the original citation of the genus (or subgenus), with its author, year, reference and pagination, and, if a subgenus, the original genus name with author and year that the subgenus was originally placed in; the type species and means of designating it (for example, by original designation, monotypy, absolute tautonymy, or subsequent designation); the number of recognized North Atlantic species in the genus; the Synonyms of genera, with their rank (genus, subgenus, or other genus-group ranking), author, year, pagination, and genus they were described in if originally ranked as subgenera or equivalents; FAO Names if they exist; Field Marks if genera are large and distinctive; Diagnostic Features of the genus; Local Names where available; a Key to North Atlantic Species if the genus has more than one species (is not monotypic); and a Remarks section.

Species Accounts include the valid modern names of the species, with author and date; the original citation of the species, with its author, year, reference pagination; the holotype, syntypes, lectotype or neotype of each species (paratypes are not listed in the present account), including the total length and sex of the specimen, its institutional deposition, and its catalogue number; the type locality including the location, coordinates and depth if available, where the holotype, syntypes, lectotype or neotype were caught; Synonyms of the species, including their names, authors and dates; a section listing other scientific names recently in use; the English, French, and Spanish FAO Names for the species; a lateral view illustration, and often other useful illustrations (lateral view drawings are given of each shark species, usually ventral views of heads, and often teeth and denticles of the shark in question); Field Marks; Diagnostic Features (except in monotypic genera); Distribution, including a map; Habitat; Biology; Size; Interest to Fisheries and Human Impact; Local Names when available; a Remarks section when necessary; and Literature.

Synonyms commonly seen in the North Atlantic literature are listed, where appropriate, and include only true taxonomic synonyms of the valid family, genus and species given. For species, another category, Other Combinations, is provided for common misidentifications of a given species with another, valid species (for example, the requiem shark Carcharhinus brachyurus (Carcharhinidae)) was often termed C. remotus in the older literature, but the latter is a junior synonym of $\boldsymbol{C}$. acronotus) as well as commonly used combinations that place a valid species in different genera (for example, Odontaspis taurus or Eugomphodus taurus for Carcharias taurus).

FAO Family and Species Names. English, French and Spanish names for each family and species, primarily for use within FAO, were selected by the following criteria: (a) each name applies to a single family or species worldwide; (b) the name conforms with FAO spelling nomenclature; (c) the name conforms to prior usage when possible. FAO names are not intended to replace local species names, but are necessary to overcome the confusion caused by the use of a single name for more than one species or several names for one species. The FAO names used here conform to prior FAO usage. The common French and Spanish names of species from the other FAO Catalogues, including the Sharks of World (Compagno, 1984, 2001; Ebert and Compagno, In press; Ebert, In preparation), and regional FAO Catalogues on the Sharks, Rays, and Chimaeras of the Eastern Central Atlantic (Compagno, 1981a, b; Stehmann, 1981), Western Central Atlantic (Compagno, 2002; Didier, 2002; McEachran, 2002), and Mediterranean and Black Sea (Serena, 2005), were used when appropriate.

Keys, Field Marks, and Diagnostic Features. These sections include identification data in different forms. Keys to families, genera and species are standard dichotomous biological keys that are followed in steps of alternate choices to single out the taxa covered. It should be noted that the Keys include only those families, genera, and species that occur in FAO Areas 21 and 27, or within the scope of the present Catalogue and does not include those groups not
occurring with the area. Field Marks generally include a few obvious characters of use in field identification, extracted from Diagnostic Features at various levels, but included in a separate section. Field Marks are listed at the ordinal, familial and species levels, and occasionally the generic level in cases of large genera with many species. The arrangement of Field Mark characters is semihierarchical and pragmatic and may include characters from a higher level such as an order in lower level taxonomic accounts such as those of species. Field Marks include characters that are obvious in live or fresh-caught individuals but may be obscure in frozen or preserved material. Diagnostic Features are lists of characters at the ordinal, familial, generic, and species level, with the character choice generally limited to external characters, particularly at the species level, because of their primary purpose of identification rather than indication of relationships. The Diagnostic Features sections are hierarchical, with characters at the ordinal level generally not duplicated at the family, genus and species levels. Monotypic orders with one family (such as Squatiniformes), monotypic families with one genus (Mitsukurinidae) or monotypic genera with one species (Pseudotriakis) all have the Diagnostic Features section present only in the highest taxon covered.

Distribution. Geographic distributions for nearly all species of sharks are given by listing the countries off the coasts of or oceanographic features, e.g. seamounts and troughs, of where the species occurs. In compiling distributional data and preparing maps it was noted that the distributions of many wide-ranging coastal and deepsea species are very spottily known as present. In many cases gaps in distribution may not indicate absence of a given species but absence of knowledge. Continental slope shark faunas are poorly known for much of the world, and a number of deepwater species probably have wider ranges than are currently known. Much effort was made to screen out distribution errors, based on misidentifications of species, at a cost of presenting distributional lists and maps that are spotty, but possibly more accurate.

Habitat. Habitat covers information on physical conditions where various sharks are found. The known depth range of the species (in metres), position in the water column, type of substrate occupied, and preferences relative to coasts are noted when available. In most cases data on salinity, oxygen content, and specific temperature of the water in which they occur was not available or was not in an easily usable form and has not been regularly compiled here.

Biology. Includes data on reproduction, age and growth, diet, and behaviour and movement patterns. Compilation of these data suggests that very few species are biologically well known, and even in the picked dogfish (Squalus acanthias), perhaps the best-known of living cartilaginous fishes, there are areas of its biology that are very poorly known (such as its behaviour and sociobiology).

Size. All size data are given as total lengths; this is the measurement most often used as an independent variable and standard measurement in the shark literature, although particularly in fisheries papers precaudal lengths, fork lengths, and other measurements have been used from
choice or necessity. Unfortunately shark workers have not agreed on a standard method of measuring total length, so total lengths from different sources in the literature may not be strictly comparable. We prefer and advocate as a standard method a direct measurement, in which the shark, batoid, or chimaera is held belly down with its dorsal caudal-fin lobe depressed into line with its body axis and total length measured as a point to point distance (not over the curve of the body) from the snout tip to the tip of the dorsal caudal-fin lobe. This method lends itself readily to quick use of a fishboard with a perpendicular front bar or plate to index the fish's snout against, a one metre or two metre ruler or folding ruler slipped under the shark, batoid, or chimaera or even a steel or cloth tape, and avoids the trouble of computation and possible errors and loss of data.

Total length data presented includes maximum size, size at maturity (in some cases, a size range at maturity, when abundant data were available) and maximum size for both sexes, and size at birth or hatching. Sometimes size at sexual maturity for either or both sexes is not known, in which cases reported minimum and maximum sizes of adult individuals are given. In some cases maximum size exceeds that recorded for either sex, in which case the sex of the outsized individual or individuals representing the maximum size measurements was not indicated. In some poorly known species only immature individuals are known, in which case the hypothetical maximum adult size is almost certainly larger than the known immature maximum.

In some species length-weight equations are presented, usually of the form $W=a+T L^{b}$, where $W$ is weight, $a$ and $b$ are constants, and TL is total length.

Interest to Fisheries and Human Impact. This section includes Fisheries information, including whether the species is taken in targeted or non-targeted (bycatch) fisheries and if taken as bycatch whether it is retained or discarded. Data on localities of fisheries, gear used, and uses of the particular species are noted when available. National fisheries data for sharks is often sketchy and combined for a number of species. Thus, catch statistics were available for relatively few species of sharks but are noted when available, with particular emphasis on data from those species reported to FAO. Additional data are increasingly available from national and regional fisheries bodies are presented when available. Other aspects of human interaction, e.g. shark attack or ecotourism, are presented, and the current conservation Red List status of each species as evaluated by the IUCN Species Survival Commission's Shark Specialist Group (http://www. iucnredlist.org). At the end of the Bibliography section an electronic reference section has been added with a link to the Red List Assessment for each species included in the Catalogue.

Local Names. Many species have no vernacular names whatsoever or are lumped under catchall names, while some species such as the white and basking sharks have dozens of names. Wherever possible common local names are presented, especially for important wide-ranging sharks. The broadening interest in sharks, batoids, and chimaeras, and urgent need to acquire species-specific data for their
management and conservation should encourage fisheries biologists and other researchers to compile local names for their own countries or regions, and add to the sketchy knowledge of local names.

Remarks. Important information, especially on systematics and nomenclature, are given in the remarks section. Also, the relative number of families per order, genera per family, and species per genus worldwide is given when appropriate for comparison to the groups occurring within FAO Areas 21 and 27.

Literature. References cited here include specific works with important information for each species and family as well as comprehensive accounts, but are not intended as a comprehensive bibliography.


Fig. 1 Map of FAO Area 21 (Western North Atlantic) and Area 27 (Eastern North Atlantic)

### 1.2 Technical Terms and Measurements: Sharks, Batoids, and Chimaeras

### 1.2.1 Picture Guide to External Terminology of Sharks



Fig. 2 Lateral view


Fig. 3 Ventral view


Fig. 4 Head of an orectoloboid shark (ventral view)


Fig. 5 Nostril


Fig. 6 Eyes


Fig. 8 Dorsal fin


Fig. 9 Caudal fin


Fig. 10 Pectoral fin


Fig. 7 Mouth corner

ANTERIOR
$<$ MEDIAL $\quad$ LATERAL $\rightarrow$


Fig. 11 Dorsal view of clasper (lamnid shark)

### 1.2.2 Picture Guide to Skeletal Terminology of Sharks



Fig. 12 Chondrocranium


Fig. 13 Aplesodic and plesodic pectoral fins


Fig. 14 Clasper skeleton of lamnid shark (right side)


Fig. 15 Tooth terminology (left upper anterolateral tooth)


Fig. 16 Oblique anterolateral view of lateral trunk dermal denticle

### 1.2.3 Measurements Used for Sharks

TL = TOTAL LENGTH
PP2 = PREPELVIC-FIN LENGTH
FL = FORK LENGTH
PCL = PRECAUDAL-FIN LENGTH
SVL = SNOUT-VENT LENGTH
PAL = PREANAL-FIN LENGTH
IDS $=$ INTERDORSAL SPACE
DCS = DORSAL CAUDAL-FIN SPACE
PPS = PECTORAL-FIN PELVIC-FIN SPACE
PAS = PELVIC-FIN ANAL-FIN SPACE
ACS = ANAL-FIN CAUDAL-FIN SPACE
PCA = PELVIC-FIN CAUDAL-FIN SPACE
VCL = VENT CAUDAL-FIN LENGTH
PD2 = PRE-SECOND DORSAL-FIN LENGTH
PD1 = PRE-FIRST DORSAL-FIN LENGTH
HDL = HEAD LENGTH
PG1 = PREBRANCHIAL LENGTH
PSP = PRESPIRACULAR LENGTH

TL


Fig. 17 Main longitudinal measures
PRN = PRENARIAL LENGTH
POR = PREORAL LENGTH
EYL = EYELENGTH
EYH = EYE HEIGHT
ING = INTERGILL LENGTH
GS1 = FIRST GILL SLIT HEIGHT
GS2 = SECOND GILL SLIT HEIGHT
GS3 = THIRD GILL SLIT HEIGHT
GS4 = FOURTH GILL SLIT HEIGHT
GS5 = FIFTH GILL SLIT HEIGHT
GS6 = SIXTH GILL SLIT HEIGHT
GS7 = SEVENTH GILL SLIT HEIGHT
P1A = PECTORAL-FIN ANTERIOR MARGIN
P1R = PECTORAL-FIN RADIAL LENGTH
$\mathrm{P} 1 \mathrm{~B}=\mathrm{PECTORAL-FIN} \mathrm{BASE}$
P1I = PECTORAL-FIN INNER MARGIN
P1P = PECTORAL-FIN POSTERIOR MARGIN
P1H = PECTORAL-FIN HEIGHT
P1L = PECTORAL-FIN LENGTH
SOD = SUBOCULAR POCKET DEPTH


Fig. 18

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CDM = DORSAL CAUDAL-FIN MARGIN
CPV = PREVENTRAL CAUDAL-FIN MARGIN
CPU = UPPER POSTVENTRAL CAUDAL-FIN MARGIN
CPL = LOWER POSTVENTRAL CAUDAL-FIN MARGIN
CFW = CAUDAL-FIN FORK WIDTH
CFL = CAUDAL-FIN FORK LENGTH
CST = SUBTERMINAL CAUDAL-FIN MARGIN
CSW = SUBTERMINAL CAUDAL-FIN WIDTH
CTR = TERMINAL CAUDAL-FIN MARGIN
D1L = FIRST DORSAL-FIN LENGTH
D1A = FIRST DORSAL-FIN ANTERIOR MARGIN
D1B = FIRST DORSAL-FIN BASE
D1H = FIRST DORSAL-FIN HEIGHT
D1I = FIRST DORSAL-FIN INNER MARGIN
D1P = FIRST DORSAL-FIN POSTERIOR MARGIN
```

D2L = SECOND DORSAL-FIN LENGTH
D2A = SECOND DORSAL-FIN ANTERIOR MARGIN
D2B = SECOND DORSAL-FIN BASE
D2H = SECOND DORSAL-FIN HEIGHT
D2I = SECOND DORSAL-FIN INNER MARGIN
D2P $=$ SECOND DORSAL-FIN POSTERIOR MARGIN
P2L = PELVIC-FIN LENGTH
P2A = PELVIC-FIN ANTERIOR MARGIN
P2B = PELVIC-FIN BASE
P2H = PELVIC-FIN HEIGHT
P2l = PELVIC-FIN INNER MARGIN [LENGTH]
P2P = PELVIC-FIN POSTERIOR MARGIN [LENGTH]
ANL $=$ ANAL-FIN LENGTH
ANA $=$ ANAL-FIN ANTERIOR MARGIN
ANB $=$ ANAL-FIN BASE
ANH $=$ ANAL-FIN HEIGHT
ANI =ANAL-FIN INNER MARGIN


Fig. 19 Measurements of caudal fin


Fig. 20 Measurements of dorsal, pelvic and anal fins


Fig. 21 Other common measurements

HDH = HEAD HEIGHT
TRH = TRUNK HEIGHT
ABH $=$ ABDOMEN HEIGHT
TAH = TAIL HEIGHT
CPH = CAUDAL-FIN PEDUNCLE HEIGHT
DAI = SECOND DORSAL-FIN INSERTION ANAL-FIN INSERTION
DAO $=$ SECOND DORSAL-FIN ORIGIN ANAL-FIN ORIGIN

DPI $=$ FIRST DORSAL-FIN MIDPOINT PECTORAL-FIN INSERTION
DPO $=$ FIRST DORSAL-FIN MIDPOINT PELVIC-FIN ORIGIN
PDI $=$ PELVIC-FIN MIDPOINT FIRST DORSAL-FIN INSERTION
PDO = PELVIC-FIN MIDPOINT SECOND DORSAL-FIN ORIGIN

```
MOL = MOUTH LENGTH
MOW = MOUTH WIDTH
ULA = UPPER LABIAL-FURROW LENGTH
LLA = LOWER LABIAL-FURROW LENGTH
NOW = NOSTRIL WIDTH
INW = INTERNARIAL SPACE
ANF = ANTERIOR NASAL-FLAP LENGTH
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```
CLO = CLASPER OUTER LENGTH
CLI = CLASPER INNER LENGTH
CLB = CLASPER BASE WIDTH
```



Fig. 22

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INO = INTERORBITAL SPACE
SPL = SPIRACLE LENGTH
ESL = EYE SPIRACLE SPACE
HDW = HEAD WIDTH
TRW = TRUNK WIDTH
ABW = ABDOMEN WVIDTH
TAW = TAIL WIDTH
CPW = CAUDAL-FIN PEDUNCLE WIDTH
```


### 1.2.4 Picture Guide to External Terminology and Measurements Used for Batoids



Fig. 25 Lower side of a typical skate


Fig. 26 Anterior part of disc of a skate


Fig. 27 Teeth of a stingray (arrows indicate method of counting pavement pattern in batoids)

### 1.2.5 Picture Guide to External Terminology and Measurements Used for Chimaeras



Fig. 28 Lateral view of a typical Chimaera


### 1.2.6 Glossary of Technical Terms

The following glossary of terms used for the anatomy and biology of shark-like fishes is modified from terms in Compagno (1984, 1988, 1999) and a short glossary in Compagno, Ebert and Smale (1989). The main glossary (1.2.4.1) duplicates that in volume 2 of the revised shark catalogue (Compagno, 2001), except that additional terms for habitat and distribution used in the text are reinstated in the glossary. Terms for photophore patterns (including photomarks) that pertain only to the Family Etmopteridae and primarily to the genus Etmopterus are discussed under that family.

Abdominal ridges or keels: In some sharks, paired longitudinal dermal ridges that extend from the bases of the pectoral fins to the pelvic-fin bases.

Abyss: The deep sea bottom, ocean basins or abyssal plain descending from 4500 m to about 6000 m .

Accessory dorsal marginal: In the clasper skeleton, a flat cartilage on the posterior end of the dorsal marginal cartilage that supports the cover rhipidion.

Adductor mandibulae muscles: Paired head muscles originating on the lateral faces of the quadrate process of the palatoquadrates and inserting on the lateral surface of the Meckel's cartilages; the primary jaw-closing muscles of sharks.

Adelphophagy: Foetus-eating, a mode of live-bearing reproduction employing uterine cannibalism; early foetuses deplete their yolk-sacks early and subsist by first eating their smaller siblings and then eating nutritive eggs produced by the mother. At present only known for certain in the sand tiger shark (Carcharias taurus), but suspected in a few other lamnoids.

Alternate teeth: Small oral teeth with asymmetrical crowns that form two interdigitated rows on the symphysis, with the cusps of each row hooked mesially towards the opposite row. Additional paired rows of alternates may be present distal to the symphysial rows.

Amphitemperate: Referring to a species that occurs in temperate water in the northern and southern hemispheres, but is absent from the tropics.

Anal fin: A single fin on the ventral surface of the tail between the pelvic fins and caudal fin of some sharks, absent in batoids, dogfish, sawsharks, angel sharks, and some chimaeras.

Annular rings or annuli: In a vertebral centrum in cross section, rings of calcified cartilage separated by uncalcified cartilage that occupy the intermedialia only, or concentric rings that cross both the intermedialia and basalia.

Anterior: Forward, in the longitudinal direction of the snout tip. Also, cranial.

Anterior fontanelle: On the elasmobranch neurocranium, an aperture on the anterodorsomedial surface, usually at the rear of the ethmoid region and forming a passage into
the internal cranial cavity. It is closed by a tough membrane, varies tremendously in shape, and may be pinched off by the medially expanded orbits in a few sharks.

Anterior margin: In precaudal fins, the margin from the fin origin to its apex.

Anterior nasal flap: A flap on the front edges of the nostrils, that serves to partially divide the nostril into incurrent and excurrent apertures or openings.

Anterior teeth: Enlarged, tall, narrow-rooted oral teeth near the symphysis, often with lingually curved cusps.

Anterodorsal palpebral depressor muscle: in the orectoloboid family Parascylliidae, paired head muscles that originate at the insertions of the preorbitalis muscles on the anterolateroventral face of the Meckel's cartilage, and insert on the skin of the upper eyelid anterior to the eye. These are possibly for depressing the upper eyelids and closing the eyes, and are not found in any other sharks.

Antorbital cartilages: On the neurocranium of sawsharks and batoids, separate cartilages attached to the sides of the nasal capsules that support the sides or front of the head.

Apex: In precaudal fins, the distal tip, which can be acutely pointed to broadly rounded.

Apical: In oral teeth, towards the tip of the crown or cusp. Can also be used as indicating direction towards the apex or tip of a fin, fin-spine, etc.

Aplacental viviparity: Live-bearing in which the young do not have a yolk-sac placenta. Found in all groups of livebearing sharks.

Aplesodic fin: A pectoral, pelvic, dorsal, or anal fin in which the fin radial cartilages do not extend into the distal fin web and between the supporting ceratotrichia of the fin web. Modern sharks always have aplesodic caudal fins, in which the haemal arches of the caudal vertebrae do not support the ventral caudal lobe.

Apopyle: The anterior opening of the clasper, on the anteromesial surface of the clasper and close to the vent. The apopyle receives sperm from the cloaca and fluid from the siphons, which enter the clasper groove and are discharged through the hypopyle. Apopyle is also used for clasper skeletons for the anterior opening of the tubular shafts formed by enlarged marginal and axial cartilages.

Axial cartilage: In the clasper skeleton, the elongated ventral rod or plate-shaped cartilage that forms the main support of the clasper. Also termed appendix-stem.

Barbels: Long conical paired dermal lobes on the snouts of sharks, that may serve to locate prey. Sawsharks have barbels on the underside of the snout in front of the nostrils as in sturgeon, but most barbeled sharks have them associated with the nostrils, either as an extension of the anterior nasal flaps or as separate structures medial to the nasal apertures.

Basal: In oral teeth, a proximal direction towards the crown foot and roots.

Basal cartilages or basals: In precaudal fins the large cartilages of the fin bases, immediately distal to the pectoral and pelvic fin girdles or the vertebral column (dorsal and anal fins), on which the radials articulate distally. The paired pectoral fins of living sharks primitively have a tribasal pectoral fin, with a propterygium, mesopterygium, and metapterygium as basals, although these may be fused; in batoids, additional neopterygial basals may be added between the mesopterygium and metapterygium and the propterygium is variably expanded anterior with a propterygial basal and axis. The pelvic fins have a basipterygium that supports the pelvic radials and, in males, the claspers. The caudal fin has no basals, but these are functionally replaced by expanded neural and haemal arches of the vertebral column.

## Basal communicating canals: See subnasal fenestrae.

Basal groove: In oral teeth, a deep groove proximal to the basal ledge on the labial surface of the crown neck and apical root margin.

Basal ledge: In oral teeth, a shelf-like projection on the labial surface of the crown foot.

Basal plate: The floor of the cranial cavity of the neurocranium, a ventral, medial plate extending from the ethmoid region between the orbits and otic capsules and below the cranial cavity to the occipital condyles, occipital centrum and foramen magnum.

Basals or basalia: In a vertebral centrum, the diagonal spaces below the attachment surfaces of the basidorsal cartilages, above the basiventral cartilages, and between the two halves of the double cone. Basalia may be filled with uncalcified cartilage, may have diagonal calcifications penetrating the uncalcified cartilage, or may have calcified annuli or solid calcified cartilage that are continuous with calcification of the intermedialia. See diagonal calcifications and intermedialia.

Base: In precaudal fins, the proximal part of the fin between the origin and insertion, extending distally, and supported by the cartilaginous fin skeleton. In the caudal fin, that thickened longitudinal part of the fin enclosing the vertebral column and between the epaxial and hypaxial lobes or webs of the fin. In oral teeth, the proximal root and crown foot, in apposition to the distal cusp. In denticles, the proximal anchoring structures, often with four or more lobes, holding the denticles in the skin.

Basidorsal cartilages: A pair of wedge-shaped arched, thin cartilages articulating with the dorsolateral surfaces of a vertebral centrum and forming a continuous neural arch with the interdorsal cartilages to protect the spinal cord.

Basipterygium: The large elongate longitudinal cartilage at the fin base of the pelvic fin, attached to the posterolateral ends of the pelvic girdle or puboischiadic bar. The basipterygium has pelvic radials attached along its distal edge and has the clasper skeleton attached posteriorly in males.

Basiventral cartilages: A pair of rounded or wedge-shaped cartilages on the ventrolateral surfaces of a vertebral centrum that form the bases for attachment of ribs in monospondylous precaudal vertebrae. In diplospondylous precaudal and caudal vertebrae the basiventrals form haemal arches along with the interventral cartilages for protecting the caudal artery and vein.

Bathypelagic zone: That part of the oceans beyond the continental and insular shelves, from about 1000 m to 3000 to 6000 m and above the middle and lower continental rises and the abyssal plain, the sunless zone. Some oceanic sharks may transit the epipelagic, mesopelagic and bathypelagic zones to the bottom while migrating vertically.

Batoid: A ray or flat or winged shark, a neoselachian of the cohort Batoidea, a sawfish, sharkray, wedgefish, guitarfish, thornray, panray, electric ray, skate, stingray, butterfly ray, eagle ray, cownose ray, devil ray or Manta. Rays are closely allied to the sawsharks (Pristiophoriformes) and angel sharks (Squatiniformes), but differ from them in having the pectoral fins fused to the sides of the head over the gill openings, which are ventral rather than laterally or ventrolaterally placed.

Benthic or Demersal: referring to organisms that are bottom-dwelling.

Beta cartilage: In the clasper skeleton, a single, dorsolateral flattened, wedge-shaped or cylindrical cartilage connecting the pelvic basipterygium and axial cartilage and reinforcing the intermediate segments, possibly derived from a pelvic radial.

Blade: In oral teeth, an arcuate, convex-edged section of the cutting edge of the crown foot, without cusplets.

Body ridges: Elongated longitudinal dermal ridges on the sides of the trunk and precaudal tail in certain carpet sharks (Orectolobiformes), in the whale, zebra and some bamboo sharks.

Body: Can refer to an entire shark, sometimes restricted to the trunk and precaudal tail.

Branchial arches: The paired visceral arches behind the hyoid arch and just in front of the scapulocoracoid that support the gills. In elasmobranchs the five to seven branchial arches primitively consist of a pair of dorsomedial and wedgeshaped cartilages, the pharyngobranchials, closely situated against the roof of the pharynx, a pair of dorsolateral and more cylindrical epibranchials that are connected dorsomedially to the pharyngobranchials, a pair of ventrolateral cylindrical ceratobranchials that are connected ventrolaterally to the epibranchials, a pair of ventromedial hypobranchials that are connected ventrolaterally to the ceratobranchials, and unpaired ventromedial basibranchials that are connected ventrolaterally to the hypobranchials. The hypobranchials and basibranchials along with the expanded ventral ends of the ceratobranchials form the basibranchial skeleton of the floor of the branchial pharynx. The branchial skeleton is variably modified in elasmobranchs, with basibranchials and sometimes hypobranchials often lost, the last two pharyngobranchials and the last epibranchial often fused together, and the last basibranchial often expanded into a
long, broad copula with which the anterior hypobranchials and posterior ceratobranchials articulate.

Calcified cartilage: Shark skeletons are formed of hyaline cartilage or gristle, but this is often reinforced with layers of calcified cartilage, cartilage impregnated with a mineral, hydroxyapatite, similar to that of bone but organized differently, in a hard, tile-like pavement of tiny tesserae, or more compactly as in the calcified structures of vertebral centra.

Calcified double cones: In vertebrae, the primary calcifications of the notochordal sheath, in lateral view resembling two hollow, horizontal cones with their apices merged, or an hourglass.

## Cannibal viviparity: See uterine cannibalism.

Carcharhinoid: A ground shark, a member of the order Carcharhiniformes, and including the catsharks, false catsharks, finbacked catsharks, barbeled houndsharks, houndsharks, weasel sharks, requiem sharks and hammerheads.

Carina: On the crowns of oral teeth, a low blunt mesodistal ridge replacing the cusp and cutting edge, in sharks that eat hard-shelled invertebrate prey.

Carotid foramen: A single foramen or one of a pair of foramina that penetrate the basal plate usually near its midlength and allow passage of the internal carotid arteries into the cranial cavity. In some advanced elasmobranchs the carotid foramina shift through the stapedial foramina and onto the medial wall of the orbit.

## Cartilaginous fishes:Members ofthe classChondrichthyes.

Caudal crest: A prominent saw-like row of enlarged pointed denticles along the dorsal caudal margin and sometimes along the ventral caudal margin of the caudal fin. Found in certain sharks including hexanchoids and some carcharhinoids.

Caudal fin: The fin on the end of the tail in shark-like fishes, lost in some batoids.

Caudal keels: A dermal keel on each side of the caudal peduncle that may extend onto the base of the caudal fin, and may, in a few sharks, extend forward as a body keel to the side of the trunk.

Caudal peduncle: That part of the precaudal tail extending from the insertions of the dorsal and anal fins to the front of the caudal fin.

Central foramen: In oral teeth, a nutrient foramen on the midline of the lingual surface of the root, in the transverse groove.

Centrum (plural, Centra): A spool-shaped, partially or usually fully calcified structure that forms as a segmental constriction in the notochordal sheath of neoselachians, and which as an articulated string forms the principal structural units of the vertebral column. Centra are primarily formed by the calcified double cones in the notochordal sheath, which
may be their only calcification, but additional secondary calcification may occur in the centrum between the outer surfaces of the calcified double cones, including calcified intermedialia, radii, annuli, and diagonal calcifications.

Ceratotrichia: Slender soft or stiff filaments of an elastic protein, superficially resembling keratin or horn, from the Greek keratos, horn, and trichos, hair. Ceratotrichia run in parallel and radial to the fin base and support the fin webs. The prime ingredient of shark-fin soup.

Chimaera: A member of the order Chimaeriformes, subclass Holocephali, see also Chimaeroid, Holocephali.

Chimaeroid: A chimaera, ratfish, silver shark, ghost shark, spookfish or elephant fish, a member of the order Chimaeriformes.

Chondrichthyan: Referring to the class Chondrichthyes.
Chondrichthyes: The class Chondrichthyes, from Greek chondros, cartilage, and ichthos, fish, a major taxonomic group of aquatic, gill-breathing, jawed, finned vertebrates with primarily cartilaginous skeletons, 1 to 7 external gill openings, oral teeth in transverse rows on their jaws, and mostly small, tooth-like scales or dermal denticles. Chondrichthyes include the living elasmobranchs and holocephalans and their numerous fossil relatives, and also can be termed shark-like fishes or simply sharks.

## Chondrocranium: See neurocranium.

Circumglobal: Occurring around the world.
Circumnarial fold: A raised semicircular, lateral flap of skin around the incurrent aperture of a nostril, in heterodontoids, orectoloboids, and a few batoids, defined by a circumnarial groove.

Circumnarial groove: A shallow groove defining the lateral bases of the circumnarial folds.

Circumtropical: Occurring around the tropical regions of the world.

Clasper claws: In parascylliid orectoloboids, a longitudinal row of large anterolaterally directed claw-like denticles on the dorsolateral surface of the clasper glans, supported by the terminal ventral.

Clasper dactyI: In parascylliid orectoloboids, a large fingerlike process on the medial face of the clasper, supported by the dorsal terminal and having a mesospur, an analogue to the lateral spur or spine of the terminal 3 cartilage of other orectoloboids and other sharks.

Clasper gaff or hook: In the external clasper glans, a posterior hook-like structure, like a clasper spur but formed from the dorsal terminal cartilage, found in squaloids of the family Squalidae.

Clasper glans: The distal and dorsal part of the external clasper from the hypopyle to its tip, and including various movable terminal structures; also, the same area of the clasper skeleton.

Clasper groove: The longitudinal groove through the clasper, surrounded by the axial and marginal cartilages, and connecting the apopyle and hypopyle.

Clasper hooks: In the clasper glans of some carcharhinoid sharks, small claw-like dermal denticles arranged in a row along the ventral surface of the free edge of the exorhipidion.

Clasper sacs: Dermal sacs with longitudinally ribbed walls on the ventral and medial surfaces of the claspers of hexanchoids.

Clasper shaft: That part of the clasper skeleton from its origin on the pelvic fin basipterygium to the hypopyle; also, that part of the external clasper from its base to the hypopyle.

Clasper spine: In the external clasper, a projection of the terminal 3 cartilage on the lateral surface of the clasper glans, which forms a short to long, acutely pointed, spine that is covered with shiny hard tissue, possibly enameloid, dentine or both. In some squaloids other terminal cartilages may have spines.

Clasper spur: In the external clasper, a projection of the terminal 3 cartilage on the lateral surface of the clasper glans, which may be pointed but is not covered with shiny hard tissue.

Clasper tip: The posterior end of a clasper.
Claspers: The paired copulatory organs present on the pelvic fins of male cartilaginous fishes, for internal fertilization of eggs, also termed mixopterygia.

Classification: The ordering of organisms into groups on the basis of their relationships, which may be by similarity or common ancestry.

Cloaca: The common chamber at the rear of the body cavity of elasmobranchs through which body wastes and reproductive products including sperm, eggs, and young pass, to be expelled to the outside through a common opening or vent.

Cover rhipidion: On the external clasper glans, an elongated, longitudinal blade or flap on its dorsomedial external edge, often supported by an accessory dorsal marginal cartilage.

Cranial cavity: The central cavity of the neurocranium, containing the brain, pituitary gland, and roots of the cranial nerves. It extends posteriorly between the orbits and otic capsules to the foramen magnum.

Cranial roof: The anterior roof of the cranial cavity of the neurocranium, a dorsomedial, arched or flattened plate extending from the anterior fontanelle and between the orbits to the parietal fossa of the otic capsule. Sometimes perforated by a frontal or parietal foramen or fenestra, which may be continuous with the anterior fontanelle and can occupy most of the cranial roof.

Craniomandibular muscles: Paired head muscles in heterodontoid sharks that originate from long tendons
on the medial walls of the orbits that extend below and transverse to the levator palatoquadrati and spiracular constrictor muscles and behind the spiracles to insert on the posterodorsolateral face of the Meckel's cartilages. They are found in no other sharks and may serve to retract or elevate the jaws.

Crown: The distal part of the oral tooth, almost entirely covered with shiny enameloid except for the neck. In denticles, a flat dorsal plate-like or thorn-like structure, elevated above the denticle base on a stalk or pedicle or confluent with the base.

Crown foot: The expanded, proximal, basal part of the crown, often bearing cusplets or blades.

Cusp: A usually pointed large distal projection of the crown. A primary cusp is situated on the midline of the crown foot. Multicuspid refers to oral teeth or denticles with more than one cusp. In lateral trunk denticles, the posterior ends of the crown may have medial and lateral cusps, sharp or blunt projections associated with the medial and lateral ridges.

Cusplet: As with a cusp, but a small projection in association with a cusp, and usually mesial and distal but not medial on the crown foot.

Cutting edge: In oral teeth, the compressed sharp longitudinal ridge on the mesodistal edges of the crown.

Dentine: The primary material of shark oral teeth, a hard tissue with numerous vascular and nonvascular canals.

Dermal denticle or placoid scale: A small tooth-like scale found in cartilaginous fishes, covered with enameloid, with a core and base of dentine and usually small and often closeset to one another and covering the body. A few nonbatoid sharks, many batoids, and chimaeroids generally have them enlarged and sparse or reduced in numbers.

Dermal lobes: In wobbegongs, family Orectolobidae, narrow or broad-based, simple or branched projections of skin along the horizontal head rim and on the chin.

Diagonal calcifications: In a vertebral centrum in crosssection, plate-like (diagonal calcified lamellae) or knoblike (diagonal calcified lobes) structures of calcified cartilage that partially fills the uncalcified basalia. These have a radial orientation from the centre of the centrum.

Diphycercal: A caudal fin with the vertebral axis running horizontally into the fin base, which is not elevated.

Diplospondylous vertebrae: Vertebrae of the tail with two centra and two basidorsal and basiventral elements per segment, and mostly with a haemal arch formed by the basiventral and interventral elements. These include diplospondylous precaudal vertebrae between the monospondylous vertebrae and the base of the caudal fin, and diplospondylous caudal vertebrae in the caudal fin.

Distal: In any direction, at the far end of a structure. In oral teeth, used in a special sense for structures on the teeth towards the posterolateral mouth corners or rictuses. See apical and basal.

Dorsal: Upwards, in the vertical direction of the back. See ventral.

Dorsal fin: A fin located on the trunk or precaudal tail or both, and between the head and caudal fin. Most sharks have two dorsal fins, some batoids one or none.

Dorsal fin spine: A small to large enameloid-covered, dentine-cored spine located on the anterior margins of one or both of the dorsal fins, found on bullhead sharks (Heterodontiformes), many dogfish sharks, fossil (but not living) batoids, chimaeroids, but lost entirely or buried in the fin bases of other shark-like fishes.

Dorsal lobe: In the caudal fin, the entire fin including its base, epaxial and hypaxial webs but excepting the ventral lobe.

Dorsal margin: In the caudal fin, the margin from the upper origin to its posterior tip. Usually continuous, but in angel sharks (Squatiniformes) with their hypocercal, superficially inverted caudal fins, it is subdivided. See squatinoid caudal fin.

Dorsal marginal: In the clasper skeleton, a flat semicylindrical cartilage that is partially fused to the medial edge of the axial cartilage, and forms the medial wall of the clasper groove.

Dorsal terminal: On the skeleton of the clasper glans, an often triangular, elongated, curved, plate-like cartilage that articulates or is attached to the medial or dorsomedial edge of the end-style and anteriorly to the dorsal marginal.

Dorsal terminal 2: A flat elongated cartilage with its mesial edge attached to the floor of the glans, and supporting the rhipidion.

Ectethmoid chambers: On the neurocranium, cavities in the nasal capsule that drain the nasal sinuses through the orbitonasal canals into the orbital sinuses.

Ectethmoid processes: On the neurocranium of hexanchoid and some squaloid sharks, posteroventrolateral angular or lobular projections of the nasal capsules and the preorbital walls.

Egg case: A stiff-walled elongate-oval, rounded rectangular, conical, or dart-shaped capsule that surrounds the eggs of oviparous sharks, and is deposited by the female shark on the substrate. It is analogous to the shell of a bird's egg and is made of protein, which is a type of collagen that superficially resembles horn or keratin. Egg cases often have pairs of tendrils or horn-like structures on their ends, or flat flanges on their sides or spiral flanges around their lengths, which anchor the cases to the bottom. As the egg travels from the ovaries into the oviducts and through the nidamental glands, the egg case is secreted around it and the egg is fertilized. Live-bearing sharks may retain egg cases, and these vary from being rigid and similar to those of oviparous sharks to soft, bag-like, degenerate and membranous. Soft egg cases may disintegrate during the birth cycle.

Elasmobranch: Referring to the subclass Elasmobranchii.

Elasmobranchii: The subclass Elasmobranchii, (from Greek elasmos, plate, and branchos, gills, in allusion to their plate-like gill septa), the shark-like fishes other than the Holocephali or chimaeras, and including the living nonbatoid sharks, batoids, and a host of fossil species. They differ from holocephalans in having 5 to 7 pairs of gill openings open to the exterior and not covered by a soft gill cover, oral teeth separate and not formed as tooth plates, a fixed first dorsal fin with or without a fin spine, and a short spined or spineless second dorsal.

Embryo: An earlier development stage of the young of a live-bearing shark, ranging from nearly microscopic to moderate-sized but not like a miniature adult. See foetus.

Enameloid: The shiny hard external coating of the crowns of shark oral teeth, superficially similar to enamel in land vertebrates.

Endemic:Aspecies or higher taxonomic group of organisms that is only found in a given area. It can include national endemics found in a river system or along part or all of the coast of a given country, but also regional endemics, found off or in adjacent countries with similar habitat, but not elsewhere.

End-style: In the clasper skeleton, the posterior end of the axial cartilage, between the dorsal and ventral terminal cartilages.

Endemic: Aspecies or higher taxonomic group of organisms that is only found in a given area. It can include national endemics found in a river system or along part or all of the coast of a given country, but also regional endemics, found off or in adjacent countries with similar habitat, but not elsewhere.

Epaxial lobe or web: In the caudal fin, that part of the caudal fin between the base and dorsal margin, supported by ceratotrichia.

Epaxial web: The entire fin web above the vertebral column and caudal base.

Epipelagic zone: That part of the oceans beyond the continental and insular shelves, in oceanic waters, from the surface to the limits of where most sunlight penetrates, about 200 meters. Also known as the sunlit sea or `blue water'. Most epipelagic sharks are found in the epipelagic zone, but may penetrate the mesopelagic zone.

Epiphysial foramen or notch: On the neurocranium, a foramen or notch in the cranial roof at the dorsomedial edge of the anterior fontanelle, that houses the pineal body.

Ethmoid region: That anteriormost sector of the neurocranium including the nasal capsules, internasal plate between them, and the rostrum.

Ethmonuchal muscles: In the orectoloboid family Parascylliidae, paired head muscles that originate on the dorsal myomeres of the nape, and insert via long tendons on the nasal capsules. These are possibly for elevating the snout. Not found in any other sharks, though analogous muscles exist in batoids.

## Euselachian: Referring to the Euselachii.

Euselachii: The cohort Euselachii (Greek Eu, true, good or original, and selachos, shark or cartilaginous fish), the spined or 'phalacanthous' sharks, including the modern sharks or Neoselachii, and fossil shark groups including the hybodonts, the ctenacanths, and the xenacanths, all primitively with anal fins and having two dorsal fins with fin spines.

Excurrent apertures: The posterior and ventrally facing openings of the nostrils, which direct water out of the nasal cavities and which are often partially covered by the anterior nasal flaps. These are usually medial on the nostrils and posteromedial to the incurrent apertures, but may be posterior to the incurrent apertures only.

Exorhipidion: In claspers, a longitudinally elongated, external blade or flap with its base attached to the dorsolateral edge of the clasper glans, and with its free edge directed medially. It is supported by the ventral terminal 2 cartilage.

Eye notch: A sharp anterior or posterior indentation in the eyelid, where present cleanly dividing the upper and lower eyelids.

Filter screens: In the whale shark (Rhincodontidae) and devil rays (Mobulidae), transverse bars with lateral dermal lobes on the internal gill openings that form devices for screening out plankton.

Fin skeletons: In unpaired precaudal fins, the basal plates and radials; in the caudal fin, the vertebral column including expanded neural and haemal arches; and in the paired fins, the fin girdles, basals, and radials.

Fin web: The usually thin, compressed part of the fin, distal to the base, that is supported by ceratotrichia alone (in aplesodic fins) or by ceratotrichia surrounding expanded fin radials or by radials only (plesodic fin).

First dorsal constrictor muscles: Paired head muscles that are confluent and functionally part of the levator palatoquadrati muscles in most nonbatoid sharks, except in orectoloboids where they are discrete muscles with separate origins and insertions similar to but more lateral than the levators.

First dorsal fin: The anteriormost dorsal fin of two, ranging in position from over the pectoral fin bases to far posterior on the precaudal tail.

Foetus: A later development stage of the unborn young of a live-bearing shark, that essentially resembles a small adult. Term foetuses are ready to be born, and generally have oral teeth and denticles erupting, have a colour pattern (often more striking than adults), and, in ovoviviparous sharks, have their yolk-sacs reabsorbed.

Foramen magnum: On the neurocranium, the 'great hole' or posteromedial aperture through the occiput into the cranial cavity, above the occipital centrum and medial and usually dorsal to the occipital condyles. The spinal cord passes from the brain through the foramen magnum into the neural canal of the vertebral column.

Free rear tips: The pectoral, pelvic, dorsal, and anal fins all have a movable rear corner or flap, the free rear tip, that is separated from the trunk or tail by a notch and an inner margin. In some sharks the rear tips of some fins are very elongated.

Frontal and parietal fenestrae: On the neurocranium, medial apertures in the cranial roof between the anterior fontanelle and the parietal fossa, the frontal fenestra being closer to the anterior fontanelle and the parietal fenestra to the parietal fossa. Sometimes the two merge and become a frontoparietal fenestra, while in many batoids and in some orectoloboid sharks there is a merging of the anterior fontanelle with the frontoparietal fenestra so that it extends nearly to the parietal fossa. All of these fenestrae are closed by tough membranes.

Functional series: A series of oral teeth that are in functional position on the jaw.

## Galeomorph: Referring to the Galeomorphii.

Galeomorphii: The neoselachian superorder Galeomorphii, including the heterodontoid, lamnoid, orectoloboid, and carcharhinoid sharks.

Gill openings or slits: In elasmobranchs, the paired rows of five to seven transverse openings on the sides or underside of the head for the discharge of water through the gills. Chimaeras have their four gill openings hidden by a soft gill cover and discharge water through a single external gill opening.

Gill-raker denticles: In the basking shark (Cetorhinidae), elongated denticles with hair-like cusps arranged in rows on the internal gill openings, which filter out planktonic organisms.

Gill-raker papillae: Sparse to dense dermal papillae on the gill arches of some sharks that serve as filters to collect small food organisms.

Girdle: A bar of cartilage buried in the body wall that supports the basals of the paired fins: the pectoral girdle (scapulocoracoid) and pelvic girdle (puboischiadic bar).

Hadal: The benthic zone of the deep trenches, 6000 to about 11000 m , from which no cartilaginous fishes have been observed or recorded to date.

Hadopelagic zone: The pelagic zone inside the deep trenches, 6000 to about 11000 m , from which no chondrichthyans have been observed or recorded.

Haemal arch: The arch ventral to the notochord or vertebral centra on tail vertebrae that is formed by the basiventrals and interventrals and which houses the caudal artery and caudal vein in a haemal canal.

Haemal spines: On the haemal arches of the diplospondylous precaudal and caudal vertebrae, elongated ventral surfaces forming vertical plates, particularly welldeveloped on the caudal fin.

Head: That part of a cartilaginous fish from its snout tip to the last or (in chimaeras) only gill slits.

Heterocercal: A caudal fin with the vertebral axis slanted dorsally into the fin base, which is also dorsally elevated.

Heterodontoid: A bullhead shark, horn shark, or Port Jackson shark, a member of the order Heterodontiformes, family Heterodontidae.

Heterodonty: In oral teeth, structural differences between teeth in various positions on the jaws, between teeth in the same position during different life stages, or between teeth in the same positions in the two sexes.

Hexanchoid: A cowshark or frilled shark, members of the order Hexanchiformes, and including the sixgill sharks, sevengill sharks, and frilled sharks.

Holocephalan: Referring to the Holocephali.
Holocephali: The subclass Holocephali (from Greek holos, entire, and kephalos, head), the living chimaeras and their numerous fossil relatives, a major subdivision of the class Chondrichthyes. The name is in reference to the fusion of the upper jaws or palatoquadrates to the skull in all living species and in many but not all fossils. The living holocephalans include three families in the order Chimaeriformes. The living species differ from elasmobranchs in having four pairs of gill openings covered by a soft gill cover and with a single pair of external gill openings, oral teeth fused and reduced to three pairs of ever-growing tooth plates, an erectile first dorsal fin with a spine and a long, low spineless second dorsal.

Holotype: Either the only specimen used and mentioned in an original description of a species, with or without a designation of such, or one of two or more specimens used and mentioned in an original description of a species and designated as such. This becomes the 'name-bearer' of the species, and is used to validate the species or scientific name by anchoring it to a single specimen.

Homodonty: In oral teeth, structural similarity between teeth in various positions on the jaws, between teeth in the same position during different life stages, or between teeth in the same positions in the two sexes.

Hyoid arch: The visceral arch that supports the tongue and, in elasmobranchs, the rear of the upper jaws. The hyoid arch is between the mandibular arch and the first branchial arch, and has the spiracular pocket between it and the mandibular arch. The hyoid arch in elasmobranchs includes a medial basihyoid in the floor of the mouth and inside the tongue, a pair of elongated ceratohyals articulating with the basihyoid and the hyomandibulae, and a pair of hyomandibulae articulating with the ceratohyals and the hyomandibular facets of the neurocranium. Chimaeroids have a nonsuspensory hyoid arch similar to the gill arches, with a pair of epihyals and pharyngohyals equivalent to the hyomandibulae. Batoids have the ceratohyals reduced and separated from the hyomandibulars or absent, and functionally replaced by paired dorsal and ventral pseudohyoids.

Hyomandibular facet: On the neurocranium of elasmobranchs, a joint surface, socket or cotyle that is usually on the ventrolateral surfaces of each otic capsule
but may be extended posteriorly or arched dorsally. The heads of the hyomandibulae articulate with these facets. Chimaeras lack hyomandibular facets and differentiated hyomandibulae.

Hyomandibular nerve foramina: Foramina for the roots of the hyomandibular nerves, behind the orbital fissures. These foramina are confluent with the orbital fissure in many sharks.

Hypaxial web: The entire fin web below the vertebral column (vertebral axis) and the caudal base.

Hypercalcified structures: Parts of the skeleton that have developed extremely dense calcified cartilage, primarily during growth and maturation, which sometimes swell to knobs that distort and engulf existing cartilaginous structures. The rostrum of the salmon shark (Lamna ditropis) is a particularly impressive hypercalcified structure.

Hypocercal: A caudal fin with the vertebral axis slanted ventrally into the fin base, which is also ventrally depressed. Found only in angel sharks (Squatiniformes) among living sharks.

Hypopyle: On the external clasper and clasper skeleton, the posterior opening of the clasper groove onto the clasper glans.

Incurrent apertures: The anterior and ventrally facing openings of the nostrils, which direct water into the nasal cavities. These are usually lateral on the nostrils and anterolateral to the excurrent apertures, but may be anterior to the excurrent apertures only.

Independent dentition: Teeth along a mesodistal series in which the roots do not overlap and are separated by a space. See overlapping dentition.

Inner margin: In precaudal fins including the pectoral, pelvic, dorsal and anal fins, the margin from the fin insertion to the rear tip.

Insertion: The posterior or rear end of the fin base in precaudal fins. The caudal fin lacks insertions except with many batoids and some chimaeroids that have a caudal filament that extends posterior to the fin. See origin.

Interdorsal cartilages: A pair of wedge-shaped arched thin cartilages fitting between the basidorsal cartilages of each vertebra to complete the neural arch.

Interdorsal ridge: A ridge of skin on the midback of sharks, in a line between the first and second dorsal fins; particularly important in identifying grey sharks (genus Carcharhinus, family Carcharhinidae).

Intermedialia: In a vertebral centrum, dorsal, ventral and lateral spaces between the attachment surfaces of the basidorsal and basiventral cartilages and between the two halves of the double cone. These can be filled with uncalcified cartilage, with solid or hollow wedges of calcified cartilage, or with plate-like, branched calcified radii within uncalcified cartilage. See basalia.

Intermediate segments: In the clasper skeleton, one or more short cylindrical cartilages connecting the pelvic basipterygium to the axial cartilage of the clasper. Also termed stem-joints.

Intermediate teeth: Small oral teeth between the laterals and anteriors of the upper jaw, found in most lamnoids.

Internasal plate or septum: On the neurocranium, a plate or partition between the two nasal capsules. It ranges from a vertical plate to a broad horizontal plate.

Interventral cartilages: A pair of rounded or wedge-shaped cartilages fitting between the basiventral cartilages of each vertebra, that in diplospondylous precaudal and caudal vertebrae form the haemal arches with the basiventral cartilages.

Intestinal valve: A dermal flap inside the intestine, protruding into its cavity or lumen, and of various forms in different cartilaginous fishes. Often formed like a corkscrew or augur. See spiral, ring and scroll valves.

## Jaws: See mandibular arch.

Labial cartilages: Paired cartilages that are internal and support the labial folds at the lateral angles of the mouth. Living neoselachians typically have two pairs of upper labial cartilages, the anterodorsal and posterodorsal labial cartilages, and one pair of ventral labial cartilages, but these are variably reduced and sometimes absent in many sharks. Chimaeras have more elaborate labial cartilages than living elasmobranchs.

Labial flange: On tooth crowns of many squaloids and some orectoloboids, a narrow, vertically elongated labial basal ledge.

Labial folds: Lobes of skin at the lateral angles of the mouth, usually with labial cartilages inside them, separated from the sides of the jaws by pockets of skin (labial grooves or furrows).

Labial furrows or labial grooves: Grooves around the mouth angles on the outer surface of the jaws of many cartilaginous fishes, isolating the labial folds. Primitively there is a distinct upper labial furrow above the mouth corner and a lower labial furrow below it.

Labial: In oral teeth, the outer face of the tooth that is directed outside the mouth and towards the lips. See lingual.

Lamnoid: A mackerel shark, a member of the order Lamniformes, and including the sand tiger sharks, goblin sharks, crocodile sharks, megamouth shark, thresher sharks, basking shark, and the makos, porbeagle, salmon shark and white shark.

Lateral clasper fold: In mackerel sharks (family Lamnidae), a unique longitudinal flap of skin along the lateral edge of the external clasper shaft.

Lateral commissures: On the neurocranium, tube-like or ring-like enclosed passages for the lateral head veins, which drain the orbital sinuses, through the postorbital
walls of the orbits and below the sphenopterotic ridges and above the hyomandibular facets in neoselachians. The lateral commissures are reduced or absent in many living neoselachians.

Lateral or laterad: Outwards, in the transverse direction towards the periphery of the body. See medial.

Lateral orolabial grooves: Shallow longitudinal grooves on the lower jaw that connect the edge of the lip on each side with the medial ends of the lower labial furrows. Found in more advanced orectoloboids.

Lateral teeth: Large broad-rooted, compressed, high crowned oral teeth on the sides of the jaws between the anteriors and posteriors.

Lateral trunk denticle: A dermal denticle from the dorsolateral surface of the back below the first dorsal fin base.

Lectotype: One of two or more specimens that were syntypes in an original description, designated as a lectotype by a subsequent writer. It then becomes equivalent to a holotype, and anchors the name of the species to a specimen unless invalidated by a ruling of the International Commission on Zoological Nomenclature or a previous designation of a lectotype.

Levator palatoquadrati muscles: Paired head muscles that primitively originate on the underside of the postorbital processes and sphenopterotic ridges, extend vertically, and insert on the posteromedial surfaces of the quadrate processes of the palatoquadrates. In advanced carcharhinoids the origins of the levator palatoquadrati muscles are expanded far forwards and diagonally into the orbits. Primitively these muscles lift or retract the jaws upwards, but in advanced carcharhinoids may help rotate the jaws forwards and downwards in opposition to the levator hyomandibularis muscles, which retract the jaws.

Lingual: In oral teeth, the inner face of the tooth that is directed inside the mouth and towards the tongue. See labial.

Littoral zone: That part of the oceans over the continental and insular shelves, from the intertidal to 200 m .

Live-bearing: A mode of reproduction in which female sharks give birth to young sharks, which are miniatures of the adults. See viviparity.

Longitudinal ridges: In lateral trunk denticles, parallel ridges that extend anteroposteriorly on the distal surface of the crown. These may be in the form of a single medial ridge (sometimes paired), and paired lateral ridges, and may terminate in medial and lateral cusps.

Lower eyelid: The ventral half of the eyelid, separated by a deep pocket (conjunctival fornix) from the eyeball. In some derived batoids the pocket also fuses with the eyeball.

Lower origin: In the caudal fin, the anteroventral beginning of the hypaxial or lower web of the caudal fin, at the posterior end of the anal-caudal or pelvic-caudal space (see measurement illustrations).

Lower postventral margin: In the caudal fin, the lower part of the postventral margin of the hypaxial web, from the ventral tip to the posterior notch.

Mandibular arch: The paired primary jaw cartilages of sharks, including the dorsal palatoquadrates and the ventral Meckel's cartilages.

Mandibulocutaneous muscles: Paired head muscles in squaloid and hexanchoid sharks, that originate on the inside of the skin of the head behind the eyes and near the spiracles, and insert on the dorsoposterolateral face of the quadrate processes of the palatoquadrates.

Meckel's cartilages: The paired lower jaw cartilages, articulating mesially with each other at the midline or symphysis of the lower jaw, and articulating laterally with the distal ends of the palatoquadrates. The Meckel's cartilages are fused together at the symphysis in some shark-like fishes or are articulated to a symphysial cartilage in others.

Medial teeth: Small oral teeth, generally symmetrical and with narrow roots, in one row at the symphysis and often in additional paired rows on either side of the symphysial one.

Medial: Inwards, in the transverse direction towards the middle of the body. See lateral.

Mesial: In oral teeth, mesial structures are towards the midlines of the jaws, the symphyses. See distal.

Mesopelagic zone: That part of the oceans beyond the continental and insular shelves, in oceanic waters, from about 200 to 1000 m , the twilight zone where little light penetrates.

Mesopterygium: In the pectoral fin skeleton of living neoselachians, the middle basal cartilage, between the propterygium and metapterygium. The mesopterygium is sometimes fused to the propterygium or metapterygium, or to both.

Mesorhipidion: A knife-like or blade-like structure on the lateral clasper glans of some carcharhinoid sharks, formed from the terminal 3 cartilage, and over and partially lateral to the ventral terminal and mesial to the pseudopera.

Metapterygial axis: In the pectoral fin skeleton of living neoselachians, the posterior extension of the mesopterygium as a flattened, elongated segmented series of cartilages that supports the distal bases and free rear tips of the pectoral fins; the axis has radials along its distal edge continuous with the radials on the metapterygial basal.

Metapterygial basal: In the pectoral fin skeleton of living neoselachians, the anteriormost, expanded cartilage of the metapterygium.

Metapterygial proximal segment: In the hexanchoid pectoral fin skeleton, a short jointed segment on the proximal end of the metapterygial basal, not found in other sharks.

Metapterygium: In the pectoral fin skeleton of living neoselachians, the rearmost basal cartilage, adjacent to the posterior edge of the mesopterygium and with
several radials attached to its distal edge. It includes the metapterygial basal and the metapterygial axis.

Molariform: In oral teeth, referring to a tooth with a broad flat crown with low cusps or none, for crushing hard-shelled invertebrate prey.

Monospondylous precaudal vertebrae: Vertebrae with one centrum and one pair of basidorsals, basiventrals, and ribs per body segment (myotome), and generally extending from the occiput to the end of the body cavity and to over the pelvic girdle. However there is much variation in the position of the monospondylous-diplospondylous transition, which can range well in front or behind the pelvic girdle.

Monospondylous-diplospondylous transition: The position on the vertebral column where monospondylous centra end and diplospondylous centra begin. In lateral view the transition often appears as an abrupt decrease in length of the diplospondylous centrum compared to the last monospondylous centrum, but this can be obscure in various sharks with very numerous, very short centra. Often a centrum of intermediate length appears between a long monospondylous centrum and a short diplospondylous centrum. In a few sharks there is a stutter zone of alternating long and short centra that marks the transition. Also, the basidorsals and basiventrals have foramina for the spinal nerves on every other vertebra, rather than on each vertebra as in monospondylous vertebrae. The transition from long to short centra is generally coordinated with the transition of vertebrae with free ribs and no haemal arches to those without ribs and with haemal arches. However, in some sharks the two transitions can be anterior or posterior to each other.

Multiple oviparity: A mode of egg-laying or oviparity in which female sharks retain several pairs of cased eggs in the oviducts, in which embryos grow to advanced developmental stages. When deposited on the bottom (in captivity) the eggs may take less than a month to hatch. Found only in the scyliorhinid genus Halaelurus, with some uncertainty as to whether the eggs are normally retained in the oviducts until hatching. Eggs laid by these sharks may be abnormal, unusual, or an alternate to ovoviviparity. The whale shark (Rhincodon typus) may have multiple retention of egg cases; near-term foetuses have been found in their uteri and egg-cases with developing foetuses have been collected on the bottom.

Nasal aperture: On the neurocranium, an aperture in the anteroventral surface or floor of each nasal capsule, through which the nostril directs water into and out of the nasal organ.

Nasal capsules: On the neurocranium, a pair of spherical, oval or trumpet-shaped, thin-walled structures behind the rostrum (when present) and in front of the orbits, cranial roof and basal plate. They serve as containers for the nasal organs or organs of smell, and have passages into the cranial cavity to connect the nasal organs with the brain.

Nasal curtain: Anterior nasal flaps that are expanded medially and posteriorly and have fused with each other. Nasal curtains are found in some carcharhinoid sharks and in many batoids.

Nasal flap: One of a set of dermal flaps associated with the nostrils, and serving to direct water into and out of them, including the anterior, posterior, and mesonarial flaps.

Nasal fontanelle: On the neurocranium, an aperture in the posteroventral surface or floor of each nasal capsule, behind the nasal apertures and closed by a dermal membrane.

Nasoral grooves: Many bottom-dwelling, relatively inactive sharks have nasoral grooves, shallow or deep grooves on the ventral surface of the snout between the excurrent apertures and the mouth. The nasoral grooves are covered by expanded anterior nasal flaps that reach the mouth, and form water channels that allow the respiratory current to pull water by partial pressure into and out of the nostrils and into the mouth. This allows the shark to actively irrigate its nasal cavities while sitting still or when slowly moving. Nasoral grooves occur in heterodontoids, orectoloboids, chimaeroids, some carcharhinoids, and most batoids. Also termed oronasal grooves.

Neck: A narrow band of finely porous dull tissue (possibly orthodentine) encircling the proximal end of the crown of a tooth, and apparently covered with dental membrane.

Neoselachian: Referring to the Neoselachii.
Neoselachii: From Greek neos, new, and selachos, shark. The modern sharks, the subcohort Neoselachii, consisting of the living elasmobranchs and their immediate fossil relatives. See Euselachii.

Neotype: A specimen, not part of the original type series for a species, which is designated by a subsequent author, particularly if the holotype or other types have been destroyed, were never designated in the original description, or are presently useless.

Neural arch: In shark vertebrae, a dorsal arch formed by basidorsal and interdorsal cartilages above the centrum and forming a neural canal containing the spinal cord.

Neural spines: On the neural arches of shark vertebrae, elevated dorsal plate-like surfaces, particularly welldeveloped in many squalomorph sharks.

Neurocranium: In sharks, a box-shaped complex cartilaginous structure at the anterior end of the vertebral column, containing the brain, housing and supporting the nasal organs, eyes, ears, and other sense organs, and supporting the visceral arches or splanchnocranium. Also termed chondrocranium, chondroneurocranium, or endocranium.

Nictitating lower eyelid: In the ground sharks (order Carcharhiniformes), a movable lower eyelid that has special posterior eyelid muscles that lift it and, in some species, completely close the eye opening (or palpebral aperture). Often incorrectly termed nictitating membrane, a different, nonhomologous structure in terrestrial vertebrates.

Nictitating upper eyelid: In parascylliid orectoloboids, the upper eyelid has anterior eyelid muscles that pull it down and close the eye opening, analogous to the nictitating lower eyelids of carcharhinoids.

Nomenclature: In biology, the application of distinctive names to groups of organisms.

Nostrils: The external openings of the cavities of the nasal organs, or organs of smell.

Notochord: In embryonic sharks (and other chordates) the notochord is a fluid-filled tube below the spinal cord that has a connective-tissue notochordal sheath surrounding it. The notochord forms the primitive developmental base of the chondrichthyan vertebral column. Chimaeroids retain the notochord and its sheath without constriction (although some have ring-like centra in the sheath), but in neoselachians it is constricted by the development of double-cone calcifications of the centra within the sheath into biconical chambers between each centrum. The addition of centra to the notochordal sheath strengthens the vertebral column. Some deepwater squaloid, hexanchoid, and lamnoid sharks have the sheath constriction and calcified double cones variably reduced, sometimes to connective tissue septa only. Some of these taxa with a 'notochordal' vertebral column have been considered primitive but are apparently derived from ancestors with well-calcified, constricted vertebral centra.

Occipital centrum: On the occiput of the neurocranium, the posterior half of a calcified double cone of the vertebral column, imbedded in the basal plate and articulating with the anteriormost centrum of the vertebral column. Also termed occipital hemicentrum.

Occiput: The posteriormost sector of the neurocranium, behind and partially between the otic capsules, with its dorsal surface from the parietal fossa rearwards to the foramen magnum, and its posterior surface including the occipital condyles, the occipital centrum, the paired vagus nerve foramina, the paired glossopharyngial nerve foramina, and the rear surface of the hyomandibular facets.

Oceanic: Referring to organisms inhabiting those parts of the oceans beyond the continental and insular shelves, over the continental slopes, ocean floor, sea mounts and abyssal trenches. The open ocean.

Ocelli or eyespots: Large eye-like pigment spots located on the dorsal surface of the pectoral fins or bodies of some sharks including rays, angel sharks, and some bamboo sharks, possibly serving to frighten potential enemies.

Oophagy: From Greek oön, egg, and phagos, to eat. Eggeating, a mode of live-bearing reproduction employing uterine cannibalism; early foetuses deplete their yolk-sacks early and subsist by eating nutritive eggs produced by the mother. Known in several lamnoid sharks, the carcharhinoid family Pseudotriakidae, and in the orectoloboid family Ginglymostomatidae (Nebrius ferrugineus).

Optic nerve foramen: A large foramen usually in the middle of the orbital wall, passing the optic nerve from the brain to the eye.

Optic pedicel: On the neurocranium, a slender cartilage that projects from the medial orbital wall and articulates with the eyeball; it serves as a pivot point for the eyeball and a spacer between the eyeball and the orbital wall.

Orbital fissures: The main foramina or fenestrae that pass the trigeminal and facial nerves from the brain to the orbits, located on the posteroventral ends of the medial walls of the orbits.

Orbital notches: On the neurocranium, the paired anterior notches in the suborbital shelves that articulate with the orbital processes of the palatoquadrates. In many squalomorph sharks these are enlarged, deepened, socketlike, and posteriorly situated in the orbits, with telescoping of the suborbital shelves, and are lost in batoids.

Orbits: Large, paired cavities on the sides of the neurocranium, behind the nasal capsules, mostly in front of the otic capsules, and separated medially by the cranial cavity. They are bounded anteriorly by the preorbital walls and processes, dorsally by the supraorbital crests, ventrally by the suborbital shelves (reduced or lost in various squalomorph sharks), and posteriorly by the postorbital processes and walls. The orbits contain the eyeballs and their muscles, venous sinuses, several arteries that connect to the cranial cavity, and most of the cranial nerves.

Orectoloboid: A carpet shark, a member of the order Orectolobiformes, including barbelthroat carpet sharks, blind sharks, wobbegong sharks, bamboo sharks, epaulette sharks, nurse sharks, zebra sharks, and whale sharks.

Origin: The anterior or front end of the fin base in all fins. The caudal fin has upper and lower origins but no insertion. See insertion.

Orthodentine: A primary hard tissue comprising the crown of oral teeth in sharks, with numerous fine mostly parallel nonvascular tubules.

Orthodont: An oral tooth with its crown filled with orthodentine, and with a prominent central pulp cavity.

Osteodentine: A primary hard tissue comprising the roots and sometimes the inside of the crown in the oral tooth, with bone-like large reticulating, thick-walled tubules.

Osteodont: An oral tooth with its crown filled with osteodentine, continuous with the root, and without a pulp cavity.

Otic capsules: On the neurocranium, a pair of complex thick-walled capsules containing the inner ears, and located between the orbits and the occiput, and partially separated medially by the cranial cavity.

Overlapping dentition: Teeth along a mesodistal series in which the roots overlap and are not separated by a space. Two types of overlap patterns occur, alternate overlap, in which teeth in a series alternate from more labial to more lingual, and imbricate overlap, in which the distal end of each tooth lingually or labially overlaps the mesial end of the succeeding tooth, repeating to the distal ends of the dental band. Alternate-imbricate dentitions combine both alternate and imbricate overlap. See independent dentition.

Oviparity: A mode of reproduction in which female sharks deposit eggs enclosed in oblong or conical egg-cases on the bottom, which hatch in less than a month to more than
a year, producing young sharks which are miniatures of the adults.

Ovoviviparity: Generally equivalent to yolk-sac viviparity, live-bearing in which the young are nourished primarily by the yolk in the yolk-sac, which is gradually depleted and the yolk-sac reabsorbed until the young are ready to be born. Sometimes used to cover all forms of aplacental viviparity, including cannibal viviparity.

Paired fins: The pectoral and pelvic fins.
Palatoquadrates: The paired upper jaw cartilages, articulating mesially with each other at the midline or symphysis of the upper jaw, and articulating laterally with the distal ends of the Meckel's cartilages. The palatoquadrates are fused to the neurocranium in all living holocephalans. The palatoquadrates of neoselachians are divided into cylindrical anteromedial sectors or palatine processes, which articulate or are otherwise attached to each other at the symphysis; variably modified conical to flattened articular structures or orbital processes on the middle of the palatoquadrates for attachment to the neurocranium at the orbital notches; and often elevated posterodistal quadrate processes that articulate with the distal ends of the Meckel's cartilages and are loosely or firmly attached to the distal ends of the hyomandibulae. In a few living neoselachians, and many fossil elasmobranchs, the quadrate processes have postorbital articulations with the rear surfaces of the postorbital processes of the neurocranium.

Palpebral aperture: The eye opening, defined by the upper and lower eyelids.

Papillae: Elongated finger-like processes of skin, located around the spiracles of torpedo rays, and in the mouths and on the gill arches of other sharks.

## Papillose gill rakers: See gill raker papillae.

Paralectotype: One of two or more specimens that were syntypes in an original description, but which became a paralectotype or paralectotypes when a subsequent author designated one of the syntypes as a lectotype. Paralectotypes are equivalent to paratypes.

Paratype: Each specimen of a type series other than the holotype. Specimens other than the holotype automatically become paratypes unless the author designates them as referred specimens that are not part of the type series.

Parietal fossa: On the neurocranium, a shallow or deep depression between the otic capsules and at the rear of the cranial roof, that houses foramina for paired ducts leading to the inner ears and for the spaces around them.

Pectoral fins: A symmetrical pair of fins on each side of the trunk just behind the head and in front of the abdomen. These are present in all cartilaginous fishes and correspond to the forelimbs of a land vertebrate (a tetrapod or fourfooted vertebrate).

## Pectoral or shoulder girdle: See scapulocoracoid.

Pedicel: In lateral trunk denticles, a narrow stalk separating the crown from the base.

Pelagic: Referring to organisms that are free-swimming, not bottom-dwelling.

Pelvic fin: Asymmetrical pair of fins on the sides of the body between the abdomen and precaudal tail which correspond to the hindlimbs of land vertebrate (a tetrapod or four-footed vertebrate). Also, ventral fins.

## Pelvic girdle: See puboischiadic bar.

Photophores: Conspicuously pigmented small spots on the bodies of most lantern sharks (family Etmopteridae) and some kitefin sharks (family Dalatiidae). These are tiny round organs that are covered with a conspicuous dark pigment (melanin) and produce light by a low-temperature chemical reaction.

## Placenta: See yolk-sac placenta.

Placental viviparity: Live-bearing in which the young develop a yolk-sac placenta, which is apparently confined to the carcharhinoid sharks.

## Placoid scale: See dermal denticle.

Plesodic fin: A pectoral, pelvic, dorsal, or anal fin in which the radial cartilages of the fin skeleton extend far into the distal fin web, often near its edges, and between the supporting ceratotrichia of the fin web. Some fossil sharks also have plesodic caudal fins, in which the expanded haemal arches of the caudal vertebrae extend far into the fin web. In more advanced batoids the radials of the plesodic paired fins become highly branched and segmented, very narrow and slender, and essentially replace the ceratotrichia as supports for the fin webs.

Pores, pigmented: In a few sharks and skates, the pores for the lateral line and ampullae of Lorenzini are conspicuously black-pigmented, and look like little black specks.

Posterior: Rearwards, in the longitudinal direction of the caudal-fin tip or tail filament. Also caudal.

Posterior margin: In precaudal fins, the margin from the fin apex to either the free rear tip (in sharks with distinct inner margins) or the fin insertion (for those without inner margins).

Posterior nasal flaps: Low flaps or ridges arising on the posterior edges of the excurrent apertures of the nostrils.

Posterior notch: In the caudal fin, the notch in the postventral margin dividing it into upper and lower parts.

Posterior teeth: Small or sometimes enlarged irregular oral teeth near and at the distal ends of the dental bands, with low crowns and sometimes missing cusps.

Posterior tip: The posteriormost corner or end of the terminal lobe of the caudal fin.

Postocular eyelid muscles: A complex of paired head
muscles unique to carcharhinoid sharks that originate around the spiracles and insert on the posterior ends of the upper eyelids and nictitating lower eyelids. Primitively they depress the upper eyelid and elevate the nictitating lower eyelid to close the eye, but in more derived carcharhinoids the eye is closed only by elevation of the nictitating lower eyelid.

Postorbital processes: On the neurocranium, posterolateral projections of the supraorbital crests, below which the postorbital walls originate.

Postorbital walls: On the neurocranium, the posterior boundaries of the orbits, variously reduced vertical plates of cartilage that close the orbits between the postorbital processes and the suborbital shelves, more or less reduced in living neoselachians.

Postventral margin: In the caudal fin, the margin from the ventral tip to the subterminal notch of the caudal fin. See lower and upper postventral margins.

Preanal ridges: Apair of low, short to long, narrow ridges on the midline of the caudal peduncle extending anteriorly from the anal fin base.

Precaudal fins: All fins in front of the caudal fin.
Precaudal pit: A depression at the upper and sometimes lower origin of the caudal fin where it joins the caudal peduncle.

Precaudal tail: That part of the tail from its base at the vent to the origins of the caudal fin.

Precaudal vertebrae: Vertebrae from the occiput to the dorsal origin of the caudal fin.

Predorsal ridge: A low narrow ridge of skin on the midline of the back anterior to the first dorsal fin base.

Preorbital canals: On the neurocranium, anterior passages for the superficial opthalmic nerves out of the orbits and onto the nasal capsules and rostrum, situated at the anteromesial edges of the supraorbital crests at the rear bases of the preorbital processes; sometimes greatly expanded posteriorly.

Preorbital processes: On the neurocranium, anterolateral projections of the supraorbital crests, below which the preorbital walls originate.

Preorbital walls: On the neurocranium, the anterior boundaries of the orbits, curved vertical plates of cartilage that vary from complete to absent in neoselachians.

Preorbitalis muscles: Paired head muscles that primitively originate on the rear of the nasal capsules or on the preorbital walls, run diagonally rearwards, and insert on the adductor mandibulae at the mouth angles. Orectoloboids and heterodontoids have the preorbitalis vertical, with crossbiased fibres in the latter, and the insertions are along the ventral edge of Meckel's cartilage. In derived orectoloboids the origins of the preorbitalis are expanded onto the cranial roof and the muscles greatly expanded. Primitively the preorbitalis may primarily serve to protrude the jaws, but
they may primarily serve to increase the power of the bite in orectoloboids and heterodontoids. Also termed levator labii superioris muscles.

Preventral margin: In the caudal fin, the margin from the lower origin to the ventral tip of the caudal fin.

Pristiophoroid: A saw shark, order Pristiophoriformes, family Pristiophoridae.

Propterygium: In the pectoral fin skeleton of living neoselachians, the anteriormost basal cartilage, adjacent to the anterior edge of the mesopterygium and with one or more radials attached to its distal end. In batoids with expanded anterior pectoral fin lobes it becomes expanded and segmented into a propterygial basal and propterygial axis, similar to the metapterygial basal and axis.

Proximal: In any direction, at the near end of a structure.
Pseudopera: On the external clasper glans, a dorsally opening blind pocket along the lateral edge of the clasper, and about opposite the anterior edge of the glans.

Pseudosiphon: On the external clasper glans, a dorsally opening blind pocket along the medial edge of the clasper, and about opposite the cover rhipidion.

Pterotic horn or process: On the neurocranium, elongated posterior projections of the sphenopterotic ridges of the otic capsules.

Puboischiadic bar: A transverse flattened or cylindrical plate in the posterior body wall opposite the anterior ends of the pelvic fins, in front of the vent and at the posterior end of the body cavity, that supports a few anterior pelvic radials and a basal cartilage, the basipterygium. The pelvic girdle.

Radial cartilages or radials: The small, segmented, more distal cartilages of the precaudal fins, attached proximally to the distal edges of the basal cartilages. In the pectoral fin skeleton of living neoselachians, the radials mostly have three segments but range from no segments to 30 or more. The radial segments adjacent to the pectoral basals are the proximal radials, the radial segments furthest from the basals are the distal radials, and any segments between them are intermediate radials.

Radii: In a vertebral centrum in cross-section, branching plates of calcified cartilage in the intermedialia. These have a radial orientation from the centre of the centrum.

## Ray: See batoid.

Replacement series: A series of oral teeth that are lingual to the functional series, and not in a functional position on the jaw.

Rhipidion: In nonbatoid sharks, a longitudinal, elongated flap attached to the floor of the glans along its base and with its free edge directed laterally. In skates (Rajoidei) rhipidion is used for a soft mass of erectile tissue in the glans, not necessarily homologous to the rhipidion of nonbatoid sharks.

Rhomboidal: In the form of a rhombus or diamond.
Ribs: On the shark vertebral column, short to elongated paired and typically pointed cartilages attached to the basiventral cartilages and extending into the horizontal septum of the segmented trunk musculature or myomeres. Chondrichthyan ribs are therefore dorsal ribs rather than ventral ribs as in bony fishes (which support the body cavity).

Ring valve: A type of spiral intestinal valve in which the valve turns are very numerous and short and resemble a stack of washers.

Rise: The transitional and less steep bottom zone from the lower slope to the abyss or ocean floor, between 2250 m and 4500 m . The rise can be divided into upper ( 2250 to 3000 m ), middle ( 3000 to 3750 m ) and lower ( 3750 to 4500 $\mathrm{m})$ rises. Few sharks are known from the rise, and those mostly from the upper rise. See Abyss, Hadal, Shelf and Slope.

Root lobe: Sharks often have the roots of their oral teeth divided into separate lobes at their midlengths, which are termed mesial and distal root lobes.

Root: The proximal part of the oral tooth, made of porous osteodentine and anchoring the tooth in the dental membrane of the jaw.

Rostral keel: In the neurocranium of squaloids, a large vertical plate on the underside of the rostrum and internasal septum, sometimes reduced, and with the cavities of the subnasal fenestrae on either side of the keel.

Rostral node: On the neurocranium, the anterior end of the rostrum of cartilaginous fishes, and the plate formed by the fused anterior ends of the tripodal rostra in many galeomorph sharks.

Rostromandibular muscle: In the orectoloboid family Parascylliidae, paired head muscles that originate on the sides of the adductor mandibulae muscles and insert via long tendons on the medial rostral cartilage. These are possibly for depressing the snout. Not found in any other sharks, though analogous muscles exist in batoids.

Rostronuchal muscles: In the orectoloboid family Parascylliidae, paired head muscles that originate on the dorsal myomeres of the nape, and insert via long tendons on the medial rostral cartilage. These are possibly for elevating the snout. Not found in any other sharks, though analogous muscles exist in batoids.

Rostrum: On the neurocranium, the cartilaginous anteriormost structure which supports the prenasal snout including lateral line canals and masses of ampullae, and is located in front of the nasal capsules and anterior fontanelle. The rostrum is very variable, and in squalomorph sharks is primitively trough or basin-shaped, while it may be primitively rod-shaped or tripodal in galeomorph sharks. It is absent in a few nonbatoid sharks and in many batoids. See rostrum, tripodal.

Rostrum, tripodal: The rostrum of the neurocranium in lamnoids and carcharhinoids is primitively tripodal, with a pair of dorsolateral lateral rostral cartilages that arise from the posterolaterodorsal surfaces of the nasal capsules or from the preorbital wall, and a medial rostral cartilage that arises from the anteromedial surface of the internasal septum. The medial and lateral rostral cartilages extend anteriorly and articulate or fuse at the rostral node. Living orectoloboids have only the medial rostral cartilage although a tripodal rostrum may be present in some fossil orectoloboids, while heterodontoid sharks lack a rostrum as adults but apparently lose it as embryos.

Row: In oral teeth, a single replicating line of teeth, approximately transverse to the longitudinal jaw axis, which includes functional teeth and their replacements, derived from one tooth-producing area on the jaw.

Saw or saw-snout: The elongated snout in sawfish and sawsharks, with side and (in sawsharks) ventral teeth formed from enlarged denticles, used to kill, ensnare or dig for prey. Also termed rostral saw.

Scapulocoracoid: The primitively U-shaped cartilage in the body wall just behind the gills and at the anterior end of the pectoral bases, that supports the pectoral fins and articulates with the pectoral basals. The scapulocoracoid consists of a ventral coracoid bar connecting its paired lateral faces with articular condyles or ridges for the pectoral basals, and a pair of dorsal scapular processes dorsal to the lateral faces. The scapular processes sometimes have separate suprascapulae above them, but they are sometimes fused with the scapular processes. The coracoid bar has a medial joint or even a separate medial cartilage (sternal cartilage) in a few living sharks, as with many fossil cartilaginous fishes. The pectoral or shoulder girdle.

Scroll valve: A type of spiral intestinal valve in requiem and hammerhead sharks in which the valve has uncoiled and resembles a rolled-up bib or scroll.

Second dorsal fin: The posteriormost dorsal fin of two in cartilaginous fishes, ranging in position from over the pelvic-fin bases to far posterior on the precaudal tail.

Secondary caudal keels: Low horizontal dermal keels on the ventral base of the caudal fin in mackerel sharks (Lamnidae) and sometimes somniosids.

Secondary lower eyelid: The eyelid below or lateral to the nictitating lower eyelid, separated from it by a subocular groove or pocket, and, in many carcharhinoids with internal nictitating lower eyelids, functionally replacing them as lower eyelids. Some orectoloboids have shallow subocular grooves separating their non-nictitating lower eyelids from weakly developed secondary lower eyelids. They may, however, be able to close their eye openings by retracting the eyeballs.

Semiplesodic fin: In some sharks, a pectoral or dorsal fin with the fin radial cartilages extending partway into the fin web but not to its distal edges, essentially intermediate between plesodic and aplesodic fins.

Series: In oral teeth, a line of teeth along the jaws which is parallel to the jaw axis and includes teeth from all rows present.

Serrations: In oral teeth, minute teeth formed by the cutting edge of the crown that enhance the slicing abilities of the teeth.

Shark: Generally used for cylindrical or flattened cartilaginous fishes with 5 to 7 external gill openings on the sides of their heads, pectoral fins that are not attached to the head above the gill openings, and a large, stout tail with a large caudal fin; that is, all living elasmobranchs except the rays or batoids. Living sharks in this sense are all members of the Neoselachii, the modern sharks and rays. Shark is also used loosely for fossil chondrichthyans that are not neoselachians but have a shark-like form, and even for 'spiny sharks' (acanthodians) and for certain teleosts. Rays are essentially flattened sharks with the pectoral fins attached to their heads and are cladistically nested within the squalomorph sharks, while living chimaeras are the immediate sister group of living neoselachians and are called ghost sharks or silver sharks. Hence shark is used here in an alternate and broader sense to include the rays and chimaeras.

Shelf, continental and insular: The sloping plateaulike area along the continents and islands between the shoreline and approximately 200 m depth. It is roughly divided into inshore (intertidal to 100 m ), and offshore (100 to 200 m ) zones. The shelves have the greatest diversity of cartilaginous fishes. See Abyss, Rise and Slope.

Shoulder: In oral teeth, an arcuate or straight, convexedged section of the crown foot, without cusplets and similar to a blade but without a cutting edge.

Single oviparity: A mode of egg-laying or oviparity in which female sharks produce encased eggs in pairs, which are not retained in the oviducts and are deposited on the bottom. Embryos in the egg-cases are at an early developmental stage, and take a few months to over a year to hatch. Found in almost all oviparous cartilaginous fishes.

Siphons: A pair of dermal sacs in the ventral abdominal wall of male sharks, connecting posteriorly with the apopyles of the claspers, and extending anteriorly a variable distance from about opposite the pelvic-fin origins to opposite the pectoral-fin bases.

Skull or cranium: The skull or head skeleton of sharks includes the neurocranium and the splanchnocranium or visceral arches. The visceral arches articulate with and are associated with the neurocranium, but, except for the upper jaws of many holocephalans, are not fused to it. Also termed syncranium.

Slope, continental and insular: The precipitous bottom zone from the edge of the outer shelf down to the submarine rise, between 200 m to 2250 m . The slope can be divided into upper ( 200 to 750 m ), middle ( 750 to 1500 m ) and lower ( 1500 to 2250 m ) slopes, of which the upper and middle slope has the highest diversity of deepwater benthic sharks. See Abyss, Rise and Shelf.

Snout: That part of a cartilaginous fish in front of its eyes and mouth, and including the nostrils.

Sphenopterotic ridge: On the neurocranium, a horizontal ridge along the dorsolateral edge of each otic capsule that either ends at the occiput or terminates in an expanded pterotic process.

Spiracle: A small to large opening between the eye and first gill opening of most sharks and rays, representing the modified gill opening between the jaws and hyoid (tongue) arch. This is secondarily lost in chimaeras and some sharks.

Spiral or conicospiral valve: An intestinal valve shaped like a corkscrew or augur, with the valve angled anteriorly and medially in the intestine.

Splanchnocranium: That part of the shark skull including the visceral arches. These include the jaws or mandibular arch, the tongue or hyoid arch, and the five to seven gill or branchial arches. Also, viscerocranium.

Squalene: Along-chain oily hydrocarbon present in the liver oil of deepwater cartilaginous fishes. It is highly valued for industrial and medicinal use.

Squaloid: A dogfish shark, a member of the order Squaliformes, including bramble sharks, picked dogfish, gulper sharks, lantern sharks, viper sharks, rough sharks, sleeper sharks, kitefin sharks, and cookiecutter sharks.

## Squalomorph: Referring to the Squalomorphii.

Squalomorphii: The neoselachian superorder Squalomorphii, including the hexanchoid, squaloid, squatinoid, and pristiophoroid sharks.

Squatinoid: An angel shark, order Squatiniformes, family Squatinidae.

Squatinoid caudal fin: Angel sharks (Squatiniformes) are unique among living sharks in having hypocercal caudal fins that resemble inverted caudal fins of ordinary sharks. The dorsal margin is subdivided into a predorsal margin from the upper origin to its dorsal tip (analogous to the preventral margin and ventral tips in ordinary sharks), a postdorsal margin (like the postventral margin) from the dorsal tip to its supraterminal notch (similar to the subterminal notch), and a short supraterminal margin and large ventral terminal margin (similar to the subterminal and terminal margins) between the supraterminal notch and the ventral tip of the caudal. The ventral margin has a preventral margin forming a ventral lobe with the ventral tip and the ventral terminal margin.

Stapedial foramen or fenestra: On the neurocranium, a foramen through the posteroventromedial surface of each suborbital shelf into the orbit, for the stapedial or orbital arteries. It may be greatly expanded into a stapedial fenestra in sharks with greatly coiled stapedial arteries or lost in sharks with the suborbital shelves greatly reduced or absent.

Stapediocarotid foramen: On the neurocranium of certain sharks, fusion of the stapedial and carotid foramina on either side produces a single pair of stapediocarotid foramina.

Subcaudal keel: In a few dogfish sharks (family Centrophoridae), a single longitudinal dermal keel on the underside of the caudal peduncle.

Subethmoid fossa: On the neurocranium, a deep cavity on the ventral surfaces of the nasal capsules and the internasal plate, into which fit the palatine processes of the upper jaws.

Subnasal fenestrae: On the neurocranium of squaloids, a pair of apertures in the internasal plate between the nasal capsules that connect the cerebral cavity with two ventral fluid-filled cavities between the nasal capsules and the rostral keel. The fenestrae themselves are covered by tough membranes as with the anterior fontanelle. Subnasal fenestrae are present in most squaloids but reduced in a few derived species, and are not found in other sharks. Their function is obscure but may be sensory. Also termed basal communicating canals.

Suborbital shelf: On the neurocranium, a horizontal plate arising on the ventral junction of the orbital wall and basal plate on each side which extends from the nasal capsule to the otic capsule; it forms the floor of the orbit. A welldeveloped suborbital shelf is apparently primitive for sharklike fishes but is variably telescoped, reduced or lost in many squalomorph sharks and a few galeomorphs.

Subterminal margin: In the caudal fin, the margin from the subterminal notch to the ventral beginning of the terminal margin.

Subterminal mouth or ventral mouth: Mouth located on the underside of the head, behind the snout. Also termed an inferior mouth, in reference to its ventral position but not its function. A superior mouth (not found in living cartilaginous fishes) is on the dorsal surface of the head.

Subterminal notch: On the caudal fin of most non-batoid sharks and at least one batoid, the notch in the lower distal end of the caudal fin, between the postventral and subterminal margins, and defining the anterior end of the terminal lobe.

Superficial ophthalmic nerve foramina: Foramina for the roots of the superficial ophthalmic nerves in the medial wall of the orbits, separate from the orbital fissure. These foramina are confluent with the orbital fissure in many sharks.

Supraorbital crest: On the neurocranium, an arched horizontal plate of cartilage forming the dorsal edge of the orbit on each side; it arises from the medial orbital wall and the cranial roof and extends horizontally from the preorbital process to the postorbital process. It is apparently primitive for shark-like fishes but is variably reduced or absent in some living elasmobranchs.

Supraorbital or brow ridge: A dermal ridge above each eye, particularly well-developed in heterodontoids and some orectoloboids.

Symphyseal or symphysial groove: A longitudinal groove on the ventral surface of the lower jaw of some orectoloboid sharks, extending posteriorly from the lower symphysis.

Symphysial teeth: Larger oral teeth in one row on either side of the symphysis, distal to medials or alternates where present. Symphysials are broader than medials and usually have asymmetrical roots.

Symphysis: The midline of the upper and lower jaws, where the paired jaw cartilages articulate with each other.

Syntype: Two or more specimens used and mentioned in an original description of a species, where there was no designation of a holotype or a holotype and paratype(s) by the describer of the species.

Systematics: Scientific study of the kinds and diversity of organisms, including relationships between them.

Tail: That part of a cartilaginous fish from the cloacal opening or vent (anus in chimaeroids, which lack a cloaca) to the tip of the caudal fin or caudal filament, and including the anal fin, usually the second dorsal fin when present, and caudal fin.

Taxon, plural taxa: A taxonomic group at any level in a classification. Thus the taxon Chondrichthyes is a class with two taxa as subclasses, Elasmobranchii and Holocephali, and the taxon Galeorhinus, a genus, has one taxon as a species, G. galeus.

Taxonomy: Often used as a synonym of systematics or classification, but narrowed by some researchers to the theoretical study of the principles of classification.

Temperate: Two circumglobal bands of moderate ocean temperatures usually ranging between $10^{\circ}$ and $22^{\circ} \mathrm{C}$ at the surface, but highly variable due to currents and upwelling: including the north temperate zone between the Tropic of Cancer, $23^{\circ} 27^{\prime} \mathrm{N}$ latitude, to the Arctic Circle, $66^{\circ} 30^{\prime} \mathrm{N}$; and the south temperate zone between the Tropic of Capricorn, $23^{\circ} 27^{\prime}$ S latitude, to the Antarctic Circle, $66^{\circ} 30^{\prime} \mathrm{N}$.

## Term foetus: See foetus

Terminal 3 cartilage: A wedge-shaped or elongated cartilage articulating with the posterior edge of the ventral marginal cartilage and over the ventral terminal cartilages. It supports a variety of structures, including clasper spines and spurs, the shields of many skates (Rajoidei), and the mesorhipidion of some carcharhinoid sharks.

Terminal lobe: In the caudal fin of most non-batoid sharks and at least one batoid, the free rear wedge-shaped lobe at the tip of the caudal fin, extending from the subterminal notch to the posterior tip.

Terminal margin: In the caudal fin, the margin from the ventral end of the subterminal margin to the posterior tip.

Terminal mouth: Mouth located at the very front of the animal. Most cartilaginous fishes have subterminal mouths, but some species (viper sharks, wobbegongs, angel sharks, frilled sharks, whale sharks, megamouth sharks, and Manta) have it terminal or nearly so.

Thorn: In many batoids, most angel sharks and the bramble shark (Echinorhinus brucus), enlarged, flat conical denticles with a sharp, erect crown and a flattened base (which may grow as the shark grows).

Tongue arch: See hyoid arch.

Transverse groove: In oral teeth, a deep groove transverse on the lingual root surface, transecting it into mesial and distal root lobes.

Transverse notch: In oral teeth, a distinct notch in the proximal labial edge of the root at about its midlength.

Transverse ridges: Small narrow ridges on the labial and lingual surfaces of the crown, apicobasally oriented and sometimes extending to the cusp edges.

Tribasal pectoral fin: A pectoral fin skeleton with three basal cartilages, the propterygium, mesopterygium, and metapterygium, primitively found in most euselachians including living neoselachians.

Trilobate lower lip: In advanced orectoloboids, shallow orolabial grooves divide the lower lips into a medial section and a pair of lateral sections.

Tropeic folds: Longitudinal paired ridges on the ventral midline of the abdomen in frilled sharks (Chlamydoselachidae).

Tropical: Circumglobal band of warm coastal and oceanic water, usually above $22^{\circ} \mathrm{C}$ at the surface (but varying because of currents and upwelling), between the latitudes of $23^{\circ} 27^{\prime}$ North (Tropic of Cancer) and $23^{\circ} 27^{\prime}$ South (Tropic of Capricorn) and including the Equator.

Truncate: Blunt, abbreviated.
Trunk: That part of a cartilaginous fish between its head and tail, from the last gill openings to the vent, including the abdomen, back, pectoral and pelvic fins, and often the first dorsal fin.

Umbilical cord: A modified yolk stalk in placental viviparous sharks, carrying nutrients from the placenta to the foetus.

Unpaired fins: The dorsal, anal, and caudal fins.
Upper eyelid: The dorsal half of the eyelid, separated by a deep pocket (conjunctival fornix) from the eyeball. The upper eyelid fuses with the eyeball and the pocket is lost in all batoids.

Upper origin: In the caudal fin, the anterodorsal beginning of the epaxial or upper web of the caudal fin, at the posterior end of the dorso-caudal space (see measurement illustrations).

Upper postventral margin: In the caudal fin, the upper part of the postventral margin of the hypaxial web, from the posterior notch to the subterminal notch.

Uterine cannibalism or cannibal viviparity: A mode of reproduction in which foetuses deplete their yolk-sacks early and subsist by eating nutritive eggs produced by the mother (see oophagy) or first eat smaller siblings and then nutritive eggs (see adelphophagy).

Vent: The opening of the cloaca on the ventral surface of the body between the inner margins and at the level of the pelvic-fin insertions.

Ventral: Downward, in the vertical direction of the abdomen. See dorsal.

## Ventral fin: See pelvic fin.

Ventral lobe: In the caudal fin, the expanded distal end of the preventral and lower postventral margins, defined by the posterior notch of the caudal fin.

Ventral margin: In the caudal fin, the entire ventral margin from lower origin to posterior tip, either a continuous margin or variably subdivided into preventral, postventral, subterminal and terminal margins.

Ventral marginal: In the clasper skeleton, a flat semicylindrical cartilage that is partially fused to the lateral edge of the axial cartilage, and forms the lateral wall of the clasper groove.

Ventral terminal: On the skeleton of the clasper glans, an often triangular, elongated, curved, plate-like cartilage that articulates or is attached to the lateral or ventrolateral edge of the end-style and to the posterior end of the ventral marginal cartilage.

Ventral tip: In the caudal fin, the ventral apex of the caudal fin where the preventral and postventral margins merge.

Vertebra, plural vertebrae: A single unit of the vertebral column, including a vertebral centrum and associated cartilages that form neural arches and ribs or haemal arches.

Vertebral axis: That part of the vertebral column inside the base of the caudal fin.

Vertebral column: The entire set or string of vertebrae or 'backbone' of a shark, from the rear of the chondrocranium to the end of the caudal base. Living elasmobranchs range
from having as few as 35 vertebrae (some squaloids of the family Somniosidae) to as many as 477 vertebrae (thresher sharks).

## Visceral arches: See splanchnocranium.

Viviparity: Used in two ways in recent literature, as being equivalent to placental viviparity only, that is for carcharhinoid sharks with a yolk-sac placenta; or for all forms of live-bearing or aplacental viviparity

## Web, fin: See fin web

Yolk sac or yolk sack: Almost all sharks start embryonic development somewhat like a chicken, as a large spherical yolky egg inside an elongated shell, the egg case. A small disk of dividing cells represents the pre-embryo or blastula atop the huge yolk mass. The blastula expands around the sides and ventral surface of the yolk mass, and differentiates into an increasingly shark-like embryo, the yolk sac or baglike structure containing the yolk, and a narrow tubular yolk stalk, between the abdomen of the embryo and the yolk sac.

Yolk stalk: The connecting passage between embryo or foetus and yolk sac, which allows yolk to pass from the sac into the embryonic gut.

Yolk-sac placenta: An organ in the uterus of some ground sharks (order Carcharhiniformes), formed from the embryonic yolk-sac of the embryo and maternal uterine lining, through which maternal nutriment is passed to the embryo. It is analogous to the placenta of live-bearing mammals. There are several forms of yolk-sac placentas in carcharhinoid sharks, including entire, discoidal, globular, and columnar placentas (see Compagno, 1988).

Yolk-sac viviparity: Live-bearing in which the young are nourished primarily by the yolk in the yolk sacs, which is gradually depleted and the yolk sacs reabsorbed until the young are ready to be born.

### 1.2.7 The egg capsules of skates (Arhynchobatidae and Rajidae)

Producing relatively large horny egg capsules, which are deposited by the mother female on the sea floor and/or attached to structures on the bottom, has been developed in several groups of chondrichthyans independently and either as the initial form of reproduction, or secondarily after first viviparous reproduction. All chimaeras lay spindle-shaped egg capsules, as well as all skates (Rajiformes: families Arhynchobatidae and Rajidae) rectangular to subquadrate capsules with paired horns at both ends; among sharks, only three orders have a family each laying egg capsules (Heterodontiformes: Heterodontidae; Orectolobiformes: Orectolobidae; Carcharhiniformes: Scyliorhinidae).

Encapsulation of eggs passing from the ovaries to finally the uteri happens, while ovarian eggs pass the oviducal, or nidamental, or shell glands located between the ovaries and the uteri. In skates, a pair of eggs is encapsulated at a time, so that simultaneously one enters each uterus, and both will be extruded by the female a few days later, before the next pair will be produced. Once deposited on the sea floor, no more parental care is provided, and the embryos develop during a few months up to more than a year until hatching from the capsules; during the development period within the capsules, embryos are solely nourished by their yolk sac and even short time after. Unlike many life-bearing elasmobranchs with partly very large pups, the dorsoventrally flattened body shape of skates limits the capacity of the belly cavity and so the uteri, why egg capsules are relatively small even in large skates, as well as hatching embryos are comparatively small to fit the volume of the capsules. Initially, the huge yolk sac occupies most of the capsule's volume; while the embryo reduces the yolk sac with its growth, nevertheless space limits of the rectangular capsule volume require that the advanced embryo has one pectoral fin folded over its back, the other under his belly, and the tail is curled all around the embryo. As another consequence, the dorsal capsule surface is usually convex
to allow space for the embryo's body disc bent over the yolk sac, whereas the ventral surface is mostly even.

Unlike protection granted inside the female's belly cavity during embryonic development in viviparous species, is there a high fatal risk of deposited egg capsules to be damaged mechanically (e.g. by bottom trawl gears, or by displacement with heavy surf), or by predators like gastropods, sharks, large other skates, so that embryonic mortality is high. In view of in average, depending on size of females and size of the species, only 20 to 60 egg capsules being produced per female and a reproductive cycle, such low fecundity explains the vulnerability of skates by additional fishery impact. However, skate egg capsules are in many respects a genial evolutionary concept for protecting the embryo during the long incubation period; their construction reminds, so to speak, of a bank safe with very solid walls. Capsule walls consist of several layers of tough fibres, with orientation of each layer in different direction than neighboring layers. Antibacterial components in capsules walls are said to prevent from fatal infections during the long incubation period. The paired horns at both ends each have a slit to allow entry of water and thus oxygen, and the ventilation is provided by constant fanning of the embryo's tail. As newly hatched skates depend on small prey items, deepwater skates usually deposit their capsules at much shallower depth than regular habitat depth of the adults.

Empty skate capsules are often found washed ashore and commonly called "mermaid's purse" according to their shape. If such capsules are systematically sampled and specifically identified, the locations and seasonality of their occurrence can provide invaluable information for fishery science for assessing the fecundity of shelf species and their reproductive cycle. Most capsules can be identified rather easily at least to the genus, and field guides with good illustrations do exist for several regions. Interaction between volunteer beach samplers and fishery science can therefore only be encouraged.

## 2. SYSTEMATIC CATALOGUE - Subclass NEOSELACHII - Cohort SELACHII

### 2.1 Order HEXANCHIFORMES - Frilled and Cow sharks

Order: Hexanchiformes Garman, 1913, Mem. Mus. Comp. Zool. Harvard 36: 10, 11 (emendation of order Plagiostoma, suborder Antacea, "group" Hexanchoidei Garman, 1913).

## Number of Recognized North Atlantic Families: 2.

FAO Names: En - Frilled and Cow sharks.
Field Marks: Sharks with six or seven pairs of gill openings, one spineless dorsal fin, and an anal fin.
Diagnostic Features: Head conical to slightly depressed, not expanded laterally. Snout very short to moderately long, truncated to conical, not greatly elongated or flattened, and without lateral teeth or rostral barbels. Eyes on sides of head, without nictitating lower eyelids, secondary lower eyelids, or subocular pouches; upper eyelids not fused to eyeball. Nostrils of the ordinary shark type, transverse on snout, without barbels, nasoral grooves or circumnarial grooves, separate from mouth, anterior nasal flaps short and not reaching mouth. Six or seven paired gill openings are present on sides of head, with the last gill opening $n$ front of pectoral fin origins. Spiracles present, very small, and well behind and above level of eyes. Mouth large, arched and elongated, extending well behind eyes. Labial furrows reduced but present on both jaws. Teeth weakly to strongly differentiated along the jaws, without enlarged anterior teeth or enlarged molariform posterior teeth and without a gap or small intermediate teeth between anterior and lateral teeth in the upper jaw. Tooth row counts 19 to 46 upper jaw, 19 to 38 lower jaw. Trunk cylindrical or somewhat compressed, but not flattened and ray-like. Caudal peduncle without lateral dermal ridges or keels. Dermal denticles covering entire body, with no enlarge thorns or spines. Pectoral fins small to moderately large, not expanded and ray-like, without triangular anterior lobes that cover the gill slits. Pelvic fins small to moderately large, with vent continuous with their inner margins. Claspers without siphons in the abdomen but with large clasper sacs. A single spineless dorsal fin present, with origin over or behind pelvic-fin insertions. Anal fin is present. Caudal fin with a long dorsal lobe and the ventral lobe short to absent. Vertebral counts: total vertebral counts 118 to 171 , precaudal vertebral counts 54 to 102 , monospondylous vertebral counts 18 to 75 , diplospondylous vertebral counts 13 to 38 , and caudal vertebral counts 50 to 82 . Intestinal valve of spiral or ring type, with 14 to 49 turns. Moderate sized to very large sharks with adults 85 to 500 cm or more in length. Colour: variable depending on species from a silvery grey to reddish brown, olive grey, dark brown or black above, most species light below, but some (Chlamydoselachus) uniformly coloured; most species without prominent spotting (except Notorynchus) or saddle markings; juvenile colour pattern of some species are quite striking with darker or lighter fin edges. Reproductive mode is viviparous, fetal nutriment primarily derived from yolk sac.

Distribution: Wide-ranging in all seas with representatives of both families occurring in the North Atlantic.
Habitat: These are mostly deep water sharks occurring in a wide range of marine habitats from shallow bays and estuaries (in some parts of the world) on the continental shelves down to the continental and insular slopes and on seamounts and submarine ridges, from close inshore to at least 2500 meters; some deepwater species common down to 1100 m .

Biology: Reproduction mode is yolk-sac viviparity with litters ranging from 2 to at least 108 . These are rare to common sharks where they occur that feed on a wide variety of cephalopods, crustaceans, bony fishes, other sharks, and batoid fishes, and with the largest member of this group Hexanchus griseus also consuming marine mammals.

Interest to Fisheries and Human Impact: These sharks are relatively unimportant commercially, but are targeted by some shark fisheries and are regular bycatch components of other fisheries. They are incidentally caught in trawls, gillnets, and on long-line gear. Larger species may snap during capture, but are apparently docile when approached underwater. Ecotourism diving operations have sprung up in some areas where the larger species are known to congregate, although there are currently no known ecotourism operations involving these sharks in the North Atlantic. The conservation status of the group varies by region from Data Deficient to Near Threatened depending on the species.

Local Names: Hexanchoid sharks, Hexanchiform sharks, One-dorsaled sharks.
Remarks: The classification of hexanchiform sharks has varied tremendously over the past two centuries. Most early authors were impressed by the supposedly 'primitive' morphology of the living cowsharks, family Hexanchidae, particularly because of their 'amphistylic' jaw suspension (following Gegenbaur's 1872 monograph), and treated the cowsharks as an archaic group with possible relationships to various Paleozoic and Mesozoic shark groups such as hybodonts and paleoselachians.

The interrelationships of frilled and cow sharks was reassessed by Ebert and Compagno (In press) which built on newer findings on hexanchoid morphology by Maisey and Wolfram (1984), Ebert (1990) Shirai (1992a, b, 1996), and de Carvalho
(1996). These works, along with more recent molecular evidence (Naylor et al. 2005), tend to support the hexanchids and chlamydoselachids as a monophyletic squalomorph group, united by several derived features of their skeletal and external morphology including details of their chondrocrania, branchial skeleton, pectoral and pelvic fin skeletons, clasper morphology, and external morphology. It also suggests that both hexanchids and chlamydoselachids are highly derived and ecomorphologically divergent, and that some of the 'primitive' features that they supposedly share with various palaeoselachian and protoselachian sharks may be convergent. The present classification of the Hexanchiformes continues to rank the living taxa in a common order with two families, the Chlamydoselachidae and Hexanchidae, comprised of four genera and six species; both families, three genera and four species occur in the North Atlantic.

## Key to North Atlantic Families:

1a. Head snakelike, with short snout and terminal mouth. Teeth tricuspidate in both jaws. Body elongated and eel-like (Fig. 30a, 30b) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . family Chlamydoselachidae

a) LATERAL VIEW

b) UPPER AND LOWER TOOTH

Fig. 30 Chlamydoselachus

1b. Head not snakelike, with moderate snout and subterminal mouth. Teeth cuspidate in upper jaw and compressed and comb-like in lower jaw. Body moderately stout and not eel-like (Fig. 31a, 31b). . . . . . . . . . . . . . family Hexanchidae

a) LATERAL VIEW

b) UPPER AND LOWER TEETH

Fig. 31 Hexanchus

### 2.1.1 Family CHLAMYDOSELACHIDAE

Family: Chlamydoselachidae Garman, 1884, Bull. Essex Inst., 16: 52 (p. 8 in separate).
Type genus: Chlamydoselachus Garman, 1884.
Number of Recognized North Atlantic Genera: 1.
FAO Names: En - Frilled sharks; Fr - Requins à collerette; Sp - Tiburones anguila.
Field Marks: See genus Chlamydoselachus.
Diagnostic Features: Elongated eel-shaped sharks with the head flattened and subtrapezoidal in dorsoventral outline. A pair of longitudinal keels or tropeic folds is present on the ventral surface of the abdomen. A prominent horizontal subocular groove above the upper lip extends below the nostrils and eyes to the cheek. Snout extremely short, its tip nearly transverse and truncated. Eyes are well behind symphyses of mouth. Interbranchial septa greatly enlarged and frilly, ventral edges of those of first gill openings attached across the throat as a gular flap; gill raker papillae absent from gill arches. Nostrils are about opposite of jaw symphyses. Lateral trunk denticles with spike-like crowns; enlarged and monocuspidate denticles along the mouth edges. Mouth terminal, teeth and mouth edges exposed when mouth is closed. Upper lip not expanded below the level of tooth bases to form a prominent flange and groove; lower lip not expanded anteriorly and laterally to the teeth series; no deep groove between lower lip and teeth. Tongue prominent and with a deep sublingual groove separating it from the dental membrane. Labial cartilages complete (two pairs of uppers and one pair of lowers). Teeth are alike in both jaws, with three cusps and two cusplets on crown, and with flat, low lingually bilobate roots; no small granular posterior teeth. Total tooth counts 19 to 30 upper jaw, 21 to 29 lower jaw. Pectoral fins rounded and smaller than pelvic fins. Pelvic fins with broadly rounded anterior margins and apices, inner margin not forming expanded clasper sheath in males. Dorsal fin very low, rounded, and elongated, insertion just behind upper caudal-fin origin. Anal fin is broad-based and rounded, larger than dorsal fin; anal-fin insertion ending at the lower caudal-fin origin. Caudal peduncle is very short and compressed. Caudal fin with a vestigial subterminal notch; ventral caudal-fin lobe is essentially absent. Vertebral counts: total vertebral counts 147 to 171, precaudal vertebral counts 93 to 102, monospondylous vertebral counts 18 to 75 , diplospondylous precaudal vertebral counts 21 to 76 , and caudal vertebral counts 52 to 78 . Intestinal spiral valve turn counts 26 to 49. These are moderately large sharks, with adults up to 196 cm total length. Colour: a uniform dark chocolate brown, brownish grey or brownish black without any dark or light banding or mottled colour patterns.

Distribution: The family Chlamydoselachidae has a patchy, but almost circumglobal range with most records of this family from the Western Pacific, southern Africa, and the Eastern North Atlantic including the Mid-Atlantic Ridge.

Habitat: Frilled sharks are benthopelagic, and are often found in association with continents, islands, submarine canyons, peaks and ridges. They appear to be most common in boreal, temperate and subtropical seas.

Biology: Reproductive mode is viviparous with a yolk-sac, and litters of up to 12. The reproductive cycle may be either two years or possibly up to three and half years. Nothing is known about the age and growth of these sharks. The diet consists mainly of cephalopods, teleosts, and elasmobranchs, especially those members of the families Squalidae and Scyliorhinidae.

Interest to Fisheries and Human Impact: There are no fisheries for these sharks. They are relatively uncommon in most areas where they occur and the flesh is of little value. They are likely caught on occasion as bycatch, but are most likely discarded.

The conservation status of these sharks is poorly known due to a lack of life history data and information on population trends.

Local Names: Frill sharks, Frilled sharks, Frilled-gilled sharks (English); Akuly plaschenosnyo (Russia).
Remarks: A single genus, Chlamydoselachus.

## Chlamydoselachus Garman, 1884

Genus: Chlamydoselachus Garman, 1884, Bull. Essex Inst., 16: 47, 52 (pp. 8, 13 in separate).
Type species: Chlamydoselachus anguineus Garman, 1884, by monotypy.

## Number of Recognized North Atlantic Species: 1.

Synonyms: Genus Chlamydoselache Günther, 1887: 2. Emendation of Chlamydoselachus Garman, 1884, and hence taking the same type species, Chlamydoselachus anguineus Garman, 1884. Genus Chlamydoselachoides Fowler, 1947: 8. Type species: Chlamydoselachus lawleyi Davis, 1887 by original designation; Pliocene of Tuscany, Italy. Synonymized with Chlamydoselachus by Pfeil (1983) and Cappetta (1987), which is followed here. Genus Chlamidoselachus Cervigón, 1960: 36, 39-42. Consistent erroneous spelling of Chlamydoselachus Garman, 1884 (cited six times as such).

FAO Names: En - Frilled sharks; Fr - Requins à collerette; Sp - Tiburones anguila.
Field Marks: Eel-like sharks with 6 gill slits, terminal mouth with tricuspidate teeth in both jaws, and one dorsal fin.
Diagnostic Features: See family.
Local Names: Frilled sharks.
Remarks: Living frilled sharks had long been considered a single wide-ranging species, Chlamydoselachus anguineus Garman, 1884, but Ebert (1990) compared frilled sharks from a wide geographic range and suggested that the morphological variability of this species may represent an additional species within the genus. Further comparisons and examination of frilled sharks taken from off Angola and Namibia with Pacific specimens from Australia, California (U.S.A.), Japan, New Zealand, and Taiwan, Province of China, and from the North Atlantic revealed differences in morphometrics, size at maturity, chondrocranial morphology, vertebral counts, vertebral morphology and calcification patterns, pectoral fin skeletal morphology and radial counts, and intestinal valve counts that lead Ebert and Compagno (2009) to separate the southern African frilled shark (Chlamydoselachus africana) into a distinctly different species.

The common, wide-ranging frilled shark (Chlamydoselachus anguineus) is the only known representative in the North Atlantic. However, specimens from the North Atlantic should be compared and closely examined to Chlamydoselachus species from elsewhere to confirm $\boldsymbol{C}$. anguineus is the only frilled shark species occurring in the North Atlantic, or whether a second (C. africana), or a possible third undescribed species of frilled shark may occur in this area. Kukuev and Pavlov (2008) reporting on a mass catch of frilled sharks ( $n=34$ ) from the mid-Atlantic Ridge north of the Azores ( $44^{\circ} 00^{\prime} \mathrm{N}, 28^{\circ}$ $37^{\prime} \mathrm{W}$ ) commented that their North Atlantic specimens differed in proportional measurements from those specimens caught in the southeastern Atlantic ( $=C$. africana?) and from the holotype of $C$. anguineus that came from off Japan.

## Chlamydoselachus anguineus Garman, 1884

Chlamydoselachus anguineus Garman, 1884, Bull. Essex Inst., 16: 47 (p. 3 in separate), Fig. Holotype, Museum of Comparative Zoology, Harvard University, MCZ-800-S, female, probably adult, ca. 151 cm (59.5") TL with caudal tip missing, from "Japanese seas" (probably southeastern Honshu), now in pieces (Ebert, 1990; Hartel and Dingerkus, in Garman, 1997, The Plagiostoma: xxxvii).

Synonyms: Chlamydoselache anguinea Günther, 1887: 2 (emended spelling).
Other Combinations: Didymodus anguineus (Garman, 1884). Cope (1884: 412) placed Chlamydoselachus in synonymy of a Permian American xenacanth genus, Didymodus Cope, 1883, and placed the living $\mathscr{C}$. anguineus in Didymodus. Although, this combination has generally been rejected by subsequent authors. See Garman (1885) and Gudger and Smith (1933) for a discussion of the supposed xenacanth and cladodont affinities of the frilled shark.

FAO Names: En - Frilled shark; Fr - Requin lézard; Sp - Tiburón anguila.


Fig. 32 Chlamydoselachus anguineus

Field Marks: Eel-like shark with 6 gill slits, snakelike terminal mouth with tricuspidate teeth in both jaws, and one dorsal fin. Colour uniform brown with dark brown fins and prominent lighter lateral line.

Diagnostic Features: Body long, slender, eel-like, compressed behind the pelvic fins. Pectoral-pelvic space elongated 26.4 to $31.0 \%$ total length. Head broad, flattened, wider than high, slightly convex; head length 13.1 to $16.2 \%$ TL. Preoral snout length 0.1 times mouth width. Snout tip broadly rounded. Nostrils lateral, width 6.3 to 7.9 in internarial width. Eyes large, rounded, length approximately 10.1 times in head length. Spiracle present or absent. Height of gill openings descending in length; first gill opening extends across throat. Mouth broadly rounded, large, distensible. Teeth are similar in both upper and lower jaws, each tooth with three long, slender, smooth-edged cusps, and a small pointed cusplet between each cusp; upper medial teeth paired, form similar to anterolateral teeth, but noticeably reduced; lower jaw with a single medial tooth row undifferentiated from anterolaterals; teeth on upper and lower jaws are curved inwards and set on a broad base that projects behind and interlocks with the tooth base posterior to it; tooth count is 19 to 28 upper jaw, 21 to 29 lower jaw. Lateral trunk denticles lanceolate, single cusped, with flattened bases; crown slightly projected above the body with four longitudinal ridges extending from the base to the cusp; denticle crowns widely spaced. Pectoral fins are broad, rounded and low on body; pectoral-fin length 7.6 to $8.6 \% \mathrm{TL}$; pectoral fins smaller than pelvic fins; pectoral-fin origin is posterior to sixth gill opening. Pelvic fins large and broadly rounded; anterior and posterior margins convex. Anal fin very large, broadly rounded, its height is 1.5 to 2.0 times dorsal-fin height, base length 1.2 to 1.6 in dorsal-fin base; anterior and posterior fin margins are rounded and convex; an acute angle forms at the tip of the posterior and inner margins. Dorsal fin is set far back, about 54.3 to $65.0 \%$ TL from snout tip; anterior margin is rounded and convex with posterior margin. Caudal fin elongated, subtriangular, and without a subterminal lobe; length of dorsal margin 2.5 times in precaudal length. Vertebral counts: total vertebral counts 160 to 171 , precaudal vertebral counts 93 to 102 , monospondylous vertebral counts 72 to 75 , diplospondylous precaudal vertebral counts 21 to 27 . Spiral valve turns 35 to 49 . A large species, adults 196 cm total length. Colour: dark chocolate brown, brownish grey or brownish black.

Distribution: North Atlantic wide ranging, but spottily distributed. Eastern North Atlantic: from northern Norway (Varanger Fjord), the Atlantic Slope off northern Scotland and western Ireland, France, Spain, and Portugal. Also captured along the mid-Atlantic Ridge north of the Azores. Western North Atlantic: off New England and North Carolina (Sedberry, Meister, and Loefer, 2007), U.S.A. World-wide sporadically distributed.

Habitat: A rare to locally common, deepwater epibenthic, and occasionally epipelagic shark on offshore continental and insular shelves, seamounts, and along mid-ocean ridges. At depths of between 20 and 1500 m , but occasionally taken at the surface. Usually caught near the bottom, individuals are known to migrate into the water column, venturing at least 1500 m , or more, off the bottom and into the midwater. A remote operated vehicle videotaped a frilled shark swimming a couple meters off the bottom off North Carolina, U.S.A.


Fig. 33 Chlamydoselachus anguineus
$\square$ Known distribution
Biology: Yolk-sac viviparous, with the number of young ranging from 2 to 15 per litter, six being the average. Virtually nothing is known in the North Atlantic about its reproductive cycle or life history. Kukuev and Pavlov (2008) based on the catch of 34 frilled sharks in a single bottom trawl tow suggested that seamounts along the Mid-Atlantic Ridge were areas where mating activity occurred. In Japanese waters this species appears to reproduce year-round with mating thought to occur from March to June. The gestation period is probably very long, on the order of one to two years, by extrapolating the observed growth rate of early embryos artificially kept alive for up to 3 months. Tanaka et al. (1990) suggested that the total gestation period may be as long as 3.5 years. Uterine eggs are enormous, about 11 to 12 cm long, and greatly distend the abdomens of gravid females.
The diet of North Atlantic frilled sharks is poorly known, but examination of several stomachs from individuals showed them to have consumed mostly smaller sharks, mainly squaloids and scyliorhinids (Ebert, 1990; D.A. Ebert, pers. obs.). Elsewhere, the only diet study with a reasonable sample size $(n=139)$ of frilled sharks was in Japanese waters where squids were found to be the dominant prey item, occurring in about $61 \%$ of the stomachs examined compared to $11 \%$ with fish remains (Kubota, Shiobara, and Kubodera, 1991).
The long mouth of the frilled shark can accommodate relatively large prey, and their snakelike head and firm, muscular bodies suggest that they may be able to slowly approach faster swimming epipelagic prey and make a sudden snakelike lunge to snag a potential prey item with their relatively strong, tooth-studded jaws. The mouth of a frilled shark bears a functional resemblance to a squid jig, with many needle-sharp, inward and diagonally-directed curved points on its teeth which is enhanced by the outward rotation of the tooth rows when the jaws are protruded. Even a glancing strike by a shark on a cephalopod or other soft-bodied prey could readily snag it.
Live frilled sharks have been photographed swimming in captivity with mouth agape and with lighter coloured tooth bands highlighted against the darker coloured mouth. Whether this serves to lure prey items such as squids and fishes to within striking distance is speculative at present. Also, a frilled shark caught on video by a remote operate vehicle (ROV) showed it to take flight quite rapidly as the ROV approached. There are no known predators of these sharks, but one can assume that larger sharks may on occasion consume them.

Size: Maximum 196 cm ; males adult at approximately 118 cm to 163 cm ; females maturing at 130 to 150 cm and reaching 196 cm . Size at birth about 39 to 50 cm .

Interest to Fisheries and Human Impact: Of no importance in North Atlantic fisheries as it is usually taken as bycatch in other fisheries. There are no reported landings of this species. Elsewhere, this species if taken as bycatch if not discarded is utilized for meat or fishmeal. It has occasionally been kept in aquaria in Japan. A harmless species, the needle-sharp teeth can hook and cut the hands of the unwary scientist examining its mouth.

The conservation status of this species is Near Threatened due to concerns over expansion of deepwater fisheries that may increase bycatch levels.

Local Names: Frill-shark, Scaffold shark, Lizard shark, (English); Requin-frangé, Requin lézard (France); Kragenhai (Germany); Plašcenosnaja akula (Russia); Kragehai (Norway); Kråshaj (Sweden).

Literature: Garman (1884, 1885, 1913); Gudger and Smith (1933); Gudger (1940); Wheeler (1962); Wheeler and Blacker (1969); Boeseman in Hureau and Monod (1973); Cadenat and Blache (1981); Pfeil (1983); Boeseman in Whitehead et al. (1984); Ebert (1990, 2003); Tanaka et al. (1990); Kubota, Shiobara and Kubodera (1991); Paul and Fowler (2003a); Moore et al. (2003); Sedberry, Meister, and Loefer, (2007); Gibson et al. (2008); Kukuev and Pavlov (2008); Ebert and Compagno (2009, In press); D.A. Ebert (unpubl. data).

### 2.1.2 Family HEXANCHIDAE

Family: Tribe Hexanchina Gray, 1851 (family Squalidae), List Fish British Mus., Pt. 1, Chondropterygii, Brit. Mus. (Nat. Hist.): 67, London.

Type genus: Hexanchus Rafinesque, 1810.

## Number of Recognized North Atlantic Genera: 2.

FAO Names: En - Cow sharks, Sevengill sharks, Sixgill sharks; Fr - Requins a six et sept fentes branchiales, Requins grises, Requins perlon, Requins vaches; Sp - Cañabotas.

Field Marks: Moderately slender to stocky sharks with a subterminal mouth, large compressed comb-like teeth in the lower jaw, smaller cuspidate teeth in upper jaw, 6 or 7 pairs of gill openings, one spineless dorsal fin, and an anal fin.

Diagnostic Features: Moderately elongated to stout sharks with the head flattened and conical in dorsoventral outline. No subocular groove on head. Snout moderately long; snout tip pointed to broadly round. Eyes about opposite to symphyses of mouth. Interbranchial septa moderately enlarged, without a gular flap connecting the first gill openings; gill raker papillae present on gill arches. Nostrils positioned well anterior to jaw symphyses. Mouth subterminal. Teeth and mouth edges concealed when mouth is closed. Upper lip expanded below the level of tooth bases to form a prominent flange and groove that extends posteriorly to the mouth angle and labial furrows; lower lip expanded anterior and lateral to the teeth series and separated from them by a deep groove. Labial cartilages are incomplete with one pair on the upper jaw only. Teeth dissimilar in upper and lower jaws, with lower anterolateral teeth much larger, compressed, comb-shaped, and with more cusplets than uppers; small granular posterior teeth present. Tooth counts 23 to 46 upper jaw, 15 to 38 lower jaw. No longitudinal keels on the abdomen. Caudal peduncle is moderately long and cylindrical. Enlarged and cuspidate denticles weakly developed or absent from the mouth edges. Pectoral fins angular, larger than pelvic fins. Pelvic fins with nearly straight anterior margins and narrowly rounded apices, inner margins expanded into broad clasper sheaths in males. Dorsal fin relatively high, angular, and short, insertion well anterior to upper caudal-fin origin by dorsal-fin base length or more. Anal fin is narrow-based and angular, insertion ending well anterior to the lower caudal-fin origin. Caudal fin with a well-developed subterminal notch and a ventral caudal-fin lobe weak to moderately developed. Vertebral counts: total vertebral counts 118 to 159, precaudal vertebral counts 72 to 94 , monospondylous vertebral counts 41 to 58 , diplospondylous precaudal vertebral counts 13 to 38 , caudal vertebral counts 50 to 82 . Spiral valve turns 14 to 39 . These sharks range in size from small to very large, with various species between 140 to 500 cm and more in maximum total length. Colour: uniform olive to dark grey, black or brown above, lighter to white below; some species with scattered small spots on the dorsal surface, others without any spotting.

Distribution: Worldwide in boreal and cold temperate to tropical seas.
Habitat: Most cowshark species are deepwater inhabitants of the outer continental shelves, upper continental slopes, insular shelves and slopes, and submarine canyons down to at least 2500 m depth, near the bottom or well above it. Some species also occur in shallow bays, close inshore, and near the surface.

Biology: These are sluggish to active, strong swimming sharks usually occurring near the bottom. Reproduction is yolksac viviparity with some species having relatively large litters of up to 108. The reproductive cycle although poorly known is annual or biannual for those species where some information is available. These sharks feed on a wide variety of relatively large marine organisms, including crustaceans and cephalopods, bony fishes, other sharks, rays, marine mammals including seals and dolphins, and carrion (including mammalian meat).

Interest to Fisheries and Human Impact: Cow sharks are relatively unimportant commercially but are regular components of shark fisheries and bycatch of other fisheries in temperate and tropical waters, and are usually taken by line gear, bottom and pelagic trawls, and gill nets. These sharks are excellent for human food and are utilized fresh and dried-salted; they are also processed for fishmeal, oil, and leather. Some species are subject to sports fisheries in inshore temperate waters. In the North Atlantic only the bluntnose sixgill shark (Hexanchus griseus) is recorded in landings for Area 27, no cowshark species are reported in landings for Area 21. It is likely that the bigeyed sixgill shark ( $\boldsymbol{H}$. nakamurai) is caught and landed, but reported as bluntnose sixgill do to misidentification between these two species.
Cow sharks may snap when captured and can inflict lacerations if carelessly handled; the two larger species (H. griseus and Notorynchus cepedianus) have been confirmed as biting divers in the sea. Both these two larger species have been implicated in attacks on divers elsewhere, but none reported from the North Atlantic. These two cowsharks (H. griseus
and $\boldsymbol{N}$. cepedianus) reach large sizes (from 3.0 to 5.0 m ) and feed on large prey including marine mammals. Diving with $N$. cepedianus and $H$. griseus in the sea has become a popular ecotourism attraction in some areas, especially in southern Africa and in the North Eastern Pacific. Although the paucity of confirmed attacks by cowsharks biting people suggests that they are often docile and inquisitive in their reactions to humans, large cowsharks should be treated with respect as with other big macropredatory sharks.

The conservation status of this family is poorly known. The smaller continental deep-water species are little-known but potentially vulnerable to demersal trawl and longline fisheries. The larger species have been the subject of localized fisheries from various geographic regions throughout the world. All of these targeted fisheries quickly ended when these species were subsequently overfished.

Local Names: Sixgill sharks, Sevengill sharks, Sixgill cow sharks, Sevengill cow sharks, Combtooth sharks (English); Griset, Perlon (France); Akuly drevnye, Grebnezubye akuly (Russia).

Remarks: Three living genera are currently recognized, Heptranchias, Hexanchus, and Notorynchus, of which two (Heptranchias and Hexanchus) occur in the North Atlantic. Several authors (Maisey and Wolfram, 1984; Shirai, 1992a 1996; de Carvalho, 1996) have attempted to elucidate the phylogenetic relationship of this group. Maisey and Wolfram (1984) recognized the divergence of Heptranchias from the other living hexanchids, and considered Heptranchias and Hexanchus as sister groups do to similarities in tooth morphology, with Notorynchus as a sister group of Heptranchias + Hexanchus. Heptranchias and Hexanchus have more elongated, lower anteriorlateral teeth than Notorynchus and differ from it in having a vertical cusp on the lower medial tooth (assumed to be derived, which is uncertain). Shirai (1992a, 1996) suggested that Notorynchus should be included in a separate family Notorynchidae, on a supposedly derived character, secondary loss of an ethmoidal canal in the nasal capsules. Heptranchias and Hexanchus were grouped as sister genera by two possible derived characters, lateral line canal closed, and presence of a subnasal fenestra or basal communicating canal on the ethmoid. De Carvalho (1996) recognized a single family Hexanchidae but grouped Heptranchias and Hexanchus in a subfamily Hexanchinae in apposition to its sister group Notorynchus; Hexanchinae was defined by the presence of an ethmoidal canal, a closed lateral line, a subnasal fenestra, and presence of a fossa on the ectotic process under the hyomandibular facet. There are some problems with these characters, including the apparent lack of subnasal fenestrae in any hexanchid. The so-called subnasal fenestra of hexanchids is a perforation through the dorsal wall of the ectethmoid chamber, inside rather than outside the nasal capsule and unlike the true subnasal fenestrae of squaloids. The ectotic fossa is variably developed in Hexanchus and occasionally present in Notorynchus. The ethmoidal canal is also present in Notorynchus with walls, but usually without a roof (occasionally present as a thin bar). The lateral line canals are closed on the heads of all hexanchids but are open only on the trunk and tail of Notorynchus. It is debatable whether a closed canal is derived or primitive for the trunk and tail of hexanchids. On the other hand, the neurocranium and claspers are divergent and probably highly derived in Heptranchias, while Hexanchus and Notorynchus have derived similarities in clasper morphology. Given the problems with these characters and the obvious monophyly of the living hexanchids, as well as the ease of incorporating any of the three possible phylogenic arrangements of the living genera within a single family, it is best to leave them in the Hexanchidae pending a more thorough revision and satisfactory analysis of their morphology and phylogeny.

Literature: Garman (1913); Daniel (1928, 1934); Bigelow and Schroeder (1948); Springer and Waller (1969); Compagno (1973, 1984); Maisey and Wolfram (1984); Ebert (1990); Shirai (1992a, b, 1996); De Carvalho (1996); Ebert and Compagno (In press).

## Key to North Atlantic Genera:

1a. Six pairs of gill openings (Fig. 34) . . .
. . . . . . . . . . . . . . . . . . . . . . . . Hexanchus
1b. Seven pairs of gill openings (Fig. 35)
Heptranchias


Fig. 34 Hexanchus


Fig. 35 Heptranchias

## Heptranchias Rafinesque, 1810

Genus: Heptranchias Rafinesque, 1810, Caratt. gen. sp. animal. piant. Sicilia, pt. 1: 13.
Type species: "Squalus cinereus Lacépède" by original designation, equals $S$. cinereus Gmelin, in Linnaeus and Gmelin, 1789 and a junior synonym of Squalus perIo Bonnaterre, 1788.

Synonyms: Genus Heptanchus Müller and Henle, 1837a: 115; Müller and Henle, 1837b: 398; Müller and Henle, 1838a: 88; Müller and Henle, 1838b: 64 (two species, but names not mentioned); Müller and Henle, 1839: 81. Type species not designated, two species named, H. cinereus "Raf." (Rafinesque, = Squalus cinereus Gmelin, 1789, a junior synonym of S. perlo Bonnaterre, 1788) and H. indicus Müller and Henle, 1839 (= Notidanus indicus Agassiz, 1835, usually ascribed to the genus Notorynchus). Genus Heptancus Agassiz, 1846: 178; Agassiz, 1848: 514 (emended spelling of Heptanchus "Rafinesque" and Heptranchias Rafinesque, 1810, cited as such); Jordan and Gilbert, 1883: 34. Genus Heptranchus Gray, 1851: 6 (emended spelling). Genus Heptrancus Costa, 1857: 5 (29) (emended spelling). Type species, Heptrancus angio Costa, 1857, by monotypy? Genus Heptabranchias Garman, 1884 (in part): 537, 538; Garman, 1888: 58, 67, 68, 72, 82, pl. 14. Possible emendation of Heptranchias Rafinesque, 1810, and Heptanchus Müller and Henle, 1837. No type species indicated.

Diagnostic Features: Head acutely pointed in dorsoventral view, compressed and rounded or vertically oval in section at eyes. Eyes large. Seven paired gill openings. Mouth very narrow and angular-parabolic. Five rows of lower comb-shaped anterolateral teeth on each side; these long and low, with a few short mesial cusplets, and an abruptly high cusp, up to 7 or 8 distal cusplets in adults that increase and then decrease in size distal to cusp; total tooth counts including smaller posteriorlateral teeth 23 to 43 upper jaw, 20 to 33 lower jaw. Caudal peduncle elongated. Lateral line canal closed. Clasper apopyle dorsal, clasper groove and hypopyle dorsolateral; hypopyle without a lateral flap on its dorsal edge; clasper sack small, not pleated, not expanded far onto dorsomedial surface of clasper, and without a large dorsal fold; clasper with three enlarged mucous glands with corrugated surfaces along the clasper groove, a dorsal gland near the apopyle, a ventral gland on midlength of clasper, and a terminal gland at the clasper tip; clasper shaft large and stout. Vertebral counts: total vertebral counts 141 to 159 , precaudal vertebral counts 72 to 94 , monospondylous vertebral counts 51 to 58 , diplospondylous precaudal vertebral counts 28 to 38 , caudal vertebral counts 60 to 67 . Intestinal valve count ranges from 18 to 22 . Size at maturity between 85 and 137 cm . Colour: uniform pale grey to olive above, lighter to white below; spots absent from body, dorsal fin and upper caudal-fin lobe with black tips, faded or absent in adults but prominent in young.

Local Names: Sharpnose sevengill sharks.
Remarks: Following Garrick and Paul (1971), Bass, D'Aubrey and Kistnasamy (1975), Ebert (1990) and Ebert and Compagno (In press), only a single wide-ranging species is recognized for this genus, Heptranchias perlo (Bonnaterre, 1788). Earlier references (Bigelow and Schroeder, 1948; Whitley, 1931) to other regional species within this genus prove to be related to sexual dimorphism with the position of the anal fin (more posterior in males than in females) relative to the dorsal fin (Garrick and Paul, 1971; Bass, D'Aubrey and Kistnasamy, 1975; Ebert, 1990).

## Heptranchias perlo (Bonnaterre, 1788)

Squalus perlo Bonnaterre, 1788, Tabl. encyclop. method. trois reg. Nat., Ichthyol., Paris: 10. Holotype unknown. Type locality: "La Méditerranée", = Mediterranean Sea.

Synonyms: Squalus cinereus Gmelin, in Linnaeus and Gmelin, 1789: 1497. Holotype unknown. Type locality "in Mari Mediterraneo", = Mediterranean Sea. Squalus cinereus Walbaum, 1792: 517. No locality, independently proposed from $S$. cinereus Gmelin, 1789 and possibly not conspecific or confamilial according to Eschmeyer (1998). Heptrancus angio Costa, 1857: 5, pl. 13, 14, Fig. 3. Existance of types uncertain. Type locality, Mediterranean Sea. Notidanus (Heptanchus) cinereus, var. pristiurus (var. aetatis) Bellotti, 1878: 60. Syntypes: Two, whereabouts unknown according to Eschmeyer (1998). Type locality, Mediterranean Sea.

Other Combinations: Heptanchus perlo (Bonnaterre, 1788), Heptanchus or Heptranchias cinereus (Gmelin, 1789).
FAO Names: En - Sharpnose sevengill shark; Fr - Requin perlon; Sp - Cañabota bocadulce.


Fig. 36 Heptranchias perlo


UPPER AND LOWER TEETH ON LEFT SIDE

Field Marks: A narrow-headed, big-eyed, small seven-gilled shark with one dorsal fin, no dark spots, and a black blotch on the dorsal fin (inconspicuous in large individuals).

## Diagnostic Features: See genus Heptranchias.

Distribution: Found on both sides of the Atlantic. Eastern North Atlantic: Ireland, England and Wales, south to Bay of Biscay and Straits of Gibraltar. Western North Atlantic: New England, USA, where it is rare, to Florida, Bahamas, Cuba and the northern Gulf of Mexico. Elsewhere this wide-ranging but somewhat spottily distributed sevengill shark is found in most tropical and warm temperate seas except in the Eastern Central and North Pacific.

Habitat: A primarily deepwater benthic and epibenthic species on the continental and insular shelves and upper slopes. Possibly moving well off the bottom but details little known. Depth mostly between 27 to 720 m , but usually below 100 m and down to 1000 m , although sometimes in shallower water close inshore.

Biology: Yolk-sac viviparous, with 6 to 20 young per litter. Reproductive cycle in the North Atlantic unknown, but in the Mediterranean Sea and off Japan they seem to be reproductively active throughout the entire year.


Fig. 37 Heptranchias perlo
$\square$ Known distribution Their diet includes crustaceans mostly shrimps, crabs, lobsters, and cephalopods including squid (Ommastrephidae and Loliginidae) and cuttlefish (Sepiidae), and a wide variety of small to moderately large demersal and pelagic bony fishes, including lanternfish (Myctophidae), lightfishes (Phosichthyidae), cods (Gadidae), lings (Phycidae), hake (Merluccidae), grenadiers (Macrouridae), roughies (Trachyichthyidae), hairtails (Trichiuridae), jack mackerel (Trachurus, Carangidae), scorpionfish (Scorpaenidae), flatfish (Pleuronectiformes), dragonets (Callionymidae), and small elasmobranchs including catsharks (Scyliorhinidae), lanternsharks (Etmopterus, Etmopteridae), smaller hexanchids (including other Heptranchias perlo), and skates (Rajidae). The presence of pelagic bony fishes, cephalopods and crustaceans in their diet suggest that these sharks are feeding well off the bottom (Ebert, 1990). In the Mediterranean Sea off Tunisia bony fishes are the most important prey, followed by small sharks and rays, crustaceans and cephalopods. Eighty-four percent of 125 of these sharks examined by Capapé (1980) had full stomachs. Around the Great Meteor Seamount, Central Eastern Atlantic, teleosts followed by cephalopods were found to constitute the main portion of the diet (Frentzel-Beyme and Köster, 2002). The narrow jaws and prominent narrow needle-sharp cusps and cusplets on the teeth of these sharks suggest that they are well equipped for grabbing, holding and swallowing small, soft-bodied prey, but less capable of dismembering large-bodied tough prey than Hexanchus griseus.

Size: Maximum total length is about 139 cm ; reports of it reaching a total length of 214 cm or over 3 m in literature (see Bigelow and Schroeder, 1948) are most likely erroneous. Size at maturity varies slightly by region, but generally males adolescent between 70 and 78 cm , adult at 75 to 107 cm ; females adolescent between 89 and 98 cm , but adult at 97 cm and larger. Size at birth is about 26 to 27 cm .

Interest to Fisheries and Human Impact: Of no importance commercially in North Atlantic fisheries, this species is likely caught in small numbers as a bycatch of deepwater bottom trawl and longline fisheries. It is not reported in landings for either Areas 21 or 27 . In other areas where it is more frequently taken as bycatch its flesh is utilized for human consumption and presumably for fishmeal. There are no data available on current and past catches, although species-specific catch data for this species are desirable.
It has been maintained occasionally in captivity at public aquariums in Japan. Although this shark is very active and will snap vigorously when captured, and may on occasion bite its captor, there are no records of it having attacked divers. Its deepwater habitat likely precludes it from coming into contact with divers.

Conservation status is considered Near Threatened due to suspected declines that may have occurred in places such as southern Mozambique and Taiwan, Province of China, where deepwater demersal trawl fisheries for shrimp and bony fishes have been operational over the past few decades. This shark is wide-ranging but relatively uncommon in most places where it occurs, but may be affected by a wide variety of deepwater demersal fisheries.

Local Names: Perlon shark, Sharphead sevengill, Sharp-snouted seven-gilled shark, Sharpsnouted sevengill, Narrowheaded sevengilled shark, Seven-gilled shark, Seven-gilled cow shark (English); Perlon, Monge gris (France); Boca dolça (Spain); Boca doce, Cacao severino, Ohlo branço, Bico doce (Portugal); Albafar bravo, Bico doce, Sharpnose seven-gill shark (Azores).

Literature: Lo Bianco (1909); Bigelow and Schroeder (1948); Garrick and Paul (1971); Boeseman in Hureau and Monod (1973); Capapé (1980); Cadenat and Blache (1981); Boeseman in Whitehead et al. (1984); Cappetta, Du Buit and Quéro (1985); Lloris (1986); Compagno, Ebert and Smale (1989); Ebert (1990); Du Buit (1991); Henderson and Williams (2001); Frentzel-Beyme and Köster (2002); Paul and Fowler (2003b); Braccini (2008); Gibson et al. (2008); Ebert and Compagno (In press); D.A. Ebert (unpubl. data).

## Hexanchus Rafinesque, 1810

Genus: Hexanchus Rafinesque, 1810, Caratt. gen. sp. anim. piant. Sicilia, Palermo, pt. 1: 14.
Type species: "Squalus griseus Lacépède", by original designation, a junior synonym of Squalus griseus Bonnaterre, 1788.

## Number of Recognized North Atlantic Species: 2.

Synonyms: Subgenus Monopterhinus Blainville, 1816 (Genus Squalus Linnaeus, 1758): 121. Type species: Squalus griseus Blainville, 1816, by subsequent designation of Jordan and Evermann, 1917: 95. Subgenus Notidanus Cuvier, 1817 (Genus Squalus Linnaeus, 1758): 128. Type species, Squalus griseus Bonnaterre, 1788, by subsequent designation of Jordan and Evermann, 1917: 97. Genus Hexanchias Swainson, 1838: 148 (emended or erroneous spelling of Hexanchus Rafinesque, 1810). Genus Holodus Agassiz, 1845: 3; Agassiz, 1846: 183; Agassiz, 1848: 529. Attributed by Agassiz, 1845 to "Msc. Coll." and indicated as "= Notidanus". Apparently a manuscript name without description, but a valid junior synonym of Notidanus Cuvier, 1817 and a senior homonym of the lungfish genus Holodus Pander, 1858 according to Jordan (1923: 97) and White and Moy-Thomas (1940: 101). Genus Notidamus Münster, 1842: 66 (erroneous or emended spelling of Notidanus Cuvier, 1817). Genus Hexancus Agassiz, 1846: 181; Agassiz, 1848: 522 (emended spelling of Hexanchus Rafinesque, 1810).

Nomen nudum: Squalus (Monopterhinus) Colombinus Blainville, 1816: 121 (referred to Hexanchus). This nomen nudum was included by Blainville (1816) in his subgenus Monopterhinus, but is of uncertain identity and may not be based on a hexanchid shark.

Diagnostic Features: Head narrowly or broadly parabolic in dorsoventral view, depressed and transversely oval in section at eyes. Eyes small to large. Six paired gill openings. Mouth moderately wide to very wide and parabolic or arcuate. Five or 6 rows of lower comb-shaped anterolateral teeth on each side, these long and low in adults but higher in young; mesial edge smooth in young but with serrations in adults; a low to moderately high cusp, 8 to 10 distal cusplets present in adults that decrease in size distal to the cusp; total tooth counts including smaller posteriorlateral teeth 25 to 46 upper jaw, 15 to 38 lower jaw. Caudal peduncle is short to elongated. Lateral line canal closed. Clasper apopyle ventral, clasper groove ventral, hypopyle ventrolateral; hypopyle with a large triangular lateral flap on its dorsal edge; clasper sack greatly enlarged and baglike, pleated, expanded far onto dorsomedial surface of clasper and outside clasper sheath, and with a large dorsal fold; clasper without mucous glands; clasper shaft slender. Vertebral counts: total vertebral counts 118 to 155, precaudal vertebral counts 67 to 87 , monospondylous vertebral counts 41 to 57 , diplospondylous precaudal vertebral counts 18 to 30 ,
caudal vertebral counts 50 to 77 . Intestinal valve counts 22 to 39 . Maximum size depending on the species can be either about 180 or up to 500 cm or more in length. Colour: body without spots or with irregular brown spots, no black tips on fins.

Local Names: Sixgill sharks.
Remarks: Following Springer and Waller (1969), Bass, D'Aubrey and Kistnasamy (1975), Compagno (1984), Ebert (1990), and Ebert and Compagno (In press) two living species are recognized here for this genus, Hexanchus griseus (Bonnaterre, 1788) and H. nakamurai Teng, 1962 (senior synonym of H. vitulus Springer and Waller, 1969); both species occur in the North Atlantic.

## Key to North Atlantic Species:

1a. Snout shorter, blunt and broad; lower jaw usually with 6 rows of large, comb-like anterolateral teeth on each side; dorsal-fin base separated from upper caudal-fin origin by a distance about equal to or slightly greater than its length; size very large, up to at least 4.8 m TL (Fig. 38).

Hexanchus griseus


Fig. 38 Hexanchus griseus


Fig. 39 Hexanchus nakamurai

## Hexanchus griseus (Bonnaterre, 1788)

Squalus griseus Bonnaterre, 1788, Tabl, encyclop, method. trois reg. Nat., Ichthyol., Paris: 9. Types unknown according to Boeseman in Hureau and Monod (1973, CLOFNAM. Check-list fish. NE Atlantic Mediterranean, 1: 9). Type locality: "La Méditerranée", = Mediterranean Sea.

Synonyms: Squalus vacca Bloch and Schneider, 1801: 138. Types unknown? No locality, presumably European Seas. Notidanus monge Risso, 1826: 129. Existance of types unknown. Type locality, Mediterranean Sea. Also N. monge Risso and N. monge var. albescens Risso (nomen nudum) in Bonaparte, 1846: 17 in synonymy (Eschmeyer, 1998)

Other Combinations: Notidanus griseus (Bonnaterre, 1788).
FAO Names: En - Bluntnose sixgill shark; Fr - Requin griset; Sp - Cañabota gris.


Field Marks: A heavy-bodied, broad-headed sixgill shark. Mouth is ventral with 6 rows of lower bladelike, comb-shaped teeth on each side. One dorsal fin. Dark pupil prominently ringed with white. Colour grey or tan to blackish with a conspicuous lighter lateral line and sometimes with darker spots on the sides. Underside often lighter than the dorsal surface in newborn young but more uniform in larger juveniles and adults.

Diagnostic Features: Head broadly parabolic or bluntly pointed in dorsoventral view. Snout bluntly rounded to roundedangular in dorsoventral view, preoral length shorter and 4.3 to $5.4 \%$ of TL. Eyes small. Mouth very broad with width over 2 times mouth length. Upper jaw and dental arcade is a rounded v-shape in ventral view. Six rows, usually, of lower comb-shaped anterolateral teeth; total tooth counts, including smaller posterior lateral teeth 26 to 46 upper jaw, 19 to 38 lower jaw. Body rather stout, body and fins very soft and supple. Caudal peduncle is short and stout. Pectoral fins broadly triangular. Ventral caudal lobe poorly developed at all stages, postventral margin weakly concave to straight and not subdivided. Vertebral counts: total vertebral counts 118 to 148 , precaudal vertebral counts 67 to 77 , monospondylous precaudal vertebral counts 41 to 52 , diplospondylous precaudal vertebral counts 18 to 30 , caudal vertebral count 50 to 77. Intestinal valve counts 35 to 39. A giant shark, size at maturity in males about 310 cm and in females 480 cm , size at birth between 65 and 70 cm . Colour: body not sharply bicoloured (except in some neonatal animals), either dark above and below or with underside somewhat lighter than dorsal surface; fins with light posterior margins but not abruptly white (except in some neonates).

Distribution: Worldwide, but somewhat patchily distributed in boreal, temperate and tropical seas, possibly absent in the Arctic and Antarctic oceans. Eastern North Atlantic: Iceland, Faroe Islands, Norway, northern North Sea, Ireland, Scotland, England and Wales, France, Spain and Portugal, including the Mediterranean. Central Atlantic: Azores and along the Mid-Atlantic Ridge. Western North Atlantic: Nova Scotia, Canada to North Carolina and Florida, USA, and southwards to at least northern Argentina.

Habitat: This is a mostly deepwater demersal and pelagic shark of the continental and insular shelves and slopes and off seamounts and underwater ridges, found close to and well off the bottom. Occurs on occasion in cold temperate waters at the surface and close inshore inside bays and estuaries, especially in areas where the continental shelf is narrow and at the heads of submarine canyons. Depth range extends down to at least 2500 m on the upper continental slope. It may


Fig. 41 Hexanchus griseus show equatorial submergence in the tropics as with some other deepwater sharks, and may not normally penetrate warm tropical inshore waters although it has been known to rise to the surface offshore in response to fishing operations.

Young are often found close inshore, occasionally in enclosed bays; adults, especially males are often in deeper water below 200 m in temperate areas, although adults and sub adults will enter shallow water in open and enclosed bays with adjacent deep-water canyons. These sharks are often associated with areas of upwelling and high biological productivity. Hydrographic data variously taken in areas where bluntnose sixgill sharks occur reveals a bottom temperature of 6.1 to $10.0^{\circ} \mathrm{C}$ in waters with high nutrient levels.

Biology: Yolk-sac viviparous, with litters very large, 47 to 108 . Reproductive cycle poorly defined, but may be biannual with females having a 12 month resting phase followed by a 12 month gestation period. Pupping grounds occur on the upper slopes and outer continental shelves, the Bay of Biscay may be one such pupping area as neonate bluntnose sixgill sharks appear seasonally (Desbrosses, 1938). Ebert (1994, 2002, 2003) suggested that this shark segregates over its life cycle with neonates living near the bottom on the upper slopes, outer shelves, and in high latitude nearshore areas where the continental shelf is relatively narrow to the continental landmass. Neonates and younger bluntnose sixgills feed largely on cephalopods and teleosts, but with growth in size larger individuals move into deeper water and feed on a wide range of benthic and pelagic marine vertebrates and cephalopods. This species may be long-lived but it has yet to be aged. A study by McFarlane et al. (2002) found bands on the neural arches of these sharks, but were unable to determine if they were related to age.

The bluntnose sixgill shark is a voracious feeder consuming a wide range of marine organisms, but principally cephalopods and marine vertebrates, with cartilaginous fishes, bony fishes, marine mammals and cephalopods being the most important prey categories. It eats other cartilaginous fishes including catsharks (Scyliorhinidae), spurdogs (Squalus, Squalidae), houndsharks (Triakidae), skates (Rajidae), elephantfish (Callorhinchidae), hooked conspecifics (which it attacks and sometimes follows up to the surface from deep water); demersal and pelagic bony fish including anchovies (Engraulidae), sardines and round herrings (Clupeidae), lanternfish (Myctophidae), hake (Merluccidae), cod and ling (Gadidae), grenadiers (Macrouridae), mackerel (Scombridae), snoek (Thyrsites, Gempylidae), swordfish (Xiphiidae), marlin (Istiophoridae), dolphinfishes (Coryphaenidae), flounders (Pleuronectidae), gurnards (Triglidae) and anglerfish (Lophiidae); marine mammals including unspecified seals (probably Phocidae), Cape fur seals (Arctocephalus p. pusillus, Otariidae), and dolphins (Delphinidae); carrion; gastropods, squids (Ommastrephidae and Loliginidae), crabs, and shrimp.
The diet of bluntnose sixgills changes with growth as those below 1.2 m feed primarily on cephalopods and secondarily on bony fish, with very little chondrichthyan prey evident, while those 1.2 to 2 m long feed primarily on cephalopods, bony fishes and chondrichthyans with small marine mammals comprising a small component. Large sixgills, those above 2 m , feed primarily on marine mammals (Cape fur seals and cetaceans) and large pelagic teleosts, with smaller components of cartilaginous fishes and cephalopods (Ebert, 1994). An indication of the voracious dietary nature of these sharks was demonstrated by an electric ray (Torpedo cf. nobiliana) that had the distinct scars of an immature Hexanchus griseus, estimated at about 1 m in length, but apparently was able to fend off the attacking predator by discharging an electric shock to halt the attack. A larger bluntnose sixgill likely would have been more successful. Sixgills apparently feed on the bottom and well above it, and may be able to take large active prey such as eared seals, cetaceans, and large pelagic bony fishes by stealthy stalking them. This is an infrequently taken bycatch species on pelagic longlines where these sharks are often caught hundreds of meters off the bottom.
Bluntnose sixgill sharks in some areas exhibit both seasonal and diurnal activity with these sharks appearing in high concentrations during summer months, but disappearing during the rest of the year. When present these sharks appear to respond to environmental signals whereby they move onto relatively shallow reefs during the afternoon, but retreat later in the day. The wide bathymetric and geographic range of the species, the large size of adults, its ability to prey on pelagic organisms, and its scattered occurrence off seamounts and oceanic islands and well away from the bottom suggest that it may be capable of long-distance migration in the open ocean.
Larger captive individuals become greatly disturbed at even moderately high light levels, indicating a great sensitivity to light at very low levels, while those attracted to baits near submersibles either did not react or gave a minor to violent response when the lights were turned on. Smaller individuals in public aquaria appear to adapt better to artificial light with some individuals having been maintained for nearly a year. Large individuals offer little resistance when captured, but small ones may snap and thrash vigorously when boated.
The bluntnose sixgill shark has been observed both singly and in groups, and will readily attack conspecifics especially if injured, however very little else is known of their social behavior.

Size: Maximum TL at least 482 cm and probably to about 550 cm (large, possibly gravid female sighted from a submersible). Males immature up to 281 cm , adolescent at 273 to 308 cm , mature at 309 to 330 cm and possibly reaching about 430 cm ; females immature up to 320 cm , possibly adolescent or newly mature at 350 to 420 cm , mature at 421 cm , and reaching about 550 cm . Size at birth about 61 to 74 cm .

Interest to Fisheries and Human Impact: The bluntnose sixgill shark can be a locally common species in the Eastern North Atlantic and along the Mid-Atlantic Ridge, and although there are no directed fisheries for these sharks in the North Atlantic they are sporadically taken as bycatch, mostly by French, Portuguese, and United Kingdom fisheries in ICES Subareas VII, VIIIa, and X. Reported landings in Area 27 for this species are quite small varying from between 0 and 30 tonnes per year (average 7.8 tonnes per year) between 2000 and 2009. The species is rare to uncommon in the Western North Atlantic and as such catch or landing records are generally not reported.
Bluntnose sixgill sharks are typically taken by line gear, gillnets, traps and pelagic and bottom trawls and utilized fresh, frozen, and dried and salted for human consumption, and for fishmeal and oil. These sharks are largely caught as a bycatch of other fisheries.
Bluntnose sixgill sharks have been the subjects of ecotourism dive operations, especially in British Columbia, Canada, but there are no similar ecotourism activities in the North Atlantic. Although the bluntnose sixgill is largely docile when confronted by divers, young sharks will snap vigorously when captured. There is at least one confirmed non-fatal attack by this species on a diver gathering clams in Puget Sound, Washington, USA. As it is among some of the larger known shark species caution should be taken if encountered while diving.

The global conservation status of the bluntnose sixgill shark is listed as Near Threatened. Although the species is taken in small numbers regionally, mostly as retained bycatch in other fisheries, there is inadequate population and fisheries data to show declines in its population. There is no regional conservation assessment for this species in the North Atlantic.

Local Names: Sixgill shark, Six-gilled shark, Cow shark, Griset or Griset shark, Mud shark (English); Griset, Bouca douça, Mounge gris, Hexanche (France); Boquidulce, Boca dolça, Bastriuvaca (Spain); Grauhai, Stumpfnasen-Sechskiemerhai (German); Albafar, Albafora, Olho verde (Portugal); Albafar, Six-gill shark (Azores); Seksgaellet haj (Denmark); Kamtannhai (Norway); Sexbågig kamtandhaj (Sweden).

Remarks: The bluntnose sixgill shark is one of the most common and wide-ranging shark species worldwide, ranking alongside the picked dogfish (Squalus acanthias) and blue shark (Prionace glauca). Small Hexanchus griseus, usually less than 120 cm in length, may be confused with the bigeyed sixgill shark, $\boldsymbol{H}$ nakamurai.

Literature: Bigelow and Schroeder (1948); Springer and Waller (1969); Wheeler and Blacker (1969, 1972); Boeseman in Hureau and Monod (1973); Cadenat and Blache (1981); Boeseman in Whitehead et al. (1984); Compagno (1984); Ebert (1984, 1986a, b, 1990, 1994, 2002, 2003); Gilhen and Coad (1989); Merrett et al. (1991a); Michael (1993); Carey and Clark (1995); McFarlane, King, and Saunders (2002); Cook and Compagno (2005a); Andrews et al. (2007); Gibson et al. (2008); ICES (2010); Ebert and Compagno (In press); D.A. Ebert (unpubl. data).

## Hexanchus nakamurai Teng, 1962

Hexanchus griseus nakamurai Teng, 1962, Class. Dist. Chond. Taiwan: 30, Fig. 5. Holotype: Taiwan Fisheries Research Institute, TFRI 2515, 750 mm TL male, probably juvenile, Keelung, Taiwan, Province of China. Possibly lost according to Ebert (1990, Taxonomy, biogeography and biology of cow and frilled sharks, Chondrichthyes: Hexanchiformes: 55), who searched for it while on a fellowship in Taiwan, Province of China.

Synonyms: Hexanchus vitulus Springer and Waller, 1969: 160, Figs. 1, 2A, 3-4. Holotype: U.S. National Museum of Natural History, USNM 200674, 148 cm adult male, off Bimini, Bahamas, in about 350 m depth, confirmed by Howe and Springer (1993: 14).

Other Combinations: None.
FAO Names: En - Bigeyed sixgill shark; Fr - Requin vache; Sp - Cañabota ojigrande.


Fig. 42 Hexanchus nakamurai

Field Marks: A slender-bodied, narrow-headed sixgill shark, with one dorsal fin, a mouth ventrally situated, and a lower jaw consisting of 5 rows of bladelike, comb-shaped teeth on each side.

Diagnostic Features: Head narrowly parabolic or bluntly pointed in dorsoventral view. Snout narrowly rounded to rounded-angular in dorsoventral view. Eyes large. Mouth narrower with width about 1.5 times mouth length. Upper jaw and dental arcade $v$-shaped in ventral view. Lower anterolateral teeth in five rows and comb-shaped; total tooth counts, including smaller posterior lateral teeth 25 to 32 upper jaw, 9 to 32 lower jaw. Body rather slender, body and fins relatively hard and firm. Caudal peduncle is long and slender. Pectoral fins narrowly triangular and semifalcate. Ventral caudal-fin lobe short and strong in adults but weak in young, postventral margin deeply notched in adults and subdivided into upper and lower parts. Total vertebral counts 155, precaudal vertebral count 87 , monospondylous precaudal vertebral count 57, diplospondylous precaudal vertebral count 30 , caudal vertebral count 68 . Intestinal valve counts 22 to 28 . A moderately large shark, with a maximum length of 180 cm . Colour: usually sharply bicoloured with underside lighter than dorsal surface; most fins with prominent white posterior margins and tips but sometimes dusky.

Distribution: Spottily distributed worldwide in most warm temperate and tropical seas, although absent from the Eastern Pacific. In the Eastern North Atlantic from the Bay of Biscay (France), Spain, Portugal and Gibraltar, but not recorded in the area from the Western North Atlantic. Occurs in the Eastern Central Atlantic from off Morocco, possibly the Ivory Coast and Nigeria, and also in the Western Mediterranean. Patchily distributed throughout the Western Central Atlantic, especially from off Florida, USA and the Bahamas, northern Cuba, Cayman and Virgin Islands, Yucatan and Gulf coast of Mexico, Nicaragua, Costa Rica, Venezuela and the Guyana's.

Habitat: A little-known, primarily deepwater shark of continental and insular shelves and slopes from 90 to 621 m depth, usually on or near the bottom, but occasionally moving to near the surface or inshore in the tropics.

Biology: Yolk-sac viviparous, fecundity much lower in this species than in Hexanchus griseus with the number


Fig. 43 Hexanchus nakamurai
$\square$ Known distribution of young between 13 and 26. The reproductive cycle is unknown for this species. Diet sketchily known, but includes small to medium-sized bony fishes, including hairtails (Trichiuridae), a small tuna (Euthynnus, Scombridae), and crustaceans.
This shark when it has been observed at bait stations set by submersibles it appears to be more cautious than H. griseus in the same area, with individuals not taking baits although still approaching the bait stations and the submersible closely (Clark and Kristof, 1990a, b).

Size: Maximum total length about 180 cm ; males mature at 123 to 157 cm and females mature at 142 to 178 cm in length. Size at birth is about 40 to 43 cm in length.

Interest to Fisheries and Human Impact: It probably is a very minor bycatch component of offshore demersal trawl and line fisheries where it occurs, but no catch statistics are available. It is relatively uncommon in Area 27 as far as known, and it has not been reported as occurring in Area 21.

The conservation status of this shark is Data Deficient due to a lack of sufficient biological and population information on this species. It is uncommon to rare where it occurs, but may be affected by bottom fisheries. Similarly, as with Heptranchias perlo, species-specific catch data is desirable for this species. It may be more common than thought, but is often misidentified with smaller juveniles of its larger relative Hexanchus griseus.

Local Names: Bigeye sixgill shark (English); Canhabota olho grande (Portugal).
Remarks: The species name Hexanchus vitulus (Springer and Waller, 1969) is often cited in the literature, but this name is a junior synonym of $\boldsymbol{H}$. nakamurai(Teng, 1962). Ebert (1990; unpubl. data) investigated and examined material, including the types of $\boldsymbol{H}$. vitulus from the Bahamas and compared it with specimens from Australia, Florida, USA, Indonesia, Kenya, Philippines, South Africa, Taiwan, Province of China (including the type locality of H. nakamurat), the northern Gulf of Mexico, and the U.S. Virgin Islands and concluded that these two species were one in the same based on morphological evidence, including tooth morphology.

Literature: Bigelow and Schroeder (1948); Teng (1962); Springer and Waller (1969); Boeseman in Whitehead et al. (1984); Ebert (1990); Clark and Kristof (1990a, b); Ebert, Serena, and Mancusi (2008a); Gibson et al. (2008); ICES (2010); Ebert and Compagno (In press); D.A. Ebert (unpubl. data).

### 2.2 Order SQUALIFORMES - Dogfish sharks

Order: Squali, suborder Squali: Gill, 1862, Ann. Lyc. Nat. Hist. New York, 7: 367, 394, 396.
Number of Recognized North Atlantic Families: 7.
FAO Names: En - Dogfish sharks; Fr - Squales; Sp - Galludos.
Field Marks: Small to very large sharks with a cylindrical or compressed body, a flattened or conical snout, five paired lateral gill openings, two dorsal fins with or without spines, and no anal fin.

Diagnostic Features: Head conical to moderately depressed, but not expanded laterally. Snout short to moderately long, conical to moderately depressed, not laterally expanded and without sawteeth or rostral barbels. Eyes lateral or slightly dorsolateral on head, without nictitating lower eyelids, secondary lower eyelids or subocular pouches; upper eyelids not fused to eyeballs. Spiracles small to very large, close behind and about opposite level of eyes. Five pairs of gill openings present on sides of head, last in front of pectoral-fin origins. Nostrils transverse on snout, without separate barbels but with anterior nasal flaps expanded into barbels and reaching mouth in Cirrhigaleus barbifer but not in other squaloids; nasoral grooves and circumnarial grooves and folds absent from nostrils. Mouth small to large, usually subterminal on head (terminal in Trigonognathus), Y-shaped, narrowly to broadly arched and parabolic to transverse and nearly straight, ending below or behind eyes. Labial furrows well developed on both jaws. Teeth weakly to strongly differentiated along the jaws, with (Trigonognathus) or usually without enlarged anterior teeth and without enlarged molariform posterior teeth; without a gap or small intermediate teeth between anterior and lateral teeth in the upper jaw. Trunk cylindrical to slightly depressed or somewhat compressed but not depressed and ray like. Tail without long thick lateral dermal folds that reach to caudal base but sometimes with short caudal keels. Denticles covering almost entire body (sparsely distributed in one species of Centroscyllium), usually not enlarged as thorns or spines (except in Echinorhinus brucus). Pectoral fins small to moderately large, not expanded and ray-like, without triangular anterior lobes that cover the gill slits. Pelvic fins small to moderately large, inner margins continuous with margin of vent. Two dorsal fins present, with spines on both fins in many taxa, a spine on the first dorsal fin only in one genus (Squaliolus), and spines absent in most Dalatiidae and some Somniosidae; origin of first dorsal fin varying from over the pectoral-fin bases or gill slits to over the anterior halves of the pelvic-fin bases. Anal fin absent. Caudal fin with a moderately long dorsal lobe and the ventral lobe absent to strong. Vertebral counts: total vertebral counts 35 to 131 , precaudal vertebral counts 44 to 95 , monospondylous vertebral counts 29 to 67 , diplospondylous vertebral counts 4 to 49 , and caudal vertebral counts 50 to 82 . Intestinal valve of conicospiral or ring type, with 4 to 42 turns. Dwarf to very large sized sharks with adults ranging from 22 cm to 600 cm or more in length. Colour: variable but may range from light to very dark hues or with intermediate shades of grey, brown, or black; some species uniformly coloured, while others are lighter below; prominent markings such as spots are present on some species, while others are relatively plain coloured. Reproductive mode is viviparous with a yolk-sac.

Distribution: Circumglobal in all seas, with representatives of all seven families occurring in the North Atlantic.
Habitat: These sharks occur in most marine habitats from shallow enclosed and open bays, on continental shelves, slopes and rises of continental and insular waters, on submarine ridges, and in epipelagic, mesopelagic and bathypelagic zones. They inhabit rocky reefs, estuaries, sandy beaches, and under pack ice in Arctic waters. They range in depth from the intertidal to the outer shelves, slopes and rises to below 4000 m . Dogfish sharks generally dominate deepwater benthic shark faunas in diversity and abundance, and are the only sharks present in polar seas.

Biology: Reproductive mode is yolk-sac viviparity, with litters ranging from 1 to perhaps 300 in some of the larger species. Dogfish feed on small to large bony fishes and invertebrates, with some of the larger species known to consume chondrichthyans and, at least as carrion, marine mammals. Many are formidable predators, having large teeth and efficient cutting dentitions, with the lower teeth or teeth of both jaws forming a sawlike cutting edge. A few species are facultative parasites, and core plugs of flesh out of other chondrichthyans, large bony fishes, seals, and cetaceans. Dogfish sharks are active to sluggish swimmers and highly varied in size, however most species are small. Information on movements is limited or absent for most species; the picked dogfish (Squalus acanthias) is migratory, and changes habitat seasonally. Many dogfishes are social and are found in aggregates or schools, some of which are huge, but the sociobiology of most species is poorly known as is most other aspects of their behaviour.

Interest to Fisheries and Human Impact: Several members of this shark group are of moderate to major importance to fisheries, particularly members of the Squalidae. Some species are regular components of targeted shark fisheries and as utilized or discarded bycatch of other fisheries targeting teleost fishes or marine invertebrates. These sharks are caught in bottom and pelagic trawls, in fixed and pelagic gillnets, in fish traps, on bottom longlines, with harpoons, with hook and line and rod and reel. Several species are used for human consumption; the flesh of some species is excellent. Most are small (less than 1 m long), have relatively small fins, and seem to have very limited importance for the oriental soup-fin trade.
North Atlantic countries reporting dogfish catches to FAO from 1950 to 2001 include Canada, Channel Islands, Denmark, France, Germany, Greenland, Iceland, Ireland, the Isle of Man, the Netherlands, Norway, Poland, Portugal, the Russian Federation (and former USSR), Spain, Sweden, the Ukraine, the United Kingdom, and the United States of America.

Dogfish catches reported to FAO from 1950 to 2001 ranged from 35945 to 75464 tonnes, averaging 52646 tonnes during that period. Catch trends are erratic but show increased catches, with a levelling-off during the 1980s and early 1990s and a declining trend from 1996 ( 64977 tonnes) to 2001 ( 42774 tonnes). From 2002 to 2009 the trend in dogfish catches generally declined from 45252 tonnes (2002) to 34623 tonnes (2009), with a spike in 2005 of 47248 tonnes being reported. The decline in dogfish landings over the past decade is a result of regulations implemented by the USA and the European Community.

The conservation status for the majority of dogfish sharks is Least Concern or Data Deficient due to a lack of life history information and data on population trends. However, several species are considered Endangered to Critically Endangered due to impacts from either targeted or non-targeted fishing.

Local Names: None.

Remarks: The arrangement of the order as restricted here follows Compagno (1984, 1999), Compagno, Dando, and Fowler (2005), and Ebert and Compagno (In press) in recognizing seven families in the order, all of which have representatives in the North Atlantic.

Key to Families Occurring in the North Atlantic:
1a. First dorsal fin originating posterior to pelvic-fin origins (Fig. 44). . . . family Echinorhinidae

1b. First dorsal fin originating anterior to pelvic-fin origin (Fig. 45) 2

2a. Body very high and compressed, triangular in cross-section. Dorsal fins extremely high
(Fig. 45)
family Oxynotidae
2b. Body low and more cylindrical in crosssection. Dorsal fins low 3

3a. Dorsal-fin spines without grooves. Teeth similar in both jaws. Upper precaudal pit usually present on caudal-fin base; strong lateral caudal keels always present on caudal peduncle. Subterminal notch absent from caudal fin (Fig. 46)
family Squalidae
3b. Dorsal-fin spines, if present, with lateral grooves. Teeth dissimilar in upper and lower jaws (Fig. 48 \& 49). Upper precaudal pit absent from caudal-fin base; strong lateral caudal keels generally absent (Fig. 47) 4

4a. Underside of body, flanks, and tail usually with more or less conspicuous black markings with light organs (photophores)

## family Etmopteridae

4b. Underside of body, flanks, and tail without conspicuous black markings with light organs (photophores)

5a. Upper teeth relatively broad and bladelike, lowers low and wide (Fig. 48)
family Centrophoridae

5b. Upper teeth relatively narrow and not blade-like, lowers high and wide (Fig. 49) 6


Fig. 44 Echinorhinus


Fig. 45 Oxynotus


Fig. 46 Squalus


Fig. 47 Etmopterus


UPPER AND LOWER TEETH
Fig. 48 Centrophorus


UPPER AND LOWER TEETH
Fig. 49 Isistius

6a. Head moderately broad and somewhat flattened or conical. Snout flat and narrowly rounded to elongate-rounded in dorsoventral view. Abdomen usually with lateral ridges. Both dorsal fins either with or without fin spines (Fig. 50).
family Somniosidae


Fig. 50 Somniosus


Fig. 51 Dalatias

### 2.2.1 Family ECHINORHINIDAE

Family: Echinorhinoidae Gill, 1862, Ann. Lyc. Nat. Hist. New York, 7(32): 406.
Type genus: Echinorhinus Blainville, 1816. Emended to family Echinorhinidae by Gill, 1893, Natn. Acad. Sci. USA, Mem. 6, 6: 129.

## Number of Recognized North Atlantic Genera: 1.

Synonyms: None.
FAO Names: En - Bramble sharks; Fr - Squales bouclés; Sp - Tiburones espinosos.
Field Marks: Short-nosed and flat-headed with a cylindrical, heavy-body. Short-tailed with no anal fin. Two very small, spineless, posterior dorsal fins, the first behind the pelvic origins, and covered with coarse spiky denticles or enlarged tacklike thorns.

Diagnostic Features: Head broad and flat. Snout flat and broadly rounded in dorsoventral view. Spiracles very small and far behind eyes. Fifth gill opening much larger than first four. Nostrils wide-spaced with internarial width much greater than nostril width; nostrils with small, simple anterior nasal flap. Mouth broadly arched, elongated, with thin, non-papillose lips. Labial furrows short, not encircling mouth, confined to mouth corners and falling well behind level of eyes, not elongated posteriorly into postoral grooves or anteriorly into preoral grooves. Labial folds thin and not papillose. Teeth with dignathic heterodonty. Poorly developed upper teeth about as large as lowers. Total tooth row counts 18 to 28 upper jaw, 18 to 27 lower jaw. Teeth of both jaws compressed, low-crowned, broad, bladelike, and forming a sawlike cutting edge, not arranged in a quincunx pattern but forming a single flat nonimbricated series in either jaw. Teeth with an oblique compressed, sharp-edged cusp (smooth-edged, undulated or serrated); one to three (usually two) pairs of mesial and distal cusplets on anterolateral teeth of adults (absent mesially and distally replaced by a blade in posterior teeth) but cusplets absent in young which have undivided mesial edges and distal blades on most teeth. Trunk broad and cylindrical with a circular cross section. Abdomen with weak lateral ridges. Interdorsal space very short and less than half the length of first dorsal base. Pelvic-caudal space very short and less than half length of pelvic bases. Caudal peduncle compressed, very short, and without lateral keels and precaudal pits. Body without photophores. Denticles large to enormous, sessile and without pedicellate. Denticle crowns flattened and leaf-shaped, but with a median cusp. Pectoral fins low, broadly rounded-angular and not falcate or leafshaped, anterior margins moderately large and about equal to or somewhat smaller than the prespiracular length, rear tips rounded and not elongated. Pectoral fin skeleton unibasal with propterygium. Mesopterygium and metapterygium fused to form a single basipterygium. Mesopterygial radials not fused to the basipterygium. Metapterygial axis greatly elongated, distal end of basipterygium not expanded and fanlike. Pelvic fins about as large or slightly larger than pectoral fins, over twice area of dorsal fins. Claspers with a lateral spine only. Dorsal fins rounded-angular, not falcate, and without spines. First dorsal fin very small, with length less than prespiracular length. First dorsal-fin base over the pelvic-fin bases and origin behind the pelvic-fin origins. Second dorsal fin about as large as first dorsal fin, base mostly behind pelvic-fin bases with origin over to slightly anterior or posterior to pelvic-fin insertions. Caudal fin moderately heterocercal, with ventral lobe poorly developed in adults, but absent in young and with subterminal notch absent or barely indicated. Chondrocranium with large, basin-like and broad rostrum, with large rostral appendices and lateral wings, anterior to and between the laterally situated nasal capsules, with a strong and broad medial keel. Precerebral fossa very large; nasal capsules not expanded medially and far lateral to each other. Internasal septum high at keel but low and depressed between keel and capsules. Basal communicating canals very large. Anterior fontanelle moderately large and U-shaped. Basal plate very broad in front of and between basitrabecular cotyles for orbital processes. No ventrally projecting, suborbital stay on basal plate. No basal angle on basal plate. Basitrabecular cotyles of palatoquadrate orbital processes very small and
weakly developed in anterior half of orbits. Optic nerve foramen above orbital processes. Suborbital shelves moderately large and well developed, with stapedial foramina. Postorbital processes very broad, ventrally keeled, and subquadrate with broad winglike tips. Sphenopterotic ridges high and strong. Jaws very long and anteriorly narrow, extending behind cranium. Palatoquadrates with short orbital processes, slender palatine processes, and high quadrate processes. Meckel's cartilages low and with shallow symphyses. Vertebral centra poorly calcified, primary double cones not calcified or weakly developed. Vertebral counts: total vertebral counts 86 to 102; monospondylous vertebral counts 50 to 59 ; diplospondylous precaudal counts only 4 to 10 . Intestinal valve with 8 to 16 turns. Adults between 150 to about 400 cm long. Colour: light grey to blackish, plain or mottled, without black photophore markings on tail.

Distribution: This family includes two large, inshore to deep-water species with a spotty but virtually circumglobal distribution in cold temperate to tropical seas.

Habitat: Bramble sharks are found on the continental and insular shelves and upper slopes, at the heads of submarine canyons, down to at least 900 m , and on or near soft bottom substrate. They move up submarine canyons into shallow water and in cold-temperate areas with strong upwelling. They appear to occupy a similar habitat to sleeper sharks (Somniosus) and the bluntnose sixgill shark (Hexanchus griseus).

Biology: The biology of bramble sharks is poorly known. They exhibit yolk-sac viviparity in their reproductive mode, but little else is known about their reproductive cycle. Bramble sharks are large, soft-bodied and sluggish, but are formidable bottom predators that reach a maximum size of 310 to 450 cm . They feed on a variety of benthic and neritic bony fishes, other sharks, chimaeroids, as well as crabs and cephalopods. They have a moderately large mouth, a very large and long pharynx, and are believed to suck in their prey by suddenly expanding their mouths and pharynxes.

Interest to Fisheries and Human Impact: Bramble sharks attain a large size ( 310 to 450 cm ), and are uncommon to rare in most areas where they occur, hence they are of minimal interest to fisheries. They generally occur as a sporadic and largely unutilised bycatch of other fisheries, including those for other sharks, although targeted fisheries for bramble sharks have existed outside the North Atlantic, most notably from off of south-western India and Namibia. They are taken on longline gear, deepset gillnets, and bottom trawls.

The conservation status is essentially unknown, and no world or local fisheries records are available for these sharks.
Local Names: Bramble sharks, Prickly sharks; Shipovatye akuly (Russia).
Remarks: This family has a single living genus Echinorhinus with two valid species, one of which occurs in the North Atlantic. The family and genus Echinorhinus is divergent from all other squaloids and has been placed in its own separate order (Echinorhiniformes) by some authors (Shirai, 1992a, 1996; de Carvalho, 1996; Nelson, 2006) or separate suborder (Echinorhinoidei) by others (Günther, 1870; Woodward, 1889, 1898; Zittel et al., 1902; Regan, 1906a; Goodrich, 1909; Bridge, 1910; Engelhardt, 1913; Hubbs and McHugh (1951); Bigelow and Schroeder, 1957; Norman, 1966; Nelson, 1976, 1984, 2006; de Carvalho, 1996) with the remaining families being placed in the suborder Squaloidei as their probable primitive sister group.

Literature: Garman (1913); Bigelow and Schroeder (1948, 1957); Cadenat and Blache (1981); Compagno (1984); Shirai (1992a, 1996); Ebert and Compagno (In press).

## Echinorhinus Blainville, 1816

Genus: Subgenus Echinorhinus Blainville, 1816, Bull. Sci. Soc. Philomat. Paris, (8): 121 (genus Squalus Linnaeus, 1758).
Type species: "Spinosus" = Squalus spinosus Gmelin, in Linnaeus and Gmelin, 1788, by monotypy.

## Number of Recognized North Atlantic Species: 1.

Synonyms: Genus Goniodus Agassiz, 1835: PI. E, Fig. 13. Genus name only, with illustration of entire tooth set. Ibid., 1838, 94. Apparently proposed as a replacement name for Echinorhinus Blainville, 1816, as this name was mentioned as being equivalent to Goniodus. No type designation, but the only species mentioned was "Sq. spinosus Schn." (= Squalus spinosus Gmelin, in Linnaeus and Gmelin, 1788) as the type of Echinorhinus. Ibid., 1843, Tab. Mat.: 12. Type species: "Squalus spinosus de Blainville", by original designation, = Squalus spinosus Gmelin, in Linnaeus and Gmelin, 1788. Genus Echinorrhinus (Blainville) Müller and Henle, 1837a: 116; Müller and Henle, 1837b: 399. Probable emendation of or error for Echinorhinus Blainville, 1816. Müller and Henle (1838b: 65; 1839: 96) reverted to Blainville's original spelling. Genus Echinarrhinus (Blainville) Müller and Henle, 1838a: 89. Probable error for EChinorrhinus Müller and Henle, 1837.

Field Marks: See Family account above.

Diagnostic Features: See Family account above
Local Names: See Family account above.

## Echinorhinus brucus (Bonnaterre, 1788)

Squalus brucus Bonnaterre, 1788, Tabl. Encyclop. Method. Trois Reg. Nat., Ichthyol., Paris: 11. Holotype lost according to Krefft and Tortonese (1973b, in J. C. Hureau and T. Monod, eds., CLOFNAM. Check-list fish. NE Atlantic Mediterranean, 1: 45) and Eschmeyer (1998, Cat. Fish.). Type locality: "L’Océan" (= Eastern North Atlantic).

Synonyms: Squalus spinosus Gmelin, in Linnaeus and Gmelin, 1788: 1500. Holotype lost, based on same specimen as $S$. brucus Bonnaterre, 1788 according to Krefft and Tortonese (1973: 45). Type locality: "In Oceano" (= Eastern North Atlantic.); Lacepède, 1798: 167, pl III (Fig. 2); Schneider, 1801: 136; Risso, 1810: 42-43. Echinorhinus spinosus Blainville, 1816: 121; Blainville, 1820-1830: 66-68, pl. XVI (Fig. 1-2); Müller and Henle, 1841: 96; Duméril, 1865: 459461, pl. XII (Fig, 16-20); Bocage and Capello, 1866: 35; Günther, 1870: 428-429; Canestrini, 1872: 42; Doderlein, 1881: 104-105; Moreau, 1881: 365-367, Fig. 64-65; Day, 1884: 323-325, pl CLXII (Fig. 2); Goode and Bean, 1896: 8-9, pl III (Fig. 9); Regan, 1908: 42; Roule, 1912: 18, 25; Lozano Rey, 1928: 485-490, Fig. 161-163; Nobre, 1935: 463-464, pl. LXIV (Fig. 201); Ehrenbaum, 1936: 290-291, Fig. 255; `Soljan, 1963: 68, Fig. Scymnus spinosus Cuvier, 1817: 131; Risso, 1826: 136.

Other Combinations: None.
FAO Names: En - Bramble shark; Fr - Squale bouclé; Sp - Tiburón de clavos.



UNDERSIDE OF HEAD


UPPER AND LOWER TOOTH


DERMAL DENTICLES

Fig. 52 Echinorhinus brucus

Field Marks: A large, short-nosed and flat-headed, cylindrical, heavy-body shark. No anal fin, two spineless dorsal fins, the origin of the first set far posterior, originating behind the pelvic-fin origins. Denticles enlarged, tack-like, conspicuous and scattered over body and fins. Colour light to medium grey, grey-brown, brownish or blackish on the dorsal surface, often lighter below, sometimes with red or black spots or blotches on the body; fin edges blackish.

Diagnostic Features: Dermal denticles on body and fins in adults and large juveniles above 90 cm total length varying from small to very large, with many large, widely spaced, thorn or buckler-like denticles with bases not stellate and over a centimetre wide; some of these enlarge denticles are fused in groups of 2 to 10 and may form large plates over 25 mm across. Newborn specimens have no large plates and are densely covered with small and high denticles with narrow, semi-stellate bases. Ventral surface of snout and area around mouth with close-set small denticles in young, and large conspicuous denticles or thorns in larger juveniles and adults. Teeth similar in both jaws, cusps strongly oblique outwardly, with 1 to 3 lateral cusplets flanking a flat cutting edge; tooth row counts 20 to 26 upper jaw, 21 to 26 lower jaw. Vertebral
centra poorly calcified, primary double cones not calcified or weakly developed. Total vertebral count 102. Intestinal valve 12 to 16 turns. Maximum total length to about 310 cm . Colour: uniformly grey or brownish to black or grey-black, usually lighter ventrally; photophores absent.

Distribution: Wide ranging, but patchy distribution throughout the Atlantic, western Indian, and western Pacific oceans, and in the Mediterranean Sea. Eastern North Atlantic: Norway and Northern Sea, Scottish and Irish Atlantic slopes, south-west England, France, Spain, and Portugal, including the Azores. Western North Atlantic: North Carolina to Massachusetts.

Habitat: This bottom-dwelling shark may occur in shallow water, inshore in cold-temperate areas and in places with upwelling, but primarily it is a deep-water species, occurring on the continental and insular shelves and the upper slopes. It is encountered on continental slopes usually between 200 to 900 m , but may extend inshore in cold water to 18 m or less and possibly into the surfline.

Biology: Yolk-sac viviparity, with the number of young per litter ranging from 15 to 26 . Nothing is known of its reproductive cycle in the North Atlantic, but in Indian waters it may breed in


Fig. 53 Echinorhinus brucus
$\square$ Known distribution the spring months (Silas and Severaj, 1972). Its diet is primarily benthic and littoral bony fishes, smaller sharks (including Squalus acanthias), and crustaceans (including crabs).

Size: Maximum TL about 305 to 310 cm but most reports below 300 cm ; females adult at about 213 cm and larger, males adult at between 150 and 175 cm TL. Size at birth between 45 and 50 cm .

Interest to Fisheries and Human Impact: In the Eastern North Atlantic it is caught occasionally, as bycatch in bottom fisheries, but there is no catch information available for it. In the Western North Atlantic it is very rarely caught, even as a bycatch species.

The conservation status of this large, sluggish, poorly known shark is currently Data Deficient.
Local Names: Bramble shark, Spiny shark, Spinous shark, (England and USA); Bilan, Chenille, Bouclé, Requin bouclée, Squale bouclé, Mounge clavelat (France); Cassò, Pez clavo (Spain); Peixe prego, Prego, Tubarão-prego (Portugal); Bramble shark (Azores); Nagelhai (Germany); Tagghaj (Sweden); Braamhaai (the Netherlands).

Remarks: Late foetuses and small free-living Echinorhinus brucus ( 40 to 50 cm ) lack the large platelike denticles of juveniles ( 90 cm and larger) and adults.

Literature: Bonnaterre (1788); Smith (1849); Duméril (1865); Lo Bianco (1909); Bigelow and Schroeder (1948, 1957); Musick and McEachran (1969); Cadenat and Blache (1981); Compagno (1984); McEachran and Branstetter, in Whitehead et al. (1984); Springer in Quero et al. (1990); Bernardi and Powers (1992); Bianchi et al. (1993); Schwartz (1993); Santos, Porteiro, and Barreiros (1997); Hernandez et al. (1998); Hemida and Capapé (2002); Paul (2003a); Gibson et al. (2008); Ebert and Compagno (In press).

### 2.2.2 Family SQUALIDAE

Family: Genus or family Squalus Blainville, 1816, Bull. Sci. Soc. Philomat. Paris, (8): 121.
Type genus: Squalus Linnaeus, 1758.

## Number of Recognized North Atlantic Genera: 1.

FAO Names: En - Dogfish sharks; Fr - Squales; Sp - Galludos, Tollos.
Field Marks: Short-nosed, cylindrical body with no anal fin. Two dorsal fins with strong ungrooved spines. First dorsal fin with origin opposite or slightly behind the pectoral fins, second dorsal fin strongly falcate and with its origin opposite or well behind the pelvic-fin inner margins. Low, strong keels on the caudal peduncle. Caudal fin without a subterminal notch. Small to moderately large denticles with leaf-shaped, tricuspidate, lanceolate or cross-shaped crowns.

Diagnostic Features: Head moderately broad and flattened. Snout flat and broadly to narrowly rounded or angular in dorsoventral view. Spiracles large and close behind eyes. Fifth gill opening about as large as first four. Nostrils wide-spaced with internarial width greater than nostril width; anterior nasal flaps more or less bilobate, usually with short to greatly elongated medial barbels, these sometimes absent. Mouth nearly transverse and very short, with thin, non-papillose lips. Labial furrows short, not encircling mouth, confined to mouth corners but extending below eyes, and elongated posteriorly into postoral grooves. Labial folds thin. Teeth of both jaws compressed, low-crowned, broad and bladelike and forming a sawlike cutting edge with deep, imbricated series. Teeth not arranged in a quincunx pattern, are sharp-edged in both jaws, with an oblique compressed cusp, a distal blade, and no cusplets. Tooth rows 21 to 30 upper jaw, 19 to 27 lower jaw. Trunk cylindrical, and abdomen with or without inconspicuous lateral ridges. Interdorsal space elongated and greater than length of first dorsal base. Pelvic-caudal space elongated and several times length of pelvic-fin bases. Caudal peduncle cylindrical, elongated, and with lateral keels. Upper precaudal pits present in Squalus and absent or faintly indicated in Cirrhigaleus. Body without photophores. Denticles small to moderate-sized and pedicellate, with flattened, narrow to broad-keeled, leaf-shaped, lanceolate or cross-shaped crowns and low bases. Pectoral fins moderately high, angular, falcate or subtriangular, anterior margins moderately large and subequal or slightly greater than the prespiracular length, rear tips rounded to angular but not greatly elongated. Pelvic fins smaller than pectoral fins and first dorsal fin, and subequal to or smaller than second dorsal fin. Claspers with a lateral spine on the accessory terminal cartilage (T3) and a medial hook-like process on the dorsal terminal cartilage. Dorsal fins falcate-angular and with strong ungrooved spines. First dorsal fin large, with length somewhat less than or subequal to the prespiracular space. First dorsal-fin base over pectoral-pelvic space and origin over pectoral-fin bases, inner margins or just behind pectoral-fin rear tips. Second dorsal fin about as large as first dorsal fin or considerably smaller, with base behind pelvic-fin bases and origin varying from about over pelvic-fin insertions to well behind pelvic-fin rear tips. Caudal fin strongly heterocercal, with ventral lobe weakly to strongly developed in adults, and with subterminal notch absent. Vertebral counts: total vertebral counts 96 to 124, monospondylous vertebral counts 37 to 53 , diplospondylous precaudal counts 29 to 49 . Intestinal valve with 8 to 14 turns. Adults may be up to 180 cm and possibly to 200 cm , but mostly between 40 and 120 cm in total length. Colour: plain or with light or dark markings on fins and sometimes with white spots on body, without black photophore markings on tail or flanks.

Distribution: Globally the family Squalidae has an almost circumglobal range in boreal, temperate and tropical seas often in association with continents, islands, submarine peaks and ridges. Members of the Squalidae are known from all temperate seas and the tropics of the Western and Eastern Atlantic, the Indian Ocean, and Western-Central Pacific but apparently are absent from the tropical Eastern Pacific.

Habitat: Members of the Squalidae are found on continental and insular shelves and upper slopes near the bottom and in the water column, they also occur on submarine ridges and seamounts that extend to near the surface. They may range close inshore and in shallow bays in cool temperate waters but are usually demersal and well offshore in the tropics, where they may be mostly replaced in inshore habitats by small species of the families Carcharhinidae, Sphyrnidae, and other carcharhinoid families. Squalids are mostly demersal although some species have pelagic young that live well off the bottom in inshore and offshore continental waters (Squalus acanthias, S. megalops, and S. suckleyi). Some species occur near the bottom on seamounts far from land, and at least one species ranges into the epipelagic zone in the middle of the North Pacific. Squalids range in depth from the intertidal and near the surface of the epipelagic zone to 1446 m on the deep slope, with most species on the shelves and uppermost slopes down to about 600 m. Squalids overlap in habitat on the slopes with other, more deep-dwelling squaloids of the families Centrophoridae, Etmopteridae, Oxynotidae, Somniosidae, and Dalatiidae, but are apparently largely replaced by members of these families below 700 to 1000 m .

Biology: Several dogfish sharks are social, with some species apparently forming large to immense schools that are highly nomadic and migratory, moving locally and on regular annual migrations. Others are suspected of being solitary or occurring in small aggregations at most. All members of this family in which reproduction is known are viviparous with a yolk-sac, having one to 32 young in a litter. Some squalid species are very slow growing, maturing at over 30 years in age, and are very long-lived, up to 100 years in age. Squalids feed on a wide variety of prey, chiefly bony fishes, cephalopods and crustaceans but also other cartilaginous fishes and other invertebrates. Several species apparently feed communally, and may locally exhaust or drive away neritic prey species such as bony fishes. All species have powerful jaws with shear-
like cutting dentitions in both jaws and can dismember relatively large prey including fishes and cephalopods larger than themselves.

Interest to Fisheries and Human Impact: Dogfishes are taken in target fisheries and are often an important bycatch in mixed demersal fisheries targeting benthic and pelagic bony fishes. These sharks are primarily caught in bottom trawls, but also by deep-set longlines, bottom longlines, handlines, pelagic and demersal gill nets, seines, pelagic trawls, and fish traps. They are caught on rod and reel by sports anglers in some areas. Some dogfish species, particularly several Squalus species, are among some of the most important fisheries for elasmobranchs globally, and are rivalled only by some of the carcharhinoid families (Triakidae, Carcharhinidae, and Sphyrnidae), the skates (especially Rajidae), and the longtailed stingrays (Dasyatidae) in world fisheries catches. The flesh is used for human consumption which is prepared fresh, fresh-frozen, smoked, dried-salted, boiled-marinated, and as fish cakes. Other products prepared from dogfish include liver oil for vitamins (and potentially squalene), fishmeal, pet food, fertilizer and leather.
Dogfishes have supported some of the largest shark fisheries, particularly in the North Atlantic, over the past 60 years with catches for Squalus acanthias from 1950 to 2001 ranging from 20300 to 54150 tonnes, averaging 37066 tones. FAO catch trends from 2002 to 2009 showed an overall decline in dogfish landings in the North Atlantic from about 23300 tonnes in 2002 to about 9800 tonnes in 2009, an average of slightly over 14000 tonnes during this time. Part of this decline in landings was due to increasingly restrictive management measures.
Dogfishes can be a hazard to people who have to handle them since some species use their mildly toxic fin-spines and sharp teeth to defend themselves when captured and can inflict punctures or lacerations on unwary fishers. They also can cause damage to fishing gear while preying on the catch, and may drive away more desirable fisheries species. A few species are regularly kept in public aquaria for display in North America and Europe, and do reasonably well in captivity.

The conservation status of the group ranges from Data Deficient to Endangered depending on the species and in some cases the regional assessment will also vary due to local fishing practices.

Local Names: Dogfish, Dog sharks, Spurdogs, Spiny dogfish; Requins épineux (France); Chiao sha k'o, Kolyuchie akuli (Russia).

Remarks: The family consists of two genera, Squalus and Cirrhigaleus, which comprise 28 species. The Squalus is the more speciose genera with 27 species, a number likely to increase. The family is represented in the North Atlantic by the genus Squalus with three species recognized. However, the taxonomic status of one species is in question, and a regional revision of the group in the North Atlantic should be conducted with redescriptions of each species.

Literature: Garman (1913); Fowler (1941, 1968); Bigelow and Schroeder (1948, 1957); Garrick (1960a, 1961); Bass, D'Aubrey and Kistnasamy (1976), Chen, Taniuchi and Nose (1979); Cadenat and Blache (1981); Compagno (1984); Myagkov and Kondyurin (1986); Parin (1987); Muñoz-Chapuli and Ramos (1989a); Ebert et al. (2010); Ebert and Compagno (In press).

## Squalus Linnaeus, 1758

Genus: Squalus Linnaeus, 1758, Syst. Nat., ed. 10, 1: 233.
Type species: Squalus acanthias Linnaeus, 1758, by subsequent designation of Gill, 1862, Ann. Lyceum Nat. Hist. New York, 7(32): 405.

## Number of Recognized North Atlantic Species: 3.

Synonyms: Genus Squallus Scopoli, 1777: 464. Emended spelling for Squalus Linnaeus, 1758, according to Bigelow and Schroeder (1948: 452). Genus Acanthorhinus Blainville, 1816: 121 (genus Squalus Linnaeus, 1758). Type species: "Squalus acanthias Lacépède", $=\boldsymbol{S}$. acanthias Linnaeus, 1758, designated by Jordan (1919: 95). Genus Acanthias Leach, 1818: 62. Type species: Acanthias antiquorum Leach, 1818, by monotypy; a junior synonym of Squalus acanthias Linnaeus, 1758. Genus Acanthias Risso, 1826: 131. Type species: Squalus acanthias Linnaeus, 1758, by subsequent designation of Jordan and Evermann (1917:119), equivalent to Acanthias vulgaris Risso, 1826. Genus Acanthias Bonaparte, in Müller and Henle, 1837a: 115; also Bonaparte, in Müller and Henle, 1837b: 398 (no species mentioned); Bonaparte, 1838: 207. Proposed as a new name; type species: Squalus acanthias Linnaeus, 1758, by absolute tautonymy and monotypy. Genus Carcharias Gistel, 1848: x. Replacement name for Acanthias (probably of Risso, 1826), supposed by Gistel to be a junior synonym of Acanthia Fabricius, in Insecta; and hence taking the same type species, Acanthias vulgaris Risso, 1826, a junior synonym of Squalus acanthias Linnaeus, 1758. Not Carcharias Rafinesque, 1810 (Odontaspididae). Genus Acantias Vaillant, 1888: (c5) c13. Probably erroneous spelling, as correctly spelled in Vaillant (1888: 75). Subgenus Acantherinus (Blainville) Bigelow and Schroeder, 1948: 471. Error for Acanthorhinus Blainville, 1816.

Field Marks: Short to rather long snouts. Short anterior nasal flaps with very small medial barbels. Low bladelike cutting teeth in both jaws. Rather slender sharks, with lateral keels on caudal peduncle and a precaudal pit. Stout, ungrooved fin-spines on both dorsal fins, with second dorsal fin smaller than first. No anal fin, and caudal fin without a subterminal notch.

Diagnostic Features: Head flat and rounded angular to conical in dorsoventral view. Snout flattened and rounded to narrowly pointed and short to very elongated. Anterior nasal flaps with medial barbels variably developed but always short and narrow. Upper labial furrows longer, more than nostril width. Tooth counts 21 to 30 upper jaw, 19 to 27 lower jaw. Dermal denticles small, crowns of lateral trunk denticles in adults usually less than 0.5 mm long, with low, pedicellate, lanceolate or tricusped and triridged flat leaf-shaped crowns; skin smooth. Pectoral-fin free rear tips narrowly rounded to acutely angular. Pelvic fins low and obtusely triangular, with anterior margins about a third to one-half length of pectoral-fin anterior margins. Second dorsal fin smaller than first dorsal fin and with base length about three-fourths of first dorsal-fin base; second dorsal-fin origin usually behind free rear tips of pelvic fins, but occasionally over them. Caudal peduncle elongated and with dorso-caudal space much greater than second dorsal-fin base; upper precaudal pit prominently developed on caudal peduncle. Caudal fin with more or less slightly elongated, narrower dorsal lobe. Ventral caudal lobe strong; postventral caudal-fin margin usually deeply concave in adults. Vertebral counts: total vertebral counts 93 to 127, precaudal vertebral counts 67 to 93 , monospondylous vertebral counts 35 to 51 . Intestinal valve with 8 to 14 turns. Moderately large, adults up to 180 cm total length. Colour: blackish brown or greyish brown above, lighter below; fins plain or with conspicuous white and black margins or tips but usually without continuous broad white posterior margins.

Local Names: None.
Remarks: The present taxonomic arrangement of Squalus follows the recent work by Last, White, and Pogonoski (2007), and the various publications therein that volume, and Ebert et al. (2010) in recognizing 24 valid species worldwide. Three species are recognized in the North Atlantic, but some of these species including Squalus blainville and S. megalops may represent species complexes.

The below key to North Atlantic Squalus species is provisional pending a review and resolution of the S. blainville and $S$. megalops complexes.

## Key to North Atlantic Species:

1a. First dorsal fin more posteriorly situated on body, with fin origin usually behind or sometimes over pectoral free rear tips. Origin of first dorsal spine well behind pectoral free rear tips. Medial barbel minute or absent from anterior nasal flaps. Usually white spots present on sides of body (Fig. 54). . . . . . .

Squalus acanthias


a) LATERAL VIEW

b) UNDERSIDE OF HEAD

Fig. 55 Squalus megalops


UNDERSIDE OF HEAD
Fig. 56 Squalus blainville

## Squalus acanthias Linnaeus, 1758

Squalus acanthias Linnaeus, 1758, Syst. Nat., ed. 10, 1: 233. Possible syntypes (2): Linnaean Collection in Uppsala, no. 159 (alcohol), no. 160 (dried), according to Krefft and Tortonese (1973, in J. C. Hureau and T. Monod, eds., CLOFNAM. Check-list fish. NE Atlantic Mediterranean, 1:37). Type locality: "Habitat in Oceano Europaeo".

Synonyms: Squalus spinax Olavius, 1780: 562, pl. 7. A junior homonym of Squalus spinax Linnaeus, 1758. Squalus achantias Latreille, 1804: 72. Error for Squalus acanthias Linnaeus, 1758. Acanthias antiquorum Leach, 1818: 62. Holotype: No type material. According to Leach applies to "the piked dogfish of the fishermen", which is Squalus acanthias Linnaeus, 1758. Acanthias vulgaris Risso, 1826: 131. Apparently a replacement name for Squalus acanthias Linnaeus, 1758. Holotype?: 800 mm female mentioned, presumably from the Mediterranean Sea, but possibly not extant. No types known according to Eschmeyer (1998). Acanthias americanus Storer, 1846: 506. No type material, New York to Labrador and beyond. Several syntypes but whereabouts unknown according to Eschmeyer (1998). Acanthias linnei Malm, 1877: 624. Apparently a replacement name for Squalus acanthias Linnaeus, 1758, as this name is listed in synonymy.

Other Combinations: Acanthias acanthias (Linnaeus, 1758), Squalus (Acanthorhinus) acanthias Linnaeus, 1758, Spinax acanthias (Linnaeus, 1758), Spinax vulgaris (Risso, 1826).

FAO Names: En - Picked dogfish; Fr - Aiguillat commun; Sp - Mielga.


Fig. 57 Squalus acanthias

Field Marks: A moderate-sized to very large dogfish, with a moderately long, narrow, angular or subangular snout. Preoral length about 1.1 to 1.4 times mouth width, with oblique-cusped cutting teeth in both jaws. Pectoral fins narrow and falcate or semifalcate, with straight to concave posterior margins. Somewhat slender body, with two unequal-sized dorsal fins with ungrooved, strong spines. First dorsal fin fairly long and low, with fin origin usually behind pectoral-fin rear tips and fin spine origin always behind them. First dorsal-fin spine slender and very short. No anal fin, and no subterminal notch on caudal fin. Upper precaudal pit and lateral keels on caudal peduncle. White spots usually present on sides, and dorsal fins with dusky fin edges in adults, black in young. No blackish bar along caudal-fin base, caudal web dusky, ventral caudal-fin lobe not black.

Diagnostic Features: Moderately broad head, with oblique distance from snout tip to orbit subequal to interorbital space. Snout is subangular, pointed, narrow, and moderately long. Preoral length about 1.1 to 1.4 times mouth width; preorbital length about 1.5 to 2.0 times eye length. Diagonal distance from snout tip to excurrent aperture of nostril slightly greater than or approximately the same length as that from excurrent aperture to anterior end of upper labial furrow. Eyes about equidistant between snout tip and first gill openings or slightly closer to snout tip. Nostrils are usually slightly nearer snout tip than mouth. Anterior nasal flap with medial barbel is minute or absent. Teeth with a single oblique cusp, blade-like, and similar in both the upper and lower jaws; tooth counts 26 to 30 upper jaw, 22 to 24 lower jaw. Lateral trunk denticles small, with crowns of adult denticles less than 0.5 mm long. Denticle crowns narrow, lanceolate or cross-shaped in young, but broad and leaf-shaped in adults; crowns with scalloped (young) to convex (adults) anterior margins, a medial cusp and two lateral cusps in adults (lateral cusps absent in young), and a medial keel and two lateral keels in adults (lateral keels absent in young). A fairly slender bodied shark, with pectoral fins narrow and falcate or semifalcate, posterior margins weakly to moderately concave, free rear tips narrowly rounded, and inner margins about 1.8 to 2.7 in pectoral anterior
margins. Pelvic midbases closer to second dorsal-fin base than to first. First dorsal fin more posteriorly situated, with origin over or usually behind pectoral-fin free rear tips. First dorsal fin low in height, usually less than 0.5 (but sometimes up to 0.7 ) of its length, with anterior margin low and oblique. Second dorsal fin with height less than $5 \%$ of total length. Dorsal-fin spines slender, tapering gradually towards tip. First dorsal-fin spine low, with length of anterior margin of exposed spine less than 0.33 of fin base; spine tip falling far below apex of fin; spine origin behind pectoral-fin free rear tips. Second dorsal-fin spine with tip approximately the same height or slightly higher than fin apex; spine anterior margin less than $5 \%$ of total length; spine narrow-based with anterior margin over four times its base length. Caudal fin short, with an elongated, lanceolate dorsal lobe. Vertebral counts: total vertebral counts 109 to 116 (average $=112$ ), precaudal vertebral counts 68 to 85 , monospondylous vertebral counts 40 to 48 . Spiral valve turn counts 12 to 13 . Size of adults may vary depending on the population and whether they are referable to this species, but most are smaller than 130 cm . Colour: grey or bluish grey above and lighter to white below. Sides of body usually with a conspicuous line of white spots or dashes (occasionally absent in large adults). Pectoral fins dusky above with light posterior margins in adults, but with black proximal web and broad white posterior margin in young. Dorsal fins plain or with dusky tips in adults, with conspicuous black apices and white posterior margins and free rear tips in young. Caudal fin with a dusky proximal web, a lighter base, dark dorsal and terminal edges, and light lower postdorsal margin in adults; young with conspicuous black proximal web and terminal lobe, white upper postventral margin, white ventral caudal-fin lobe, and a black patch at subcaudal notch. No conspicuous bar on lower edge of caudal-fin base or black patch on apex of ventral lobe.

Distribution: Widespread and common on both sides of the North Atlantic. Eastern North Atlantic: Iceland, the Barents Sea, Murmansk Coast and White Sea (Russia) to Norway, Sweden, Denmark (rarely in the western Baltic Sea), Germany, the Netherlands, Belgium, Orkneys, Faroe Islands, Scotland, England and Wales, Ireland, France, Portugal, possibly the Azores, Spain, Morocco, the Canary Islands, Madeira Islands, Mauritania, Western Sahara, and Senegal; throughout the Mediterranean and Black Seas. Western North Atlantic: Western Greenland, Canada (Labrador, Newfoundland, New Brunswick, Nova Scotia) and USA (Maine south to Florida with records from Maine, New Hampshire, Massachusetts, Rhode Island, New York, New Jersey, Delaware, Virginia, North and South Carolina, Georgia, and Florida to the Dry Tortugas), Cuba, and Bahamas. Elsewhere, antitropical with apparent isolated populations or subpopulations of uncertain taxonomic status in the South Atlantic, and the South Pacific.


Fig. 58 Squalus acanthias
Habitat: The picked dogfish is found in boreal to warm-temperate waters, from inshore and offshore demersal and apparently epipelagic zones, continental and insular shelf waters. It occurs from the surface down to the bottom, possibly to 1446 m on the deep slopes, but mostly on the shelf and upper slope above 600 m . It usually occurs on or near the bottom in continental waters and near the surface in oceanic waters. Squalus acanthias gives birth in some areas in deep water on the outer shelves and uppermost slopes, and the young range in depth from the bottom to near the surface.
It is is caught on a variety of substrates on the continental shelf, and may also be found in sea lochs, bays and outer limits of estuaries (although it seems to have a low tolerance for reduced salinities). It may tolerate exposures to brackish water but apparently cannot survive fresh water for more than a few hours and may not regularly occur there.

Biology: This shark is viviparous with a yolk-sac, and with litters of 1 to 32 young. In general, larger mother sharks have larger litters of fetuses that attain a larger size before birth than smaller ones. There is also regional variation in reported litter sizes, for example the north-east Atlantic stock produces up to 21 pups. The gestation period is generally reported as 18 to 24 months, and may vary in different areas, with a period as short as 12 months. Mating of dogfish may occur in the winter with birth primarily during the cold months of the year, however there is considerable variation with some young produced in spring and summer. The sex ratio at birth is 1:1.

Age of picked dogfish is commonly determined by counting annual growth rings on the exterior of the fin spines, though wear of the spines in large specimens may limit the usefulness of this method. Tetracycline has been used to validate the spine rings as being annual, and spine rings have also been studied by sectioning. This is apparently a slow growing and maturing species that is very long-lived. Ages at maturity may vary markedly in different regions and populations, and has been variously reported as 10 to 20 years for females and 11 or more years for males. Based on tag returns, maximum age is at least 40 years.
This shark is a powerful, voracious predator that feeds primarily on bony fishes, and is capable of dismembering rather large prey with its strong jaws and clipper-like teeth. It is thought to prey on most available bony fishes smaller than itself, and will often prey heavily on abundant schooling fishes, but newborn picked dogfish are known to attack herring larger than themselves, as adults do to cod and haddock. They often scavenge fish caught on longlines and in seines. The invertebrate prey of this species include squid (ommastrephids and other families), octopuses, crabs, natantid shrimps, amphipods, euphausiid shrimps, sea snails (gastropods), scallops, polychaete worms, sea cucumbers (Holothuria), jellyfish and comb jellies. In the Western North Atlantic these sharks may feed very little in the winter in their deepwater wintering grounds as judged by their thinness when they return to shallow water. Predators on the picked dogfish include larger bony fishes, sharks, and cetaceans.
The picked dogfish forms immense feeding aggregations, packs or schools in rich foraging grounds and may be present in thousands or even millions. Longline sets of 700 to 1500 hooks with nearly every hook bearing a picked dogfish have been reported from the Western North Atlantic. This species often occurs in schools segregated by size and sex, including those of small juveniles of both sexes in equal numbers, mature males, larger immature females, and large mature females. Mixed schools of adults have also been reported, but at best these are probably less common than segregated schools. These schools are dense and localized in a given area, and move erratically over short periods of time, possibly reflecting pursuit of schooling prey fishes. In general, males occur in shallower water than females, with the exception of large pregnant females.
Much has been written of the seasonal, bathymetric, and localized movements of this shark. An important correlate of its movements seems to be water temperature; the sharks prefer a temperature range with a minimum of 7 to $8{ }^{\circ} \mathrm{C}$ and maximum of 12 to $15^{\circ} \mathrm{C}$, and apparently make latitudinal and depth migrations to stay within their optimum range. Thus in the Western North Atlantic, they move inshore from their wintering grounds in deep water off the middle US Atlantic and southern States as the water warms in spring, pressing northwards along the coasts of Newfoundland and Labrador and southwards along the US Atlantic coast occasionally to Cuba. As the water warms in the south over the optimum in late spring and summer, they apparently retreat into deep water, reappear coastally in autumn as the water temperature descends to optimum, and disappear into deep water when the surface temperature goes below optimum. In the northern part of their range in the Western North Atlantic, large females appear first inshore, followed by adult males. There may be unseasonal invasions of dogfish inshore during the winter for unknown reasons.
Tagging studies off the British Isles suggests separate winter migrations of stocks to the Irish Sea and the Norwegian coast and a return and mixing of these stocks on fishing grounds northwest of the British Isles in summer.

Size: Maximum total length varies regionally, but in the North Atlantic about 121 cm ; males mature from 52 to 70 cm with a maximum length of about 95 cm ; females mature at 66 to 82 cm , with a maximum length of about 122 cm . Size of young at birth is 18 to 30 cm .

Interest to Fisheries and Human Impact: This is possibly the single most important species of shark for targeted and utilized bycatch fisheries because of its abundance, utilization in various commercial fisheries (particularly in the North Atlantic), easy access by recreational anglers, and damage it causes to gear and catches of other fishes. It has been heavily fished in the Western North Atlantic off the United States and Canada, and currently supports a sizeable fishery in the Eastern North Atlantic. Between 2000 and 2009 the yearly catch of North Atlantic picked dogfish declined each year from about 33000 tonnes in 2000 to 9900 tonnes in 2009, with an annual average landing of 17800 tonnes (FAO Fishstats). Cumulative catches of Eastern North Atlantic Squalus acanthias averaged 12000 tonnes between 2000 and 2009 (range 4000 to 22000 tonnes). However, actual Eastern North Atlantic catches are probably far higher, as several countries report this species under 'dogfish sharks', 'dogfish sharks, etc.', and 'dogfishes and hounds' to FAO, which may also include Scyliorhinus, other Squalus species, and other small demersal sharks. Reported catches of $\boldsymbol{S}$. acanthias in the Western North Atlantic have been much less than the Eastern North Atlantic, averaging 5900 tonnes annually between 2000 and 2009 (range 3700 to 12000 tonnes).
The picked dogfish is captured primarily in bottom trawls, gillnets and with longlines and handlines, but is also commonly taken with seines, fish traps, and other gear. It is often caught with rod and reel by recreational anglers in the United States, the European Community including the United Kingdom, and probably elsewhere. It is utilized fresh, fresh-frozen, smoked, boiled-marinated, dried-salted, and in the form of fish cakes for human consumption. The fins are also used for soup-base. It is under TAC regulation in EU (in 2012, TAC=0). If accidentally caught this species should not be harmed and specimens shall be promptly released (EU, 2010). Under TAC regulation in Canada and USA and finning prohibited (2012). Directed fisheries banned in Norway (2012).

The picked dogfish can curl itself and whip its tail about to inflict wounds with the long, sharp, second dorsal spine. The toxin is mildly irritating to most people, but some people can have a strong allergic reaction to it and may require medical attention. With care to minimize capture trauma and with a sufficiently large and appropriately shaped aquarium, it is an attractive public exhibit and is kept by various aquaria in the United States, Canada and Europe. It is also kept in research aquaria to study its physiology and biochemistry.

The global conservation status of Squalus acanthias is Vulnerable, but in the Eastern North Atlantic it is considered Critically Endangered due to steep declines in its population. Included in Appendix II of the Convention on Migratory Species.

Local Names: Spiny dogfish or Dog fish, Spotted spiny dogfish, Dogfish, Common spiny dogfish, Pacific spiny dogfish, Piked dogfish, Piked shark, Picked dogfish, Spiky jack, Grayfish, Spiked dogfish, Spined dogfish or dog fish, Whitespotted dogfish, Spurdog, Horned dogfish, Bonedog, Skittle-dog or Skittle dog, Cod shark, Codfish shark, Thornback shark, Victorian spotted dogfish, Rock salmon (England); Ci pigog, Picewd (Wales); Cu maire, Sea dog (Scotland); Cu maire, Gobag, Biorach, Fiógach (Ireland); Hoe (Orkneys); Pighaj (Denmark); Háfur (Iceland); Dornhai (Germany); Doorn haai (the Netherlands); Spoorhai, Speerhai (Belgium); Havúr (Faroe Islands); Haakatt, Hafskatt, Haaa Haafisk, Pigghaa, Pigghaj (Sweden); Pigghå (Norway); Aiguillat, Aiguillat tacheté, Bilan, Epinette, Chien broquu, Chien de mer, Chien de mer epineux (France); Aguilat, Agullat, Ahullat, Casso, Farró, Guissona, El ferron, Jérron, Quelve, Quisona (Spain); Cação galhudo, Malhado melga (Portugal); Galludo (Canaries); Spurdog, Spiny dogfish (Azores); Koljuchaja akula (Russia).

Remarks: The North Pacific spiny dogfish has recently been distinguished as a separate species, Squalus suckleyi(Ebert et al. 2010) from $\boldsymbol{S}$. acanthias species from elsewhere. This is not surprising given that the life history characteristics of these two species are strikingly different.

Literature: Bigelow and Schroeder (1948, 1957); Holden and Meadows (1962); Templeman (1963); Holden (1968, 1973, 1974, 1977); Wheeler (1978, 1991); Cadenat and Blache (1981); Compagno (1984); McEachran and Branstetter in Whitehead et al. (1984); Muñoz-Chapuli and Ramos (1989a); Santos, Porteiro and Barreiros (1997); Ellis et al. (2005); Hammond and Ellis (2005); Campana et al. (2006a); Fordham et al. (2006); Ward et al. (2007); Ellis and Keable (2008); Gibson et al. (2008); Pawson, Ellis, and Dobby (2009); Ebert et al. (2010); EU (2010); ICES (2010); Ebert and Compagno (In press).

## Squalus blainville (Risso, 1827)

Acanthias blainville Risso, 1827, Hist. nat. Princip. Prod. Europe Méred, Paris, Poissons: 133, pl. 3, Fig. 6; plate legend, p. 478 as Acanthias blainvillii. No type material available, according to Krefft and Tortonese, In J. C. Hureau and T. Monod (eds.), CLOFNAM. Check-list fish. NE Atlantic Mediterranean, 1: 38, and Eschmeyer (1998, Cat. Fish.).

Synonyms: Uncertain.
Other Combinations: Squalus fernandinus, not Molina, 1782 (= Squalus acanthias Linnaeus, 1758); Squalus blainvillii or $\boldsymbol{S}$. blainvillei (variant and emended spellings of $\boldsymbol{S}$. blainville).

FAO Names: En - Longnose spurdog; Fr - Aiguillat coq; Sp - Galludo.


Fig. 59 Squalus blainville



NOSTRIL

Field Marks: A large dogfish species with a wide head. Moderately long, rounded-parabolic mouth. Preoral length about 1.0 to 1.3 times mouth width. Oblique-cusped cutting teeth in both jaws. Stocky to moderately slender body. Pectoral fins are broad, semifalcate and with slightly concave posterior margins. Two unequal-sized dorsal fins with ungrooved high spines. First dorsal fin very high and short, with slender and very tall spine with spine origin over pectoral inner margins. No anal fin or subterminal notch on caudal fin. Upper precaudal pit and lateral keels on caudal peduncle. No white spots on sides, dorsal fins without conspicuous dark markings, dusky edges and tips, caudal fin without conspicuous dark markings.

Diagnostic Features: Broad head with oblique distance from snout tip to orbit less than interorbital space. Moderately long, rounded-parabolic mouth. Preoral length about 1.0 to 1.3 times mouth width. Preorbital length less than twice eye length. Diagonal distance from snout tip to excurrent aperture of nostril greater than that from excurrent aperture to anterior end of upper labial furrow. Eyes nearer the snout tip than the first gill openings. Nostrils closer to snout tip than mouth; anterior nasal flap with rather large medial barbel. Teeth with a single, smooth-edged, bladelike cusp, imbricated; upper and lower teeth similar in shape; tooth counts 27 upper jaw, 23 lower jaw. Lateral trunk denticles large but size of crowns uncertain; crowns broad and leaf-shaped in adults, with convex anterior margins, a medial cusp and keel, and two lateral cusps and keels. Fairly stout body with pectoral fins broad and semifalcate, with posterior margins slightly concave, and free rear tips narrowly rounded. Inner margins about 1.8 to 2.0 in pectoral anterior margins. Pelvic midbases about equidistant between first and second dorsal bases. First dorsal fin more anteriorly situated, with fin origin about over pectoral insertions or just behind them. First dorsal fin very high with height over $0.75 \%$ of its length, with anterior margin low and oblique. Second dorsal fin with height more than $6 \%$ of its total length. Dorsal-fin spines slender, tapering gradually towards tip. First dorsal-fin spine high; length of anterior margin of exposed spine nearly or as long as fin base and spine tip falling a short distance below apex of fin. Spine origin over pectoral-fin inner margins and well in front of their rear tips. First dorsal-fin spine anterior margin subequal to that of second dorsal-fin spine. Second dorsal-fin spine with tip slightly higher than fin apex; spine anterior margin usually more than $6 \%$ of total length. Spine narrow-based with anterior margin over four times its base length. Caudal fin moderately long, 4.2 to 4.9 times in total length, with an elongated, lanceolate dorsal lobe. Vertebral counts: total vertebral counts 118 to 125 , precaudal vertebral counts 88 to 90 , monospondylous vertebral counts 44 to 46 (Atlantic and Mediterranean Sea specimens). Size of adults up to between 80 and 100 cm long. Colour: grayish brown above and lighter below with no white spots on sides of body. Pectoral fins dusky above with light posterior margins. Dorsal fins with white edges. No conspicuous dark markings on dorsal or caudal fins.

Distribution: Eastern Atlantic: Bay of Biscay to Mediterranean (Mediterranean coast of France type locality) and Black Seas, Morocco, Canaries, Senegal, to the Congo and possibly Namibia but probably based on a different species. Absent from the Western Atlantic. Records of Squalus blainville from the Eastern South Atlantic, Western Indian Ocean, Western and Central Pacific, and Eastern South Pacific are based in large part on S. mitsukurii or close relatives. Western North Pacific records of this species are attributable to an undescribed highfin species currently under investigation (W.T. White, pers. comm.).

Habitat: Squalus blainville is nominally recorded from the continental shelves and upper slopes, at or near the bottom at depths of 16 to at least 440 m and probably deeper.

Biology: Details of the biology of this shark are uncertain because of taxonomic problems. Viviparous with yolk-sac, litters of 1 to 9 ( 1 to 6 in the Eastern Mediterranean Sea), with a two year reproductive cycle. Although a recent study in the eastern Mediterranean Sea found a continuous reproductive cycle. Females mature at about 5.1 years and males at 3.3 years in the Mediterranean. The maximum estimated age for this species is 13.5 years for females and 12.8 years for males, with a possible maximum age of 15 years. The diet of Squalus blainville includes a variety of bony fishes, as well as crabs, lobsters, and octopuses. In the Eastern North Atlantic and Mediterranean nominal S. blainville is reported to form large schools.

Size: Maximum total length is about 92 cm for females and 80 cm for males; males adult at 43 to 56 cm , females possibly adult at 52 to 56 cm , but size uncertain due to confusion with other Squalus species occurring within its range in the Eastern North Atlantic and Mediterranean Sea. Size at birth between 19 and 22 cm .

Interest to Fisheries and Human Impact: Interest to fisheries uncertain since sharks referred to Squalus blainville are common in the temperate to tropical Eastern Atlantic and Mediterranean and are fished there with bottom trawls, gillnets and line gear. This shark is mostly caught in the southern portion of ICES Subarea IX as part of a mixture of
several, possibly two or three, different Squalus species including high and low-finned species of the $\boldsymbol{S}$. megalops and $\boldsymbol{S}$. mitsukurii groups. It is uncertain whether the eastern North Atlantic population is part of the same population occurring in the Mediterranean. These sharks are utilized fresh, dried salted and smoked for human consumption, but are of limited importance in comparison to S. acanthias.

In the Mediterranean, this shark represents about $3 \%$ (about 1500 mt ) of the mean total biomass of elasmobranchs caught in fisheries. It ranks $12^{\text {th }}$ overall in elasmobranch abundance in the Mediterranean. However, catch data are unreliable, and likely underrepresented, as Squalus blainville is usually taken as part of a mixed species complex in the Mediterranean and it is not usually separated out and reported to species.

The conservation status of this species is currently considered to be Data Deficient since two or three different species may be involved in the Eastern Atlantic. As


Fig. 60 Squalus blainville
Known distribution discussed in the 'Remarks' section this species or species complex is in need of a critical revision with the designation of a type specimen and a redescription.

Local Names: L'aigullat de blainville, Aguiat, Mangin (France); Agullat, Agulat, Ahullat, Galluate, Galludo, Pinchuo, Quisona (Spain); Ferrânho, Galhudo, Melga de ferrâo (Portugal). It is likely that several of these names are based on Squalus mitsukurii-like or S. megalops-like dogfishes.

Remarks: The status of this widely cited species is uncertain at present and as of this writing, Squalus blainville remains somewhat an enigma since it was inadequately described, is currently without types, and has been identified by various authors as two or possibly three different species in the Eastern North Atlantic and Mediterranean and possibly as more species elsewhere. Despite detailed morphological comparisons of Eastern Atlantic dogfish (S. blainville and S. megalops) by Muñoz-Chapuli and Ramos (1989a), and others, much still remains unanswered as to what Squalus species exactly constitutes $S$. blainville. Ebert and Compagno (In press) provide a detailed overview on the checkered taxonomic history of this species.

Literature: Lozano y Rey (1928); Bigelow and Schroeder (1948, 1957); Poll (1951); Cadenat (1957); Compagno (1984); Muñoz-Chapuli and Ramos (1989a); Cannizzaro, Rizzo, Levi, and Gancitano (1995); Sion et al. (2003); Ebert, Serena, and Mancusi (2008b); Gibson et al. (2008); Serena et al. (2009); ICES (2010); Kousteni and Megalofonou (2011); Ebert and Compagno (In press).

## Squalus megalops (Macleay, 1881)

Acanthias megalops Macleay, 1881, Proc. Linn. Soc. New South Wales, 1882 (Feb. 23, 1881), 6(2): 367, also Descr. Cat. Australian Fish. 2: 303. Type specimens not mentioned, type locality "Port Jackson" [= Sydney Harbor, Australia]. Holotype: Australian Museum, Sydney, AMS I.16255-001 according to Paxton et al. (1989) and Eschmeyer (1998, Cat. Fish.).

Synonyms: ?Squalus uyatus Rafinesque, 1810, Sicily, Mediterranean Sea.
Other Combinations: Squalus blainville, not Risso, 1826, S. fernandinus, not Molina, 1782, Acanthias vulgaris, not Risso, 1826.

FAO Names: En - Shortnose spurdog; Fr - Aiguillat nez court; Sp - Galludo ñato.


Fig. 61 Squalus megalops

Field Marks: A small species with a wide head, a short, broad, rounded-parabolic snout. Preoral length about 1.2 to 1.4 times mouth width, with oblique-cusped cutting teeth in both jaws. Body moderately slender. Pectoral fins broad and falcate, with moderately concave posterior margins. Two unequal-sized dorsal fins with ungrooved high spines. First dorsal fin moderately high. First and second dorsal-fin spines slender, first dorsal-fin spine low and gradually tapering with origin over pectoral-fin inner margin. No anal fin. Upper precaudal pit and lateral keels on caudal peduncle, and no subterminal notch on caudal fin. No white spots on sides, dorsal fins with blackish tips and edges but not conspicuous blotches. No blackish bar along caudal-fin base; caudal fin with dusky web and a white posterior margin. Ventral lobe with a white posterior margin and not black-tipped. Dark blotch at subcaudal notch.

Diagnostic Features: Head broad, with oblique distance from snout tip to orbit less than interorbital space. Snout subangular, slightly pointed, fairly broad, and moderately long. Preoral length about 1.2 to 1.4 times mouth width. Preorbital length subequal to eye length in adults. Diagonal distance from snout tip to excurrent aperture of nostril much less than that from excurrent aperture to anterior end of upper labial furrow. Eyes closer to snout tip than first gill openings. Nostrils closer to snout tip than mouth. Anterior nasal flap with a small medial barbel, bifurcate. Body moderately slender. Lateral trunk denticles small, crowns in adults less than 0.5 mm long; crowns narrow, lanceolate or cross-shaped in adults, with deeply scalloped anterior margins, a medial cusp but no lateral cusps, and a medial keel but no lateral keels. Pectoral fins fairly broad but falcate; posterior margins moderately concave; rear tips angular and pointed, sometimes narrowly rounded; inner margins 1.2 to 1.5 in pectoral-fin inner margins. Pelvic-fin midbases closer to first dorsal-fin base than second. First dorsal fin anteriorly situated, with fin origin over pectoral-fin inner margins; first dorsal fin moderately high, height about half its length, anterior margin low and oblique. Second dorsal fin with height less than $5 \%$ of total length. Dorsal-fin spines slender, tapering gradually towards tip. First dorsal-fin spine moderately high, length of anterior margin of exposed spine about 0.3 to 0.5 of fin base; spine tip falling well short of apex of fin; spine origin over pectoral-fin inner margins and well in front of their rear tips; spine anterior margin shorter ( 0.75 or less) than that of second dorsal-fin spine. Second dorsal-fin spine with tip about as high as fin apex; spine anterior margin less than $5 \%$ of total length; spine narrow-based with anterior margin over four times its base length. Caudal fin short, 4.7 to 5.1 in total length, with an elongated, lanceolate dorsal lobe. Vertebral counts (based on Eastern North Atlantic form): total vertebral counts not available, precaudal vertebral counts 78 to 82 , monospondylous vertebral counts 38 to 41 . Size of adults small, 34 to 77 cm long. Colour: light grey-brown to dark brown above, lighter below. No white spots on sides of body. Pectoral fins dusky above with light posterior margins. Dorsal fins with black tips and white posterior margins and rear tips but these are often inconspicuous in adults or may be lacking. Caudal fin with light dorsal margin, dark web on hypural and epural lobes; dusky terminal margin, broad white lower postventral margin and narrower white upper postventral and terminal margin, and sometimes a darker bar on dorsal edge of fin base.

Distribution: Eastern Atlantic and Mediterranean: Southern Portugal, Spain south to Mauritania, Alboran Sea, Western Mediterranean, Guinea, Gabon to Angola, Namibia, and South Africa (Western and Northern Cape Provinces). Absent from the Western Atlantic. Elsewhere, this or a similar species occurs in the Western Indian Ocean, Western Pacific, and along the south Australian coast.

Habitat: A common to abundant small species of temperate and tropical seas, found on the inner and outer continental shelves and upper slopes. Generally found on or near the bottom at depths from close inshore and the intertidal down to 732 m .

Biology: Viviparous with a yolk-sac, with the number of young per litter ranging from 1 to 6 , but generally 2 or 3 . The gestation period is uncertain, although it has been estimated as two years. Adult females are apparently continuously reproducing, without a gap between pregnancies. Age at maturity for the Eastern Central Atlantic population has been estimated for males and females at between 4 and 15 years, with a maximum age estimate of 26 years for males and 32 years for females. The high degree of variation in the age and size at maturity suggests that either multiple species may be involved or different regional subpopulations occur within this species.

This shark eats a variety of bony fishes and on rare occasions also eats other elasmobranchs, including


Fig. 62 Squalus megalops
 torpedo rays (Torpedo, Torpedinidae), eagle rays (Myliobatis, Myliobatidae), and skates (Rajidae, this and the previous batoids possibly scavenged), but apparently does not cannibalize its own young. Invertebrate prey includes a variety of crustaceans such as amphipods (Amphipoda), mysid shrimp (Mysidacea), manis shrimps (Stomatopoda), crabs (Mersia and Goneplax, Brachyura), carid and penaeid prawns, and hermit crabs (Anomura); molluscan prey includes sea hares (Aplysia, Gastropoda), squid (Loligo, Loliginidae), octopods, and cuttlefish (Sepia, Sepiidae); other invertebrates include brittle stars (Ophiuroidea) and especially bristleworms (Polychaeta), which are common prey items.
This is a social shark that often forms large, dense schools where it occurs.
Size: Maximum total length for both sexes about 77 cm , though most are smaller than 65 cm . Males mature at about 34 to 51 cm , females at 37 to 66 cm . Size at birth about 23 to 28 cm .

Interest to Fisheries and Human Impact: This shark is common to very abundant where it occurs, and may be taken in substantial quantities in bottom trawls. In the Eastern North Atlantic it is possibly taken as part of a species complex that may include two or three species. As discussed below in the 'Remarks' section Squalus megalops in the Eastern North Atlantic may represent a different species than what occurs in Australian and South African waters. Landing of this species are not reported to ICES since it is caught in low numbers and is not separated from other Squalus species.
The conservation status of this species is Data Deficient due to taxonomic uncertainty.
Local Names: None.
Remarks: The taxonomic status of this species as presented here is provisional, and Squalus megalops sensu lato appears to be a species complex rather than a single species with a very wide-range that spans the Eastern Atlantic and Indo-West Pacific. Last, Edmunds, and Yearsley (2007) and Last and Stevens' (2009) stated that typical S. megalops is possibly an Australian endemic, with very similar nominal megalops-like species from off southern Africa, the Eastern North Atlantic, and the Western North Pacific. Muñoz-Chapuli and Ramos (1989a) discussed the classification of S. megalops in the Eastern Atlantic, and presented northern range extensions of the species from Mauritania to Portugal and from the Western Mediterranean. However, members of the $\boldsymbol{S}$. megalops group from southern Africa have been distinguished as a separate species: $\boldsymbol{S}$. acutipinnis following Regan (1908). If found to be true and $\boldsymbol{S}$. acutipinnis is eventually determined to be a valid species it would open up the question as to the status of Squalus cf. megalops from the Eastern North Atlantic. Representatives of this species complex are in need of critical taxonomic evaluation with regards to their status.

Literature: Macleay (1881); Regan (1908, 1921); Bigelow and Schroeder (1957); Compagno (1984); Myagkov and Kondyurin (1986); Parin (1987); Muñoz-Chapuli and Ramos (1989a); Fischer et al. (1990); Springer in J.-C. Quero et al. (1990); Bianchi et al. (1993); Cavanagh and Lisney (2003); Gibson et al. (2008); Last and Stevens (2009); Pajuelo et al. (2011); Ebert and Compagno (In press).

### 2.2.3 Family CENTROPHORIDAE

Family: Centrophoroidei Bleeker, 1859, Act. Soc. Sci. Ind. Neerl. 4(3): xii.
Type genus: Centrophorus Müller and Henle, 1837

## Number of Recognized North Atlantic Genera: 2.

FAO Names: En - Gulper sharks; Fr - Squales-chagrins; Sp - Quelvachos.
Field Marks: Short to long-nosed, cylindrical to somewhat compressed sharks with no anal fin. Denticles small to large and variable in shape, with leaf-shaped, tricuspidate or polycuspidate crowns and slender pedicels, high pitchfork-shaped erect crowns on high pedicels, or low ridged sessile crowns. No keels on the caudal peduncle. Two dorsal fins with strong grooved spines; first dorsal fin with origin usually opposite the pectoral-fin bases or pectoral inner margins and exceptionally just behind the pectoral-fin free rear tips; second dorsal fin not falcate and with its origin usually opposite the pelvic-fin bases or inner margins, but exceptionally somewhat behind the pelvic-fin free rear tips. Caudal fin with a strong subterminal notch.

Diagnostic Features: Head moderately broad to narrow and somewhat flattened. Snout flat and narrowly rounded to elongate-rounded in dorsoventral view. Spiracles large, close behind eyes. Fifth gill opening about as large as first four. Nostrils wide-spaced with internarial width greater than nostril width. Nostrils with simple anterior nasal flaps and no medial barbels. Mouth nearly transverse and very short, with thin, non-papillose lips. Labial furrows short, not encircling mouth, confined to mouth corners but extending anteriorly to below eyes, elongated posteriorly into postoral grooves and sometimes anteromedial preoral grooves (Deania); thin labial folds. Teeth with dignathic heterodonty well developed, upper teeth much smaller than lowers. Teeth of both jaws moderately compressed, high-crowned, broad-based and bladelike; upper teeth not imbricated or weakly so, with broad high roots that are closely adjacent and sometimes overlapping and not forming a quincunx pattern; lower teeth forming a deep, strongly imbricated series and a continuous sawlike cutting edge; all teeth with a compressed cusp, a distal blade, sometimes a medial blade, and no cusplets; upper cusps narrow, erect to oblique, and broad-based; lower cusps oblique to semierect. Tooth rows 22 to 45 upper jaw, 24 to 35 lower jaw; upper teeth usually somewhat more numerous than lowers (averaging 1.2:1). Trunk cylindrical or slightly compressed, abdomen without lateral ridges. Interdorsal space elongated and usually greater than length of first dorsal base but subequal to or slightly longer than it in a few species. Pelvic-caudal space moderately long and about two or three times pelvic bases. Caudal peduncle slightly compressed, short to moderately elongated, and without lateral keels or precaudal pits. Body without photophores. Denticles moderate-sized and pedicellate or sessile, when pedicellate having flattened, narrow to broad-keeled, leaf-shaped (Centrophorus) or pitchfork-like (Deania) crowns, slender pedicels and low bases. Pectoral fins low, angular or rounded, and not falcate; anterior margins moderately large and about 0.5 to 1.2 times the prespiracular length; pectoral-fin rear tips rounded and short to angular and greatly elongated. Pelvic fins smaller than pectoral and first dorsal fins, and subequal to or smaller than second dorsal fin. Claspers with a lateral spine only (Centrophorus), or with no spine (Deania). Dorsal fins large, broad, angular or rounded-angular but not falcate, with strong grooved spines. First dorsal fin large, with length usually greater than prespiracular space, exceptionally slightly shorter, and up to over 2.5 times its length; first dorsal-fin base over pectoral-pelvic space and well anterior to pelvic fins; first dorsal-fin origin over pectoral-fin bases or inner margins (slightly behind them in some Deania species). Second dorsal fin usually smaller than or sometimes as large as first dorsal; second dorsal-fin base partly over or just behind pelvic-fin bases; second dorsal-fin origin usually over rear halves of pelvic-fin bases, pelvic insertions, or pelvic inner margins but sometimes slightly behind pelvic-fin free rear tips (some C. moluccensis specimens). Caudal fin heterocercal, with ventral lobe poorly to strongly developed in adults, and with a strong subterminal notch. Vertebral centra strongly calcified, primary double cones well developed. Vertebral counts: total vertebral counts 106 to 131 , monospondylous vertebral counts 49 to 65 , diplospondylous precaudal counts 24 to 37 . Intestinal valve with 10 to 25 turns. Adults are small to moderate-sized, between 43 to 169 cm long. Colour: plain or with light or dark markings on fins, without black photophore markings on tail or flanks.

Distribution: The family Centrophoridae has an almost circumglobal range in cold temperate to tropical seas, in association with landmasses including continents, islands, sea mounts and ridges. Gulper sharks are generally absent from very high latitudes, except Centrophorus squamosus which ranges up to Iceland in the North Atlantic, and are most diverse in warm temperate waters and in the tropics. Several of the species are wide-ranging in the Atlantic but the greatest known diversity of the family is in the Indo-West Pacific. These sharks are apparently absent from the Eastern North Pacific, though C. squamosus and Deania calcea occur in the Eastern South Pacific off South America. Geographic and bathymetric ranges are imperfectly known for most species, a result of problems in identifying individual centrophorid species and uneven sampling of deepwater slope-dwelling sharks. Several species may be regional endemics.

Habitat: Members of the Centrophoridae are primarily bottom dwelling, deepwater demersal inhabitants of the continental and insular slopes and more rarely the upper rises, but also occur on submarine ridges and seamounts. They range in depth from 200 to below 4000 m , but most species do not appear to extend below 1500 m . These sharks occasionally occur on the continental and insular shelves offshore in water up to 50 m depth, although this is most exceptional. The family apparently lacks specialized epipelagic species but at least one bottom dwelling centrophorid may venture into the open ocean: Centrophorus squamosus was once collected at a depth between the surface and 1250 m in water about 4000 m deep.

Biology: Reproductive mode is viviparous with a yolk-sac, with females having from one to 17 young in a litter. There have only been a few studies on the age and growth of these sharks, but most appear to be very slow growing, maturing between 8.5 and 30 years, with a maximum age estimated at 70 years or more for at least one species. Gulper sharks feed mostly on bony fishes and cephalopods but also eat crustaceans (lobsters and shrimps), small sharks (including batoids and chimaeras), and tunicates. Centrophorids have moderately strong to very powerful jaws with a shear-like cutting dentition in the lower jaw, and holding or cutting dentition in the upper jaw.
Several centrophorids are social, and form small to huge schools or aggregations, making them among the commonest deep-water sharks in temperate and tropical seas, but their general biology, including behaviour and population structure is little known.

Interest to Fisheries and Human Impact: Globally, the Centrophoridae are perhaps one of the most important families of deepwater sharks as they are the subject of targeted and non-target deepwater fisheries. In the Eastern North Atlantic, these sharks were commonly fished as part of targeted deepwater shark fisheries and also formed an important bycatch of deepwater fisheries for bony fishes until restrictive management measures were established. Some species are caught regularly as discarded bycatch of fisheries for deepwater teleosts. They are caught with longlines, bottom trawls, and fixed bottom gillnets. Landings over the past decade in the North Atlantic according to FAO fisheries statistics averaged about 2237 tonnes with a high of 4142 tonnes reported in 2003 . The majority of these landings were in Portuguese waters. The reported landings however are likely underestimated since prior to 2010 many deepwater sharks were classified as "deepwater siki sharks" which may include any number of deepwater squaloid species. However, in an attempt to move away from non-scientific classification and develop better stock assessments the leafscale gulper shark (Centrophorus squamosus), among other abundant deepwater squaloids, was separated by species and its landings are now report separately. Gulper sharks are used for human consumption: dried-salted or fresh, for fishmeal, and for their livers, which are extremely large, oily, and have a high squalene content.

The conservation status of gulper sharks is poorly known largely due to the poor taxonomic resolution of this group, inadequate monitoring in most areas, and limited knowledge on their biology, and possibly from the extreme limits in life-history parameters such as fecundity, life span, age at maturity, and gestation period. One species, the Eastern North Atlantic gulper shark, Centrophorus granulosus, is currently listed as critically endangered due to sharp declines in its population (Gibson et al., 2008).

Local Names: Gulper sharks, Birdbeak dogfish, Oil tankers.
Remarks: The current arrangement of the Centrophoridae is comprised of two genera, both represented in the North Atlantic, and with 17 nominal species currently recognized. However, several of these appear to be species-complexes and may involve several as yet undescribed species. One such species, Centrophorus uyato, is often cited in the literature, but in fact is not a valid species (see Remarks section for the genus Centrophorus below).

Literature: Müller and Henle (1839); Gray (1851); Dumeril (1865); Günther (1870); Regan (1908); Garman (1913); Fowler (1941, 1968, 1969); Bigelow and Schroeder (1948, 1957); Cadenat (1959a, b, c), Garrick (1959a, 1960b); Cadenat and Blache (1981); Compagno (1984); Muñoz-Chapuli and Ramos (1989b); Shirai (1992a, 1996); Last and Stevens (2009); Compagno and Niem (1998); Hernández et al. (1998); Clarke and Stenberg (2006); Gibson et al. (2008); Kyne and Simpfendorfer (2010); ICES (2010); Ebert and Compagno (In press).

## Key to North Atlantic Genera:

1a. Preoral snout length less than distance from mouth to pectoral-fin origins (Fig. 63a). Dermal denticles of back leaf-shaped with pedicels, or sessile with low ridges, and without erect pitchfork-shaped crowns (Fig. 63b).

Centrophorus

a) LATERAL VIEW
b) DERMAL DENTICLES

Fig. 63 Centrophorus
1b. Preoral snout length greater than distance from mouth to pectoral-fin origins (Fig. 64a). Dermal denticles of back with tall, slender pedicels and pitchfork-shaped crowns (Fig. 64b) . Deania

a) LATERAL VIEW
b) DERMAL DENTICLES

Fig. 64 Deania

## Centrophorus Müller and Henle, 1837

Genus: Centrophorus Müller and Henle, 1837a, Ber. K. preuss. Akad. wiss. Berlin, 2: 115; Müller and Henle, 1837b, Arch. Naturg. 3: 398.

Type species: Squalus granulosus Bloch and Schneider, 1801, by monotypy. "Sq. squamosus BI. Schn." (= Squalus squamosus Bonnaterre, 1788) was mentioned by Müller and Henle (1837a, b) in the account of Centrophorus, but who thought a new genus was required. Müller and Henle (1838a, Mag. Nat. Hist., n. ser., 2: 89) confusingly included one species in Centrophorus, "S. squamosus, BI. Schn." (possibly a mistake for S. granulosus), but also noted that "Squalus squamosus, BI. Schn." was allied to Centrophorus but probably belonged to a new genus. Bonaparte (1838, Nuov. Ann. Sci. Nat. Bologna, ser. 1, 2: 207) apparently followed their suggestion and named a new genus Lepidorhinus for $\boldsymbol{S}$. squamosus, but Müller and Henle (1839, Syst. Beschr. Plagiost., pt. 2: 90) reversed their previous opinion and included S. squamosus in Centrophorus.

## Number of Recognized North Atlantic Species: 4.

Synonyms: Lepidorhinus Bonaparte, 1838: 207; Machephilus Johnson, 1867: 713; Entoxychirus Gill 1862: 496, 498.
Field Marks: Deepwater sharks with a moderately long and broad snout, and huge, iridescent green eyes. Bladelike upper and lower teeth without cusplets; lower teeth imbricated and much larger than uppers. Cylindrical bodies with very tough skin and large leaf-like, thornlike or pebble-shaped denticles. Pectoral-fin free reartips more or less angular to attenuated. Two dorsal fins each with strong grooved spines, no anal fin, and caudal fin with strong subterminal notch. Body coloration light grey or grey-brown to blackish grey, sometimes lighter below. Fin webs dusky or with dark and light bars.

Diagnostic Features: Snout flattened and broadly parabolic to slightly pointed in dorsoventral view, angular to roundedangular in lateral view; snout short to moderate with preoral length less than distance from mouth to pectoral origins and half length of head or less. Labial furrows not extended anteromedially as elongated preoral grooves. Upper and lower teeth with broader, thicker crowns and roots. Lower teeth with vertical basal grooves on their lingual roots and with broader cusps than the upper teeth; edges of lower teeth often serrated in adults. Tooth rows 30 to 45 upper jaw, 24 to 35 lower jaw. Dermal denticles with low, flat, ridged crowns, varying from leaf-shaped and with low pedicels and posterior cusps, to cuspless, block-shaped, and without pedicels; denticle crowns flat and not elevated or pitchfork-like, with a short medial cusp (sometimes absent), lateral cusps short or absent, and single or multiple ridges; denticle bases broader and quadrangular. Surface of skin rough in the leaf-scaled Centrophorus squamosus but smooth in species with sessile crowns and low bases. Pectoral fins with free rear tips varying from squared-off and angular to elongated and acutely pointed, not broadly lobate. Claspers with a lateral spine. Second dorsal fin smaller than first and with its base about half to $3 / 4$ length of first dorsal-fin base; second dorsal-fin origin varying from over last third of pelvic-fin bases to slightly posterior to pelvic-fin free rear tips; second dorsal-fin spine equal to or slightly larger than first dorsal-fin spine but not greatly enlarged, spine moderately curved, spine apex usually falling well below fin apex. Vertebral counts: total vertebral counts 106 to 131, precaudal vertebral counts 77 to 92 , monospondylous vertebral counts 49 to 64 . Intestinal valve with 10 to 29 turns. Adults are small to moderately large from 90 to 170 cm total length. Colour: light to dark grey, greyish brown to black above, usually lighter below; depending on the species fin edges may be plain to light or dark edged.

## Local Names: Gulper sharks.

Remarks: The genus has 13 recognized species, of which at least four occur in the North Atlantic, possibly more, but the taxonomic status of North Atlantic Centrophorus species, like most of the genus, is very poor with most species having been inadequately described and with type material missing or in poor condition. Muñoz-Chapuli and Ramos (1989b) reviewed the systematics of Centrophorus from the Eastern North Atlantic and recognized four readily separable species, C. squamosus, C. granulosus, C. lusitanicus, and C. niaukang However, recent studies indicate that C. niaukang may be restricted to the Western Indo-Pacific. Furthermore, C. granulosus and C. lusitanicus are still poorly known taxonomically, making it difficult to manage these species as separate stocks. Another species name frequently seen in the literature, Centrophorus uyato, is not actually a Centrophorus species, but rather a Squalus of uncertain identity. Ebert and Compagno (In press) provided a detailed overview of the taxonomic issues relating to this genus, including the North Atlantic. The current key and arrangement of species below is provisional, pending further examination of adequate growth series of several of the species, improved sampling, and exploration of deepwater habitats where these sharks occur. A comprehensive systematic review of Centrophorus, including detailed consideration of external morphological, anatomical and molecular characters (extending Muñoz-Chapuli and Ramos' 1989b regional study), is necessary to elucidate the variation and interrelationships of Centrophorus species and to rectify several outstanding problems within the genus. These include the confused systematics of Western North Atlantic, including the Gulf of Mexico, Centrophorus species referred to as $C$. cf. acus, $C$. cf. granulosus, $C$. cf. uyato, and $C$. cf. tessellatus as well a long-snouted species very similar to C. cf. harrissoni that also occurs in the area.

Key to North Atlantic Species:
1a. Lateral trunk denticles with leaf-like flattened crowns on elevated narrow to broad pedicels extending above the denticle bases; crowns with strong medial and lateral cusps on their posterior ends (Fig. 65)

Centrophorus squamosus

1b. Lateral trunk denticles with flat sessile crowns on the denticle bases, without separate pedicels; crowns usually with or sometimes without a posterior medial cusp but no lateral cusps (Fig. 66)

2a. Free rear tips of pectoral fins moderately elongated and attenuated, usually not extending behind first dorsal-fin spine (Fig. 67). Lateral trunk denticles with more or less elongated crowns and a prominent angular cusp in adults (Fig. 66). A large species with adults about 110 to 169 cm long.

Centrophorus niaukang

2b. Free rear tips of pectoral fins greatly elongated and usually extending well behind first dorsal-fin spine (Fig. 70). Lateral trunk denticles with rounded or oval crowns and a low obtusely angular cusp (sometimes absent in large adult C. granulosus) (Fig. 68). Smaller species, with adults usually below 100 cm but possibly up to 110 cm .

3a. First dorsal fin very low and greatly elongated, first dorsal-fin height 2.4 to 3.8 in base length, first dorsalfin base 16.2 to $22.4 \%$ of total length (Fig. 69) . . .

## Centrophorus lusitanicus

3b. First dorsal-fin base higher and shorter, first dorsal-fin height 1.7 to 2.5 in base length, first dorsal-fin base 8.8 to $15.8 \%$ of total length (Fig. 70)

Centrophorus granulosus


DERMAL DENTICLES
Fig. 65 Centrophorus squamosus


Fig. 66 Centrophorus niaukang


Fig. 67 Centrophorus niaukang


DERMAL DENTICLES
Fig. 68 Centrophorus granulosus


Fig. 69 Centrophorus Iusitanicus


Fig. 70 Centrophorus granulosus

Centrophorus granulosus (Bloch and Schneider, 1801)
Squalus gramulosus Schneider in Bloch and Schneider, 1801, Syst. Ichthyol.: 135. No locality mentioned. Holotype: A single large stuffed specimen without jaws, "5 ped. longum" or 1570 mm long; lost according to Krefft and Tortonese (1973, In J. C. Hureau and T. Monod, eds., CLOFNAM. Check-list fish. NE Atlantic Mediterranean, 1:38) and Paepke and Schmidt (1988, Mitt. Zool. Mus. Berlin 64[1]: 161).

Synonyms: Dalatias nocturnus Rafinesque, 1810: 11, pl. 14, Fig. 3; ?Centrophorus bragancae Regan, 1906b: 438; Centrophorus machiquensis Maul, 1955: 5, Fig. 13-16.

Other Combinations: Centrophorus or Entoxychirus uyato or uyatus (not Squalus uyato Rafinesque, 1810).

FAO Names: En - Gulper shark; Fr - Squale-chagrin commun; Sp - Quelvacho.



UNDERSIDE OF HEAD


UPPER AND LOWER TEETH


DERMAL DENTICLES

Fig. 71 Centrophorus granulosus

Field Marks: Snout moderately long and thick. Bladelike monocuspidate teeth in upper and lower jaws, with lowers much larger than uppers. Low rhomboidal monocuspidate lateral trunk denticles. Rear tips of pectoral fins narrowly angular and greatly elongated. Two dorsal fins with large grooved spines, first dorsal fin higher than second dorsal fin; first dorsal fin short and high, second dorsal fin with spine base over pelvic-fin inner margins. No anal fin. Colour dark grey or grey-brown above, lighter below, with dusky fin webs but no prominent blackish fin markings.

Diagnostic Features: Snout moderately long, preoral length 0.9 to 1.2 times mouth width, 1.0 to 1.4 in space from mouth to pectoral origins, and 0.7 to 0.9 times head width at mouth. Snout broadly parabolic in dorsoventral view, broadly wedge-shaped in lateral profile, depth at mouth 1.3 to 1.9 in preoral length. Mouth width 7.4 to $8.8 \%$ of total length. Upper anterolateral teeth with erect to semioblique cusps, lower teeth with oblique or semioblique cusps; tooth row counts 36 to 43 upper jaw, 28 to 32 lower jaw. Body moderately stocky to slender. Distance from first dorsal insertion to second dorsal spine origin 24.7 to $29.0 \%$ of total length. Dorsal-caudal space 6.1 to $8.0 \%$ of total length. Lateral trunk denticles with rhomboidal to nearly circular sessile crowns on very low, thick pedicels; crowns close-set but not overlapping one another, with a narrow to broad, very short, thornlike to blunt or obsolete medial cusp (broader and shorter in adults than young), no lateral cusps, and several low blunt ridges. Pectoral-fin free rear tips elongated into narrow, angular lobes that reach behind first dorsal-fin spine base; pectoral-fin inner margin 10.1 to $15.6 \%$ of total length. First dorsal fin moderately high and short, height 1.7 to 2.5 in base; base 11.0 to $15.8 \%$ of total length. Second dorsal-fin height about 0.7 to 0.8 times first dorsal-fin height; second dorsal-fin base 7.6 to $10.5 \%$ of total length and about 0.5 to 0.8 times first dorsal-fin base; second dorsal-fin spine origin over inner margins of pelvic fins. Caudal fin with broadly notched postventral margin in adults. Vertebral counts: total vertebral counts 113 to 125 , monospondylous vertebral counts 53 to 59 , precaudal vertebral counts 79 to 89 . Intestinal valve counts 11 to 14 . Size large, adults to 166 cm . Colour: body dark grey or grey-brown above, slightly lighter below; fins with dark grey or blackish webs but without prominent black tips and margins.

Distribution: Possibly widespread in the Atlantic, Indian, and western Pacific oceans, but geographic range uncertain due to misidentification with similar species. Eastern Atlantic: France, Spain, Portugal, Madeira Islands, the Mediterranean Sea (including Algeria, Spain, France, Tunisia, Italy, and Israel, but absent from the Black Sea), Canary Islands, Morocco, Sahara Republic, Senegal, Liberia, Ivory Coast to Nigeria, Cameroon to Congo, Angola, Namibia, and the west coast of South Africa (Northern Cape Province). Western Atlantic: There are many nominal records of Centrophorus granulosus and C. "uyato" in the Western North Atlantic mostly based on specimens collected by research vessels that need to be verified and could possibly include C. cf. niaukang and other species along with the present species; localities include the northern mid-Atlantic Bight, Gulf of Mexico off the USA (Louisiana, Mississippi, Alabama, and northern Florida) and Mexico (Tamaulipas and Yucatan Provinces), the north coast of Cuba, and the Caribbean off the Lesser Antilles, possibly Colombia and Venezuela, off French Guiana and northern Brazil.

Habitat: A common to uncommon deepwater gulper shark of the outer continental shelves and upper slopes, usually on or near the bottom at depths from 50 to 1440 m , but most records between 200 to 600 m .

Biology: Viviparous with a yolk-sac, number of young per litter 1 to 6, averaging 3 , in the Galician waters (Eastern North Atlantic), but in the Mediterranean females only have a single young per litter. Elsewhere, the number of young is only one or two for the species. Nothing is known of its reproductive cycle. Like other members of this genus, Centrophorus granulosus is slow growing, with females maturing in about 16.5 years and males in about 8.5 years. The maximum estimated age for this shark is 39 and 25 years for females and males, respectively. Its diet includes bony fishes, cephalopods, and crustaceans.
Confusion in the literature between C. granulosus and other Centrophorus species contributes to a sketchy knowledge of its biology.

Size: Maximum total length varies regionally from 110 to 166 cm . Males mature at 80 to 118 cm , females mature at 100 to 138 cm total length. The size at maturity varies regionally, but this is likely due to misidentification of this species


Fig. 72 Centrophorus granulosus with other similar looking species.
Eastern North Atlantic males are reported to be mature at 118 cm , but immature at 115 cm , while Mediterranean and southern African specimens of C.cf. granulosus are mature between 80 and 94 cm . Size at birth between 30 and 47 cm ; smallest free-swimming individuals, with open umbilical scars, were 39 to 44 cm .

Interest to Fisheries and Human Impact: Primarily fished in the eastern Atlantic with bottom trawls, long lines, and fixed bottom nets, but also caught as discarded or utilized bycatch of deepwater slope fisheries elsewhere. This species is usually included in generic landings categories, except for Portugal and the United Kingdom where species-specific landings over the past decade (2000 to 2009) averaged 164 and 130 tonnes, respectively. Landings from the UK may, however, be confounded with Centrophorus squamosus. Hence reliable landings data are not readily available, due to continuing taxonomic problems in identifying this species from other Centrophorus species and the widespread use of generic landings categories. This species, if it even occurs in the Western North Atlantic, is relatively uncommon and is only likely taken as bycatch on occasion. The flesh of this species is utilized smoked and dried salted for human consumption or processed for fishmeal and liver oil. It is also valuable for its large oily liver with high squalene content.
Under TAC regulation in EU (in 2012, TAC=0) (EU, 2010). Technical measures in force in EU waters and NEAFC regulatory area (2012).

The conservation status is Critically Endangered in the Eastern North Atlantic due to massive, expanding, and often uncontrolled deepwater fisheries in many parts of its range, including European seas. Globally this species is considered Vulnerable.

Local Names: Little gulper shark; Petit squale-chagrin (France, as Centrophorus uyato); Galludito (Spain); Quelmo (Madeira Islands, as C. machiquensis); Quelma, Gulper shark (Azores); Lixa granulosa, Lixa-de-lei, Lixa pequena (as C. uyato); Quelme (Canaries); Barroso, Xara branca (Portugal).

Remarks: The nomenclature and systematic status of this species is sketchy and convoluted. Ebert and Compagno (In press) provide an overview on the taxonomic status of this species.

Literature: Bloch and Schneider (1801); Rafinesque (1810); Blainville (1825); Müller and Henle (1839); Gray (1851); Dumeril (1865); Günther (1870); Regan (1908); Lo Bianco (1909); Garman (1913); Lozano y Rey (1928); Poll (1951); Maul (1955); Bigelow, Schroeder and Springer (1955); Tortonese (1956); Bigelow and Schroeder (1957); Cadenat (1959a, b, c); Maurin and Bonnet (1970); Kreff and Tortonese in Hureau and Monod (1973b); Capapé (1974, 1975); Compagno (1984); Cadenat and Blache (1981); McEachran and Branstetter in Whitehead et al. (1984); Muñoz-Chapuli and Ramos (1989b); Fischer et al. (1990); Springer in Quero et al. (1990); Bianchi et al. (1993); Santos, Porteiro and Barreiros (1997); Hernández et al. (1998); McEachran and Fechhelm (1998); Guallart and Vicent (2001); Clarke and Stenberg (2006); Guallart et al. (2006); Bañón, Piñeiro, and Casas (2008); Gibson et al. (2008); EU (2010); ICES (2010); Ebert and Compagno (In press).

## Centrophorus Iusitanicus Bocage and Capello, 1864

Centrophorus lusitanicus Bocage and Capello, 1864, Proc. Zool. Soc. London, 24: 260, Fig. 1. Syntype: British Museum (Natural History), BMNH-1867.7.23.2, 75 cm immature male, examined by D.A. Ebert; other type material in Museu Bocage, Lisbon, probably lost in fire; type locality off Portugal.

Synonyms: None.

## Other Combinations: None. Sometimes confused with Centrophorus granulosus and C. niaukang.

FAO Names: En - Lowfin gulper shark; Fr - Squale-chagrin longue dorsale; Sp - Quelvacho lusitánico.


UNDERSIDE OF HEAD
Fig. 73 Centrophorus Iusitanicus
Field Marks: Snout moderately long and flat. Teeth are blade-like, monocuspidate in upper and lower jaws, with lowers much larger than uppers. Low rhomboidal monocuspidate lateral trunk denticles. Rear tips of pectoral fins narrowly angular and greatly elongated. Two dorsal fins with large grooved spines, first dorsal fin very long, high and higher than second dorsal fin, second dorsal fin with spine base over pelvic-fin inner margins. No anal fin. Colour grey-brown or grey above, slightly lighter below, with dusky fin webs.

Diagnostic Features: Snout moderately long, preoral length 1.1 to 1.3 times mouth width, 0.8 to 1.2 times space from mouth to pectoral origins, and 0.9 to 1.0 times head width at mouth. Snout broadly parabolic in dorsoventral view, fairly narrow and slender in lateral profile, depth at mouth 1.6 to 2.2 in preoral length. Mouth width 6.9 to $7.8 \%$ of total length. Upper anterolateral teeth with erect to semioblique cusps, lower teeth with oblique cusps; tooth row counts 36 to 44 upper jaw, 27 to 32 lower jaw. Body relatively slender. Distance from first dorsal insertion to second dorsal spine origin 21.6 to $24.6 \%$ of total length. Dorsal-caudal space 5.9 to $8.1 \%$ of total length. Lateral trunk denticles with thornlike to rhomboidal or rounded sessile crowns on very low, thick pedicels; crowns close-set but not overlapping one another, with a narrow to broad, very short, thornlike to blunt medial cusp (broader in adults than young), no lateral cusps, and several low blunt ridges. Pectoral-fin free rear tips elongated into narrow, angular lobes that reach opposite or somewhat behind first dorsalfin spine base; pectoral-fin inner margin 10.7 to $12.4 \%$ of total length. First dorsal fin very low and long, height 2.4 to 3.8 in base; base 16.2 to $22.4 \%$ of total length. Height of second dorsal fin 0.7 to 0.9 times first dorsal-fin height; second dorsalfin base 9.4 to $11.7 \%$ of total length and about 0.5 to 0.6 of first dorsal-fin base; second dorsal-fin spine origin over inner margins or free rear tips of pelvic fins. Caudal fin with weakly notched postventral margin in adults. Total vertebral counts 119 to 125, monospondylous vertebral counts 58 to 64, precaudal vertebral counts 84 to 92 . Intestinal valve counts 12 to 13. Size is moderate, with adults 75 to 95 cm long. Colour: grey-brown or dark grey above, slightly lighter below; fins with darker webs or tips but without prominent markings in adults, late foetuses with prominent black bars on dorsal-fin webs and terminal caudal-fin lobe.

Distribution: Eastern North Atlantic: Portugal, Morocco, Canary Islands, Senegal, Nigeria, Ivory Coast, Ghana, Gulf of Guinea, and Cameroon; not known from the Mediterranean Sea. Records C. cf. Iusitanicus-like species from outside the eastern Atlantic, including those from the Western Indian Ocean, Indonesia, and the Western Pacific may represent one or more different species. Absent from the Western North Atlantic.

Habitat: A deepwater species of the outer continental shelves and upper slopes at depths between 300 to 1400 m , but mostly between 370 to 610 m in the Eastern North Atlantic.

Biology: Virtually nothing is known about this species. Viviparous with a yolk-sac, number of young may be 1 per litter. Diet uncertain, probably consists of bony fishes, small cartilaginous fishes and cephalopods.

Size: Maximum size uncertain but possibly 100 cm or more. A late juvenile male (surviving syntype) is 75 cm long and an adult male was also 75 cm . Adult females (including a pregnant female) were between 86 and 95 cm long (D.A. Ebert, unpubl. data). Size at birth uncertain but a near-term foetus from an 86 cm female was 33 cm long.

Interest to Fisheries and Human Impact: Interest to fisheries limited. Primarily utilized in the Eastern North Atlantic, where it is captured in bottom trawls and with fixed bottom nets and


Fig. 74 Centrophorus Iusitanicus
$\square$ Known distribution longline gear. Landings of this species, along with Centrophorus granulosus (see above), are usually not reported by individual species categories. Although in recent years (2007 to 2009) it has been reported in Portuguese landings where a steady, sizeable, increase has been observed from 180 to 423 tonnes between 2007 and 2009. Its flesh is utilized dried and salted for human consumption, and processed for fishmeal.

Conservation status is Vulnerable due to its restricted range, extremely low fecundity, and it being the subject of deepwater fisheries in the Eastern North Atlantic.

Local Names: Barroso, Lixa, Lixa-de-lei, Quelme, Tubarão-lusitano (Portugal); Remudo (Canary Islands).
Remarks: Muñoz-Chapuli and Ramos (1989b) gave a detailed morphological and anatomical description of this shark based on Eastern Atlantic examples and considered it a valid species that has often been confused with Centrophorus granulosus and C. niaukang in the past. Ebert and Compagno (In press) concurred on its validity after comparing specimens collected off South Africa and Mozambique of C. niaukang and C.granulosus. Apart from the Eastern North Atlantic, Centrophorus Iusitanicus or C. Iusitanicus-like species are also reliably known from Taiwan (Province of China), Indonesia, and Mozambique (D.A. Ebert and W.T. White, unpubl. data).

Literature: Bocage and Capello (1864); Regan (1908); Garman (1913); Bigelow and Schroeder (1957); Cadenat (1959b, c); Teng (1962); Krefft and Tortonese in Hureau and Monod (1973b); Cadenat and Blache (1981); Compagno (1984); McEachran and Branstetter in Whitehead et al. (1984); Muñoz-Chapuli and Ramos (1989b); Springer in Quero et al. (1990); Clarke, White, and Compagno (2008); Gibson et al. (2008); ICES (2010); Ebert and Compagno (In press); W.T. White (pers. comm.).

Centrophorus niaukang Teng, 1959
Centrophorus niaukang Teng, 1959, Taiwan Fish. Res. Inst., Keelung, Lab. Fish. Biol. Rep., (9): 1. Holotype: Taiwan Fisheries Research Institute, TFRI-3612, 1540 mm TL adult female, $24^{\circ} 48^{\prime} \mathrm{N}, 121^{\circ} 54^{\prime} \mathrm{E}$, northeast coast of Taiwan (Province of China), 250 m .

Synonyms: None.
Other Combinations: None.

FAO Names: En - Taiwan gulper shark; Fr - Squale-chagrin quelvacho; Sp - Quelvacho chino.



UNDERSIDE OF HEAD


UPPER AND LOWER TEETH


DERMAL DENTICLES

Fig. 75 Centrophorus niaukang

Field Marks: Snout short and thick. Teeth are blade-like, monocuspidate in upper and lower jaws, with lowers much larger than uppers. Low thornlike to semi-rhomboidal, monocuspidate lateral trunk denticles. Rear tips of pectoral fins narrowly angular and slightly elongated. Two dorsal fins with large grooved spines, first dorsal fin slightly higher and larger than second dorsal fin, first dorsal fin very long and high, second dorsal fin with spine base usually behind pelvic-fin rear tips. Colour dark grey or grey-brown above, slightly lighter below, with dusky fin webs but no prominent markings.

Diagnostic Features: Snout short and thick. Preoral length 0.8 to 1.2 times mouth width, 1.0 to 1.7 in space from mouth to pectoral origins, and 0.6 to 0.9 times head width at mouth. Snout broadly parabolic in dorsoventral view, broadly and bluntly wedge-shaped in lateral profile, depth at mouth 1.2 to 1.7 in preoral length. Mouth width is 8.0 to $9.3 \%$ of total length. Upper anterolateral teeth with erect to semi-oblique cusps, lower teeth with oblique cusps; tooth row counts 32 to 37 upper jaw, 29 to 31 lower jaw. Body relatively stocky in adults and subadults. Distance from first dorsal insertion to second dorsal spine origin is 22.3 to $25.9 \%$ of total length; dorsal-caudal space 4.6 to $7.7 \%$ of total length. Lateral trunk denticles of adults with thornlike to semi-rhomboid sessile crowns on very low, thick pedicels; crowns close-set but not overlapping one another, with a narrow to broad, very short, thornlike to bluntly conical medial cusp (broader in adults than young), no lateral cusps (except in late foetuses), and several low blunt ridges. Pectoral-fin free rear tips variably elongated into short narrow, angular lobes that reach opposite, slightly anterior, or slightly posterior to first dorsal-fin spine base. Pectoral-fin inner margin is 9.1 to $13.8 \%$ of total length. First dorsal fin relatively low and long, height 2.6 to 4.0 in base; base 13.9 to $24.5 \%$ of total length. Second dorsal-fin height 0.8 to 1.0 times first dorsal-fin height; second dorsal-fin base 9.3 to $12.3 \%$ of total length and about 0.5 to 0.8 times first dorsal-fin base; second dorsal-fin spine origin over inner margins of pelvic fins. Caudal fin in adults have a straight to shallowly concave postventral margin. Total vertebral counts 111 to 120 , monospondylous vertebral counts 55 to 60 , precaudal vertebral counts 81 to 90 . Intestinal valve counts 14 . Size very large, with adults 110 to 169 cm . Colour: dark grey or grey-brown above, slightly lighter below; fin webs and margins dusky, without prominent markings.

Distribution: Eastern Atlantic: Morocco, off the Canary Islands, and possibly Portugal. Western North Atlantic: Atlantic coast of the United States (off Virginia and North Carolina), but likely to be more widespread there because of confusion with the sympatric Centrophorus granulosus or "C. uyatd", and possibly other species. At one time this species was known only from the type locality off north-eastern Taiwan (Province of China) (ROC) (Compagno, 1984), but since then it, or a closely related species, has been found to have a wide if not sporadic range in the Atlantic and Indo-West Pacific. Therefore, records of this species from the North Atlantic should be considered tentative at this time.

Habitat: A little-known deepwater shark found on or near the bottom on the outer continental shelves and upper slopes at 98 to about 1000 m .

Biology: An uncommon large gulper shark. Viviparous with a yolk-sac, the number of young is from one to six (mostly four to six) per litter. Eats bony fishes including cod-like fish (Gadiformes) and anglerfish (Lophiformes), small dogfish sharks (Squaliformes), skates (Rajidae), squid, and lobsters. Females from the Canary Islands ate about 57\% bony fishes, $14 \%$ cartilaginous fishes, and $29 \%$ cephalopods (Hernández et al., 1998) with food items ranked by category.

Size: Maximum total length to at least 170 cm . Males mature at 110 to 128 cm and females mature at 130 to 140 cm . Size at birth 35 to 45 cm .

Hernández et al. (1998) gave a lengthweight equation: $\mathrm{Wt}(\mathrm{gm})=6.94435 \mathrm{x}$ $10^{-7} \mathrm{TL}(\mathrm{mm})^{3.323665}(\mathrm{n}=30)$, for females only.

Interest to Fisheries and Human Impact: Moderate interest to fisheries. Regularly fished with line gear off Taiwan (Province of China), for its large liver with oil rich in squalene; utilized in the Eastern North Atlantic for liver oil and for human consumption.


Fig. 76 Centrophorus niaukang


Conservation status Near Threatened due to concerns over deepwater fisheries and the vulnerability of most gulper sharks to intense fisheries, but an assessment of Data Deficient may be more appropriate do to taxonomic misidentification with other similar Centrophorus species.

Local Names: Giant gulper shark; Remudo, Remudo blanco (Canaries).
Remarks: Centrophorus niaukang has been confused with C. Iusitanicus, C. granulosus and possibly other species in the North Atlantic and the Indo-West Pacific. Muñoz-Chapuli and Ramos (1989b) in their revision of Eastern North Atlantic Centrophorus did not directly compare Taiwanese C. niaukang specimens with those from the Eastern North Atlantic. More recently, Last and Stevens (2009) considered this species to have a more restricted distribution occurring only in the Western Pacific.

Literature: Teng (1959); Compagno (1984); Muñoz-Chapuli and Ramos (1989b); Hernández et al. (1998); Fowler (2003); Kiraly et al. (2003); Compagno, Dando, and Fowler (2005); Last and Stevens (2009); Ebert and Compagno (In press); W.T. White (pers. comm.).

## Centrophorus squamosus(Bonnaterre, 1788)

Squalus squamosus Bonnaterre, 1788, Tabl. Encyclop. Method. Trois Reg. Nat., Ichthyol., Paris: 12. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN-A7829, head only, no locality, according to Krefft and Tortonese in Hureau and Monod (1973, CLOFNAM. Check-list fish. NE At/antic Mediterranean, 1: 44) and Eschmeyer (1998, Cat. Fish.).

Synonyms: Machephilus dumerilli Johnson, 1867: 713. Holotype: British Museum (Natural History), BMNH1865.5.20.14, 111 cm ( $431 / 2^{\prime \prime}$ ) adult male, Madeira Islands. Holotype catalogue number according to Krefft and Tortonese in Hureau and Monod (1973: 44) and Eschmeyer (1998). Species name apparently corrected by Günther (1870: 422) and species reallocated to Centrophorus as C. dumerilii.

Other Combinations: Centrophorus dumerilli (Johnson, 1867); Lepidorhinus foliaceus (Günther, 1877); Lepidorhinus squamosus (Bonnaterre, 1788); Squalus (Acanthorhinus) squamosus Bonnaterre, 1788.

FAO Names: En - Leafscale gulper shark; Fr - Squale-chagrin de l'Atlantique; Sp - Quelvacho negro.


Field Marks: Snout short and thick or somewhat flattened. Blade-like, monocuspidate teeth in upper and lower jaws, with lowers much larger than uppers. High rough leaf-shaped, tricuspidate or multicuspidate lateral trunk denticles. Rear tips of pectoral fins hardly angular and slightly elongated. Two dorsal fins with large grooved spines; first dorsal fin very long and low, usually slightly lower although larger than second dorsal fin; second dorsal fin with spine base usually opposite pelvicfin inner margins or free rear tips. Colour grey, grey-brown or reddish brown above, usually similar below, with dusky fin webs and margins but no prominent markings.

Diagnostic Features: Snout short and thick. Preoral length 0.8 to 1.3 times mouth width, 0.9 to 1.8 in space from mouth to pectoral origins, and 0.6 to 0.9 times head width at mouth. Snout broadly parabolic in dorsoventral view, broad to narrow and wedge-shaped in lateral profile, depth at mouth 1.2 to 2.3 in preoral length. Mouth width 6.4 to $10.3 \%$ of total length. Upper anterolateral teeth with erect to semi-oblique cusps, lower teeth with oblique cusps; tooth row counts 30 to 38 upper jaw, 24 to 32 lower jaw. Body relatively stocky. Distance from first dorsal insertion to second dorsal spine origin 22.2 to $27.7 \%$ of total length. Dorsal-caudal space 3.8 to $7.0 \%$ of total length. Lateral trunk denticles with flat, leaflike crowns on narrow, high pedicels; crowns of lateral trunk denticles partly overlapping one another, with an angular medial cusp, either a pair of lateral cusps (young) or several small lateral cusps like large serrations (adults), and a strong high medial ridge. Pectoral-fin free rear tips not greatly elongated, forming angular corners to very short narrow, angular lobes that end well in front of first dorsal-fin spine base. Pectoral fin inner margin 5.4 to $8.8 \%$ of total length. First dorsal fin low and long, height 2.7 to 4.6 in base; base 11.9 to $21.6 \%$ of total length. Second dorsal fin 0.9 to 1.3 times first dorsal-fin height (usually slightly higher than first); second dorsal-fin base 9.4 to $18.2 \%$ of total length and about 0.5 to 0.9 times first dorsal-fin base; second dorsal-fin spine origin usually opposite pelvic-fin inner margins or free rear tips, sometimes just behind tips. Caudal fin with nearly straight to weakly concave postventral margin in adults. Vertebral counts: total vertebral counts 106 to 120 , monospondylous vertebral counts 55 to 60 , precaudal vertebral counts 82 to 88 . Intestinal valve counts 12 to 14 . Size relatively large, adults 103 to 160 cm . Colour: uniform dark grey, medium to light greyish brown, brown or reddish-brown above and below, underside may be slightly lighter although not conspicuously so. Fin webs may be slightly darker than body, but without prominent markings on fins.

Distribution: Eastern Atlantic: Iceland and the Atlantic Slope to Norway, Sweden, Denmark, Germany, Faroe Islands, England and Wales, Ireland, France (Bay of Biscay), Portugal, Spain (absent from the Mediterranean Sea), Madeira Islands, Canary Islands, Cape Verde, Azores, Morocco, Mauritania, Senegal, Gabon to Zaire, Namibia, South Africa (Western and Northern Cape Provinces). Western North Atlantic absent, but one record of this species from off Venezuela (G. Bianchi, pers. comm., 1989; RV F. Nansen sta. 1142. 2 Dec. $1988,10^{\circ} 53^{\prime} \mathrm{N}, 67^{\circ} 50^{\prime} \mathrm{W}$, between 462 to 508 m ). Also, occurs in the Western Indian and Western Pacific oceans.

Habitat: A large deepwater gulper shark of the continental slopes from 229 to 2359 m deep, but rare above 1000 m depth in the Eastern North Atlantic. Also found in the epipelagic or mesopelagic zone between the surface and 1250 m depth in the North-Central Atlantic over water 4000 m deep, but it is uncertain if this species regularly occurs in oceanic waters. A common species in some localities where it occurs.

Biology: Viviparous with a yolk-sac, with litters of four to eight or possibly nine young. Age at maturity is about 30 years for males and 35 years for females, with a maximum estimated age of 70 years. Eats bony fishes including hake (Merluccidae), codfish (Gadidae), grenadiers (Macrouridae), slickheads (Alepocephalidae), horse mackerel (Carangidae: Trachurus), and spinyfins (Diretmidae), also chimaeras (Chimaeridae), cephalopods (including ommastrephid and histioteuthid squid), and crustaceans (euphausiid and penaeid shrimp).

Size: Maximum total length about 164 cm . Males maturing at about 100 to 110 cm , and adult females 110 to 125 cm . Size at birth between 30 to 40 cm . Hernández et al. (1998) give a lengthweight equation: Wt $(\mathrm{gm})=3.00253 \mathrm{x}$ $10^{-9} \mathrm{TL}(\mathrm{mm})^{4.073401}(\mathrm{n}=31)$, for both sexes.

Interest to Fisheries and Human Impact: In the Eastern Atlantic, fished with bottom trawls, line gear and fixed bottom nets, and utilized fresh, frozen or dried salted for human consumption and for fishmeal. Landings of this gulper shark over the past decade peaked in 2003 at 3042 tonnes and have declined since to 243 tonnes in 2009, in line with more restrictive management. This species, based on FAO catch data, is landed mainly by Portugal (average 893 tonnes per year from 2000 to 2009), the United Kingdom (average 336 tonnes per year), and Spain (average 189 tonnes per year), although France also has important fisheries for this species. Landings are likely underestimated since issues remain with separating out this species from the generic "siki sharks" category; a category which refers to mixed


Fig. 78 Centrophorus squamosus deepwater shark species mainly comprised of Centrophorus squamosus and Centroscymnus coelolepis Under TAC regulation in EU (in 2012, $\mathrm{TAC=0}$ ) ( $\mathrm{EU}, 2010$ ). Technical measures in force in EU waters and NEAFC regulatory area (2012).

Conservation status is listed as Vulnerable globally, although regionally its status in the Eastern North Atlantic is Endangered because of deepwater bycatch and targeted deep-shark fisheries.

Local Names: Lixa, Arreganhada, Sapata preta (Portugal); Xara branca (Madeira Islands); Remudo, Remudo rasposo (Canaries); Lixa de escama, Leafscale gulper shark (Azores); Düsterer Dornhai, Blattschuppen-Schlingerhai (Germany); Brun pigghaj (Sweden); Schubzwelghaai (the Netherlands), Rauð̌háfur (Iceland).

Literature: Bonnaterre (1788); Müller and Henle (1839); Gray (1851); Dumeril (1865); Johnson (1867); Günther (1870, 1877, 1887); Garman (1913); Lozano y Rey (1928); Bigelow and Schroeder (1957); Cadenat and Blache (1981); Mauchline and Gordon (1983); Muñoz-Chapuli and Ramos (1989b); Ebert, Compagno and Cowley (1992); Bianchi et al. (1993); Santos, Porteiro and Barreiros (1997); Hernández et al. (1998); Clarke, Connolly, and Bracken (2001, 2002a); White (2003); Bañón, Piñeiro, and Casas (2006); Figueiredo et al. (2008); Gibson et al. (2008); Last and Stevens (2009); EU (2010); ICES (2010); Ebert and Compagno (In press); G. Bianchi (pers. comm.); W.T. White (pers. comm.).

## Deania Jordan and Snyder, 1902

Genus: Deania Jordan and Snyder, 1902, Proc. U.S. Natn. Mus. 25(1279): 80.
Type species: Deania eglantina Jordan and Snyder, 1902, by monotypy, a junior synonym of Acanthidium calceum Lowe, 1839.
Number of Recognized North Atlantic Species: 3.
Synonyms: Genus Acanthidium Lowe, 1839, Proc. Zool. Soc. Lond., pt. 7: 92, Type species: without designation of type species, new based in part on Acanthidium calceus and A. pusillum Type location Madeira Islands.

Field Marks: Deepwater sharks with an extremely long, broad snout, bladelike upper and lower teeth without cusplets, and lower teeth much larger than uppers and imbricated. Cylindrical or compressed bodies with delicate but rough skin and large erect or semierect denticles with pitchfork-like crowns and three sharp cusps. Pectoral-fin free rear tips rounded, not angular or attenuated. Two dorsal fins with strong grooved spines on both dorsal fins but with the second dorsal-fin spine much larger than the first. No anal fin. Caudal fin with strong subterminal notch. Body colour is light grey or grey-brown to blackish; fin webs dusky and without conspicuous markings. Eyes huge and iridescent green or yellowish.

Diagnostic Features: Snout spatulate in dorsoventral view, a thin depressed elongated wedge in lateral view; snout greatly elongated with preoral length over half head length and greater than distance from mouth to pectoral origins. Labial furrows extended anteromedially as elongated preoral grooves. Upper and lower teeth with narrower and more compressed crowns and roots. Tooth rows 22 to 36 upper jaw, 24 to 32 lower jaw. Dermal denticles with high pedicels, high erect crowns resembling tiny pitchforks, with slender narrow elongate triple cusps and ridges; bases narrow and stellate. Surface of skin very rough due to the erect large denticles. Pectoral fins with narrowly rounded or angular free rear tips but not acutely attenuated. Claspers without a lateral spine. Second dorsal fin about as large or slightly larger than first, with its base subequal to about $2 / 3$ length of first dorsal-fin base. Second dorsal-fin origin about over middle of pelvic-fin bases; second dorsal-fin spine usually over twice as long as first and with a broader base, strongly curved and with spine usually reaching apex of fin. Vertebral counts: total vertebral counts 118 to 128 , precaudal vertebral counts 85 to 95 . Intestinal valve turn counts not available. Moderately large, with adults from 97 to 122 cm total length. Colour: blackish brown or grey to greyish brown above and below.

Local Names: Arrowhead dogfishes, Birdbeak dogfishes.
Remarks: Currently, four species are recognized for the genus Deania of which three occur in the North Atlantic.

Key to North Atlantic Species:
1a. A subcaudal keel on the lower surface of the caudal peduncle (Fig. 79) . . . . . Deania profundorum

1b. No subcaudal keel on the lower caudal peduncle. . 2


Fig. 79 Deania profundorum
2a. Lateral trunk denticles moderately large, crown length about 0.5 mm (Fig. 80). Colour often medium grey-brown, sometimes light grey to dark brown . . . . . . . . . . . . . . Deania calcea

2b. Lateral trunk denticles very large, crown length about 1 mm (Fig. 81). Colour often blackish-brown, sometimes lighter . Deania hystricosa


DERMAL DENTICLES
Fig. 80 Deania calcea


DERMAL DENTICLES
Fig. 81 Deania hystricosa

## Deania calcea (Lowe, 1839)

Acanthidium calceumLowe, 1839, Proc. Zool. Soc. London, 1839 (7): 92. No type material, Madeira Islands. Eschmeyer (1998, Cat. Fish.) noted that the whereabouts of types for this species was unknown.

Synonyms: None.
Other Combinations: Centrophorus crepidalbus Bocage and Capello, 1864: 262, Fig. 2. Centrophorus calceus (Lowe, 1839); Centrophorus rostratus (Garman, 1906); Deania calceus (Lowe, 1839); Deania calceus calceus (Lowe, 1839).

FAO Names: En - Birdbeak dogfish; Fr - Squale savate; Sp - Tollo pajarito.


Fig. 82 Deania calcea


## UPPER AND LOWER TEETH

Field Marks: Extremely long flat snout. Compressed cutting teeth in both jaws. Small pitchfork-shaped denticles make the skin rough. Extremely long and low first dorsal fin, grooved dorsal-fin spines with the second dorsal-fin spine much higher than the first. No anal fin and no subcaudal keel on caudal peduncle. Coloration is often grey or grey-brown.

Diagnostic Features: Snout extremely long and flattened. Teeth dissimilar in shape; upper teeth with a single, erect cusp, lowers with a single smooth-edged, blade-like cusp; tooth counts 25 to 35 upper jaw, 27 to 33 lower jaw. No subcaudal keel on underside of caudal peduncle. Denticles fairly small, crown length about 0.5 mm long in adults. First dorsal fin long and low, origin over bases of pectoral fins; distance from origin of first dorsal-fin spine to first dorsal rear tip much greater than distance from free rear tip to second dorsal spine. Vertebral counts: total vertebral counts 118 to 127, precaudal vertebral counts 85 to 95 . Intestinal valve counts not available. Maximum size about 122 cm . Colour: varying from uniform light or dark grey or grey-brown above and below to dark brown, fins darker, fin webs dusky to blackish.

Distribution: Eastern Atlantic: Iceland along Atlantic slope to Faroe Islands, Scotland, Ireland, France, Spain, Portugal, Morocco, Azores, Madeira Islands, Mauritania, Senegal, Gabon, Namibia, South Africa (Northern and Western Cape). Apparently does not occur in the Mediterranean. Absent from the Western Atlantic. Also, occurs in the Western Indian, Western North Pacific, and South Pacific oceans.

Habitat: A common deepwater dogfish, sometimes collected in large groups, of the outer continental and insular shelves and upper, middle, and lower slopes from 60 to 1490 m depth, on or near the bottom or well above it. In the Eastern North Atlantic this species is most abundant between 750 and 800 m .

Biology: Viviparous with a yolk-sac, with litters of 1 to 17, averaging 7. In Irish seas estimated ages ranged from 11 to 35 years for females and 13 to 29 years for males. Length at fifty-percent maturity for females in Irish waters is estimated at 105 cm total length and at 25 years. Age


Fig. 83 Deania calcea at maturity in Australia waters is about 14 years for males and 22 years for females with a maximum age of 33 and 37 years. Diet includes hatchetfish (Sternoptychidae), scaly and black dragonfishes (Stomiidae), barracudinas (Paralepididae), lanternfish (Myctophidae), cod-like fishes (Gadiformes), scorpionfish (Scorpaenidae), squids (Ommastrephidae and Abraliopsis sp.) and shrimps (including penaeids). Off the west coast of South Africa a single species of lanternfish (Diaphus ostenfeldi) was by far the dominant prey, with small fractions of cephalopods, black dragonfish (Melanostomias spilorhynchus), and other fishes and penaeid shrimps (Ebert, Compagno and Cowley, 1992).

Size: Maximum total length about 122 cm ; males mature at 81 to 94 cm ; females mature at 99 to 106 cm . Size at birth about 29 to 34 cm .

Interest to Fisheries and Human Impact: Interest to fisheries moderate. Caught in bottom trawls, by longline and gillnet fisheries in the Eastern North Atlantic. Small numbers of this shark have been reported over the past decade, with an average of 119 tonnes being reported between 2000 and 2009 by FAO. Most reported landings of Deania calcea were by Portugal (between 2000 and 2009 an average of 74 tonnes), followed by Spain (average 26 tonnes) and the United Kingdom (average 17 tonnes). However, these numbers are likely underestimated due to it being included in uncategorized landings with other mixed deepwater squaloid species. Under TAC regulation in EU (in 2012, TAC=0). When accidentally caught with longlines, this species shall not be harmed. Specimens shall be promptly released (EU, 2010). Technical measures in force in EU waters and NEAFC regulatory area (2012).

The global conservation status is Least Concern, but in the Eastern North Atlantic it is has been assessed as Vulnerable.
Local Names: Forreta, Sapata, Sapata branca (Portugal); Pifaro, Pife, Sapata, Tutia, Birdbeak dogfish, Shovel nosed shark (Azores); Evhávur (Faroe Islands); Vogelschnabel-Dornhai (Germany); Flatnefur (Iceland); Skednoshaj (Sweden).

Literature: Lowe (1839); Garman (1906, 1913); Lozano y Rey (1928); Belloc (1934); Bigelow and Schroeder (1957); Cadenat (1957); Maurin and Bonnet (1970); Krefft and Tortonese in Hureau and Monod (1973b); Cadenat and Blache (1981); Mauchline and Gordon (1983); Compagno (1984); McEachran and Branstetter in Whitehead et al. (1984); Springer in Quero et al. (1990); Merrett et al. (1991); Du Buit (1991); Kong and Melendez (1991); Yano (1991); Ebert, Compagno and Cowley (1992); Bianchi et al. (1993); Santos, Porteiro and Barreiros (1997); Clarke, Connolly, and Bracken (2002b); Stevens (2003); Ivine (2004); Gibson et al. (2008); Last and Stevens (2009); EU (2010); ICES (2010); Ebert and Compagno (In press).

## Deania hystricosa (Garman, 1906)

Acanthidium hystricosum Garman, 1906, Bull. Mus. Comp. Zool. Harvard, 46(11): 206. Holotype: Museum of Comparative Zoology, Harvard, MCZ-1130, 92 cm ( 36 1/4") adult female, Sagami Bay, Japan, illustrated by Garman (1913, Mem. Mus. Comp. Zool. Harvard 36: pl. 12, Fig. 5-8. Holotype missing according to Hartel and Dingerkus (1997, in Garman, The Plagiostoma: xI).

Synonyms: Deania mauli Cadenat and Blache, 1981: 72, Fig. 47b, 50b, b1, b2, c, c1, c1, 51, 53c1, c2. Holotype: Possibly Museum National d'Histoire Naturelle, Paris, number uncertain, 835 mm adult male, off Camara de Lobos, Madeira Islands, 600-1000 m. Paratypes includes MNHN 1969-296, 298, 299, and 300 according to Eschmeyer (1998). Deania histricosa Compagno, 1984: 66, 67. Typographical error for D. hystricosa, spelled correctly elsewhere (Compagno, ibid.: 65).

Other Combinations: Centrophorus hystricosus (Garman, 1906).
FAO Names: En - Rough longnose dogfish; Fr - Squale-savate rude; Sp - Tollo raspa.


Fig. 84 Deania hystricosa

Field Marks: Extremely long flat snout. Compressed cutting teeth in both jaws. Large pitchfork-shaped denticles make the skin extremely rough. Extremely long and low first dorsal fin, grooved dorsal-fin spines with the second dorsal-fin spine much higher than the first. No anal fin, no subcaudal keel on caudal peduncle, and dark blackish-brown or grey-brown coloration.

Diagnostic Features: No subcaudal keel on underside of caudal peduncle. Denticles very large, crowns length about 1 mm long in adults. First dorsal fin long and low, origin over bases of pectoral fins; distance from origin of first dorsal-fin spine to first dorsal-fin rear tip much greater than distance from free rear tip to second dorsal-fin spine. Vertebral and intestinal valve counts not available. A moderate sized species, adults 84 to about 111 cm . Colour: blackish brown to grey-brown, fins slightly darker than body.

Distribution: Patchily distributed. Eastern Atlantic: Occasional records from south-west of the British Isles, Bay of Biscay, Azores, Madeira Islands, Canary Islands, Namibia, and South Africa (Northern Province). Western North Pacific: Japan, New Zealand.

Habitat: A little-known benthic and probably epibenthic dogfish of the upper and middle continental and insular slopes, at depths of 471 to 1300 m .

Biology: Viviparous with a yolk-sac, litter sizes not known but a female with 12 large ovarian eggs suggests moderatesized litters. Food not recorded.

Size: Maximum total length 111 cm . Males reported to mature at 81 to 84 cm and females maturing at 92 to 106 cm . Size at birth uncertain.
Hernández et al. (1998) give a lengthweight equation: Wt $(\mathrm{gm})=6.71652$ $\times 10^{-6} \mathrm{TL}(\mathrm{mm})^{2933160}(\mathrm{n}=44)$, for both sexes.

Interest to Fisheries and Human


Fig. 85 Deania hystricosa
$\square$ Known distribution
Possible distribution

Caught with deep-set longlines off Madeira Islands and the Canary Islands, and probably as bycatch of deepwater fisheries elsewhere. Utilized for liver oil and meat in the Canary Islands. Reported as occurring in ICES subarea XII as bycatch with other Deania species, but there is no information available on the percent composition D. hystricosa makes up of the overall bycatch of this genus. It appears that this species and $D$. profundorum are far less abundant that the more common D. calcea in the North Atlantic.

The conservation status of this poorly known birdbeak dogfish is Data Deficient due to a lack of information on its biology, although it may be of concern due to extensive deepwater fisheries where it occurs.

Local Names: Pejepato, Picopato, Zapata, Tollo raspa (Canaries).
Remarks: This species has been synonymized with Deania calcea (as its synonym D. eglantina) by Bigelow and Schroeder (1957). Cadenat and Blache (1981) named a new species, D. mauli, from Madeira Islands, which chiefly differs from $D$. calcea in its much larger denticles and perhaps a darker coloration. However, reference to Garman $(1906,1913)$ shows that $D$. mauli agrees in its large denticles and coloration with $D$. hystricosa and is otherwise not different from it. Deania mauli was tentatively synonymized with $D$. hystricosa by Compagno (1984), but was in turn recognized as separate from $D$. calcea. The characters that distinguish this species from $D$. calcea need to be examined in more detail than have been possible here. Lighter-coloured individuals with large denticles have been identified as D. hystricosa by Hernández et al. (1998) off the Canary Islands. This species may be wider ranging than indicated above.

Literature: Garman (1906, 1913); Bigelow and Schroeder (1957); Cadenat and Blache (1981); Compagno (1984); Cappetta, Du Buit and Quéro (1985); Springer in Quero et al. (1990); Hernández et al. (1998); Compagno, Dando, Fowler (2005); Ebert et al. (2008b); Gibson et al. (2008); ICES (2010); Ebert and Compagno (In press).

## Deania profundorum(Smith and Radcliffe, 1912)

Nasisqualus profundorum Smith and Radcliffe, in Smith, 1912, Proc. U.S. Nat. Mus. 41(1877): 681, Fig. 3, pl. 53. Holotype: United States National Museum of Natural History, USNM-70258, 430 mm adult male, Albatross Sta. 5491, between Leyte and Mindanao, Philippine Islands, $9^{\circ} 24^{\prime} \mathrm{N}, 125^{\circ} 12^{\prime} \mathrm{E}$, in beam trawl fished on green mud and coral bottom at 1347 m depth. Status of holotype confirmed by Howe and Springer (1993, Smiths. Contr. Zool. [540): 12).

Synonyms: Deania elegans Springer, 1959: 31, Fig. 1.
Other Combinations: None.
FAO Names: En - Arrowhead dogfish; Fr - Squale-savate lutin; Sp - Tollo flecha.



UNDERSIDE OF HEAD


UPPER AND LOWER TEETH

Fig. 86 Deania profundorum

Field Marks: Extremely long flat snout, compressed cutting teeth in both jaws, pitchfork-shaped small denticles that makes the skin rough, short, moderately high first dorsal fin, grooved dorsal-fin spines with the second dorsal-fin spine much higher than the first, no anal fin, a distinct subcaudal keel on caudal peduncle, and grey or grey-brown coloration.

Diagnostic Features: A subcaudal keel present on underside of caudal peduncle. Denticles small, crown length about 0.25 mm long in adults. First dorsal fin short and high, origin over inner margins of pectoral fins; distance from origin of first dorsal-fin spine to first dorsal-fin free rear tip slightly greater than distance from free rear tip to second dorsal-fin spine. Vertebral counts: total vertebral counts 118 to 122 , precaudal vertebral counts 85 to 93 . Intestinal valve counts not available. Size smaller than other Deania, adults 43 to 97 cm , mostly below 80 cm . Colour: medium to dark grey or grey brown above and below, fins dusky.

Distribution: Eastern Atlantic: the Azores, Canary Islands, Western Sahara, Mauritania, Senegal, Nigeria, Gabon, the Congo, Namibia, South Africa (Northern and Western Provinces). Western Atlantic: USA (Atlantic coast off Virginia and North Carolina, Gulf of Mexico off Mississippi), and the LesserAntilles (Dominica). Patchy distribution in the Western Indian and Western Pacific oceans.

Habitat: A little-known deepwater demersal dogfish of the upper continental and insular slopes found on or near the bottom at depths from 275 to 1785 m on the upper, middle and lower slopes. In the Western North Atlantic it occurs at 412 to 617 m , while off the Canary Islands it has been caught at 600 to 1500 m . It has been trawled on green mud and coral bottom in the Philippines.

Biology: Viviparous with a yolk-sac, probable number of young 5 to 7 based on fertilized eggs in the uteri. Diet includes small benthic and midwater bony fishes, including lanternfish, as well as squids and crustaceans. This shark sometimes occurs in huge aggregations or schools.

Size: Maximum total length about 97 cm , but most smaller. Males adult at 43 to 67 cm , females adult at 62 to 80 cm . Size at birth above 31 cm . Hernández et al. (1998) gave a length-weight equation: $\mathrm{Wt}(\mathrm{gm})=3.34938 \times 10^{-8} \mathrm{TL}(\mathrm{mm})^{3.713050}(\mathrm{n}=$ 32), for both sexes.

Interest to Fisheries and Human Impact: Interest to fisheries minimal. Caught on longlines off the Canary Islands. Possibly taken as bycatch with other Deania species in ICES subarea XII, but species-specific catch data not available. Utilized for liver oil and meat, probably caught as bycatch of fisheries elsewhere.

Conservation status Least Concern due to a lack of deep-water fisheries in those areas where it occurs, but may eventually be of concern if deep-water fisheries develop in areas where it occurs.

Local Names: Arrowhead dogfish, Sapata (Azores); Pejepato, Picopato, Zapata (Canaries).

Literature: Smith and Radcliffe in Smith (1912); Bigelow and Schroeder (1957); Springer (1959); Cadenat (1960, 1961); Maurin and Bonnet (1970); Bass et al. (1976); Cadenat and Blache (1981); Compagno (1984); Compagno, Ebert and Smale (1989); Springer in Quero et al. (1990); Compagno, Ebert and Cowley (1991);


Fig. 87 Deania profundorum
$\square$ Known distribution

Yano (1991); Ebert, Compagno and Cowley (1992); Bianchi et al. (1993); Santos, Porteiro and Barreiros (1997); Hernández et al. (1998); McEachran and Fechhelm (1998); Compagno, Dando, and Fowler (2005); Ebert, McCormack, and Samiengo (2008); Gibson et al. (2008); ICES (2010); Ebert and Compagno (In press).

### 2.2.4 Family ETMOPTERIDAE

Family: Subfamily Etmopterinae Fowler, 1934, Proc. Acad. Nat. Sci. Philadelphia, 85: 239 (family Squalidae).
Type genus: Etmopterus Rafinesque, 1810.

## Number of Recognized North Atlantic Genera: 2.

FAO Names: En - Lanternsharks.
Field Marks: Dwarf to moderate-sized sharks (usually less than 1 m long and mostly below 80 cm long) with short to long snouts, cylindrical to slightly depressed bodies and no anal fin. Teeth similar in both jaws or varying between jaws; upper teeth with a cusp and sometimes cusplets; lower teeth similar to upper teeth (Aculeola, Centroscyllium, Trigonognathus) or compressed and bladelike (Etmopterus, Miroscyllium) with a cusp and cusplets (Miroscyllium) or a cusp and blade (Etmopterus). Denticles small to moderately large and variable in shape, with slender to stout, pointed, wedge-shaped or hooked erect crowns without pedicels, or with low concave sessile crowns. No keels on the caudal peduncle. Two dorsal fins with strong grooved spines; the first dorsal fin usually smaller than the second and with origin varying from opposite the pectoral-fin inner margins or somewhat behind the pectoral-fin free rear tips; the second dorsal fin falcate or not and with its origin usually opposite the pelvic-fin bases or inner margins. Caudal fin with subterminal notch moderately strong to lacking; body and fin bases with photophores, inconspicuous and diffuse or in black photophore patches on the ventrolateral surface.

Diagnostic Features: Head moderately broad to narrow and somewhat flattened or cylindrical. Snout flat to conical and narrowly to broadly rounded, undulated or distally truncated in dorsoventral view. Spiracles moderate-sized to large and close behind eyes. Fifth gill opening not enlarged relative to first four but gill openings may increase slightly in width from first to fifth. Nostrils wide-spaced and with internarial width greater than or subequal to nostril width. Nostrils with simple, anterior nasal flaps that lack medial lobes or barbels. Mouth varying from broadly arched or Y -shaped and elongated to nearly transverse and very short, with thin, non-papillose lips. Labial furrows rudimentary to short, not encircling mouth, confined to mouth corners and under or exceptionally posterior to level of eyes, elongated posteriorly into postoral grooves or not; labial folds thin where present. Teeth with dignathic heterodonty well developed or not, upper teeth as large as
lowers or with uppers smaller than lowers. Upper teeth high-crowned, never compressed and blade-like and not forming a cutting edge, usually arranged in a quincunx pattern and not overlapping, with narrow erect or flexed conical cusps and often one to three pairs of conical cusplets (Centroscyllium); lower teeth either similar to upper teeth (Centroscyllium) or compressed, high-crowned, broad and blade-like, imbricating, and forming a saw-like cutting edge, with a compressed oblique cusp and either a distal blade (Etmopterus) and no cusplets or with compressed cusplets. Tooth rows 15 to 68 upper jaw, 15 to 68 lower jaw, upper teeth about as numerous as lowers or much fewer than lowers. Trunk cylindrical and without lateral ridges on abdomen. Interdorsal space usually longer than first dorsal base but ranging from about 0.6 to several times its length; pelvic-caudal space elongated or short and equal to about twice pelvic bases. Caudal peduncle cylindrical or slightly compressed, short to moderately elongated, and without lateral keels or precaudal pits. Head, trunk, and tail with photophores in many species and possibly all members of the family; denticles small to moderate-sized, either sessile and without cusps or with spike-like hooked crowns on low bases; denticles without flattened leaf-shaped crowns and slender pedicels and low bases. Pectoral fins low, rounded-angular or almost circular, not falcate, anterior margins shorter than the prespiracular length, rear tips rounded or rounded-angular and not greatly elongated. Pelvic fins subequal in size or larger than pectoral fins. Claspers usually with both medial and lateral clasper spines. Dorsal fins small to moderately large, broad, angular or rounded-angular, both with strong grooved spines; second dorsal spine usually much larger than the first dorsal spine. First dorsal fin small, not falcate, with length usually less than prespiracular space; first dorsal base over pectoralpelvic space and well anterior to pelvic fins; first dorsal-fin origin varying from exceptionally over pectoral-fin bases to more commonly over pectoral-fin inner margins or behind pectoral-fin rear tips. Second dorsal fin usually much larger than first dorsal fin but sometimes about as large as it; second dorsal-fin base partly over or just behind pelvic-fin bases with second dorsal-fin origin over pelvic-fin bases or above inner margins of pelvic fins. Caudal fin heterocercal, with ventral lobe weakly to moderately developed in adults, and with subterminal notch weak to (usually) strong. Vertebral counts: total vertebral counts 71 to 99 , monospondylous vertebral counts 35 to 56 , diplospondylous precaudal counts 7 to 27 . Intestinal valve with 7 to 19 turns. Adults dwarf to moderate-sized and between 16 to 107 cm long but mostly below 80 cm long. Colour: plain or with conspicuous light or dark markings on fins and body. Head, trunk, tail and fin bases with photophores, sometimes forming distinct black photomarks or broad black areas on the ventrolateral surface of the abdomen, flanks or tail. Photophores sometimes confined to ventral surface but often-denser there than on dorsal surface.

Distribution: Lantern sharks have an essentially circumglobal range in boreal, austral, temperate and tropical seas.
Habitat: These are primarily bottom-dwelling deepwater bathic inhabitants of the continental and insular slopes and more rarely the upper rises, but also occur on submarine ridges and seamounts and on the outer continental shelves in water greater than 50 m deep. They range in depth between 70 to at least 2250 m , with one species (Etmopterus princeps) descending to between 3550 and 4500 m on the lower rises of the eastern North Atlantic but with most species not found below 1500 m or above 200 m . A few species (E. gracilispinis, E. pusillus, and possibly several others) are semioceanic and occur in the epipelagic and mesopelagic zones of the open ocean as well as on the continental and insular slopes, but as currently known the family apparently lacks specialized oceanic species such as some members of Somniosidae and most Dalatiidae.

Biology: Reproductive biology is sketchily known for most species, but those species for which information is available they are viviparous with a yolk-sac, and have between 3 and 20 young per litter. The reproductive cycle for most species is unknown, while other species for which some data is available have an undefined reproductive cycle. Age and growth studies for this group are few, but depending on the species may have a maximum longevity of 13 years or as long as 57 years.
Lantern sharks feed mostly on bony fishes including sardines (Clupeidae), lanternfish (Myctophidae), viperfish (Stomiidae), barracudinas (Paralepididae), cod-like fishes (gadoids) including grenadiers (Macrouridae), mackerel (Scombridae), and cephalopods (including cuttlefish and histioteuthid squids), but also eat small squaloid sharks, crustaceans (decapod crabs, penaeid and euphausiid shrimp), jellyfish, and brittle stars. Several etmopterid species are highly social, and form small to huge schools or aggregations, and it has been hypothesized that these sharks may hunt in packs to subdue larger prey items such as cephalopods.
Recent studies by Claes et al. (2010a, b, 2011) and Claes and Mallefet (2008, 2010a, b) have demonstrated the functionality and bioluminescence of the photophores of Etmopterus spinax. It appears that at least for $\boldsymbol{E}$. spinax, and likely many other etmopterids, the photophores provide a means of camouflage for these sharks in the midwater. This ability allows them to both hide from potential predators and ambush prey items. The diet of many etmopterids, which includes midwater fishes, crustaceans, and cephalopods, supports this foraging behaviour.

Interest to Fisheries and Human Impact: Lantern sharks have little importance for fisheries because of the generally small size (below 60 cm ) of most species. In part because of limited fisheries interest, the biology of the family is sketchily known compared to other, more important fisheries for dogfish such as members of the families Squalidae and Centrophoridae. Lantern sharks are often caught and discarded as bycatch of fisheries utilizing bottom trawls, pelagic trawls, fixed bottom nets, line gear including hook-and-line, and in sablefish traps. Some of the more abundant species are dried-salted for human consumption and processed for fishmeal and probably liver oil, which has a high content of squalene. However, the livers of most species are small and probably not of much commercial use except for the few relatively large (over 60 cm maximum length) species of Etmopterus and Centroscyllium. Separate fisheries statistics are seldom reported for the family or for individual species at present, although separate statistics for small catches of some lantern shark species have been recently reported to ICES (2010), including Centroscyllium fabricii, Etmopterus princeps, E. pusillus, and
E. spinax from Denmark, France, Portugal, Norway, Spain, and the United Kingdom; additional countries are probably catching lantern sharks but not reporting them.

The conservation status of lantern sharks globally is very poorly known, but with expanding deepwater fisheries worldwide, inadequate monitoring of deepwater sharks in most areas, limited interest in this group, a high degree of regional endemism, and low public profile these sharks may be of concern. Some etmopterid species may have protection and management under existing European and United States legislation, but imperfect monitoring of etmopterid bycatch and mortality from trawling makes conservation difficult even in protected areas. Of the species occurring in the North Atlantic most are currently assessed as Least Concern or Data Deficient, with the exceptions of Centroscyllium fabricii and Etmopterus spinax, both of which are considered Near Threatened in the Eastern North Atlantic.

Local Names: Lanternsharks or Lantern sharks (general).
Remarks: The present arrangement of the family Etmopteridae follows the cladistic analyses of Shirai and Nakaya (1990b) and Shirai (1992a) in comprising five genera, two of which, Centroscyllium and Etmopterus, occur in the North Atlantic. The other three genera, Aculeola, Miroscyllium, and Trigonognathus, are monotypic and as far as known are confined to the Western North Pacific or Eastern South Pacific. However recent molecular and morphological analysis by Straube et al. (2010) has suggested that Miroscyllium should be transferred to the Etmopterus.

Most etmopterids have distinctive black patches with densely arrayed spherical, multicellular light-emitting organs or photophores on the ventral and lateral surfaces of the body and caudal fins. These luminescent markings are useful for the systematics of many etmopterids, particularly the genus Etmopterus. The use of photophores or photomarks, and there terminology, in etmopterid taxonomy and identification is presented in Ebert and Compagno (In press).

Literature: Müller and Henle (1839, 1841); Günther (1870); Regan (1906a, 1908); Garman (1913); Bigelow and Schroeder (1948, 1957); Bigelow, Schroeder and Springer (1953); Compagno (1984); Cadenat and Blache (1981); Springer and Burgess (1985); Burgess and Springer (1986); Yamakawa, Taniuchi, and Nose (1986); Tachikawa, Taniuchi and Arai (1989); Shirai and Nakaya (1990a, b); Shirai (1992a, 1996); Shirai and Tachikawa (1993); Schofield and Burgess (1997); Last, Burgess, and Seret (2002) Compagno, Dando and Fowler (2005); Schaaf-Da Silva and Ebert (2006); Last and Stevens (2009); Claes and Mallefet (2008, 2010a, b); Claes et al. (2010a, b, 2011); Straube et al. (2010, 2011); Ebert and Compagno (In press).

## Key to North Atlantic Genera:

1a. Lower teeth similarto uppers, not compressed and blade-like, and overlapping or abutting one another (Fig. 88). Mouth arcuate and moderately long . . . . . . . . . . . . . . . . . . . . . Centroscyllium

1b. Lower teeth dissimilar to uppers, compressed, blade-like, and with adjacent teeth overlapping or abutting one another (Fig.
89). Mouth short, nearly straight and transverse


Fig. 88 Centroscyllium


Fig. 89 Etmopterus

## Etmopterus

## Centroscyllium Müller and Henle, 1841

Genus: Centroscyllium Müller and Henle, 1841, Syst. Beschr. Plagiost., pt. 3, suppl.: 191.
Type Species: Centroscyllium fabricii Müller and Henle, 1841 (new combination) by monotypy, equals Spinax fabricii Reinhardt, 1825.

## Number of Recognized North Atlantic Species: 1.

Synonyms: None.
Field Marks: Greyish or blackish-brown, no anal fin, dorsal-fin spines present and large, short to moderately long snout, comb-like teeth with cusps and cusplets in both jaws.

Diagnostic Features: Head broad and flattened, wider than deep. Snout moderately rounded or slightly pointed, flattened and truncated; snout short, preoral length about 0.5 to 1.0 of mouth width. Gill openings about equally wide or increasing in width posteriorly. Spiracles subangular-oval and much shorter than eyes. Mouth subterminal on head, not extending anterior to eye and ending far behind nostrils; mouth broadly arcuate and relatively long to short, length 0.2 to 0.5 of width. Labial furrows
usually with post-labial grooves present. A shallow groove between upper lips and upper jaws. Teeth similar in upper and lower jaws, not fang-like, small, with conical straight cusps and one or two pairs of prominent cusplets, not compressed and blade-like and not imbricated; tooth row counts 45 to 75 upper jaw, 43 to 76 lower jaw. Body stocky to moderately slender. Lateral trunk denticles, where present, with bluntly conical, thorn or bristle-like cusps and stellate bases, denticles usually sparse and spaced well apart. Dorsal-fin spines long, usually stout, and curved, second dorsal-fin spine much larger than the first and with its tip extending just below or opposite apex of second dorsal fin. Dorsal fins high and short, first dorsal-fin length much less than interdorsal space; first dorsal-fin origin usually about opposite or just behind pectoral-fin free rear tips; second dorsal fin usually larger than first but slightly larger or subequal in some species. Vertebral column with primary calcification present, including centra with calcified double cones, notochord constricted, without septa; vertebral column with haemal arches not extending anterior to the monospondylous-diplospondylous transition. Vertebral counts: total vertebral counts 81 to 97 , monospondylous vertebral counts 37 to 46 , diplospondylous precaudal counts 14 to 22 , precaudal vertebral counts 54 to 67 . Intestinal valve with 4 to 10 turns. Body with photophores more dense on the ventral surface than the dorsal surface or absent from the dorsal surface, but usually no conspicuous black photomarks on underside of head and body, flanks, tail and caudal fin (except in Centroscyllium ritteri, which has discrete photomarks). Colour: greyish to blackish-brown above and below; fin webs varying from mostly about as dark as bases to abruptly white or with black and white markings; no naked patch of white skin on edge of upper eyelid.

Local Names: Combtooth dogfishes.
Remarks: Seven species are currently recognized, of which Centroscyllium fabricii(Reinhardt, 1825) is the only species known to occur in the Atlantic, all other six members of the genus occur in the Pacific or Indian oceans.

## Centroscyllium fabricii (Reinhardt, 1825)

Spinax fabricii Reinhardt, 1825, Overs. K. Danske Vidensk. Selsk. Forh. (1824-1825): 3. Syntypes (1): Kobenhavns Universitet Zoologisk Museum (Zoological Museum, University of Copenhagen), Copenhagen, Denmark, UZMK or ZMUK 185, stuffed specimen, Julianehaab, West Greenland. Type status from Krefft and Tortonese 1973: 40 and Eschmeyer (1998, Cat. Fish.).

## Synonyms: None

## Other Combinations: None.

FAO Names: En - Black dogfish; Fr - Aiguillat noir; Sp - Tollo negro merga.


Fig. 90 Centroscyllium fabricii
Field Marks: No anal fin. First dorsal fin with a low subangular fin web. Two grooved dorsal-fin spines, the first low and the second moderately high. Teeth with narrow cusps and cusplets in both upper and lower jaws. Denticles high, conical and sharp-cusped, dense and numerous on dorsal and ventral surfaces of body; skin firm. Abdomen long, caudal peduncle short. Colour uniform blackish-brown above and below, without white fin markings or discrete black photomarks on body.

Diagnostic Features: Preoral snout about 32 to $36 \%$ of head length. Mouth moderately arched and about 35 to $38 \%$ as long as wide. Body moderately stout and compressed; caudal peduncle short with pelvic-caudal space about 11 to $14 \%$ of total length. Teeth similar in upper and lower jaws, with a single large, acutely pointed central cusp, flanked by 1 or 2 lateral cusplets; tooth count from a single individual was 68 (upper jaw) and 68 (lower jaw). Denticles close-set and numerous on body; lateral trunk denticles conical and with sharp hooked cusps. Pectoral-fin apices when laid back ending well anterior to first dorsal-fin spine origin. First dorsal fin low with height about 0.4 times base length, fin semi-elliptical or subtriangular in shape; first dorsal-fin
spine short, much lower than second dorsal-fin spine, and ending below first dorsal-fin apex and far anterior to it. Second dorsal fin considerably larger than first dorsal fin; second dorsal-fin spine short to elongated, extending to below or about the height of second dorsal-fin apex but ending far anterior to it; origin of second dorsal-fin spine over or just behind pelvic-fin insertions. Vertebral counts: total vertebral counts 87 to 97 , precaudal vertebral counts 60 to 67 , monospondylous vertebral counts 43 to 46. Intestinal valve counts 7 to 10 . Size moderate, with adults to 107 cm . Colour: blackish brown above and below, without conspicuous black markings on ventral surface or sides of tail; fins without white markings.

Distribution: Eastern Atlantic: from Iceland along the Atlantic Slope, including the Iceland-Faroe Ridge, to the Faroe Islands, southern Norway, Rockall Trough and Porcupine Seabight to Morocco, Mauritania, Senegal, Guinea, Sierra Leone, Namibia, and South Africa. Western North Atlantic: it occurs from Greenland south to Canada (Baffin Island, Labrador, Newfoundland, and Nova Scotia) and the USA (south to Virginia and possibly North Carolina) and in the northern Gulf of Mexico. Western South Atlantic records from off Argentina (Beagle Channel) should be closely examined to determine whether this or a similar, but different species occurs there.

Habitat: One of the most abundant deepwater schooling shark of the outermost continental shelves and slopes at depths ranging from 180 to 2250 m , but mostly below 275 m . At high latitudes in the North Atlantic it may move up to near the surface, especially during the winter and when darkest at night. This species at its northern most extremes does not range into truly Arctic


Fig. 91 Centroscyllium fabricii
Known distribution waters but occurs on the fringe in the boreal North Atlantic. Water temperatures at the bottom where these sharks are most commonly caught are 3.5 to $4.5^{\circ} \mathrm{C}$, but sometimes down to $1.0^{\circ} \mathrm{C}$.

Biology: Yolk-sac viviparous, with late term embryos to at least 18 cm long, but free-swimming between 16 and 19 cm in length. Litter size varies by location, with those off western Greenland having up to 40 eggs or near-term embryos having been found in utero, but off southern Africa females have been found with 7 and 8 embryos, with up to 14 eggs in the oviducts. In the North Atlantic there does not appear to be a defined reproductive season, although more gravid females appear to be present between August and November than at other times of the year. Hermaphrodism has been observed in this species with individuals having both ovaries and testes.
Food items reported from North Atlantic specimens primarily include teleosts (gadoids mackerel, myctophids), crustaceans (pelagic crustaceans and demersal decapod crabs), and cephalopods. Elsewhere, off Namibia and the West Coast of South Africa this shark feeds primarily on crustaceans, especially penaeid shrimp but also euphausiids and secondarily on cephalopods, lanternfish (Myctophidae, including Diaphus sp.), barracudinas (Paralepididae) and unidentified teleosts. Behaviorial observations of Centroscyllium fabricii from submersibles reveal these sharks to be quite active swimmers, often occurring above the bottom. These observations combined with known prey items including myctophids, pelagic crabs, and cephalopods suggest that these sharks are active feeders in the midwater. Fish offal also appears to be a major component of the diet of this shark where bottom trawling occurs such as in the Flemish Pass in Canadian waters where C. fabricii larger than 69 cm were found to primarily consume Greenland halibut (Reinhardtius hippoglossoides) and macrurid heads. The North Atlantic population exhibits strong evidence of segregation by sex and size within populations and of movements of schools into shallower water and increase in school size during winter and spring. This shark appears to segregate with smaller individuals ( $<48 \mathrm{~cm}$ total length) occurring shallower (mostly less than 800 m ) than the adults which occur mostly over 750 m . In the northwest Atlantic as the Laurentian Channel (entrance to Gulf of St. Lawrence) small juveniles (young of the year, $15-30 \mathrm{~cm}$ ) are highly concentrated in the deepest parts of the channel while mature females distribute on the slope of the channel. Fish $<30 \mathrm{~cm}$ only rarely occur outside the Channel (and in close proximity). So, it appears that females, from as far as thousands of km away, come to the channel to give birth. These observations are from the spring (Kulka, 2006). In Icelandic waters, females tend to predominate at depths below 1000 m , while males were more abundant in shallower waters. Also, adult females appear to segregate into the eastern waters off Iceland, while in the waters westward mostly males of all maturity stages and immature females occurred.
This shark has luminescent organs (photophores) scattered randomly over its skin, but apparently not arranged in regular photomarks as in some other Centroscyllium species.

Size: Maximum total length about 107 cm in the North Atlantic; males mature at about 55 to 57 cm and females at about 65 to 70 cm ; size at birth 15 to 20 cm .

Interest to Fisheries and Human Impact: Interest to fisheries limited, although it is taken as retained bycatch mainly by French trawl fisheries operating in the Eastern North Atlantic. Between 2000 and 2009 an average of 73 tonnes were landed annually, but the highest landings were between 2000 and 2004 (average 136 tonnes) prior to total allowable catch (TACs) regulations being implemented and set for deepwater sharks in ICES subareas V, VI, VII, VIII, and IX. After TACs were established the approximate average landings of Centroscyllium fabricii declined to about 23 tonnes between 2005 and 2009. However, the estimated landing is likely underestimated, and this species is still likely taken as bycatch, and landed, but not identified to species. In the Western North Atlantic this is a very abundant and commonly taken as bycatch in a number of groundfish fisheries. The biomass of this species, which is taken in these fisheries, is unknown, but considered to be substantial. However, the adult population appears to be stable in the Western North Atlantic. Under TAC regulation in EU (in 2012, $\mathrm{TAC=0}$ ) ( $\mathrm{EU}, 2010$ ). Technical measures in force in EU waters and NEAFC regulatory area (2012).

Conservation status is Least Concern globally, but in the Eastern North Atlantic, where it is taken as bycatch in other fisheries, it is listed as Near Threatened because of intensive fisheries on the deep slopes following depletion of demersal fish stocks on the continental shelves and fishing banks.

Local Names: Svart piggaj (Sweden); Fabricius-Dornhai (Germany); Svartháfur (Iceland).
Remarks: It is uncertain if North Atlantic, Western South Atlantic, and Eastern South Atlantic representatives of this species form discrete populations, or may represent different species. They should be critically compared to determine if they comprise a single species.

Literature: Goode and Bean (1895, 1896); Jordan and Evermann (1896); Regan (1908); Garman (1913); Fowler (1936); Bigelow and Schroeder (1948, 1954, 1957); Templeman (1963); Krefft and Tortonese in Hureau and Monod (1973b); Markle and Musick (1974); Sedberry and Musick (1978); Cadenat and Blache (1981); Mauchline and Gordon (1983); Lleonart and Rucabado (1984); McEachran and Branstetter in Whitehead et al. (1984); Haedrich and Merrett (1988); Shirai and Nakaya (1990a); Springer in Quero et al. (1990); Merrett et al. (1991a): Ebert, Compagno and Cowley (1992); Bianchi et al. (1993); Menni, Burgess and Garcia (1993); Yano (1995); Punzón and Herrera (2000); Jakobsdóttir (2001); Compagno, Dando and Fowler (2005); Kulka (2006); Ebert et al. (2008a); Gibson et al. (2008); Baker, Devine, and Haedrich (2009); EU (2010); ICES (2010); Ebert and Compagno (In press); D.A. Ebert (unpubl. data).

## Etmopterus Rafinesque, 1810

Genus: Etmopterus Rafinesque, 1810, Caratt. gen. sp. anim. piant. Sicilia, Palermo, pt. 1: 14.
Type Species: Etmopterus aculeatus Rafinesque, 1810, by monotypy, equals Squalus spinax Linnaeus, 1758.

## Number of Recognized North Atlantic Species: 5.

Synonyms: Genus or subgenus Spinax Cloquet, 1816, Dict. Sci. Nat., ed. 1 (2?), 1, suppl., 93 (not seen); Subgenus Spinax Cuvier, 1817, Reg. Anim., ed. 1, 2: 129 (genus Squalus Linnaeus, 1758). Type species: Squalus spinax by absolute tautonymy. Probably also subgenus Spinax Bosc et al. 1816-1819, Nouvelle Dictionnaire d'Histoire Naturelle, according to Whitley (1935, Aust. Zool. 8[2]: 136). Genus Centrina Lowe, 1833, Proc. Zool. Soc. London, 1833 (1): 144; not Centrina Cuvier 1817 = Oxynotus Rafinesque, 1810. Genus Acanthidium Lowe, 1839, Proc. Zool. Soc. London, 1839 (7): 91. Type species: A. pusillum Lowe, 1839 (= Etmopterus pusillus), by subsequent designation by Jordan and Evermann (1896, Bull. U.S. Natn. Mus. (47, pt. 1): 55) and Goode and Bean (1896, Oceanic Ichthyol., Smithson. Inst. Spec. Bull:: 10); genus Acanthidim Sollas, 1906, Zool. Rec. 43, Pisces, 1907: 58. Erroneous spelling.

Field Marks: Moderately long snout. Upper teeth with cusp and cusplets, lower teeth blade-like. No anal fin. Second dorsal fin and fin spine larger than first dorsal fin and spine.

Diagnostic Features: Head broad and flattened, wider than deep, or cylindroconical and about as wide as deep. Snout broadly rounded to slightly pointed and with a wedge-shaped tip, flattened or subconical; snout moderately elongated, preoral length about 0.9 to 1.7 of mouth width. Spiracles subangular-oval and much shorter than eyes. Gill openings about equally wide. Mouth subterminal on head, not extending anterior to eye and ending far behind nostrils; mouth short and very broadly arched, nearly transverse, length 0.2 to 0.5 of mouth width. Labial furrows with postlabial grooves present. A shallow groove between upper lips and upper jaws. Teeth strongly differentiated in upper and lower jaws, upper teeth small, not fang-like, with a strong, conical nearly straight cusp and one, two or several pairs of prominent cusplets; lower dentition compressed, imbricated, and blade-like, with a flattened cusp, no cusplets, and a distal blade; tooth row counts upper jaw 18 to 38, lower jaw 24 to 55 . Body stocky to slender. Lateral trunk denticles with thorn or bristle-like conical or hooked cusps, or flat, truncate, and without cusps, bases cross-shaped; denticles usually spaced close together. Dorsal spines usually large and strongly curved; second dorsal-fin spine usually much larger than first and extending to apex of
second dorsal fin. Dorsal fins high and short; first dorsal-fin length much less than interdorsal space; first dorsal-fin origin varying from opposite pectoral-fin free rear tips to well behind them; second dorsal fin noticeably larger than first. Vertebral column with primary calcification present, including centra with calcified double cones, notochord constricted, without septa; vertebral column with haemal arches extending five to nine centra anterior to the monospondylous-diplospondylous transition. Vertebral counts: total vertebral counts 68 to 99 , precaudal vertebral counts 53 to 73 , monospondylous vertebral counts 36 to 56 . Intestinal valve with 9 to 19 turns. Body often with photophores more dense on the ventral surface than the dorsal surface, conspicuous black photophore patches often present on underside of head and abdomen, flanks, tail and caudal fin but obscure or absent in some species. Colour: variable, from blackish to tan above, often black below; fin webs varying from not much lighter than the bases to abruptly lighter; a hemicircular or elongated patch of white skin on edge of upper eyelid in some species.

Biology: Reproduction is yolk-sac viviparous with litters ranging from 1 to 21 . Virtually nothing is known on the reproductive cycle of these sharks. Most of those whereby some data is available indicates that they have an undefined reproductive cycle with gravid females being present in some populations year round. Virtually nothing is known about the age and growth of these sharks. Depending on the species some may mature in as little as 5 to 8 years or as much as 20 to 30 years. Some species may live for only 13 years while others may have longevity of up to 57 years.

It has long been speculated that the social behavior of some Etmopterus species to forage in packs (pack-hunting) allows these relatively small sharks to capture and consume prey items that a single individual would not be able to capture alone. The elaborate photomarks and photolines of many Etmopterus species may help groups or schools to coordinate their movements while hunting or when engaged in other social activities. Etmopterus species may be successful by combining relatively small size, social feeding, and powerful feeding structures (a grabbing, cutting and dismembering dentition in strong, short jaws), which allows them to take advantage of a broad variety of small to large prey on the slopes including bony fish and invertebrates that are larger than they can swallow whole and are too large for a single individual to overcome.

## Local Names: Lantern sharks (general).

Remarks: This is one of the most speciose genera of sharks worldwide with 37 nominal species currently recognized. The genus has several species-complexes that will likely reveal additional species making it, along with the Apristurus, among the most species-rich genera of sharks. The group appears to exhibit a high degree of endemism with several species having a restricted distributional range. In the North Atlantic five species are currently recognized, with only Etmopterus princeps known to occur in both Areas 21 and 27.

The vernacular name 'lantern shark' is descriptive of the minute photophores of these sharks that are also found in other members of the family.

## Key to North Atlantic Species:

1a. Skin smooth, denticles with low, flat, concave, sessile crowns atop low bases (Fig. 92) . . . . .

## Etmopterus pusillus

1b. Skin with a fuzzy or rough texture, denticles with erect, thorn-like, cuspidate crowns, more or less elevated from their bases (Fig. 93) . . . . . . . . . . 2

2a. Denticles on flanks, caudal peduncle, and caudal bases in regular longitudinal lines (Fig. 93)

## Etmopterus princeps

2b. Denticles on sides of body randomly arranged, not in regular lines 3

3a. Distance from pelvic-fin insertions to lower caudal origin only about half as long as distance between pectoral and pelvic-fin bases (Fig. 94)

## Etmopterus spinax

3b. Distance from pelvic-fin insertions to lower caudal-fin origin at least $2 / 3$ and often as long as distance between pectoral and pelvic-fin bases


DERMAL DENTICLES (Dorsal view)
Fig. 92 Etmopterus pusillus


DERMAL DENTICLES (Lateral view)
Fig. 93 Etmopterus princeps
(Fig. 96) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4


Fig. 94 Etmopterus spinax

4a. Colour black or grey above and below, without prominent markings, obscure pelvic markings present in some species; first dorsal-fin spine well behind pectoral-fin rear tips (Fig. 95)

Etmopterus gracilispinis

4b. Colour lighter above and with prominent black markings below; first dorsal-fin spine about opposite pectoral-fin rear tips (Fig. 96)

Etmopterus hillianus


Fig. 95 Etmopterus gracilispinis


Fig. 96 Etmopterus hillianus

## Etmopterus gracilispinis Krefft, 1968

Etmopterus gracilispinis Krefft, 1968, Arch. Fischereiwiss. 19(1): 3, Figs. 2, 3a, 4, 5a. Holotype: Institut für Seefischerei, Hamburg, ISH-1051/66, 255 mm TL subadult male, $34^{\circ} 01^{\prime} \mathrm{S}, 51^{\circ} 20^{\prime} \mathrm{W}, 600 \mathrm{~m}$.

Synonyms: None.
Other Combinations: None.
FAO Names: En - Broadbanded lanternshark; Fr - Sagre rubané; Sp - Tollo lucero bandoneado.




UPPER AND LOWER TEETH


DERMAL DENTICLES

Fig. 97 Etmopterus gracilispinis
Field Marks: A small stout bodied species with a short slender tail; a short, bulbous stout, and a very short gill openings. Lateral trunk denticles irregular. A blackish brown body dorsally becoming black ventrally, with an inconspicuous elongated black flank markings extending anterior and posteriorly; anterior marking longer than posterior.

Diagnostic Features: Head fairly deep and flattened-conical; head relatively long, 22 to $25 \%$ of total length and about 2.7 times in snout-vent length; head width about 1.3 times preoral snout; head low with height about $9 \%$ of total length. Prespiracular length subequal to spiracle-pectoral space. Snout somewhat bulbous; preoral length short and about 9\% of total length. Eyes narrow and elongated-oval; upper eyelid without a pale naked patch. Gill openings about as wide as spiracle; width of third gill opening one-third eye length or less. Mouth relatively broad and 1.5 times eye length. Upper teeth generally with less than 3 pairs of cusplets and with cusps greatly expanded, about 2.5 times higher than adjacent cusplets; condition of upper teeth in mature males uncertain. Total tooth row counts upper jaw 24 to 27, lower jaw 25 to 32. Body moderately firm, cylindrical, not compressed, and moderately slender. Predorsal spine length about 39 to $41 \%$ of total length; interdorsal space less than prebranchial length and subequal to prespiracular space; pectoral-pelvic space about 1.3 times head length in adults; snout tip to rear flank marking base slightly greater than snout tip to second dorsal-fin spine origin; dorso-caudal space 9 to $12 \%$ of total length and about 1.6 in interdorsal space; pelvic-caudal space 15 to $16 \%$ of total length, about 1.5 times first dorsal-fin length, about 1.1 times interdorsal space, shorter than prebranchial length
and much shorter than head, and 1.4 to 1.6 in pectoral-pelvic space. No rows of greatly enlarged denticles on flanks above pectoral fins; denticles largely covering underside of snout; denticles not in regular longitudinal rows on head, flanks, caudal peduncle, and caudal base; denticles present on second dorsal fin, apparently densely covering it; lateral trunk denticles short, small and slender, closely spaced, with very slender, high, hooked conical crowns. Distal margins of fins fringed with a broad band of naked ceratotrichia. Pectoral fin small with anterior margin length about 8 to $9 \%$ of total length, subangular in shape. First dorsal-fin origin well behind pectoral-fin free rear tips, base slightly closer to pelvic-fin bases than pectorals; first dorsal-fin spine slender, short, and lower than first dorsal-fin apex, with origin about equidistant between upper caudal-fin origin and snout tip or closer to the caudal-fin origin. Second dorsal fin much larger than first and about twice its area, height about 23 to $32 \%$ of second dorsal-fin length, apex rounded-angular, posterior margin shallowly concave; second dorsal-fin spine slender and slightly recurved, with its tip diagonally vertical in adults. Dorsal caudal-fin margin about equal to head length. Vertebral counts: total vertebral counts 71 to 83 , precaudal vertebral counts 53 to 57 , monospondylous vertebral counts 37 to 41 . Intestinal valve counts 9 to 11 . Size small with adults 26 to 33 cm . Colour: dark brown to blackish-brown on dorsal surface, underside of snout and abdomen black, dorsal surface lighter, ventral surface conspicuously dark; fins light distally, terminal lobe and proximal web of caudal fin dark, but no conspicuous dark bands at tip and through middle of caudal fin; a small conspicuous triangular white pineal blotch present on dorsal surface of head. No conspicuous photolines on body. Suprapelvic photomark present and running behind pelvic fins. Flank photomarks present; flank photomark base very broad and extending anterior and posterior to second dorsal-fin spine; anterior branch of flank photomark moderately long and very broad, longer than posterior branch; posterior branch about $50 \%$ as long as anterior branch; posterior branch broad and bluntly pointed, conspicuous, merging ventrally with post-pelvic photomark and not extending behind free rear tip of second dorsal fin. Ventral saddle-shaped precaudal photomark absent from middle of caudal peduncle. Caudal photomarks present; caudal base photomark present, with anterior branch broad, enveloping ventral surface and extending onto lateral surfaces of caudal peduncle; caudal base photomark with a blunt-tipped, elongated posterior branch about $6 \%$ of total length. No oval central caudal photomark. Straight upper caudal photomark.

Distribution: Western Atlantic: Atlantis Canyon ( $39^{\circ} 57^{\prime} \mathrm{N}, 70^{\circ} 18^{\prime} \mathrm{W}$ ) off New England (USA) southward to Florida and the northern Gulf of Mexico and from off Surinam, Brazil (Rio Grande do Sul), Uruguay and Argentina. Absent from the Eastern North Atlantic.

Habitat: From the outer continental shelves and upper-middle slopes, on or nearthe bottomatdepths of 100 to 1000 m ; also epipelagic and mesopelagic at depths of 70 to 480 m over water 2240 m deep off Argentina.

Biology: Almost entirely unknown, except that it is viviparous with a yolksac.

Size: Maximum total length about 33 cm ; males mature at or above 26 cm ; females mature at 33 cm ; size at birth unknown, but the smallest freeswimming individual was 13 cm in length.

Interest to Fisheries and Human Impact: Interest to fisheries none given its small size, although it may be taken as bycatch on occasion in some fisheries.


Fig. 98 Etmopterus gracilispinis
$\square$ Known distribution

Conservation status of this species is Least Concern although it may on occasion be taken as bycatch its small size and widespread distribution across the Western Atlantic minimize it vulnerability to fishing pressure.

Local Names: Broadband lanternshark.
Remarks: Namibian and South Africa records of this species are most likely that of a different species, Etmopterus compagnoi.

Literature: Kreff (1968, 1980); Schwartz and Burgess (1975); Cadenat and Blache (1981); Compagno (1984); Sadowsky, Arfelli and Amorim (1986); Kiraly, Moore, and Jasinski (2003); Moore et al. (2003); Burgess et al.(2007); Gianeti and Vooren (2008); Ebert and Compagno (In press).

## Etmopterus hillianus(Poey, 1861)

Spinax hillianus Poey, 1861. Memorias Hist. Nat. Cuba, 2: 340, pl. 19, Figs. 13-14. Holotype: Museum of Comparative Zoology, Harvard, MCZ-1025, 269 mm TL female, off Havana, Cuba.

## Synonyms: None.

## Other Combinations: None

FAO Names: En - Caribbean lanternshark; Fr - Sagre antillais; Sp - Tollo lucero antillano.



UNDERSIDE OF HEAD

Fig. 99 Etmopterus hillianus

Field Marks: A very small lantern shark with a stout body, short, flattened snout, and a moderately long tail. Dermal denticles covering snout; denticles not arranged in longitudinal rows along trunk. Gill openings very short. Interdorsal space short. Grey to brown dorsally, black ventrally. Flank markings include a long, broad anterior branch extending over the pelvic fins and a short, truncated posterior branch that is less than $50 \%$ the length of the anterior branch.

Diagnostic Features: Head broad and flattened, not conical; head relatively long, about 21 to $22 \%$ of total length and 2.2 to 2.4 times in snout-vent length; head width about 1.3 to 1.4 times preoral snout; head low, height about 9 to $10 \%$ of total length. Prespiracular length 1.4 to 1.7 times spiracle-pectoral space. Snout flattened, not bulbous; preoral length short and 9 to $10 \%$ of total length. Eyes narrow and elongate-oval; upper eyelid apparently without a pale naked patch. Gill openings somewhat wider than spiracle; width of third gill opening one-third eye length or less. Mouth relatively broad and 1.3 to 1.6 times eye length. Total tooth row counts upper jaw 24 to 26 , lower jaw 36 to 38 ; upper teeth generally with less than 3 pairs of cusplets ( 2 to 4 pairs), cusps greatly expanded, about 1.5 to 2 times higher than adjacent cusplets; upper teeth of mature males large with a cusp and two pairs of short cusplets. Body moderately firm, cylindrical, and moderately slender. Predorsal spine length about 35 to $37 \%$ of total length; interdorsal space slightly longer than prebranchial length and shorter than head length; pectoral-pelvic space about 0.9 to 1.2 times head length in adults; snout tip to rear flank marking base over $100 \%$ of snout tip to second dorsal-fin spine origin; dorso-caudal space 10 to $13 \%$ of total length, about 1.4 to 1.9 in interdorsal space; pelvic-caudal space 19 to $21 \%$ of total length, about 2.1 to 2.2 times first dorsal-fin length, about 1.0 to 1.2 times interdorsal space, longer than prebranchial length, subequal to head length, and subequal to about 1.3 in pectoral-pelvic space. No rows of greatly enlarged denticles on flanks above pectoral fins; denticles largely covering underside of snout; denticles on head, flanks and tail not arranged in regular longitudinal rows; denticles present on second dorsal fin, densely covering it; lateral trunk denticles elongated, wide-spaced, and with slender, hooked conical crowns. Distal margins of fins not fringed with naked ceratotrichia. Pectoral fins moderately small with anterior margin length 8.5 to $11 \%$ of total length, rounded-subangular in shape. First dorsal-fin origin just behind or about opposite pectoral-fin free rear tips, base closer to pectoral-fin bases than pelvic fins; first dorsal-fin spine stout, short, and usually lower than first dorsal-fin apex, spine origin nearer snout tip than upper caudal-fin origin. Second dorsal fin much larger than first but less than twice its area, height 39 to $43 \%$ of second dorsal-fin length; apex narrowly rounded, and posterior margin broadly to deeply concave; second dorsal-fin spine stout and moderately recurved, with its tip obliquely vertical in adults. Dorsal caudal-fin margin about equal to head length or slightly shorter. Vertebral counts: precaudal vertebral counts 54 to 59 . Size small with adults 20 to 28 cm . Colour: grey or dark brown on dorsal surface, underside of snout and abdomen abruptly black, dorsal surface lighter, ventral surface conspicuously dark, with a light lateral band on head, flank and tail base separating the two; precaudal fins light distally, abruptly dark basally; conspicuous dark bands across terminal lobe and through anterior half of caudal fin, with a light band between them; condition of white pineal blotch unknown. Horizontal photolines of dashes and individual photophores present on back and dorsal flanks. Suprapelvic photomark present and running behind pelvic fins. Flank photomarks present; flank
photomark base opposite and behind second dorsal-fin spine; anterior branch of flank photomark long and broad, much longer than posterior branch, posterior branch less than $50 \%$ of anterior branch; posterior branch of flank photomark truncate, merging ventrally with post-pelvic photomark, and not extending behind free rear tip of second dorsal fin. Ventral saddleshaped precaudal photomark absent from middle of caudal peduncle. Caudal photomarks present; caudal-base photomark present, with anterior branch broad but not enveloping ventral surface of caudal peduncle and not extending onto its sides; caudal-base photomark with a short posterior branch less than $2 \%$ of total length that has a bluntly angular or truncate rear tip. Central caudal photomark absent. Upper caudal photomark present, this long and straight.

Distribution: Western North Atlantic: Virginia at about $38^{\circ} \mathrm{N}$ to southern Florida (USA), Bahamas, Cuba, Bermuda, Hispanola, and northern Lesser Antilles. Also the northern Gulf of Mexico from the Florida Panhandle to the Mississippi River Delta; not known from western or southern Caribbean.

Habitat: A species of the upper continental and insular slopes, on or near bottom, at 311 to 695 m depth (average 481 m ), with most records above 641 m .

Biology: Viviparous with a yolk-sac, number of young per litter between 4 and 5.

Size: Maximum total length at least 28 cm for females and 26 cm for males; males mature at about 20 cm TL; size at birth about 9 cm . Reports of this species reaching a maximum total length of 50 cm are likely through confusion with Etmopterus robinsi, a sympatric congener from the southern portion of $E$. hillianus distribution.


Fig. 100 Etmopterus hillianus
Known distribution

Interest to Fisheries and Human Impact: Interest to fisheries none given its very small size. It is likely caught on occasion as bycatch in bottom trawl fisheries, but discarded.

The conservation status of this species is Least Concern.
Local Names: None.
Literature: Bigelow and Schroeder (1948, 1957); Schwartz and Burgess (1975); Cadenat and Blache (1981); Springer and Burgess (1985); Schofield and Burgess (1997); Kiraly, Moore, and Jasinski (2003); Herndon and Burgess (2006a); Ebert and Compagno (In press).

## Etmopterus princeps Collett, 1904

Etmopterus princeps Collett, 1904, Christ. Vidensk-Selsk. forhandl. 1904(9): 3. Syntypes (4): Zoologisk Museum, Oslo, ZMO 364 (2 specimens), ZMO-365 (1 specimen), Zoologisk Museum Universetet i Bergen UBNM-3496 (1 specimen), lectotype apparently not designated, all from Faroe Channel, Faroe Bank, 750-1200 m.

Synonyms: None.
Other Combinations: Spinax princeps Regan, 1908; Koefoed 1927.

FAO Names: En - Great lanternshark; Fr - Sagre rude; Sp - Tollo lucero raspa.


## Fig. 101 Etmopterus princeps

Field Marks: A very large, heavy-bodied, broad-headed, short-tailed, uniform-coloured, blackish lanternshark with a short thick flat snout. Upper teeth with a cusp and one or more pairs of cusplets, lower teeth compressed, knife-like, and with a cusp and blade. Lateral trunk denticles wide-spaced and moderately large, with stout cusps, giving the body a rough texture, forming inconspicuous, regular longitudinal rows on caudal peduncle and caudal-fin base. Two dorsal fins with fin spines, first dorsal fin smaller than second dorsal fin, second dorsal-fin spine recurved and pointing posterodorsally in adults. No anal fin. Discrete photomarks absent.

Diagnostic Features: Head fairly deep but not conical; head relatively long, 19 to $25 \%$ of total length and 2.4 to 3.0 times in snout-vent length; head width about 1.5 to 1.6 times preoral snout; head low, height 10 to $12 \%$ of total length. Prespiracular length 1.6 to 1.7 times spiracle-pectoral space. Snout flattened and semibulbous, not conical; preoral length short and about 9 to $10 \%$ of total length. Eyes narrow and elongated; upper eyelid apparently without a pale naked patch. Gill openings much wider than spiracle; width of third gill opening about a third to half eye length. Mouth relatively broad and 1.4 to 1.7 times eye length. Total tooth row counts upper jaw 29 to 32, lower jaw 40 to 50 . Upper teeth generally with one or two pairs of cusplets, cusps moderately expanded and about 1.5 to 3 times higher than adjacent cusplets; upper teeth of mature males large with a cusp and a pair of long cusplets. Body moderately firm, cylindrical, and stout. Predorsal spine length about 33 to $37 \%$ of total length; interdorsal space usually greater than prebranchial length, slightly shorter to slightly longer than head length; pectoral-pelvic space about 1.3 to 1.5 times head length in adults; snout tip to rear flank marking base not comparable to snout tip to second dorsal spine origin; dorso-caudal space 8.6 to $9.8 \%$ of total length and about 2.0 to 2.6 in interdorsal space; pelvic-caudal space 12 to $15 \%$ of total length, about 1.2 to 1.7 times first dorsal-fin length, 1.4 to 1.8 in interdorsal space, subequal to or slightly greater than prespiracular space and less than or subequal to prebranchial length, and 1.7 to 2.4 times in pectoral-pelvic space. No rows of greatly enlarged denticles on flanks above pectoral fins; denticles largely covering underside of snout, except for naked areas at lips and sometimes in the midline of the snout; denticles not in regular longitudinal rows on head and flanks but with linear denticles on caudal peduncle and base of caudal fin; denticles present on second dorsal fin, mostly covering it except for outer margin of fin web; lateral trunk denticles short, robust, wide-spaced, and with stout, hooked conical crowns. Distal margins of fins not fringed with naked ceratotrichia. Pectoral fin small with anterior margin length about 8.0 to $8.9 \%$ of total length, broadly rounded or rounded-angular in shape. First dorsal-fin origin behind pectoral-fin free rear tips, base somewhat closer to pectoral-fin bases than pelvic fins; first dorsal-fin spine stout, short, and usually lower than first dorsal-fin apex, spine origin nearer to snout tip than upper caudal-fin origin. Second dorsal fin much larger than first but less than twice its area, height 32 to $40 \%$ of second dorsal-fin length, apex more or less pointed or rounded angular, and posterior margin nearly straight to deeply concave; second dorsal-fin spine stout and recurved, with its tip diagonally vertical in adults. Dorsal caudal-fin margin about equal to head length. Vertebral counts: total vertebral counts 81 to 86 , precaudal vertebral counts 58 to 60 , monospondylous vertebral counts 44 to 47 . Size large with adults to about 89 cm . Colour: black or blackish-brown on dorsal surface, underside of snout, abdomen and tail blackish, dorsal and ventral surfaces dark, ventral surface not conspicuously darker than dorsal surfaces; fins dark distally, except second dorsal rear tip which is sometimes lighter, no conspicuous dark bands on caudal fin; no light pineal blotch on dorsal surface of head. No photolines on body. Suprapelvic black bar absent. Flank photomarks absent. Ventral saddle-shaped precaudal photomark absent from caudal peduncle. Caudal photomarks absent.

Distribution: Eastern North Atlantic: Denmark Strait between Greenland and Iceland, southern Iceland along Atlantic slope to Faroe Islands, Norway, Scotland (including Rockall Trough), Ireland, south-west England, Bay of Biscay, France, Spain, Portugal, Gibraltar, the Azores, and southward to Morocco, Mauritania, Canary Islands, and possibly Sierra Leone. Western North Atlantic: Nova Scotia (Canada) to Massachusetts, Connecticut, New York, and New Jersey (USA).

Habitat: A lanternshark of the continental slopes, on or near bottom at depths of 350 to 2213 m, also Lower Rise between 3750 and 4500 m in North Atlantic. In the North Atlantic these sharks are most abundant between 800 and 1000 m . The population in the North Atlantic around Iceland appears to segregate by depth and size, with larger individuals occurring shallower than 600 m , but the mean size range progressively decreases with increasing depth.

Biology: Viviparous with yolk-sac, litters average 10. There appears to be at least two peak seasons annually when the majority of these sharks appear to reproduce, in June and July, and again in October. The diet includes teleosts (mostly Myctophidae), cephalopods, and crustaceans. The high proportion of teleosts, particularly myctophids, suggests that Etmopterus princeps may feed far off the bottom, possibly in the midwater.

Size: Maximum total length about 89 cm ; $50 \%$ maturity is attained by males at about 57.3 cm and females at 62.2 cm . Size at birth 12 to 17 cm .


Fig. 102 Etmopterus princeps
Known distribution

Interest to Fisheries and Human Impact: Interest to fisheries limited. It is taken, as bycatch and retained, in groundfish fisheries in the Eastern Atlantic but species-specific details are poorly known. Approximately 20 tonnes of this species were landed in 2008, but fishing mortality from discards is likely much higher. Under TAC regulation in EU (in 2012, TAC=0). When accidentally caught with longlines, this species shall not be harmed and specimens shall be promptly released (EU, 2010). Technical measures in force in EU waters and NEAFC regulatory area (2012).

Conservation status is Data Deficient due to a lack of information on its biology and fisheries data.
Local Names: Rough sagre, Great lantern shark (USA); Dökkháfur (Iceland);Großer scwarzer Dornhai (Germany); Collett's búksvarti háur (Faroe Islands).

Literature: Bigelow, Schroeder and Springer, (1953); Bigelow and Schroeder (1957); Krefft and Tortonese (1973b); Cadenat and Blache (1981); Haedrich and Merrett (1988); Santos, Porteiro and Barreiros (1997); Jakobsdóttir (2001); Kiraly, Moore, and Jasinski (2003); Moore et al. (2003); Herndon and Burgess (2006b); Kulka (2006); Gibson et al. (2008); EU (2010); ICES (2010); Ebert and Compagno (In press).

## Etmopterus pusillus (Lowe, 1839)

Acanthidium pusillum Lowe, 1839, Proc. Zool. Soc. London, 1839 (7): 91. Replacement name for Centrina nigra Lowe, 1833. Syntypes: Four specimens mentioned by Lowe, 1839, 11-12" long, from Madeira Islands. Two specimens in British Museum (Natural History), BMNH-1855.11.29.27 from Madeira and presumably received from Lowe are considered syntypes by Krefft and Tortonese (1973, in Hureau and Monod, Check-list fish. NE Atlantic Mediterranean, 1: 43) and by Shirai and Tachikawa (1993, Copeia 1993[2]: 484-485) but these specimens, a 332 mm female and a 213 mm immature male, do not fall in the size range indicated by Lowe (1839, loc. cit.) if he is taken literally ( $280-305 \mathrm{~mm}$ ). Günther (1870, Cat. Fish. British Mus. 8: 425) noted the following material: "a, b, c, d, e-f, g-i, k-m. Adult examples ( 12 inches long). Madeira. Among them the typical examples". This suggests that some eleven examples of the species were received from Madeira (possibly all from Lowe) by Günther's time, and that the specimens considered as types by Krefft and Tortonese may not be so. A search of the $\mathrm{BM}(\mathrm{NH})$ collection will be necessary to see if any additional Lowe specimens are present that might be the real syntypes. According to P. Whitehead in Shirai and Tachikawa (1993, Copeia 1993[2]: 489), two of the syntypes of this species were lost.

Synonyms: Centring nigra Lowe, 1833, Proc. Zool. Soc. London, 1833 (1): 144. 10" individual mentioned, Madeira Islands, but there is no type material according to Krefft and Tortonese (1973, in Hureau and Monod, Check-list fish. NE Atlantic Mediterranean, 1: 43). Not Squalus niger Gunnerus, 1763, Cloquet, 1817, and subsequent authors, = Squalus spinax Linnaeus, 1758. Spinax pusillus Günther, 1870: 425. Vaillant, 1888: 72. Regan, 1908: 44.

Other Combinations: None
FAO Names: En - Smooth lanternshark; Fr - Segre ain; Sp - Nolo lucero lis.


Fig. 103 Etmopterus pusillus

Field Marks: A moderately large, slender, broad-headed, long-tailed, lanternshark with a short thick flat snout. Upper teeth with a slender cusp and one or more pairs of cusplets, lower teeth compressed and knife-like, with a cusp and blade. Lateral trunk denticles cuspless, truncated, and wide-spaced, giving the body a smooth texture, not in longitudinal rows on head, body or tail. Two dorsal fins with fin spines, first dorsal fin smaller than second dorsal fin, first dorsal-fin spine slender and lower than fin, second dorsal-fin spine slightly recurved and pointing posterodorsally. No anal fin. Flank and caudal photomarks present and inconspicuous.

Diagnostic Features: Head flattened and moderately broad, not deep and conical; head relatively long, 22 to $26 \%$ of total length and 2.2 to 2.8 times in snout-vent length; head width 0.9 to 1.4 times preoral snout; head low, height 6 to $9 \%$ of total length. Prespiracular length 1.2 to 1.4 times spiracle-pectoral space. Snout flattened and broadly rounded, not bulbous; preoral length moderately long and 9 to $11 \%$ of total length. Eyes narrow and elongated-oval; upper eyelid with a pale naked patch. Gill openings slightly wider than spiracle; width of third gill opening one-third eye length or less. Mouth relatively broad and 1.2 to 1.7 times eye length. Total tooth row counts upper jaw 23 to 30 , lower jaw 35 to 44 ; upper teeth generally with less than 3 pairs of cusplets, with cusps greatly expanded, over twice as high as adjacent cusplets; upper teeth of mature males large with a cusp and a pair of long cusplets. Body moderately firm, slightly compressed, and moderately slender. Predorsal spine length about 36 to $39 \%$ of total length; interdorsal space about 1.2 to 1.5 times prebranchial length, subequal to head length; pectoral-pelvic space about 1.1 to 1.4 times head length in adults; snout tip to rear flank marking base about $103-106 \%$ of snout tip to second dorsal spine origin; dorso-caudal space 9 to $11 \%$ of total length, about 1.8 to 2.9 in interdorsal space; pelvic-caudal space 15 to $18 \%$ of total length, about 1.8 to 2.3 times first dorsal-fin length, about 1.1 to 1.6 in interdorsal space, subequal or somewhat shorter than prebranchial length, and about 1.5 to 2.0 times in pectoral-pelvic space. No rows of greatly enlarged denticles on flanks above pectoral fins; denticles covering underside of snout; denticles on head, flanks and tail not in regular longitudinal rows; denticles present on second dorsal fin, densely covering base but absent from posterior margin; lateral trunk denticles short, robust, close-set but not overlapping, with truncated, hollow, sessile, low crowns, not thorn or bristle-like. Distal margins of fins not fringed with naked ceratotrichia. Pectoral fin small with anterior margin length 8 to $9 \%$ of total length, rounded-angular in shape. First dorsal-fin origin just behind pectoral-fin free rear tips, base much closer to pectoral-fin bases than pelvic fins; first dorsal-fin spine stout, short, and usually lower than first dorsal-fin apex, spine origin nearer to snout tip than upper caudal-fin origin. Second dorsal fin much larger than first and nearly or quite twice its area, height 32 to $39 \%$ of second dorsal-fin length, apex more or less pointed or narrowly rounded, posterior margin usually deeply concave; second dorsal-fin spine stout and recurved, with its tip diagonally vertical. Dorsal caudal-fin margin about 0.8 of head length. Vertebral counts: total vertebral counts 82 to 88 , precaudal vertebral counts 59 to 66 , monospondylous vertebral counts 47 to 53 . Intestinal valve counts 10 to 13 . Size moderate with adults to about 48 cm . Colour: pale or dark brown to blackish on dorsal surface, underside of snout and abdomen abruptly black, dorsal surface dark in life, conspicuously lighter in preservative, ventral surface conspicuously dark; precaudal fins light distally, no
conspicuous dark bands at tip and through middle of caudal fin; a small conspicuous round white pineal blotch on dorsal surface of head. No conspicuous photolines on body. Suprapelvic photomark present but not running behind pelvic fins. Flank photomarks present; flank photomark base opposite and behind second dorsal-fin spine; anterior branch of flank photomark long and broad, much longer than posterior branch, posterior branch about $10 \%$ of anterior branch and truncate, merging ventrally with post-pelvic photomark, and not extending behind free rear tip of second dorsal fin. Ventral saddle-shaped precaudal photomark absent from middle of caudal peduncle. Caudal photomarks present; caudal-base photomark present, with anterior branch broad, partly enveloping ventral surface of caudal peduncle but not extending onto its sides; caudal-base photomark with elongated, blunt-tipped posterior branch over $7 \%$ of total length. No central caudal photomark. Upper caudal photomark present and straight.

Distribution: Eastern Atlantic: Portugal and the Azores, to Madeira Islands, Canaries, Liberia, Ivory Coast to Gabon, Zaire, Angola, Namibia, and west coast of South Africa. Absent from the Western North Atlantic, but with scattered records from the northern Gulf of Mexico to the Florida Straits, and southern Brazil to Argentina. Also, known from the Central South Atlantic (oceanic), between Argentina and South Africa. Elsewhere widespread but scattered in the Indian, Central and Western Pacific oceans.

Habitat: A species of the continental slopes, on or near bottom at a depth of 274 to 1000 m or more (possibly to 1998 m ); also oceanic in the central South Atlantic and central North Pacific, at depths between the surface and 110 to 708 m over deep water (Krefft, 1980; D.A. Ebert, unpubl. data).

Biology: Viviparous with yolk-sac, litters range from 1 to 6 with an average of 3.5 embryos; the number of ovarian eggs present in adult females is slightly higher, ranging from 2 to 18 (averaging 10 to 11), suggesting that fecundity may be slightly higher than reported. Reproductive seasonality has not been confirmed in this species, but in the eastern North Atlantic gravid females are most common between November and April, while males appeared to be most active reproductively during August.
Males mature between 5 and 9 years, and females between 8 and 11 years. Maximum age estimates range up to 13 years for males and 17 years for females.
Diet includes fish eggs, lanternfish, squid, and other small dogfish. Off Namibia and South Africa this shark eats cephalopods, hake (Merluccidae, Merluccius), and lanternfish (Myctophidae, Diaphus), and small squaloid sharks.

Size: Maximum total length at least 50.2 cm ; males immature at 15.8 to 41.7 cm , adult at 31.0 to 47.9 cm ; females immature 15.9 to 45.5 cm and adult at 38 to 50.2 cm . Size at maturity may vary regionally. Size at birth is from 15 to 16 cm .

Interest to Fisheries and Human Impact: Interest to fisheries limited. In the Eastern Atlantic captured as bycatch in bottom trawls and nets, and on longline gear. It is mostly taken off southern Portugal as retained bycatch in several fisheries, but species-specific landings data is difficult to come by since it is retained in mixed deepwater shark catches and not identified to species.

This species is listed as Least Concern given its widespread geographic and bathymetric distribution.
Local Names: Lixinha-da-fundura (Portugal); Lixinha da fundura, Quelmazinha, Smooth lanternshark (Azores); Gata preta (Madeira Islands).

Remarks: Examination of regional E. pusillus specimens, especially from the central and western North Pacific and Indian Ocean suggests that this species may form a complex that may include multiple species. One form has a more angular pectoral fin and is generally found to occur in association with continental slopes, while a second form with broadly rounded pectoral fins seems to inhabit a more oceanic environment usually occurring around offshore islands, seamounts, and deepsea ridges far from continental land masses (D.A. Ebert and J.D.S. Knuckey, unpubl. data).

Literature: Bigelow and Schroeder (1957); Cadenat (1957); Cadenat and Blache (1981); Ebert, Compagno, and Cowley (1992); Shirai and Tachikawa (1993); Coelho and Erzini (2005, 2007, 2008a); Coelho, Tanaka, and Compagno (2008); Gibson et al. (2008); Last and Stevens (2009); ICES (2010); Ebert and Compagno (In press); D.A. Ebert and J.D.S. Knuckey (unpubl. data).

## Etmopterus spinax(Linnaeus, 1758)

Squalus spinax Linnaeus, 1758, Syst. Nat., ed. 10, 1: 233. Holotype unknown, type locality: "Habitat in Europa".
Synonyms: Squalus niger Gunnerus, 1763: 293, pls 7-8, Norway. Spinax niger Cloquet, 1816, Dict. Sci. Nat., 1 (suppl.): 93, possibly nomen nudum? Spinax niger Bonaparte, 1836, Iconog. Fauna Italica, 3, Pesci, fasc. 14, 17, pta. 84, 2 p., Fig. 1, and subsequent authors. Etmopterus aculeatus Rafinesque, 1810, Caratt. gen. sp. anim. piant. Sicilia, Palermo, pt. 1: 14, pl. 13, Fig. 3. No type material, off Sicily, Mediterranean Sea. Squalus infernus Blainville, 1825, in Vieillot et al., Faune Francaise, liv. 13-14: 59, pl. 14, Fig. 2. Holotype: A specimen 10 in long to end of truncated tail mentioned, lost?, Mediterranean Sea. This was erroneously and inexplicably placed by Compagno (1984) in questionable synonymy of Centrophorus uyato (= C. granulosus) but from examination of the original description is clearly not a centrophorid. Spinax gumneri Reinhardt, 1825, Overs. K. Danske Vidensk. Selsk. Forh. (1824-1825): 3. New name only, on Squalus spinax Gunnerus, 1765, Drontheim Gesell. Schrift., 2: 284-290, pl. 4. ?Spinax vitalinus de la Pylaie, 1835, Rech. France Poiss., 1832-1833, Congr. Sci. France Poitiers, 1834: 527. Fide Jordan, 1919, Stanford U. Pub., U. Ser., Gen. Fish.(2): 182. Possible replacement name for Squalus spinax Linnaeus, 1758? Spinax linnei Malm, 1877, Göteborgs Bohusläns Fauna, 626. Apparent replacement name for Squalus spinax Linnaeus, 1758.

Other Combinations: None.
FAO Names: En - Velvet belly; Fr - Sagre commun; Sp - Negrito.


Fig. 105 Etmopterus spinax
Field Marks: Two spined dorsal fins. No anal fin. Blade-like unicuspidate teeth in lower jaw and teeth with cusps and cusplets in upper jaw. Denticles not in lines and with long slender cusps. Abdomen long, tail short, black markings on underside of body and sides of tail prominent.

Diagnostic Features: Head broad and flattened, not deep and conical; head relatively long, 19 to $23 \%$ of total length and about 2.3 to 2.8 times in snout-vent length; head width about 1.3 to 1.4 times preoral snout; head low, height 9 to $11 \%$ of total length. Prespiracular length 1.4 to 1.7 times spiracle-pectoral space. Snout broad, thick and spatulate, not bulbous; preoral length short and 8.1 to $9.3 \%$ of total length. Eyes narrow and elongated; upper eyelid possibly without a pale naked patch. Gill openings about as wide as spiracle; width of third gill opening less than one-third eye length. Mouth relatively broad and 1.3 to 1.4 times eye length. Total tooth row counts upper jaw 22 to 32 , lower jaw 26 to 40 ; upper teeth generally with 3 pairs of cusplets or less, cusps expanded, about three times higher than adjacent cusplets; sexual dimorphism in upper teeth uncertain. Body moderately firm, cylindrical, and moderately stout. Predorsal spine length about 31 to $37 \%$ of total length; interdorsal space 0.6 to 1.4 times head length and usually longer than prebranchial length; pectoral-pelvic space about 0.8 to 1.4 times head length in adults; snout tip to rear flank marking base subequal to snout tip to second dorsal spine origin; dorso-caudal space 10 to $12 \%$ of total length, about 1.4 to 2.0 in interdorsal space; pelvic-caudal space 19 to $21 \%$ of total length, about 2.0 to 2.2 times first dorsal-fin length, 0.7 to 1.7 in interdorsal space, about as long as prebranchial length, subequal to about 1.4 in pectoral-pelvic space. No rows of greatly enlarged denticles on flanks above pectoral fins; denticles largely covering underside of snout; denticles on head, flanks and tails not in regular longitudinal rows; denticles present on second dorsal fin, covering it; lateral trunk denticles high, slender, and close-set, with very slender, strongly hooked conical crowns. Distal margins of fins not fringed with naked ceratotrichia. Pectoral fin
small with anterior margin length about 8 to $9 \%$ of total length, rounded-subangular in shape. First dorsal-fin origin about opposite or just behind pectoral-fin free rear tips, base much closer to pectoral-fin bases than pelvic fins; first dorsal-fin spine stout, short, and usually lower than first dorsal-fin apex, spine origin nearer to snout tip than upper caudal-fin origin. Second dorsal fin much larger than first and about twice its area, height about 38 to $42 \%$ of second dorsal-fin length, apex narrowly to broadly rounded, posterior margin deeply concave; second dorsal-fin spine stout and strongly recurved, with its tip obliquely vertical in adults. Dorsal caudal-fin margin about equal to head length. Vertebral counts: total vertebral counts 81 to 91 , precaudal vertebral count 55. Intestinal valve count unknown. Size moderately large with adults rarely above 45 cm but reaching 60 cm . Colour: brown on dorsal surface, underside of snout and abdomen abruptly black, dorsal surface light, ventral surface conspicuously dark; precaudal fins dark distally, webs sometimes conspicuously lighter than bases or body; a conspicuous or obscure dark band on the terminal caudal lobe and often a dark blotch on ventral caudal lobe, but no dark band through middle of caudal fin; presence of light pineal blotch on dorsal surface of head uncertain. No conspicuous photolines on body. Suprapelvic photomark possibly absent. Flank photomarks present; flank photomark base forward and under second dorsal-fin spine; anterior branch of flank photomark long and broad, much longer than posterior branch, posterior branch 38 to $53 \%$ of anterior branch; posterior branch broadly lobate but not truncate, merging ventrally with postpelvic photomark and not extending behind free rear tip of second dorsal fin. Ventral saddle-shaped precaudal photomark absent from middle of caudal peduncle. Caudal photomarks present; caudal-base photomark present, with anterior branch broad but not enveloping ventral surface of caudal peduncle and extending onto its sides; caudal-base photomark with a sharp or blunt-tipped, greatly elongated posterior branch that is 9 to $10 \%$ of total length and extends nearly to elongated upper caudal photomark. Central caudal photomark absent. Upper caudal photomark present, this straight and greatly elongated.

Distribution: Eastern Atlantic: Iceland and Norway to Gabon, including the Azores and Cape Verde. Widespread and very common in the Western Mediterranean.

Habitat: A common species found on, near or well above the bottom on the outer continental shelves and upper slopes at depths of 70 to 2000 m , mostly between 200 to 500 m .

Biology: Viviparous with yolk-sac development, litter sizes from 1 to 21 with the litter size increasing with the total length of the female. The age at first maturity for males is about 4 years with a maximum estimated age of 7 to 8 years. Females mature at about 4.7 years with a maximum estimated age of 9 to 11 years. Adult females in various maturity stages, including those in both pregnant and resting stages, are found throughout the year in Portuguese waters, although fully developed embryos are only seen in June. Mating activity appears to be highest during the winter. Development of embryos is estimated to take about 12 months, and


Fig. 106 Etmopterus spinax
Known distribution
Possible distribution may be followed by an additional resting time period before they can become pregnant again. If true, the species may only be able to reproduce every 2 to 3 years and with a maximum age of 9 to 11 years for females an individual female may only give birth 2 or 3 times during her life span. This species shows strong population structure segregation by depth with larger, mature females occurring deeper. Etmopterus spinax appears to be highly segregated by depth depending on its maturity stage and sex with older mature segments of the population occurring predominantly in deeper water, below 600 m , than smaller immatures which prefer shallower water less than 600 m . As this shark ages and matures it moves from about 300 m depth progressively into deeper water below 600 m . Pregnant females appear to migrate into shallow water to give birth, but move back into deeper water where mating occurs.
The diet of $E$. spinax consists mostly of benthopelagic prey items including small fishes, squids, and crustaceans suggesting that these sharks forage away from the bottom. Furthermore, it appears that $E$. spinax, and most likely other etmopterids, not only migrate vertically into the water column to capture midwater prey, and avoid predators, they do so by counter illuminating themselves by use of their ventral photophores (Claes et al., 2010a). The main prey items of $\boldsymbol{E}$. spinax in Norwegian fjords are krill and pearlfish, both of which make vertical diel migrations and are luminous, and would not be unexpected for these sharks to follow their prey on their daily migration.
The diet of this species however changes ontogenetically with small sharks ( 9 to 17 cm total length) feeding almost exclusively on euphausiids, medium sized sharks ( 17 to 28 cm total length) consuming mostly natantid decapods and teleosts, and large (over 28 cm total length), mostly mature, sharks feeding on natantids, gadoids, and cephalopods. Larger sharks tend to have a broader more diversified diet.

Size: Maximum total length confirmed to 41 cm , but reported to about 60 cm , although this latter number may be based on a different species. Males mature at 24.2 to 33.9 cm , and females at 30.5 to 41.1 cm . Size at maturity differs between some populations of Etmopterus spinax with males and females reaching $50 \%$ maturity at 24.2 cm and 30.9 cm , respectively, off southern Portugal, but in the Western Mediterranean Sea the average size at maturity for males and females is 28.3 and 34.2 cm , respectively. Size at birth are about 9 to 14 cm .

Interest to Fisheries and Human Impact: Interest to fisheries minor. It is taken in the Eastern North Atlantic by bottom and pelagic trawls, and on longline gear. Like other members of this genus these sharks are generally reported as part of a deepwater species complex, with very little species-specific information available. These sharks are commonly taken as retained bycatch in several fisheries off southern Portugal, but elsewhere in the North Atlantic they are frequently discarded in other fisheries. Under TAC regulation in EU (in 2012, TAC=0) (EU, 2010). Technical measures in force in EU waters and NEAFC regulatory area (2012).

In the North Eastern Atlantic this species has been assessed as Near Threatened due to significant fishing pressure and possible declines in its population within this region. Globally it has been assessed as Least Concern.

Local Names: Lantern shark, Black spiny shark, Spinax, Velvetbelly shark (English); Épineux de fond (France); Kleiner schwarzer Dornhai (German); Sorthaj (Denmark); Blåmage, Svarthả (Norway); Blåkäxa (Sweden); Lixinha da fundura, Quelmazinha, Velvet belly (Azores); Búksvarti hávur (Faroe Islands).

Remarks: Records of this species from the west coast of South Africa are apparently based on other species, primarily on Etmopterus compagnoi.

Literature: Bigelow and Schroeder (1957); Kreff (1968a); Wheeler (1978); Cadenat and Blache (1981); Macpherson (1980a); Compagno (1984); Compagno, Ebert and Cowley (1991), Bello (1997); Coelho and Erzini (2005, 2008a, b); Neiva, Coelho, and Erzini (2006); Gennari and Scacco (2007); Claes and Mallefet (2008); Coelho et al. (2008); Coelho, Bladesdale, Crozier, and Stenberg (2008); Gibson et al. (2008); Claes et al. (2010a); Coelho and Erzini (2010); Coelho et al. (2010); EU (2010); ICES (2010); Ebert and Compagno (In press).

### 2.2.5 Family SOMNIOSIDAE

Family: Somniosidae Jordan, 1888, Man. Vert. Eastern U.S., ed. 5: 15.
Type genus: Somniosus Lesueur, 1818.

## Number of Recognized North Atlantic Genera: 6.

FAO Names: En - Sleeper sharks; Fr - Laimargue dormeurs; Sp - Tiburones Tollos.
Field Marks: Short to long-nosed, cylindrical to somewhat compressed sharks with no anal fin, two dorsal fins with or without spines, first dorsal fin with origin in front of pelvic-fin origins, and small to moderately large denticles variable in shape, with leafshaped, tricuspidate or polycuspidate crowns and slender pedicels, high pitchfork-shaped erect crowns on high pedicels, or low ridged sessile crowns; no keels on the caudal peduncle and caudal fin with a strong subterminal notch. Colour grey to brownish or black, most without mottling, spotting, or other distinctive markings; without photophores.

Diagnostic Features: Head moderately broad and somewhat flattened or conical. Snout flat and narrowly rounded to elongaterounded in dorsoventral view. Spiracles large, close behind eyes. Fifth gill opening about as large as first four. Nostrils wide-spaced with internarial width greater than nostril width; nostrils with simple anterior nasal flaps. Mouth nearly transverse and usually very short (more elongated in Scymnodon ringens), with thin, non-papillose lips. Labial furrows short to greatly elongated, encircling mouth or not, confined to mouth corners or extending partway around mouth (Centroselachus crepidater) and under posterior corners of eyes, elongated posteriorly into postoral grooves and also anteromedial preoral grooves ( C crepidater); labial folds thin. Teeth with dignathic heterodonty well-developed, upper teeth much smaller than lowers. Teeth of upper jaw lanceolate, high-crowned, needlelike, with narrow erect to semioblique cusps and no cusplets or blades, in quincunx arrangement and not imbricated; lower teeth compressed, high-crowned, narrow and bladelike, imbricated, forming a sawlike cutting edge, with a compressed erect to oblique cusp, a distal blade, and no cusplets. Tooth rows 30 to 70 upper jaw, 31 to 68 lower jaw. Trunk cylindrical or slightly compressed, abdomen with lateral ridges. Interdorsal space elongated and greater than length of first dorsal base; pelvic-caudal space short and between one and two times pelvic-fin bases. Caudal peduncle slightly compressed, short to moderately elongated, and without lateral keels or precaudal pits (some Somniosus with low keels on the caudal base). Body without photophores. Denticles moderate-sized and pedicellate, with flattened, narrow to broad-keeled or smooth leaf-shaped, round, or narrow thornlike crowns, slender pedicels and low bases. Pectoral fins low, angular or rounded, and not falcate, anterior margins moderately large and shorter or equal to the prespiracular length, rear tips rounded and short. Pelvic fins subequal or larger than pectoral fins and first dorsal fin and subequal to or smaller than second dorsal fin. Claspers with a lateral spine only. Dorsal fins small, broad, rounded-angular but not falcate, with small grooved spines on both dorsal fins or no spines. First dorsal fin length variable from slightly larger, subequal to, or slightly smaller than second dorsal fin in size; first dorsal-fin base over pectoral-pelvic space and well anterior to pelvic fins, origin over pectoral-fin bases or inner margins. Second dorsal fin usually
smaller than first dorsal fin or about as large, base partly over pelvic-fin bases with origin over to slightly anterior to pelvic-fin insertions. Caudal fin heterocercal, with ventral lobe weakly to strongly developed in adults, and with subterminal notch strong. Vertebral counts: total vertebral counts 35 to 120 , monospondylous vertebral counts 43 to 67 , diplospondylous precaudal vertebral counts 13 to 23 . Intestinal valve with 12 to 41 turns. Adults small to gigantic, total length to between 49 and 600 cm or more. Colour: plain or with light or dark markings on fins and body, without photophores and black photomarks on tail or flanks.

Distribution: The family has an almost circumglobal range in polar (boreal and austral) to tropical seas, mostly in association with land masses including continents, islands, sea mounts and ridges. The giant sleeper sharks of the genus Somniosus(subgenus Somniosus) are among the few non-rajiform elasmobranchs penetrating deeply into polar waters, but the family is most diverse in cool to warm temperate seas and possibly in the tropics (in deep water, but with distributions poorly known). Several of the species are wide-ranging in the Atlantic but the greatest known diversity of the family is in the Indo-West Pacific. Geographic and bathymetric ranges are imperfectly known for most species, and reflect uneven sampling of deepwater slope-dwelling sharks as well as problems in identifying somniosid species.

Habitat: The Somniosidae are primarily bottom dwelling, deepwater inhabitants of continental and insular slopes and occasionally on the upper rises (Centroscymnus coelolepis and possibly Somniosus species), but also occur on submarine ridges and seamounts. They range in depth between 200 to at least 3675 m but with most species not known to extend below 1000 to 1500 m . Most species are bottom dwellers, but some species are apparently oceanic. These sharks occasionally occur on the continental and insular shelves offshore in water up to 50 m depth, although this is most exceptional. In high latitudes members of the genus Somniosus occur on the continental shelves to the intertidal.

Biology: Reproduction is yolk-sac viviparous, with 4 to 59 young per litter. Virtually nothing is known about the age and growth of these sharks although where some information is available (particularly for the large Somniosus species) they appear to be quite long-lived and very slow growing. Sleeper sharks feed on bony fishes, other chondrichthyans, cephalopods and other molluscs, crustaceans, seals, whale meat, carrion, sea birds, echinoderms and jellyfish; at least one species (Centroscymnus coelolepis) takes chunks of meat out of living marine mammals and bony fishes.

Interest to Fisheries and Human Impact: In the Eastern Atlantic these sharks are fished with line gear and bottom trawls for human consumption and for their livers, which are extremely large, oily, and have high squalene content.

Local Names: Sleeper sharks, Gurry sharks, Velvet dogfishes.
Remarks: The family is small, but rather diverse with seven genera and about 17 species. The family is well represented in the North Atlantic with six genera and eight species.

Literature: Müller and Henle (1839); Gray (1851); Dumeril (1865); Günther (1870); Regan (1908); Garman (1913); Bigelow and Schroeder (1948, 1957); Garrick (1959b, c, 1960b); Cadenat and Blache (1981); Compagno (1984, 2005); Shirai (1992a, 1996); Compagno and Niem (1998); Hernández et al. (1998); Yano, Stevens, and Compagno (2004); Last and Stevens (2009); Ebert and Compagno (In press).

## Key to North Atlantic Genera:

1a. Dorsal-fin spines present, though sometimes short and partly covered by skin (Fig. 107a) 2

1b. Dorsal-fin spines absent 5

2a. Snout greatly elongated, preoral length about equal to distance from mouth to pectoral-fin origins. Upper labial furrows greatly elongated, their lengths greater than distance between their anterior ends (Fig. 107b) . . Centroselachus

2b. Snout shorter, preoral length much less than distance from mouth to pectoral-fin origins. Upper labial furrows shorter, their lengths less than distance between their anterior ends (Fig. 108) 3

a) LATERAL VIEW

b) UNDERSIDE OF HEAD

Fig. 107 Centroselachus


Fig. 108 Centroscymnus

3a. Lower teeth with relatively low, more or less oblique cusps (Fig. 109) Centroscymnus

3b. Lower teeth with relatively high, more or less erect cusps (Fig. 110) 4

4a. Snout very short. Mouth very large and broadly arched. Caudal fin with a weak subterminal notch (Fig. 111)

Scymnodon

4b. Snout moderately long. Mouth rather small and nearly transverse. Caudal fin with a strong subterminal notch (Fig. 112)

Zameus

5a. Lower teeth with high, erect cusps. Ventral caudal-fin margin half as long as dorsal caudalfin margin. Eyes horizontally elongated (Fig. 113 \& 114)

Scymnodalatias

5b. Lower teeth with low, oblique cusps. Ventral caudal margin about $2 / 3$ as long as dorsal caudal margin. Eyes nearly circular (Fig. 115 \& 116)

Somniosus


Fig. 109 Centroscymnus


Fig. 110 Scymnodon


Fig. 111 Scymnodon


Fig. 112 Zameus


LOWER TEETH
Fig. 113 Scymnodalatias


LOWER TEETH
Fig. 115 Somniosus


Fig. 114 Scymnodalatias


Fig. 116 Somniosus

## Centroscymnus Bocage and Capello, 1864

Genus: Centroscymnus Bocage and Capello, 1864, Proc. Zool. Soc. London, 24: 263.
Type species: Centroscymnus coelolepis Bocage and Capello, 1864, by monotypy.

## Number of Recognized North Atlantic Species: 2.

Synonyms: None
Field Marks: Short to moderately long snout, slender-cusped teeth without cusplets in upper jaw, bladelike, oblique and short-cusped, interlocked cutting teeth in lower jaw, caudal fin with a strong subterminal notch, and pectoral fins with broadly rounded free rear tips. Colour greyish or blackish-brown, no anal fin, small fin spines present on both dorsal fins though sometimes inconspicuous (Centroscymnus owstoni).

Diagnostic Features: Anterior nasal flaps short, not expanded as barbels; snout flattened, broadly parabolic, length varying from about equal to distance from mouth to pectoral origins to considerably less than that space, and about half length of head or less; gill openings moderately wide and about equal-sized; lips thick but not pleated or suctorial; teeth very different in upper and lower jaws, uppers with very slender, acute cusps and no cusplets, not bladelike, lower teeth high compressed, bladelike, interlocked with short, oblique cusps, distal blades, and no cusplets; tooth rows 39 to 70 upper jaw, 32 to 42 lower jaw. Small, grooved fin-spines present on both dorsal fins, these sometimes covered with skin and inconspicuous; first dorsal-fin origin varying from over the pectoral-fin bases to well posterior to their free rear tips, insertion well in front of pelvic-fin origins and closer to the pectoral-fin bases than the pelvic-fin bases; second dorsal-fin origin about over the middle of the pelvic-fin bases; second dorsal fin about as large or slightly smaller than first, but first often with an anteriorly elongated base up to about twice as long as that of first; pectoral fins with short, broadly rounded free rear tips and inner margins, not broadly lobate or acute and attenuated; caudal fin asymmetrical, not paddle-shaped, upper lobe long, lower lobe short but well-developed, subterminal notch present and strong. No precaudal pits or lateral keels on caudal peduncle. Dermal denticles with low, pedicellate, flat, ovoid crowns, varying from triridged and tricuspidate to smooth and acuspidate in adults, triridged and tricuspidate in young. Cloaca without a luminous gland. Vertebral counts: total vertebral counts 96 to 114 , monospondylous vertebral counts 54 to 64, precaudal vertebral counts 68 to 84 . Intestinal valve with 11 to 21 turns. Moderately large, adults up to 122 cm total length. Colour: blackish brown or greyish brown above and below.

Local Names: Portuguese sharks.

Remarks: The genus has two species recognized, both of which (Centroscymnus coelolepis and C. owstoni) occur in the North Atlantic. The arrangement of this genus and its separation from the genus Scymnodon follows Ebert and Compagno (In press).

## Key to North Atlantic Species:

1a. Snout short, preoral length about $2 / 3$ as long as distance from mouth to first gill slits, and less than mouth width (Fig. 117). Centroscymnus coelolepis


UNDERSIDE OF HEAD


UNDERSIDE OF HEAD
Fig. 118 Centroscymnus owstoni

## Centroscymnus coelolepis Bocage and Capello, 1864

Centroscymnus coelolepis Bocage and Capello, 1864, Proc. Zool. Soc. London, 24: 263, Fig. 4. Holotype: Museu Bocage, Lisbon, MB T113, destroyed in fire, off Portugal.

Synonyms: Scymnodon melas Bigelow, Schroeder, and Springer, 1953, Bull. Mus. Comp. Zool. Harvard, 109(3): 233, Fig. 5. Holotype: Museum of Comparative Zoology, Harvard, MCZ-37452, 462 mm TL immature female, $40^{\circ} 00^{\prime} \mathrm{N}, 68^{\circ}$ $52^{\prime}$ W, off Georges Bank, 769 to 878 m.

Other combinations: None.
FAO Names: En - Portuguese dogfish; Fr - Pailona commun; Sp - Pailona.


Fig. 119 Centroscymnus coelolepis
Field Marks: Body stocky, not tapering abruptly from pectoral region, snout very short, lanceolate upper teeth and bladelike lower teeth with short, oblique cusps, very large lateral trunk denticles with smooth, circular, acuspidate crowns in adults and subadults; dorsal fins with very small fin spines, no anal fin. Colour a uniformly light to dark brown.

Diagnostic Features: Body stocky, not strongly tapering back from pectoral region. Snout short, preoral length much less than distance from mouth to first gill slits and less than mouth width. Lips not thick and fleshy. Upper labial furrows very short, their lengths much less than distance between their front ends. Lower teeth with very short, strongly oblique cusps and high, narrow roots; total tooth counts for upper jaw 43 to 68 and lower jaw 29 to 42. Lateral trunk denticles very large, with smooth, circular, ridgeless and acuspidate crowns, giving shark an almost teleost-like appearance. Pectoral fins moderately large, apices falling well in front of first dorsal-fin spine when laid back. Free rear tips of pelvic fins extending behind second
dorsal-fin insertion. Dorsal fins about equal in size and height, fin spines very small but with tips protruding from fins. First dorsal-fin base not extending forwards as a prominent ridge, origin behind pectoral fins. Second dorsal-fin base shorter than space between it and upper caudal-fin origin, free rear tip well in front of upper caudal origin. Vertebral counts: total vertebral counts 102 to 114, monospondylous vertebral counts 56 to 64 , precaudal vertebral counts 68 to 84 . Intestinal valve with 16 to 21 turns. Moderately large, up to 122 cm total length. Colour: uniformly light to blackish brown.

Distribution: Eastern Atlantic: Denmark Strait and Iceland to Portugal and the Azores, western Mediterranean and from Morocco to Sierra Leone, including the Canary Islands and Madeira Islands. Also, occurs off Namibia and the west coast of South Africa. Western Atlantic: from Canada (Grand Banks and Newfoundland) to the Florida Straits between Florida (USA) and Cuba, and from off French Guiana. Elsewhere, this common to rare deep-sea shark occurs in the Indian and Western Pacific oceans.

Habitat: A common, wide-ranging but little-known deepwater shark, on or near the bottom on the continental slopes and upper and middle rises. Occurs mostly at depths below 400 m , but with a depth range of 128 to 3675 m . Bottom water temperatures where this species has been captured range from 5 to $13^{\circ} \mathrm{C}$.

Biology: Viviparous with a yolk-sac, with 1 to 29 young per litter, but mostly from 12 to 14 . The number of embryos per litter increases slightly with the total length of the mother. There does not


Fig. 120 Centroscymnus coelolepis appear to be a defined reproductive cycle as females give birth year-round. These sharks segregate by size, sex, and reproductive stage with depth. Feeds mostly on bony fishes including hake (Merluccidae), epigonids (Epigonidae) and bramids (Bramidae), other sharks, benthic invertebrates including squid, octopuses, gastropods, and crabs. Similar to the cookiecutter sharks (Isistius species) this shark will core flesh out of live cetaceans, deep-diving pinnipeds, and possibly large driffishes (Stromateidae).

Size: Maximum total length about 122 cm ; males mature at 85 to 100 cm ; females mature at 95 to 110 cm . Size at birth about 23 to 35 cm ; smallest free swimming individual was 34 cm total length.

Interest to Fisheries and Human Impact: A common deepwater shark, caught in bottom trawls, fixed bottom nets, and longline gear, in targeted deepwater shark fisheries and as bycatch in other deepwater demersal fisheries. Over the past decade (2000 to 2009) an average of 2163 tonnes (as reported to FAO) of this shark was landed in the Eastern North Atlantic, with the United Kingdom (average 896 tonnes) and Portugal (average 674 tonnes) reporting the largest landings in this region, although important French and Spanish fisheries also operated. Most of the fishery appears to take place west of Ireland, and off France, Spain, and Portugal. This species along with Centrophorus squamosus make up the largest biomass component of the mixed deepwater shark fisheries in this area. The stock appears to be highly depleted, and in 2008 it was listed as a Threatened and Declining species by OSPAR. Despite concerns over the population status of this species issues still remain in separating out landings of this species from the generic "siki" category. In the eastern Atlantic it is utilized for fishmeal, dried salted for human consumption, and for its squalene-rich liver oil. Under TAC regulation in EU (in 2012, TAC=0). When accidentally caught with longlines, this species shall not be harmed and specimens shall be promptly released (EU, 2010). Technical measures in force in EU waters and NEAFC regulatory area (2012).

Conservation status is Near Threatened globally, but is considered Endangered in the Eastern North Atlantic due to apparent steep declines in its population and continued deepwater fishing in this region.

Local Names: Portugese shark (English); Portugiesenhai (Germany); Palluda, Rasqueta (Spain); Xara preta (Madeira Islands); Carocho, Xara preta (Portugal); Tubarão português, Portugese dogfish, Portugese shark (Azores); Gljáháfur (Iceland).

Literature: Bigelow and Schroeder (1948, 1957); Kreff and Tortonese (1973b); Cadenat and Blache (1981); Yano and Tanaka (1983, 1987, 1988); Ebert, Compagno and Cowley (1992); Santos, Porteiro and Barreiros (1997); Girard and Du Buit (1999); Clarke, Connolly, and Bracken (2001);Stevens and Correia (2003); Verissimo, Gordo, and Figueiredo (2003); Bañón, Piñeiro and Casas (2006); Gibson et al. (2008); Last and Stevens (2009); EU (2010); ICES (2010); Kyne and Simpfendorfer (2010); Ebert and Compagno (In press); D.A. Ebert (unpubl. data).

## Centroscymnus owstoni Garman, 1906

Centroscymnus owstonii Garman, 1906, Bull. Mus. Comp. Zool. Harvard, 46(11): 207, January, 1906. Holotype: Museum of Comparative Zoology, Harvard, MCZ-1037, 79 cm ( 31 1/4") adult male, Yenoura, Suruga Gulf, and Sagami Bay, Japan.

Synonyms: Centroscymnus cryptacanthus Regan, 1906b, Ann. Mag. Nat. Hist. (7), 18(108): 437, December, 1906. Holotype: British Museum (Natural History), BMNH-1865.5.20.14, 780 mm adult male, off Madeira Islands.

Other combinations: None.
FAO Names: En - Roughskin dogfish; Fr - Pailona rapeux; Sp - Sapata lija.


Fig. 121 Centroscymnus owstoni
Field Marks: Dorsal fins with fin spines buried in the fins or with tips slightly protruding, moderately long snout, lanceolate upper teeth and bladelike lower teeth with short, oblique cusps, fairly stocky body that does not taper abruptly from pectoral region, large lateral trunk denticles with mostly smooth, circular, cuspidate and acuspidate crowns in adults and subadults. Uniformly dark brown to black with no conspicuous markings.

Diagnostic Features: Body stocky, not strongly tapering back from pectoral region. Snout moderately long, preoral length about as long as distance from mouth to 1 st gill slits and about equal to mouth width. Lips moderately thick and fleshy. Upper labial furrows very short, their lengths much less than distance between their front ends. Lower teeth with short, oblique cusps and fairly high, narrow roots; total tooth counts for upper jaw 36 to 39 and for the lower jaw 32 to 40 . Lateral trunk denticles large, with mostly smooth, oval, partly ridged and cuspidate or ridgeless and acuspidate crowns. Pectoral fins moderately large, apices falling well in front of first dorsal-fin spine when laid back. Free rear tips of pelvic fins below or slightly in front of second dorsal insertion. Second dorsal fin considerably higher than first, fin spines small and with tips protruding from fins or buried in the skin. First dorsal fin extending forwards as a short and inconspicuous to prominent ridge, origin behind or over pectoral-fin bases. Second dorsal-fin base much longer than space between it and upper caudal-fin origin, free rear tip just in front of or about opposite upper caudal-fin origin. Vertebral counts: total vertebral counts 96 to 114, monospondylous vertebral counts 54 to 60, precaudal vertebral counts 71 to 82 . Intestinal valve with 11 to 15 turns. Moderately large, with adults up to 120 cm . Colour: light grey or brown to dark brown or black, without any conspicuous markings.

Distribution: Wide ranging, but patchy, in the North Atlantic known only from off the Azores. Also in the Eastern Atlantic from off Madeira Islands, Senegal, Canary Islands, Namibia, and South Africa. Western Atlantic not known to occur in Area 21, but found in the northern Gulf of Mexico (USA), French Guiana, Brazil, and Uruguay. Elsewhere found in the Western Pacific from off Japan, New Caledonia, New Zealand, Australia, and southern seamounts.

Habitat: A little known deepwater dogfish of the outer continental shelves and upper continental slopes on or near bottom at depths of 150 to 1459 m , but mostly below 600 m .

Biology: Viviparous with yolk-sac, females with litters of 5 to 31 fertilized eggs or embryos in utero, but females may have as many as 34 ovarian eggs. The number of embryos or eggs increases slightly with the total length of the mother. There does not appear to be a defined reproductive season since partition appears to occur year-round. These sharks segregate by size, sex, and reproductive stage with depth with adult females occurring at greater depths than males.
The diet of this shark is poorly known, but includes bony fish and cephalopods. As far as known it does not appear to remove core flesh from live cetaceans, deep-diving pinnipeds, or large fishes, as does its congener Centroscymnus coelolepis.

Size: Maximum total length about 120 cm ; adult males 67 to 84 cm ; adult females 95 to 104 cm . Size at birth about 25 to 35 cm .

Interest to Fisheries and Human Impact: This species is of no fisheries interest in the Eastern North Atlantic since it is only known from the Azores. It may occur elsewhere in the region, and may be taken on, but misidentified with other mixed deepwater sharks.

The conservation status of this species is currently listed as Least Concern.

Local Names: Rough dogfish, Roughskin dogfish, Shortnose velvet dogfish (English), Pailona sans epine (French); Pailona ñata (Spain); Xara-preta-de-natura (Azores)

Literature: Garman (1906, 1913); Regan (1906); Bigelow and Schroeder (1957); Krefft (1968a); Cadenat and Blache (1981); Yano and Tanaka (1983, 1987, 1988); Compagno (1984); Parin (1991); Santos, Porteiro and Barreiros (1997); McEachran and Fechhelm (1998); Paul (2003b); Gibson et al. (2008); Last and Stevens (2009); ICES (2010); Kyne and Simpfendorfer (2010); Ebert and Compagno (In press).

## Centroselachus Garman, 1913



Fig. 122 Centroscymnus owstoni

Genus: Centroselachus Garman, 1913, Mem. Harvard Mus. Comp. Zool., 36: 206.
Type species: Centroselachus crepidater Garman, 1913, new combination, by monotypy, equals Centrophorus crepidater Bocage and Capello, 1864 (listed in synonymy).

Number of Recognized North Atlantic Species: 1.
Synonyms: None.
Field Marks: See the single species.
Diagnostic Features: Body fairly slender, not strongly tapering back from pectoral region. Snout very long, preoral length about equal to distance from mouth to pectoral-fin origins and much greater than mouth width. Lips not thick and fleshy. Upper labial furrows very long, their lengths greater than distance between their front ends. Lower teeth with moderately long, semioblique cusps and moderately high, fairly broad roots; total tooth counts for upper jaw 36 to 51 and for the lower jaw 30 to 36 . Lateral trunk denticles moderately large, with anteriorly smooth but posteriorly ridged, oval, cuspidate crowns. Pectoral fins moderately large, apices falling well in front of first dorsal-fin spine when laid back. Free rear tips of pelvic fins extending to about opposite second dorsal-fin insertion. Dorsal fins about equal in size and height, fin spines very small but with tips protruding from fins. First dorsal-fin base expanded forwards as a prominent ridge, origin over pectoral-fin bases. Second dorsal-fin base longer than space between it and upper caudal origin, free rear tip nearly reaching upper caudal-fin origin. Vertebral counts: total vertebral counts 105 to 119 and precaudal vertebral counts 73 to 85 . Intestinal valve turn counts unavailable. Moderate sized, with a maximum length of 105 cm . Colour: blackish brown.

## Centroselachus crepidater (Bocage and Capello, 1864)

Centrophorus crepidater Bocage and Capello, 1864, Proc. Zool. Soc. London, 24: 262, Fig. 3. Holotype: Museum Bocage, Lisbon, MB T112 (49), destroyed in fire, off Portugal.

Synonyms: Centrophorus jonssonii Jensen, in Saemundsson, 1922, Vidensk. Meddel. Dansk Naturhist. Foren. Kobenhaven, 74: 192, pl. 5, Fig. 1-2. Holotype: 81 cm , from off Vestmannaeyjar, Iceland, $700-920 \mathrm{~m}$, probably lost, according to Krefft and Tortonese, in Hureau and Monod, 1973, Check-list fish. NE Atlantic Mediterranean, 1: 41. Centrophorus jonsonii Ibid.: 178, is apparently an error for jonssonii, which is consistently spelled as such elsewhere in the text and is named after Th. Jonsson.

Other combinations: None.
FAO Names: En - Longnose velvet dogfish; Fr - Pailona à long nez; Sp - Sapata negra.


Fig. 123 Centroselachus crepidater
Field Marks: Dorsal fins with very small fin spines, very long snout, greatly elongated labial furrows that nearly encircle mouth, lanceolate upper teeth and bladelike lower teeth with moderately long, oblique cusps, fairly slender body that does not taper abruptly from pectoral region, moderately large lateral trunk denticles with partly smooth, oval, cuspidate crowns in adults and subadults. Colour is a uniform black or blackish brown.

## Diagnostic Features: See genus Centroselachus.

Distribution: Eastern Atlantic: Denmark Straits, Iceland, and Faroe Islands south along the Atlantic slope to Rockall Trough, Porcupine Seabight, Portugal, Morocco, Senegal, Madeira Islands, Azores, Gabon to Zaire, Namibia, and South Africa (west coast). Absent from the Western Atlantic. Elsewhere, wide-ranging but scattered throughout the Indo-Pacific and Eastern South Pacific from off Chile.

Habitat: Occurs along upper continental and insular slopes on or near the bottom at depths of 200 to 1500 m .
Biology: A little-known but common deepwater dogfish, with yolk-sac viviparity; litters range from 1 to 9 , with an average of 6 . Females appear capable of breeding throughout the year. Age at maturity is about 9 years for males and 20 years for females; oldest individual was a female estimated at 54 years and the oldest male about 34 years. Diet consists of bony fishes, including lanternfishes (Myctophidae), and cephalopods.

Size: Maximum total length about 105 cm ; males mature at 60 to 68 cm ; females mature at 77 to 88 cm ; size at birth about 28 to 35 cm .

Interest to Fisheries and Human Impact: Interest to fisheries limited, it is caught as bycatch with reported landings of just over 500 tonnes to near zero over the past decade (2000 to 2009). The reduction in landings is most likely due to a ban on deepwater set gillnets and a reduced total allowable catch limit for deepwater sharks. It is likely that this species is part of the deepwater mixed "siki sharks" landings, but there is no estimate as to what proportion of the landings they may represent. Under TAC regulation in EU (in 2012, TAC=0) (EU, 2010). Technical measures in force in EU waters and NEAFC regulatory area (2012).

Conservation status for this species is Least Concern due to its wide, but patchy distribution and apparent population increase in some regions.

Local Names: Sapata preta (Portugal), Sapata de natura (Madeira Islands), Sapata preta, Longnose velvet dogfish (Azores); Porsteinsháfur (Iceland); Langitrantur (Faroe Islands).

Literature: Bigelow and Schroeder (1948, 1957); Garrick (1959b); Krefft and Stehmann (1973); Cadenat and Blache (1981); Ebert, Compagno and Cowley (1992); Santos, Porteiro and Barreiros (1997); Stevens et al. (2003); Invine, Stevens, and Laurenson (2006b); Last and Stevens (2009); Kyne and Simpfendorfer (2010); Gibson et al. (2008); EU (2010); ICES (2010); Ebert and Compagno (In press).


Fig. 124 Centroselachus crepidater

## Scymnodalatias Garrick, 1956

Genus: Scymnodalatias Garrick, 1956, Trans. Roy. Soc. New Zealand, 83(3): 564.
Type species: Scymnodon sherwoodiArchey, 1921, by original designation.

## Number of Recognized North Atlantic Species: 1.

Synonyms: None
Field Marks: Snout broadly rounded, elongated, somewhat flattened, not bulbous. Mouth long and broadly arched. Eyes horizontally elongated. Upper teeth small than lowers, narrow, acute, without cusplets; lower teeth larger, blade-like, lacking serrations, imbricate. Two spineless dorsal fins, the second being slightly larger than the first; first dorsal fin originates about mid-body. Pectoral fins elongated. Caudal fin asymmetrical, upper caudal-fin margin nearly twice the length of the lower caudal-fin margin with a short lower lobe. Colour is dark brown to mottled grey above, lighter below; fins with or without conspicuous fin markings or prominent light edges and light blotches on caudal base.

Diagnostic Features: Head length 17.8 to $28.1 \%$ of total length, snout moderately long, pointed and flattened, preorbital snout 4.2 to $8.4 \%$ of total length. Anterior nasal flaps short, not expanded into barbels. Gill openings moderately wide, fifth one slightly broader than first four. Upper teeth with straight slender cusps; cusps of lower teeth erect or slightly oblique, cusp covering root and apparently without small distal blade; tooth row counts upper jaw 33 to 62 , lower jaw 32 to 42 , upper rows more numerous than lowers. Dermal denticles with moderately high, narrow pedicels and broad, flat, leaf-shaped, tricusped and triridged crowns. Predorsal length less than to nearly half of total length. Both dorsal fins spineless; first dorsal-fin free rear tip anterior to pelvic-fin origins. Second dorsal-fin origin above rear third of pelvic-fin base, free reartip just anterior to upper caudal-fin origin; second dorsal-fin origin above pelvic-fin midbase, free rear tip just anterior to upper caudal-fin origin. Pectoral fins broadly angular or leaf-shaped, with angular or bluntly rounded apices, anterior margins 10.6 to $18.6 \%$ of total length. Cloaca normal, not expanded as a luminous gland. No precaudal pits, lateral or midventral keels on caudal peduncle. Caudal fin asymmetrical. Vertebral counts: total vertebral counts 81 to 84 , monospondylous vertebral counts 43 to 45 , and precaudal vertebral counts 57 to 61 . Adult size to at least 110 cm . Colour: dark brown or mottled grayish above, dark to lighter brown or grey below; fins with or without whitish grey margins, or conspicuous white blotches on caudal-fin base.

## Local Names: None.

Remarks: The arrangement of this genus as presented here follows Ebert and Compagno (In press) in considering this to be a separate genus, apart from the genus Scymnodon, as proposed by Garrick (1956) and subsequent authors. The genus has four species recognized, of which only one is known to occur in the North Atlantic.

## Scymnodalatias garricki Kukuev and Konovalenko, 1988

Scymnodalatias garricki Kukuev and Konovalenko, 1988, Vopr. Ikthiol. (2): 315, Fig. 1. Holotype: Zoological Institute, Leningrad, ZIL(ZIN)-48190, 377 mm TL possibly adolescent male, North Atlantic Ridge north of Azores, $40^{\circ} 22^{\prime} \mathrm{N}, 30^{\circ} 10^{\prime} \mathrm{W}$, 300 m .

Synonyms: None.
Other combinations: None
FAO Names: En - Azores dogfish; Fr - Squale grogneur des Açores; Sp - Bruja de Azores.


Fig. 125 Scymnodalatias garricki

Field Marks: A long head, with a broad, rounded, elongated snout. Eyes horizontally elongated. Mouth long and broadly arched. Upper teeth very small, narrow, lower teeth larger, blade-like and imbricate. First dorsal fin originates about midbody, with free rear tip of first dorsal fin terminating anterior to origin of pelvic fins. No dorsal-fin spines.

Diagnostic Features: Head length $28.1 \%$ and preorbital snout $6.6 \%$ of total length. Upper teeth with straight slender cusps; cusps of lower teeth erect or slightly oblique, cusp covering root and apparently without small distal blade; tooth row counts 43 to 44 upper jaw, 32 lower jaw, upper rows more numerous than lowers. Predorsal length nearly half or $49 \%$ of total length. Pectoral fins broadly angular and not leaf-shaped, with bluntly rounded apices, anterior margins $11.5 \%$ of total length. First dorsal-fin free rear tip just anterior to pelvic-fin origins. Second dorsal-fin origin above rear third of pelvic fin base, free rear tip just anterior to upper caudal-fin origin. Ventral caudal-fin lobe short and strong. Vertebral counts not available. Adult size at least 41 cm . Colour: dark brown above and below, no white blotches on caudal fin.

Distribution: Eastern North Atlantic: known from two specimens both taken along the North Atlantic Ridge near the Azores. A possible third specimen of this rare shark is from the South Pacific requires confirmation.

Habitat: Apparently oceanic or deep-benthic, in the open ocean over seamounts along the Mid-Atlantic Ridge near the Azores at 300 to 580 m , with bottom depths in the vicinity of approximately 2000 m or more.

Biology: Essentially unknown. An 80 cm female reported to be of this species had "several" embryos (Kukuev, 2006).
Size: Maximum to 40.6 cm total length, possibly 80 cm ; adult males 40.6 cm , but adolescent at 37.7 cm . Female size at maturity unknown.

Interest to Fisheries and Human Impact: None as currently known.
Conservation status is Data Deficient, as this rare deepsea species is only known from two, possibly three, specimens.

## Local Names: None.

Remarks: The only member of this genus occurring in the northern hemisphere as the other three known Scymnodalatias species all occur in the southern hemisphere; mostly at latitudes higher than $35^{\circ} \mathrm{S}$. There is one unconfirmed report of $S$. garricki occurring in the South Pacific, but unfortunately only the skin of this specimen was retained (Kukuev, 2006).

Literature: Kukuev and Konovalenko (1988); Santos, Porteiro and Barreiros (1997); Kukuev (2006); Gibson et al. (2008); Séret, McCormick, and Pinho (2008); Ebert and Compagno (In press).


Fig. 126 Scymnodalatias garricki
Known distribution

## Scymnodon Bocage and Capello, 1864

Genus: Scymnodon Bocage and Capello, 1864, Proc. Zool. Soc. London, 24: 263.
Type species: Scymnodon ringens Bocage and Capello, 1864, by monotypy.
Number of Recognized North Atlantic Species: 1.
Synonyms: None.
Field Marks: See species account below.
Diagnostic Features: Head rather thick and high. Snout broad and short, preoral length less than mouth width and less than distance from lower symphysis to first gill slits. Mouth very wide, rather long and broadly arched. Postoral grooves very short, much shorter than upper labial furrows. Teeth small, lanceolate, without lateral cusplets in upper jaw; lower teeth relatively large, triangular, blade-like. Total tooth counts from a single specimen, upper jaw 50 , lower jaw 29 . Gill slits rather long, longest over half eye length. Lateral trunk denticles tridentate in shape, but without cross-ridges on crowns. Caudal peduncle short, distance from second dorsal-fin base to upper caudal-fin origin about half second dorsal-fin base. Pectoral fins narrow and leaf-shaped; apices of pectoral fins nearly reaching base of first dorsal-fin spine. Caudal fin with a weak subterminal notch and no lower lobe. Vertebral counts: total vertebral count 111, monospondylous vertebral count 58, precaudal vertebral count 78. A moderate-size shark with a maximum known length of 110 cm . Colour: uniformly black with conspicuous markings.

Local Names: Velvet dogfishes.
Remarks: The genus as restricted here follows Ebert and Compagno (In press) and most recent authors in recognizing a single species within this genus.

## Scymnodon ringens Bocage and Capello, 1864

Scymnodon ringens Bocage and Capello, 1864, Proc. Zool. Soc. London, 24: 263, Fig. 5. Syntypes: One in Bocage Museum, Lisbon, destroyed by fire; possible syntype in British Museum (Natural History), BMNH-1867.7.23.3; off Portugal.

Synonyms: None.
Other combinations: None.
FAO Names: En - Knifetooth dogfish; Fr - Squale-grogneur commun; Sp - Bruja.


Fig. 127 Scymnodon ringens

Field Marks: Head high, robust, snout broad, short, and mouth broadly arched. Upper teeth small, lanceolate, without lateral cusplets; lower teeth relatively large, triangular, blade-like. Gill openings rather long, greater than one-half eye width. Fin spines preceding each dorsal fin, the second being slightly larger than the first. Caudal peduncle asymmetrical, not paddle-shaped, with weak subterminal notch and no lower lobe. Coloration is black with no conspicuous markings.

Diagnostic Features: See genus account above.

Distribution: Eastern Atlantic: along the Atlantic slope from Scotland to Spain, Portugal, Mauritania, and Senegal. Absent in the Western Atlantic. Western South Pacific: a single record of this species has been from the Southern Campbell Plateau, New Zealand.


Fig. 128 Scymnodon ringens

Habitat: A relatively common, little known deepwater, temperate to subtropical shark of the Eastern Atlantic continental slope, on or near the bottom at depths of 200 to 1600 m .

Biology: Viviparous with a yolk-sac, but little else known. The immense, triangular, razor-edged lower teeth of this shark suggest that it is a formidable predator capable of attacking and dismembering large prey.

Size: Maximum total length about 110 cm .
Interest to Fisheries and Human Impact: This species is of limited fisheries interest. It is caught as bycatch in bottom trawls and nets, and by longline gear, but rarely reported separately and is generally included with other deepwater sharks in mixed landings. Since 2006, an average of 205 tonnes in landings was reported to FAO, with most of the landings coming from Portugal and Spain. Nothing is known about its life history or population structure. It is utilized dried salted for human consumption and for fishmeal. Under TAC regulation in EU (in 2012, TAC=0) (EU, 2010). Technical measures in force in EU waters and NEAFC regulatory area (2012).

The conservation status of this species is Data Deficient due to insufficient information on its life history and abundance within fishery areas.

Local Names: Arreganhada (Portugal); Messerzahnhai (Germany); Knorrhaj (Sweden).
Literature: Bigelow and Schroeder (1957); Maurin and Bonnet (1970); Krefft and Stehmann (1973); Taniuchi and Garrick (1986); Blasdale and Valenti (2008); Gibson et al. (2008); EU (2010); ICES (2010); Ebert and Compagno (In press); A. Stewart (pers. comm.).

## Somniosus Lesueur, 1818

Genus: Somniosus Lesueur, 1818, J. Acad. Sci. Philadelphia 1(2): 222. Proposed as a subgenus of Squalus Linnaeus, 1758, but used in generic form.

Type species: Somniosus brevipinna or Squalus brevipinna Lesueur, 1818, by monotypy; a junior synonym of Squalus microcephalus Bloch and Schneider, 1801.

## Number of Recognized North Atlantic Species: 2.

Synonyms: Subgenus Somnolentus (Lesueur) Swainson, 1838, Nat. Hist. Fish. Amphib. Rept, Monocard. Anim., 1: 146. Apparently an erroneous misspelling or correction of Somniosus Lesueur, 1818; regarded by Swainson as a synonym of Scymnus Cuvier, 1817. Genus Laemargus Müller and Henle, 1837, Ber. K. preuss. Akad. wiss. Berlin, 2: 116; Müller and Henle, 1837, Arch. Naturg. 3: 399; Müller and Henle, 1838, Mag. Nat. Hist., n. ser., 2: 89; Müller and Henle, 1838, L'Institut, 6: 65 (no species mentioned). Reduced to subgenus Laemargus Müller and Henle, 1839, Syst. Beschr. Plagiost., pt. 2: 93 (Genus Scymnus Cuvier, 1817), with three species. Type species: "Squalus borealis Scoresby", by subsequent designation of Jordan, 1919, Stanford U. Pub., U. Ser., Gen. Fish. (3): 192, equals Scymnus borealis Fleming, 1828 as cited by Müller and Henle, 1839, a junior synonym of Squalus microcephalus Bloch and Schneider, 1801. Genus Leiodon Wood, 1846, Proc. Boston Soc. Nat. Hist, 2, 174. Type species: Leiodon echinatum Wood, 1846, by monotypy. Genus Rhinoscymnus Gill, 1864 (published 1865?), Proc. Acad. Nat. Sci. Philadelphia: 264, ftn. 5. Type species: Scymnus rostratus Risso, 1826, by monotypy. Subgenus Brevisomniosus Quéro, 1976, Rev. Trav. Inst. Peches Marit. 39(4): 463, 467. (Genus Somniosus Lesueur, 1818). Type species not indicated, two species, Somniosus rostratus (Risso, 1827) and S. bauchotae Quéro, 1976, included in it.

Field Marks: Short to moderately long snout, no fin spines on dorsal fins, no anal fin, slender-cusped teeth without cusplets in upper jaw, bladelike, oblique and relatively short-cusped teeth in lower jaw, denticles with narrow, hooked, cuspidate crowns, lips not fringed and pleated, first dorsal fin on middle of back and usually behind pectoral fins, but well ahead of pelvic fins, second dorsal fin slightly smaller than first, caudal fin somewhat paddle-shaped, with a long lower lobe, size moderate large to very large.

Diagnostic Features: Anterior nasal flaps short, not expanded into barbels; snout short to moderately long, broadly rounded to pointed and somewhat flattened, length $2 / 5$ to less than $1 / 3$ of head length and $2 / 3$ to less than $2 / 5$ of distance from mouth to pectoral origins; gill openings moderately wide, last one about as long as first four; lips thin, not fringed, pleated or suctorial; teeth strongly different in upper and lower jaws, upper small, with narrow, acute, erect cusps and no cusplets, not bladelike, lowers much larger, bladelike, interlocked, with a low to moderately high, oblique or semierect cusps and distal blade, edges serrated or not; tooth rows 30 to 60 upper jaw, 31 to 63 lower jaw. Both dorsal fins spineless; first dorsal fin on middle of back, with origin sometimes extended forward as a low ridge over pectoral-fin bases but usually well behind pectoral fins, insertion far in front of pelvic-fin origins but slightly closer to pelvic-fin bases than pectoral fins; second dorsal fin slightly smaller than first and with base $3 / 4$ length of first dorsal-fin base or less; origin of second dorsal fin varying from over anterior half of pelvic-fin bases to somewhat posterior to pelvic-fin free rear tips; pectoral fins with short, narrowly to broadly rounded free rear tips and inner margins, not expanded and acute or lobate; caudal fin semi-symmetrical and paddle-shaped, with a relatively short upper lobe and long lower lobe, and a strong subterminal notch. No precaudal pits, or lateral keels, or midventral keels on caudal peduncle.

Dermal denticles with oblique to erect, ridged hooked, cuspidate narrow crowns, not flat, depressed and block-like. Cloaca normal, not expanded as a luminous gland. Vertebral counts: total vertebral counts 35 to 78 , monospondylous vertebral counts 21 to 46 , and precaudal vertebral counts 28 to 59 , caudal vertebral counts 6 to 10 . Intestinal valve with 23 to 41 turns. Moderate to gigantic sharks with adults from 140 to more than 600 cm total length. Colour: medium grey to blackish, without conspicuous light fin edges

Local Names: Sleeper sharks, Greenland sharks, Gurry sharks.
Remarks: Following Yano, Stevens and Compagno (2004), five species are recognized with two species occurring in the North Atlantic. A sixth species, based on an illustration by Capello (1870), of a specimen captured off Portugal, and held in the collection at the Bocage Museum in Lisbon, Portugal, was lost in a fire that destroyed the Bocage Museum; no other specimens like it are in existence to the best of our knowledge in other museum collections.

## Key to North Atlantic Species:

1a. Lower teeth with low roots and high, slender, semierect cusps. Number of tooth rows 57 to 63 upper jaw, 31 to 36 lower jaw. Intestinal valve count less than 27. Vertebral centra well-calcified, with notochord constricted between the calcified double cones. Small sharks, with adults less than 140 cm long (Fig. 129) . . . . . . . . . Somniosus rostratus

1b. Lower teeth with high roots and low, broad, oblique cusps. Number of tooth rows 35 to 52 upper jaw, 45 to 63 lower jaw. Intestinal valve count more than 27 . Vertebral centra not calcified, with notochord greatly expanded between the septate centra. Gigantic sharks, with adults to 500 cm or more long (Fig. 130) . . Somniosus microcephalus


Fig. 129 Somniosus rostratus


LOWER TEETH
Fig. 130 Somniosus microcephalus

## Somniosus microcephalus(Bloch and Schneider, 1801)

Squalus microcephalus Bloch and Schneider, 1801, Syst. Ichthyol.: 135. Holotype lost, "habitat in mari glaciali".
Synonyms: Squalus carcharias Gunnerus, 1765, Drontheim Gesell. Schrift, 2: 299-207, pl. 10-11. Not Squalus carcharias Linnaeus, 1758, = Carcharodon carcharias. Squalus squatinaPallas, 1814, Zoogr. Rosso Asiat., 3: 64. White and Arctic Seas. Not Squalus squatina Linnaeus, 1758, = Squatina squatina. Squalus (Acanthorhinus) norwegianus Blainville, 1816, Bull. Sci. Soc. Philomat. Paris, (8): 121, Nomen nudum, placed here by reference to Blainville, 1825 (below). Squalus brevipinna Lesueur, 1818, J. Acad. Sci. Philadelphia 1(2): 222. Also as Somniosus brevipinna Lesueur, 1818, Ibid., pl. Holotype: 196 cm specimen, near Marblehead, Massachusetts, probably not saved. Squalus borealis Scoresby, 1820, Arctic regions, 1:538-540, pl. 15, Fig. 3-5. No type material, Spitzbergen Sea. Squalus (Acanthorhinus) norwegianus Blainville, 1825, in Vieillot et al., Faune Francaise, liv. 13-14: 61. No type material, "mers du Nord". Sq[ualus] arcticus (Scoresby) Blainville, 1825, in Vieillot et al., Faune Francaise, liv. 13-14: 61. Attributed to Scoresby's treatise on whale fisheries. Scymnus gumneri Thienemann, 1828, Lehrb. Zool., 3: 409. On Squalus carcharias Gunnerus, 1765? Scymmus glacialis Faber, 1829, Fische Islands: 23. No type material? Iceland, Polar seas. Scymnus micropterus Valenciennes, 1832. Nouv. Ann. Mus. Natn. Hist. Nat. Paris, 1: 458-468, pl. 20. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN-9857, "estuarie de la Seine". Leiodon echinatum Wood, 1846, Proc. Boston Soc. Nat. Hist, 2, 174. Description of a 16 ' specimen, no type material? Portland, Maine.

Other Combinations: Laemargus borealis (Scoresby, 1820).
FAO Names: En - Greenland shark; Fr - Laimargue du Groenland; Sp - Tollo de Groenlandia.


Fig. 131 Somniosus microcephalus


Field Marks: Short, rounded snout, heavy cylindrical body and small precaudal fins, two spineless, equal-sized dorsal fins, no anal fin, long ventral caudal-fin lobe, first dorsal fin on back slightly closer to pelvic fins than pectoral fins, interdorsal space greater than distance from snout to second gill slits, no keels on base of caudal fin, upper teeth lanceolate, lower teeth with short, low, strongly oblique cusps and high, narrow roots.

Diagnostic Features: Snout short and broadly rounded. Head moderately long, length from snout to pectoral fins 20.7 to $28.8 \%$ total length. Cusps of lower teeth short and low, strongly oblique, roots very high. Total tooth rows upper jaw 35 to 39 and for lower jaw 45 to 57 . Lateral trunk denticles with erect, narrow-crowns and hooked cusps, giving skin a rough, bristly texture. Insertion of first dorsal fin slightly closer to pelvic bases than pectoral bases. Interdorsal space greater than distance from snout tip to second gill slits. No lateral keels present on base of caudal fin. Caudal peduncle short, distance from second dorsal-fin insertion to upper caudal-fin origin less than twice second dorsal-fin base, distance from pelvic-fin insertions to lower caudal-fin origin less than dorsal caudal-fin margin. Vertebral column without well-defined calcified centra, notochord secondarily expanded. Vertebral counts: total vertebral counts 41 to 44 , monospondylous vertebral counts 25 to 29, precaudal vertebral counts 31 to 36 , caudal vertebral counts 7 to 10 . Spiral valve turns: 29 to 34 . Size very large, exceeding 600 cm and possibly exceeding 730 cm . Colour: grey to medium brown, sometimes with transverse dark bands, small dark and light spots, and blotches.

Distribution: As presently known, endemic to the North Atlantic and Arctic from Georgia (USA) to the Gulf of Maine and Gulf of St. Lawrence to Ellesmere Island, Greenland, Iceland, Spitzbergen, the Arctic coast of Russia (Bear Island, White Sea), and Norway to the North Sea and Ireland, with occasional specimens recorded further south.

Habitat: An abundant deepwater shark of continental and insular shelves and upper slopes down to at least 1400 m and possibly to 2647 m . The Greenland shark is one of the larger sharks and by far the largest of North AtlanticArctic fishes with the exception of the basking shark (Cetorhinus maximus). In the Arctic and boreal Atlantic it occurs inshore in the intertidal and at the surface in shallow bays and river mouths during the colder months but tends to retreat into water 180 to 550 m deep when the temperature rises. At lower latitudes in the North Atlantic (Gulf of Maine and North Sea) it inhabits the continental shelves, and may move into shallower water in the spring and summer. Recent records of a large


Fig. 132 Somniosus microcephalus
 unidentified Somniosus species from off Savannah, Georgia (U.S.A.) and in the northern Gulf of Mexico suggest that much like the North Pacific Somniosus pacificus, this species or one of the other large Somniosus species exhibits tropical submergence in warm temperate and tropical seas. Yano, Stevens, and Compagno (2007) showed that at lower latitudes this species tends to occur in deeper water. The water temperature typically preferred by these sharks ranges from 0.6 to $12^{\circ} \mathrm{C}$. Remote operated vehicles operating in the northern Gulf of Mexico recorded large Somniosus species occurring to great depths (to 2647 m ) and usually where the water temperate is less than $5^{\circ} \mathrm{C}$. Also, these videos show a large Somniosus swimming 10 m or more off the bottom.

Biology: Viviparous with a yolk-sac, but there is very little information on fecundity available. Three large females were found to have large numbers ( 2689 to 2931) of large, yolky ovarian eggs. One female over 500 cm long had 10 young each about 37 cm long in 1 uterus; and these were presumably full term because their yolk-sacs were resorbed and their denticles were erupted and their teeth were visible. Growth rates although poorly documented for this species appears to be quite slow, with individuals from one tag and recapture study growing only 8 to 15 cm after being at liberty for 16 and 14 years, respectively.
Important food items include fishes such as herring, spiny eels, salmon and char, smelt, a variety of gadoids including cod, ling, pollock, and haddock, several flatfish including Atlantic and Greenland halibut, wolf-fish, redfish (Sebastes), sculpins, lumpfish, and skates and their egg-cases. The Greenland shark regularly devours marine mammals, including seals (a common prey item) and small cetaceans (possibly mostly as carrion). Although seemingly slow moving, this shark is apparently able to capture large and active prey. Tracking studies have shown the Greenland shark will frequently move to the surface in areas where ringed seals (Phoca hispida) are abundant, and by stealth and cryptic coloration ambush these seals as they enter the water. These sharks have also been implicated in attacks on at least five different pinniped species around Sable Island, especially during the winter months. Greenland sharks voraciously devour carrion and offal of all sorts from whaling, sealing, and fishing operations, and will gather to feast in great numbers around whaling stations, whale kills, fish processing operations, and ice flows with skinned seal carcases. Parts of drowned horses and an entire reindeer were found in large Greenland sharks. Other prey includes sea birds, squid, crabs, amphipods, marine snails, brittle stars, sea urchins, and jellyfish.
The Greenland shark has an unusual copepod (Ommatokoita elongata) parasite that attaches itself to the corneas of the eyes; usually a single copepod is present on each eye. The copepods are highly conspicuous and may even be luminescent. It has been speculated that their relationship to the shark is mutualistic and beneficial, with the copepods serving as lures to bring prey species in proximity to their hosts. Field observations are necessarily, however, to determine if the parasites actually serve as lures.

Size: Maximum at least 640 cm and possibly to 730 cm , but most adults between 300 to 450 cm ; adult males mature at about 300 cm or greater in length, and adult females at a length of about 450 cm or more. Size at birth about 40 cm , but full-term foetuses were 37 cm long and free-swimming neonates were 40 to 50 cm in length.

Interest to Fisheries and Human Impact: Small numbers of these sharks are landed, mainly in Icelandic waters where the catch has been relatively stable, averaging about 43 tonnes annually over the past decade. It is likely caught in much higher numbers as discarded bycatch, but there are not estimates available. Historically, this shark was caught in large numbers for its liver oil in Greenland, Iceland, and Norway, in the early part of the 20 th century with catches of up to 32000 sharks per year. Some Norwegian fisheries targeted them as they viewed them as a pest. Although fished in Greenland, Iceland and northern Norway for its liver oil, its meat is also used fresh and dried for human and sled-dog food. The meat is toxic when fresh, unless carefully washed, but is harmless dried or semi-putrid. Eskimos have used the skin of the Greenland shark for making boots, and used the sharp lower dental bands as knives for cutting hair. The Greenland shark is mostly fished with hook and line, longline gear or gaffs, but is often taken in seal and whale nets and cod traps.
Fishermen consider the Greenland shark as harmless, but there are old, unsubstantiated and possibly mythical tales of Greenlanders in kayaks being attacked by these sharks. Under TAC regulation in EU (in 2012, TAC=0) (EU, 2010).

The global conservation status of this species is Near Threatened based on possible population declines and its limiting life history characteristics.

Local Names: Gurry shark, Sleeper, Sleeper shark, Large sleeper shark, Nurse shark, Nurse, Ground shark (English); Laimargue, Laimargue atlantique, Laimargue du Groenland (France); Eishai (Germany); Håkjerring, Håkäring (Sweden, Norway); Tiburón boreal (Spain); Tubarão da gronêlandia, Pailona (Portugal); Ekalugssuak (Greenland); Poljarnaja akula (Russia); Hákarl (Iceland); Hákelling (Faroe Islands); Havkal (Denmark).

Literature: Bigelow and Schroeder (1948); Bjerkan (1957); Koefoed (1957); Hansen (1961); Garrick and Schultz (1963); Templeman (1963); Beck and Mansfield (1969); Lineaweaver and Backus (1970); Quero (1976); Herdendorf and Berra (1995); Skomal and Benz (2004); Yano, Stevens and Compagno (2004, 2007); Kyne, Sherrill-Mix and Burgess (2006); Benz, Hoffmayer, Driggers et al. (2007); Benfield, Thompson, and Caruso (2008); Gibson et al. (2008); Skomal (2008); EU (2010); ICES (2010); Lucas and Natanson (2010); Ebert and Compagno (In press).

## Somniosus rostratus(Risso, 1827)

Scymnus rostratus Risso, 1827, Hist. nat. Princip. Prod. Europe Méred., Paris, Poissons: 138. No type material. Mediterranean Sea, deep water.

Synonyms: Somniosus bauchotae Quero, 1976, Rev. Trav. Inst. Peches Marit. 39(4): 455, Figs. 1-8. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN-1976-12, 130 cm adult (?) female, $46^{\circ} 50^{\prime} \mathrm{N}, 5^{\circ} 10-15^{\prime} \mathrm{W}$, Bay of Biscay, 220 m.

Other Combinations: None.
FAO Names: En - Little sleeper shark; Fr - Laimargue de la Méditerranée; Sp - Tollo boreal.


Fig. 133 Somniosus rostratus

Field Marks: Short, rounded snout, two spineless, equal-sized dorsal fins, no anal fin, long ventral caudal lobe, first dorsal fin on back closer to pectoral fins than pelvic fins, short keels on base of caudal fin.

Diagnostic Features: Snout short and broadly rounded. Head short, length from snout to pectoral fins 20 to $23 \% \mathrm{TL}$ in specimens above 70 cm TL. Cusps of most lower teeth large, high, and semioblique, roots low. Total tooth rows upper jaw 53 and for lower jaw 31 to 36. Lateral trunk denticles with flat, wide, crowns and horizontal cusps, giving skin a smooth texture. Insertion of first dorsal fin closer to pectoral-fin bases than pelvic-fin bases. Interdorsal space equal or greater than distance from snout tip to second gill slits. A short lateral keel present on base of caudal fin. Caudal peduncle short, distance from second dorsal-fin insertion to upper caudalfin origin 2 times second dorsal-fin base or less, distance from pelvic-fin insertions to lower caudal-fin origin subequal to dorsal caudal-fin margin. Vertebral column with well-defined centra. Vertebral counts: total vertebral count 78 , precaudal vertebral count 58. Spiral valve turns: 23. Size small, not exceeding 140 cm . Colour: uniformly blackish without transverse dark bands, small light spots, and blotches.

Distribution: Eastern Atlantic: France, Portugal, and Madeira Islands, and the western Mediterranean. Western Central Atlantic: possibly from off Cuba.


Fig. 134 Somniosus rostratus
Known distribution

Habitat: A rare to sporadically common, little-known small sleeper shark of the outer continental shelves and upper slopes, occurring on or near the bottom at depths of 180 to 2200 m .

Biology: Development viviparous with a yolk-sac, and with litters of 6 to 9 . Probably eats deepwater bottom fishes and invertebrates. This species thought at one time to have luminous organs, but Fulgosi and Gandolfi (1983) showed that the structures in question are really pit organs. Hence this species agrees with the large species of Somniosus (subgenus Somniosus) in lacking light organs.

Size: Maximum about 143 cm ; adult males 71 cm ; adult females 82 to 134 cm . Size at birth 21 to 28 cm .
Interest to Fisheries and Human Impact: Interest to fisheries minimal, caught on longlines and with bottom trawls in the Eastern Atlantic. Small numbers, less than 3 tonnes annually, of this shark are landed in Spain and it is likely taken as bycatch by others, but is not reported separately.

The conservation status of this species is currently Data Deficient due to the rarity of this species.
Local Names: Sleeper shark, Frog shark.
Remarks: The Japanese Heteroscymnus longus(= Somniosus longus) and the Mediterranean Somniosus bauchotae have been synonymize with $S$. rostratus by previous authors (Bigelow and Schroeder 1957; Quero, 1976; Compagno, 1984), but subsequent work by Yano, Stevens, and Compagno (2004) confirm that $S$. Iongus is in fact distinct. However, Yano et al. (2004) also concluded that $S$. bauchotae, described by Quero (1976) from a single specimen from the Bay of Biscay, was indistinct from $S$. rostratus and therefore is considered a junior synonymy.

Literature: Bigelow and Schroeder (1948, 1957); Maul (1955), Quero (1976); Cadenat and Blache (1981); Fulgosi and Gandolfi (1983); Barrull and Mate (2001a); Yano, Stevens, and Compagno (2004); Gibson et al. (2008); Séret et al. (2008); Ebert and Compagno (In press).

## Zameus Jordan and Fowler, 1903

Genus: Zameus Jordan and Fowler, 1903, Proc. U.S. Natn. Mus. 26 (1324): 632.
Type species: Centrophorus squamulosus Günther, 1877, by monotypy.

## Number of Recognized North Atlantic Species: 1.

Synonyms: Scymnodon Barbosa du Bocage and Brito Capello, 1864, Proc. Zool. Soc. Lond., 24: 263.
Field Marks: Small to moderate, slender bodied sharks, with low flat head, snout moderately long to short. Mouth short, narrow, transverse; upper labial furrows short. Teeth of upper jaw small, spear-like, lower jaw teeth larger, highly erect, knife-like. Fin spine preceding each dorsal fin. Pectoral fins small, leaf-shaped to rounded. Caudal fin with strong subterminal notch and short lower lobe. Colour is a uniform black to dark brownish.

Diagnostic Features: Head rather low and flat. Snout narrow, relatively long to short. Eyes moderately large. Mouth broad to fairly narrow and transverse. Teeth dissimilar in upper and lower jaws; upper teeth small, single cusp, smooth-edged, lanceolate, lower teeth triangular, oblique, erect-cusped, knife-like. Tooth counts for upper jaw 42 to 60 , lower jaw 28 to 38 . Gill slits rather short, longest less than half eye length. Lateral trunk denticles with or without tricupid ridges. First dorsal fin dissimilar in shape to second dorsal fin; length of first dorsal-fin base greater than second. Dorsal-fin spines present; first dorsal-fin spine relatively large, but decreases proportionally with growth; second dorsal-fin spine slightly shorter than first. Pectoral fins narrow to moderately broad, rounded, or leaf-shaped; apices of pectoral fins fall anterior to, or posterior to origin of first dorsal-fin spine. Pelvic fins small, about equal to second dorsal fin. Caudal peduncle long, distance from second dorsal-fin base to upper caudal-fin origin about equal to second dorsal-fin base. Caudal fin with a strong subterminal notch and a short lower lobe. Spiral valve turns: 12 to 16 . Vertebral counts: total vertebral counts 93 to 105 , precaudal vertebral counts 66 to 76 , monospondylous vertebral counts 50 to 57 . Small to moderate size sharks between 84 to 101 cm . Colour: uniformly black to dark brownish with no conspicuous markings.

Local Names: Velvet dogfish.
Remarks: Taniuchi and Garrick (1986) based on distinct morphological, including dermal denticles, and meristic (tooth and vertebral) differences from Scymnodon resurrected the genus Zameus. The genus as presently restricted includes two species, Zameus ichiharai known only from the Western North Pacific (Japan) and a wide ranging, but sporadically distributed species $Z$ squamulosus. The species name Scymnodon (=Zameus) obscurus is sometimes seen in the literature for the North Atlantic, but that species appears to be a junior synonym of $Z$ squamulosus (See Remarks section below species account).

## Zameus squamulosus (Günther, 1877)

Centrophorus squamulosus Günther, 1877, Ann. Mag. Nat. Hist. ser. 4, 20(119): 433. Holotype: British Museum (Natural History), BMNH-1880.5.1.1, 670 mm female, Challenger sta. 232, off Inosima, Japan, $35^{\circ} 11^{\prime} \mathrm{N}, 139^{\circ} 28^{\prime} \mathrm{E}, \mathrm{BT}-41.4^{\circ} \mathrm{F}, 631 \mathrm{~m}$.

Synonyms: Centroscymnus obscurus Vaillant, 1888, Exped. Sci. Travailleur et Talisman, Zool., Poiss. 67-68, pl. 2, Fig. 2a-e. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN-84-388, 590 mm female, `côtes du Soudan', 1400-1435 m.

Other combinations: Scymnodon squamulosus (Regan, 1908), Scymnodon obscurus Bigelow and Schroeder (1957).
FAO Names: En - Velvet dogfish.


Fig. 135 Zameus squamulosus
Field Marks: A small slender bodied shark, with a low flat head, fairly long snout, short narrow mouth, post oral grooves much longer than the short upper labial furrows. A small spine preceding each dorsal fin, no anal fin, small lanceolate teeth without cusplets in upper jaw and large high, knife-cusped cutting teeth in lower jaw, mouth moderately wide and nearly transverse, caudal fin with strong subterminal notch and short lower lobe. Uniformly black to dark brownish in colour.

Diagnostic Features: Head rather low and flat. Snout rather narrow and long, preoral length greater than mouth width and almost equal to distance from lower symphysis to first gill slits. Mouth fairly narrow, short and transverse. Postoral grooves very long, much longer than upper labial furrows. Teeth of upper jaw small, spear-like, lower jaw high-cusped, knife-like. Tooth counts for upper jaw 47 to 60, lower jaw 32 to 38 . Gill slits rather short, longest less than half eye length. Lateral trunk denticles with cross-ridges on crowns. Dorsal-fin spines present, relatively small. Pectoral fins narrow to moderately broad and leafshaped; apices of pectoral fins falling well in front of first dorsal-fin spine. Pelvic fins small, about equal to second dorsal fin. Caudal peduncle long, distance from second dorsal-fin base to upper caudal-fin origin about equal to second dorsal-fin base. Caudal fin with a strong subterminal notch and a short lower lobe. Spiral valve turns: 16. Vertebral counts: total vertebral counts 93 to 105, monospondylous vertebral counts 50 to 54 , precaudal vertebral counts 66 to 76 . Moderate size with a maximum total length of 84 cm . Colour: uniformly black to dark brownish with no conspicuous markings.

Distribution: Eastern Atlantic: Iceland and Faroe Ridge to Madeira Islands, Morocco, Cape Verde, Senegal, Namibia, and west coast of South Africa. Western Atlantic: absent from Area 21, but known from the northern Gulf of Mexico, Surinam, and southern Brazil. Elsewhere, widely and sporadically distributed in most seas except the Eastern Pacific.

Habitat: A poorly known epipelagic and oceanic deepwater sharkusually found off continental and insular slopes, on or near the bottom at depths of 550 to 1450 m , but also well off the bottom at depths between 0 to 580 m in water 2000 to 6000 m deep.


Fig. 136 Zameus squamulosus
Known distribution $\square$ Possible distribution

Biology: Viviparous with a yolk-sac, litter possibly 3 to 10 based examination of mature females with ovarian eggs. A predator on bottom fishes and invertebrates, but its smaller teeth and mouth, and weaker jaws suggest that it is a predator less capable of killing large prey than its congener $\boldsymbol{S}$. ringens.

Size: Maximum total length about 84 cm ; adult males 47 to 51 cm , and adult females 59 to 69 cm long. Size at birth about 20 cm .
Interest to Fisheries and Human Impact: This relatively small shark is of limited fisheries interest. It is caught incidentally in bottom trawl and set gillnets, and by bottom and pelagic longline gear in the Eastern North Atlantic. There is no speciesspecific information on the numbers of these sharks that are caught as bycatch, but it is likely low since the do not seem to be abundant where they are known to occur.

Conservation status is Data Deficient due to a lack of information on the life history, abundance, and population status of this widespread, but sporadically distributed shark.

Local Names: Smallmouth velvet dogfish (English); Squale-grogneur à queue échancrée; Squale grogneur velouté (France); Bruja terciopelo, Bruja bocachica (Spain), all for Scymnodon obscurus.

Remarks: The Japanese Scymnodon (=Zameus) squamulosus and the eastern North Atlantic Scymnodon obscurus were considered to be separable by the supposed presence ( $\boldsymbol{S}$. obscurus) or absence ( $\boldsymbol{S}$. squamulosus) of transverse ridges on their dermal denticles; a character said by Bigelow and Schroeder (1957) to differentiate these two species. However, comparison of dermal denticles between $S$. (=Z.) squamulosus and $S$. obscurus by several authors (Krefft, 1980; Yano and Tanaka, 1984; Taniuchi and Garrick, 1986) revealed the presence of transverse ridges on the denticles of both species. Furthermore, comparison of proportional measurements of the type specimen of $Z$. squamulosus to North Atlantic specimens of $\boldsymbol{S}$. obscurus further confirmed that there were no differences between these species, thus $\boldsymbol{S}$. obscurus is considered a junior synonym of $Z$. squamulosus.

Literature: Bigelow and Schroeder (1957); Krefft and Stehmann (1973); Kreff (1980); Yano and Tanaka (1984); Taniuchi and Garrick (1986); Wetherbee and Crow (1996); Burgess and Chin (2006); Gibson et al. (2008); Last and Stevens (2009); Ebert and Compagno (In press).

### 2.2.6 Family OXYNOTIDAE

Family: Oxynotidae Gill, 1872, Smiths. Misc. Coll. (247): 24. Also separately proposed as Subfamily Oxynotinae Fowler, 1934, Proc. Acad. Nat. Sci. Philadelphia, 85: 239 (Family Squalidae).

Type genus: Oxynotus Rafinesque, 1810.

## Number of Recognized North Atlantic Genera: 1.

FAO Names: En - Rough sharks; Fr - Centrines; Sp - Cerdos marinos, Tiburones ojinotos.
Field Marks: Unmistakable compressed, rough-skinned small sharks with high, sail-like spined dorsal fins and no anal fin.
Diagnostic Features: Head moderately broad and somewhat flattened. Snout flat and bluntly rounded or roundedangular in dorsoventral view. Spiracles large to enormous, close behind eyes. Fifth gill opening about as large as first four. Nostrils close together with internarial width much less than nostril width; nostrils with simple but enlarged anterior nasal flaps. Mouth nearly transverse and very short and small, with thick, papillose lips. Labial furrows elongated, entirely encircling mouth, and under posterior halves of eyes, elongated posteriorly into postoral grooves but not anteromedial preoral grooves; labial folds thick and papillose. Teeth with dignathic heterodonty well-developed, upper teeth much smaller than lowers. Upper teeth small, lanceolate, with narrow erect uncompressed, stout smooth-edged cusps and no cusplets or blades, in quincunx formation in a narrow triangular pad and not imbricated; lower teeth highly compressed, high-crowned, broad and bladelike, and imbricated, a single series of functional teeth forming a continuous sawlike cutting edge, teeth with a compressed, medially erect but distally mostly oblique broad, sharp-edged, serrated cusp, a short distal blade (except medial tooth with a pair of distal blades), and no cusplets; tooth row counts 9 to 18 upper jaw, 9 to 15 lower jaw. Trunk strongly compressed, very high, with a triangular cross-section, abdomen with strong lateral ridges. Interdorsal space short and variably less than or somewhat larger than length of first dorsal-fin base; pelvic-caudal space short and subequal to less than twice length of pelvic-fin bases. Caudal peduncle slightly compressed, short, and without lateral keels or precaudal pits. Body without photophores. Denticles large and pedicellate, with flattened, broad-keeled, erect or semierect, trident-like crowns with medial and lateral cusps, sometimes auxillary anterior and posterior cusps, slender tall pedicels and low bases; surface of skin extremely rough. Pectoral fins high, narrow, distally lanceolate, leaf-shaped, subangular or falcate, length of anterior margins varying from about equal to the prespiracular length to about equal to the head length, rear tips rounded and not elongated. Pelvic fins smaller than pectoral fins and dorsal fins. Claspers with a lateral spine only. Dorsal fins very large, broad, angular, high, sail-like and often falcate, with strong stout spines nearly completely buried in the fins and with ungrooved exposed tips. First dorsal fin large, with length greater than prespiracular
space and sometimes slightly longer than head; first dorsal-fin base over pectoral-fin bases and pectoral-pelvic space and well anterior to pelvic fins, origin over pectoral-fin bases and sometimes anterior to pectoral-fin origins. Second dorsal fin smaller than first dorsal fin, base over pelvic-fin bases with origin about opposite to well in front of pelvic-fin origins. Caudal fin heterocercal, with ventral lobe weakly developed in adults, and with subterminal notch strong. Vertebral counts: total vertebral counts 84 to 94 , monospondylous vertebral counts 41 to 50 , diplospondylous vertebral counts 16 to 18, total precaudal vertebral counts 58 to 66 , caudal vertebral counts 26 to 31 . Intestinal valve with 9 to 11 turns. Adults small to moderately large, 49 to 150 cm long. Colour: plain or with light and dark markings on body, without black photophore markings on tail or flanks.

Distribution: Rough sharks as currently known are mostly regional endemics scattered throughout the Eastern Atlantic, including the Mediterranean, Western Central Atlantic, Western Pacific, and possibly the South-western Indian Ocean off Mozambique. Three of the five known species occur in the Atlantic, with species from off the British Isles to South Africa in the Eastern Atlantic, and Venezuela and Mexico in the Western Central Atlantic. Two species occur in the Western Pacific off Japan, Australia, and New Zealand.

Habitat: These are poorly known deepwater bottom sharks, with a distinctive appearance, that live on the upper continental and insular slopes and outer shelves at depths of 40 to 1067 m .

Biology: The reproductive mode is yolk-sac viviparity, with litters of 7 to 23 , but little else is known about the biology of these sharks. These are small sharks, with all five known species maturing at a size mostly smaller than 70 cm but exceptionally up to 118 to 150 cm in two species.

The feeding habits of rough sharks are little known, but include polychaetes, crustaceans and molluscs. The mouth of these sharks is very small, have papillose lips, and their teeth are small though strong and confined to the tips of the stout jaws. This suggests a primary diet of small bottom invertebrates and possibly small benthic fishes that are dismembered by the clipper-like lower cutting teeth and retained by the broad triangular pad of short-cusped lanceolate teeth on the upper jaw. The very large nostrils and nasal organs (exceptionally large for squaloids and more resembling those of benthic scyliorhinids) and unusual labial structures may be especially important in locating prey. The large close-set denticles, with erect crowns and sharp, very prickly cusps, may serve as armor to protect these sharks from benthic predators.

The behaviour of these unusual sharks is poorly known, but judging from their distinct body form and rough scales, they are likely sluggish swimmers. They may rely on their expanded body cavities and large oily livers, estimated at 16 to $23 \%$ of total weight in one species, to attain neutral buoyancy, so they can hover and slowly swim above the substrate without needing forward motion for lift. Underwater videos of Oxynotus species in situ show that they hover or slowly swim off the bottom and tip their heads downwards to feed on the bottom. The strong pectoral radial muscles, expanded lanceolate pectoral fins and fanlike pectoral radials suggest that the pectoral fins may be actively used for manoeuvring off the substrate, but this needs to be studied by analysing videos of live animals in the wild or in captivity.

Interest to Fisheries and Human Impact: Rough sharks are of limited interest to fisheries since they do not appear to occur in concentrated numbers or in any abundance, and are a relatively uncommon bycatch of bottom trawl fisheries. In the Eastern Atlantic where they are occasionally retained they are utilized mostly for fishmeal and oil, but also are prepared smoked and dried-salted for human consumption. World and local catch statistics are limited to non-existent for these sharks.

The conservation status of rough sharks is poorly known, but may be of concern since they seem to be rare to uncommon where they occur, have limited geographic and bathymetric ranges, and occur in areas with significant demersal trawl fisheries that take them as bycatch. However, given their apparent ability to gain neutral buoyancy and to 'hover' they may occur more commonly in areas of rocky, high relief bottom substrates that precludes them from being caught in bottom trawls and given their relatively small mouths they would likely not be as vulnerable to longline gear as would other large-mouth shark species. This combination of characteristics, habitat preference and body morphology, may therefore minimize the bycatch of these sharks.

## Local Names: Rough sharks, Prickly dogfishes, Sea pigs or Porkfishes.

Remarks: This monotypic family includes the distinctive living genus Oxynotus. This small family with a single genus currently has five recognized species, but depending on the taxonomic resolution of the group one or two additional species may eventually be described. Two of the five known species occur in Area 27, but there are no records of this group occurring in Area 21 although one species Oxynotus caribbaeus does occur in the Western Central Atlantic (Area 31).

Literature: Garman (1913); Norman (1932); Bigelow and Schroeder (1957); Cadenat and Blache (1981); Compagno (1984); Yano and Murofushi (1985); Ebert and Compagno (In press).

## Oxynotus Rafinesque, 1810

Genus: Oxynotus Rafinesque, 1810, Indice Ittiol. Sicil.: 45, 60
Type species: Oxynotus centrina Rafinesque, 1810, by monotypy, equals Squalus centrina Linnaeus, 1758.
Number of Recognized North Atlantic Species: 2.
Synonyms: Subgenus Centrina Cuvier, 1816: 130. Type species: Squalus centrina Linnaeus, 1758, by absolute tautonymy. Genus Centrinus Swainson, 1838: 151. Apparent erroneous spelling of Centrina Cuvier, 1817, as Centrina is consistently used elsewhere in Swainson's work (vols. 1 and 2, 1838 and 1839).

Remarks: Several prominent 19th and early 20th Century researchers followed Cuvier $(1817,1829)$ in using Centrina rather than Oxynotus Rafinesque, 1810 for these sharks, including Bonaparte (1838, 1839), Müller and Henle (1839), Bleeker (1859), Günther (1870), and Goodrich (1909). However, Oxynotus achieved recognition as a senior synonym of Centrina following the reviews of Gray (1851), Gill (1862b), Dumeril (1865), Regan (1906a), and Garman (1913).

## Key to North Atlantic Species:

1a. Spiracle very large, vertically elongated and slit-like or D-shaped, height nearly equal to eye length (Fig. 138). Supraorbital ridges greatly expanded posteriorly, forming a prominent rounded knob just in front of spiracle on each side that is covered with enlarged denticles. . Oxynotus centrina

1b. Spiracle smaller and circular or vertically oval, height less than half eye length (Fig. 139). Supraorbital ridges not greatly expanded and not forming a rounded knob in front of spiracle

Oxynotus paradoxus


Fig. 138 Oxynotus centrina


Fig. 137 Oxynotus paradoxus

## Oxynotus centrina(Linnaeus, 1758)

Squalus centrina Linnaeus, 1758, Syst. Nat., ed. 10, 1: 233. Holotype unknown (see also Eschmeyer, 1998, Cat. Fish.) Type locality: "Habitat in mari Mediterraneo".

Synonyms: Oxynotus centrina Rafinesque, 1810: 45. Probably a new combination based on Squalus centrina Linnaeus, 1758, although Rafinesque did not mention Linnaeus' species as such. Centrina salviani Risso, 1827: 135. No type material (see also Eschmeyer). Type locality: Mediterranean Sea. Squalus centrina Linnaeus, 1758 not mentioned in account, but possible replacement name for Linnaeus' species. Centrina oxynotus Swainson, 1839: 315. No type material or locality, probably Europe by reference to "Bloch, 115" (see also Eschmeyer, 1998). Centrina vulpecula Moreau, 1881: 335, Fig. 61. Mediterranean Sea. Apparently an unjustified replacement name for Squalus centrina Linnaeus, 1758, as both Linnaeus' species and C. salviani Risso, 1826 are listed in its synonymy. Syntypes: whereabouts unknown according to Eschmeyer (1998).

## Other Combinations: Squalus (Acanthorhinus) centrina Linnaeus, 1758, Centrina centrina (Linnaeus, 1758)

FAO Names: En - Angular roughshark; Fr - Centrine commune; Sp - Cerdo marino.


Fig. 139 Oxynotus centrina


UNDERSIDE OF HEAD


UPPER AND LOWER TEETH

Field Marks: Short, blunt snout, high, sail-like dorsal fins with spines, no anal fin, first dorsal spine inclined forwards, high, thick, triangular body with large, rough denticles, massive knobs on supraorbital ridges, vertically elongated spiracles, lanceolate upper teeth, lower bladelike teeth in nine rows, colour pattern of darker marks on a light background, sometimes obscure.

Diagnostic Features: Spiracle large and vertically elongated, crescent or oval in shape. Supraorbital ridges enlarged over eyes, with a knoblike posterior expansion studded with large denticles and ending in front of spiracles. Teeth on upper and lower jaws dissimilar; uppers smaller than lowers, lanceolate, narrowly erect, awl-shaped in the central rows, broadly triangular and blade-like in the posterior rows, smooth-edged cusps and no lateral cusplets or blades, in quincunx formation in a narrow triangular pad and not imbricated; lower teeth imbricated, with a medially erect, distally oblique broad, sharpedged, serrated cusp, with no lateral cusplets; tooth row counts upper jaw 9 to 11, lower jaw 9 . Predorsal spine length from snout to first dorsal spine 2.6 to 2.8 in precaudal length. Pectoral fins leaf-shaped, not strongly falcate. Apices of dorsal fins broadly triangular, posterior margins shallowly concave. First dorsal-fin spine inclined forwards. First dorsal-fin anterior margin from spine to apex 0.8 to 1.0 in first dorsal-fin spine height, second dorsal-fin anterior margin from spine to apex 0.6 to 0.8 in second dorsal-fin spine height. Second dorsal-fin base 1.5 to 1.8 in interdorsal space, second dorsal-fin origin well anterior to pelvic-fin origins. Vertebral counts: total vertebral counts 91 to 94 , monospondylous vertebral counts 46 to 50 , total precaudal vertebral counts 61 to 66, caudal vertebral counts 26 to 30 . Intestinal valve turn counts unavailable. Adults to 150 cm . Colour: grey or grey-brown above and below, with darker blotches on head and sides (sometimes obscure particularly in adults); a light horizontal line separates dark areas on head and another crosses cheeks below eyes.

Distribution: A rare to uncommon species throughout its range. Eastern Atlantic from Norway to Portugal and extending southward to Madeira Islands, the Canary Islands, Morocco, Mauritania, to the Gulf of Guinea region, south to Gabon, Angola, Namibia, and South Africa (Western Cape). Also, throughout the Mediterranean Sea along the entire coast from the Straits of Gibraltar to Israel, but absent from the Black Sea. Possibly off Mozambique in the Western Indian Ocean, but whether it is this or a different species requires confirmation.

Habitat: A bottom shark of the continental shelves and upper slope at depths of 50 to 777 m , mostly below 100 m . Found mostly on coralline algal and muddy bottoms.

Biology: Viviparous with a yolk-sac, litters of 7 to 23 ; ovarian eggs may be up to 40 to 60 mm in diameter. In the Mediterranean mating is reported to occur in February with parturition possibly occurring three to 12 months later. Bith appears to occur in the spring. The liver weight as a percent of body weight (hepatosomatic index) is 16


Fig. 140 Oxynotus centrina
$\square$ Known distribution to 23 percent enabling this shark to attain neutral buoyancy so that it can 'hover' and slowly swim above the substrate without needing forward motion for lift. This allows these sharks to tip their heads downwards to feed on the bottom. Based on their diet, primarily consisting of polychaetes (60\%) along with crustaceans and teleosts making up a smaller portion, Oxynotus centrina like other oxynotids is thought to be a suction feeder. They are also known to consume the egg cases of Scyliorhinus canicula and in one occasion a newborn skate (Rajidae) was found the stomach of one individual.

Size: Maximum about 150 cm , but most individuals less than 100 cm long. Females maturing at about 65 cm in the northern part of their range, but in the southern part of their range two Angolan adult females reported to have large eggs were smaller at 52 and 58 cm in length (Poll, 1951). Males maturing at about 60 cm total length. Size at birth is 21 to 24 cm .

Interest to Fisheries and Human Impact: Interest to fisheries limited, and apparently primarily caught in the Mediterranean Sea and the Eastern North Atlantic. Caught as bycatch in bottom and pelagic trawls and utilized for fishmeal, oil, and smoked and dried-salted for human consumption. Records of this, and other oxynotids being caught within ICES fishing areas may be overestimated due to confusion with the common Portuguese name peixe-porco, which is also used for triggerfish (Balistes spp.) which constitute most of the large scale landings.

The conservation status is considered to be Vulnerable since this shark occurs in areas with intense deepwater demersal fisheries and suspected local population declines. In the Eastern North Atlantic there is no data regarding population trends, but given its population decline elsewhere most notably in the Mediterranean, a possible decline may be inferred in this area.

Local Names: Humantin, Prickly dogfish (England); Bernardet, Centrine, Cochon de mer, Coffre, La centrine humantin, Le squale humantin, Le humantin, Péi porc, Porc, Porc marin (France); Gefleckte Meersau, Meersau (Germany); Cerdo marino, Cochino, Guarrito, La mielga, Porc, Porch marí, Truchona, Truja (Spain); Peixe-porco (Portugal).

Remarks: Oxynotus centrina or a similar species reported from off southern African (Angola to South Africa) has been described as a different species, Oxynotus shubnikovi, based on the largely on the latter species having a shorter interdorsal space. However, comparison of southern African and Eastern North Atlantic $O$. centrina specimens reveal this characteristic to be variable. Therefore, lacking any other characteristics to separate the southern African Oxynotus from the Eastern North Atlantic and Mediterranean forms $O$. centrina is considered a junior synonym of $\boldsymbol{O}$. centrina Records of an Oxynotus from Mozambique, also similar in form to $\boldsymbol{O}$. centrina need to be further investigated.

Literature: Linnaeus (1758); Müller and Henle (1839); Gray (1851); Dumeril (1865); Günther (1870); Moreau (1881); Garman (1913); Lozano y Rey (1928); Norman (1932); Fowler (1936, 1969a); Bigelow and Schroeder (1957); Maurin and Bonnet (1970); Capapé (1974, 1975); Cadenat and Blache (1981); Quéro in Whitehead et al. (1984d); Springer (1990); Bianchi et al. (1993); Hernandez et al. (1998); Capapé et al. (1999); Barrull and Mate (2001b); Yano and Matsuura (2002); Megalofonou and Damalas (2004); Bradaï et al. (2007); Capapé (2008); Gibson et al. (2008); ICES (2010); Ebert and Compagno (In press).

## Oxynotus paradoxus Frade, 1929

Oxynotus paradoxus Frade, 1929, Bull. Soc. Port. Sci. Nat., 10(22): 267, Fig. 1. Holotype: Museu Bocage, Lisbon, Portugal, MB-T114, probably female, 78 cm TL, apparently lost in a fire that destroyed the museum, off Morocco (status confirmed by Eschmeyer, 1998, Cat. Fish.).

Synonyms: None.
Other Combinations: Centrina paradoxa (Frade, 1929).
FAO Names: En - Sailfin roughshark; Fr - Humantin; Sp - Cerdo marino velero.


Fig. 141 Oxynotus paradoxus

Field Marks: Short, blunt snout, high, sail-like dorsal fins with spines, strongly falcate pectoral fins, no anal fin, round spiracle, first dorsal-fin spine inclined rearwards, high, thick, triangular body with large, rough denticles, lanceolate upper teeth, lower bladelike teeth; tooth counts 13 in upper jaw and 11 to 15 in lower jaw. Coloration is uniformly blackish to dark brown.

Diagnostic Features: Spiracle small and circular. Supraorbital ridges not greatly expanded and not forming a knob in front of spiracles. Teeth on upper and lower jaws dissimilar; uppers smaller than lowers, lanceolate, broadly erect, triangular in medial rows, narrow and blade-like in posterior rows, cusps smooth-edged, with no lateral cusplets or blades, in quincunx formation in a narrow triangular pad and not imbricated; lower teeth imbricated, with a


UNDERSIDE OF HEAD medially erect, distally oblique broad, sharp-edged, serrated cusp, and no lateral cusplets; tooth counts upper jaw 13, lower jaw 9 . Predorsal spine length from snout to first dorsal-fin spine 2.7 in precaudal length. Pectoral fins strongly falcate. Apices of dorsal fins narrowly triangular, posterior margins strongly concave. First dorsal-fin spine inclined rearwards. First dorsal-fin anterior margin from spine to apex 2.5 in first dorsal-fin spine height, second dorsal-fin anterior margin from spine to apex 2.1 in second dorsal-fin spine height. Second dorsal-fin base 1.6 to 2.0 in interdorsal space, second dorsal-fin origin opposite pelvic-fin origins. Vertebral counts: total vertebral count 95 , monospondylous vertebral counts 46 to 50 , precaudal vertebral counts 62 to 64 , caudal vertebral count 31. Intestinal valve turn counts unavailable. Adults to 118 cm . Colour: blackish or dark brown, without prominent markings

Distribution: Endemic to the Eastern Atlantic, found along the Atlantic Slope from Scotland (including the northern North Sea), to Ireland, southern England, France, Spain, Portugal, and the Azores. Also, occurs off Madeira Islands, the Canary Islands, Morocco, Mauritania, Western Sahara, Senegal, and possibly southwards to the Gulf of Guinea region. Apparently absent from the Mediterranean.

Habitat: A deepwater bottom shark found on the Atlantic continental slope at depths from 265 to 720 m .

Biology: Yolk-sac viviparous, but nothing else known of its biology. This species was once filmed off the Azores by a remote operated vehicle, which showed the shark swimming near the bottom and tipping its head downwards to the substrate.

Size: Maximum about 118 cm ; an adult male was 75 cm long. Size at birth about 25 cm .


Fig. 142 Oxynotus paradoxus
$\square$ Known distribution

Interest to Fisheries and Human Impact: An uncommon bycatch of offshore trawling fleets and possibly longliners targeting deep-benthic squaloids. Under TAC regulation in EU (in 2012, TAC=0) (EU, 2010). Technical measures in force in EU waters and NEAFC regulatory area (2012).

Conservation status Data Deficient but may be of concern because this shark occurs in areas with intense demersal fisheries.

Local Names: Paradox dogfish, Kite-fin shark, Sharp-back shark, Sailfin roughshark (British Isles); Graue Meersau (Germany); Peixe-porco-de-vela (Portugal); Spetsfenad haj (Sweden).

Literature: Frade (1920); Norman (1932); Krefft (1955); Bigelow and Schroeder (1957); Cadenat (1961); Wheeler and Blacker (1969); Blache et al. (1970); Maurin and Bonnet (1970); Krefft and Tortonese (1973a); Wheeler (1978); Cadenat and Blache (1981); Compagno (1984); Quéro in Whitehead et al. (1984d); Yano and Murofushi (1985); Springer (1990); Du Buit (1991); Santos, Porteiro and Barreiros (1997); Hernandez et al. (1998); Azevedo, Souse, and Brum (2003); Gibson et al. (2008); Soldo and Freitas (2008); EU (2010); Ebert and Compagno (In press).

### 2.2.7 Family DALATIIDAE

Family: Tribe Dalatiana Gray, 1851, List Fish British Mus., Pt. 1, Chondropterygii, British Mus. (Nat. Hist.): 74 (Family Squalidae).

Type genus: Dalatias Rafinesque, 1810.

## Number of Recognized North Atlantic Genera: 3.

## FAO Names: En - Kitefin sharks.

Field Marks: Short to moderately long-nosed, usually cylindrical or somewhat compressed sharks with no anal fin; snout and head narrow and conical; denticles small and mostly sessile, but with short pedicels and elongated lanceolate crowns in a few genera; keels present or absent on the caudal peduncle; two dorsal fins usually without spines (Squaliolus with spined first dorsal fin but with spineless second dorsal fin); the first dorsal fin with origin varying from opposite the pectoral-fin bases to far behind the pectoral fins and somewhat anterior to the pelvic-fin origins; the second dorsal fin not falcate and with its origin usually opposite the pelvic-fin bases or inner margins, but exceptionally slightly anterior to the pelvic-fin origins; caudal fin with a strong subterminal notch. Mostly small ( 50 cm long or less) to dwarf (less than 30 cm ) oceanic species, often dark brown or blackish with light fins and ventral photophores (Dalatias moderately large at up to 182 cm long and without photophores).

Diagnostic Features: Head narrow and rounded-conical. Snout conical and narrowly rounded to elongate-rounded in dorsoventral view. Photophores on the ventral surface of the head and body dense in the genera Euprotomicrus, Isistius and Squaliolus, but Dalatias apparently lack them. Spiracles large, close behind eyes. Fifth gill opening about as large as first four in most genera; Euprotomicroides with gill openings increasingly wider posteriorly. Nostrils wide to narrow-spaced with internarial width equal to or much greater than nostril width; nostrils with simple anterior nasal flaps. Mouth nearly transverse and short, with lips thin and smooth or thickened and fringed or pleated. Labial furrows short to moderately long, not encircling mouth or partially encircling it, confined to mouth corners and under or behind posterior corners of eyes, elongated posteriorly into postoral grooves and anteromedial preoral grooves; labial folds thin or thickened. Teeth with dignathic heterodonty well-developed, upper teeth much smaller than lowers; tooth row counts 16 to 37 upper jaw, 17 to 34 lower jaw. Upper teeth small, lanceolate, with narrow erect cusps and no cusplets or blades, in quincunx formation and not imbricated; lower teeth highly compressed, high-crowned, broad and bladelike, imbricated, forming a sawlike cutting edge, teeth with a compressed, erect to oblique cusp, a distal blade present or absent, and no cusplets. Trunk cylindrical or slightly compressed, abdomen without lateral ridges. Interdorsal space elongated and usually much greater than length of first dorsal-fin base (subequal to it in Isistius plutodus); pelvic-caudal space short to moderately long and about equal to over twice pelvic-fin bases. Caudal peduncle cylindrical, short to moderately elongated, with or without lateral keels but without precaudal pits. Body with or without photophores. Denticles small and usually with low ridged sessile crowns but some genera (Dalatias and Mollisquama) with leaf-shaped, monocuspidate and lanceolate crowns on low pedicels. Pectoral fins rounded-angular or rounded-lobate, not lanceolate or falcate, anterior margins short and mostly shorter than or sometimes subequal to the prespiracular length, rear tips rounded and short. Pelvic fins subequal to or smaller than pectoral fins, smaller to larger than dorsal fins. Claspers with or without a lateral spine. Dorsal fins small or moderate-sized, angular or rounded-angular but not falcate, without spines except for a small fin spine on the first dorsal fin of Squaliolus. First dorsal fin small to moderate-sized, with length less than prespiracular space; first dorsal-fin base usually over pectoral-pelvic space and behind pectoral-fin bases and well anterior to or partially over pelvic fins, first dorsal-fin origin usually behind pectoral fins (over pectoral-fin inner margins in Squaliolus and over the pectoral-fin bases in Heteroscymnoides). Second dorsal fin subequal, slightly larger, or much larger than first dorsal fin, second dorsal-fin base over or just behind pelvic-fin bases, second dorsal-fin origin slightly anterior to pelvic-fin origins to posterior to pelvic-fin insertions. Caudal fin markedly heterocercal to almost diphycercal, with ventral lobe low (Dalatias) to strongly developed in adults, and with subterminal notch weak to strong. Vertebral counts: total vertebral counts 60 to 92 , monospondylous vertebral counts 29 to 46, diplospondylous precaudal counts 8 to 22 . Intestinal valve with 6 to 42 turns. Adults dwarf to moderately large, between 15 to about 182 cm long. Colour: plain or with fin edges transparent, without black photophore markings on tail or flanks but with photophores, where present, often very closely spaced on the ventral surface.

Distribution: Dalatiids have an almost circumglobal range in temperate to tropical seas, either in the open ocean or demersally in association with landmasses. The kitefin sharks as presently defined are represented by three genera Dalatias, Isistius, and Squaliolus in the North Atlantic. Of the other genera in this family, Euprotomicroides, Euprotomicrus, and Heteroscymnoides are known to occur in the Central and Southern Atlantic Ocean and it would not be surprising if vagrant species of these genera were eventually found to occur in the North Atlantic. The rare and poorly known genus Mollisquama is only known from an ocean ridge in the South Pacific.

Habitat: The Dalatiidae include species that represent at least two ecomorphotypes (Compagno, 1990b), with most showing the oceanic or microceanic habitus of spindle-shaped bodies, large eyes, small smooth denticles, long abdomens, small precaudal fins (often transparent), and more or less symmetrical caudal fins and the bathic or bathic habitus with larger fins but resembling oceanic dalatiids in having a narrower head and stronger jaws and larger teeth than is typical of other bathic squaloids such as echinorhinids, large centrophorids, and many somniosids. The oceanic species are best known
from epipelagic records with some species being caught at or near the surface at night drawn by surface lights or in surface gill-nets; trawl records of these sharks extend down to at least 3500 m , and they have been caught near the surface at night in waters over 9000 m deep. Some oceanic species seem to be vertical migrants with a daily cycle, and may make transits of 1500 to 3000 m or more to rise to the surface at night and descend to the ocean bottom during the day. The bottom-dwelling deepwater bathic species are mostly inhabitants of continental and insular slopes, submarine ridges and seamounts, with occasional records from inshore in shallow water on the continental shelves (Dalatias). The bathic species range in depth between 20 m to at least 1800 m but with most records between 200 and 1000 m .

Biology: The family is very poorly known biologically. Reproduction is yolk-sac viviparous with litters of six to 16 young, but virtually nothing is known about the life cycle or age and growth of these sharks. These sharks, relative to their size, proportionally have very powerful jaws with large teeth interlocked to form a shear-like cutting dentition in the lower jaw, and a holding dentition of very small hooklike teeth in the upper jaw, which allow them to capture and dismember relatively large prey. Dalatias licha feeds on a wide variety of bony fishes, cartilaginous fishes, crustacea, cephalopods, polychaetes, siphonophores, and tunicates. Species of Isistius are ectoparasitic on larger pelagic marine vertebrates including cetaceans, phocid seals, elasmobranchs, and especially large bony fishes and attach to the skin of these animals with their suctorial lips and cut out plugs of flesh with their lower teeth; they can also catch and consume smaller fishes and cephalopods. Proportionately, Isistius species have the largest teeth relative to their body-size of any modern shark species. Their mouth and jaw apparatus are uniquely designed to remove large chunks of flesh from prey items many times their size. Very little is known of their socio-biology except that of the commoner species, Dalatias licha may be solitary while Isistius and Squaliolus species may occur in aggregations as well as single individuals.

Interest to Fisheries and Human Impact: This family is of limited interest for fisheries purposes, as most of the species are apparently oceanic or semioceanic and are far too small to be caught in conventional pelagic fishing gear. Most catches of the small species are from research vessels, at nightlights at the surface or with pelagic or bottom trawls. Exceptions include species of Isistius and Squaliolus that are caught as bycatch by commercial bottom trawlers and oceanic gillnets. The large bathic Dalatias licha is an exception by being the only known commercial species in the family. It is commonly fished in targeted deepwater shark fisheries in many places where it occurs and also taken as bycatch in deep benthic fisheries for bony fishes.
Kitefin sharks are not regularly kept in public aquaria and are apparently too deep-dwelling or sparse in oceanic waters to be a current subject of conventional ecotouristic diving. There is at least one confirmed account of a cookie-cutter shark (Isistius spp.) biting a swimmer at the surface in the open ocean off the Hawaiian Islands as well as several anecdotal accounts of this species biting swimmers in the open ocean.

The conservation status of kitefin sharks is poorly known, but given their general small size and the rarity that many are caught most are either Least Concern or Data Deficient. The one exception though is Dalatias licha, which is listed as Data Deficient worldwide, but Vulnerable in the Eastern North Atlantic.

Local Names: Kitefin sharks, Black sharks, Spineless dogfish, Scymnoid sharks (English); Pryamorotye akuly (Russia).
Remarks: The Family Dalatiidae is comprised of seven genera, five of which are monotypic genera, and ten species worldwide. Three of these genera, and three species occur in the North Atlantic. However, it would not be unexpected if two additional wide-ranging oceanic southern Atlantic genera, Euprotomicroides or Euprotomicrus, were to eventually turn up in the North Atlantic since the geographic and bathymetric ranges are sketchily to poorly known for all species within this family.

Literature: Müller and Henle (1839); Gray (1851); Bleeker (1859); Gill (1862); Dumeril (1865); Günther (1870); Regan (1908); Garman (1913); Bigelow and Schroeder (1948, 1957); Hubbs and McHugh (1951); Garrick (1956, 1960b); Hubbs, Iwai and Matsubara (1967); Cadenat and Blache (1981); Compagno (1984); Shirai (1992, 1996); Hernández et al. (1998); Compagno, Dando, and Fowler (2005); Ebert and Compagno (In press).

## Key to North Atlantic Genera:

1a. First dorsal insertion about over pelvic-fin origins. Cusps of lower teeth covering the entire crown foot, without a convex accessory blade separated from the cusp by a notch (Fig. 143)

Isistius


Fig. 143 Isistius


LOWER TOOTH
Fig. 144 Dalatias

2a. First dorsal fin with a spine (sometimes concealed by skin). Second dorsal-fin base at least twice as long as first dorsal-fin base. Upper caudal-fin lobe shortened, caudal fin paddle-shaped (Fig. 145)

Squaliolus

2b. Dorsal fins spineless. Second dorsal-fin base as long as first dorsal-fin base or shorter. Caudal fin not paddleshaped, its upper lobe not shortened (Fig. 146) . . . . . Dalatias


Fig. 145 Squaliolus


Fig. 146 Dalatias

## Dalatias Rafinesque, 1810

Genus: Dalatias Rafinesque, 1810, Caratt. gen. sp. anim. piant. Sicilia, Palermo, pt. 1: 10.
Type species: Dalatias sparophagus Rafinesque, 1810, by subsequent designation of Jordan, Tanaka and Snyder, 1913, J. Coll. Sci. Imp. U. Tokyo, 33(1): 22, considered by these authors to be equivalent to Squalus licha Bonnaterre, 1788.

## Number of Recognized North Atlantic Species: 1.

Synonyms: Subgenus Scymnus Cuvier, 1817, Reg. Anim., ed. 1, 2: 130. (Genus Squalus Linnaeus, 1758). Type species: Squalus americanus Gmelin, 1789, by monotypy, a junior synonym of Squalus licha Bonnaterre, 1788. Whitley (1935, Australian Zool. 8[2]: 137) and [Eschmeyer (1998, Cat. Fish.)] note that Lesson (18, Dict. Class. Hist. Nat. 14: 598) selected Squalus americanus"Broussonet" as type species of Scymnus Cuvier. Genus Scimnus S.D.W., 1837, no reference, fide Fowler, 1969, Quart. J. Taiwan Mus. 22 (1 and 2): 68; cited by Whitley, 1955, Proc. Roy. Soc. New S. Wales, 1953-4: 44-57, 8 Figs. Genus Scymnium Valenciennes in Cuvier, 1838, Reg. Anim., ed. 3, Poiss.: legend to pl. 115, Fig. 5, as "Scymnium niciense Cuv.". Scymnus was used consistently elsewhere in the text (ibid, p. 367) and in the plate legend as "S.-Genre des Leiches. Scymnus. Cuv." (loc. cit.), suggesting that Scymnium nicense (= Squalus nicaeensis Risso, 1810) is a mispelling for Scymnus nicense. Cited by Fowler, 1969, Quart. J. Taiwan Mus. 22 (1 and 2): 68. Genus Dalatius Agassiz, 1845, Nomencl. Zool., pisc., 21. Emendation for Dalatias Rafinesque, 1810. Genus Scymnorhinus Bonaparte, 1846, Cat. Metod. Pesc. Europa: 16. Type species: Scymnorhinus licha Bonaparte, 1846, by monotypy, equals Squalus licha Bonnaterre, 1788. Proposed as a replacement for Scymnus Cuvier, 1817. Genus Borborodes Gistel, 1848, Naturg. Thier. Schul.: x. Replacement name for Scymnus Cuvier, 1817, a junior homonym of Scymnus Kugelmann, 1794 (Coeleoptera), and hence taking the same type species, Squalus americanus Gmelin, 1789. Genus Scymnorhynus Nobre, 1935, Faun. Mar. Portugal 1: Vert: 410. Erroneous spelling of Scymnorhinus Bonaparte, 1846. Genus Barborodes (Gistel) Bigelow and Schroeder, 1948, Mem. Sears Fnd. Mar. Res. (1), 1: 501. Erroneous spelling of Borborodes Gistel, 1848.

Diagnostic Features: Anterior nasal flaps short, not expanded into barbels; snout broadly conical, rounded, and short, length much less than distance from mouth to pectoral origins and about $1 / 4$ of head length; gill openings moderately broad and about equally wide; lips very thick, fringed or pleated, not suctorial; teeth very different in upper and lower jaws, uppers small, with narrow, hooked, needle-shaped cusps and no cusplets, lowers very large, bladelike, interlocked, with broad, erect, triangular cusps, small distal blades, and serrated edges; tooth row counts 16 to 21 upper jaw, 17 to 20 lower jaw. Both dorsal fins without spines; first dorsal-fin origin somewhat behind free rear tips of pectoral fins, first dorsal-fin insertion well anterior to pelvic-fin origins, closer to pectoral-fin bases than pelvic fins; second dorsal-fin origin about over middle of pelvic-fin bases; second dorsal fin only slightly larger than first, its base less than 1.5 times first dorsal-fin base; pectoral fins with short, broadly rounded free rear tips, not broadly lobate or acute and elongated; caudal fin asymmetrical, not paddle-shaped, upper lobe long, lower lobe very short or virtually absent, subterminal notch well-developed. No precaudal pits or lateral keels on caudal peduncle. Dermal denticles with low flat, ridged, unicuspid crowns, not pedicellate. Cloaca is without a luminous gland. Vertebral counts: total vertebral counts 69 to 85 , precaudal vertebral counts 47 to 55 . A moderately large shark with a maximum length of 180 cm . Colour: greyish to black or blackish brown, sometimes violet with black spots.

## Dalatias licha(Bonnaterre, 1788)

Squalus licha Bonnaterre, 1788, Tabl. Encyclop. Method. Trois Reg. Nat., Ichthyol., Paris: 12. Holotype: Lost, from "Le cap Bretan".

Synonyms: Squalus americanus Gmelin, in Linnaeus and Gmelin, 1789, Syst. Nat., ed. 13, Pisces 1(3): 1503. Holotype: Same as for S. licha, lost, from "Le cap Bretan". ?Dalatias sparophagus Rafinesque, 1810, Caratt. gen. sp. anim. piant. Sicilia, Palermo, pt. 1: 10, pl. 13, Fig. 2. No type material, Sicily. Squalus nicaeensis Risso, 1810, Ichthyol. Nice, Paris: 43, pl. 4, Fig. 6. One syntype: MNHN no. B 842(?), Nice, France. Scymnus vulgaris Cloquet, 1822 (1823), Dict. Sci. Nat. 25: 433. European seas, general. Scymnus scymnus Voigt, in Cuvier, 1832, Tierreich 2: 512. Replacement name for Squalus Iichia Bonnaterre, 1788. ?Scymnus aquitanensis de la Pylaie, 1835, Rech. France Poiss., 1832-1833, Congr. Sci. France Poitiers, 1834: 527. Fide Jordan, 1919, Stanford U. Pub., U. Ser., Gen. Fish. (2): 182. Possible replacement name for Squalus lichia Bonnaterre, 1788. Scymnus lichia Bonaparte, 1836, Iconog. Fauna Italica, 3, Pesci, fasx. 16, pta. 85,4 p., 1 pl. Emended spelling.

Other Combinations: None.
FAO Names: En - Kitefin shark; Fr - Squale liche; Sp - Carocho.


Fig. 147 Dalatias licha
Field Marks: A moderate-sized, short- and blunt-snouted shark with two almost equal-sized spineless dorsal fins, no anal fin, papillose thick lips, small slender-cusped upper teeth and very large lower teeth with erect triangular serrated cusps and distal blades, first dorsal fin on back with its origin behind the pectoral rear tips and its base closer to the pectoral-fin base than the pelvic fins, and caudal fin with the ventral lobe not expanded.

Diagnostic Features: See genus account above.
Distribution: Atlantic slope of the British Isles (with occasional records from the continental shelf, including the North Sea and Celtic Sea), to Spain and Portugal, including the Azores and Madeira Islands, and Mid-Atlantic Ridge. Also occurs in the western Mediterranean, and from off Morocco to Cameroon. Western North Atlantic: Georges Bank off New England, USA, in the northern Gulf of Mexico, and from southern Brazil. Elsewhere, occurs in the central and western Pacific, and Indian oceans.

Habitat: A common but sporadically distributed deepwater, warm-temperate and tropical shark of the outer continental and insular shelves and slopes from 37 to at least 1800 m depth, but commonest below 200 m . It occurs most frequently on or near the bottom but readily ranges well off the substrate. Its large oily liver allows it to attain neutral buoyancy, so it can move or hover above the bottom without the necessity of utilizing dynamic lift from its fins and body.

Biology: Development is yolk-sac viviparous, with litters of 3 to 16 young, but nothing is known about its reproductive cycle or age at maturity.

A powerful and versatile deep-sea predator, D. licha is equipped with huge serrated teeth and compact, heavy jaws of enormous power. It feeds primarily on deepwater bony fishes, including deepwater smelt (Argentinidae), viperfishes, scaly
dragonfishes, barracudinas, greeneyes, lanternfishes, gonostomatids, cod, ling, whiting and other gadoids, hake, grenadiers, deepwater scorpionfishes, bonito, gempylids, epigonids, and chaunacid anglers, but also skates, catsharks (Galeus), spiny dogfish (Squalus, Etmopterus and Centrophorus), squid, octopus, amphipods, isopods, shrimp and lobsters, and even polychaetes and siphonophores. The recorded diet is fairly representative of the bottom and midwater fauna where it occurs, but the presence of fast-swimming epipelagic fishes such as bonito may indicate either scavenging or some means of ambushing or otherwise overcoming such prey. Often chunks of large fish are found in the stomach of this shark, as well as small whole fish, suggesting that it may take chunks out of live fish prey in "cookiecutter" fashion as in Isistius species and Centroscymnus coelolepis, though to date bite-sized chunks of cetacean have not been found in this shark. In the western Mediterranean bony fishes are a staple primary fare throughout the year.


Fig. 148 Dalatias licha
$\square$ Known distribution Sharks are consumed more commonly as secondary prey in spring and winter, but crustaceans become more important in the summer and cephalopods in the fall. Adult sharks eat more crustaceans and sharks and less cephalopods than young. Male Dalatias for some reason are more frequently found to have full stomachs more commonly than females.
Catch records in the Mediterranean Sea suggest that this is primarily a solitary shark, not found in large schools as with many other dogfish.

Size: Maximum to at least 159 cm , possibly to 182 cm ; males mature at about 100 cm and females mature at about 120 cm . Size at birth about 30 to 40 cm .

Interest to Fisheries and Human Impact: A directed fishery off the Azores collapsed after nearly 30 years of fishing pressure, with catches declining from over 800 tonnes in the mid-1980s to less than 1 tonne in 2000 and 2001. A comparison of trawl surveys west of the British Isles revealed an apparent decline of $94 \%$ over a similar 30 year time frame, but this latter study should be viewed with caution as the underlying reason for this decline had more to do with a low market value for the liver of this shark; also the area west of the British Isles is at the edge of this species range.
The Azores kitefin shark fishery suggests that targeted fisheries for this species are capable of reducing its population quite rapidly. The life history of this species is expected to result in a slow recovery after depletion. An increasing trend for fisheries to move into deeper water on continental shelves and slopes suggests that fishing pressure on this species may increase. The Eastern North Atlantic kitefin shark population is considered to be a single stock and is managed as part of the deepsea shark fisheries. It has been recommended by ICES $(2006,2010)$ that no targeted fisheries for this species be permitted until reliable estimates of current exploitation rates and sufficient data are available to assess its productivity. These sharks are caught with longline gear, demersal and pelagic trawls, and fixed bottom gillnets. They are used for human consumption dried-salted or fresh, or as fish meal, leather, and their livers, which are extremely large, oily, and have a high squalene content. Under TAC regulation in EU (in 2012, TAC=0) ( $E$ U, 2010). Technical measures in force in EU waters and NEAFC regulatory area (2012).

The conservation status is Near Threatened globally, but in the Eastern North Atlantic it is Vulnerable due to steep declines in its population and limited life history characteristics.

Local Names: Black shark, Darkie charlie (English); Schokoladenhai (Germany); Ga gatte, Gatte, Gatta causiniera, La liche, La scymne commune, Liche, Liche ordinaire (France); Chokladhaj (Sweden); Cassó, Cazon Catalán, Negret, Negritu, Pastiu (Spain); Carocho, Carôxo (male), Pailoma (female), Lixa de pau (Portugal); Gata-lixa, Gata, Gato, Kitefin shark (Azores).

Literature: Bigelow and Schroeder (1948, 1957); Maurin and Bonnet (1970); Wheeler (1978); Macpherson (1980a); Cadenat and Blache (1981); Matallanas (1982); Compagno (1984); Compagno, Dando, and Fowler (2005); Blasdale et al. (2006); Capapé et al. (2008c); Gibson et al. (2008); EU (2010); ICES (2006, 2010); Kyne and Simpfendorfer (2010); Ebert and Compagno (In press); D.A. Ebert (unpubl. data).

## Isistius Gill, 1865

Genus: Isistius Gill, 1865 (listed 1864), Proc. Acad. Nat. Sci. Philadelphia: 264, ftn. *2.
Type species: Scymnus brasiliensis "Müller and Henle, 1839", by monotypy, equals Scymnus brasiliensis Quoy and Gaimard, 1824. Published Nov. 22, 1864 according to Garman, 1899, Mem. Mus. Comp. Zool. Harvard, 24: 33; listed as 1865 according to Dean, 1916, Bibliogr. Fish., 1: 460 and Eschmeyer, 1998, Cat. Fish.

## Number of Recognized North Atlantic Species: 1.

Synonyms: Genus Leius Kner, 1864, Anz. Akad. Wiss. Wien, 1: 186; Kner, 1864, Ann. Mag. Nat. Hist., 3, ser. 15: 185187; Kner, 1864, Denkschr. Akad. Wiss. Wien, Math.-nat. Kl. 24: 9, pl. 4, Figs. 2-2a. Type species: Leius ferox Kner, 1865, by original designation? The latter was published Nov. 10, 1864 according to Garman, 1899, Mem. Mus. Comp. Zool. Harvard, 24: 33; 1865, according to Dean, 1916, Bibliogr. Fish., 1: 695. See also Eschmeyer, 1990, Cat. Gen. Fish. 212, who indicates type by monotypy.

Field Marks: Small size, cigar-shaped body with long abdomen and short tail, small, spineless, nearly equal-sized dorsal fins far posterior on back, no anal fin, large to huge, triangular-cusped lower teeth without blades, suctorial lips, short, bulbous snout, caudal fin with short to long ventral lobe.

Diagnostic Features: Anterior nasal flaps very short, not expanded into barbels; snout short, bulbously conical, length less than $2 / 5$ of head length and much less than distance from mouth to pectoral origins; gill openings small, uniformly broad; lips expanded, fleshy, suctorial, allowing the shark to attach to its prey like a lamprey; teeth strongly different in upper and lower jaws, uppers small, with narrow, acute, erect cusps and no cusplets, not bladelike, lowers very large, bladelike, interlocked, with a high broad, erect cusp but no blade, edges not serrated; tooth row counts 29 to 43 upper jaw, 17 to 31 lower jaw. Both dorsal fins spineless; first dorsal fin far posterior, origin far behind pectoral fins and somewhat anterior to pelvic-fin origins, insertion over pelvic-fin bases; second dorsal fin slightly larger than first but with base about equal to first dorsal-fin base; origin of second dorsal fin about over pelvic-fin rear tips; pectoral fins with short, narrowly to broadly rounded free rear tips and inner margins, not expanded and acute or lobate; caudal fin varying from asymmetrical to nearly symmetrical, paddle-shaped or not, with a short upper lobe, short to long lower lobe, and a strong subterminal notch. No precaudal pits but with low lateral keels on caudal peduncle, no midventral keel. Dermal denticles flat and block-like, not pedicellate, no posterior cusps on flat, depressed crowns. Cloaca normal, not expanded as a luminous gland. Vertebral counts: total vertebral counts 81 to 92 , precaudal vertebral counts 60 to 66 , caudal vertebral counts 20 to 27 . Intestinal valve turn counts 8 to 10 . Small sharks with a maximum length of about 50 cm . Colour: medium grey or grey-brown with light-edged fins; usually with a dark collar-like band around the gill region.

Local Names: Cookiecutter sharks.
Remarks: The arrangement of this genus follows Garrick and Springer (1964).

## Isistius plutodus Garrick and Springer, 1964

Isistius plutodus Garrick and Springer, 1964, Copeia 1964 (4): 679, Figs. 1A, 2A, 2C. Holotype: U.S. National Museum of Natural History, USNM-188386, 423 mm TL adult female, Oregon Sta. 3102, off Mississippi Delta, $28^{\circ} 58^{\prime} \mathrm{N}, 88^{\circ} 18^{\prime} \mathrm{W}$, bottom depth 814-997 m but depth of capture unknown.

Synonyms: None.
Other combinations: None.
FAO Names: En - Largetooth cookiecutter shark; Fr - Squalelet dentu; Sp - Tollo cigarro dentón.


Fig. 149 Isistius plutodus


Field Marks: Small size, cigar-shaped body, very short bulbous snout, suctorial lips, small, spineless, nearly equal-sized dorsal fins far posterior on back, no anal fin, asymmetrical caudal fin with short ventral lobe; huge, triangular-cusped lower teeth without blades and in 17 to 19 rows. A prominent dark collar-marking variably developed and sometimes absent over branchial region.

Diagnostic Features: Snout very short, about length of eye. Eyes set well forward on head, with extensive anterior binocular field. Tooth row counts 21 to 29 upper jaw, 17 to 19 lower jaw; lower teeth enormous. Interdorsal space subequal to first dorsal base, space between second dorsal insertion and upper caudal origin about equal to second dorsal base. Pectoral fins rounded, pelvic fins smaller than dorsal fins. Second dorsal-fin height about 1.3 times first. Caudal fin small, noticeably asymmetrical, with a short ventral caudal-fin lobe less than one-half length of dorsal caudal-fin margin. Vertebral counts: total vertebral count 92 , precaudal vertebral count 65 , caudal vertebral count 27 . Intestinal valve turn counts unavailable for this species. A small shark with a maximum length of 42 cm . Colour: a uniform dark brown with conspicuous dark collar-like marking around the gill region variably absent or present; fin margins pale to translucent.

Distribution: Possibly circumglobal in
distribution but so far known from only a few scattered localities. The only Eastern North Atlantic record is from north of the Azores ( $43^{\circ} 58^{\prime} \mathrm{N}, 28^{\circ} 32^{\prime} \mathrm{W}$ ). There are no records of this species from the Western North Atlantic. The holotype of this species was collected in the Western Central Atlantic off the Mississippi Delta in the northern Gulf of Mexico and there is a record of it from off the coast of the Western Sahara Republic. Elsewhere, known from the Western South Atlantic and from a few scattered localities in the western Pacific.

Habitat: A little-known epibenthic, epipelagic and possibly bathypelagic shark, known from a few scattered localities and currently from less than 10 specimens. Presently known to be pelagic or epibenthic near continents, with most collected close to land (unlike Isistius brasiliensis), except for one specimen caught north of the Azores between 90 and 100 m deep over water 890 to 980 m deep. Continental shelf near bottom at about 100 m , epipelagic zone at


Fig. 150 Isistius plutodus depths of 60 to 120 m above continental slopes at bottom depths of 815 to 2060 m , epipelagic at about 200 m with a bottom depth of 6440 m . Its infrequency of capture compared to I. brasiliensis suggests that it may be localized or more limited in its distribution and habitat, and might occur in deeper water than its congener. It may also occur in areas less heavily fished than $I$. brasiliensis therefore reducing the likelihood of it being captured by fishing gear.

Biology: Virtually nothing known about its biology. The small dorsal and caudal fins of this shark suggest that it is a weaker, less active swimmer than Isistius brasiliensis, and that also takes advantage of a 'hepatic float'. However, its larger, more
powerful jaws, bigger mouth and gigantic lower teeth (proportionately the largest in any living shark) equip it for taking larger bites out of its prey, something shown by a huge plug of bony fish flesh taken from the stomach of the holotype. This was as high and wide as the diameter of its mouth but over twice as long, and indicates with its suctorial lips and feeding apparatus that this shark is probably at least a facultative ectoparasite like its congener. Similar to the better-known I. brasiliensis this species appears capable of gouging elongated plugs out of its victims, perhaps using a different action than the twisting motion required to cut out cones.
A curious feature of this shark is its extremely short snout and anteriorly positioned eyes. When viewed frontally the largetooth cookiecutter apparently has a broad anterior field of vision, unlike I brasiliensis with its longer snout and more posterolaterally positioned eyes; this apparently allows for binocular vision, and may be helpful in precisely locating its victims prior to attacking them.

Size: Maximum total length at least 42 cm for females and 34 cm for males. Size at birth unknown.
Interest to Fisheries and Human Impact: Interest to fisheries none, except as a possible causative agent of "crater wounds" or elongate gouges on fishes such as scombrids and billfishes, and hence of negative interest to fisheries. One was caught while biting a chunk out of a blue shark (Prionace glauca).

The conservation status of this small, epibenthic and epipelagic cookiecutter shark is Least Concern. It may be an occasional bycatch in bottom and midwater trawl fisheries and by longline fisheries, but given its circumglobal, but scattered distribution and small size there does not appear to be any significant threats fishing pressures at this time.

Local Names: Gulf dogfish, Longtooth cookiecutter shark (English).
Remarks: This is one of three species known in this genus. The other two species include the wide-ranging Isistius brasiliensis, which does occur in the Eastern and Western Central Atlantic (Areas 31 and 37) and I. Iabialis known from only a single specimen in the Western Central Pacific (Area 61). Care should be taken in examining any Isistius species observed in the North Atlantic as I brasiliensis would not be unexpected to occur here.

Literature: Garrick and Springer (1964); Parin (1975); Cadenat and Blache (1981); Compagno (1984); Golovan and Pakhorukov (1986); McGrouther (2001); Zidowitz et al. (2004); Kyne, Gerber, and Sherrill-Mix (2006); Last and Stevens (2009); Ebert and Compagno (In press).

## Squaliolus Smith and Radcliffe, 1912

Genus: Squaliolus Smith and Radcliffe, in Smith, 1912, Proc. U.S. Nat. Mus. 41(1877): 683.
Type species: Squaliolus laticaudus Smith and Radcliffe, in Smith, 1912, by original designation.

## Number of Recognized North Atlantic Species: 1.

Synonyms: Euprotomicrus laticaudus Garman, 1913, Plagiostoma. Mem. Mus. Comp. Zool. Harvard, 36: 235-236.
Field Marks: The only sharks with a fin spine on their first dorsal fins but not on their second; very small size, spindle-shaped body, long, bulbously conical, pointed snout, second dorsal fin with base about twice as long as that of first, first dorsal fin with origin opposite inner margins or rear tips of pectoral fins, no anal fin, dark colour with conspicuously light-margined fins.

Diagnostic Features: Head cylindrical, snout very long, bulbously conical but slightly pointed, length about half head length and about equal to distance from mouth to pectoral fins. Eye variably small to large depending on species; upper margin of orbit nearly straight to broadly arched or angular and chevron shaped. Anterior nasal flaps very short, not expanded into barbels; gill openings very small, uniformly wide; lips thin, not fringed, pleated or suctorial, upper lip with or without paired lateral papillae. Teeth strongly different in upper and lower jaws, uppers small, with narrow, acute, erect cusps and no cusplets, no bladelike, lowers much larger, bladelike, interlocked, with a high, moderately broad, nearly erect cusp and distal blade, edges not serrated; tooth row counts 21 to 23 upper jaw, 16 to 21 lower jaw. Lateral dermal denticles flat, block-like, not pedicellate, with no posterior cusps on flat, depressed crowns. First dorsal fin with a spine, covered by skin or not, but second dorsal without a spine; first dorsal fin well anterior, origin about opposite inner margins or free rear tips of pectoral fins, insertion well anterior to pelvic-fin origins and closer to pectoral-fin bases than pelvic fins; second dorsal fin much larger than first, base about twice as long as first dorsal-fin base; origin of second dorsal fin over from half of pelvic-fin bases; pectoral fins with short, narrowly rounded free rear tips and inner margins, not expanded and acute or lobate. Cloaca normal, not expanded as a luminous gland. No precaudal pits or midventral keels, but with low lateral keels on caudal peduncle. Caudal fin nearly symmetrical, paddle-shaped, with a short upper and long lower lobe and a strong subterminal notch. Vertebral counts: total vertebral counts 55 to 62 , precaudal vertebral counts 44 to 48 , monospondylous vertebral counts 27 to 32 , diplospondylous vertebral counts 26 to 32. Spiral valve turn counts 13 . These are among the smallest known of living shark species. Colour: blackish to blackish-brown with conspicuously light-margined fins.

Local Names: Spined pygmy sharks.
Remarks: The present arrangement of this genus includes two valid species, Squaliolus aliae confined to the Western Pacific and Eastern Indian Ocean, and S. laticaudus, a near circumglobal species that occurs in the North Atlantic. A third species, Squaliolus sarmenti, described from off Madeira Islands is recognized by some authors, but Seigel et al. (1977) and Seigel (1978) demonstrated that $S$. sarmenti is a junior synonym of $S$. laticaudus. The arrangement of this genus follows Sasaki and Uyeno (1987).

## Squaliolus laticaudus Smith and Radcliffe, 1912

Squaliolus laticaudus Smith and Radcliffe, in Smith, 1912, Proc. U.S. Nat. Mus. 41(1877): 684, Fig. 4, pl. 50, 54. Holotype: United States National Museum of Natural History, USNM-70259, 146 mm male, Albatross Sta. 5268, Batangas Bay, Luzon, Philippine Islands, $13^{\circ} 42^{\prime} \mathrm{N}, 120^{\circ} 57^{\prime} 15^{\prime \prime} \mathrm{E}$, in beam trawl fished on bottom at 311 m . depth. Status of holotype confirmed by Howe and Springer (1993, Smiths. Contr. Zool. [540]: 8).

Synonyms: Squaliolus sarmenti di Noronha, 1926, Ann. Carnegie Mus. 16(3-4): 386, pl. 35. Holotype: Field Museum of Natural History, Chicago, FMNH-58862, 246 mm female, Madeira Islands, caught on an espada (Aphanopus carbo) longline somewhere between 0-1464 m depth, and probably between 915 to 1464 m .

Other combinations: Euprotomicrus laticaudus Garman, 1913. Euprotomicrus sarmenti Fowler, 1936; Belloc, 1937; Sigalas, 1939-1940; Albuquerque, 1954-1956.

FAO Names: En - Spined pygmy shark; Fr - Squale nain; Sp - Tollo pigmeo espinudo.



UNDERSIDE OF HEAD


UPPER AND LOWER TEETH

Fig. 151 Squaliolus laticaudus
Field Marks: Very small size, spindle-shaped body, long, bulbously conical, pointed snout, second dorsal fin with base about twice as long as that of first, first dorsal fin with origin opposite inner margins or rear tips of pectoral fins, and no anal fin. This is one of only two sharks (the other being Squaliolus aliae see above) with a fin spine on its first dorsal fin but not its second. Dark coloured with conspicuously light-margined fins.

Diagnostic Features: Head cylindrical, snout very long, bulbously conical but slightly pointed, length about half head length and about equal to distance from mouth to pectoral fins. Eye large, diameter 73 to $86 \%$ of interorbital width and 61 to $82 \%$ of preorbital snout length; upper margin of orbit nearly straight and broadly arched. Anterior nasal flaps very short, not expanded into barbels; gill openings very small, uniformly wide; lips thin, not fringed, pleated or suctorial, upper lip without a pair of lateral papillae. Teeth strongly different in upper and lower jaws, uppers small, with narrow, acute, erect cusps and no cusplets, no bladelike, lowers much larger, bladelike, interlocked, with a high, moderately broad, nearly erect cusp and distal blade, edges not serrated; tooth row counts 22 to 23 upper jaw, 16 to 21 lower jaw. Dermal denticles flat and block-like, not pedicellate, no posterior cusps on flat, depressed crowns. First dorsal fin with a spine, covered by skin or not, but second dorsal fin without a spine; first dorsal fin well anterior, origin about opposite inner margins or free rear tips of pectoral fins, insertion well anterior to pelvic-fin origins and closer to pectoral bases than pelvic fins; second
dorsal fin much larger than first, base about twice as long as first dorsal-fin base; origin of second dorsal fin over from half of pelvic-fin bases; pectoral fins with short, narrowly rounded free rear tips and inner margins, not expanded and acute or lobate. Cloaca normal, not expanded as a luminous gland. No precaudal pits or midventral keels, but with low lateral keels on caudal peduncle. Caudal fin nearly symmetrical, paddle-shaped, with a short upper and long lower lobe and a strong subterminal notch. Vertebral counts: total vertebral counts 55 to 62 , monospondylous vertebral counts 27 to 32, diplospondylous vertebral counts 26 to 32 , precaudal vertebral counts 44 to 48 . Spiral valve turn counts 13 . One of the smallest known sharks, to at least 28 cm . Colour: blackish or blackish-brown with conspicuously light-margined fins.

Distribution: Oceanic and nearly circumtropical. Eastern North Atlantic records are patchy, with records from the Bay of Biscay, France and the Azores and from the Eastern Central Atlantic off Madeira Islands, Canary, and Cape Verde. Western North Atlantic from scattered records off the Scotian Shelf of Canada, the Grand Banks, Virginia (USA), several Western North Atlantic seamounts, Bermuda, Sargasso Sea, the Gulf of Mexico, and Suriname. Also, occurs in the Western South Atlantic and from scattered records in the Western Indian and Pacific oceans.

Habitat: A wide-ranging, warm temperate to tropical epipelagic species that occurs near continental and island archipelagos, sometimes over the shelves, with a preference for areas of high productivity. In the North Atlantic this species appears to have a strong association with insular landmasses. Unlike Euprotomicrus bispinatus it appears to avoid central ocean basins.


Fig. 152 Squaliolus laticaudus
$\square$ Known distribution $\square$ Possible distribution Squaliolus laticaudus does appear to migrate vertically on a diel cycle, travelling from at least 500 to as much as 2000 m depth during the day to about 200 m at night. This shark has been captured on bottom longlines between 700 and 750 m deep. It has been caught on pelagic longline between 60 and 80 m over water approximately 1220 m deep. The bottom temperature where some of these sharks have been taken ranged from 11.2 to $26.3^{\circ} \mathrm{C}$. These sharks unlike their close relatives $\boldsymbol{E}$. bispinatus and Isistius brasiliensis tend to avoid the surface and are not attracted to night-lights from ships.

Biology: Development is viviparous with yolk-sac, with a litters of 3 to 5. A 21.5 cm female from the northern Gulf of Mexico had three near-term embryos, one male and two females, measuring between 8.6 and 9.1 cm in length, while another female from the same area had 5 uterine eggs, two in left and three in the right uteri, and a third reported gravid female from southern Brazil had four embryos; 3 of the embryos were females and the fourth was a male. Two additional adult females were found to have 12 large mature ova in a single ovary. Although nothing is known of the breeding behaviour of this shark, all known records of gravid females to date came from between $27^{\circ}$ and $32^{\circ}$ north or south latitude. Nothing else is known about the reproductive cycle of this shark.

The spined pygmy shark eats cephalopods, including the deepsea squid (Abralia redfieldii), lanternfish, gonostomatids and idiacanthids, and probably follows its prey on their diel migrations. This shark has well-developed photophores, densely covering the ventral surface of the body but sparse on the sides and hardly developed on the dorsal surface. Such photophore patterns in this and other bioluminescent sharks and mesopelagic teleosts has been explained as 'photophore counter-shading', in which the light-producing underside eliminates the shadow normally formed when the fish is illuminated from above, and hence makes it less conspicuous to potential predators. However, this species has been found in the stomachs of pelagic fish caught by longlines. In one instance two individuals were found in the stomach of a swordfish (Xiphias gladius) and 45 in the stomach of a bigeye tuna (Thunnus obesus). The occurrence of large numbers in the stomach of the bigeye tuna suggests that these sharks aggregate in schools perhaps for foraging.

Size: Maximum total length about 28 cm ; males maturing at about 15.2 cm and reaching 22.3 cm ; females maturing between 17 and 20 cm and reaching 27.5 cm . Size at birth 8 to 10 cm in length as smallest free-swimming individual measured 8.1 cm , but near-term embryos from a single female were between 9 and 9.7 cm total length. This shark is often cited in popular literature as 'the smallest living shark', but according to Compagno (1988) it is closely rivalled for the
title by Squaliolus aliae, several lanternsharks (Etmopterus, Family Etmopteridae), and Eridacnis radcliffei (Family Proscylliidae).

Interest to Fisheries and Human Impact: Interest to fisheries none, although it is likely taken as bycatch in some bottom trawl fisheries.

Conservation status is Least Concern due to its small size and wide distribution.
Local Names: Dwarf shark (Azores).
Literature: Bigelow and Schroeder (1957); Siegel et al. (1977); Siegel (1978); Kukuyev (1982); Compagno (1984, in part); Glukhov and Kuz'michev (1984); Sadowsky, Amorim, and Arfelli (1985); Sasaki and Uyeno (1987); Vinnichenko (1997); Aires Da Silva et al. (1998); Moore et al. (2003); Cunha and Gonzales (2006); Kyne and Burgess (2006); Gibson et al. (2008); Driggers et al. (2010); Ebert and Compagno (In press).

### 2.3 Order SQUATINIFORMES - Angel sharks

Order: Tectospondyli, Suborder Squatinoidei: Jordan, 1923, Stanford Univ. Publ., Univ. Ser., Biol. Sci., 3: 102, emended to Order Squatiniformes.

## Number of Recognized North Atlantic Families: 1.

FAO Names: En - Angel sharks.
Field Marks: Sharks with a flattened batoid-like form but with free anterior pectoral lobes lateral to gills and lower lobe of caudal fin longer than upper lobe.

Diagnostic Features: Head greatly depressed and expanded laterally. Snout extremely short and truncated, without lateral teeth or rostral barbels. Eyes dorsolateral on head, without nictitating lower eyelids, secondary lower eyelids, or subocular pouches; upper eyelids not fused to eyeball. Spiracles large, close behind and at level of eyes. Five pairs of gill openings present on sides of head, with the posteriormost in front of pectoral-fin origins. Nostrils terminal on snout, with barbels on anterior nasal flaps but no nasoral grooves or circumnarial grooves; nostrils separate from mouth but with anterior nasal flaps overlapping mouth. Mouth large, terminal on head, broadly arched and subangular, terminating about opposite or slightly behind eyes. Labial furrows very large and present on both jaws. Teeth moderately differentiated along the jaws, with slightly enlarged anterior teeth, no enlarged molariform posterior teeth, and without a gap or small intermediate teeth between anterior and lateral teeth in the upper jaw; teeth with orthodont histological structure. Trunk greatly depressed and raylike. Caudal peduncle without elongated lateral dermal ridges but with short thick keels at the caudal base. Dermal denticles either covering entire body or absent from lower surface, some denticles more or less enlarged as thorns or spines on head and midline of back. Pectoral fins very large, expanded and raylike, with unique triangular anterior lobes that cover the gill openings. Pectoral girdle (scapulocoracoid) low, wide, C-shaped and depressed, without a medial joint, and with superscapulae directed posterodorsomedially and not contacting vertebral column. Pectoral-fin skeleton tribasal, with propterygium in contact with radials and metapterygium without a proximal segment; pectoral fins semiplesodic, with radials partially extending into fin webs; radial counts 47 to 52 with mostly 4 or 5 but up to 8 segments. Pelvic fins very large, with inner margins lateral to vent. Claspers with siphons in the abdomen below the pelvic-fin bases but without clasper sacs; clasper glans lacking a pseudosiphon or clasper spurs or spines but with a cover rhipidion and rhipidion; dorsal and ventral marginals of clasper skeleton well-developed but not rolled into a tube for the clasper canal. Two spineless dorsal fins present, with origin of first on tail over or behind pelvic-fin free rear tips. Anal fin absent. Caudal fin with a long dorsal lobe and an expanded ventral lobe; vertebral axis depressed into the ventral caudal lobe (hypocercal caudal fin). Vertebral calcification very strong, secondary calcification in the form of concentric annuli that fill the intermedial and basal spaces. Vertebral counts: total vertebral counts 119 to 146 , monospondylous vertebral counts 43 to 52 , diplospondylous precaudal vertebral counts 48 to 65 , precaudal vertebral counts 90 to 115 , caudal vertebral counts 26 to 31 . Intestinal valve of conicospiral type, with 7 to 12 turns. Medium sized sharks from just over 100 cm to about 240 cm in length. Colour: light grey to yellow-brown, reddish-brown, or tan above, usually lighter below; most species have some saddles, spots, or blotches on dorsal surface. Reproduction viviparous with a yolk-sac.

Distribution, Biology, Size, Interest to Fisheries and Human Impact: See Family Squatinidae.

### 2.3.1 Family SQUATINIDAE

Family: Subfamily Squatinini Bonaparte, 1838, Nuov. Ann. Sci. Nat. Bologna, ser. 1, 2: 206 (Family Squalidae). Also Subfamily Squatinae Swainson, 1839, Nat. Hist. Fish. Amphib. Rept., Monocard. Anim., 2: 321 (Family Raidae Swainson, 1839), and Family Squatinae Müller and Henle, 1841, Syst. Beschr. Plagiost., pt. 3: 99.

Type genus: Squatina Dumeril, 1806.

## Number of Recognized North Atlantic Genera: 1.

FAO Names: En - Angelsharks, Sand devils; Fr - Anges de mer; Sp - Angelotes, Peces ángel.
Local Names: Angel sharks, Angelsharks, Angelfish, Monkfishes (English), Angeli morskie (Russia).
Field Marks: See order.
Diagnostic Features: See ordinal diagnosis.

Distribution: Angel sharks occur in most oceans including the Eastern and Western Pacific, Eastern and Western Atlantic, and in the extreme Southwestern and Southeastern Indian Ocean. They are not known from most areas of the Indian Ocean or in the Central Pacific reaches of Oceania.

Habitat: Angel sharks have a mostly amphitemperate range, with few species being known from tropical equatorial waters, but several occur in warm temperate seas and a few range into cold northern boreal waters. They range in depth from close inshore down to about 1300 m on the continental slopes. They are often found buried in mud and sand on the bottom during the daytime, but are night-active and may swim off the bottom after dusk.

Biology: Most angel shark species are sketchily to poorly known biologically. The reproductive mode is viviparous with a yolk-sac and they may have litters from 1 to 25 young, but very little is known of their reproductive cycle. Those angel shark species that have been studied appear to have an annual reproductive cycle, with birth usually occurring in the spring and summer months. Angel sharks are mostly moderate in size, 120 to 160 cm total length, but at least one European species (Squatina squatina) may exceed 200 cm . Attempts to age these sharks using vertebral centra have been unsuccessful since it has been shown in at least two species that the banding is not temporal. Angel sharks feed on a variety of small bony fishes, crustaceans, cephalopods, gastropods and bivalves, and use their flexible 'necks' and highly protrusible, traplike jaws to suddenly raise their heads and snap up prey above or in front of them at high speed.

Interest to Fisheries and Human Impact: Several angel shark species are intensively fished, especially by bottom trawl, line gear and fixed bottom nets, as both targeted catch and bycatch of trawl fisheries for other demersal fishes. World catch of angel sharks averaged approximately 5275 tonnes according to FAO with an increase of $63 \%$ in landings from 3375 tonnes in 2000 to 6335 tonnes in 2009, with a high of 6835 tonnes in 2007. The actual landed catch of angel sharks is probably much greater because many countries where angel sharks are caught do not report separate statistics for them. There is no targeted fishery for angel sharks in the Western North Atlantic, and in the Eastern North Atlantic only small numbers are occasionally reported (see Squatina squatina account below). They are used for human consumption, oil, fishmeal, leather and shagreen for woodworking and artistry. Shagreen of certain angel sharks is of use in preparing the bristles of artistic brushes in the Orient.

Angel sharks are harmless to people unless disturbed or provoked, but if aroused they can bite and are capable of causing serious cuts with their small but sharp teeth and strong jaws. Their relatively small size and bottom habitat makes them of little concern to swimmers and bathers, and they primarily pose a minor hazard to fisheries personnel that have to remove live individuals from demersal fishing gear.

The conservation status of angel sharks is poorly known for most species, but some species are considered Critically Endangered. In those areas where fisheries for angel sharks have occurred the fishery usually collapses within a few years.

## Local Names: None.

Remarks: The Squatinidae is a small, but highly distinctive group of batoid-like sharks that have usually been recognized as a discrete taxon at the genus, family, and higher level. The family has a monotypic genus with 20 valid taxon currently recognized. Two species occur in the North Atlantic.

Literature: Regan (1908); Garman (1913); Fowler (1941, 1969); Lindberg (1971); Roux (1977); Capapé and Roux (1980); Compagno (1984); Ebert and Compagno (In press).

## Squatina Dumeril, 1806

Genus: Squatina Dumeril, 1806, Zool. Analyt:: 102. No species. Genus Squatina Dumeril in Risso, 1810, Ichthyol. Nice, Paris: 45.

Type species: Squatina vulgaris Risso, 1810, by subsequent monotypy; a junior synonym of Squalus squatina Linnaeus, 1758 and unnecessary replacement according to Eschmeyer (1998). Eschmeyer also noted that Dumeril applied the species name angelus to Squatina in 1808, with $\boldsymbol{S}$. angelus an unneeded substitute for $\boldsymbol{S}$. squatina, but neither Eschmeyer or the writers were able to examine Dumeril's account. If correct this shifts the type allocation from Risso to Dumeril. Squatina was originally proposed by Valmont, 1768, Dict. Hist. Nat. 1: 117, without species, but Valmont's names are unavailable by ruling of the International Commission on Zoological Nomenclature (Opinion 89, 1925: 27.).

## Number of Recognized North Atlantic Species: 2.

Synonyms: Genus Rhina Rafinesque, 1810: 14. Type species: "Squalus squatinus" Linnaeus, 1758, by original designation. A junior homonym of Rhina Bloch and Schneider, 1801 (a batoid). Genus Squatina Blainville, 1816: 121. Type species: Squatina angelus Blainville, 1816, by monotypy. Genus Rhina Klein, in Gill, 1862: 408. Type species: "Rhina squatina Raf." by designation of Gill, 1862, equals Squalus squatina Linnaeus, 1758. Also Rhina Klein, in

Garman, 1913: 5, 250. Both are revivals of Rhina Schaeffer, 1760: 20; Klein, 1776: 587; and Walbaum, 1792: 580. Schaeffer's Rhina had no species, according to Bigelow and Schroeder (1948: 534, ftn. 12). Klein and Walbaum's names are unavailable by rulings of the International Commission on Zoological Nomenclature (Opinion 21, 1910: 51; Opinion 89, 1925: 27.). Rhina Klein in Gill and Garman are junior homonyms of Rhina Bloch and Schneider, 1801 (a batoid). Genus Squalraia de la Pylaie, 1835: 526. Type species: Squalraia acephala de la Pylaie, 1835, = Squalus squatina Linnaeus, 1758, by subsequent designation of Jordan (1919: 183).

Field Marks: See order.
Diagnostic Features: See ordinal diagnosis.
Local Names: Angel sharks, Angelsharks, Angelfish, Monkfishes (English), Angeli morskie (Russia).

## Key to North Atlantic Species:

1a. Lateral head folds without lobes (Fig. 153).
Squatina dumeril (Western North Atlantic)


Fig. 153 Squatina dumeril


Fig. 154 Squatina squatina

## Squatina dumeril Lesueur, 1818

Squatina dumerilLesueur, 1818, J. Acad. Sci. Philadelphia 1(2): 225, pl. 10. Specimen depicted an adult male. Syntypes: Three, according to Eschmeyer (1998, Cat. Fish.), including Museum National d'Histoire Naturelle, Paris, MNHN A. 9692 (1), a 122 cm dry-mounted male in good condition from the coast of New York State (Bertin, 1939b, Bull. Mus. Nat. Hist. Nat., 2 e ser., 12(6): 77).

Synonyms: None.

## Other Combinations: Rhina dumeril (Lesueur, 1818).

FAO Names: En - Sand devil; Fr - Ange de mer de sable; Sp - Tiburón ángel.


Fig. 155 Squatina dumeril

Field Marks: An angel shark with simple, tapering nasal barbels and weakly fringed or smooth anterior nasal flaps, lateral head folds without triangular lobes, large eyes with eye-spiracle space less than 1.5 times eye length, fairly broad and posteriorly angular pectoral fins without an anterior shoulder, rough, hooked dorsal denticles, and nearly plain dorsal coloration without elaborate spotting or ocelli on body.

Diagnostic Features: Interorbital space strongly concave. Head width about 3.1 in precaudal length. Head length to notch about 4.0 in precaudal length and 1.4 in head width. Lateral head folds low, without triangular lobes. Eye length 4.1 in interorbital space; preorbital length greater than eye length; eye-spiracle space less than 1.5 times eye length. Spiracle width greater than eye length; spiracles with 10 pseudobranchial folds; interspiracular space slightly greater (about 1.1 times) than interorbital space. Nasal barbels with simple tapering tips; posterior edges of anterior nasal flaps low and weakly fringed; tips of anterior nasal flaps narrow and hardly fringed, not strongly lobate; posterior nasal flaps moderately enlarged, not fringed. Nostril width about 4.5 in internarial width. Exposed upper lip between bases of anterior nasal flaps forming a low, broad, rounded arch. Tooth row counts 38 upper jaw, 40 lower jaw. Body width at pectoral-fin insertions about 0.9 times head length to upper notch and 4.4 in precaudal tail. Tail length from pelvic-fin insertions to upper caudalfin origin 1.1 to 1.2 times trunk length from pectoral-fin origins to pelvic-fin insertions. Small but prominent thorns present on snout, interorbital space, and with a few between spiracles, fewer and more discrete in young but more numerous and forming patches in adults; small but prominent thorns present on midline of back in front of first dorsal fin, between dorsal fins, and on postdorsal space in young, but adults have these reduced and inconspicuous. Dorsal denticles loosely spaced, surface slightly rough; denticles fairly sharp-cusped, broadly hooked, and with 4 or more anterior ridges. Adult males with enlarged thorns on anterior margins and apices of pectoral fins. Underside of body naked except for anterior margins of pectoral and pelvic fins, ventral surface of tail, and scattered patches on the abdomen and fin bases. Angle of pectoralfin apex narrowly obtuse, slightly greater than a right angle. Pectoral-fin anterior margins straight, not forming a distinct anterior shoulder, apices narrowly rounded, posterior margin slightly concave, rear tips narrowly rounded or subangular, inner margins broadly convex and rounded. Distance from anterior tip of pectoral fin to insertion about 0.6 of maximum pectoral-fin length from anterior tip to free rear tip; maximum pectoral-fin length about $39 \%$ of maximum total length to tip of lower caudal-fin lobe. Free rear tip of pectoral fin closer to pelvic-fin apex than pelvic-fin origin. First dorsal-fin origin posterior to pelvic-fin free rear tips by about half interorbital. First dorsal-fin base about 2 in interdorsal space, 2.0 to 2.1 times in postdorsal space. Postventral caudal-fin margin nearly vertical and truncate, or diagonal. Vertebral counts: total vertebral counts 132 to 137 , total precaudal counts 101 to 107 , monospondylous vertebral counts 45 to 48 , diplospondylous precaudal counts 55 to 59 . A large sized angel shark, possibly reaching a maximum total length of 152 cm . Colour: bluish grey or ashy grey dorsally when fresh, chocolate brown in preservative, underside white with red spots on throat, abdomen, and on tail behind the vent; pectoral and pelvic fins with reddish ventral margins; faint symmetrical white spotting on dorsal surface in young but not adults; no discrete darker spotting on dorsal surface; no ocelli on back; pectoral and pelvic-fin webs with pale reddish brown anterior and posterior margins; dorsal-fin webs darker and bases and rear tips light, unspotted; caudal fin with light base and darker web, without numerous dark or pale spots.

Distribution: Endemic to the Western North and Central Atlantic (Areas 21, 31) from southern New England to Florida, USA and the Gulf of Mexico. Also, unconfirmed records from Cuba, Jamaica, Nicaragua, and Venezuela.

Habitat: A moderately common but rather poorly known temperate and subtropical angel shark of the Western North Atlantic continental shelf and slope, on or near the bottom from close inshore to exceptionally down to 1290 m depth, most records between 40 to 250 m . During the spring and summer months this shark moves close inshore, but retreats to deeper water at other times of the year.

Biology: Viviparous with yolk-sac and only the left ovary functional. The reproductive cycle is at least biennial (possibly triennial) with a 12 month gestation period followed by a 12 month resting phase after giving birth. Parturition in the Gulf of Mexico occurs during the late winter to mid-summer months (February to June). Litters range from 4 to 25 embryos in the


Fig. 156 Squatina dumeril

Western North Atlantic and from 4 to 10 in the northern Gulf of Mexico (average 7), but there does not appear to be any relationship between the size of the female and the number of embryos per litter. As with other squatinids (Squatina californica), attempts to age $\boldsymbol{S}$. dumeril using vertebrae were unsuccessful as deposition of vertebral bands are not associated with age, but rather size.

The diet consists primarily of benthic bony fishes, followed by squids, and crustaceans. However, the diet composition changes in these sharks with increasing size, with crustaceans becoming less important with increasing size. In addition to ontogenetic shifts in diet, there is a seasonal change with squid predominating in their diet during the winter and spring, but teleosts (Stromateidae, Mullidae, and Sciaenidae) becoming prominent in the diet during the spring and fall.

Size: Maximum total length at least 134 cm , but possibly to 152 cm ; males mature at about 85 to 93 cm total length, a length slightly larger than females that mature at about 85 cm ; size at birth is 25 to 30 cm in length.

Interest to Fisheries and Human Impact: Squatina dumeril is only taken as a bycatch species, mainly in the butterfish (Peprilus burti) bottom trawl fishery and to a lesser extent by shallow water shrimp trawls. It is currently listed as a prohibited species from directed commercial fisheries in United States waters. This is largely due to a lack of life history information and as a precautionary approach to managing its population. Like most squatinids for which some life history information is available, its characteristics make $\boldsymbol{S}$. dumeril potentially vulnerable to fishing pressures. Not dangerous to people when undisturbed, but readily snaps at fishermen that catch it (hence the common name sand devil) and can inflict severe lacerations. Listed as a prohibited species from directed commercial fisheries in the US (2012).

The conservation status is currently Data Deficient, but its status should be reassessed since additional life history information has been gathered since it has been originally assessed (Heupel and Carlson, 2006).

Local Names: West Atlantic angel shark, Atlantic angel shark, Angel shark, Angelfish, Nurse fish, Monkfish, Sand devil, Ange de mer d'Amérique.

Literature: Lesueur (1818); Garman (1913); Bigelow and Schroeder (1948); Springer and Bullis (1956); Bullis and Thompson (1965); Cervigon (1966); Schwartz and Burgess (1975); Compagno (1984); Heupel and Carlson (2006); Baremore, Murie, and Carlson (2008, 2010); Baremore, Andrews, and Hale (2009); Baremore (2010); I.E. Baremore (pers. comm.).

## Squatina squatina (Linnaeus, 1758)

Squalus squatina Linnaeus, 1758, Syst. Nat., ed. 10, 1: 233. Possible syntypes: Uppsala Universitet, Zoologiska Museet, Uppsala, Sweden, ZMUU Linnaean coll. 161 (1, dry) and Naturhistoriska Riksmuseet, Stockholm, Sweden, NHRM L-87 (1), according to Eschmeyer (1998, Cat. Fish.). "Habitat in Oceano Europaeo."

Synonyms: Squatina vulgaris Risso, 1810: 45. No type material, off Nice, France. Squatina angelus Blainville, 1816: 121. Nomen nudum. Blainville, 1825: 53 , pl. 13, fig. 1. Holotype: 58 cm ( 23 ") specimen mentioned, France. Squatina laevis Cuvier, 1817: 131. Apparently a replacement name for Squalus squatina Linnaeus, 1758, as the latter is placed in synonymy of S. laevis. Squatina lewis Couch, 1825: 90. England, possibly an error for Squatina laevis? ?Squalraia acephala de la Pylaie, 1835: 527. Fide Jordan, (1919: 182). ?Squalraja cervicata de la Pylaie, 1835, Rech. France Poiss., 1832-1833, Congr. Sci. France Poitiers, 1834: 527. Fide Jordan (1919: 182). Crossorhinus (or Cestracion?) angelorum Swainson, 1838: 137, fig. 13; also Squatina angelorum Swainson, 1838, ibid:: 184, fig. Probably a replacement name for $S$. squatina; "Our European species, C. angelorum, is generally called the angel-fish" (Swainson, 1838, ibid.: 137). Squatina europaea ("BI. 116"), Swainson, 1839: 321. Based on an illustration in Bloch (1785: pl. 118) according to Eschmeyer (1998), and probably a synonym of Squalus squatina Linnaeus, 1758. Squatina angelus Gronow, in Gray, 1854: 14. Syntype: British Museum (Natural History), BMNH 1853.11.12.207 (Gronovius coll.), a skin from European seas (Eschmeyer, 1998). Apparently a synonym of Squalus squatina Linnaeus, 1758.

Other Combinations: Rhina squatina (Linnaeus, 1758), Rhina vulgaris (Risso, 1810).

FAO Names: En - Angelshark; Fr - Ange de mer commun; Sp - Angelote.


Fig. 157 Squatina squatina
Field Marks: An angel shark with a broad trunk, simple nasal barbels with a simple, straight or spatulate tip, smooth or weakly fringed anterior nasal flaps, lateral head folds with a single triangular lobe on each side; very sharp, hooked dorsal denticles giving it a very rough surface, large thorns absent from middle of back (small thorns present in young but lost in juveniles and adults); very high broad pectoral fins, and dorsal surface with small spots but no ocelli.

Diagnostic Features: Interorbital space weakly concave, nearly flat. Head width 3.2 to 3.6 in precaudal length. Head length to notch about 4.4 to 4.6 in precaudal length and 1.3 to 1.5 in head width. Lateral head fold with a triangular lobe. Eyes relatively small, length about 3.5 (small juveniles) to 5.3 to 5.5 (large immature specimens) in interorbital; preorbital length greater than eye length; eye-spiracle space over 1.5 times eye length. Spiracle width greater than eye length, up to 1.6 times it. Spiracle with 10 pseudobranchial folds; interspiracular space subequal to interorbital space. Nasal barbels simple and with straight or slightly expanded spatulate tips, no lobate fringes; posterior edges of anterior nasal flaps weakly fringed; tips of anterior nasal flaps narrow and not fringed and lobate; posterior nasal flaps small and weakly fringed. Nostril width 6.0 to 7.0 in internarial width. Exposed upper lip between bases of anterior nasal flaps forming a broad, low rounded arch. Total tooth row counts similar for upper and lower jaws at 36 to 44 . Body very broad, width at pectoral insertions about 0.7 times head length to upper notch and 3.6 to 4.0 in precaudal tail in moderate-sized specimens but possibly down to 5.0 in young. Tail length from pelvic-fin insertions to upper caudal-fin origin 0.8 to 1.0 times trunk length from pectoral-fin origins to pelvic-fin insertions (usually less than trunk). Patches of small thorns on snout and on interorbital space; small thorns or enlarged denticles present on the midline of the back and between fin bases in newborn young, but inconspicuous or absent in larger individuals. Dorsal denticles closely spaced, surface very rough; denticles with very narrow, sharp-cusped hooked crowns with weak anterior ridges. Presence of enlarged thorns on paired fins of adult males uncertain. Underside of body covered with denticles. Angle of pectoral apex approximately a right angle. Pectoral-fin anterior margins straight to slightly convex, not forming a distinct anterior shoulder, apices rounded-angular, posterior margin slightly concave or nearly straight, rear tips broadly rounded, inner margins broadly convex and rounded. Distance from anterior tip of pectoral fin to insertion 0.5 to 0.6 of maximum pectoral-fin length from anterior tip to free rear tip; maximum pectoral-fin length about 26 to $29 \%$ of maximum total length to tip of lower caudal-fin lobe. Free rear tip of pectoral fin closer to pelvic-fin origin than pelvic-fin apex. First dorsal-fin origin usually opposite pelvic-fin free rear tips but occasionally slightly posterior. First dorsal-fin base about 1.7 to 2.1 in interdorsal space, 1.4 to 1.5 times in postdorsal space. Postventral caudal-fin margin nearly vertical and truncate. Vertebral counts: total vertebral counts 119 to 125, precaudal counts 91 to 96 , monospondylous vertebral counts 43 to 46 , diplospondylous precaudal counts 48 to 50 . Orbital fenestra of supraorbital crest not open laterally, postorbital process contacting anterior part of crest. A very large angel shark, attaining a maximum total length of at least 183 cm and possibly up to 244 cm . Colour: grey to reddish-brown or yellow-green dorsally, white below, fin margins dusky; small symmetrical white spots loosely scattered on dorsal surface of head, trunk, and paired fins in young; white nuchal spot may be present; young often with white reticulations, adults more uniform; small blackish dots and spots densely scattered on dorsal surface; young with large dark blotches on head, pectoral-fin bases, pelvic-fin bases, and below dorsal fins; no ocelli on back; pectoral and pelvic-fin webs with lighter posterior margins; dorsal-fin bases and webs dark anteriorly, pale distally, not regularly spotted. Caudal fin with dark base, dark dorsal and preventral margins, light medial and posterior web, and no dense dark or light spots.

Distribution: Eastern North Atlantic: Southern Norway, Sweden, Denmark and Shetland Islands south to the United Kingdom, Ireland, Germany, the Netherlands, Belgium, France, Portugal, and Spain. Also, Eastern Central Atlantic including Morocco, Western Sahara, Mauritania, and the Canary Islands, and the entire coast of the Mediterranean and Black Seas.

Habitat: A temperate-water bottomdwelling angelshark of the European and North African continental shelves, on or near the bottom from close inshore in the intertidal or subtidal to at least 150 m depth. This shark prefers mud or sandy bottom, where it lies buried with little more than its eyes protruding. It may penetrate estuaries and brackish water.

Biology: This shark is yolk-sac viviparous, with both ovaries functional. It has moderate-sized litters of 7 to 25 young which vary according to the size of the female. Gestation period is 8 to 10 months, born in December to February in the Mediterranean but apparently later in northern parts of its range (July in England).

The angelshark is nocturnal and can be found swimming strongly up off the bottom at night, but is torpid in the daytime and rests on the bottom. In the northern parts of its range it is seasonally migratory, and makes northwards incursions during the summer.


Fig. 158 Squatina squatina
$\square$ Known distribution

The angelshark feeds primarily on bony fishes, especially flatfishes but also other demersal fishes and skates, crustaceans and molluscs. Specific items include hake (Merluccius merluccius, Merluccidae), sparids (Pagellus erythrinus, Sparidae), grunts (Pomadasys sp., Haemulidae) flatfish (Bothus sp., Bothidae, Citharus linguatula, Citharidae, Limanda limanda, Pleuronectidae), sole (Solea solea, Soleidae), squid (Loligo vulgaris), cuttlefish (Sepia officinalis, Sepiola sp.), and crustaceans (Dorippe lanata, Geryon tridens, Dromia personata, Goneplax rhomboides, Liocarcinus corregatus, Atelecyclus rotundatus). It occasionally swallows odd items, including eelgrass and seabirds (a cormorant was once recorded).

Size: Maximum total length at least 183 cm and possibly to 244 cm . Males mature between 80 and 132 cm , with a maximum length of 183 cm ; females maturing at 126 to 167 cm and generally larger than males; size at birth about 24 to 30 cm .

Interest to Fisheries and Human Impact: Fisheries for angel shark in the Eastern North Atlantic has largely ceased with the species having been extirpated from large areas of its distribution over the past 100 years. Reported landings of this species declined from 15 to 20 tonnes in the 1980s to only 1 or 2 tonnes in the 1990s. Over the past decade ( 2000 to 2009) reported landings were mostly 0 to a high of 4 tonnes in 2005. As of this writing, the angel shark has largely been banned from being retained in European fisheries, and fishers are encouraged to release this shark in the best possible condition (ICES, 2010). The status and current exploitation off NW Africa are uncertain. The EU has prohibited the fishing for, retaining on board, transhipments or to land this species in and from EU waters (2012).

The conservation status of this species is listed as Critically Endangered as it has apparently been locally extirpated from large areas of the Mediterranean and North Sea. It is now considered uncommon throughout much of its range.

Local Names: European angel shark, Angel fish, Fiddle fish, Kingston, Little bullhead shark, Mongrel skate, Monk fish, European monkfish, Monkey fish, Angel ray, Squanto, Puppy fish, Shark ray (England); Maegli (Wales); Ange de mer, Ange, Angel, Antjou, Bourgeois, Bourget, L'ange, L'anelot, Martrame, Mordacle, Squatine occelée (France); Meerengel, Engelhai, Gemeiner meerengel (Germany); Havengel (Denmark, Norway); Zeeängel, Shoorhaai (the Netherlands); Bergelote, Speelman, Zeeduyvel (Belgium); Angel, Angelot, Angelote, Escat, Mennejuela, Pardón, Peje ángel, Vexigall (Spain); Anjo, Peixe anjo, Viola (Portugal); Angel evropeiskii morskie (Russia).

Literature: Garman (1913); Lozano y Rey (1928); Belloc (1934); Fowler (1936); Iselstöger (1937); Bigelow and Schroeder (1948); Wheeler and Blacker (1969, 1972); Krefft in Hureau and Monod (1973a); Capapé (1974, 1975); Roux (1977); Wheeler (1978); Capapé and Roux (1980); Compagno (1984); Roux in Whitehead et al. (1984); Springer (1990); Capapé, Quignard, and Mellinger (1990); Ellis, Pawson and Shackley (1996); Bridge, Mackay and Newton (1998); Rogers and Ellis (2000); Morey et al. (2006); Gibson et al. (2008); ICES (2010); Ebert and Compagno (In press).

### 2.4 Order ORECTOLOBIFORMES

Order: Orectolobiformes Applegate, 1972, J. Mar. Biol. Ass. India, 14(2): 743; also Compagno, 1973, J. Linn. Soc. (Zool.), 53, suppl. 1: 28.

## Number of Recognized North Atlantic Families: 2.

FAO Names: En - Carpet sharks; Fr - Requins-tapis; Sp - Tiburones tapiceros and Gatas nodrizas.
Field Marks: These are moderate to enormous sharks with the combined characteristics of nostrils with barbels (rudimentary in Rhincodon typus), nasoral grooves connecting the nostrils to the mouth, relatively short truncated mouth terminating in front of eyes, no nictitating eye membranes, five paired gill openings, two spineless dorsal fins, and an anal fin. Many members of this order have rather striking colour patterns.

Diagnostic Features: Body shape cylindrical, depressed, or somewhat ray-like in the Orectolobidae. Head conical to depressed, relatively short, expanded laterally in some species, but not in others. Snout short to very snout, conical, truncated, or flattened, but not elongated or blade-like. Nostrils with barbels (rudimentary in Rhincodon), circumnarial grooves present around incurrent aperture but absent in some taxa; nasoral grooves present and connecting excurrent apertures of nostrils with mouth; anterior nasal flaps short to elongate and reaching mouth. Eyes dorsolateral to lateral on head, and without nictitating membranes. Spiracles small to relatively large, located close behind and about opposite level of eyes. Five paired gill openings present on side of head; length relatively small to very long, but not encircling head; posterior most two to four above pectoral-fin origins. Mouth small to large, usually subterminal, except in Rhincodon it is terminal, and arched to nearly transverse and short, and ending in front of eyes. Labial furrows well develop. Teeth weakly to strongly differentiated along the jaws, with or usually without enlarged anterior teeth and without enlarged molariform posterior teeth; without a gap or small intermediate teeth between anterior and lateral teeth in the upper teeth in the upper jaw; tooth counts from 23 to over 300 upper jaw, and 19 to over 300 lower jaw. Caudal peduncle with or without lateral dermal ridges or lateral keels. Dermal denticles covering entire body. Pectoral fins small to large, somewhat expanded and ray-like in some species. Pelvic fins small to large, with vent usually continuous with their inner margins, but may be separate in the Orectolobidae. Dorsal fins spineless, with origin of first dorsal fin varying from anterior to pelvic-fin origins to behind pelvic-fin insertions. Anal fin present. Caudal fin with a long dorsal lobe. Vertebral counts: total vertebral counts 117 to 243, monospondylous vertebral counts 32 to 138, diplospondylous precaudal vertebral counts 38 to 95 , precaudal vertebral counts 69 to 138, and caudal vertebral counts 49 to 154 . Intestinal valve of conicospiral type, with 6 to 74 turns. Size small, maturing about 34 cm in length, to gigantic, maturing at over 1000 cm in length. Colour: colour pattern may be obscure or plain, with very few light or dark spots to rather striking with prominent dark saddles with or without numerous small to large dark or light spots, blotches, rings, or reticulations, and collar markings around the gill region on some species; dark spotting or darker and lighter blotches on some species may vary depending on size and stage of development. Reproductive mode depending on the species may be oviparous, viviparous with yolk-sac, or in the genus Nebrius oophagous, with embryos consuming uterine eggs.

Distribution: Most members of this shark group occur throughout the Indo-western Pacific where several species are regional endemics. The only exceptions are the wide-ranging whale shark (Rhincodon typus) found in most tropical and warm-temperate seas, and the nurse shark (Ginglymostoma cirratum) found primarily in the tropical and warm temperate Atlantic and tropical eastern Pacific.

Habitat: These are mostly tropical to warm temperate sharks, many are regional endemics. They occur from the intertidal zone down to about 200 m depth. Most species are bottom dwelling, occurring on coral or rocky reefs, on mud or sandy bottoms, but the whale shark is oceanic, travelling great distances, even crossing ocean basins making ling distant migratory movements.

Biology: Development may be oviparous or viviparous with a yolk-sac. Virtually nothing is known about the reproductive cycle of most species, length of gestation, or fecundity of most species. Age and growth parameters are only known for a few species, while most are unknown. The diet, depending on the species, is rather broad ranging from invertebrates, including mostly crustaceans, cephalopods, to teleosts and small chondrichthyans. The whale shark unlike most members of this group feeds on plankton, copepods, invertebrate larvae, and gametes from spawning fishes, pelagic crustaceans, cephalopods, and small fishes on occasion.

Interest to Fisheries and Human Impact: Most of the families in this order are of relatively minimal fisheries importance as they are typically discarded. However, some of the most colorful species are highly valued in the aquarium trade and as such are taken in fisheries targeting them. Some species have been maintained in captivity in public aquaria for years and do quite well. Other species, particularly the whale shark (Rhincodon typus) is popular with ecotourist divers in those regions where they occur.

Remarks: The arrangement of this order follows Compagno $(1984,2001)$ with some modifications. The order has seven families of which two are represented in the North Atlantic.

## Key to North Atlantic Families:

1a. Mouth very large and terminal; gill slits very large; caudal peduncle with strong lateral keels; caudal fin without subterminal notch; flanks of body with lateral ridges present; body colour a distinct checkerboard pattern (Fig. 159)
family Rhincodontidae


Fig. 159 Rhincodon


Fig. 160 Ginglymostoma

### 2.4.1 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 North Atlantic Genera: 1.

FAO Names: En - Nurse sharks; Fr - Requins nourrices; Sp - Gatas nodriza.
Field Marks: Small to moderate sized sharks, with a broad, flattened head, rounded or truncated snout, with well developed nasoral grooves but no circumnarial grooves or folds, short to long nasal barbels, small, subterminal, transverse mouths not extending behind the eyes; no nictitating membrane over eyes, small spiracles behind and level to slightly above the eyes, no lateral skin flaps on head; five small gill openings, the fifth nearly overlapping the fourth; two spineless dorsal fins and an anal fin; second dorsal fin originates anterior to anal-fin origin; precaudal tail length much shorter than the head and body; caudal fin elongated.

Diagnostic Features: Small to moderately large sharks, with bodies cylindrically stout or moderately depressed, and without lateral ridges on back or sides of trunk. Head short, broadly flattened, without lateral skin flaps; snout broadly rounded or truncated. Eyes relatively small, situated dorsolaterally on head, with or without strong subocular ridges below them; eyes without nictitating eyelids or subocular pockets. Spiracles minute, much smaller than eyes, without raised external rims; located behind and about level to eyes but not below them. Gill openings small, first four openings evenly spaced, fifth gill opening closer, nearly overlapping fourth; internal gill openings without filter screens. Nostrils short to moderately long with pointed barbels; circumnarial folds or grooves absent. Nasoral grooves long and well developed. Mouth subterminal on head, transverse, moderately large, and situated well in front of eyes; 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 not continuous, ending well lateral to symphysis and not connected medially by a mental groove or groove and flap. Teeth similar in upper and lower jaws, with symphysial teeth not enlarged or fang-like, but with a strong medial cusp, 1 to 7 pairs of short lateral cusplets. Tooth row count 24 to 38 upper jaw, 22 to 32 lower jaw. Precaudal tail length shorter than body. Caudal peduncle without lateral keels or precaudal pits. Pectoral fins moderately large broadly rounded to narrowly falcate. Pelvic fins much smaller than pectoral fins, with anterior margins 0.4 to 0.7 times pectoral-fin anterior margins; pelvic fins somewhat larger or smaller than dorsal fins and anal fin. Dorsal fins either equal-sized (Pseudoginglymostoma) or with second dorsal fin considerably smaller than first (Ginglymostoma and 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. Second dorsal fin about equal size to anal fin; origin of second about opposite or midbase anal-fin origin. Anal fin with angular apex and broad base, insertion separated by a space much less than its base length from lower caudal-fin origin. Caudal fin elongated horizontally, heterocercal, but not crescentic, its upper lobe moderately angled above the body axis; dorsal caudal-fin margin less than two-fifths length of 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, forming a continuous curve (Pseudoginglymostoma and subadult Ginglymostoma and Nebrius) or may be weakly differentiated in adults (Ginglymostoma and Nebrius). Caudal keels absent. Vertebral counts: total vertebral count 135 to 195 , monospondylous vertebral counts 35 to 57 , diplospondylous precaudal vertebral counts 41 to 53 , diplospondylous caudal vertebral counts 49 to 96 , precaudal vertebral counts 85 to 103. Valvular intestine of ring type with 15 to 24 turns. Small to moderately large sharks with adults from 53 to 320 cm . Colour: plain with no prominent saddles, reticulations or white spots; young may have a few dark spots.

Distribution: Circumglobal in subtropical and tropical waters of the Atlantic, and the Eastern, Central and Indo-Western Pacific. Only the genus Ginglymostoma occurs in the Atlantic, primarily in tropical Atlantic waters, but vagrants are known to wander into warm temperate waters particularly during summer months. Eastern Atlantic: Tropical West Africa, from Gabon to Senegal, the Cape Verde Islands and rarely north to the Bay of Biscay, France. Western Atlantic: New England, U.S.A., southwards to the Gulf of Mexico, throughout the Caribbean and to Brazil.

Habitat: A group of common to rare inshore sharks usually found from the intertidal down to at least 130 m deep, but mostly in water less than 70 m deep. These sharks are usually found on rocky or coral reefs, in reef lagoons, mangroves, and in sandy areas between reefs. These are mostly tropical to subtropical sharks found on continental and insular waters, but on occasion individual vagrants have been found in warm temperate to temperate waters.

Biology: Development is viviparous with a yolk-sac, at least for Ginglymostoma and Nebrius, and possibly Pseudoginglymostoma, but this latter genus may be oviparous based on a single female that laid unfertilized egg cases in captivity; more information is required for Pseudoginglymostoma to better determine its reproductive mode. Nebrius is also unusual in that it exhibits a form of oophagy whereby the developing foetuses, numbering 1 or 2 per uterus, one they have reabsorbed their yolk-sac will feed on other large, encased uterine eggs; this is the only orectoloboid known to have uterine cannibalism.
The diet of these sharks includes reef fishes, crustaceans, cephalopods, molluscs, and various other reef associated invertebrates.

Interest to Fisheries and Human Impact: Interest to fisheries limited. They are utilized for human consumption, liver oil, and for their tough hides that make good leather products. The two larger species are very hardy and have been maintained in public aquaria for 10 years or more. The smaller Pseudoginglymostoma is rarely kept in captivity, but also appears to be quite hardy as one individual was maintained for 33 years at the Artis Zoo, Amsterdam. Although these sharks are considered docile to harmless, the two larger species, if provoked will bite and clamp down on their victim and hold on until their jaws are pried open.

The conservation status of this family is poorly known with Ginglymostoma and Pseudoginglymostoma being Data Deficient, and Nebrius, being considered Vulnerable due to possible local extirpations within its known distribution range.

## Local Names: None.

Remarks: This small orectoloboid family is comprised of three monotypic genera, each with a single species. The Ginglymostoma is the only genus of this family represented in the Atlantic. The other two genera, Nebrius and Pseudoginglymostoma, occur in the Central Pacific and Indo-Western and the Western Indian oceans, respectively. The above family account is modified after Compagno (2001).

Literature: Bigelow and Schroeder (1948); Compagno (1984, 2001); Dingerkus (1986); Compagno, Dando, and Fowler (2005).

## 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 $S$. 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 $\boldsymbol{S}$. cirratus, and Eschmeyer (1998, Cat. Fish.).

## Number of Recognized North Atlantic Species: 1.

Synonyms: Genus Ginglimostoma Agassiz, 1838: 85. Error or emendation of Ginglymostoma. Genus Ginglyostoma Springer, 1938: 13. Apparent error for Ginglymostoma.

Field Marks: See species account below.

Diagnostic Features: Body trunk rather stout anteriorly, tapering posteriorly behind first dorsal fin; caudal peduncle strongly compressed laterally and without lateral ridges or precaudal pits. Head somewhat compressed, more so in males than in females; in dorsal or ventral view adults narrow and U-shaped, broadly arcuate in smaller individuals. Snout broadly rounded, very short, and blunt; mouth width about 2.3 to 2.6 times preoral length. Eyes oval shaped and small, located dorsolaterally on head, subocular ridges strong; eye width about two times height. Spiracles minute, set behind and about level with eyes. Gill openings dorsolaterally situated on head, third opening about over pectoral-fin origin, first four evenly space apart, fourth and fifth openings close-set, partially overlapping; fifth gill opening about 1.7 times height of first gill. Nostrils nearly terminal on snout; nasoral grooves deep, extending posteriorly and connecting to front of mouth; anterior nostril margin with moderately elongated, slender barbel tapering posteriorly and extending past mouth; barbel length slightly more than $1 \%$ of total length. Mouth nearly transverse, lower lip trilobate and divided by shallow orolabial grooves connecting mouth with lower labial furrows. Upper labial furrows extending inwards to edge of nostrils; lower labials about equal to or slightly longer than uppers in length; distance between lower labial furrows about 1.5 times their length. Teeth in both jaws similar in shape, moderately compressed, with alternating overlap pattern, but not imbricated; teeth with erect central cusp, flanked by 2 to 6 lateral cusplets; tooth counts 30 to 42 upper jaw, 28 to 34 lower jaw. Dermal denticles on body trunk close-set, somewhat overlapping, with parallel three ridges, the median being the longest; cusp blunt and very short; pedicels high, slender, and on broad stellate bases; denticle size varies with growth, with adults being broad and rhomboid shaped. Pectoral fins semifalcate, with broadly rounded apices and a straight or nearly so posterior margin; in small sharks pectoral fins are broadly rounded and angular; pectoral-fin origin about under third gill opening. Pelvic fins broadly rounded at apices, size about two-thirds that of first dorsal fin. Dorsal fins apically rounded; first dorsalfin origin about over or slightly behind pelvic-fin origins; second dorsal fin much smaller than first dorsal fin, origin slightly anterior to above anal-fin origin. Anal fin about one-half as large in area as second dorsal fin, rounded at apices, with free rear tip extending posterior to level of lower caudal-fin origin. Caudal fin narrow, elongated, with dorsal caudal-fin margin over $25 \%$ total length (adults); dorsal caudal-fin margin 3.2 to 3.6 times caudal-fin depth; ventral caudal-fin lobe in young sharks absent, but weak in adults; preventral caudal-fin margin much shorter than postventral margin and 43 to $67 \%$ of it; terminal lobe short, 15 to $19 \%$ of dorsal caudal-fin margin. Vertebral counts: total vertebral counts 168 to 175, monospondylous vertebral counts 48 to 50 , diplospondylous caudal vertebral counts 73 to 83 , precaudal vertebral counts 92 to 98 , caudal vertebral counts 73 to 83 . Intestinal valve count 16 to 17 . Size to 308 cm total length. Colour: yellow to greyish brown above, becoming light yellow or whitish brown below, with no spots, saddles or other prominent markings, except for small dark, light ringed spots and obscure saddle markings on juveniles.

## Local Names: None.

Remarks: A single living species. The genus description is modified from Compagno (2001).

## Ginglymostoma cirratum (Bonnaterre, 1788)

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., $2 e$ ser., 12(6): 51-98) by M.L. Bauchot (pers. comm. to L.J.V. Compagno, 2001), also Eschmeyer (1998, Cat. Fish.). Separately described as Squalus cirratus Gmelin, in Linnaeus and Gmelin, 1788, Syst. Nat., ed. 13, Pisces 1(3): 1492. Types?

Synonyms: Ginglymostoma caboverdianus Capello, 1867: 167. Cape Verde. Three syntypes according to Eschmeyer (1998), but status of these types otherwise uncertain.

Other Combinations: Nebrius cirratum (Bonnaterre, 1788); Scyllium cirratum (Bonnaterre, 1788).
FAO Names: En - Nurse shark; Fr - Requin nourrice; Sp - Gata nodriza.


Fig. 161 Ginglymostoma cirratum


FRONTO-LATERAL VIEW OF HEAD


UPPER AND LOWER TEETH

Field Marks: Snout broad, bluntly rounded and very short; nasoral grooves present, but not circumnarial, nostrils with relatively long barbels, eyes well posterior to mouth; spiracles minute; fourth and fifth gill openings close-set, nearly overlapping; dorsal fins broadly rounded, first much larger than second; caudal fin more than $25 \%$ of total length. Colour yellow to greyish or brown above, lighter below, without spots or saddles except in young.

Diagnostic Features: As for genus.
Distribution: Eastern Atlantic: Gabon to Senegal, and Cape Verde Islands, rarely to Bay of Biscay, France. Western Atlantic: Rhode Island, USA, to southern Brazil, most common in the Caribbean. Eastern Pacific: Gulf of California to Peru.

Habitat: A nearshore, coastal mostly tropical shark usually found around coral and rocky reefs, and in soft sediment channels and sand flats between mangroves. These sharks appear to be most active at night when foraging, but during daylights hours are often seen resting on the bottom. They also show a high degree of site fidelity during the day resting in caves and crevices, and are extremely social sharks, as they will aggregate in considerable numbers. These sharks may occur in quite shallow water, less than 1 meter deep, but are more common from 10 to 40 m deep, with a maximum depth of at least 130 m .

Biology: Development is viviparous with young nourished on yolk-sac only, litter size 21 to 34 ; a report of 50 young in one litter appears based on erroneous data. Gestation is about 5 to 6 months, with females giving birth every other year. Multiple paternity has been reported for this species with up to at least four males fathering offspring from a single litter. Nurse sharks show a high degree of site fidelity with males returning annually to mate at specific locations, while females only return to these same sites every other year. Age at maturity is estimated at 10 to 15 years for males and 15 to 20 years for females.

Nurse sharks feed primarily on bottom invertebrates such as crustaceans, molluscs, sea urchins, and reef dwelling bony fishes; they occasionally have been found to have stingrays in their stomach. The jaws and buccal cavity of these sharks design for powerful suction feeding which allows them to extract thick-shelled bivalves and gastropods from their shell. These sharks appear to be opportunistic nocturnal feeders consuming prey items, such as bony fishes that are resting at night or invertebrates that are active at night.

Size: Maximum length 308 cm ; unconfirmed records of this shark to 430 cm are likely incorrect; males mature at 210 to 220 cm , maximum length at least 257 cm ; females mature at 220 to 240 cm , maximum length over 259 cm . Size at birth is 27 to 30 cm .

Interest to Fisheries and Human Impact: Fisheries for this shark are limited and mostly artisanal. However, the species appears to show strong site fidelity, possibly making it vulnerable to local, intensive fishing pressure. The meat is consumed fresh or salted by humans, but its thick skin is also used to make leather products. In the North Atlantic (Areas 21 and 27) these sharks are rare to uncommon and of no interest to fisheries other than being caught on occasion as bycatch.
Nurse sharks are considered harmless to humans given their slow almost lethargic behaviour, relatively small mouth and teeth. However, there have been a few unprovoked, non-fatal attacks (often provoked) with this shark biting divers and swimmers. These sharks have also become a popular attraction for ecotourist divers throughout the Caribbean, Florida (USA), and the Bahamas.
The nurse shark is a common, popular species in many public aquaria throughout North America and Europe. They are very hardy and have been maintained in captivity for at least 25 years. Nurse sharks given their hardiness in captivity are frequently used for experimental behavioural and physiological research studies.

The global conservation status for Ginglymostoma cirratum is Data Deficient due to a lack of information on its life history. Regional assessments for the Western North Atlantic is Least Concern, but for its population off Central and South America it has been assessed as Vulnerable due to potential threats throughout this area.

## Local Names: None.

Literature: Bigelow and Schroeder (1948); Clark and von Schmidt (1965); Cadenat and Blache (1981); Compagno (1984, 1988, 2001); Quéro in Whitehead et al. (1984b); Carrier and Luer (1990); Carrier, Pratt, and Martin (1994); Carrier and Pratt (1998); McEachran and Fechhelm (1998); Castro, Woodley, and Brudek (1999); Saville, Lindley, Maries, Carrier, and Pratt (2002); Pratt and Carrier (2001, 2007); Carrier, Pratt, and Castro (2004); Rosa et al. (2006); Gibson et al. (2008).

### 2.4.2 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 North Atlantic Genera: 1.

FAO Names: En - Whale sharks; Fr - Requins baleine; $\mathbf{S p}$ - Tiburones ballena.
Field Marks: See species account below.
Diagnostic Features: Body moderately stout, fusiform-shaped, with prominent longitudinal ridges along its upper flanks. Head broad and strongly flattened; snout indistinct, truncated. Eyes minute, diameter less than one-tenth nostril length, situated laterally on head just posterior to angle of mouth, and without moveable upper eyelids or subocular pockets and ridges. Spiracles moderate-sized, about equal to or smaller than eyes, without raised external rims, and located behind and slightly above eye level. Gill openings very long, relatively straight vertically, high up on sides, widely separated ventrally, fourth and fifth gill openings not overlapping; internally with uniquely modified transverse lamellae crossing each gill opening to form filter. Nostril barbels rudimentary with no circumnarial folds and grooves; nasoral grooves very short and shallow. Mouth terminal or nearly so on head, transverse, very large, and situated in front of eyes; lower lip not trilobate, without lateral orolabial grooves connecting edge of lip with medial ends of lower labial furrows, no longitudinal symphysial groove in chin. Lower labial furrows short, extending only slightly beyond corner of mouth, not connected medially by a mental groove or groove and flap. Teeth similar in upper and lower jaws, minute, hook-shaped, with a strong medial cusp, no lateral cusplets, and 10 to 15 functional rows along dental band; labial roots absent; teeth osteodont with partially filled crown and a plug of osteodentine; tooth counts 300 or more rows on upper and lower jaws. Precaudal tail length shorter than body. Caudal peduncle with strong lateral keels and a distinct precaudal pit above, but absent below. Dermal denticles small, slightly overlapping, erect, with long medial cusp flanked by 1 to 2 lateral cusplets. Pectoral fins falcate, very large, length about $15 \%$ of total length; plesodic with fin radials expanded into fin web. Pelvic fins smaller than first dorsal fin; anterior margin length only about 0.3 times anterior margin of pectoral fins; size about equal to subequal second dorsal and anal fins. Dorsal fins subtriangular, with rounded apices, dissimilar in size; first dorsal fin very large, much larger than second, set posteriorly on body, with origin of first dorsal fin well anterior to pelvic-fin bases. Second dorsal fin about onethird size of first, its insertion about over anal-fin base. Anal fin similar in shape and size to second dorsal fin, origin about opposite anterior third of second dorsal-fin base. Caudal fin very large, crescent-shaped, upper lobe less than one-third of total length, lower lobe less than one-half length of upper; terminal caudal-fin lobe indistinct; upper lobe in very small juveniles much longer than lower lobe. Vertebral counts: total vertebral counts 153 to 174, monospondylous vertebral count 42 , diplospondylous precaudal vertebral count 40 , precaudal vertebral counts 81 to 82 , caudal vertebral count 92 . Valvular intestine of ring type with 68 to 74 turns. The largest fish in the world, reaching a maximum length of 1800 cm . Colour: unique checkerboard pattern consisting of prominent white or yellow spots between vertical and horizontal stripes offset by a background colour that ranges from dark grey to bluish or brown above, becoming white below.

Distribution: A wide-ranging circumglobal species occurring in most tropical and warm temperate seas.
Habitat: The whale shark is an oceanic and coastal species often observed at or near the surface from close inshore, including bays and lagoons, to far offshore. In nearshore waters it is usually found where the temperate is between $18^{\circ} \mathrm{C}$ and $30^{\circ} \mathrm{C}$, with a preference for mixing layers of cool upwelled oceanic water.

Biology: See species account.
Interest to Fisheries and Human Impact: See species account.

## Local Names: None

Remarks: The family Rhincodontidae has only a monotypic genus with a single species, the wide ranging and charismatic whale shark, Rhincodon typus. Andrew Smith (1828) described the new genus and species in a Cape Town newspaper, basing his description on a specimen that was stranded on a beach in Table Bay, South Africa. A new family (Rhinodontes) was erected for this shark by Müller and Henle (1839) using a variation on the generic spelling of Rhinodon. The spelling of the family name has several spelling variants, much of it do to variations in the spelling of the genus, which has caused confusion in the literature. The International Commission on Zoological Nomenclature (1984, Opinion 1278) finally stabilized the spelling of the family, Rhincodontidae, and genus, Rhincodon.

The family, genus, and species accounts are modified and updated after Compagno (2001) who also provides a detailed account on the history of the spelling and usage of the various scientific names for this shark.

The family has a single genus and species, which occurs all major oceans including the North Atlantic.
Literature: Bigelow and Schroeder (1948); Compagno (2001); Ebert (2003); Last and Stevens (2009).

## Rhincodon Smith, 1829

Genus: Rhincodon Smith, 1829, Zool. J., 4: 443. Placed on the Official List of 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 North Atlantic Species: 1.

Synonyms: None.
Field Marks: See species account below.
Diagnostic Features: See family account above.
Local Names: None.

## Rhincodon typus Smith, 1828

Rhincodon typus Smith, 1828, S. African Comm. Adv., 3(145): 2. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN 9855, 4600 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.

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


Fig. 163 Rhincodon typus

Field Marks: This is an unmistakable shark with its unique checkerboard colour pattern of horizontal and vertical stripes with white or yellow spots, offset by a bluish to grey background colour, a broad flattened head, wide terminal mouth, long vertical gill slits, prominent longitudinal ridges on its back and large semicrescent caudal fin.

Diagnostic Features: See family Rhincodontidae above.
Distribution: Eastern Atlantic: Azores, Senegal, Mauritania, Cape Verde Islands, Gulf of Guinea, Gabon, and southward to South Africa. Western North Atlantic: south of Nova Scotia, Canada to the Gulf of Maine and New York to Florida and the Gulf of Mexico.

Habitat: The whale shark is an oceanic to coastal species found in most tropical and warm temperate seas where it is often seen at or near the surface from close inshore, including bays and lagoons, to far out at sea. It is usually found in nearshore waters where the temperature is between 18 and $30^{\circ} \mathrm{C}$, but will


LATERAL VIEW OF HEAD occasionally migrate to higher latitudes where the water temperatures are cooler. They are known to make deep dives, to over 700 m , to where the water temperature may drop below $10^{\circ} \mathrm{C}$. In the Azores these sharks often associate with schools of tuna that aggregate close to the whale shark.

Biology: Viviparous without a yolk-sac placenta, with litters of at least 300 from one specimen, making it one of the most fecund species of cartilaginous fish. Embryos are retained within a leathery egg case inside the uterus, emerging from this egg case just prior to birth. Whale sharks do not appear to have a defined birthing season as newborns are found nearly year-round in the tropics.
Whale sharks grow quite rapidly their first several years of life, averaging 20 to 30 cm annually. A single newborn held in captivity more than doubled its length in 90 days growing from 60 to 126 cm . Males mature in about 20 years and live at least 31 years or more. Female age at maturity is uncertain, but immature females at 800 to 900 cm are estimated to be 27 years old.
Whale shark diet includes a variety of zooplanktonic organisms, including copepods, jellyfish, invertebrate larvae, pelagic crabs, euphasiids, squid, and small to medium size pelagic fishes including anchovies, sardines, mackerels, small tunas, and albacore. When targeting dense patches of their primary prey they at times forage in groups, often with other fishes and seabirds, numbering in the hundreds. Whale sharks will often aggregate when other fishes or corals are spawning, feeding on the gametes as they are being released. These sharks will often appear in the same locations seasonally, especially when plankton patches, spawning activity or other ecological processes concentrate potential food resources. Whale sharks are suction feeders and rather than passively swimming to ingest prey items, they actively draw in water at a high velocity by suction. They have dense gill rakers that act as sieves to screen out prey items as water passes over their gill rakers. In captivity these sharks will ingest 8 to $11 \%$ of their body weight per week.
Adult whale sharks have few known predators, with orcas known to prey on adults; however, small juveniles are more vulnerable and have been fed upon by blue shark and blue marlin.
Whale sharks are highly mobile and will travel thousands of kilometre, often migrating in groups of similar size and sex, to specific locations for feeding. Their movement patterns seem to be correlated with oceanographic features such as seamounts and boundary currents where their preferred food items are abundant. When migrating in groups, these groups
may number from a few individuals up to several hundreds at a time. Migrating whale sharks average about 25 km per day, but may move up to 100 km in a single day. Adults have been known to migrate over $11,000 \mathrm{~km}$, but smaller juveniles tend to show more localized movement patterns.

Size: An enormous shark, the largest living fish in the world reaching up to 1800 cm or more in length. Males mature at 850 to 900 cm , and females at 1000 cm or more. Size at birth is from 55 to 64 cm total length.

Interest to Fisheries and Human Impact: Whale sharks are still fished in some areas of the world for their flesh as food for human consumption and for their fins, which bring a relatively high value. However, they have also become a popular ecotourist attraction in many areas of the world where they are known to congregate. In the North Atlantic, whale sharks are relatively uncommon.


Fig. 164 Rhincodon typus
Known distribution

This shark has been maintained in captivity at several aquariums around the world. Once they have acclimatized, mainly by learning how to feed in their new surroundings, to the tank they appear to do very well.

Conservation status is Vulnerable. These sharks are a protected species U.S. Atlantic and Gulf of Mexico waters, and in 2003 they were added to the Convention on International Trade in Endangered Species (CITES) Appendix II for protection.

Local Names: Tubarâo baleia, Pintado (Azores).
Literature: Bigelow and Schroeder (1948); Compagno (1984, 2001); Eckert and Stewart (2001); Joung et al. (1996); Chang, Leu, and Fang (1997); Clark and Nelson (1997); Santos, Porteiro, and Barreiros (1997); McEachran and Fechhelm (1998); Wintner (2000); Ebert (2003); Ebert et al. (2004); Norman (2005); Turnbull and Randell (2006); Graham and Roberts (2007); Nelson and Eckert (2007); Stevens (2007); Brunnschweiler et al. (2009); Last and Stevens (2009); Ebert and Winton (2010); Rohner et al. (2011); Rowat and Brooks (2012).

### 2.5 Order LAMNIFORMES - Mackerel sharks

Order: Lamniformes Garman, 1885, Bull. Mus. Comp. Zool. Harvard, 12(1): 30 (emendation by Compagno 1984 of "group" Lamnae Garman, 1885).

## Number of Recognized North Atlantic Families: 5.

FAO Names: En - Mackerel sharks.
Field Marks: External appearance of several members of this group each appears to be unique and unrelated to each other, but they are united by several features including a short to moderately long pointed snout, eyes usually lateral on the head (except dorsal lateral on Carcharias), eyes without a nictitating membrane, spiracles if present are usually very small and located behind the eyes, no nasal barbels, a large to very large mouth extending well behind the eyes, five paired gill openings with the last two in some groups occurring above the pectoral-fin origins, two spineless dorsal fins, and an anal fin. Colour may range from blue-grey, light to dark brown, reddish, yellowish, or even pink above, usually lighter below; some species may have spots or light and dark blotches, and with darker or lighter fin edges.

Diagnostic Features: Body shape cylindrical, fusiform, or somewhat compressed, but not flattened or ray-like; body stout to very slender, and firm or very soft and flabby. Head conical to moderately depressed, relatively short to very long, but not expanded laterally. Snout relatively short to extremely long, flattened and blade-like. Eyes nearly circular, relatively small to very large, located lateral on head, except dorsolateral on Carcharias, without nictitating lower eye membrane. Nostrils without barbels, nasoral or circumnarial grooves, and separated from mouth; anterior nasal flaps short and not reaching mouth. Gill openings numbering 5 on each side of head; length short to extremely long, nearly encircling the head; posteriormost two-gill openings located just anterior to or above pectoral-fin origins. Spiracles, if present, very small and situated behind and level to eyes. Mouth very large, broadly rounded and highly protrusible. Labial furrows very small or absent. Teeth weakly to strongly differentiated along jaws, usually with a gap or small intermediate teeth between anterior and lateral teeth of upper jaw; tooth counts number from 19 to over 200 rows in upper jaw, and 20 to over 200 rows in lower jaw. Caudal peduncle with lateral keels, depending on the family, present or absent, if present may number 1 or 2; precaudal pits variably present or absent depending on the group. Dermal denticles covering entire body, small and relatively smooth or enlarged, very rough and thorn-like. Pectoral fins small to very long, and broadly rounded to moderately angular. Pelvic fins small to moderately large. Two spineless dorsal fins; first dorsal fin may be much larger than second dorsal fin, very high, erect, and nearly triangular or small, rounded and similar in size to second; first dorsal fin originating over abdomen, well in front of pelvic-fin origins. Second dorsal fin may be minute, much smaller than first dorsal fin or similar in size. Anal fin present; size may be similar to second dorsal fin or possibly larger depending on species. Caudal fin with long to extremely long upper dorsal lobe and a strong to absent ventral lobe. Vertebral counts: total vertebral counts 107 to 477, precaudal vertebral counts 50 to 126, and caudal vertebral counts 55 to 356 . Intestinal valve of conicospiral type, with 18 to 55 turns. Size small, from less than 100 cm in length, to gigantic, up to 1000 cm in length. Colour: dorsal surface ranges from a pinkish white, bluish, grey, grey-brown, brown or blackish, ventral surface may be similar in colour to dorsal surface or lighter to white; dark spotting or darker and lighter blotches may be present on some species and may vary depending on size and stage of development. Reproductive mode yolk-sac viviparity with oophagy and, in some species, adelphopahgy (intra-uterine cannibalism).

Distribution: Circumglobal from cold temperate to tropical seas, with some species occurring in polar seas.
Habitat: Mackerel sharks occur from close inshore, in shallow bays and estuaries to the outer coast, and the open ocean. They are found over sandy beaches, rocky and coral reefs, and in pelagic waters far from landmasses, and from the surface to over 1600 m deep and over bottom depths of over 5000 m . No mackerel sharks are known to occupy freshwater habitats, such as rivers and lakes.

Biology: Mackerel sharks, with a few exceptions, are highly active, fast swimming, migratory sharks, with most being quite wide-ranging in their geographic distribution. They are viviparous in their reproductive mode, but have uterine cannibalism with the young embryos consuming uterine eggs (oophagy) or feeding on other embryos (adelphophagy). The reproductive cycle of most species is unknown, although in some species they are known to make long distance migrations to specific nursery areas. The number of young per litter is not well known, but appears to be relatively small, and depending on the species, may only be from 2 to 16 young per cycle. Depending on the species maturity is attained in 4 to 5 years with a maximum estimated longevity of 20 to 30 years. The diet of these sharks may range from small planktonic organisms to invertebrates, large bony and cartilaginous fishes, and even marine mammals, reptiles, and sea birds.

Interest to Fisheries and Human Impact: Some mackerel shark species are the subject of important target and nontarget fisheries worldwide, especially members of the families Alopiidae and Lamnidae. Other groups, Cetorhinidae and Odontaspididae, were the subjects of intense fisheries previously, but they are largely protected in many areas of the world since their populations have declined from previous fisheries exploitation.

Several species, particularly the white shark (Carcharodon carcharias) is well known to attack humans engaged in ocean activities including swimming, diving, surfing, kayaking, and boating, among other activities. In temperate waters the white shark has been implicated in more attacks on people than any other shark species. This is most likely due to its being more
easily recognized and a lack of other species, mainly Carcharhinidae species that tend to be more prominent in tropical seas. In recent years, the white shark and shortfin mako shark, among other lamnoids, have become popular ecotourist attractions for thrill seeking cage divers. The sand tiger shark (Carcharias taurus) is another popular species and one that has been maintained in public aquaria for decades. Small white sharks have recently been maintained at the Monterey Bay Aquarium, California (USA), for short time periods, of up to about six months. However, they usually out grow their surroundings and are released back into the wild.

The conservation status of mackerel sharks have been a concern for several species, but some such as the white shark and basking shark have due to their high-profile have received considerable protection through the Convention on International Trade of Endangered Species (CITES) and more regional protective measures. The conservation status of other poorly known species such as the goblin (Mitsukurina owstoni), megamouth (Megachasma pelagios), and bigeye sand tiger (Odontaspis noronhai) sharks are uncertain due to a lack of information on their populations and basic biological information.

Local Names: None.
Remarks: The present account is modified from, and follows Compagno (1984, 1999, 2001) in recognizing seven families of which five occur in the North Atlantic. See Compagno (2001) for detailed discussion of the order.

## Key to Families Occurring in the North Atlantic:

1a. Snout extremely elongated, flat, and blade-like Precaudal pits and ventral lobe absent (Fig. 165).

## family Mitsukurinidae

1b. Snout short to moderately long, but not greatly elongated or blade-like, and broadly rounded. Precaudal pits and ventral caudal lobe present $\qquad$ . 2

2a. Caudal fin about as long as trunk of body (Fig. 166).
family Alopiidae

2b. Caudal fin much shorter than trunk of body
3

3a. Upper precaudal pit present; lower pit and lateral keels absent; caudal fin heterocercal, not crescent shaped (Fig. 167)
family Odontaspididae

3b. Upper and lower precaudal pits and strong lateral keel present; caudal fin crescent shaped. $\qquad$ . 4

4a. Teeth large, pointed or triangular and blade-like; gill slits large, but not extending onto dorsal surface of head or nearly across throat, and without internal gill rakers (Fig. 168a \& 168b) . . . . . . family Lamnidae

4b. Teeth minute, hook shaped, and not blade-like; gill slits extremely large, extend dorsally onto surface of head and first nearly extending across the throat, and with internal gill rakers (Fig. 169a \& 169b) . .
family Cetorhinidae


Fig. 165 Mitsukurina


Fig. 166 Alopias


Fig. 167 Odontaspis


Fig. 168 Lamna


Fig. 169 Cetorhinus

### 2.5.1 Family ODONTASPIDIDAE

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

Type genus: Odontaspis Agassiz, 1838.

## Number of Recognized North Atlantic Genera: 2.

FAO Names: En - Sand tiger sharks; Fr - Requins de sable; Sp - Solrayos, Toros.
Field Marks: Large fusiform-shaped sharks, with a conical snout, large subterminal mouth, teeth large with slender cusps and lateral cusplets, eyes small to moderately large without nictitating membranes, five moderately long paired gill slits that do not extend onto the dorsal surface of head, two large spineless dorsal fins, an anal fin, upper precaudal pit present, lower precaudal pit absent, caudal fin asymmetrical, upper margin less than one-third total length.

Diagnostic Features: Body fusiform, moderately stout, and firm. Head relatively short to moderately long; snout short to moderately long, conical and pointed, not greatly elongated, or flattened. Eyes are small to moderately large, without nictitating membranes, diameter length 1.4 to $4.1 \%$ precaudal length. Spiracles present, but very small. Gill openings relatively long, but not extending onto dorsal surface of head; first gill opening 6.2 to $9.2 \%$ precaudal length; fifth gill openings anterior to pectoral-fin bases; no internal gill rakers. Nostrils subterminal, entirely separate from mouth, no nasoral grooves, and anterior margins without barbels. Mouth large, broadly arched, subterminal on head; jaws strongly protrusible. Teeth large, awl-shaped, with lateral cusplets present; 2 to 3 rows of large anterior teeth on each side of jaw followed by 1 to 5 rows of smaller intermediate teeth; tooth counts 34 to 56 upper jaw, 36 to 46 lower jaw. Caudal peduncle not greatly compressed or laterally expanded; upper precaudal pit present, but without lower precaudal pit or precaudal keels. Dermal denticles smooth and moderately large; crowns flattened and with small ridges and cusps; flank denticles posteriorly directed. Pectoral fins broadly angular and moderately long, origin posterior to fifth gill opening. Pelvic fins relatively large, similar in size to first dorsal fin. Dorsal fins large, angular, relatively high and erect; fin spines absent; first dorsal fin originates over or posterior to pectoral-fin free rear tips. Second dorsal and anal fins size similar to or smaller than first dorsal fin; second dorsal and anal fins with broad non-pivoting bases. Caudal fin asymmetrical, upper lobe moderately long, less than one-third length of precaudal length, ventral lobe much shorter. Vertebral counts: total vertebral counts 156 to 183 , precaudal vertebral counts 80 to 95 , diplospondylous caudal vertebral counts 71 to 88 . Intestinal valve with 28 to 34 turns. Size large with adults to at least 450 cm total length. Colour: light grey, grey-brown, to dark reddish brown or black above; ventral surface lighter or similar to dorsal colour; spots present on some species.

Distribution: Wide-ranging, but patchily distributed, in most warm-temperate and tropical waters.
Habitat: Sand tiger sharks occur mostly in tropical to warm-temperate seas and depending on the species inhabit nearshore coastal areas including bays and harbors, but also offshore, on outer continental shelves, upper slopes, and on seamounts down to 1600 m . The bigeye sand tiger (Odontaspis noronhai) may be oceanic in the epipelagic and possibly the mesopelagic zone. These are relatively slow moving, but active sharks.

Biology: Viviparous with oophagy, with litters of possibly only two very large young, but little else known about the reproductive biology of this shark family. The diet of sand tiger sharks mostly consists of other elasmobranchs, bony fishes, cephalopods, and crustaceans.

Interest to Fisheries and Human Impact: Most species within this family tend to occur in deeper water and have a very scattered distribution, and as such are generally not important in fisheries other than being taken on occasion as bycatch. Virtually nothing is known about the population trends for Odontaspis ferox or O. noronhai. However, Carcharias taurus is an exception in that it occurs mostly in nearshore waters, may be quite common where it occurs, and has been targeted by commercial and recreational fishers in some areas or has been subjected to eradication programs.

Despite their fearsome, toothy appearance and large size, these sharks are generally not aggressive towards swimmers or divers and in fact $\boldsymbol{C}$. taurus and $\boldsymbol{O}$. ferox have become the popular subjects for ecotourism by divers in Australia, Mediterranean Sea, South Africa, the east coast of the U.S.A. and in the eastern Pacific off Malpelo Island. There have been a few incidents of people being bitten by $\boldsymbol{C}$. taurus, but no reported incidents by either of the Odontaspis species. Carcharhias taurus is also a common and popular species in public aquaria given their hardiness and longevity.

The conservation status for some of these sharks is considered Vulnerable since species have been experienced declines due to overfishing.

Local Names: Sand tigers, Nurse sharks, and Sand sharks.
Remarks: The family has two genera and three species of which two species occur in Areas 21 and 27. A third member of this family (bigeye sand tiger, Odontaspis noronhai) is known from just south of the present areas, central Atlantic, but may eventually be found to occur within Areas 21 and 27 . The family account is modified after Compagno (2001).

A detailed discussion of the nomenclature for this family is given in Compagno (2001).
Literature: Garman (1913); Bigelow and Schroeder (1948); Compagno (1973, 1984, 1999, 2001); Quéro in Whitehead et al. (1984a); Ebert (2003); Last and Stevens (2009).

## Key to North Atlantic Genera:

1a. First dorsal fin similar in size to second dorsal and anal fins, and closer to pelvic-fin bases than pectoral-fin bases; snout short and slightly depressed; three rows of large upper teeth on each side of jaw symphysis (Fig. 170)

Carcharias



Fig. 170 Carcharias


Fig. 171 Odontaspis

## Carcharias Rafinesque, 1810

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

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

## Number of Recognized North Atlantic Species: 1.

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

Field Marks: See species account below.
Diagnostic Features: Body fusiform-shaped, moderately stout. Head moderately flattened; snout short, somewhat flattened and conical, but not bulbous; preoral length 3.2 to $4.7 \%$ of total length and 0.3 to 0.5 times mouth width. Eyes dorsolateral on head, with prominent lateral head ridges ventrally, relatively small and rounded, diameter about 0.9 to $1.4 \%$ of total length. Spiracles very small, about level with upper eye margin and posterior by a distance about equal to upper eye margin length. Gill openings relatively large, but not extending onto dorsal head surface; fourth opening largest, fifth shortest. Nostrils transverse, with small rounded flap on inner anterior margin. Mouth broadly rounded, subterminal on head. Labial furrow prominent on lower jaw, but indistinct (especially when mouth closed) on upper. Teeth awl-shaped with long central cusp, flanked on either side by a smaller cusplet, shape similar in both jaws; upper jaw without medial teeth, but anterior teeth with three rows of large, stout, broad-tipped cusps, flanked by short, strongly hook-shaped
cusplets; lateral teeth compressed, blade-like, with flattened cusps; posterior teeth molariform, with cusps and cusplets greatly reduced or absent, and strongly differentiated from lateral teeth. Tooth counts 36 to 54 upper jaw, 32 to 46 lower jaw. Caudal peduncle with well-defined upper precaudal pit, but without lower precaudal pit; without lateral keels. Dermal denticles somewhat broad and loosely spaced, with 3 ridges, the medial ridge very prominent. Pectoral fins relatively large, length nearly as broad as width, anterior margin nearly straight; apices rounded. Pelvic fins about as large as first dorsal fin, with origin slightly posterior to first dorsal-fin base. First dorsal fin originates closer to pelvic-fin bases than pectoral-fin bases. Second dorsal fin nearly as large as first. Anal fin similar in size to dorsal fins, origin about under midpoint of second dorsal-fin base. Vertebral counts: total vertebral counts 156 to 186, precaudal vertebral counts 80 to 97 , caudal vertebral counts 71 to 85 . Spiral valve turn count 29 to 30 . A large shark with adults to 320 cm or more in length. Colour: light brown to bronzy above, lighter below, often with dark reddish or brown spots scattered on body; irises of eyes light green.

Local Names: See species account below.

## Carcharias taurus Rafinesque, 1810

Carcharias taurus Rafinesque, 1810, Caratt. gen. sp. anim. piant. Sicilia, Palermo, pt. 1: 10, pl. 14, fig. 1. Holotype unknown; type locality, Sicily, Mediterranean Sea. Placed on the Official list of Specific names in Zoology by the International Commission on Zoological Nomenclature 91987, Opinion 1459.4, Bull. Zool. Nomencl., 44(3): 216.

Synonyms: Squalus americanus Mitchell, 1815: 483. No types known according to Eschmeyer (1998). Type locality, New York. Not Squalus americanus Gmelin, 1788, = Dalatias licha (Bonnaterre, 1788). Squalus macrodous Mitchell, 1818: 328. Replacement name for S. americanus Mitchell, 1815. Squalus littoralis Lesueur, 1818: 224. Holotype: 91 cm specimen, New York, possibly not extant. Squalus Iittoralis Mitchell, 1818: 328. Types unknown. Apparently a junior homonym of S. Iittoralis Lesueur, 1818 according to Eschmeyer (1998). Carcharias griseusAyres, 1842: 58-59 (nomen nudum); Ayres, 1843a: 288 (no distinguishing features), Ayres, 1843b: 293, pl. 12, fig. 4. Type locality, Long Island, New York. No types according to Eschmeyer (1998). Odontaspis americanus Abbott, 1861: 400 (new combination validates name?).

Other Combinations: Eugomphodus taurus (Rafinesque, 1810), Odontaspis taurus (Rafinesque, 1810), Triglochis taurus (Rafinesque, 1810), Synodontaspis taurus (Rafinesque, 1810), Carcharias Iittoralis (Le Sueuer, 1818), Odontaspis griseus (Ayres, 1843), Eugomphodus griseus (Ayres, 1843), Odontaspis littoralis (Le Sueuer, 1818), Eugomphodus littoralis (Lesueur, 1818), Carcharias americanus (Mitchell, 1815).

FAO Names: En - Sand tiger shark; Fr - Requin taureau; $\mathbf{S p}$ - Toro bacota.



UNDERSIDE OF HEAD


UPPER AND LOWER TEETH

Fig. 172 Carcharias taurus

Field Marks: A large stout bodied shark with a short, slightly flattened snout, mouth long with large distinctly prominent teeth, similar sized dorsal and anal fins, first dorsal fin is closer to pelvic fins than pectoral fins, upper precaudal pit present, lateral keels absent, and an asymmetrical caudal fin. Dorsal surface colour light brown to bronzy, sometimes with scattered small brown or reddish spots; ventral surface lighter.

Diagnostic Features: See genus Carcharias above
Distribution: Eastern Atlantic: unknown from Area 27, but does occur in the Mediterranean Sea, off the Canary Islands, Morocco, Western Sahara, Mauritania, Sao Tome and Principe, and the Cape Verde Islands, and south to Namibia and South Africa. Western Atlantic: off New Brunswick, Canada and the Gulf of Maine southwards to Florida and the Gulf of Mexico and from southern Brazil to Argentina. Elsewhere, found scattered throughout the IndoWestern Pacific, but not in the central or eastern Pacific.

Habitat: A common nearshore, coastal shark of warm temperate and tropical seas where it occurs. It occurs in bays and estuaries, on sandy or muddy areas, and on rocky or coral reefs. These sharks may occur quite close inshore, in water less than one meter deep or offshore down to at least 191 m , but they appear to be most common between 15 and 25 m depth. Although these sharks are usually seen in association with reefs they occasionally make excursions into the midwater or to the surface.


Fig. 173 Carcharias taurus
Known distribution

Biology: Reproductive mode is oophagous, but is unique among lamnoids in exhibiting adelphophagy; a form of oophagy in which the largest developing embryo in each uterus consumes all the smaller embryos and then relies on maternal production of unfertilized eggs for the remainder of their development. This results in a single very large embryo, approximately 100 cm in length, developing within each uterus. The reproductive cycle is thought to be two years in the Western North Atlantic, but some studies have suggested it may only be one year. Courtship and mating has been observed. In North American waters mating is believed to occur between late March and April, with birth occurring after a 9 to 12 month gestation period and from about December to March. Nursery areas are not well defined along the Atlantic coast of North America, but juveniles appear to be abundant in Delaware Bay, and other estuaries, from March-April through October, with peak abundance in June.
Age at maturity has been estimated at 9 to 10 years for females and 6 to 7 years for males, with females and males reaching a maximum estimated age of 17 and 15 years, respectively. However, captive sand tigers have been found to live for more than 30 years in some public aquaria.
Sand tiger sharks have a broad diet consisting mostly of smaller sharks, batoids, teleosts, and invertebrates including cephalopods and crustaceans. A sevengill shark (Notorynchus cepedianus) was once found to have bite marks from a sand tiger, and sand tigers have been observed to bear the scars from white shark (Carcharodon carcharias) encounter. On rare occasions they have been found to have pinniped remains and wounds from this shark have been observed on dolphins. These sharks may form small groups and have been observed to feeding cooperatively on schooling fishes by herding them into a tight group and then consuming them.
Sand tiger sharks are often observed in small to moderate sized groups of up to 80 individuals. They are frequently observed in gullies, at the mouths of rocky caves, or on rocky reefs usually hovering motionlessly or slowly moving just above the bottom. These sharks are highly migratory, making seasonal movements to higher latitudes during the summer, but retreating to lower latitudes during the fall and winter. Sexual segregation seems to be pronounced with adult males and females forming separate aggregations along the coast.

Size: Maximum total length about 320 cm , with unconfirmed reports to 430 cm ; males mature at 190 to 195 cm with maximum length of at least 257 cm ; females mature at 220 to 230 cm and exceeding 300 cm or more in maximum length. Size at birth 85 to 105 cm total length.

Interest to Fisheries and Human Impact: Sand tiger sharks were once abundant in the coastal waters of Massachusetts, U.S.A. and supported a fishery in the early 1900's in Nantucket Sound, but they were fished out and none of these sharks has been caught since 1989 in this area. Furthermore, along the U.S. east coast these sharks experienced sharp declines in abundance due to increased exploitation during the 1980s and 1990s with some estimates suggesting that their abundance had declined by $90 \%$ from virgin stocks. However, a recent status report (Carlson et al., 2009) concluded that although previous estimates of declines were not as severe as once thought, the sand tiger shark should remain a species of concern due to their low productivity and inconclusive trends in abundance. The sand tiger shark is presently listed as a "Species of Concern" in North American waters. They are protected and managed in U.S. waters, since 1997, under the Highly Migratory Species Fishery Management Plan (FMP) whereby it is illegal to land this species or any parts of it either by commercial or recreational fishers.
Sand tiger sharks are a popular display species in public aquaria given their large size and fearsome appearance. Also these are relatively docile sharks that keep well in captivity as exhibited by individuals that have been maintained in large aquariums for over 30 years. Adults have been observed to mate and subsequently give birth in captivity.

The conservation status of the sand tiger shark is considered Vulnerable due to significant declines in its abundance in North American waters and elsewhere, especially in Australian waters. Its populations have been severely depleted in several locations due to fishing activities, both commercial and recreational, from spearfishing, and by protective beach netting. These various activities have lead to management restrictions limiting the capture and retention of this species.

Local Names: Sand shark, Sand tiger (USA); Lamio, Verdoun, Odontaspide taureau, Requin sable (France); Pez toro (Spain); Grauer Sandhai, Schnauzenhai, Stierhai (Germany); Sarda (Canaries).

Literature: Garman (1913); Bigelow and Schroeder (1948); Gilmore, Dodrill, and Linley (1983); Compagno (1984, 2001); Quéro in Whitehead et al. (1984a); Gilmore (1986, 1990, 1993); Governder, Kistnasamy, and van der Elst (1991); Gilmore (1993); Gordon (1993); Musick, Branstetter, and Colvocoresses (1993); Branstetter and Musick (1994); Gelsleichter, Musick, and Nichols (1999); Collette and Klein-MacPhee (2002); Musick and Ellis (2005); Goldman, Branstetter, and Musick (2006); Skomal (2007); Carlson et al. (2009); Last and Stevens (2009).

## Odontaspis Agassiz, 1838

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

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

## Number of Recognized North Atlantic Species: 1.

## Synonyms: None.

Field Marks: Large stout-bodied sharks with conical, bulbous snout, first dorsal fin closer to pectoral fins than to pelvic fins, and much larger than second dorsal and anal fins, caudal peduncle with precaudal pit present, lateral keels absent, and caudal fin asymmetrical but with a strong ventral lobe. Colour greyish brown, dark brown or blackish above, and depending on species ventral surface may be lighter; scattered dark brown to reddish spots may be present on some species.

Diagnostic Features: Body fusiform and stout, with head slightly to strongly depressed. Snout moderately long, conical, preoral length 0.8 to 1.2 times mouth width, 4.4 to $7.8 \%$ total length. Eyes small to moderately large, less than 3 to more than 4 times snout length, and about 1.6 to $2.8 \%$ total length. Teeth similar in both jaws; awl-shaped, with a long central cusp, flanked by 2 to 3 lateral cusplets. Tooth counts 34 to 56 upper jaw, 36 to 48 lower jaw. First dorsal fin closer to pectoral-fin bases than to pelvic fins. Second dorsal fin about one-half size of first dorsal fin. Anal fin smaller than second dorsal fin, origin over or posterior to second dorsal-fin origin. Vertebral counts: total vertebral counts 177 to 183, precaudal vertebral counts 95 to 98 , caudal vertebral counts 71 to 85 . Spiral valve turn counts 30 to 34 . Large sharks with adults to 450 cm in length. Colour: dorsal surface light grey, greyish-brown to dark brown or black; ventral may be lighter or same colour as dorsal surface; depending on species, scattered dark brown or reddish spots may be present and posterior edges of fins may be darker. Iris of eyes dark brown or black with lighter tones.

Local Names: Deepwater sand tigers.
Remarks: The genus as restricted here consists of two species, one of which occurs in the North Atlantic (FAO Areas 21 and 27), but the bigeye sandtiger shark (Odontaspis noronhai) is confirmed from the eastern and western Central Atlantic and may eventually be found to occur within these areas.

## Odontaspis ferox (Risso, 1810)

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

Synonyms: None.
Other Combinations: None.

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


Fig. 174 Odontaspis ferox

Field Marks: A large, stout-bodied shark with a conical to slightly flattened snout, a long mouth extending past the eyes, a first dorsal fin that originates over the pectoral-fin free rear tips, and is much larger than the second dorsal and anal fins. Teeth are prominent, long and narrow with a central cusp flanked by two or three smaller cusplets on each side. Coloration is grey, brownish grey or olive above, lighter below; some specimens have dark reddish spots scattered over their body.

Diagnostic Features: Head flattened, snout conical and relatively long. Eyes small, without nictitating membrane. Teeth awl-shaped, with long central cusp, flanked by two to three smaller cusplets on each side, similar in both jaws; upper intermediate two to five tooth rows much smaller than anterior or posterior tooth rows; tooth counts 46 to 56 upper jaw, 36 to 48 lower jaw. Dorsal fins subangular, weakly falcate; first dorsal fin much larger than second dorsal and anal fins. Anal-fin posterior margin strongly concave, height 4.6 to $6.0 \%$ total length. Caudal fin asymmetrical, with slight bump posterior to upper precaudal pit; ventral caudal lobe short, stout. Vertebral counts: total vertebral counts 177 to 183, precaudal vertebral counts 95 to 98 , caudal vertebral counts 71 to 85 . Spiral valve turn count 32 to 34 . A large shark with adults to 450 cm total length. Colour: light grey to grey brown above, lighter below, sometimes with dark reddish or brown spots scattered on the body; fin tips in young juveniles darker with black edges. A piebald colored specimen has been reported.

Distribution: Circumglobal, but patchily distributed in most temperate and tropical seas. Eastern North Atlantic records includes the Azores, Bay of Biscay, northern Spain and France, with the French specimen the most northern verified record at approximately $46^{\circ} \mathrm{N}, 04^{\circ} \mathrm{W}$. In 2012, a dead Odontaspis sp., presumably this species, was washed ashore on the coast of Normandy (western English Channel), but no living individuals have been reported this far north. More common in the Mediterranean Sea and off North Africa. Western North Atlantic not recorded from Area 21, but there is a record of this species from just south of Cape Hatteras, North Carolina ( $34^{\circ} 51^{\prime} \mathrm{N}, 75^{\circ} 26^{\prime} \mathrm{W}$ ).

Habitat: A large, wide ranging shark found in most warm-temperate and tropical seas on continental and insular shelves
and upper slopes. A survey of known records by Fergusson, Graham, and Compagno (2008) found smalltooth sand tiger sharks range from 10 to 883 m , but with most specimens being found at less than 300 m deep. There appears to be some segregation by size and depth as small juveniles, less than about 150 cm total length mostly occur between 300 and 600 m deep, while those over about 350 cm in length also tended to occupy a similar depth range. However, individuals over 150 cm to about 350 cm appear to be more common at shallower depths of less than 150 m . Although usually associated with mud, sand, or rocky reef bottom habitats, smalltooth sand tiger sharks appear to make excursions into the water column as demonstrated by individuals having been caught in midwater trawls within 70 to 500 m of the surface over water depths of 2000 to 4000 m . Water temperature where these sharks have been caught show a broad range from about $6^{\circ} \mathrm{C}$ to more than $20^{\circ} \mathrm{C}$.


Fig. 175 Odontaspis ferox
Biology: Very little is known about their reproductive cycle or litter size, as few mature females have been observed. The
 cm individual, teleosts, cephalopods, and crustaceans. There are no known predators on smalltooth sand tiger sharks, but an Isistius spp. bite wound was observed on one individual caught off the Canary Islands. Nothing is known about the movements of these sharks, but Fergusson et al. (2008) speculated that these sharks might move over large distances by following submarine ridges, adjacent island archipelagoes, or seamounts. Support for this comes from captures of these sharks in mid-ocean waters on or adjacent to deepsea ridges and seamounts.

Size: Maximum length to 450 cm ; males mature at 200 to 250 cm , with a maximum length of 344 cm ; females mature at 300 to 350 cm , and have a maximum length of 450 cm . Size at birth about 100 cm .

Interest to Fisheries and Human Impact: Smalltooth sand tiger sharks are taken incidentally in longline and trawl fisheries, but are too spottily distributed to be of interest for directed fisheries. However, with increasing deepwater fishing efforts these sharks may become more susceptible fishing pressure than is currently assumed. Currently, there are no estimates as to the numbers of these sharks that may be caught incidentally as bycatch.
Interestingly, in recent years smalltooth sand tiger shark aggregations in relatively shallow waters off Lebanon in the Mediterranean, Malpelo Island in the Eastern Pacific, and elsewhere have enabled SCUBA divers to regularly encounter these sharks.

The conservation status of this species is Vulnerable due to suspected declines in its population in the Mediterranean and Eastern North Atlantic. However, given the patchy distribution and occurrence of this species, much still remains to learn about its population structure.

Local Names: Bumpytail sandtiger shark; Ragged-tooth shark; Ragged-tooth sandtiger shark, Fierce shark (English); Salroig, Surraig, Solraig (Spain); Smalltooth sand tiger, Ragged-tooth shark; Tubarão-areia (Azores, Portugal); Schildzahnhai (Germany); Odontaspide féroce (France).

Remarks: Individuals of this species may or may not have dark scattered spots. This variation has lead to some authors to consider those individuals with spots to be a different species, Odontaspis herbsti, however, the presence of spots appears to reflect individual variation within a single species.

Literature: Garman (1913); Maul (1955); Compagno (1984, 2001); Quero in Whitehead et al. (1984); Santos, Porteiro, and Barreiros (1997); Sheehan (1998); Ebert (2003); Pollard et al. (2007); Fergusson, Graham, and Compagno (2008); Gibson et al. (2008); Last and Stevens (2009).

### 2.5.2 Family MITSUKURINIDAE

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

## Number of Recognized North Atlantic Genera: 1

FAO Names: En - Goblin sharks; Fr - Requins lutin; Sp - Tiburones duende.
Field Marks: See species account below.
Diagnostic Features: Body compressed, slender, very soft and flabby. Head nearly as long as the body trunk. Snout greatly elongated, flattened, blade-like. Eyes small. Gill openings short, with gill filaments partially exposed; no internal gill rakers; all gill openings anterior to pectoral-fin bases. Mouth large, broadly arched, with highly protrusible jaws. Teeth large, anteriors and laterals very narrow with a single cusp; shape similar in both jaws. Tooth counts 35 to 53 upper jaw, 31 to 62 lower jaw. Caudal peduncle compressed and without keels or precaudal pits. Dermal denticles small, with erect, narrow, spike-like cusps and ridges; cusps of lateral denticles pointing perpendicular to surface of skin making it rough. Pectoral fins small, broadly rounded at apices. Pelvic fins large, larger than dorsal fins. Dorsal fins small, rounded, nearly equal in size, but smaller than pelvic and anal fins. Caudal fin long, dorsal margin elongate but less than one-half body length, ventral lobe absent. Vertebral counts: total vertebral counts 122 to 125 , precaudal vertebral counts 53 to 56 , monospondylous vertebral count 37, diplospondylous caudal vertebral counts 66 to 69 . Intestinal valve of ring type with 18 to 23 turns. Size large, with adults to 550 to 620 cm in length. Colour: freshly caught specimens are a uniform pinkishwhite above and below, with bluish fins. After preservation this spectacular coloration fades to a uniform brown or grey.

Distribution: Wide-ranging, but patchily distributed in all major oceans. Most specimens have been reported from Japanese and Taiwanese (Province of China) waters.

Habitat: See Species Account.
Biology: See Species Account.
Interest to Fisheries and Human Impact: See Species Account.
Local Names: None.
Remarks: The taxonomic history of this uniquely distinct, monotypic family, its relationship to the fossil genus Scapanorhynchus and its relationship among the extant lamniform sharks is summarized by Compagno (1984, 2001). The family has a single genus and species, which occurs all major oceans including the North Atlantic.

Literature: Compagno (1984, 2001); Ebert (2003); Yano, Miya, Aizawa, and Noichi (2007); Last and Stevens (2009).

## Mitsukurina Jordan, 1898

Genus: Mitsukurina Jordan, 1898, Proc. Calif. Acad. Sci, ser. 3 (Zool.), 1: 199.
Type species: Mitsukurina owstoni Jordan, 1898, by monotypy.
Number of Recognized North Atlantic Species: 1.
Synonyms: None.
Field Marks: See species account.
Diagnostic Features: See family Mitsukurinidae above.
Local Names: Goblin sharks.

## Mitsukurina owstoni Jordan, 1898

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

Synonyms: Odontaspis nasutus de Bragança, 1904: 49, 104, pl 1, figs. 1-1c. Type locality, Mare de Sezimbra Portugal, 603 m. Types unknown according to Eschmeyer (1998). Mitsukurina nasutus Albuquerque, 1954-56, Port. Acta. Boil., ser. $B, 5: 82-83$, fig. 47.

Other Combinations: Scapanorhynchus owstoni (Jordan, 1898).
FAO Names: En - Goblin shark; Fr - Requin lutin; Sp - Tiburón duende.


Fig. 176 Mitsukurina owstoni
Field Marks: A distinctive, unmistakable shark with its soft flabby body, elongated, flattened, bladelike snout, relatively small eyes, and highly protrusible jaws. The teeth are long and narrow, with a single cusp; two spineless dorsal fins, similar in size and about equal to large rounded anal fin; the second dorsal fin originates posterior to the pelvic fins. Colour in life is a spectacular pinkish-white to white with bluish fins.

## Diagnostic Features: As for Family Mitsukurinidae.

Distribution: Eastern Atlantic from the Bay of Biscay (France) to Portugal, Madeira Islands, Senegal and southward to the Gulf of Guinea and South Africa. Western Atlantic not recorded from Area 21, but from the northern Gulf of Mexico, Belize (?), Guiana, Suriname, and French Guiana.

Habitat: The goblin shark is a poorly known deepwater shark found on the outer continental shelf and upper slopes down to at least 1300 m , but most records are from between 100 and 960 m deep. Although little is known about the habitat of this rare species in the North Atlantic, in Japanese waters subadults have commonly been taken between 100 and 350 m deep taken in the Tokyo Submarine Canyon. Although considered a deepwater shark, the goblin shark has been taken as shallow as 40 m or less. It has been previously speculated that these sharks may occupy more of a midwater habitat than is generally assumed based on their soft-flabby body, light body colour, and diet that includes midwater fishes and invertebrates. The capture of at least one individual in a midwater drift gill net between 12 and 47 m deep over water between 200 and 2000 m deep tends to support this view.

Biology: Virtually nothing is known about the biology of these sharks, although like all other lamniforms for which information is available, they are assumed to be oophagous and have small litters, but this needs to be confirmed. Nothing is known of the reproductive cycle of this shark. The vertebrae of these sharks as with other lamnoids have well defined banding patterns that would lend themselves well to ageing, but whether these band pairs are related to age or somatic growth is unknown. Although rare in the Eastern North Atlantic and most places where it occurs, in Japanese waters subadult goblin sharks appear to be most abundant in bottom set gillnets between October and April.
Goblin sharks feed mostly on bony fishes (Macrouridae, Stomiidae), cephalopods, and crustaceans, including midwater teleosts and crustaceans. Based on the prey items often consumed by these sharks it appears that they may forage off the bottom for food and may in fact occupy more of a midwater habitat than is generally assumed. The goblin shark jaws
are highly specialized (similar to some mesopelagic fishes) for rapid projection from the head. The rapid projection of the jaws from the head may allow this apparently sluggish, slow swimming shark to closely approach potential prey items and quickly subdue them. Compagno (2001) provides an overview of the jaw morphology and structure that enables this shark to rapidly project its jaws.

Size: Maximum total length at least 550 to 620 cm . Males possibly adult at 260 to 380 cm , female size at maturity uncertain, but likely at over 400 cm . Size at birth uncertain, but the smallest freeswimming individuals were an 81.7 cm male and a 92.8 cm female.

Interest to Fisheries and Human Impact: Interest to fisheries none, it is usually taken as bycatch of deepwater trawl and longline fisheries. The softbodied flesh of this species makes it a relatively undesirable species for human consumption. Where it is consumed it is utilized dried-salted. It jaws are highly sought after by collectors.


Fig. 177 Mitsukurina owstoni
$\square$ Known distribution

The goblin shark has been kept in public aquaria where it was observed that in life this shark swims with its jaws tightly retracted; this as opposed to most illustrations of this shark with its jaws protruded.

The goblin shark has been listed as Least Concern given its global distribution, deepwater habitat, and rarity in most locations where it has been captured. Also, most specimens that have been captured are subadult suggesting that adults occur outside the depth range where most fisheries take place.

Local Names: Nasuta, Tubarão-demónio, Tubarão-gnomo (Portugal).
Remarks: Despite its general rarity, there is one record of these sharks being caught in large numbers (between 100 and 300) over a two-week period in April 2003 by Taiwanese fishers from about 600 m depth. Prior to this apparent anomalous event, goblin sharks had never been reported from Taiwanese waters. The capture of such a large number of goblin sharks, some up to between 350 and 400 cm , followed a strong earthquake centered in the area. Jaws from these sharks were reportedly sold for between US $\$ 1,500$ and $\$ 4,000$ depending on the size and quality of the jaws.

Literature: Jordan (1898); Bean (1905); Garman (1913); Duffy (1997); Compagno (2001); Parsons, Ingram, and Havard (2002); Ebert (2003); Yano et al. (2007); Duffy, Ebert, and Stenberg in Gibson et al. (2008); Last and Stevens (2009); R. Graham (pers. comm.); D.A. Ebert (unpubl. data).

### 2.5.3 Family ALOPIIDAE

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

Type genus: Alopias Rafinesque, 1810.
Number of Recognized North Atlantic Genera: 1.
FAO Names: En - Thresher sharks; Fr - Renards; Sp - Zorros.
Field Marks: See generic account below.

Diagnostic Features: Body cylindrical, moderately stout, firm and not flabby. Head short, length one-third of total length; snout conical, moderately long, not flattened or blade-like. Eyes large to extremely large; diameter 1.8 to $4.3 \%$ precaudal length; nictitating membrane absent. Spiracles present, but small, pore-like. Gill openings relatively short, first opening 3.1 to $5.2 \%$ precaudal length, third to fifth openings over pectoral-fin bases; no gill rakers on internal gill slits. Nostrils small and with nasal flaps, but without barbels or oronasal grooves. Mouth small, broadly arched, below and extending posterior to eyes. Labial furrows variably present of absent. Teeth small, blade-like, with a single erect cusp; depending on species cusplets may or may not present; tooth counts 19 to 52 upper jaw, 20 to 51 lower jaw. Caudal peduncle moderately compressed laterally, with crescentic shaped upper and lower precaudal pits and no lateral keels. Dermal denticles very small, smooth, with small ridges and cusps pointed posteriorly on lateral flanks. Pectoral fins very long and narrow, anterior margins nearly straight to curved, apices broadly tipped to pointed. Pelvic fins very large, similar in size to first dorsal fin. Dorsal fins noticeably dissimilar on size; first dorsal fin very large, erect, high, and subtriangular. Second dorsal fin minute, low and with pivoting bases; base anterior to anal-fin base. Anal fin very small, similar in size to second dorsal fin. Caudal fin extremely elongated, dorsal lobe length about equal to precaudal length; ventral lobe much shorter. Vertebral counts: total vertebral counts 278 to 477 , precaudal vertebral counts 98 to 126, diplospondylous caudal vertebral counts 180 to 356 . Intestinal valve with 33 to 45 turns. Size moderately large to very large with adults up to 550 cm long. Colour: depending on the species dorsal colour can range from a brilliant dark metallic blue, to a silvery bluish grey or a violet to purplish brown; ventral surface white.

Distribution: Wide ranging in most tropical to temperate seas.
Habitat: Thresher sharks occur from nearshore coastal waters, including bays, to oceanic habitats far from land. They occur from near the surface to depths of at least 500 m , but most are found within 65 m of the surface. Like many other lamnoids for which information is available these sharks are able to maintain their body temperatures above that of the surrounding seawater. The habitats of these sharks broadly overlap with each other in some areas, but differences in their spatial distribution and foraging behaviour suggests that they partition the available habitat and preferred prey items.

Biology: Reproductive mode is yolk-sac viviparous with oophagy. Litters are small, ranging from 2 to 7 depending on the species. Gestation is from nine to 12 months with a defined birthing only known for one species (Alopias vulpinus), while the other two species do not appear to have a defined birthing season. Thresher sharks feed on a wide variety of schooling fishes and cephalopods. These are the only modern sharks, along with the sawsharks (Pristiophoridae), known to use a structure other than their jaws and teeth to subdue their prey. Thresher sharks use their elongated caudal fins to herd prey species into a tight school and then by rapidly whipping their tails stun and kill their prey before consuming it.

Interest to Fisheries and Human Impact: Worldwide, the thresher sharks are important fisheries because their meat is of high quality for human consumption and the long fins are highly desirable in the shark fin trade. In the North Atlantic two species occur, the bigeye thresher (Alopias superciliosus) and common thresher (A. vulpinus), of which the latter is the more dominant of the two species in terms of reported landings. However, despite their being a common bycatch component in drift gillnet and longline fisheries, they are often reported in mixed catches with little detailed species-specific information.

All members of the genus Alopias are considered Vulnerable globally due to apparent declining populations.
Local Names: Fox sharks, Threshers, Renards de mer.
Remarks: The genus can be subdivided into two distinct groups; one group consisting of those thresher sharks with relatively small eyes, a thin caudal fin, and no marked grooves on the top of the head. This group includes the thresher (Alopias vulpinus) and the pelagic thresher (A. pelagicus). The other group includes the bigeye thresher (A. superciliosus) with its extremely large eyes, broad caudal fin, and distinct grooves on the top of the head, running from a central point over the eyes, out and back over the gill region.
The family has a monotypic genus Alopias with three described species, two of which occur in the North Atlantic. The pelagic thresher shark (A. pelagicus) is the only member of this family that does not occur in the Atlantic Ocean. The family, genus, and species accounts are modified and updated from Compagno (1984, 2001).

Literature: Bigelow and Schroeder (1948); Gruber and Compagno (1981); Compagno (1984, 2001); Quéro in Whitehead et al. (1984a); Ebert (2003, In preparation); Gibson, Valenti, Fowler, and Fordham (2008); Last and Stevens (2009).

## Alopias Rafinesque, 1810

Genus: Alopias Rafinesque, 1810, Caratt. gen. sp. anim. piant. Sicilia, Palermo, pt 1: 13.
Type species: Alopias macrourus Rafinesque, 1810, by monotypy, a junior synonym of Squalus vulpinus Bonnaterre, 1788, Tabl. Encyclop. Method. Trois Reg. Nat. Ichthyol., Paris: 9.

Number of Recognized North Atlantic Species: 2.
Synonyms: Genus Vulpecula Jarocki, 1822: 454. Probably based on Vulpecula marina Valmont, 1768 (work not consistently binomial), equivalent to Squalus vulpinus Bonnaterre, 1788. Genus Alopecias Müller and Henle, 1837a: 114. Type species: "Carcharias vulpes Cuv[ier]" by original designation, equals Squalus (Carcharias) vulpes Cuvier, 1816. Genus Alopius Swainson, 1838: 91 (unjustified emendation of Alopias Rafinesque, 1810). Genus Vulpecula Garman, 1913: 3, 30. Type species: Vulpecula marina Garman, 1913, by monotypy: "Valmont, 1768, gives a description of $V$ marina of earlier authors. His species is Squalus vulpinus Bonn., 1788, the Alopias macrourus Raf., 1810, A. vulpes Bonap. 1841. The genus and species are adopted from Valmont" (Garman, 1913: 3). Revival of Vulpecula Valmont (1768: 740). Valmont's names were rejected as being inconsistently binomial by the International Commission on Zoological Nomenclature (1925, Opinion 89: 27-33).

Field Marks: A distinctive shark group with extremely long caudal fin that is about as long as the body trunk, very long, narrow pectoral fins, a very large first dorsal fin and comparatively minute second dorsal fin, and large to very large eyes.

Diagnostic Features: See family account above.
Local Names: None.

## Key to North Atlantic Species:

1a. Head with a deep horizontal groove extending around each side. Eyes are very large, with orbits expanded onto the dorsal head surface. Base of first dorsal fin closer to pelvic bases than to pectoral bases (Fig. 178)

Alopias superciliosus

1b. Head without a deep horizontal groove extending around each side. Eyes relatively smaller, with orbits not expanded onto the dorsal head surface. Base of first dorsal fin about equidistant between pectoral and pelvic-fin bases or closer to pectoral-fin bases (Fig. 179)

Alopias vulpinus


Fig. 178 Alopias superciliosus


Fig. 179 Alopias vulpinus

## Alopias superciliosus Lowe, 1841

Alopecias supercilious Lowe, 1840, Proc. Zool. Soc. London, 1840(8): 39 (1841?). Also Lowe, 1849, Trans. Zool. Soc. London, 3(1): 18 (sometimes dated 1839). Holotype unknown (Eschmeyer, 1998, Cat. Fish.), type locality Madeira, Eastern Atlantic.

Synonyms: None.

## Other Combinations: None.

FAO Names: En - Bigeye thresher; Fr - Renard à gros yeux; $\mathbf{S p}$ - Zorro ojón.


Fig. 180 Alopias superciliosus
Field Marks: A large thresher shark with extremely large eyes extending onto the dorsal head surface; head with distinct lateral grooves extending from above the eyes to behind the gill slits (appearing helmet-like). Pectoral fins with curved anterior margin and broadly tipped at the apices. Caudal fin extremely long, about same length as precaudal length; caudal fin broad at fin tip. Colour purplish brown to violet above, light below; without white patches extending above pectoral or pelvic fins.

Diagnostic Features: Body stout, cylindrical. Head broad with deep grooves extending along each side of head from behind eyes to above gill openings. Snout moderately long and bulbous. Eyes huge, extending onto the dorsal


DORSAL VIEW OF HEAD head surface; interorbital space nearly flat. Labial furrows absent. Teeth large, with a long slender, smooth-edged cusp, no lateral cusplets, similar in both jaws; no symphysial or intermediate teeth; tooth count 19 to 27 upper jaw, 19 to 24 lower jaw. Pectoral fins falcate with curved anterior margins and broadly tipped apices. Claspers moderately slender, not whip-like. First dorsal midbase closer to pelvic-fin bases than to pectoral-fin bases. Caudal tip broad with wide terminal lobe. Vertebral counts: total vertebral counts 278 to 308, monospondylous vertebral count 66, diplospondylous vertebral count 39, total precaudal vertebral counts 98 to 106, caudal vertebral counts 175 to 204. Intestinal valve count 43 to 45 . Colour: upper body surface violet to purplish-brown, fading to grey or white on sides, becoming lighter ventrally, but not extending over pectoral-fin bases; no white blotches or spots extending onto upper pectoral-fin tips.

Distribution: Worldwide in all major oceans. Eastern Atlantic: occasional records from waters south-west of the British Isles, Bay of Biscay, Spain, Portugal, Azores, Madeira Islands, Canary Islands, and from Morocco to Angola and South Africa. Also, found throughout the Mediterranean Sea. Western Atlantic: New England to Florida, Bahamas, Cuba, and the Gulf of Mexico, and south to southern Brazil.

Habitat: Bigeye threshers are usually found over continental shelves, but also on the high seas in the open ocean far from land. They may occur at the surface and down to at least 723 m over very deep water. They are usually found in areas where the surface temperature ranges from 16 to $25^{\circ} \mathrm{C}$. This shark appears to exhibit a strong diel movement pattern by remaining at depth, usually between 300 and 500 m where the water temperature is between 6 and $12^{\circ} \mathrm{C}$, during the day, but at night migrates to within 10 and 100 m of the surface where the water temperature warms to between 20 and $26^{\circ} \mathrm{C}$.

Biology: Viviparous with yolk-sac, but oophagous, and with litters of 2 to 4, mostly 2 . The gestation period may be 12 months, but since there does not appear to be a defined birthing season this has not been confirmed. Gravid females with embryos in various developmental stages are found year-round. Males mature in about 9 to 10 years and live at least 19 years, while females mature in 12 to 14 years and live about 20 years.

The diet of bigeye threshers consists primarily of demersal and pelagic fishes, cephalopods, and crustaceans. The large eyes are especially well adapted for low light levels, and the expanded orbits allow the eyes to roll upward enabling these sharks to hunt by searching for silhouettes of potential prey items above it.
The bigeye thresher as with the other members of this genus and the family Lamnidae are able to maintain their body temperature several degrees above that of the surrounding water.

Size: Maximum total length about 484 cm ; males adult between 270 to 290 cm ; females mature 332 to 356 cm . Size at birth 100 to 140 cm .

Interest to Fisheries and Human Impact: The bigeye thresher is taken in drift gillnets and by longline, but very little is known as to how many are typically caught since landings are not generally reported to species. In the Eastern North Atlantic relatively small numbers of this shark, ranging from a peak of 74 tonnes to a low of 1 ton has been reported since 2004 (average of 37 tonnes annually),


Fig. 181 Alopias superciliosus but this may be an underestimate as it is landed with the common thresher shark. In the Western North Atlantic this is a prohibited species in U.S. waters. The EU has prohibited directed fishery and retaining on board, transhipping or landing any part or whole carcass of this species in the ICCAT Convention Area EU (EU, 2012).

The conservation status of this thresher shark species is Vulnerable due to apparent declining populations, possibly resulting from a combination of its life history characteristics and lack of information on its population structure.

Local Names: Bigeyed thresher (UK, USA); Tubarao raposo (Portugal, Azores).
Literature: Bigelow and Schroeder (1948); Stillwell and Casey (1976); Gruber and Compagno (1981); Branstetter and McEachran (1983); Compagno (1984, 2001); Gilmore (1983, 1993); Moreno and Moron (1992a); Santos, Porteiro, and Barreiros (1997); Thorpe (1997); Ebert (2003); Weng and Block (2004); Amorim et al. (2007); Gibson et al. (2008); Last and Stevens (2009); NMFS (2010); EU (2012).

## Alopias vulpinus (Bonnaterre, 1788)

Squalus vulpinus Bonnaterre, 1788, Tabl. Encyclop. Method. Trois Reg. Nat., Ichthyol., Paris: 9. Types unknown according to Eschmeyer (1998, Cat. Fish.), type locality, Mediterranean Sea.

Synonyms: Squalus vulpes Gmelin, 1788: 1496. Types unknown according to Eschmeyer (1998). Alopias macrourus Rafinesque, 1810: 12. Type locality, Sicily. No types. Galeus vulpecula Rafinesque, 1810: 13, equivalent to "Squalus vulpecula di Linnao", which does not exist. Type locality, Sicily. No Types. Squalus alopecias Gronow, 1854: 7. No types known, according to Eschmeyer (1998). Vulpecula marina Garman, 1913: 30, pl. 7, fig 1. Holotype: Museum of Comparative Zoology, Harvard, MCZ 1166-S (Eschmeyer, 1998), juvenile $1321 / 1346 \mathrm{~mm}$ long or 546 mm PCL, from Massachusetts Bay. Revival of Vulpecula marinaValmont, 1768: 740, rather than a description of a new species. Valmont's name were rejected as being not consistently binomial by the International Commission on Zoological Nomenclature (1925, Opinion 89: 27-33).

Other Combinations: Alopias vulpes (Gmelin, 1788), Alopecias vulpes (Gmelin, 1788), Carcharias vulpes (Gmelin, 1788).

FAO Names: En - Thresher; Fr - Renard; Sp - Zorro.


Fig. 182 Alopias vulpinus
Field Marks: Long curving dorsal caudal-fin lobe about as long as rest of shark, relatively small eyes, falcate pointed pectoral fins, white colour of abdomen extending over pectoral-fin bases.

Diagnostic Features: Body moderately stout and cylindrical. Head broad, but without deep grooves extending along each side of head. Snout conical, pointed, and relatively short. Eyes moderately large, but not expanded onto dorsal surface of head. Labial furrows present. Teeth relatively small, with a single smooth-edged, slightly oblique, triangular cusp; symphysial and intermediate tooth rows usually present; tooth counts 32 to 52 upper jaw, 25 to 51 lower jaw. Pectoral fins falcate with curved anterior margins and pointed tips. Claspers very slender and whip-like. First dorsal-fin midbase closer to pectoral-fin bases than to pelvic-fin bases. Caudal-fin tip slender with moderately broad terminal lobe. Vertebral counts: total vertebral counts 322 to 364 , total precaudal vertebral counts 112 to 123 , caudal vertebral counts 240 to 243 . Intestinal valve count 33 to 34 . Colour: upper body surface silvery to bluish grey or dark grey, ventral surface white, with conspicuous white patches extending over pectoral and pelvic-fin bases.

Distribution: Circumglobal in most cold temperate to tropical seas. Eastern North Atlantic: Norway to the British Isles, Spain, Portugal, and the Azores. Also, found in the Mediterranean. Western North Atlantic: Newfoundland to the Gulf of St. Lawrence (Canada) southward along the Atlantic coast of the U.S.A. to the Gulf of Mexico.

Habitat: Typically associated with the continental shelf, and appears to be most abundant within 70 km of land, including inshore areas (including enclosed bays, lagoons and outer estuaries), but also occurs far from landmasses. They are usually found at or near the surface, but have been taken down to nearly 400 m deep. A strong swimming, active shark, the thresher makes pronounced seasonal migrations northwards following warmwater masses.

Biology: Oophagous, with litters of 2 to 7; gestation appears to be about nine months with birth occurring in the spring and summer. Males mature in 3 to 7 years and females in 3 to 9 years; size and age at maturity varies by region. The maximum age is at least 24 years and


Fig. 183 Alopias vulpinus possibly 50 years.
Thresher sharks feed mainly on small schooling pelagic fishes, including anchovies, herring, mackerel, hake, lancetfish, lanternfishes, sardines, and invertebrates including cephalopods and pelagic crabs.

Size: Maximum size is somewhat in question, and varies regionally, but is at least 575 cm and possibly 635 cm . Males mature from 260 to 420 cm and females from 260 to 465 cm in length. Size at birth 120 to 150 cm .

Interest to Fisheries and Human Impact: There are no directed fisheries for thresher sharks in the Eastern North Atlantic, but they are retained as bycatch in longline and drift gillnet fisheries for swordfish and tunas, and are occasionally taken as bycatch in inshore fisheries. In U.S. Atlantic waters recreational fishers who have a limit of one shark per day land relatively low numbers of this thresher shark. Commercial fisheries for this in U.S. Atlantic waters are managed under the Highly Migratory Species act which has an annual landing quota for pelagic sharks. The EU has prohibited directed fishery and retaining on board, transhipping or landing any part or whole carcass of this species in the ICCAT Convention Area (EU, 2012).

The global conservation status of this species is Vulnerable, but in the Eastern North Atlantic it is listed as Near Threatened.
Local Names: Common thresher shark, Fox shark, Thrasher shark, Long-tailed shark, Slasher (UK); Lluynog (Wales); Singe de mer, La faux, Poisson épée, Péi aspasu ratou, Touille à l'épée (France); Drescherhai (Germany); Rabosa, Pez espada, Zorra de mar, Pez zorro, Zorro blanco (Spain); Arequim, Peixe alecrim, Peixe raposo, Peixe zorra (Portugal); Tubarâo raposo, Romano, Româo, Zorro (Azores); Rävhaj (Sweden); Revehai (Norway).

Literature: Bigelow and Schroeder (1948); Gilmore (1983, 1993); Santos, Porteiro, and Barreiros (1997); Compagno (1984, 2001); Ebert (2003); Ellis (2004); Gibson et al. (2008); Goldman et al. (2008); Last and Stevens (2009); EU (2012); ICES (2012); L.J. Natanson (pers. comm.).

### 2.5.4 Family CETORHINIDAE

Family: Subfamily Cetorhinidae Gill, 1862b, Ann. Lyceum Nat. Hist. New York, 7(32): 397-398 (Family Lamnoidae). Emended to Family Cetorhinidae Gill, 1862, by Gill (1872, Smiths. Misc. Coll., [247]: 24).

Type genus: Subgenus Cetorhinus Blainville, 1816 (Genus Squalus Linnaeus, 1758).

## Number of Recognized North Atlantic Genera: 1.

FAO Names: En - Basking sharks; Fr - Requins pélerin; Sp - Peregrinos.
Field Marks: See species account below.
Diagnostic Features: Body fusiform, stout, and firm, not flabby; body stoutest from about pectorals to first dorsal fin, tapering posteriorly to moderately stout; dorso-ventrally flattened caudal peduncle. Head moderately long, much shorter than trunk length, and slightly compressed laterally opposite mouth. Snout short, conical with rounded tip in larger specimens (over 360 cm ), but in smaller individuals (less than about 360 cm ) snout length much longer, forming a subcylindrical proboscis, becoming oblique, truncated, and terminating in a acutely pointed tip. Eyes nearly circular, relatively small, diameter about 0.8 to $1.3 \%$ of precaudal length, located just posterior to front of mouth. Spiracles minute, circular, about opposite to or just posterior to front of mouth. Gill openings enormous, nearly encircling the head; first gill opening largest, each subsequent opening descending in length to the fifth (smallest) opening; all five paired gill openings anterior to pectoral-fin base; internal gill openings with modified gill rakers. Nostrils small, transverse, closer to mouth than to snout tip. Mouth huge, rounded in adults, but variable in young juveniles. Lower labial furrow at mouth corners very short, upper labial furrows absent. Teeth minute, with a single smooth-edged, hook-shaped cusp, similar shaped in both jaws; tooth counts number over 200 rows on upper and lower jaws. Caudal peduncle with strong lateral keels and crescentic shaped upper and lower precaudal pits. Dermal denticles close-set, numerous, varying in size, very rough, erect and thorn-like with strong cusps and ridges; cusps of lateral denticles angled in various directions. Pectoral fins very large and broad, less than head length. Pelvic fins about two-thirds height of first dorsal-fin anterior margin. Anal fin similar in size to second dorsal fin; origin below posterior half of second dorsal fin. First dorsal fin very high, erect, nearly triangular; midbase between snout tip and caudal fork. Second dorsal-fin anterior margin only about $20 \%$ to $25 \%$ height of first dorsal fin. Caudal fin crescentshaped, large, but less than one-third length of shark; dorsal lobe about one-third longer than ventral lobe. Vertebral counts: total vertebral counts 107 to 116 , precaudal vertebral counts 50 to 54 , diplospondylous caudal vertebral counts 55 to 62 . Intestinal valve of ring type with 47 to 51 turns. The second largest fish in the world with adults to about 1000 cm and possibly to 1200 cm long. Colour: mottled bluish grey to grey or brown above, becoming variably lighter or darker below.

Distribution: Circumglobal most commonly observed in temperate and boreal waters, but known to occur at depth, usually below 300 m in tropical seas.

Habitat: Pelagic in coastal, shelf and oceanic waters, these sharks will dive to several hundred meters and remain at depth as they move through warm temperate to tropical waters migrating between hemispheres. In cooler waters they are often seen slowly cruising at the surface. These sharks are known to make transoceanic and trans-equatorial migrations. Often associate with fronts and other oceanographic features that support locally high concentrations of zooplanktonic prey.

Biology: See species account below.
Interest to Fisheries and Human Impact: See species account below.
Local Names: None.
Remarks: The family, genus, and species accounts are modified and updated after Compagno (2001) who also provides a detailed account on the history of the spelling and usage of the various scientific names for this shark.

The family has a single genus and species, which occurs all major oceans including the North Atlantic.
Literature: Bigelow and Schroeder (1948); Compagno (1984, 2001); Ebert (2003); Last and Stevens (2009).

## Cetorhinus Blainville, 1816

Genus: Subgenus Cetorhinus Blainville, 1816 (Genus Squalus Linnaeus, 1758), Bull. Sci. Soc. Philomat. Paris, (8): 121.
Type species: not designated; Blainville included the species "Gunneri, Peregrinus, Shavianus, Homianus?" in Cetorhinus without further comment. Gill (1862b, Ann. Lyceum Nat. Hist. New York, 7(32): 398), designated Squalus maximus "Linnaeus" (=Gmelin, 1788) as type of Cetorhinus, but this was not an included species. Jordan and Gilbert (1883, Bull. U.S. Nat. Mus., 16: 31) designated "Cetorhinus gunneri Blainv. = S. maximus L." (a junior synonym of Squalus maximus Gunnerus, 1765) as type of Cetorhinus, which may be the earliest valid type designation. Eschmeyer (1998, Cat. Fish.) cited Jordan and Evermann (1896, Bull. U.S. Natn. Mus., (47), pt. 1:51) as a later, similar type designation.

## Number of Recognized North Atlantic Species: 1.

Synonyms: Subgenus Selache Cuvier, 1816 (Genus Squalus Linnaeus, 1758): 129. Type species, "Sq. maximus L." by monotypy (Squalus maximus Gmelin, 1788, a junior synonym of Squalus maximus Gunnerus, 1765). Genus Selanche Jarocki, 1822: 452 (error for Selanche, Cuvier, 1816). Genus Selanchus Minding, 1832: 52 (unjustified emendation of Selache Cuvier, 1816). Genus Polyprosopus Couch, 1862: 67.

Field Marks: See species account below.
Diagnostic Features: See family account above.
Local Names: None.

## Cetorhinus maximus (Gunnerus, 1765)

Squalus maximus Gunnerus, 1765, K. Norske Vidensk-selsk. Scr. Trondh.: 33, pl. 2. Holotype, apparently none. Type Locality: Trondhjem, Norway.

Synonyms: Squalus gunnerianus Blainville, 1810 (71): 256, pl. 2, fig. 3; Types? Squalus homianus Blainville, 1810: 257, pl. 2, fig. 1. Types? Squalus pelegrinus Blainville, 1810: 256, pl. 2, fig. 2. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN 9853. Halsydrus pontoppidiani Fleming, 1817: 713. Stronsa, Orkney Islands. Holotype: National Museum of Scotland, NMSZ-1979.012. Squalus elephas Lesueur, 1822: 350, pl. Types: based on a large adult male specimens, about 1000 cm TL from the New Jersey coast, not saved. Squalus rashleighanus Couch, 1838: 51. Type locality, Cornwall. Types? Polyprosopus macerCouch, 1862: 68, pl. 15, fig. 2. Type locality, Startpoint, Cornwall, England. No types. Cetorhinus blainvillei Capello, 1870: 233, 1 pl. Type locality, Portugal. Types? Selachus pennantii Cornish, 1885: 351. Type locality: Cornwall. No types. Other Combinations: Halsydrus maximus (Gunnerus, 1765), Selache maxima, Selache maximus or Selache maximum (Gunnerus, 1765), Selache elephas (Lesueur, 1822).

FAO Names: En - Basking shark; Fr - Pélerin; Sp - Peregrino.


Fig. 184 Cetorhinus maximus
Field Marks: The great size, enormous gill slits that virtually encircle the head, modified gill rakers, pointed snout, huge, subterminal mouth with minute hooked teeth, caudal peduncle with strong lateral keels, and lunate caudal fin distinguish this shark from all others. Colour blackish to grey-brown, grey or blue-grey above and below on body and fins, undersurface sometimes lighter, often with irregular white blotches on the underside of the head and abdomen; flanks sometimes with lighter linear striping and spots.

Diagnostic Features: See family Cetorhinidae above.
Distribution: Eastern North Atlantic: Arctic Ocean, southeast Greenland, Iceland, Faroe Islands, Norway, Russia (western Barents Sea and White Sea), south to Sweden, British Isles, France, Spain, and Portugal, including the Azores, to Morocco and Senegal. Also, found throughout the Mediterranean Sea. Western North Atlantic: southwest Greenland, Newfoundland, Nova Scotia, and New Brunswick, Canada to New England and southwards to the Gulf of Mexico, U.S.A.

Habitat: Basking sharks are coastal pelagic, usually observed at the surface in areas where the water temperature is between 5 and $21^{\circ} \mathrm{C}$. They may be found close inshore, including enclosed bays, from the surfline and over the continental shelf, to well offshore at depths of over 1200 m . This is a very social species and is often seen swimming in small groups of 3 to 10 or in larger groups numbering in the hundreds. At lower latitudes these sharks will dive to depth and remain between 250 and about 1000 m deep for five months or more without coming to the surface. In warm temperate and tropical seas these sharks tend to follow distinct water masses while at depth; one shark was found to follow the $5{ }^{\circ} \mathrm{C}$ thermocline at 300 to 400 m deep off Brazil, while another individual followed the same $5^{\circ} \mathrm{C}$ thermocline at 750 to 1000 m depth off the Bahamas.

Biology: Reproduction oophagous, with 1 to 6 young per litter; reproductive cycle including gestation period unknown. Records of juvenile sharks less than 300 cm for this species are rare, suggesting pupping and nursery grounds are located in planktonic-rich oceanic waters far from populated coastal area. Previous age estimates for this species are now known to be erroneous as vertebral bands are associated with growth and not age.
These filer-feeding giants consume vast quantities of zooplankton including copepods and planktonic larvae. An individual basking shark may have half a ton of food in its stomach at any time. Adult basking sharks when feeding will cruise at a speed of about two knots per hour and will pass about 2,000 tons of water over its gills per hour. They will close their mouths every 30 to 60 seconds to ingest the filtered plankton that is trapped in their gill rakers. Basking sharks feed along thermal fronts where their food may be especially abundant. They will dive to great depths in warm temperature and tropical seas following thermoclines and will remain at depth for extended periods of time.

Basking sharks appear to have few natural predators, although white sharks (Carcharodon carcharias), killer whales (Orcinus orca), and sperm whales (Physeter macrocephalus) are known predators; a 250 cm juvenile was once found in a sperm whale stomach in the Azores.
Basking sharks are now known to make extensive transoceanic and transequatorial movements in the Atlantic often moving thousands of kilometres. The North Atlantic population may be contiguous with evidence of movements between the eastern and western North Atlantic. Also, some sharks tagged off southern New England, U.S.A., were found to move southwards to the Caribbean and as far as Brazil, South America.

Size: Maximum total length about 1000 to 1200 cm ; males mature at about 400 to 500 cm and females at about 800 to 900 cm TL . Size at birth about 150 to 200 cm total length; smallest free-swimming individual measured 170 cm in length.


Fig. 185 Cetorhinus maximus

Interest to Fisheries and Human Impact: Fisheries for basking sharks historically began at least during the seventeenth and eighteenth centuries primarily for their liver oil for vitamin A, and lamp oil, skin for leather, and flesh for human consumption. In recent years, their fins have become quite valuable in the shark fin trade industry. The primary fisheries occurred off Norway, with other local fisheries off Iceland, Ireland, Scotland, Spain, and the east coasts of Canada and the United States. Since 2003 basking sharks have been largely protected by most North Atlantic nation states with only bycatch landings allowed for in some regions. In Canada basking sharks are considered endangered, while in the U.S.A. they are listed as a species of concern. In European waters, since 2003 the landings have declined appreciably from 175 tonnes in 2003, to zero in 2009, as fishing opportunities were restricted. ICES in 2006 recommended that no targeted fishing for basking shark should be permitted, with additional measures implemented to prevent it being taken as bycatch. The basking shark is quite docile allowing boats and ecotourist divers to approach them. Although considered harmless divers approaching these sharks should take care as the extremely rough dermal denticles on its skin can cause severe abrasions and lacerations to uncovered human skin.

It has been estimated that the global population of these sharks may be quite low, which raises concerns over its conservation status. It is considered Vulnerable globally, but in the Eastern North Atlantic it is listed as Endangered. In 2002, the basking shark was listed by the convention in international trade of endangered species (CITES) on its Appendix II list of endangered species. Most nation states in the North Atlantic (Canada, U.S.A., and the European Union) have implemented laws strictly prohibiting the directed commercial fishing, landing, and sale of this shark, and it is protected on national wildlife legislation of some nations. The EU has prohibited to fish for, to retain on board, to tranship or to land this species in EU and non-EU waters (2012). Directed fishery banned in Norway (2012).

Local Names: Brugde (Denmark, Norway); Eqalussuarsuaq (Greenland); Reuzenhaai (the Netherlands); Riesenhai (Germany); Beinhákarl (Iceland); Brudga (Faroe Islands); Frade, Peixe frade, Tubarão frade (Portugal, Azores).

Literature: Bigelow and Schroeder (1948); Matthews (1950, 1962); Matthews and Parker (1950a, b); Parker and Stott (1965); Springer and Gilbert (1976); Compagno (1984, 1990c, 2001); Quéro in Whitehead et al. (1984a); Izawa and Shibata (1993); Choy and Adams (1995); Martin and Naylor (1997); Santos, Porteiro, and Barreiros (1997); Sims, Fox, and Merrett (1997); Sims and Merrett (1997); McEachran and Fechhelm (1998); Sims and Quayle (1998); Harvey-Clark et al. (1999); Sims (1999, 2000, 2003); Sims et al. (2000); Ebert (2001a, 2003); Collette and Klein-MacPhee (2002); Sims et al. (2003); Speedie (2003); Skomal, Wood, and Caloyianis (2004); Fowler (2005); Southall et al. (2005); Hoelzel et al. (2006); ICES (2006, 2010); Southall et al. (2006); DFO (2008); Gibson et al. (2008); Gore et al. (2008); Natanson et al. (2008); Last and Stevens (2009); Priede and Miller (2009); Skomal et al. (2009); Lacey et al. (2010).

### 2.5.5 Family LAMNIDAE

Family: Lamnoidea Müller and Henle, 1838a, Mag. Nat. Hist., new ser., 2: 36. Also Subfamily Lamnini Bonaparte, 1838, Nuov. Ann. Sci. Nat., Bologna, ser., 1, 2: 20 (Family Squalidae); Family Hasse, 1879, Nat. Syst. Elasmobr., (1): 52. Emended to Family Lamnidae Müller and Henle, 1838 by Richardson, 1846, Ichthyol. China Japan: 195.

Type genus: Lamna Cuvier, 1816.

## Number of Recognized North Atlantic Genera: 3.

FAO Names: En - Mackerel sharks, Porbeagles, White sharks; Fr - Requins taupe; Sp - Jaquetones, Marrajos.
Field Marks: Large, heavy-bodied, fusiform-shaped sharks with a long, conical snout, large mouth with protrusible jaws, large teeth that are either narrow and sharply pointed or triangular and blade-like, small to moderately large eyes, large gill slits, strong lateral keels, and a short, nearly symmetrical, crescent-shaped caudal fin. Dorsal surface colour, depending on the species, ranges from a brilliant blue to bluish-grey, dark grey, brownish-grey, or blackish-grey, ventral surface lighter to white; some species have dark blotches ventrally.

Diagnostic Features: Body fusiform, slender to stout, with moderately long head. Snout conical, moderately long and pointed. Eyes small to moderately large, diameter 0.9 to $3.4 \%$ precaudal length. Gill openings long, but not extending onto dorsal surface of head or nearly across throat, and without internal gill rakers; fifth gill openings anterior to pectoral-fin origin. Nostrils separate from mouth, without barbels. Mouth large, broadly rounded, subterminal on head, extending past eyes; labial furrows present; jaws moderately protrusible. Teeth very large, broadly triangular and serrated or long and slender, with smooth-edged cusps; tooth counts range from 22 to 32 upper jaw, 20 to 30 lower jaw. Dermal denticles very small and smooth. Caudal peduncle strongly depressed dorso-ventrally, and widely expanded laterally, forming a prominent keel, with upper and lower crescentic-shaped precaudal pits. Pectoral fins very long and narrow. Pelvic fins small, much smaller than first dorsal fin but larger than second dorsal and anal fins. First dorsal fin subtriangular to somewhat rounded, large, high, and erect. Second dorsal and anal fins minute, much smaller than first dorsal fin. Caudal fin crescent-shaped, upper lobe moderately long, less than one-third trunk length, ventral lobe nearly as long as upper lobe. Total vertebral counts 150 to 197, precaudal vertebral counts 84 to 114, diplospondylous caudal vertebral counts 66 to 86 . Intestinal valve of ring type with 37 to 55 turns. Size large to very large, from 300 to possibly more than 600 cm total length. Colour: blue, bluish-grey, grey, greyish-brown to blackish-grey above, sharply demarcated on lateral flanks and becoming light to white below; some species have dark blotches or speckles ventrally; fins tips may be slightly darker to dusky.

Distribution: Worldwide in most cold temperate and tropical seas, with members of one genus (Lamna) even ranging into polar seas.

Habitat: Coastal nearshore, including enclosed bays and estuaries, to outer continental shelves and insular slopes from the surf zone to the open ocean far from continental landmasses. The members of this family have a wide temperature tolerance as members of the genus Lamna occur in high latitude seas, including polar and cold temperate seas, while isurids (Isurus) are most commonly found in warm temperate to tropical seas. Overlapping the distribution of both these genera, Carcharodon has perhaps one of the broadest ranges of any large shark, as it inhabits both tropical to boreal seas.

Biology: Viviparous with oophagy, whereby developing embryos are nourished by a yolk-sac initially, but once the yolksac is exhausted they consume unfertilized eggs. Litter size is poorly known, but appears to range from 1 to 17 (possibly up to 25). Reproductive cycle may be up to three years for some species, with a gestation of 8 to 18 months depending on the species. Age at maturity ranges from five to 18 years. These are very active swimming, voracious sharks that consume a broad range of prey items including marine mammals, cetaceans as carrion, sea birds, marine reptiles, other sharks, batoids, chimaeras, a variety of bony fishes including both large, active, fast swimming species, as well as benthic species. Invertebrates including cephalopods, crustaceans, and other molluscs are frequently consumed. On occasion these sharks are also well known to attack humans engaged in water activities.

Interest to Fisheries and Human Impact: Several species within this family, especially the porbeagle (Lamna nasus) and shortfin mako shark (Isurus oxyrinchus) in the North Atlantic, are considered of high value for their meat and fins, and as such they are targeted in high seas fisheries. Besides their meat and fins, the jaws and teeth will often bring a high value from collectors of such curios.

Members of this family, particularly the white shark (Carcharodon carcharias) and shortfin mako (Isurus oxyrinchus) are well known to attack people, bathers, swimmers, divers, and in some instances boats. The porbeagle has been involved in at least one attack on a diver, but generally has not been implicated in attacks on humans, although this also may be do to the fact this high latitude species does not come into contact with bathers and divers as frequently as other members of this family.
In recent years several of these sharks have become popular ecotourist attractions especially for divers looking to experience the thrill of a life time getting up close to white sharks from the protective surroundings of a dive cage.

The conservation status of all the members of this family in the Eastern North Atlantic is considered Vulnerable, except for the porbeagle that is listed as Critically Endangered in this region.

Local Names: Mackerel sharks, Man-eaters sharks, Man-eating shark (English); Lamie, Requin-bleu, Taupe (France)
Remarks: All three genera and four of the five species within this family are represented in the North Atlantic. The arrangement of this family follows Compagno (1984, 2001).

Literature: Bigelow and Schroeder (1948); Garrick (1967a); Compagno (1984, 2001); Ebert (2003); Musick and Ellis (2005); Gibson, Valenti, Fowler, and Fordham (2008); Last and Stevens (2009); Ebert and Winton (2010).

## Key to North Atlantic Genera:

1a. Upper teeth broadly triangular and serrated (Fig. 186)

Carcharodon

1b. Upper teeth long, narrow, and without 1b. Upper teeth long
serrations (Fig. 187) 2


UPPER TOOTH
Fig. 186 Carcharodon


UPPER TOOTH
Fig. 187 Lamna

2b. Origin of first dorsal fin over base or inner margin of pectoral fins; caudal peduncle with two keels, and teeth with small lateral cusplets (although these cusplets can be partially obscured in juveniles)(Fig. 187 \& 188).

Lamna


Fig. 188 Lamna
2b. Origin of first dorsal fin posterior to rear tip of inner margin of pectoral fin; no secondary keel on caudal peduncle, and teeth without small lateral cusplets (Fig. 189) Isurus


Fig. 189 Isurus

## Carcharodon Smith, 1838

Genus: Carcharodon Smith, in Müller and Henle, 1838a, Mag. Nat. Hist., new ser., 2: 37. Placed on the Official List of Generic Names in Zoology (Name no. 1658) by the International Commission on Zoological Nomenclature (1965, Opinion 723.3b, Bull. Zool. Nomencl., 22(1): 32).

Type species: Squalus carcharias Linnaeus, 1758, by subsequent monotypy through Carcharias lamia Rafinesque, 1810 (International Commission on Zoological Nomenclature, 1965, loc. cit.).

## Number of Recognized North Atlantic Species: 1.

Synonyms: Subgenus Carcharias Cuvier, 1816 (Genus Squalus Linnaeus, 1758): 125, in part. Placed on the List of Rejected and Invalid Names in Zoology (Name no. 811) by the International commission on Zoological Nomenclature
(1965, Opinion 723.5c: 33). Cuvier's Carcharias had only three species, Squalus carcharias, S, vulpes (= Alopias vulpinus), and S. glaucus (= Prionace glauca). Squalus carcharias is the type of Carcharias Cuvier by absolute tautonymy, but is a junior homonym of Carcharias Rafinesque, 1810 (Carcharias taurus, type species by monotypy). Carcharias Cuvier was used extensively for carcharhinids following Müller and Henle (1839: 27).

Field Marks: See species account below.
Diagnostic Features: Body fusiform, moderate to very stout. Snout bluntly conical and relatively short. Eyes circular, relatively small, diameter about 0.7 to $1.8 \%$ total length. Nostrils transverse, narrow, closer to mouth than snout tip, anterior margin with low subtriangular lobe. Mouth broadly rounded, width slightly more than 1 to 2 times length; labial furrows very short, lowers concealed except with mouth is open. Teeth very large, erect, subtriangular, with edges coarsely serrated; similar in both jaws except lowers more slender than uppers. Tooth counts 23 to 29 upper jaw, 21 to 25 lower jaw. First dorsal-fin origin usually over the pectoral-fin inner margins. Second dorsal and anal fins minute relative to first dorsal fin; second dorsal-fin insertion under or slightly anterior to anal-fin origin. Secondary caudal keels absent. Vertebral counts: total vertebral counts 170 to 187 , precaudal vertebral counts 100 to 108 , and caudal vertebral counts 68 to 83 . Intestinal valve count 47 to 55 . Very large sharks, with a maximum total length of about 600 cm . Colour: grey, brownish-grey, to blue-grey above, becoming white below; transition from dorsal to ventral colour sharply demarcated. A black axillary spot often at pectoral-fin insertions; pectoral-fin tips usually abruptly black on their ventral surfaces.

Local Names: None.
Remarks: Genus and species account modified after Compagno (1984, 2001).

## Carcharodon carcharias (Linnaeus, 1758)

Squalus carcharias Linnaeus, 1758, Syst. Nat. ed. 10, 1: 235. Placed on the Official List of Species Names in Zoology (Name no. 2056) by the International Commission on Zoological Nomenclature, (1965, Opinion 723.4b, Bull. Zool. Nomencl., 22(1): 32). Holotype unknown, type locality "Europa". Also no types known according to Eschemeyer (1998, Cat. Fish.).

Synonyms: Carcharias lamia Rafinesque, 1810b: 44. Type locality: Sicily. No types? Placed on the list of Rejected and Invalid Species Names in Zoology (Name no. 811) by the International Commission on Zoological Nomenclature, (1965, Opinion 723.6: 33). ?Squalus (Carcharhinus) lamia Blainville, 1816: 121 (in part?). Name only. Carcharias verus Cloquet, 1817: 69. Europe. No types. Squalus(Carcharhinus) lamia Blainville, 1825: 88, pl. 22, fig. 2 (in part?). No types? Carcharias rondeletti Bory de Saint-Vincent, 1829: 596. Europe. Types? Squalus (Carcharias) vulgaris Richardson, 1836: 288. All seas. An unexplained name, without types according to Eschmeyer (1998). Carcharias atwoodi Storer, 1848: 72. Type locality, Provincetown, Massachusetts. Holotype: Museum of Comparative Zoology, Harvard, MCZ 89505 (missing), jaws may be MCZ 775-S (Eschmeyer, 1998).

Other Combinations: None.
FAO Names: En - Great white shark; Fr - Grand requin blanc; $\mathbf{S p}$ - Jaquetón blanco.


Fig. 190 Carcharodon carcharias


UNDERSIDE OF HEAD


UPPER AND LOWER TEETH

Field Marks: A stout spindle-shaped body, with a conical snout, teeth large, triangular, and serrated, a large erect, triangular first dorsal fin, minute second dorsal and anal fins, no secondary caudal keel, and a large crescent-shaped caudal fin. Dorsal surface grey, grey-brown to bluish-grey, ventral surface white; colour transition from dorsal and ventral surface sharply demarcated; iris of eyes are a conspicuous black.

## Diagnostic Features: See genus Carcharodon above.

Distribution: Circumglobal, common in most temperate seas, less common in tropical regions, but this is possibly due to subtropical submergence. Eastern North Atlantic: Bay of Biscay, France to Gibraltar, Azores, Madeira Islands, and Canary Islands, and throughout the Mediterranean; no confirmed records from the British Isles. Western North Atlantic: Newfoundland, Canada to Florida and the northern Gulf of Mexico.

Habitat: Carcharodon carcharias has one of the broadest habitat ranges of any elasmobranch species. They occur in coastal nearshore waters, including bays and estuaries, but are also oceanic, in the open ocean far from landmasses and around islands far from any mainland. These sharks range from the surface to at least 1280 m depth. Large great white sharks (over 300 cm total length) can tolerate a broader temperature range and may be found in boreal seas on occasion, but small juveniles tend to prefer warm temperate waters. In tropical seas great white sharks tend to remain at depth, usually at more than 100 m , but


Fig. 191 Carcharodon carcharias occasionally will come to the surface or into nearshore areas particularly around oceanic islands far from land.

Biology: Very little known despite the high profile of this species. Viviparous, with oophagy and litters ranging from 3 to 14. The gestation period is unknown, but thought to be about two years based on occurrence of females returning to specific areas every other year, but this has not been confirmed. Age at maturity has been estimated at 9 to 10 years for males and at about 14 years for females, with a maximum estimated age (based on vertebral bands) of 23 years for a 600 cm female; maximum age possibly 30 years. The growth rate of the white shark is quite rapid in juveniles, from 25 to 30 cm per year, but slows considerably once they reach maturity.

Carcharodon carcharias is one of the most formidable large marine predators in the ocean today, rivalled only by the killer whale (Orcinus orca) that is a known predator on great white sharks. These are large, fast swimming, powerful predators, that combined with their powerful jaws and large triangular teeth make them a super-predator. Great white sharks feed on a broad spectrum of prey items including bony fishes, other chondrichthyans, pinnipeds and small cetaceans, and large whales as carrion. These sharks have been observed to grab and release possible prey items, including other sharks and marine mammals, but not consume them suggesting another behavioural pattern may be involved. They will attack, but not consume inanimate objects such as boats, kayaks, and buoys. Occasionally, sea turtles and sea birds have been found in their stomach, but these do not appear to make up a considerable part of their diet. Invertebrates are also on occasion
found in their diet, but these items appear to be rare. The diet of the great white sharks changes with growth as individuals less than 300 cm in length feed more heavily on bony and cartilaginous fishes, but as they grow marine mammals become more important in their diet.

Great white sharks may occur singly, but often will occur in loosely organize groups, especially around seal rookeries and whale carcasses that may be scavenged. When they occur in groups a social hierarchy may prevail where larger sharks feed first followed in order of size by smaller sharks. The tiger shark (Galeocerdo cuvier) and blue shark (Prionace glauca), although displaced at times by great white sharks, have been observed to feed on whale carcasses where white sharks have been feeding.

Great white sharks are known to travel long distances, including crossing ocean basins, and to make long annual seasonal migrations. Although very little is known about their movements patterns in the North Atlantic, off the U.S. Atlantic coast, mating seems to take place in the feeding grounds of the mid-Atlantic Bight which also serves as a nursery ground. However, gestation and parturition takes place further south, in an area off the Atlantic coasts of Georgia and Florida (U.S.A.).

Size: Maximum length debatable, but estimated at 600 to 640 cm . Males mature between 360 and 400 cm total length with a maximum length of about 550 cm . Females maturity uncertain, but thought to be between 450 and 500 cm in length, and a maximum length of 600 cm or more. Birth size is about 120 to 150 cm in length.

Interest to Fisheries and Human Impact: Great white sharks are a protected species by most countries fronting the North Atlantic in Areas 21 and 27, and as such are not targeted, but they are occasionally caught as bycatch by gillnets and longline fisheries targeting other fish species.

The great white shark is a fearsome predator and is considered one of the most dangerous shark species, along with the bull and tiger sharks, swimming in the ocean today. The media attention garnered by this species has created an image of almost mythical proportions. In temperate waters the great white shark has probably been responsible for more attacks on people, boats, and kayaks, than any other shark species. Despite its fearsome reputation divers, surfers, kayakers, and others on or in the water have observed them without incident. In some areas ecotourism operations have develop where these sharks can be observed either from boats or for those more adventurous people from a submerged shark cage.
The EU has prohibited to fish for, to retain on board, to tranship or to land this species in EU and non-EU waters (2012).
The conservation status of the great white shark is Vulnerable due to its apparent low reproductive rate and vulnerability in some fisheries. However, it is now a protected species throughout much of its range with bans on targeted fishing, and the removal and sale of fins and jaws for trade. This species is included in Appendix I of CITES-listed animals and plants (2012).

Local Names: White shark, Maneater shark, Man-eater shark (English); Ami, Lamea, Lamie, Lameo, Le Carcharodonte lamie, Le grand requin, Pei can, Requin blanc (France); Menschen fresser, Menschenhai, Merviel fras, Weißer Hai (Germany); Ca mari, Marraco, Salroig, Salproig, Salproix, Taburo, Tiburo, Tiburón blanco, Tauró blanc (Spain); Tubarão-come-homens, Tabarao (Portugal); Tubarâo branco, White shark (Azores).

Literature: Bigelow and Schroeder (1948); Compagno (1984, 2001); Quéro in Whitehead et al. (1984a); Cailliet, Natanson, Welden, and Ebert (1985); Casey and Pratt (1985); Gilmore (1993); Santos, Porteiro and Barreiros (1997); Ebert (2003); Compagno, Dando, and Fowler (2005); Ferguson, Compagno and Marks (2005); Gibson et al. (2008); Last and Stevens (2009); J. Ellis and A. Henderson (pers. comm.); D.A. Ebert (unpubl. data).

## Isurus Rafinesque, 1810

Genus: Isurus Rafinesque, 1810a, Caratt. gen. sp. anim. piant. Sicilia, Palermo, pt. 1: 11.
Type species: Isurus oxyrinchus Rafinesque, 1810, by monotypy.

## Number of Recognized North Atlantic Species: 2.

Synonyms: Genus Oxyrhina Agassiz, 1838: 86, pls. 33-34. Type species: "Lamna oxyrhina Cuvier and Valenciennes, MS." by absolute tautonymy, a junior synonym of Isurus oxyrinchus Rafinesque, 1810. Genus Oxyrrhina Bonaparte, 1846: 17. Type species: Oxyrhina gomphodon Muller and Henle, 1839, a junior synonym of Isurus oxyrinchus Rafinesque, 1810. Genus Plectrostoma Gistel, 1848: 10. Replacement name for Oxyrhina Agassiz, 1835, and thereby taking the same type species, Lamna oxyrhina Cuvier and Valenciennes, 1838, a junior synonym of Isurus oxyrinchus Rafinesque, 1810. Genus Isuropsis Gill, 1862b: 397. Type species: Oxyrhina glauca Muller and Henle, 1839, by original designation. Genus Plectrosoma Bigelow and Schroeder, 1948: 123 (error for Plectrostoma Gistel, 1848).

Field Marks: Origin of first dorsal fin posterior to inner corner of pectoral fin, teeth smooth-edged and without lateral cusplets, and no secondary caudal keel. Dorsal surface blue, bluish grey, to blackish grey; ventral surface mostly white.

Diagnostic Features: Body fusiform, moderately slender. Snout long, narrow, acute to bluntly point snout. Eyes relatively large, diameter less than to more than one-third snout length; 1.3 to $3.1 \%$ of total length. Nostrils nearly transverse. Mouth subterminal, broadly rounded, width about 0.9 to 1.5 times length; upper labial furrows about twice as long as lowers; teeth similar in both jaws, smooth-edged, acutely pointed, without lateral cusplets; anterior teeth may or may not be recurved. Tooth counts 24 to 26 upper jaw, 22 to 32 lower jaw. First dorsal-fin origin about over to behind pectoral-fin free rear tips. Second dorsal fin much smaller than first dorsal fin, origin anterior to anal fin. Anal-fin origin about under second dorsal-fin midbase or slightly posterior to second dorsal-fin insertion. Secondary caudal keels absent. Vertebral counts: total vertebral counts 182 to 197 , precaudal vertebral counts 107 to 112 . Intestinal valve count 47 to 54 . Large sharks with a maximum length of over 400 cm . Colour: a brilliant blue to grey-blue or blackish dorsally, becoming lighter, to white, ventrally.

Local Names: Makos, Mako sharks, Mackerel sharks.
Remarks: The genus Isurus is comprised of two wide-ranging species, both of which occur in the North Atlantic. The genus account follows Compagno (1984, 2001) and Ebert (2001b, 2003) with some modifications.

## Key to North Atlantic Species:

1a. Ventral surface of snout and mouth white, anterior teeth recurved forward, pectoral fins much shorter than head length, and anal fin originating below second dorsal-fin base (Fig. 192) Isurus oxyrinchus

1b. Ventral surface of snout and mouth dusky, anterior teeth straight, pectoral fins about equal to head length, and anal fin originating below or posterior to second dorsal-fin insertion (Fig. 193)

Isurus paucus


Fig. 192 Isurus oxyrinchus


Fig. 193 Isurus paucus

## Isurus oxyrinchus Rafinesque, 1810

Isurus oxyrinchus Rafinesque, 1810a, Caratt. gen. sp. anim. piant. Sicilia, Palermo, pt. 1: 12, pl. 13, fig. 1. Also Rafinesque, 1810b, Indice Ittiol. Sicil.: 45. Holotype unknown, type locality Sicily, Mediterranean Sea. Variant spellings include Lamia oxyrhinus Bory de St. Vincent, 1829, and Isurus oxyrhynchus Jordan and Evermann, 1896.

Synonyms: Isurus spallanzanii Rafinesque, 1810b: 45, 60. Type locality: Sicily. No types known according to Eschmeyer (1998). Oxyrhina gomphodon Müller and Henle, 1839: 68, pl 28 . Holotype, Zoologisches Museum, Museum für Naturkunde der Humboldt-Universitat, Berlin, ZMB 4528, a stuffed adult male $1650 \mathrm{~mm}+$, without head, jaws separate according to Paeke and Schmidt (1988: 163), from "Ocean". Carcharias tigris Atwood, 1865: 81. No distinguishing features; also Atwood, 1869: 268. Types: None, from the Gulf of Mexico and Cape Cod, Massachusetts.

Other Combinations: None

FAO Names: En - Shortfin mako; Fr - Taupe bleu; Sp - Marrajo dientuso.


Fig. 194 Isurus oxyrinchus

Field Marks: Body moderately slender to relatively robust (especially in very large females), with a long, acutely pointed snout, eyes less than one-third snout length, pectoral fins less than head length, a high, erect first dorsal fin, an anal fin originating under midbase of second dorsal fin, and a crescent-shaped caudal fin. Colour a brilliant blue above, becoming lighter blue on the flanks, and white below; ventral surface of snout usually white.

Diagnostic Features: Body moderately slender but more robust when compared to similar sized Isurus paucus. Snout long and acutely pointed. Eyes relatively small, diameter less than $33 \%$ snout length. Mouth broadly rounded. Teeth similar in both jaws, narrow, slender, flexuous and more oblique. Tooth counts 24 to 26 upper jaw, 22 to 32 lower jaw. First dorsal-fin origin over or just posterior to pectoral-fin free rear tip; height of first dorsal fin greater than base length, except in individuals less than 185 cm total length. Pectoral fins relatively narrow at tips, length considerably less than head length. Pelvic-fin anterior margins distinctly shorter than posterior margins. Anal-fin origin under midbase of second dorsal fin. Vertebral counts: total vertebral counts 182 to 196, precaudal vertebral counts 107 to 112 . Spiral valve turn count 47 to 48 . Colour: dorsal surface a brilliant bright blue, becoming lighter blue laterally and white on ventral surface; ventral surface of snout usually white.

Distribution: Circumglobal in most tropical and temperate seas from $50^{\circ} \mathrm{N}$ (up to $60^{\circ} \mathrm{N}$ Eastern North Atlantic) to $50^{\circ} \mathrm{S}$. Eastern North Atlantic: occasional records from Norway (from about $60^{\circ} \mathrm{N}$ ) and British Isles; more common further south, including Bay of Biscay, Spain, Portugal, the Azores, and off Northwest Africa, including the Mediterranean Sea. Western North Atlantic: Newfoundland, Canada, south along the Atlantic coast to Florida, U.S.A., and the Gulf of Mexico.

Habitat: A common, coastal to offshore, oceanic, epipelagic shark that occurs from the surface to at least 600 m deep.
Biology: Viviparous with oophagy, but much of their reproductive cycle remains unknown. Litter size is between 4 and 25, with a gestation period of 15 to 18 months, followed by a resting period, making the overall time between birthing events as long as 3 years. Litter size increases with size of the female. Birth usually occurs in the spring and summer, but nursery grounds are poorly known other than they appear to be located close to coastal areas; the area off Gibraltar appears to be a possible nursery area.
Age estimates have been validated for this species in the North Atlantic, with males maturing at about 8 years and living to at least 29 years, and females maturing at 18 years with a maximum age of at least 32 years. Shortfin mako shark grow quite rapidly in their first few years of life, averaging a little over 60 cm per year the first year and over 40 cm in year two. Growth appears to be quite rapid until they approach and reach maturity.

The diet consists mainly of bony fishes, with crustaceans and cephalopods making up a lesser component of their diet; elasmobranchs are not a common component of their diet. Juvenile and neonates tend to consume crustaceans and cephalopods in higher proportion and larger quantities than adults, and there appears to be a seasonal shift in diet preference depending on the season and prey availability and abundance. Larger shortfin makos, 300 cm or more, have broader, more flattened and triangular teeth; their diet reflects this in being much broader, and with larger prey items being consumed. Blue marlin (Makaira nigricans) and sailfish (Istiophorus platypterus) bills have been found embedded in shortfin makos suggesting possible predation events. Shortfin makos have few predators, but great white sharks (Carcharodon carcharias) and killer whales (Orcinus orca) are known predators; killer whales have been observed to prey on them off the Azores and New Zealand.


Fig. 195 Isurus oxyrinchus

The North Atlantic is considered one single stock based on genetic (Heist et al. 1996; Schrey and Heist, 2003) and tagging data, but is separate from those from other oceans outside the North Atlantic. The southern limit of the North Atlantic stock is at about $5^{\circ} \mathrm{N}$. The relationship between the North Atlantic and Mediterranean is not certain. The shortfin mako shark is known to make trans-Atlantic movements with some individuals moving more than 4500 km .

Size: Maximum length about 400 cm ; size at maturity varies slightly between regions, but in the North Atlantic males mature at about 195 cm with a maximum length of 285 cm , while females mature at between 270 and 300 cm , with a maximum length of about 400 cm . Size at birth from 60 to 70 cm in length.

Interest to Fisheries and Human Impact: Shortfin mako sharks are one of the most important targeted shark species in open ocean pelagic fisheries. They are taken in both targeted and non-targeted fisheries with longline and drift gillnets. They are also frequently taken in recreational fisheries and are a popular and exciting game fish for anglers. Landing records however have been underestimated historically due to a lack of accurate species identification, but in recent years (since about 2005) they have improved due to increased reporting requirements adopted by ICCAT. No catch limitations imposed by EU, but removal of fins and discarding of body is prohibited by EU and non-EU vessels in EU waters (2012). The US National Marine Fisheries Service encourages the live release of shortfin mako sharks (2012).

Attacks by shortfin mako sharks on bathers, divers, and swimmers are rare, but have been confirmed in several instances. There have also been a number of documented attacks on boats.

The conservation status of this shark is Vulnerable globally and in the North Atlantic do to suspected declines in its population.
Local Names: Mako shark, Atlantic mako shark, Mackerel shark, Blue shark, Mackerel porbeagle (English); Anequin (Portugal); Marracho, Rinquim, Mako, Marrajo criollo (Azores); Sobraig, Sobratg, Ludia marraco, Marraquet, Marrajo, Tiburón (Spain); Makrellhai (Norway); Makrelenhai (Germany).

Literature: Bigelow and Schroeder (1948); Garrick (1967a); Stillwell and Kohler (1982); Compagno (1984, 2001); Quéro in Whitehead et al. (1984a); Moreno and Morón (1992b); Gilmore (1993); Fierstine, Cailliet, and Neer (1997); Heist et al. (1996); Henderson, Quigley, and Flannery (1999); Mollet et al. (2000); Visser et al. (2000); Ebert (2001b, 2003); Campana, Natanson, and Myklevoll (2002); Schrey and Heist (2003); Cailliet et al. (2004, 2006); Campana, Marks, and Joyce (2005); Loefer, Sedberry, and McGovern (2005); Ardizzone et al. (2006); Maia et al. (2006); Natanson et al. (2006); Maia et al. (2007); Wood, Collie, and Kohler (2007); Gibson et al. (2008); Stevens (2008, 2010); Last and Stevens (2009); Ebert and Winton (2010); ICES (2010); D.A. Ebert (unpubl. data); L.J. Natanson (pers. comm.).

## Isurus paucus Guitart, 1966

Isurus paucus Guitart, 1966, Poeyana, Ser. A, (15): 3, figs. 1, 2A, 3A, 3C. Syntypes: 2260 mm PCL adult female, 2030 mm PCL adult male, and 1955 mm PCL adult female, possibly in the Instituto de Biologia or Instituto de Oceanologia, Cuba, collected in the Caribbean near Cuba. No type known according to Eschmeyer (1998).

Synonyms: None.
Other Combinations: None.
FAO Names: En - Longfin mako; Fr - Petit taupe; Sp - Marrajo carite.


Fig. 196 Isurus paucus
Field Marks: Body relatively slender, fusiform-shaped, with a narrow to bluntly pointed snout, eye diameter more than $33 \%$ snout length, pectoral-fin length equal to head length, high, erect first dorsal fin, an anal fin originating slightly posterior to second dorsal-fin insertion, and a crescent shaped caudal fin. Dorsal surface a grayish-black, ventral surface white except for dusky coloration on the underside of snout and around mouth; especially prominent in large adults.

Diagnostic Features: Body relatively slender when compared with similar sized Isurus oxyrinchus. Snout long, narrow to bluntly pointed. Eyes relatively large, diameter more than $33 \%$ snout length. Mouth broadly rounded. Teeth similar in both jaws, broad, robust, less flexuous, and less oblique. Tooth counts 24 to 26 upper jaw, 22 to 24 lower jaw. First dorsal-fin origin distinctly posterior to pectoral-fin free rear tip; height of first dorsal fin greater than base length, in individuals at all sizes. Pectoral fins relatively straight, broadly tipped, length considerably about equal to or greater than head length. Pelvic-fin anterior margins nearly equal to that of posterior margins. Anal-fin origin slightly behind insertion of second dorsal fin. Vertebral counts: total vertebral counts 195 to 197 , precaudal vertebral counts 111 to 112 . Spiral valve turn count 54 . Colour: dorsal surface dark blue to blackish above, becoming white ventrally; ventral surface of snout distinctly dusky or dark, except in small juveniles.

Distribution: Eastern North Atlantic: Spain, Portugal, and possibly the Mediterranean. Also, from off Morocco, Western Sahara, Canary Islands, Mauritania, Guinea-Bissau, Liberia, Ghana, and possibly the Cape Verde Islands. Western North Atlantic: Newfoundland southwards along the Atlantic coast of Canada and the United States to Florida, Cuba, the Gulf of Mexico, and to Brazil. Elsewhere, known from scattered records in the Pacific and western Indian oceans.

Habitat: Little known, other than this epipelagic, oceanic shark generally occurs in tropical and warm temperate seas off the continental shelf at depths of 120 to 240 m or more. It is thought to be deeper dwelling than it sister species the shortfin mako shark, but bathymetric data confirming this is not yet available.

Biology: Oophagous with litters of 2 to 8 , but nothing is known of their reproductive cycle including gestation. Longfin mako sharks feed mostly on schooling fishes and pelagic cephalopods.

Size: Maximum length about 430 cm ; males mature at 190 to 228 cm and females at 245 cm . Size at birth 92 to 97 cm .

Interest to Fisheries and Human Impact: The longfin mako is rarely reported in fisheries landings, and they appear to be far less common relative to the shortfin mako that is the subject of major fisheries worldwide. The flesh of the longfin mako is mushy and of poorer quality than the shortfin mako, and they appear to be discarded more frequently; although it is likely their fins are retained. Seafood buyers in North America generally will not market them.
Although encounters with longfin makos are rare, a SCUBA diver in the Caribbean off Cozumel recently photographed one. They have not been implicated in any attacks on humans, but given their large size and jaws, they could be potentially dangerous.


Fig. 197 Isurus paucus

The conservation status of this shark is currently listed as Vulnerable as a precautionary measure do its apparent low reproductive rate and lack of information on its population and stock structure.

Local Names: Longfinned male shark, Taupe longue aile (France); Marrajo negro (Azores); Dientuso prieto (Cuba).
Remarks: The longfin mako shark was long recognized as being distinct from the shortin mako by Azorean fishermen who separated them long before researchers and fisheries biologists recognized them as being distinctly different species.

Literature: Guitart-Manday (1966, 1975); Garrick (1967a); Dodrill and Gilmore (1979); Gilmore (1983, 1993); Compagno (1984, 2001); Quéro in Whitehead et al. (1984a); Killam and Parsons (1985); Moreno and Morón (1992b); Ebert (2001b, 2003); Reardon, Gerber, and Cavanagh (2006); Gibson et al. (2008); Last and Stevens (2009); D.A. Ebert (unpubl. data); L.J. Natanson (pers. comm.).

## Lamna Cuvier, 1816

Genus: Subgenus Lamna Cuvier, 1816 (Genus Squalus Linnaeus, 1758), Reg. Anim., ed. 1, 2: 126.
Type species: Squalus cornubicus Bloch and Schneider, 1801 by monotypy, equals $\boldsymbol{S}$. cornubicus Gmelin, 1788: 1497, and a junior synonym of $S$. nasutus Bonnaterre, 1788.

## Number of Recognized North Atlantic Species: 1.

Synonyms: Genus Lamia Risso, 1826: 123. Type species, "L. cornubicus $\mathrm{L} "=$ Squalus cornubicus Gmelin, 1788 by monotypy. Genus Selanonius Fleming, 1828: 169. Type species, Selanonius walkeri Fleming, 1828 by monotypy (Eschmeyer, 1998), junior synonym of Squalus nasus Bonnaterre, 1788. Genus Exoles Gistel, 1848: ix. Replacement name for Lamia Risso, 1826, and hence taking the same type species, Squalus cornubicus Gmelin, 1788.

Field Marks: Stout-bodied, fusiform shaped sharks with short to long conical snout, large eyes, and two prominent caudal keels. Teeth similar in both jaws, awl-shaped, with a single narrow, smooth-edged cusp, flanked by a smaller cusplet on each side. Dorsal colour bluish grey to blackish, becoming white below; adults of Lamna ditropis with scattered dark blotches ventrally, L. nasus adult without any distinctive dark spots or blotches ventrally.

Diagnostic Features: Body fusiform, very stout. Snout acute to very bluntly conical. Eyes very large, diameter 1.6 to $2.8 \%$ of total length. Mouth parabolic, width 1.4 to 2.3 times length. Teeth slender, awl-shaped, smooth-edged, with a single
smaller lateral cusplet on each side of central cusp; shape similar in both jaws. Tooth count 28 to 32 upper jaw, 26 to 30 lower jaw. First dorsal fin originates over or just posterior to pectoral-fin insertions. Second dorsal-fin origin about over anal-fin origin. Caudal fin crescent shaped, and with secondary caudal keels present and strong. Vertebral counts: total vertebral counts 150 to 181, precaudal vertebral counts 84 to 91 , caudal vertebral counts 68 to 71 . Intestinal valve of ring type with count 37 to 41 . Length of adults to at least 310 cm . Colour: bluish grey to blackish grey above, becoming white ventrally, with or without dusky blotches present on adults; free rear tip of first dorsal fin on Lamna nasus white.

Local Names: Porbeagles, Mackerel sharks, Salmon sharks.
Remarks: The genus has two species recognized, the salmon shark (Lamna ditropis) endemic to the North Pacific, and the porbeagle (L. nasus) that occurs in the North Atlantic and Southern Oceans.

## Lamna nasus (Bonnaterre, 1788)

Squalus nasus Bonnaterre, 1788, Tabl. Encyclo. Method. Trois Reg. Nat., Ichthyol., Paris: 10, pl. 85, fig. 350. Holotype unknown, type locality probably Cornwall, England (Eschmeyer, 1998, Cat. Fish.).
Synonyms: Squalus glaucus Gunnerus, 1768: 1, pl. 1. Type locality, Norway. A junior homonym of $\boldsymbol{S}$. glaucus Linnaeus, 1758 (= Prionace glauca). Squalus cornubicus Gmelin, 1788: 1497. No types known according to Eschmeyer (1998). Type locality: Cornwall, England. Squalus pennanti Walbaum, 1792: 517. Type locality: Atlantic. No types according to Eschmeyer (1998). Squalus monensis Shaw, 1804: 350. Based on the 'Beaumaris Shark' of Pennant, a 233 cm shark observed and reported by Rev. Hugh Davies, of Beaumaris, Isle of Anglesey, Wales. No types known according to Eschmeyer (1998). Shaw thought that his S. monensis might be the same as Squalus cornubicus Gmelin, 1788 (= Lamna nasus), and that differences between them might be attributable to sexual dimorphism. Squalus cornubiensis Pennant, 1812: 152. Type locality: Cornwall. Variant spelling of $\boldsymbol{S}$. cornubicus Gmelin, 1788 according to Eschmeyer (1998). Squalus selanonus Leach, 1818: 64, pl. 2, fig. 2. Holotype: University of Edinburgh, ca. 260 cm TL adult male, Lochfyne, Scotland. Selanonius walkeri Fleming, 1828: 169. Argyll, Scotland. Based on Squalus selanonus of Walker, 1769 (manuscript name) according to Eschmeyer (1998). Lamna punctata Storer, 1839: 185, pl. 3, fig. 2. Also Storer, 1839: 534, pl. 8. New combination for and misinterpretation of Squalus punctatus Mitchill, 1815 (= Carcharhinus isodon), itself a junior homonym of S. punctatus Bloch and Schneider, 1801 (= Ginglymostoma cirratum). Type locality: Massachusetts Bay; cf. Eschmeyer (1998). Lamna pennanti Desvaux, 1851: 23. Possibly new combination based on Squalus pennanti Walbaum, 1792. Oxyrhina daekayi Gill, 1862a: 60. New name for Lamna punctata Storer, 1839 according to Eschmeyer (1998). Isuropsis dekayi Gill, 1873: 813 (emended spelling of specific name).
Other Combinations: Lamna cornubica (Gmelin, 1788).
FAO Names: En - Porbeagle; Fr - Requin-taupe commun; Sp - Marrajo sardinero.


Fig. 198 Lamna nasus


UPPER AND LOWER TEETH


Frontal view


Dorsal view

DERMAL DENTICLES
Field Marks: Stout fusiform-shaped body, with a relatively long, conical snout, teeth with large smooth-edged cusp and small lateral cusplets either side (these can be obscured in juveniles), first dorsal fin erect, high, free rear tip abruptly white, second dorsal and anal fins comparatively small, and prominent secondary caudal keels on crescent-shaped caudal fin. Dorsal surface colour dark bluish-grey, becoming white on ventral surface of body white; free rear tip of first dorsal fin prominently white.

Diagnostic Features: Body fusiform, very stout. Snout relatively long and acutely conical. Eyes very large, diameter about one-third snout length. Mouth broadly rounded, width 1.5 times length. Teeth with long narrow, smooth-edged cusp, flanked by a single lateral cusplet on each side. Tooth count 28 to 31 upper jaw, 26 to 29 lower jaw. First dorsal fin originates over or slightly posterior to pectoral-fin insertions. Second dorsal-fin origin about over or slightly anterior to anal-fin origin. Vertebral counts: total vertebral counts 150 to 162, precaudal vertebral counts 84 to 91, caudal vertebral counts 68 to 71 . Intestinal valve of ring type with count 38 to 41 . Maximum length to at least 320 cm . Colour: dark bluish grey to grey above, becoming abruptly white below; first dorsal-fin free rear tip pale to white, pectoral fins dusky; ventral surface of head and abdomen without dark or dusky blotches in North Atlantic adult population, but underside of head dusky and abdomen blotched in some adults of Southern Hemisphere population.

Distribution: Eastern North Atlantic: Greenland, Iceland, Norway, British Isles, Sweden, Germany, France, and south to Spain, Portugal (including the Azores) and Morocco, also the Mediterranean Sea. Western North Atlantic: Greenland south to the Carolina's (U.S.A.) and the Sargasso Sea as far south as about $21^{\circ} \mathrm{N}$. Also, occurs at high latitudes in the southern hemisphere.

Habitat: A wide-ranging, coastal and oceanic shark, found at high latitudes in the North Atlantic and in the southern oceans. This is one of the few, truly high latitude shark species that readily occurs at high latitudes and in Arctic waters. They prefer a water temperature usually below $18^{\circ} \mathrm{C}$, and preferably between 5 and $10^{\circ} \mathrm{C}$, but have been found to occur as low as $-1{ }^{\circ} \mathrm{C}$ and as high as $23^{\circ} \mathrm{C}$. Porbeagles, like other mackerel sharks, are endothermic and can maintain its body temperature several degrees above ambient water temperature. Recent tracking studies have shown that these sharks exhibit subtropical submergence, diving to great depths as they migrate


Fig. 199 Lamna nasus
$\square$ Known distribution $\square$ Possiblc distribution to lower latitudes to specific nursery grounds. Depth range of the porbeagle is from the surface in water less than 1 m in nearshore waters to at least 1360 m .

Biology: Viviparous, with oophagy, litters range from 1 to 5, averaging 4, with an estimated gestation period of about 8 to 9 months in the North Atlantic followed by a resting period, possibly of 12 months, between parturition and mating. Birth occurs in the Eastern North Atlantic during the spring, and in the Western North Atlantic during the spring and summer. Porbeagles
segregate by season, sex, and maturity stage, with adult males and juveniles remaining at high latitudes during the winter, while adult females migrate to lower latitudes for birthing.

Recent tracking studies in the North Atlantic have shown that adult females migrate long distances of over 2400 km to subtropical areas on both side of the North Atlantic to specific nursery grounds. These migrating sharks will dive to depths that are below the warmer Gulf Stream in the Western North Atlantic; average depth before entering the Gulf Stream is less than 248 m , but after entering the mean depth is about 845 m . In the Western Atlantic the Sargasso Sea appears to be a major pupping ground for porbeagles, while the area off Northwest Africa in the Eastern Atlantic may represent another pupping area.

The age at maturity for the North Atlantic population is from 6 to 10 years for males and 12 to 16 years for females; age at 50\% maturity is 8 years for males and 13 years for females. Maximum age is at least 26 years and possibly as much as 46 years. The diet of porbeagles consists primarily of pelagic bony fishes and cephalopods when feeding offshore in deepwater, but on the continental shelf and in shallow water they feed more on demersal bony fishes.

Size: Maximum reported length is 355 cm ; males mature at about 195 cm in the North Atlantic (slightly larger than the 165 cm in the South Pacific), and females mature at about 245 cm in the North Atlantic (at about 195 cm in the South Pacific). Size at birth is 68 to 78 cm length.

Interest to Fisheries and Human Impact: The porbeagle fishery in the North Atlantic has been the subject of intense fishing pressures over the past 50 to 60 years with the population having collapsed and recovered, and collapsed once again from heavy fishing pressure. According to the ICCAT (2009) and ICES (2010) the Eastern North Atlantic population is seriously depleted and the fishery has largely ceased as of 2009 due to restrictive management policies introduced in 2008. Historically, the main target fishery was the Norwegian fishery operating north of Scotland and west of Norway. After this fishery declined, the main fishing countries were France and, to a lesser extent Spain, the United Kingdom, and Norway. The main targeted porbeagle fishery in recent years was the French fishery in the Bay of Biscay and Celtic Sea, although some other countries have had smaller target fisheries. In addition, they are taken as bycatch in mixed fisheries in the United Kingdom, Ireland, France, and Spain (ICES, 2010).

The European Union (EU) prohibits fishing for porbeagle in EU waters and for EU vessels to fish for, retain, transship, or to land them in international waters (EU, 2012). Directed fishery banned in Norway (2012). The Eastern North Atlantic population is considered to be a single stock that occurs from Norway and Iceland to Northwest Africa. The Western North Atlantic stock however is considered to be a separate stock from the Eastern North Atlantic. This has been confirmed from tagging studies that show very little movement between stocks, although based on molecular studies there is some evidence of gene flow between these two stocks. The Mediterranean Sea population appears to be distinct from the North Atlantic with little to no mixing between stocks.

The global conservation status of porbeagles is Vulnerable, but in the Eastern North Atlantic they are considered to be Critically Endangered. It was proposed in for listing on CITES Appendix II in 2010, but the proposal did not receive the required majority support at the $15^{\text {th }}$ Conference of Parties.

Local Names: Mackerel shark, Common probeagle, Porbeagle shark, Atlantic mackerel shark, Common Atlantic mackerel shark, Salmon shark, Atlantic porbeagle, American porbeagle, Beaumaris shark, Blue shark, Blue dog (England and U.S.A.); Le lamie long nez, Lamie, Nez, Touilele boeuf taupe, Requin long nez, Loutre de mer, Nas llarg, Melantoun (France); Neushaai (the Netherlands); Sillhaj or Herring shark, Sildehaj (Denmark); Hámeri (Iceland); Håbrann (Norway); Morgi mawr (Wales); Haabranden, Haamar (Sweden); Calderon, El maarago, Ludia, Marraco, Marraquet, Marraix, Marrajo, Taulo (Spain); Anequim, Arrequim, Marracho, Sardo (Portugal); Marracho (Azores); Requiem, Nequim (Maderia); Akula sel devaia (Russia); Heringshai (Germany).

Literature: Bigelow and Schroeder (1948); Aasen (1961, 1963); Templeman (1963); Compagno (1984, 2001); Quéro in Whitehead et al. (1984a); Gauld (1989); Gilmore (1993); Ellis and Shackley (1995); Santos, Porteiro, and Barreiros (1997); Francis and Stevens (2000); Campana et al. (2002); Campana, Natanson, and Myklevoll (2002); Jensen et al. (2002); Joyce et al. (2002); Natanson, Mello, and Campana (2002); Francis and Duffy (2005); Stevens et al. (2006); Cassoff, Campana, and Myklevoll (2007); Francis, Campana, and Jones (2007); Francis, Natanson, and Campana (2008); Gibson et al. (2008); Campana, Joyce, and Fowler (2010); Ebert and Winton (2010); EU (2012); ICES (2010); Saunders, Royer, and Clarke (2011); J. Ellis (pers. comm.).

### 2.6 Order CARCHARHINIFORMES - Ground Sharks

Order: Carcharhiniformes Compagno, 1973, J. Linn. Soc. (Zool.) London, 53, suppl. 1.

## Number of Recognized North Atlantic Families: 5.

FAO Names: En - Ground sharks.
Field Marks: These sharks exhibit a wide range in external body morphology, but are generally characterized by having two spineless dorsal fins (except for 1 or 2 species which may have a single dorsal fin), five paired gill openings, a nictitating lower eyelid, a long mouth extending to or behind the eyes, and an anal fin. This group has some of the smallest and largest known shark species.

Diagnosis Features: Trunk cylindrical to slightly compressed or depressed but not raylike. Head conical to depressed and usually not anteriorly expanded, except for the prebranchial head in Sphyrnidae; 5 pairs of gill slits present on sides of head (partly dorsolateral in some Scyliorhinidae), with the last 1 to 3 over pectoral bases; spiracles present in many species, small to large and close behind eyes, or absent; nostrils usually without barbels and nasoral grooves and always without circumnarial grooves, barbels when present developed from anterior nasal flaps rather than from lateral surfaces of flaps, anterior nasal flaps varying from well separated from mouth to overlapping it posteriorly; eyes lateral or dorsolateral on head, with true nictitating lower eyelids; snout varying from very short to moderately long and almost bladelike, but not greatly elongated and not formed as a rostral saw with lateral teeth and barbels; mouth moderately large to very large, arched, and extending behind anterior ends of eyes; labial furrows varying from large and on both jaws to absent; teeth variably differentiated along jaws, but usually without enlarged molariform posterior teeth and with anterior teeth not separated by small intermediate teeth or a gap from the lateral teeth. Two dorsal fins (possibly only one in Pentanchus, family Scyliorhinidae), without spines, the first with origin varying from over the gill slits to behind the pelvic-fin bases; pectoral fins moderate-sized to large but not raylike, without triangular anterior lobes; pelvic fins small to moderately large, with vent continuous with their inner margins; anal fin present; caudal fin with a long dorsal lobe but with ventral lobe varying from long (but considerably shorter than the dorsal lobe) to absent. Vertebral counts: total vertebral counts 100 to 244 , monospondylous vertebral counts 23 to 68, diplospondylous vertebral counts 23 to 66 , precaudal vertebral counts 41 to 137. Intestinal valve of spiral or scroll type. Size small to very large sharks maturing at less than 100 cm to over 400 cm in length. Colour: depending on the family and genera these sharks are highly variable in colour ranging from rather striking brilliant colour patterns to rather plain without prominent markings. Reproductive modes are wide-ranging from oviparous egg laying species to viviparous, with one family (Pseudotriakidae) exhibiting oophagy.

Distribution: Circumglobal from cold temperate to tropical seas, with representatives of five of eight families occurring in the North Atlantic.

Habitat: Ground sharks occur in a variety of marine habitats from the intertidal and enclosed bays, estuaries, including freshwater rivers, to the deep sea, and to open ocean pelagic realm. They occur over sandy and mud bottoms, rocky and coral reefs, and in kelp forests.

Biology: These are very active to sluggish swimming sharks with some species being highly migratory while others have a more limited geographic range. They exhibit varied reproductive strategies between groups with some (Scyliorhinidae) being oviparous by depositing egg cases on the bottom while most other groups are live bearing, but exhibit various forms of viviparity with some providing nutrition by yolk-sac and others maternally with the developing embryos being supplied nutrition directly from the mother. There are no known filter feeders in this order, but ground sharks feed on a wide variety of prey items including crustaceans, cephalopods, bony fishes, other chondrichthyans, and even marine mammals in some of the larger species. Many ground sharks are social, with some species occurring in large aggregates or schools, often segregating by sex and life stage.

Interest to Fisheries and Human Impact: Many carcharhinoids are the subject of moderate to major targeted and nontargeted fisheries. Members of the families Carcharhinidae, Sphyrnidae, and Triakidae are the subject of major fisheries globally, while many of the demersal bottom-dwelling species, primarily the Scyliorhinidae, are taken in considerable numbers as by-catch. This group contains some of the most well known species that have been implicated in shark attacks around the world. The bull shark (Carcharhinus leucas), oceanic whitetip shark (C. longimanus), and tiger shark (Galeocerdo cuvier) are among the species that have been implicated in shark attack mostly in tropical and open ocean environs. Approximately 38 species of North Atlantic ground sharks are listed as being either Vulnerable or higher in terms of their conservation status.

Local Names: None.
Remarks: The present account follows Compagno (1984, 1988, 1999, 2005) in recognizing eight families of which five families occur in the North Atlantic. See Compagno (1988) for discussion of this order.

## Key to Families Occurring in the North Atlantic:

1a. Head with lateral, bladelike expansions (Fig. 200)
family Sphyrnidae

1b. Head normal, without lateral expansions . . . 2

2a. First dorsal-fin base opposite or behind pelvic-fin bases (Fig. 201) .
family Scyliorhinidae

2b. First dorsal-fin base in front of pelvic-fin bases (Fig. 202) 3

3a. Precaudal pits present. Dorsal caudalfin margin undulated (Fig. 202)
family Carcharhinidae

3b. Precaudal pits absent. Dorsal caudal-fin margin not undulated (Fig. 203) 4

4a. Labial furrows very short or absent, when present confined to mouth corners. Posterior teeth on dental bands comblike (Fig. 204)
. . . . . . . . . . . . . . . family Pseudotriakidae

4b. Labial furrows relatively long with uppers extending partway or all the way anterior to level of symphysis. Posterior teeth on dental bands not comblike (Fig. 205) . family Triakidae


UNDERSIDE OF HEAD
Fig. 200 Sphyrna


Fig. 201 Scyliorhinus


Fig. 202 Carcharhinus


Fig. 203 Pseudotriakis


UNDERSIDE OF HEAD
Fig. 204 Pseudotriakis


UNDERSIDE OF HEAD
Fig. 205 Mustelus

### 2.6.1 Family SCYLIORHINIDAE

Family: Scylliorhinoidae Gill, 1862b, Ann. Lyceum Nat. Hist. New York, 7(32): 393, 396, 406, 412.
Type Genus: "Scylliorhinus Blainville, 1816", unjustified emendation of Scyliorhinus Blainville, 1816 by Gill, ibid: 407. Emended to family Scyliorhinidae by Jordan and Fowler, 1903, Proc. U. S. Natn. Mus. 26: 600.

## Number of Recognized North Atlantic Genera: 3.

FAO Names: En - Catsharks; Fr - Chiens, Holbiches, Roussettes; Sp - Alitanes, Pejegatos, Pintarrojas.
Field Marks: Usually elongated, catlike eyes with nictitating eyelids; nostrils usually without nasoral grooves but when present these are broad and shallow; mouth long, arched and reaching past anterior ends of eyes; small cuspidate teeth; two small, spineless dorsal fins and an anal fin, the first dorsal-fin base over or behind pelvic-fin bases; no precaudal pits, and the caudal fin without a strong ventral lobe or lateral undulations on its dorsal margin.

Diagnostic Features: Head without laterally expanded blades. Eyes elongated and fusiform, oval, or slitike, with lengths over 1.5 times height. Nictitating eyelids rudimentary. Spiracles present and moderately large. Anterior nasal flaps variably formed, but not barbel-like, except for one genus (Poroderma) with a barbel formed from a separate ridge on each anterior nasal flap. Internarial width about 0.6 to 1.3 times nostril width. Labial furrows absent or very short to very long. Teeth small, with acute narrow cusps, often lateral cusplets, and basal ledges, not bladelike and similar in both jaws; posterior teeth comblike or not; tooth rows 36 to 120 upper jaw, 31 to 111 lower jaw. Precaudal pits absent. Pectoral fins with radials confined to bases of fins. First dorsal fin small and not keel-like, much shorter than caudal fin; first dorsal-fin base over or behind pelvic-fin bases, origin either slightly ahead of pelvic-fin origins (Cephalurus) or well behind them; midpoint of first dorsal-fin base always posterior to pelvic-fin origins. Ventral caudal-fin lobe absent or very weak; no undulations or ripples in dorsal caudalfin margin. Vertebral centra with or without strong, wedge-shaped intermedial calcifications. Vertebral counts: total vertebral counts 85 to 163 , monospondylous vertebral counts 28 to 48 , diplospondylous precaudal vertebral counts 24 to 61 , precaudal vertebral counts 65 to 107. Valvular intestine with a spiral valve of 5 to 23 turns. Most catsharks are small, less than 80 cm long, and while some may be mature at about 30 cm , a few may reach about 160 cm . Colour: many species with variegated colour patterns, some without them. Development usually oviparous, but some species viviparous without yolk-sac placenta.

Distribution: This is by far the largest family of sharks, with a broad worldwide geographic range in tropical to coldtemperate and arctic waters.

Habitat: Catsharks occur from the intertidal and shore side to the edges of the continental and insular shelves and down the slopes to depths greater than 2000 m . Catsharks are generally found on or near the bottom in coastal waters inshore and offshore; none are oceanic, although some deepwater species may range a considerable distance off the bottom.

Biology: Most species are very poorly known biologically. The reproductive mode for many species is single oviparity, in which only one fertilized egg enters each oviduct and is deposited on the substrate at a time; the large eggs, encapsulated in tough egg-cases with corner tendrils to anchor them, have most of their embryonic development outside the mother shark and may take two years or more to produce a hatchling shark. Others, possibly in areas of intense egg predation, have multiple oviparity, in which several encased eggs remain in the oviducts for an extended period, during which time the embryos develop to advanced stages before the eggs are laid; such eggs may hatch in less than a month. Still other species have eliminated oviparity altogether and are viviparous, retaining the eggs until the young are ready to be born. Catsharks feed chiefly on invertebrates and small fishes, and are harmless to people. Catsharks are generally weak swimmers and do not migrate over great distances; this is shown in their geographic distribution, which is often much more localized than families with strong swimming species. Some inshore species are nocturnal, sleeping often in groups in rocky crevices in the day and dispersing to feed at night.

Interest to Fisheries and Human Impact: A minority of the species in this family is of importance to fisheries, particularly the spotted catsharks (Scyliorhinus) of the eastern Atlantic, which are much utilized for human food consumption or as bait in pot fisheries for whelk Buccinum undatum. Some are rather common and regularly taken as a bycatch in the trawl fisheries worldwide, and may be used for fishmeal and oil. Many are deepwater sharks, and are not known to be utilized to any great extent, although they may be a minor component of the catch of large, deep-fishing offshore trawlers. Several inshore species are commonly caught by sportsfishers. Many species are hardy and make attractive if somewhat sluggish exhibits in public aquaria; some readily breed in captivity.

Local Names: Catsharks, Cat sharks, Marbled catsharks (English); Dogfish (England); Roussettes (France); Katzenhai (Germany); Akuly koshach'i or Koshach'i akuly (Russia).

Remarks: The Scyliorhinidae is the most diverse shark family with 17 genera and 146 species. Three genera and at least 12 species occur in Areas 21 and 27 , but it would not be unexpected that other may be found to occur within these areas.

## Key to North Atlantic Genera:

1a. Supraorbital crests present on cranium, above eyes

Scyliorhinus
1b. Supraorbital crests absent from cranium . 2

2a. Head broadly flattened and spatulate, snout elongated and usually greater than mouth width. Labial furrows very long, uppers reaching upper symphysis (Fig. 206). Apristurus

2b. Head moderately or little-flattened, not spatulate, snout equal or usually less than mouth width. Labial furrows shorter or absent, when present not reaching upper symphysis (Fig. 207).


UNDERSIDE OF HEAD
Fig. 206 Apristurus


UNDERSIDE OF HEAD
Fig. 207 Galeus

## Apristurus Garman, 1913

Genus: Apristurus Garman, 1913, Mem. Harvard Mus. Comp. Zool., 36: 96.
Type Species: Scylliorhinus indicus Brauer, 1906, by original designation.

## Number of Recognized North Atlantic Species: 6.

Synonyms: None.
Field Marks: Scyliorhinids with "the Apristurus look"- Long, laterally expanded snout and head, enlarged nostrils with reduced anterior nasal flaps, very long labial furrows, small rear-sited spineless dorsal fins, very large, elongated anal fin separated from elongated caudal fin by a notch only, and uniform coloration.

Diagnostic Features: Body not tadpole-shaped, stocky and more or less compressed, increasing in height up to the pectoral and trunk region and tapering posteriorly; body very soft and flabby, with thin skin and weakly calcified dermal denticles; stomach not inflatable. Tail short, length from vent to lower caudal-fin origin about two-fifth to three-fifth of snout-vent length. Head greatly depressed, pointed and wedge-shaped in lateral view; head rather elongated, but usually slightly less than onefourth of total length in adults. Snout elongated, about equal to mouth width or greater, greatly flattened, narrow and pointed in lateral view; snout expanded laterally, narrowly spade-shaped to broadly spatulate and usually more or less bell-shaped in dorsoventral view. Ampullae pores enlarged and prominent on snout. Nostrils more or less enlarged, with incurrent and excurrent apertures broadly open to exterior; anterior nasal flaps reduced to angular lobes, without barbels, widely separate from each other and falling far anterior to mouth; internarial space 0.8 to 1.7 times nostril width; no nasoral grooves. Eyes dorsolateral on head, broad subocular ridges present below eyes. Mouth angular or broadly arched, with lower symphysis well behind upper so that upper teeth are exposed in ventral view. Labial furrows present along both upper and lower jaws, these long and reaching nearly or quite to level of upper symphysis of mouth. Tooth rows 36 to 102 upper jaw, 31 to 106 lower jaw. Branchial region not greatly enlarged, distance from spiracles to fifth gill slits less than half head length; gill slits lateral on head. Pectoral fins variable in size, their width less to greater than mouth width. Inner margins of pelvic fins not fused over claspers in adult males. Claspers short, thick, and distally pointed, not extending more than $2 / 3$ of their lengths behind the pelvic-fin tips and sometimes not extending past their tips. Two dorsal fins present, equal-sized or with the second dorsal fin larger than the first. Origin of first dorsal fin varying from over the pelvic-fin midbases to over the pelvic-fin free rear tips. Origin of second dorsal fin about over or slightly behind the anal-fin midbase. Anal fin enlarged and more or less elongated, larger than pelvic and dorsal fins, base length at least twice second dorsal-fin base; origin of anal fin just behind pelvic-fin bases, and insertion separated from lower caudal-fin origin by a narrow notch. Caudal fin more or less elongated, over a fifth, and often over a fourth of total length. A crest of enlarged denticles absent or variably developed on the dorsal caudal-fin margin. Supraorbital crests absent from cranium. Vertebral centra with or without strong, wedge-shaped intermedial calcifications. Vertebral counts: total vertebral counts 104 to 122, monospondylous vertebral counts 28 to 47 , diplospondylous precaudal vertebral counts 24 to 44 . Valvular intestine with a spiral valve of 6 to 22 turns. Colour: uniformly jet black, brownish-black, brown, pinkish or whitish; no distinctive colour patterns.

Local Names: Demon catsharks, Ghost catsharks.
Remarks: This is one of the largest and perhaps least known of shark genera, having some 35 described species, with several additional species of uncertain validity or still remaining to be described. Six species are known to occur in the North Atlantic, but it would not be surprising if several additional species, especially deepwater forms, were eventually discovered. Recent Eastern North Atlantic examples, include the discovery and descriptions of Apristurus aphyodes and A. melanoasper over the past decade and half.

## Key to North Atlantic Species:

1a. Body slender. Upper labial furrows longer than lowers. Supraorbital sensory canal discontinuous. Spiral valve turn counts 13 to 22. Egg cases with long, coiled tendrils (Fig. 208).

2 (Apristurus brunneus-group)

1b. Body stout. Upper labial furrows subequal to or shorter than lowers. Supraorbital sensory canal continuous. Spiral valve turn counts 7 to 12. Egg cases without tendrils (Fig. 209). 3 (Apristurus spongiceps-group)


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UNDERSIDE OF HEAD
Fig. 209 Apristurus profundorum

2a. Pectoral fins relatively large, broad, and subquadrangular. Eye diameter more than onehalf interorbital space. Spiral valve turn count 16 to 20 (mostly 17 to 19). Monospondylous vertebral counts 41 to 44 (mostly 42 to 43 )(Fig. 210)

## Apristurus laurussonii

2b. Pectoral fins relatively small, narrow, and subquadrangular. Eye diameter less than one-half interorbital space. Spiral valve turn count 19 to 23 (mostly 21 to 22 ). Monospondylous vertebral counts 36 to 43 (mostly 38 to 40)(Fig. 211).

Apristurus melanoasper
3a. Body uniformly whitish. Eye diameter 1.8 to 2.5 times in interorbital width (Fig. 212)

Apristurus aphyodes
3b. Body uniformly dark. Eye diameter 2.9 to 4.0 times in interorbital width

4a. Interdorsal space equal or slightly less than first dorsal-fin base. Pectoral-fin inner margins very short, about a third of pectoral-fin bases (Fig. 213).

Apristurus microps
4b. Interdorsal space greater than first dorsal-fin base. Pectoral-fin inner margins longer, half to about equal to pectoral-fin bases (Fig. 214)

5a. Body stout and strongly tapering to head. Lateral trunk denticles very sparse on body, not overlapping. Nostrils with circular, broad incurrent and excurrent apertures. Anal fin broadly rounded, caudal fin very narrow. Tips of dorsal fins usually whitish, occasionally plain (Fig. 214)

## Apristurus manis

5b. Body slender and not strongly tapering to head. Lateral trunk denticles more close-set on body, nearly overlapping. Nostrils with elongateoval, narrow incurrent and excurrent apertures. Anal fin subangular, caudal fin broader. Tips of dorsal fins plain (Fig. 215).

Apristurus profundorum


Fig. 210 Apristurus laurussonii


Fig. 211 Apristurus melanoasper


Fig. 212 Apristurus aphyodes


Fig. 213 Apristurus microps


Fig. 214 Apristurus manis


Fig. 215 Apristurus profundorum

Apristurus aphyodes Nakaya and Stehmann, 1998

Apristurus aphyodes Nakaya and Stehmann, 1998, Arch. Fish. Mar. Res. 46(1), 1998, 77, fig. 1-9. Holotype: Institut für Seefischerei, Hamburg, ISH 71-1981, 538 mm adult male, George Bligh Bank, $58^{\circ} 42.8^{\prime} \mathrm{N}, 13^{\circ} 37.6^{\prime} \mathrm{W}, 1200$ to 1240 m .

Synonyms: Apristurus atlanticus Compagno, 1984, FAO Species Catalogue, vol. 4, pt. 2 Sharks of the World: An Annotated and Illustrated Catalogue of Shark Species Known to Date: 261, figs.

Other Combinations: None.

FAO Names: En - White ghost catshark; Fr - Holbiche spectre; Sp - Tiburó gato fantasma.


Fig. 216 Apristurus aphyodes
Field Marks: Head broad and flattened, with an elongated snout, large nostrils and a long arched mouth extending well in front of the eyes; labial furrows very long, uppers shorter in length than lowers. Colour is a uniform pale grey with slightly darker edges on some fins.

Diagnostic Features: A slender to heavy bodied Apristurus Snout relatively long, flattened; preorbital snout length slightly less than one-half head length; prenarial snout slightly longer than one-half preoral snout length. Supraorbital canals conspicuous on dorsal and ventral surface of snout. Dermal denticles along dorsal body flank small and erect, strongly tricuspidate, with a long medial cusp flanked by a single lateral cusplet on either side. Mouth broadly arched, with well developed labial furrows; uppers slightly shorter than lowers. Teeth small, similar in upper and lower jaws, with single erect, high, medial cusp flanked by 2 to 3 smaller lateral cusplets. Tooth counts 56 to 68 upper jaw, and 49 to 64 lower jaw. Eyes large and oval, with a weak subocular fold. Spiracle small, located slightly below level of horizontal axis of eye. Gill openings five, similar in size except the fifth being slightly smaller and located above the pectoral-fin base. Pectoral fins relatively small, narrow, extending to less than one-third of interspace between paired fins when pressed against body. Space between origin of pectoral and pelvic fins almost equal to head length. Dorsal fins set far back, first dorsal fin slightly smaller than second, its origin over anterior half of pelvic-fin bases; second dorsal-fin origin above middle of anal-fin base; insertion slightly anterior to above that of anal-fin base. Anal fin high, with a short base, its origin below free rear tip of first dorsal fin; posterior end of base slightly posterior or below that of second dorsal fin; anal-caudal fin space separated only by a notch. Caudal fin slender and short. Vertebral counts: monospondylous vertebral counts 34 to 37 , diplospondylous vertebral counts 24 to 28 . Spiral valve count 9 to 11. A moderate sized Apristurus to 54 cm . Colour: uniformly whitish to lead grey with fins being slightly darker.

Distribution: Eastern North Atlantic: Iceland to the northern Bay of Biscay.

Habitat: Deep Atlantic slope from 1014 to 1800 m , usually over soft bottoms. Bottom temperatures where this species has been caught range from $3.7^{\circ} \mathrm{C}$ to $9.7^{\circ} \mathrm{C}$ and with a salinity of 35.1 to 34.9 ppm.


Fig. 217 Apristurus aphyodes
$\square$ Known distribution

Biology: Very little known. Egg case morphology is consistent with those of other Apristurus spongiceps-group Apristurus in being rather small ( 5 to 7 cm long and 2 to 3 cm wide), vase-shaped, and with the posterior portion oval; horns are very short and coiled, without long tendrils (Flammang, Ebert, and Cailliet, 2007). The diet is poorly known, but includes crustaceans, mostly shrimps and euphausiids, cephalopods, and small benthic fishes.

Size: Maximum length to 54 cm . Males and females mature between 40 to 47 cm ; males are fully mature by 47 cm ; females fully mature by at least 49 cm . Maximum length males 54 cm and females 53 cm . Size at birth unknown.

Interest to Fisheries and Human Impact: Unknown, most likely caught occasionally as bycatch in deepsea fisheries. Several species of deepsea Apristurus sharks are sometimes caught in large numbers, including A. aphyodes, since deepsea trawl fisheries developed in the 1990's along the Eastern North Atlantic continental slopes. However, catches of this and other deepsea catsharks are generally not recorded as they discarded at sea due to a lack of commercial value.
A. aphyodes, as with most Apristurus species, are small and soft-bodied.

Conservation status is Data Deficient due to lack of available life history information. This species is only known from a limited number of specimens.

Local Names: None.
Remarks: The morphological and meristic characteristics of this species place it within the A. spongiceps-subgroup of this genus.

Literature: Nakaya and Stehmann (1998); Nakaya and Sato (1999); Iglésias, Du Buit, and Nakaya (2002); Duffy and Huveneers (2004); Compagno, Dando, and Fowler (2005); Flammang, Ebert, and Cailliet (2007); Gibson et al. (2008); Ebert (In preparation).

## Apristurus laurrussonii (Saemundsson, 1922)

Scyllium laurussonii Saemundsson, 1922, Vidensk. Meddel. Dansk Naturhist. Foren. Kobenhaven, 74: 73, pl. 4, fig. 1, pl. 5 , fig. 4 . Note: figure numbers on pl. 4 are apparently reversed; fig. 1 is this species and not fig. 2 as cited in the text, which is Pristiurusjensenii(= Galeus murinus). Holotype: Natural History Museum, Reykjavik, Iceland, NHMR, 673 mm female, near Vestmannaeyjar Island, southern Iceland, 560 m .

Synonyms: Scylliorhinus atlanticus Koefoed, 1927, Rep. Sci. Res. "Michael Sars" N. Atl. Deep-sea Exped., 1910, 4(1): 18, pl. 3, fig 3. Holotype: Zoological Museum, Oslo, Norway, ZMO, about 25 cm TL. Type locality: off Canary Islands, $28^{\circ}$ $08^{\prime} \mathrm{N}, 13^{\circ} 35^{\prime} \mathrm{W}$, 1365 m . Apristurus maderensis Cadenat and Maul, 1966, Bull. Inst. Fond. Afrique Noire, ser. A, 28(2): 769, figs. 1-4. Holotype: Museu Municipal do Funchal, no. 18750, 668 mm total length adult female, Camara de Lobos, Madeira Islands, 600 to 1000 m. Synonymy after Nakaya and Sato (1998, Cybium 1998, 22(2): 149-157).

Other Combinations: None.
FAO Names: En - Iceland catshark; Fr - Roussette d'Islande; $\mathbf{S p}$ - Pejegato islándico.


Fig. 218 Apristurus laurussonii

Field Marks: Head broad and rather flattened, snout relatively short, with broad nostrils, mouth long and broadly arched and extending to anterior end of eyes, labial furrows extremely long, uppers longer than lowers and reaching symphysis, eyes small, diameter more than one-half interorbital space. First dorsal fin slightly larger than second, interdorsal space less than first dorsal-fin base, pectoral fins relatively large, broad, and subquadrangular. Colouration uniform dark above and below without lighter fin edges.

Diagnostic Features: Body relatively slender, trunk slightly tapering towards head. Snout moderately long, broad, and bell-shaped, preoral snout about 7 to $8 \%$ of total length. Gill slits short, less than eye length; gill septa without projecting medial lobes or pleats, somewhat incised. Eyes rather small in adults, about $3 \%$ of total length. Nostrils fairly broad, width about 1.4 in internarial space; incurrent and excurrent apertures large and oval, anterior nasal flaps long and angular. Mouth long, moderately large, and broadly arched, with dental bands somewhat expanded and with lower ones falling well behind uppers; mouth and labial furrows about opposite eyes. Labial folds somewhat enlarged, with lowers diagonal to body axis. Mouth and teeth not greatly enlarged in males. Tooth counts 54 to 102 upper jaw, 43 to 106 lower jaw. Lateral trunk denticles of body with crowns fairly flat and closely imbricate, surface fairly smooth and without a felt-like or fuzzy texture. Pectoral fins small, anterior margins about 12 to $13 \%$ of total length; inner margins long, about length of pectoralfin bases. Interspace between pectoral and pelvic-fin bases short, slightly less than prebranchial length and about $11 \%$ of total length in adults. Pelvic fins high and broadly rounded. Interdorsal space somewhat greater than first dorsal-fin base, slightly less than preorbital snout. First dorsal fin about as large as second, bases about equally long. Origin of first dorsal fin slightly anterior to pelvic-fin midbases. Second dorsal-fin insertion about opposite anal-fin insertion. Anal fin short, fairly high, and angular, slightly more than three times as long as high, base somewhat greater than prespiracular space and 14 to $17 \%$ of total length in adults. Caudal fin fairly broad, without a dorsal crest of enlarged denticles. Vertebral counts: monospondylous vertebral counts 41 to 44 , diplospondylous counts 29 to 35 . Spiral valve counts 16 to 20 . Adults large, to 72 cm . Colour: dark brown, without light-margined dorsal fins.

Distribution: Eastern North Atlantic: Southeast Greenland, Iceland, Faroe Islands, west of Scotland and Ireland, Canary Islands, Madeira Islands. Western North Atlantic: Southwest Greenland, Davis Straight and Labrador Sea (Canada), Massachusetts, Delaware, and Gulf of Mexico. Records of this species from Honduras and Venezuela, and equatorial Africa should be carefully examined to determine if they are the same or possibly a different species.

Habitat: A little-known deepwater species, apparently fairly common on the upper continental slopes, on or near the bottom at 560 to 2060 m depth. Bottom temperatures where this shark has been captured range from $1.7^{\circ} \mathrm{C}$ to $4.3^{\circ} \mathrm{C}$.

Biology: Oviparous, but nothing else known. Egg cases have been described for this Apristurrus brunneus-group catshark. Egg case length about 25 cm , surface covered with villi-like fibres forming fine longitudinal striations; anterior end angled, with long weak fibrous threads on each corner; posterior end with two horn-


Fig. 219 Apristurus laurussonii
$\square$ Known distribution like processes and long coiled tendrils extending from each. Diet unknown, but likely consists of crustaceans, cephalopods, and other small benthic fishes.

Size: Maximum about 72 cm ; adult male 68 cm ; adult female 59 cm . Size at birth unknown, but smallest known specimen measured 24.7 cm in length.

Interest to Fisheries and Human Impact: A deepwater Apristurus relatively common as bycatch in deepsea bottom trawl fisheries, but like most other members of this genus they are generally discarded at sea because they have no commercial value. All Apristurus species are under TAC regulation in EU waters (in 2012, TAC=0). Prohibited species in the NEAFC Regulatory Area.

The conservation status of this Apristurus is considered Data Deficient due to a lack of life history information.
Local Names: Flathead catshark or Cat shark, Madeira catshark, Atlantic ghost catshark (UK, USA); Gíslaháfur (Iceland); Roussette de Madère (France); Pejegato atlántico (Spain).

Literature: Springer (1966, 1979); Nakaya and Sato (1998, 1999); Iglesias, Du Buit, and Nakaya (2002); Iglesias and Nakaya (2004); Møller et al. (2010); Compagno, Dando, and Fowler (2005); Duffy and Huveneers (2007); Gibson et al. (2008); Flammang, Ebert, and Cailliet (2007).

## Apristurus manis (Springer, 1979)

Parmaturus manis Springer, 1979, Nat. Ocean. Atmosp. Admin. Tech. Rept., Nat. Mar. Fish. Serv. Circ. (422): 102, fig. 60-63. Holotype: Museum of Comparative Zoology, Harvard, MCZ-38299, 328 mm total length immature female, $39^{\circ} 52^{\prime} \mathrm{N}$, $70^{\circ} 50^{\prime} \mathrm{W}$, S.W. of Nantucket, Massachusetts, 731 to 841 m.

Synonyms: None
Other Combinations: Apristurus profundorum (not Goode and Bean, 1896; Springer, 1966)
FAO Names: En - Ghost catshark; Fr - Holbiche fantôme; Sp - Pejegato fantasma.


Fig. 220 Apristurus manis
Field Marks: An Apristurus with a distinctively thick body tapering anteriorly as a wedge to the snout tip, very small eyes, anteriorly expanded mouth, very sparse erect denticles on body, a prominent caudal crest of denticles, and sometimes white fin tips.

Diagnostic Features: Body relatively stout (especially in adults), trunk strongly tapering towards head. Snout long, relatively narrow and bell-shaped, preoral snout about 9 to $11 \%$ of total length. Gill slits moderately large, but somewhat less than eye length; gill septa without pleats or projecting medial lobes, well incised. Eyes rather small at all sizes, between 2 to $3 \%$ of total length. Nostrils fairly broad, width about 1.1 in internarial space; incurrent and excurrent apertures very large and circular, anterior nasal flaps long and angular. Mouth long, large, and broadly arched, particularly in adult males, with dental bands prominently expanded and with lower ones falling well behind uppers; mouth and labial furrows extending well in front of eyes. Labial folds somewhat enlarged, but with lowers diagonal to body axis. Mouth and teeth enlarged in adult males. Tooth counts 59 upper jaw, 52 lower jaw. Lateral trunk denticles of body with crowns erect, unusually far from one another and not imbricate, and with a prickly but not felt-like texture. Pectoral fins small, anterior margins about 8 to $13 \%$ of total length; inner margins long, nearly length of pectoral-fin bases. Interspace between pectoral and pelvic-fins bases short, equal or less than preorbital length and about 9 to $12 \%$ of total length in young and adults. Pelvic fins high and broadly rounded. Interdorsal space slightly greater than first dorsal-fin base, about two-thirds of preorbital snout. First dorsal fin slightly smaller than second, base of first over $3 / 4$ length of second. Origin of first dorsal fin over or slightly anterior to pelvic-fin midbases. Second dorsal-fin insertion opposite to anal-fin insertion. Anal fin rather short, high, and rounded, about three times as long as high, base about equal to prespiracular space and 13 to $16 \%$ of total length in young and adults. Caudal fin long and narrow, with a conspicuous crest of enlarged denticles on its dorsal margin. Vertebral counts: total vertebral counts 110 to 121, monospondylous vertebral counts 34 to 35 . Spiral valve counts 9 to 12. Adults large, adult male 88 cm . Colour: grey or blackish, with light tips on pectorals and dorsals of young at least.

Distribution: Eastern North Atlantic: Porcupine Bank west of Ireland; nominal "Apristurus profundorum" from off Mauritania (Golovan, 1976) are possibly this species. Western North Atlantic: New England from several deepwater canyons and possibly off Nova Scotia, Canada. Several Apristurus species nominally referred to as A. manis have been
taken in deepwater off Cape Town, South Africa (L.J.V. Compagno and D.A. Ebert, unpubl. data).

Habitat: A little known but bottom catshark of the Atlantic continental slopes at depths from 600 to 1900 m , but most common at depths beyond 1500 m .

Biology: Unknown. Egg case of spongiceps-group type, small, vaselike, 6.3 to 7.1 cm in length and with both anterior and posterior ends lacking tendrils; anterior end with short horns; posterior end with 8 to 10 small hair-like filaments, about 2 to 4 mm in length. Nothing is known about its diet, but this largish Apristurus deepsea catshark likely feeds on small fishes, crustaceans, and cephalopods.

Size: Maximum length to 88 cm ; females mature at about 70 cm and to at least 76 cm in length; adult males to 85.2 cm . Size at birth unknown, but the smallest free-swimming individual was 20 cm in length.


Fig. 221 Apristurus manis
$\square$ Known distribution $\square$ Possible distribution

Interest to Fisheries and Human Impact: Interest to fisheries none. Possibly caught occasionally as bycatch of deepwater trawl fisheries and discarded.

Conservation status is Least Concern due to its very deepwater (usually over 1500 m deep) habitat being outside the main deepwater fishing grounds.

Local Names: None.
Literature: Springer (1966, 1979); Compagno (1984, 1988); Kiraly, Moore, and Jasinski (2003); Moore et al. (2003); Ebert (2004a, In preparation); Compagno, Dando, and Fowler (2005); Flammang, Ebert, and Cailliet (2007); Gibson et al. (2008).

## Apristurus melanoasper Iglésias, Nakaya, and Stehmann, 2004

Apristurus melanoasper Iglesias, Nakaya, and Stehmann, 2004, Cybium: 345-346, figs 1-11, tabs 1-5. Holotype: Paris Museum Natural History, MNHM 2000-1757, 718 mm TL, mature male, $54^{\circ} 21.5^{\prime}-54^{\circ} 22.0^{\prime} \mathrm{N}, 19^{\circ} 28.1^{\prime}-19^{\circ} 44.4^{\prime} \mathrm{W}$, Lorien Bank, 1243-1260 m.

Synonyms: Apristurus sp. B, Quero, J.-C., P. Porche, and J.-J. Vayne, 2003, Guide des Poissons de l'Atlantique europeen. 465 p. Paris, Delachaux et Niestle: 25, photo, pl. 2. Apristurus sp. 6, Iglesias, Lecointre, and Sellos, 2005, Extensive paraphylies within sharks of the order Carcharhiniformes inferred from nuclear and mitochondrial genes, Mol. Phylogenet. Evol., 34: fig. 2, tab 1.

Other Combinations: None.
FAO Names: En - Black roughscale catshark; Fr - Holbiche noire; Sp - Tiburón gato negro escamoso.


Fig. 222 Apristurus melanoasper


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UPPER AND LOWER TOOTH


DERMAL DENTICLE

Field Marks: A slender, elongated, bodied with a flattened fleshy snout, mouth length extends to just anterior of eyes, labial furrows long, lowers shorter than uppers, anal fin high, long, and angular. A uniformly dark brown to black Apristurus with black naked fin tips.

Diagnostic Features: A slender elongate bodied Apristurus. Snout relatively narrow, long, and flattened. Dermal denticles along dorsal body flank small, tricuspidate with weak ridges; close-set denticles overlapping. Mouth moderately large, broadly arched, with well developed labial furrows; uppers longer than lowers. Teeth relatively small, similar in upper and lower jaws, with single erect, high, medial cusp flanked by 1 to 2 smaller lateral cusplets on anterior teeth; more lateral cusplets on posterior teeth. Tooth counts 59 to 93 upper jaw, and 58 to 97 lower jaw. Eyes moderately sized and oval, with a weak subocular fold. Spiracle small, located slightly below level of horizontal axis of eye. Gill openings five, similar in size except the fifth being slightly smaller and located above the pectoral-fin origin. Pectoral fins relatively small, narrow, subangular, extending less than one-half length of interspace between paired fins when pressed against body. Dorsal fins set far back, first dorsal-fin about equal to slightly smaller than second, its origin over anterior one-third to one-half of pelvic-fin bases; second dorsal-fin origin above anal-fin midbase; insertion slightly anterior to anal-fin insertion. Anal fin high, base shorter than distance between pectoral-fin free rear tip and pelvic-fin origin; anal-caudal fin space separated only by a notch. Caudal fin moderately long. Vertebral counts: monospondylous vertebral counts 36 to 42, diplospondylous vertebral counts 26 to 32 . Spiral valve counts 19 to 23 . Adults large to 79 cm . Colour: uniformly dark brown to black; naked fin apices black.

Distribution: Widespread, but patchy in the North Atlantic (off the northeastern U.S.A. and off France, Ireland, and the British Isles), southeastern Atlantic (Namibia). Central Indian Ocean and south of Madagascar, and in the Western South Pacific (Australia, New Zealand, and New Caledonia and surrounding seamounts).

Habitat: Continental mid-slopes and seamounts from 512 to 1520 m .

Biology: Virtually unknown. Egg cases have been described for this species and fit the characteristics of other A. brunneus-group Apristurus with long tightly coiled tendrils posteriorly and short blunt horns anteriorly.

Size: Maximum length about 79 cm ; males and females adult between 60 to 70 cm . Size at birth unknown.

Interest to Fisheries and Human Impact: The deepwater habitat of this species likely precludes it from being impacted very much by fisheries.


Fig. 223 Apristurus melanoasper
$\square$ Known distribution

Conservation status is Data Deficient due to a lack of information on its biology, deepwater habitat, and broad geographic distribution.

Local Names: Broadmouth catshark.
Remarks: The wide, spottily distributed species likely represents a species complex of one or more similar looking, but distinct species.

Literature: Moore et al. (2003); Iglesias, Nakaya, and Stehmann (2004); Hartel et al. (2008); Gibson et al. (2008); Nakaya, Sato, and Iglésias (2008); McCormack and Iglésias (2007); Last and Stevens (2009); Ebert (In preparation).

## Apristurus microps (Gilchrist, 1922)

Scylliorhinus microps Gilchrist, 1922, Rep. Fish. Mar. Biol. Surv. Un. S. Africa, (2): 46, pl. 7, fig. 1. Holotype lost, possibly below 30 cm total length, $33^{\circ} 45.8^{\prime} \mathrm{S}, 17^{\circ} 17.1^{\prime} \mathrm{E}$, W. of Cape Town, South Africa, 1445 m .

Synonyms: None.
Other Combinations: None.
FAO Names: En - Smalleye catshark; Fr - Holbiche porc; Sp - Pejegato puerco.



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Fig. 224 Apristurus microps
Field Marks: An Apristurus with an unusually small eye, thick snout, very short interdorsal space, anteriorly projecting mouth, very short pectoral inner margins, and a supracaudal crest of denticles.

Diagnostic Features: Body relatively stout, especially in subadults, trunk slightly tapering towards head. Snout moderately long, broad, and bell-shaped, preoral snout about 9 to $10 \%$ of total length. Gill slits moderately large, somewhat less or equal to eye length; gill septa without projecting medial lobes or pleats, well-incised. Eyes very small, especially in subadults, less than $3 \%$ of total length. Nostrils broad, width about 1.2 in internarial space; incurrent and excurrent apertures very narrow and slitlike, anterior nasal flaps very low. Mouth long, large, and broadly arched, with dental bands prominently expanded and with lower ones falling just behind uppers; mouth and labial furrows extending well in front of eyes. Labial folds enlarged, but with lower diagonal to body axis. Lateral trunk denticles of body with crowns erect and not closely imbricate, skin surface with a felt-like or fuzzy texture. Pectoral fins rather small, anterior margins about 9 to $11 \%$ of total length; inner margins extremely short, about a third of pectoral-fin bases. Interspace between pectoral and pelvic-fins bases short to moderately long, two-fifths to subequal to prespiracular length and about 6 to $14 \%$ of total length in adults. Pelvic fins high and broadly rounded. Interdorsal space equal or slightly less than first dorsal-fin base, one-third to two-fifth of preorbital snout. First dorsal fin about as large or slightly smaller than second, bases about equally long or first slightly shorter than second. Origin of first dorsal fin about opposite last third of pelvic-fin bases. Second dorsal-fin insertion behind anal-fin insertion. Anal fin short, fairly high, and rounded, between three and four times as long as high, base about equal to prespiracular space and 14 to $16 \%$ of total length in adults. Caudal fin slender to moderately broad, with a loose crest of enlarged denticles on dorsal caudal-fin margin. Spiral valve counts 9 to 11. Adults large, to 61 cm . Colour: dusky brown or grey-brown to purplish-black, without conspicuous markings on fins.

Distribution: Eastern North Atlantic: between Scotland and Iceland. Western North Atlantic: Off Newfoundland, Canada and near Veatch Canyon, off Massachusetts, U.S.A. Also, along the west and south coast of South Africa.

Habitat: A bottom shark of continental slopes, on or near the bottom at depths of 700 to 2200 m . South African specimens have been collected on soft bottom between 700 to 1200 m deep.

Biology: Oviparous, females appear to deposit egg cases year-round. Egg cases for this Apristurus spongiceps-group catshark are small, 4.7 to 5.2 cm in length, broad and fairly thick, with posterior width about 32 to $37 \%$ of case length;
case surface with fine, straight, smooth longitudinal striations; both anterior and posterior end without tendrils. Adult males have cuts and scars suggesting bites by conspecifics. The diet of these catsharks includes small midwater bony fishes, shrimp, and squid. One individual was found to have a small unidentified squaloid in its stomach. The presence of prey items that are midwater inhabitants suggests these shark may forage at times far off the bottom.

Size: Maximum to 61 cm total length; males mature at about 49 to 51 cm ; females mature at 47 to 49 cm .

Interest to Fisheries and Human Impact: Interest to fisheries none. Possibly caught as discarded bycatch by deepwater trawl fisheries, particularly in the North Atlantic.

Most fisheries occur shallower than this species depth range and as such its conservation status is Least Concern.

Local Names: Pig catshark.


Fig. 225 Apristurus microps

Literature: Gilchrist (1922); Springer (1979); Compagno (1984, 1988); Ebert, Cowley and Compagno (1996); Moore et al. (2003); Ebert (2004b); Compagno, Dando, and Fowler (2005); Ebert, Compagno, and Cowley (2006); Flammang, Ebert, and Cailliet (2007); Gibson et al. (2008); Ebert (In preparation).

## Apristurus profundorum (Goode and Bean, 1896)

Scylliorhinus profundorum Goode and Bean, 1896, Oceanic Ichthyol., Smithson. Inst. Spec. Bull:: 17, pl. 5, fig. 16. Holotype: U. S. National Museum of Natural History, USNM-35646, 510 mm total length adolescent male, Albatross Sta. 2234, Western North Atlantic listed as off Delaware Bay, $39^{\circ} 09^{\prime} 00^{\prime \prime} \mathrm{N}, 72^{\circ} 03^{\prime} 15^{\prime \prime} \mathrm{W}, 1493 \mathrm{~m}$, but actually collected near Hudson Canyon and not Delaware Bay as in Goode and Bean (1896). Status of holotype and additional data from Howe and Springer (1993, Smiths. Contr. Zool. [540]: 12).

Synonyms: None.
Other Combinations: None.
FAO Names: En - Deepwater catshark; Fr - Holbiche papoila; Sp - Pejegato abisal.


Fig. 226 Apristurus profundorum

Field Marks: Thick snout, anteriorly extended mouth with expanded dental bands, rather large gill slits, narrow internarial, erect denticles and fuzzy skin texture, high rounded fins, caudal crest.

Diagnostic Features: Body relatively slender, trunk slightly tapering towards head. Snout moderately long, very broad, and bell-shaped, preoral snout about $9 \%$ of total length. Gill slits moderately large but longest somewhat less than eye length; gill septa without projecting medial lobes or pleats, but well-incised. Eyes rather small, about $3 \%$ of total length. Nostrils broad, width about equal to internarial space; incurrent and excurrent apertures rather narrowly oval, anterior nasal flaps low and broadly triangular. Mouth moderately long, large, and broadly arched, with dental bands partly expanded and with lower ones falling just behind uppers; mouth and labial furrows extending well in front of eyes. Labial folds somewhat enlarged, with lower nearly transverse to body axis. Tooth counts 50 upper jaw, and 50 lower jaw. Lateral trunk denticles of body with crowns partly erect, giving skin surface a felt-like or fuzzy texture. Pectoral fins rather small, anterior margins about $11 \%$ of total length; inner margins fairly long, about half length of pectoral-fin bases. Interspace between pectoral and pelvic-fin bases moderately long, slightly less than prespiracular length and about 15\% of total length. Pelvic fins high and broadly rounded. Interdorsal space slightly greater than first dorsal-fin base, about two-thirds of preorbital snout. First dorsal fin about as large as second, bases about equally long. Origin of first dorsal fin slightly behind pelvic-fin midbases. Second dorsal-fin insertion about opposite to anal-fin insertion. Anal fin moderately long, fairly high, and subangular, short, high, and rounded, slightly more than three times as long as high, base slightly greater than prespiracular space and $14 \%$ of total length. Caudal fin fairly broad, with a well-developed crest of enlarged denticles on dorsal caudal-fin margin, with crest denticles directed obliquely downwards. Spiral valve counts 10 . Adults moderately large, as adolescent male is 76 cm long. Colour: brownish, probably dark brown in life.

Distribution: Western North Atlantic: Hudson Canyon, not Off Delaware Bay (see comments above) is where the holotype was actually collected, also caught off Block Canyon ( $39^{\circ} 42^{\prime} \mathrm{N}$, $71^{\circ} 27^{\prime}$ W) and Bear Seamount ( $39^{\circ} 52^{\prime} \mathrm{N}$, $67^{\circ} 20^{\prime} \mathrm{W}$ ) (Atlantic coast of USA). Eastern North Atlantic: Mauritania, records need to be confirmed.

Habitat: A poorly-known species, from the Western Atlantic continental slopes at 1100 to 1830 m ; depth range in the Eastern North Atlantic (if this species and not A. manis or a different Apristurus species), 1300 to 1600 m .

Biology: Nothing known. Egg cases have not been described for this species.

Size: Maximum length about 76 cm ; males and females mature at about 55 cm .

Interest to Fisheries and Human Impact: Interest to fisheries none.


Fig. 227 Apristurus profundorum
$\square$ Known distribution

The conservation status is Data Deficient due to a lack of life history information and its deepwater habitat that likely minimizes its capture bycatch to other fisheries.

Local Names: Abyssal catshark, Deepsea shark, Deepwater cat shark.
Literature: Bigelow and Schroeder (1948); Springer (1966, 1979); Golovan (1976, 1978); Compagno (1984, 1988); Kiraly, Moore, and Jasinski (2003); Moore et al. (2003); Huveneers and Duffy (2004); Compagno, Dando, and Fowler (2005); Ebert (In preparation).

## Galeus Rafinesque, 1810a

Genus: Galeus Rafinesque, 1810a, Caratt. gen. sp. anim. piant. Sicilia, Palermo, pt. 1: 13.
Type Species: Galeus melastomus Rafinesque, 1810a, by subsequent designation of Fowler, 1908, Proc. Acad. Nat. Sci. Philadelphia, 60: 53.

## Number of North Atlantic Species: 3.

Synonyms: Subgenus Pristiurus Bonaparte, 1834 (Genus Scyllium Cuvier, 1816), Iconog. Fauna Italica, 3, Pesci, liv. 7, 4th p. Type species: Scyllium melanostomum Bonaparte, 1834, by monotypy, a junior synonym of Galeus melastomus Rafinesque, 1810a. Genus Pristidurus Bonaparte, 1838, Nuov. Ann. Sci. Nat. Bologna, ser. 1, 2: 213. Type species: Scyllium melanostomum Bonaparte, 1834, by monotypy, a junior synonym of Galeus melastomus Rafinesque, 1810. Unjustified emendation of Pristiurus Bonaparte, 1834.

Field Marks: Usually firm-bodied scyliorhinids with crests of enlarged denticles, usually rather long and wedge-shaped snouts, short labial furrows, subocular ridges virtually obsolete, large pectoral fins, large anal fin, elongated caudal fins, often barred and blotched colour pattern.

Diagnostic Features: Body not tadpole-shaped, slender and subcylindrical to rather compressed, tapering slightly to considerably to caudal fin; body firm and thick skinned, with well-calcified dermal denticles; stomach not inflatable. Tail varying from fairly short to moderately long, length from vent to lower caudal origin about $2 / 5$ to $5 / 6$ of snout-vent length. Head slightly depressed, narrowly pointed-rounded in lateral view and somewhat wedge-shaped or not; head short to moderately long, between $1 / 4$ and $1 / 5$ to less than $1 / 5$ of total length in adults. Snout fairly short to moderately elongated, $2 / 3$ to about equal to mouth width, thick to rather thin and flattened, bluntly to almost acutely pointed in lateral view; snout not expanded laterally, broadly to narrowly rounded-parabolic and usually bell-shaped in dorsoventral view. Ampullal pores not greatly enlarged on snout. Nostrils of moderate size, with incurrent and excurrent apertures only partly open to exterior; anterior nasal flaps broadly triangular and rather low, without barbels, well separated from each other and falling well anterior to mouth; internarial space about 0.7 to 1.2 times nostril width; no nasoral grooves. Eyes virtually lateral on head, subocular ridges below eyes narrow or obsolete. Mouth angular or semiangular, moderately long, with lower symphysis well behind upper so that upper teeth are exposed in ventral view. Labial furrows present along both upper and lower jaws, these very short to moderately long but ending well behind level of upper symphysis of mouth. Tooth counts 54 to 70 upper jaw, and 54 to 70 lower jaw. Branchial region not greatly enlarged, distance from spiracles to fifth gill slits $1 / 3$ to $1 / 2$ of head length; gill slits lateral on head. Pectoral fins large, their width somewhat less to considerably greater than mouth width. Inner margins of pelvic fins not fused or variably fused and forming an 'apron' over claspers in adult males. Claspers short to moderately long, fairly thick, and distally pointed and often twisted, extending from less than a fifth to about half of their lengths behind the pelvic-fin tips. Two equal-sized dorsal fins present, origin of first varying from over the first third of the pelvic-fin bases to about over their insertions. Origin of second dorsal fin varies from about over to slightly behind the anal-fin midbase. Anal fin large and more or less elongated, about as large as pelvic fins or larger, and considerably larger than the dorsal fins; base length 1.6 to slightly over 3 times second dorsal-fin base; origin of anal fin close to far behind pelvic-fin bases, and insertion separated from lower caudal-fin origin by a narrow notch to a broad space nearly equal to the anal-fin base. Caudal fin more or less elongated, over or somewhat less than a fourth of total length in adults. A well developed crest of denticles on the dorsal caudal-fin margin and sometimes the upper edge of the caudal-fin peduncle, and in some species on the preventral margin and lower edge of the caudal-fin peduncle, dorsal crest flat on its upper surface and symmetrical; small median denticles between upper crest denticles usually in less than five rows. Supraorbital crests absent from cranium. Vertebral counts: total vertebral counts 73 to 151, monospondylous vertebral counts 30 to 50 , diplospondylous precaudal vertebral counts 36 to 53 , precaudal vertebral counts 48 to 97 . Spiral valve counts 12 to 14 . Colour: light grey or brown, with or without a conspicuous colour pattern of dark saddles and blotches.

Local Names: Sawtail catsharks, Saw tail sharks, Rough cat sharks.
Remarks: The genus is comprised of 17 described species, with three known to occur in Area 27. There are no species of this genus known to occur in Area 21 at the present time, but one species, Galeus arae is known to occur just south of Area 21 off the North Carolina (U.S.A.) coast and may eventually be found to occur in the southern extreme of this area (Kiraly et al., 2003).

## Key to North Atlantic Species:

1a. A crest of denticles present on the preventral caudal margin as well as the dorsal margin. . . . . . Galeus murinus
1b. No crest of denticles on the preventral caudal margin . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
2a. Labial-furrow grooves black. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Galeus atlanticus
3b. Labial-furrow grooves white or grayish .
Galeus melastomus

## Galeus atlanticus (Vaillant, 1888)

Pristiurus atlanticus Vaillant, 1888, Expéd. sci. Travailleur et Talisman ann. 1880-1883, Poissons: 59, PI. 1, figs. a-d. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN-84-387, 440 mm total length female, Cape Spartel, Morocco.

Synonyms: None.
Other Combinations: None.
FAO Names: En - Atlantic sawtail catshark; $\mathbf{S p}$ - Olayo atlántico.


Fig. 228 Galeus atlanticus
Field Marks: Snout is long and bell-shaped, mouth cavity black, eyes lateral on edges of head, large pectoral fins, angular dorsal fins with dusky light rear webs, and a long, low anal fin, distinct crest of enlarged dermal denticles along upper caudal margin, caudal fin with dark margin, not black tipped. Colour is a dark grey-brown with about 10 darker blotches or saddles.

Diagnostic Features: Body moderately slender, with a short head, and long bell-shaped snout. Snout moderately long and pointed, preoral length about 7.2 to $8.3 \%$ of total length; prenarial snout less than eye length. Nostrils large, oblique. Eyes virtually lateral on head, without prominent subocular ridges. Mouth fairly large, broadly arched, width 6.4 to $7.6 \%$ of total length. Labial furrows moderately long, not confined to mouth corners. Pelvic fins small, low, and angular. Interspace between pelvic and anal-fins bases much shorter than anal-fin base. Anal-fin base short to long, 15.5 to $16.6 \%$ of total length, greater than interdorsal space. No subcaudal crest of enlarged denticles on preventral caudal margin. Vertebral counts: total vertebral counts 125 to 128 , monospondylous vertebral counts 34 to 35 , diplospondylous vertebral counts 43 to 44 , precaudal vertebral counts 70 to 76 . Size moderate, adults up to about 45 cm . Colour: greyish brown above, with dark grey blotches and saddles, up to 10 , along the body and caudal fin; white below.

Distribution: Eastern North Atlantic: Spain (off Galicia coast) and Portugal, northern limits of range unclear. Eastern Central Atlantic: Morocco, possibly to Mauritania, and the Mediterranean Sea around Straits of Gibraltar, Spain (Alboran Sea); possibly restricted only to this area; records from Italian waters may be of a different species.

Habitat: Continental slope from 330 to 790 m .
Biology: Oviparous, with multiple oviparity, nine egg cases were found one female. Gestation time for hatching may be short once the egg case is deposited on the sea floor. This species has a continuous reproductive cycle with females depositing egg cases year-round. Nothing is known of the diet of this species.

Size: Maximum total length to about 46 cm ; males mature at 33 to 42 cm ; females mature at 37 to 45 cm . Size at birth uncertain, but smallest free-swimming individuals were 15 and 17 cm total length.

Interest to Fisheries and Human Impact: Fisheries impact unknown due to misidentification with other similar-looking Galeus species within its narrow bathymetric and geographical range. May be caught in bottom trawls as bycatch, but usually discarded.

Conservation status is Near Threatened due to the narrow extent of its current known bathymetric and geographic range and the intense fishing pressure that takes place within its range. If the known distribution of this species eventually proves to be much broader it may be afforded more protection especially if part of the population occurs outside areas currently subjected to intense fishing pressure.

Local Names: None.
Remarks: This species has at times been considered either a valid species or at other times a synonym of Galeus melastomus. However, comparative morphological and meristic data combined with recent molecular studies confirm this as a valid species. The distribution of this species at the present appears to be restricted between the Alboran Sea, Spanish Mediterranean coast to the northwest Atlantic coast of Spain, and from off Morocco.

Literature: Munoz-Chapuli and Perez Ortega (1985); Compagno, Dando, and Fowler (2005); Rey et al. (2006); Castilho et al. (2007); Coelho et al. (2007); Gibson et al. (2008); Bañon et al. (2010); Rey et al. (2010).

## Galeus melastomus Rafinesque, 1810a

Galeus melastomus Rafinesque, 1810a, Caratt. gen. sp. anim. piant. Sicilia, Palermo, pt. 1: 13. Holotype: None. Type locality: Sicily.

Synonyms: Squalus (Scyliorhinus) delarochensis Blainville, 1816: 121 (name only); Blainville, 1825: 74, pl. 18, fig. 2. Scyllium artedii Risso, 1826: 117, pl. 3, fig. 5. Squalus prionurus 0 tto, 1821: 5. Squalus annulatus Nilsson, 1832: 114. Scyllium melanostomum Bonaparte, 1834: fasc. 7, punt. 39, PI. 131 (fig. 3). Pristiurus souverbiei LaFont, 1868: 519.

Other Combinations: Pristiurus melanostomus (Bonaparte, 1834).
FAO Names: En - Blackmouth catshark; Fr - Chien espagnol; Sp - Pintarroja bocanegra.


Fig. 230 Galeus melastomus

Field Marks: Large Galeus with long anal fin, compressed precaudal tail, striking colour pattern of numerous dark saddles and circular spots.

Diagnostic Features: Precaudal tail with base noticeably compressed. Snout moderately long and pointed, preoral length about 6 to $9 \%$ of total length; prenarial snout equal or less than eye length. Eyes lateral on head, subocular ridges obsolete. Mouth fairly large and short, very broadly arched, width 6 to $8 \%$ of total length. Labial furrows moderately long, not confined to mouth corners. Pelvic fins small, low, and angular. Interspace between pelvic and anal bases much shorter than anal base. Anal-fin base long, 13 to $18 \%$ of total length, much greater than interdorsal space; origin well in front of midlength of interdorsal space. No subcaudal crest of enlarged denticles on preventral caudal-fin margin. Vertebral counts: total vertebral counts 138 to 151 , monospondylous vertebral counts 37 to 43 , diplospondylous vertebral counts 42 to 50 , precaudal vertebral counts 78 to 90 . Size moderate, adults up to 90 cm . Colour: pattern of well-defined variegated dark saddle blotches and circular spots on body and caudal fin; saddles over 15 on back and tail; dorsal fins and caudal tip white; mouth lining dark.

Distribution: Eastern North Atlantic: Faroe Islands, Trondheim (Norway) southward to Portugal, possibly including the Azores, and to Senegal. Also throughout the Mediterranean Sea.

Habitat: A common deepwater bottom shark found on the outer continental shelves and upper slopes, mainly between 200 to 500 m but occasionally up to 55 m and down to 2000 m .

Biology: Oviparous, with up to 13 eggs present in the oviducts of a female at one time; egg case dimensions about 6 by 3 cm . Feeds mainly on bottom invertebrates, including shrimp and cephalopods, but also on small mesopelagic bony fishes (lanternfish).

Size: Maximum 90 cm ; males maturing between 34 and 42 cm and reaching at least 61 cm ; females maturing between 39 and 45 cm and reaching 90 cm .

Interest to Fisheries and Human Impact: Interest to fisheries limited in


Fig. 231 Galeus melastomus the Eastern North Atlantic where it is caught as bycatch in bottom trawls and utilized fresh and dried-salted for human consumption, and for leather. Reported landings between 2000 and 2009 averaged 154 tonnes per year (FAO landings statistics), with Spain (average 114 tonnes annually) reporting the majority of the landings followed by Portugal (average 35 tonnes annually). Fisheries further north typically discard this species. This species is under TAC regulation in EU waters (in 2012, TAC=0) (EU, 2012a) and prohibited species in the NEAFC Regulatory Area.

Conservation status is Least Concern due to its wide bathymetric and geographic distribution, and small size.

Local Names: Blackmouthed dogfish or Black mouthed dog fish, Spotted shark, Blackmouth shark (UK); Pristiure a bouche noire, Pristiure, Bardoulin, Lambardà, Chien à gueule noire (France); Rodhaae (the Netherlands); Ringhaj (Denmark); Hågäl (Sweden); Schwarzmaul-Katzenhai (Germany); Pata roxa, Cacão, Leitão, Litão (Portugal); Black-mouthed dogfish (Azores); Leitāo do Mar (Madeira Islands); Gata, Gata moixa, Mocina, Muxina, Olayo (Spain); Pilokhvost (Russia).

Literature: Springer and Wagner (1966); Wheeler (1969, 1978); Springer (1979); Munoz-Chapuli and Perez Ortega (1985); MacPherson (1980a); Capapé and Ben Brahim (1984); Bello (1995, 1997); Santos, Porteiro, and Barreiros (1997); Compagno, Dando, and Fowler (2005); Costa, Erzini, and Borges (2005); Olaso et al. (2005); Rey, Gil de Sola, and Massuti (2005); Rey et al. (2006); Capapé, Ben Salem, and Ben Amor (2007); Castilho et al. (2007); Capapé et al. (2008a); Gibson et al. (2008); Serena et al. (2008); EU (2012a); Ebert (In preparation).

## Galeus murinus (Collett, 1904)

Pristiurus murinus Collett, 1904, Christiana Vidensk.-Selsk. Forhand. 1904 (9): 4. Holotype: Zoologisok Museum, ZMUO J22, Oslo, Norway, ZMO Michael Sars stn. 76, 222 mm immature female, 150 km northwest of Hebrides, Eastern Atlantic, Faroe Channel at 1200 m. Holotype figured in Collette, 1905: PI. 1 (fig. 3)

Synonyms: Pristiurus jensenii Saemundsson, 1922, Vidensk. Meddel. Dansk Naturhist. Foren. Kobenhaven, 74: 169, pl. 4, fig. 2, pl. 5, fig. 3. Note: figure numbers on pl. 4 are apparently reversed; fig. 2 is this species and not fig. 1 as cited in the text, which is Apristurus laurussonii. Holotype: Possibly in Natural History Museum, Reykjavik, Iceland, 630 mm adult male, off Vestmanneyjar Island, Iceland, 380 m .

Other Combinations: Galeus melastomus murinus (see Springer, 1979).
FAO Names: En - Mouse catshark; Fr - Chien islandais; $\mathbf{S p}$ - Pintarroja islándica.


UNDERSIDE OF HEAD
Fig. 232 Galeus murinus
Field Marks: Galeus with large round pelvic fins, a cylindrical precaudal tail, a subcaudal crest of denticles, and no colour pattern.

Diagnostic Features: Precaudal tail not noticeably compressed at base. Snout moderately long and parabolic, preoral length about 7 to $8 \%$ of total length; prenarial snout less than eye length. Eyes slightly dorsolateral, subocular ridge very narrow. Mouth fairly large and long, broadly arched, width 7 to $8 \%$ of total length. Labial furrows moderately long, not confined to mouth corners. Pelvic fins very large, high, and broadly rounded. Interspace between pelvic and anal-fins bases much shorter than anal-fin base. Anal-fin base short, about 12 to $13 \%$ of total length, but much greater than interdorsal space; anal-fin origin just behind first dorsal-fin insertion. A strong subcaudal crest of enlarged denticles on preventral caudal-fin margin and underside of caudal peduncle. Size moderate, adults to at least 63 cm . Colour: uniform brown above, slightly lighter below, without black tips on dorsal and caudal fins; mouth lining dark.

Distribution: Eastern North Atlantic: west coast of Iceland to the Faroe Islands, and recently it has been found off Scotland, the Hebrides Islands, Ireland, France, Spain, Morocco, and Western Sahara (Iglésias, 2008).

Habitat: A little-known deepwater shark of the Eastern Atlantic continental slopes, on or near bottom at depths of 380 to 1250 m .

Biology: Moderately common where it occurs, but its biology is virtually unknown. Egg cases for this species have been described as being relatively small and slender ( 54 to 56 mm long and 14 to 17 mm wide), with a weak constricted neckline about one-fifth the length of the anterior end; the capsule is finely covered by fibres giving it a rough-looking texture; egg case without long fibrous tendrils at either end; colour is a uniform yellowish gold.

Size: Maximum at least 63 cm (adult male); males mature between 50 to 63 cm ; females to at least 50 cm , but maturity unknown.

Interest to Fisheries and Human Impact: Interest to fisheries minimal. It is taken as bycatch on occasion, with small quantities having been reported by France and Spain, but its small size and deepwater habitat likely precludes it from being taken in large numbers. However, its distribution overlaps that of Galeus melastomus and it is likely that $G$. murinus is
a common component of mixed catshark catches that possibly also includes G. atlanticus.

Conservation status is Least Concern due to its being relatively fecund, wide bathymetric and geographic distribution, and relatively small size.

Local Names: Doublesaw catshark.
Literature: Springer and Wagner (1966); Springer (1979); Compagno (1984, 1988); Iglésias, Du Buit, and Nakaya (2002); Compagno, Dando, and Fowler (2005); Gibson et al. (2008); Iglésias (2008).


Fig. 233 Galeus murinus
$\square$ Known distribution

## Scyliorhinus Blainville, 1816

Genus: Subgenus Scyliorhinus Blainville, 1816 (Genus Squalus Linnaeus, 1758), Bull. Sci. Soc. Philomat. Paris, (8): 121.
Type Species: "Scylliorhinus canicula Blainville", by subsequent designation of Gill, 1862b, Ann. Lyceum Nat. Hist. New York, 7(32): 407; equals Squalus canicula Linnaeus, 1758.

## Number of Recognized North Atlantic Species: 3.

Synonyms: Subgenus Scyllium Cuvier, 1816: 124. Subgenus Catulus Willoughby in Smith, 1837: 85.
Field Marks: Scyliorhinids without trilobate, barbeled anterior nasal flaps, labial furrows on lower jaw only, second dorsal fin much smaller than first.

Diagnostic Features: Body not tadpole-shaped, moderately stout to slender and cylindrical or spindle-shaped, tapering considerably to caudal fin; body firm and thick skinned, with well-calcified dermal denticles; stomach not inflatable. Tail moderately long, length from vent to lower caudal origin between $3 / 5$ to $3 / 4$ of snout-vent length. Head slightly to moderately depressed, narrowly rounded and not wedge-shaped in lateral view; head short, less than $1 / 5$ of total length in adults. Snout short, less than $3 / 4$ of mouth width, thick, and slightly flattened, bluntly pointed in lateral view; snout not expanded laterally, rounded-parabolic in dorsoventral view. Ampullal pores not greatly enlarged on snout. Nostrils not enlarged to moderately enlarged, with incurrent and excurrent apertures only slightly open to exterior; anterior nasal flaps more or less triangular, sometimes slightly elongated, without a prominent barbel, well separated from each other and ending somewhat anterior to mouth but close together and reaching it in Scyliorhinus canicula; internarial space 0.3 to 0.8 times nostril width; nasoral grooves usually absent, except $S$. canicula in which broad grooves are present. Eyes dorsolateral on head, broad subocular ridges present below eyes. Mouth angular or broadly arched, moderately long, with lower symphysis somewhat behind upper so that upper teeth are well-exposed in ventral view (except $\boldsymbol{S}$. canicula, in which upper teeth are obscured by lower jaw). Labial furrows present along lower jaw only, these short to moderately long; vestigial uppers occasionally present. Tooth counts 40 to 65 upper jaw, 38 to 65 lower jaw. Branchial region not greatly enlarged, distance from spiracles to fifth gill slits $1 / 2$ to $2 / 5$ head length; gill slits lateral on head. Pectoral fins large, their width about as great or considerably greater than mouth width. Inner margins of pelvic fins more or less fused over claspers in adult males, forming an 'apron'. Claspers short, relatively thick, and distally pointed or rounded, extending less than half their lengths behind the pelvic-fin tips. Two dorsal fins present, with the second considerably smaller than the first. Origin of first dorsal fin varying from over last half of pelvic-fin bases to over pelvic-fin free rear tips. Origin of second dorsal fin over last third of anal-fin base to slightly behind anal-fin insertion. Anal fin moderately large but not greatly elongated, subequal to pelvic and first dorsal fins but much larger than second dorsal fin, base length 1.3 to 2.4 times second dorsal-fin base; origin of anal fin well behind pelvic-fin bases, and insertion separated from lower caudal-fin origin by a space varying from half as long to
slightly longer than the anal-fin base. Caudal fin short and fairly broad, between $1 / 4$ to $1 / 5$ to less than $1 / 5$ of total length in adults. No crests of denticles on the caudal-fin margins. Supraorbital crests present on cranium. Vertebral counts: total vertebral counts 107 to 144, monospondylous vertebral counts 30 to 47, precaudal vertebral counts 65 to 95 . Spiral valve counts 6 to 11. Colour: pattern extremely variable, ranging from simple dark saddles, reticulating dark bars, or large dark spots on a light background to combinations of light and dark spots and saddles.

Local Names: Spotted dogfishes, Roussettes.
Remarks: The genus has 15 species currently recognized with three occurring in the North Atlantic.

## Key to North Atlantic Species:

1a. Anterior nasal flaps contacting each other at upper symphysis; shallow nasoral grooves present between nostrils and mouth (Fig. 234). . . . Scyliorhinus canicula (NE Atlantic)

1b. Anterior nasal flaps not contacting each other at upper symphysis; no nasoral grooves between nostrils and mouth (Fig. 235) $\qquad$ 2


Fig. 234 Scyliorhinus canicula


Fig. 235 Scyliorhinus stellaris


Fig. 236 Scyliorhinus retifer


Fig. 237 Scyliorhinus stellaris

## Scyliorhinus canicula (Linnaeus, 1758)

Squalus caniculaLinnaeus, 1758, Syst. Nat., ed. 10, 1: 234. Holotype unknown, type locality: "Habitat in Oceano Europae".
Synonyms: Scyllium elegans Blainville, 1825, in Vieillot et al., Faune Francaise, liv. 13-14: 73, pl. 18, fig. 1. Holotype: Adult male, lost? Type locality: Marseille, France. ?Scyllium acutidens Vaillant, 1888, Exped. sci. Travailleur et Talisman ann. 1880-1883, Poissons: 60, PI. 1, fig. 4. Eastern Atlantic. Holotype: MNHN 1884-0385 (poor condition). Paratypes: MNHN 1884-0384 (1), 1884-0385 (1, poor condition), 1884-0386 (1). Scylliorhinus canicula var. albomaculata Pietschmann, 1906, Annalen des Naturhistorischen Museums in Wien v. 21: 98. West coast of Morocco, eastern Atlantic. No types known. Catulus duhamelii Garman, 1913, Mem. Harvard Mus. Comp. Zool., 36: 73. Syntypes: In Museum of Comparative Zoology, Harvard? $43 \mathrm{~cm}\left(17^{\prime \prime}\right)$ TL female, Adriatic, $34 \mathrm{~cm}\left(131 / 2^{\prime \prime}\right)$ TL adult male, Nice, France. Apparently based on the Catulus saxatilis and "petite rousette ou chat rochier" of Duhamel (1777, Traite 3(9): 304, pl. 22, fig. 2-3), and distinguished as a smaller southern race of $S$. canicula.

Other Combinations: None.
FAO Names: En - Small-spotted catshark; Fr - Petite roussette; Sp - Pintarroja.


Fig. 238 Scyliorhinus canicula

Field Marks: A slender, dark-spotted species with greatly expanded anterior nasal flaps, reaching mouth and covering shallow nasoral grooves, labial furrows on lower jaw only, second dorsal fin much smaller than first.

Diagnostic Features: Head and body relatively deep, slender and narrow; greatest width of head less than $2 / 3$ of head length. Shallow nasoral grooves present between excurrent apertures of nostrils and mouth; anterior nasal flaps broadly expanded medially and posteriorly, nearly meeting each other medially and extending to the mouth. Tooth counts 46 upper jaw, 40 lower jaw. Denticles small, skin not extremely rough. First dorsal-fin origin well behind pelvic-fin insertions. Second dorsal-fin origin over anal-fin insertion. Interdorsal space slightly greater than anal-fin base. Vertebral counts: total vertebral counts 121 to 127, monospondylous vertebral counts 37, precaudal vertebral counts 83 to 84 . Spiral valve counts 6 to 8 . Size moderate, to 85 cm , records of larger specimens $(100 \mathrm{~cm})$ may result from misidentifications with Scyliorhinus stellaris Colour: pattern of numerous small dark spots, usually about size of eye pupil; 8 or 9 dusky saddle marks


UNDERSIDE OF HEAD sometimes present but often obscure or obsolete; scattered white spots sometimes present.

Distribution: Eastern North Atlantic: Norway and British Islesto Mediterranean, possibly Azores, Senegal, ?lvory Coast.

Habitat: An abundant temperate bottom species of the European continental shelves and uppermost slopes, on sandy, coralline algal, gravelly or muddy bottoms at depths from a few meters commonly down to 110 m and exceptionally to 400 m .

Biology: Oviparous, laying one egg case per oviduct at a time; egg-cases are deposited on algal substrates and hatch in 5 to 11 months (most in 8 to 9 months). Eggs may be laid all year but most are deposited from November to July. Eggs are laid on macroalgae (in shallow water) and on erect sessile invertebrates (hydroids, sponges, bryozoans etc.) further offshore. Eggs vary in size according to locality and size of female. In Mediterranean waters, with smaller females than the Eastern Atlantic, eggcases are about 4 by 2 cm . Young sharks and hatchlings are found in shallower water than adults, which often occur in


Fig. 239 Scyliorhinus canicula unisexual schools.
Feeds mostly on bottom invertebrates, including hermit crabs (Paguridae), swimming crabs (Portunidae) and other small crabs, shrimps, whelks (Buccinum) and other gastropods, small cephalopods, and polychaete worms (including Aphrodita), bottom-dwelling bony fishes and clupeids. The egg cases of this shark have been found in the stomach of Oxynotus centrina.

Size: Maximum total length about 85 cm (British Isles and North Sea), but maximum size and length at maturity is less than in Mediterranean than elsewhere. North Eastern Atlantic males mature at 49 to 55 cm , with females maturing at 52 to 65 cm ; maximum length at least 80 cm and possibly 85 cm . In the Mediterranean Sea males mature at 39 cm and reach 60 cm , and females mature at 44 cm and reach at least 60 cm ; size at hatching 9 to 10 cm .

Interest to Fisheries and Human Impact: This is a moderately important commercial species in European waters, particularly around the British Isles, France and Iberian peninsula. It is primarily taken by bottom trawls, but also fixed bottom nets and longline. It is utilized fresh and dried-salted for human consumption, also for oil and fishmeal. It is often used as pait in the pot fishery for whelk Buccinum undatum. Over the past decade (2000 to 2009) an average of just over 6000 tonnes (FAO landings statistics) has been landed annually, with France reporting the highest average annually landings at over 5500 tonnes. Catches have been relatively even and stable during this time.
This species is hardy in captivity and is a popular display species in public aquaria in the UK and Europe. It readily breeds in captivity, and, with care, the eggs can be hatched and the young grown to adulthood in aquaria.

Conservation status is Least Concern as the overall population appears to be stable or possibly increasing with no evidence of it having declined. This is one of the most abundant and common catsharks in the Eastern North and Central Atlantic.

Local Names: Lesser spotted dogfish, Smaller spotted dogfish, Small-spotted dogfish, Spotted dogfish, Rough hound, Dogfish, Nurse, Sandy dog, Rock salmon, Robin huss, Suss, Land dog, Row hound, Cur fish, Kennet, Daggar (English); Morgay, Blin e es (Scotland); Daw fish (Orkneys); Morghi meiaf (Wales); Squale roussette, La rousette tigre, La rousette a petites taches, Petit rousette, Charon, Charotel, Chat marin, Cata roussa, Pintou roussou, Rousse (France); Katzenai, Kleiner Katzenhai (Germany); Hondshaai (the Netherlands); Zee hond (Belgium); Småplettet rødhaj (Denmark); Deplaháfur (Iceland); Cat, Gat, Gatet, Gat vaire, Pinta rotja, Pintarrosa, Pintarroja (Spain); Pata roxa, Pintarroxa (Portugal); Lesser spotted dogfish, Dogfish, Sandy dogfish (Azores); Småfläckig rödhaj (Sweden); Morskoy pes (Russia).

Literature: Garman (1913); Wheeler (1969, 1978); Springer (1979); Compagno (1984); Lyle (1983); Ellis and Shackley (1995, 1997); Barrull and Mate (2001b); Olaso et al. (2005); Ellis et al. (2005, 2005a) Revill, Dulvy, and Holst (2005); Capapé et al. (2008b, d); Ellis et al. (2008); Gibson et al. (2008); ICES (2010); Ebert (In preparation).

## Scyliorhinus retifer (Garman, 1881)

Scyllium retiferum Garman, 1881, Bull. Mus. Comp. Zool. Harvard, 8(11): 233. Holotype: Museum of Comparative Zoology, Harvard, MCZ-825, 307 mm TL male, $38^{\circ} 22^{\prime} 35^{\prime \prime} \mathrm{N}, 73^{\circ} 33^{\prime} 40^{\prime \prime} \mathrm{W}, 163 \mathrm{~m}$.

Synonyms: None.
Other Combinations: Catulus retifer (Garman, 1881).
FAO Names: En - Chain catshark; Fr - Roussette maille; Sp - Alitán mallero.


Fig. 240 Scyliorhinus retifer

Field Marks: The striking bold chain colour pattern of black lines outlining faint dusky saddles unique to this shark distinguishes it from all other Atlantic catshark species.

Diagnostic Features: Head and body relatively deep, slender and narrow; greatest width of head about $2 / 3$ of head length. No nasoral grooves; anterior nasal flaps not expanded and falling somewhat anterior to mouth. Tooth counts 42 to 54 upper jaw, 40 to 48 lower jaw. Denticles small and flat, surface of skin relatively smooth. First dorsal-fin origin somewhat behind pelvic-fin insertions. Second dorsal-fin origin somewhat anterior to anal-fin insertion. Interdorsal space considerably greater than anal-fin base. Vertebral counts: total vertebral counts 122 to 134, monospondylous vertebral counts 39 to 43. Spiral valve 8 to 10 . Size moderate, adults below 50 cm . Colour: pattern of bold black lines, outlining obscure dusky saddles and sometimes extending over lateral surfaces and back as a reticular network; no light or dark spots.

Distribution: Western North Atlantic: Southern New England (Georges Bank, Massachusetts) to Florida, northern Gulf of Mexico to Nicaragua.

Habitat: A common, sluggish, inactive deepwater species of the outer continental shelf and upper slope, found on or near the bottom at depths of 73 to 550 m . These sharks mostly rest on the bottom and only occasionally swim off it. At the northern end of its range this shark occurs on the outer continental shelf but southwards it is a slope species generally found below 450 m . Its distribution is irregular, with areas where it is common being interspersed with those where it is rare or absent. There is some evidence that it is commonest on extremely rough, rocky bottom where trawl hauls are difficult or impossible to make. Adults may prefer untrawlable grounds because they offer places to attach eggs to biogenic features (e.g. corals). Water temperatures where it occurs range from 8.5 to $11.3^{\circ} \mathrm{C}$.

Biology: Development is single oviparity with one egg per oviduct. Females can store sperm for extended periods and produce viable eggs without males for 2.3 years or more. Egg cases are about 2.7 by 6.5 cm , with tendrils up to 35 cm long. Courtship and copulation have been observed for this species in captivity. During courtship the male and female swim together or rest on the bottom beside each other, with the male occasionally biting the female. The male eventually bites and holds the female by the tail, and transfers his bite anteriorly to the pectoral region along the flank, wrapping his body around the female, and copulating with her using only his left clasper. In captivity, females have been observed to lay pairs of eggs every 8 to 15 days, with an annual fecundity of approximately 44 to 52 eggs per year. Eggs are laid in pairs, with the second egg laid between a few minutes to eight days after the first. Females in the process of laying an egg begin to eject the egg case so that the posterior tendrils protrude from their cloaca. They then seek vertical projections on the bottom


Fig. 241 Scyliorhinus retifer
$\square$ Known distribution and circle them rapidly, wrapping and catching the tendrils on them. When the tendrils catch, the female pulls vigorously, extracting the egg, and continues circling until the anterior tendrils also catch. The female then stops swimming and rests on the bottom. Eggs have been found anchored to corals. In captivity egg cases hatch after about seven months at 11.7 to $12.8^{\circ} \mathrm{C}$, but development may take longer in some nursery areas, possibly up to a year, because of lower temperatures down to $7^{\circ} \mathrm{C}$. A trawl haul of numerous hatchlings off Cape Hatteras, North Carolina, USA suggests that there is a limited 'nesting' and nursery area there. Reproductively active females have been collected in the spring and summer, but it is not known if reproduction continues all year. In captivity young grow to 25 to 30 cm in two years, but age and growth is unknown in the wild. Captive specimens have lived for more than 9 years.
Stomach contents of 81 specimens examined by Castro, Bubucis and Overstrom (1988) included $64 \%$ with squid remains including beaks, $55 \%$ with bony fish material, $32 \%$ polychaetes or other annelids, and $21 \%$ crustaceans. Springer (1979) examined 38 specimens, all of which had empty stomachs, but half had small pebbles in their stomachs. It is not known why such a large percentage of these sharks may have had small pebbles in their stomach, but Springer hypothesized that these might be useful as ballast.

Size: Maximum total length about 59 cm . Adult males 37 to 58 cm , adult females 35 to 59 cm . Individuals from the MidAtlantic Bight mature at a smaller size, 38 cm for males and 35 cm for females, than those off South Carolina and Florida, which may mature at about 50 cm for males and 52 cm for females. Size of hatchlings about 10 to 11 cm at birth.

Interest to Fisheries and Human Impact: Interest to fisheries none, may be taken on occasion as bycatch in other fisheries. This rather attractive little catshark is frequently kept in public aquaria in the United States.

Conservation status is Least Concern.
Local Names: Chain dogfish.
Literature: Bigelow and Schroeder (1948); Springer (1966, 1979); Springer and Sadowsky (1970); Compagno (1984, 1988, 1989); Castro, Bubucis and Overstrom (1988); Able and Flescher (1991); Sminkey and Tabbit (1992); Sherril-Mix, Myers and Burgess (2006).

## Scyliorhinus stellaris (Linnaeus, 1758)

Squalus stellaris Linnaeus, 1758, Syst. Nat., ed. 10, 1:235. Holotype unknown, type locality: "Habitat in Mari Europaeo."
Synonyms: Squalus catulus Linnaeus, 1758, Syst. Nat., ed. 10, 1: 235. Holotype unknown, type locality: "Habitat in Oceano Europae".

Other Combinations: None.
FAO Names: En - Nursehound; Fr - Grande roussette; Sp - Alitán.


Fig. 242 Scyliorhinus stellaris

Field Marks: A large, fairly stocky species with large and small black spots and sometimes white spots covering dorsal surface, saddle markings obsolete, small anterior nasal flaps that don't reach mouth, no nasoral grooves, labial furrows on lower jaw only, second dorsal fin much smaller than first.

Diagnostic Features: Head and body moderately broad, greatest width of head about 2/3 of head length. No nasoral grooves; anterior nasal flaps not expanded and falling just short of mouth. Tooth counts 49 upper jaw, 44 lower jaw. Denticles fairly large and semierect, surface of skin relatively rough. First dorsal-fin origin opposite pelvic-fin insertions. Second dorsal-fin origin well anterior to anal-fin insertion. Interdorsal space subequal or less than anal-fin base. Total vertebral counts 129 to 134. Spiral valve 11. Size large, adults to 160 cm . Colour: pattern of numerous small and large black spots sometimes interspersed with white spots, the large spots often irregular, subangular, and sometimes expanded into large blotches that may totally cover the body in some individuals; saddle markings indistinct or absent.


UNDERSIDE OF HEAD

Distribution: Eastern North Atlantic: Southern Scandinavia and British Isles to Mediterranean, Morocco, Senegal, ?Gambia to Guinea, ?Liberia, ?Gabon to Zaire (tropical West African records = Scyliorhinus cervigoni?).

Habitat: A common inshore and offshore shark of the eastern Atlantic continental shelf, but less abundant than Scyliorhinus canicula; found at depths of 1 or 2 m to at least 125 m , but commonest in depths of less than 60 m . It often occurs on rough or rocky bottoms or that with algal cover. In the Eastern North Atlantic it appears to prefer rocky or cobble bottom substrate, while in the Mediterranean it is apparently found of coralline algal bottom.

Biology: Development oviparous, with a single egg laid at a time per oviduct. The large thick-walled egg-cases, 10 to 13 cm long and with strong tendrils at each corner, are deposited on macroalgae in the subtidal or extreme lower intertidal in spring and summer and may take 9 months to hatch. These sharks use different habitats within a home range, moving between different rock refuges between nocturnal and diurnal cycles.
Eats mostly cephalopods (squid and octopi), crustaceans, including hermit crabs, swimming crabs, cancrid crabs, and large shrimps, and a variety of bony fish including mackerel, epigonids, dragonets, gurnards, flatfish, herring, and small codfish and other bottom fishes, and other sharks (Scyliorhinus canicula).

Size: Maximum total length to 162 cm . Size at hatching about 16 cm ; adults common to 125 cm .
Interest to Fisheries and Human Impact: In European Atlantic waters this species is locally abundant in some regions, but is of limited fisheries importance relative to Scyliorhinus canicula. It is occasionally taken in bottom trawls and fixed bottom nets, but its preference for rough or rocky bottom habitat likely reduces its vulnerability to these fishing practices. Groundfish surveys around the United Kingdom report less 100 individuals were taken annually between 2002 and 2009. However, FAO catch statistics show that an annual average of 405 tonnes was reported landed between 2000 and 2009, with France and Portugal reporting the most landings at 172 and 202 tonnes, respectively. It is utilized fresh and dried-
salted for human consumption, and made into fishmeal.

The conservation status of this species is Near Threatened as its population appears to have declined in some regions of the Mediterranean Sea. There are no population estimates for this species from the European Atlantic seas.

Local Names: Large spotted dogfish, Larger spotted dogfish, Greater spotted dogfish, Nurse hound, Bull huss, Catfish or Cat fish, Bounce, Huss, Spotted dogfish (England); Morgi brych (Wales); Le squale rochier, Chat rochier, Rousette a grandes taches, Panthêre de mer, Cat rouquiera, Pinto reussou, Vache (France); Pantherhai, Hundshai, Großgefleckter Katzenhai (Germany); Grote gevlekte hondshaai (the Netherlands); Bounce (Belgium); Bruxa, Cacâo, Carraca, Cascarra, Gata, Bata roxa, Pata roxa denisa (Portugal); Alitán, Gat, Gatet, Gato, Gaton, Muxina, Pintarroja (Spain).

Literature: Ford (1921); Orton (1926);


Fig. 243 Scyliorhinus stellaris
Known distribution

Cadenat (1957); Wheeler (1969, 1978); Springer (1979); Compagno (1984, 1988); Ellis, Pawson and Shackley (1996); Ellis et al. (2005); Ellis et al. (2005a); Sims et al. (2005); Ellis et al. (2006a); Gibson et al. (2008); ICES (2010).

### 2.6.2 Family PSEUDOTRIAKIDAE

Family: Subfamily Pseudotriacinae Gill, 1893, Natn. Acad. Sci. USA, Mem. 6, 6: 130 (Family Scylliorhinidae). Emended and raised in rank as the family Pseudotriakidae by Jordan and Evermann, 1896, Bull. U.S. Nat. Mus. (47), 1: 26.

Type Genus: Pseudotriakis Capello, 1867, J. Sci. Math. Phys. Nat. Lisboa, ser. 2, (4): 321.

## Number of Recognized North Atlantic Genera: 1.

FAO Names: En - False catsharks; Fr - Requins à longue dorsale; $\mathbf{S p}$ - Musolones.
Field Marks: A distinctive group of small to large sharks with a narrowly rounded head and more or less elongated bell-shaped snout, a deep groove anterior to elongated, slit-like eyes and very large spiracles, first dorsal fin more or less elongated, with the base closer to the pectoral fins than the pelvic-fin bases, no precaudal pits, and a weak or absent ventral lobe on the caudal fin. Coloration is usually plain brown, grey, or black with no distinct markings.

Diagnostic Features: Head narrowly rounded with a more or less elongated bell-shaped snout, a deep groove in front of elongated, slit-like eyes; nictitating eyelids rudimentary. Spiracles very large. Anterior nasal flaps broadly angular, not barbel-like. Internarial space over 1.5 times nostril width. Mouth long, angularly arched, and extending posteriorly to eyes, no papillae inside mouth and none on edges of gill arches. Labial furrows very short. Teeth small, with acute narrow cusps, lateral cusplets, and strong basal ledges and grooves, not bladelike and similar in both jaws; posterior teeth comblike; tooth rows very numerous, upper jaw 96 to 294, lower jaw 108 to 335 . Pectoral fins with radials confined to bases of fins. First dorsal fin more or less elongated, base closer to pectoral-fin bases than to pelvic-fin bases. Precaudal pits absent. Caudal fin with weak ventral lobe or lobe absent; no undulations or ripples in dorsal caudal-fin margin. Valvular intestine with a spiral valve of 11 to 17 turns. Vertebral centra without strong, wedge-shaped intermedial calcifications. Colour: plain grey to brown or blackish.

Distribution: Wide ranging, but scattered for the large Pseudotriakis microdon, but the smaller Gollum attenuatus is restricted to New Zealand and adjacent waters.

Habitat: Poorly known deepwater sharks of the outer continental and insular shelves and slopes, on or near the bottom from 129 to 1890 m .

Biology: Development is a unique form of oophagy as early in development the embryos are nourished by a yolk-sac, but as development proceeds oophagy commences. This is the only family of sharks, other than the lamnoids, to exhibit this reproductive mode. Diet consists mostly of fishes, cephalopods, and crustaceans.

Interest to Fisheries and Human Impact: A poorly known group of sharks occasionally captured incidentally by fisheries and in fishery surveys, but likely not impacted much by fishing activity.

Local Names: Gollumsharks, Keelbacked catsharks (English); Lozhnokun'i akuly (Russia).
Remarks: The family is comprised of two genera, each monotypic with a single species. The only other species Gollum attenuatus is restricted to New Zealand waters. The unique form of oophagy exhibited by these sharks unites them in this family.

Literature: Compagno (1988); Compagno, Dando, and Fowler (2005); Musick and Ellis (2005).

## Pseudotriakis Capello, 1868

Genus: Pseudotriakis Capello, 1868, J. Sci. Math. Phys. Nat. Lisboa, (2), 1: 321.
Type species: Pseudotriakis microdon Capello, 1868, by monotypy
Number of Recognized North Atlantic Species: 1.
Synonyms: Genus Pseudotriacis Günther, 1870, Cat. Fish. British Mus. 8: 395. Emended spelling of Pseudotriakis Capello, 1868, and therefore taking the same type species, $P$ microdon Capello, 1867.

## Pseudotriakis microdon Capello, 1868

Pseudotriakis microdon Capello, 1868, J. Sci. Math. Phys. Nat. Lisboa, (2), 1: 321, pl. 5, fig. 1. Holotype in Museum Bocage, Lisbon, Portugal, 2310 mm adult male, lost in fire that destroyed this museum; collected off Setubal, Portugal.

Synonyms: None.
Other Combinations: None.
FAO Names: En - False catshark; Fr - Requin à longue dorsale; Sp - Musolón de aleta larga.



DORSAL VIEW OF HEAD


UNDERSIDE OF HEAD


LOWER TOOTH

Fig. 244 Pseudotriakis microdon

Field Marks: A large, bulky, dark-brown, soft-bodied shark with elongated, catlike eyes and nictitating eyelids, large spiracles, a huge, wide, angular mouth that reaches behind eyes, very short labial furrows, numerous small cuspidate teeth in 200 or more rows in each jaw, two large spineless dorsal fins and an anal fin, a low, long, keel-like first dorsal fin on back, no precaudal pits, and a caudal fin without a strong ventral lobe or lateral undulations on its dorsal margin. Colour is a uniform dark brown to black without any mottling, spots or other patterns.

Diagnostic Features: Head without laterally expanded blades. Eyes elongated and slit-like, with lengths over two times height. Nictitating eyelids are rudimentary. Spiracles are present and very large. Anterior nasal flaps broadly angular, not barbel-like. Internarial width about 2.8 times nostril width. Labial furrows very short. Teeth small, with acute narrow cusps, lateral cusplets, and strong basal ledges and grooves, not bladelike and similar in both jaws; posterior teeth comblike; tooth rows very numerous, upper jaw 202 to 294 , lower jaw 258 to 335 . Precaudal pits are absent. Pectoral fins with radials confined to bases of fins. First dorsal fin very large, low and formed as a rounded keel, about as long as caudal fin; first dorsal-fin base on back with insertion just opposite pelvic-fin origins and origin about opposite free rear tips of pectoral fins; midpoint of first dorsal-fin base well in front of pelvic-fin origins. Ventral caudal-fin lobe absent or very weak; no undulations or ripples in dorsal caudal-fin margin. Neurocranium with supraorbital crests. Vertebral centra without strong, wedge-shaped intermedial calcifications. Total vertebral counts 180 to 186 . Valvular intestine with a spiral valve of 17 turns. Colour: uniform plain dark brown to blackish except for darker fins.

Distribution: Sporadic but wide-ranging in most oceans, except so far not recorded in the South Atlantic or Eastern Pacific. Eastern North Atlantic: Atlantic Slope off Iceland, British Isles, France, and Portugal, including the Azores. Western North Atlantic: New York to New Jersey.

Habitat: A large deepwater bottom shark of the continental and insular slopes at depths from 100 to 1890 m ; occasionally wandering onto continental shelves, even in shallow water (possibly abnormally or possibly in situations where submarine canyons extend close to shore). Bottom temperature for one individual capture at 830 m was recorded as $6^{\circ} \mathrm{C}$.

Biology: Reproductive mode is oophagous, with litters of 2, but little else known. The gestation period for this species is unknown, but may last one year or more. Feeding habits little known, although it was once photographed in deep water eating a bony fish used as bait on the camera. It has also been photographed from a submersible poking


Fig. 245 Pseudotriakis microdon
$\square$ Known distribution $\square$ Possible distribution its nose into a trap and eating prawns in its entrance. Probably feeds on a variety of deepwater bony fishes, elasmobranchs and invertebrates. Its teeth are small but sharp cusped, and its mouth is very large, which may allow prey organisms of considerable size to be ingested. Seemingly uncommon or rare wherever it occurs. The large body cavity, soft fins, and soft skin and musculature of this shark suggest that it is relatively inactive and sluggish, and can hover off the bottom at virtually neutral buoyancy.

Size: Maximum total length 295 cm ; adult males reported at 200 to 269 cm ; adult females reported at 212 to 295 cm ; size at birth variably between 70 and 138 cm ; smallest free-swimming specimen measured 96 cm .

Interest to Fisheries and Human Impact: Interest to North Atlantic fisheries none since it is only taken incidentally by bottom fisheries usually operating at depths below 600 m . Utilization not reported.

The conservation status is Data Deficient due to its rarity, scattered distribution, and a lack of biological and population data.

Local Names: False cat shark, Atlantic false catshark, Keel-dorsal shark (English); Kambháfur (Iceland); Kamhaj (Denmark); Atlantischer Falscher Marderhai (Germany); Peixe carago (Portugal); Mamòna, False cat shark (Azores).

Literature: Capello (1868); Günther (1870); Bean (1883); Goode and Bean (1895); Jordan and Evermann (1896); Garman (1913); Lozano y Rey (1928); Bigelow and Schroeder (1948); Compagno (1984, 1988); Cadenat and Blache (1981); Yano and Musick (1992); Yano (1992); Santos, Porteiro and Barreiros (1997); Kyne, Yano and White (2004); Ebert (In preparation).

### 2.6.3 Family TRIAKIDAE

Family: Tribe Triakiana Gray, 1851 (Family Squalidae), List Fish British Mus., Pt. 1, Chondropterygii: 108.
Type genus: Triakis Müller and Henle, 1838.

## Number of Recognized North Atlantic Genera: 2.

FAO Names: En - Houndsharks, Smooth-hounds, Topes, Whiskery sharks; Fr - Emissoles, Hâs; Sp - Cazones, Tollos.
Field Marks: Small to moderate-sized sharks with horizontally oval eyes, nictitating eyelids, no nasoral grooves, anterior nasal flaps usually not barbel-like (except in Furgaleus), a long, angular or arched mouth that reaches past anterior ends of eyes, moderate to very long labial furrows, small to moderately large molariform, bladelike or cuspidate teeth, two moderate to large-sized, spineless dorsal fins and an anal fin, the first dorsal-fin base well ahead of pelvic-fin bases, no precaudal pits, and caudal fin without a strong ventral lobe or lateral undulations on its dorsal margin.

Diagnostic Features: Head without laterally expanded blades. Eyes elongated and fusiform, horizontally oval, or slitike, with lengths over 1.5 to 2.5 times height. Nictitating eyelids external, transitional or internal. Spiracles present and small to moderately large. Anterior nasal flaps varying from elongated to lobular to vestigial, barbel-like in one genus (Furgaleus). Internarial width about 0.5 to 3.0 times nostril width. Labial furrows moderately long to very long. Teeth small to moderately large, with acute and narrow to moderately large cusps and lateral cusplets in some species, but with these structures reduced or absent in others; teeth with strong basal ledges and grooves; teeth cuspidate and not bladelike, compressed and bladelike, or thickened and molariform; usually similar in both jaws but differentiated in a few species; posterior teeth not comblike; tooth rows 18 to 42 upper jaw, 27 to 106 lower jaw. Precaudal pits absent. Pectoral fins with radials confined to bases of fins. First dorsal fin moderately large to very large but not keel-like, usually much shorter than caudal fin (except in the genus Gogolia); first dorsal-fin base well ahead of pelvic-fin bases, usually closer to pectoral-fin bases than pelvic fins but sometimes slightly closer to pelvic fins; midpoint of first dorsal-fin base always in front of pelvic-fin origins. Ventral caudal-fin lobe varying from absent to well-developed; no undulations or ripples in dorsal caudal-fin margin. Vertebral counts: total vertebral counts 120 to 193 , monospondylous vertebral counts 25 to 52 , diplospondylous precaudal vertebral counts 28 to 61, precaudal vertebral counts 65 to 131. Valvular intestine with a spiral valve of 4 to 10 turns. Colour: some species with variegated colour patterns, others without them. Development viviparous with or without a yolk-sac placenta.

Distribution: This is one of the larger families of sharks, with many species found in all warm and temperate coastal seas.
Habitat: Most species occur on the continental and insular waters from the shoreline and intertidal to the outermost shelf, often close to the bottom, but a few deepwater species range down the continental slopes to considerable depths, possibly to over 2000 m . None of the species are coral reef specialists or are oceanic, but many are found in sandy, muddy and rocky inshore habitats, including enclosed bays. Although a few species have been recorded from up river mouths, none can apparently tolerate fresh water for extended periods.

Biology: Houndsharks are variably viviparous with yolk-sac or placental viviparity without a yolk-sac, and with litters of young ranging from 1 or 2 to 52 . Some species are relatively fast growing, maturing within 2 to 3 years while others may take more than 10 years to mature. The longevity for this shark group is also variable with some Mustelus species living only 5 to 9 years and one species (Galeorhinus galeus) perhaps living up to 60 years. A few houndsharks may reach almost two meters in length, but most are smaller and some mature at about 35 cm .
Houndsharks feed primarily on bottom and midwater invertebrates and bony fishes, with some species taking largely crustaceans, some mainly fishes, and a few primarily cephalopods; none eat mammalian meat or garbage to any extent. They feed on a wide variety of small to medium-sized bony fishes (both demersal and pelagic) and fish eggs, small sharks (including batoids), chimaeroids, crustaceans (including brachyuran crabs, hermit crabs, lobsters, slipper lobsters, king crabs, mantis shrimps, ghost shrimps, shrimps and prawns, and isopods), gastropods, bivalves (whole bivalves and their siphons), cephalopods (squids and octopi), tunicates, cephalochordates, polychaete worms, echiurid worms, sipunculid worms, holothurians, coelenterates, and rarely garbage.
These are fairly strong swimmers with most species occurring in small to large schools or singly. Some are very active species, like the tope shark (Galeorhinus), and may swim more or less continuously, but species of Mustelus and Triakis can rest on the bottom; some species are more active at night than the day. Many are more active at night than the day, and many tend to habitually swim close to the bottom.

Interest to Fisheries and Human Impact: Several genera within this family are of considerable importance to fisheries worldwide, especially members of the genera Galeorhinus and Mustelus, both of which have species that are fished in the North Atlantic. These sharks are caught with line gear, bottom and floating gillnets, set bottom nets, bottom trawls, and sportsfishing gear. They are primarily utilized for their meat, but also for liver oil, for processing into fishmeal, and for sharkfin soup base. None of the species are dangerous to people.

The conservation status of many species in this family is listed as Least Concern or Data Deficient, but some species are considered Near Threatened or Vulnerable.

Local Names: Houndsharks, Little nurse sharks, Smooth hounds, Smooth dogfishes, Gummy sharks.
Remarks: The family is comprised of nine genera, two of which occur in the North Atlantic, and nearly 50 species worldwide, with several still remaining to be described; four species are known to occur in the North Atlantic.

## Key to North Atlantic Genera:

1a. Ventral caudal-fin lobe very long at all stages. Second dorsal fin markedly smaller than first, half its area or less (Fig. 246)

Galeorhinus


1b. Ventral caudal-fin lobe absent to short in adults, weak or absent in young. Second dorsal fin nearly or quite as large as first, two-thirds to about equal its area (Fig. 247)

Mustelus


## Galeorhinus Blainville, 1816

Genus: Subgenus Galeorhinus Blainville, 1816, Bull. Sci. Soc. Philomat. Paris, (8): 121 (Genus Squalus Linnaeus, 1758).
Type species: "Galeorhinus galeus Blainville, 1816" by subsequent designation of Gill, 1862b, Ann. Lyceum Nat. Hist. New York, 7(32): 402, equals Squalus galeus Linnaeus, 1758.

## Number of Recognized North Atlantic Species: 1.

Synonyms: Subgenus Galeus Cuvier, 1816 (Genus Squalus Linnaeus, 1758), Reg. Anim., ed. 1, 2: 127. Type species: Squalus galeus Linnaeus, 1758 by monotypy and absolute tautonymy. A junior homonym of Genus Galeus Rafinesque, 1810. Genus Eugaleus Gill, 1863, Proc. Acad. Nat. Sci. Philadelphia 16: 148. Type species: Squalus galeus Linnaeus, 1758 by original designation.

Field Marks: See single species account below.
Diagnostic Features: Snout moderately long and parabolic in dorsoventral view, preoral length about equal to mouth width. Eyes horizontally oval and lateral, subocular ridges obsolete. Anterior nasal flaps vestigial, formed as small, low, angular points, well separated from each other and mouth; no nasoral grooves. Internarial width over 2.5 times nostril width. Mouth broadly arched and long. Labial furrows moderately long, uppers ending well behind level of upper symphysis. Teeth bladelike, compressed, and cuspidate, similar in upper and lower jaws, anteroposteriors with oblique cusps and cusplets; medial teeth well differentiated from anteroposteriors; total tooth counts 30 to 41 upper jaw, 31 to 46 lower jaw. First dorsal fin moderately large, base half length of dorsal caudal-fin margin or less; origin over or slightly behind pectoral-fin free rear tips, midbase slightly closer to pectoral-fin bases than pelvic fins. Second dorsal fin much smaller than first, less than half height of first. Anal fin about as large as second dorsal fin. Ventral caudal-fin lobe strong in young and adults; terminal lobe of caudal fin long and about 2 times in dorsal caudal-fin margin. Vertebral counts: total vertebral counts 123 to 146 (Eastern North Atlantic 134 to 136), precaudal vertebral counts 79 to 87 . Spiral valve turn counts 4 to 6 . Development viviparous without a yolk-sac placenta. Size large, adults 175 to 195 cm . Colour: uniform grey or bronze above, white below, without spots or dark bars.

Remarks: Molecular systematics of this genus suggests that apparently isolated populations of these animals from the Eastern Atlantic, Western Indian Ocean, Australasia, and the Western South Atlantic and Eastern South Pacific each may represent possibly distinct regional species. Further examination of regional Galeorhinus galeus species may be warranted to determine the status of the various nominal regional species. If some of these nominal regional species in fact turn out to be different species or subspecies, G. galeus as described by Linnaeus from European waters would retain its scientific name.

## Galeorhinus galeus (Linnaeus, 1758)

Squalus galeus Linnaeus, 1758, Syst. Nat., ed. 10, 1: 234. Holotype unknown, type locality: "Habitat in Oceano Europae".
Synonyms: ?Squalus rhinophanes Peron, 1807, Voy. Australes, 1: 337. Holotype unknown, type locality, Adventure Bay, Tasmania. Galeus vulgaris Fleming, 1828, British Anim.: 165 (Britain). Type; Unknown. Galeus canis Bonaparte, 1834, Iconog. Fauna Italica, Pesci, 3: 8, fig. 3 (Italy). Type: Unknown. Galeus nilssoni Bonaparte, 1846, Atti della Settima Adunanza degli Scienziati Italiani Settima Adunanza, Napoli: 19. Northern Ocean. Galeus communis Owen, 1853, Descr. cat. osteol. ser. coll. Roy. Coll. Surgeons: 92-93. Galeus linnei Malm, 1877, Göteborgs Bohusläns Fauna, 618. Apparently an unjustified replacement name for Squalus galeus Linnaeus, 1758, as this species is listed in synonymy.

Other Combinations: None.
FAO Names: En - Tope shark; Fr - Requin-hâ; Sp - Cazón.


Fig. 248 Galeorhinus galeus
Field Marks: A slender, long-nosed species with vestigial anterior nasal flaps, large horizontally oval eyes with internal nictitating lower eyelids, subocular ridges obsolete, an arched mouth, moderately long upper labial furrows that fall short of lower symphysis, bladelike compressed teeth with oblique cusps and distal cusplets in both jaws, second dorsal fin much smaller than first and about as large as anal fin, and an extremely long terminal caudal-fin lobe about half the dorsal caudal-fin margin.

Diagnostic Features: See genus account above.
Distribution: Eastern Atlantic: Iceland, Norway, Faroe Islands, and the British Isles to the Mediterranean and Senegal, but records from the Ivory Coast, Nigeria, and from Gabon to Zaire need confirmation. Globally, wide-ranging in most temperate seas except Western North Atlantic and Western North Pacific (but see Remarks for the genus).

Habitat: A coastal-pelagic shark of temperate continental and insular waters, often found well offshore (but not oceanic) as well as at the surfline, in shallow bays, and in submarine canyons; often occurs near the bottom, at depths of 2 to 471 m . It is very abundant in cold to warm temperate continental seas.

Biology: Development viviparous, without a yolk-sac placenta; number of young 6 to 52 per litter, increasing with the size of the mother; European topes usually have less than 20. Age at maturity varies by region, but for males they mature at 8 to 13.2 years, while females mature in 11 to 17.5 years; life expectancy is at least 45 years, but may be up to 60 years. A recaptured adult male school shark tagged with an internal tag was at large for 35.4 years, grew about 17 cm to 152 cm during this time, and was estimated from the size at tagging as being over 45 years old; its vertebral growth rings however, suggested an age of only 18 to 20 years. Tagged tope in northern Europe have been recaptured after 40 years at liberty.

Tope sharks prey heavily on bony fishes, taking a wide variety of bottom and schooling midwater fishes, but also cephalopods (most importantly squid), marine snails, crabs, shrimp, lobsters, annelid worms, echinoderms, and uncommonly other chondrichthyans (ratfish, sharks and small stingrays and skates). Young sharks may take more invertebrate prey than adults, and in some areas crabs and squid may be important prey items.
Natural predators of this shark include larger and more macropredatory sharks found in temperate waters, such as the great white shark (Carcharodon carcharias) and probably marine mammals.

Size: Maximum length 195 cm ; males maturing between about 120 to 170 cm and reaching a maximum length of 155 to 175 cm ; females maturing between about 130 to 185 cm and reaching a maximum length of 174 to 195 cm . Size at maturity varies regionally. Size at birth about 30 to 40 cm total length.


Fig. 249 Galeorhinus galeus
$\square$ Known distribution

Interest to Fisheries and Human Impact: The tope shark is not targeted in the Eastern North Atlantic, but it is taken as bycatch in trawl, gillnet, and longline fisheries. It is sometimes retained as landed bycatch, but is discarded in some fisheries. This is an important target species in recreational fisheries with most anglers following catch and release protocols. Globally, this species in most areas is an important commercial fishery in most areas where it occurs. Its meat is excellent for human consumption and is eaten fresh, fresh frozen, or dried salted; its liver contains oil that is extremely high in vitamin A, and its fins are used for sharkfin soup.
Although moderately large and active the tope shark has never been reported to bite people in the water. It will, however, snap when captured and has sufficiently large teeth to invite respect.

The conservation status globally is Vulnerable, although in some regions the populations have less fishing pressure and as a consequence these stocks are in a better state, while in other regions they are still subject to intensive fishing pressure. The Eastern North Atlantic population is considered Data Deficient because it is of limited fisheries importance and is typically landed as a bycatch in mixed demersal and pelagic fisheries. Landings data are limited as this shark is usually reported generically with other dogfish and hound shark species. However, between 2000 and 2009, annual landings of about 750 tonnes were reported, with most reported landings coming from France and Spain.

Local Names: Tope shark, Tope, Toper, Penny dog, Whitehound, Miller's dog, Rig, Liver-oil shark, Sweet William (British Isles); Milandre, Chien de mer, Palloun, Cagnot, Haut, Touille, Canicule (France); Hundshai, Gemeine meersau (Germany); Roofhaai, Steenhaei (the Netherlands); Graahaj (Denmark); Haastoerjen or Sturgeon shark, Bethaj or Bait shark (Sweden); Cacao, Ca mari, Casso, Cazón, Bosti, Bostrich, Gat, Musola, Musola corallo, Pez peine (Spain); Cacao, Cascarra, Chiâo, Chona, Chonâo, Dentudo, Perna-de-moça (Portugal); Caçao, Tope (Azores); Caçao (Madeira Islands).

Remarks: Although Galeorhinus galeus has been well studied in other parts of the world, especially Australia and in the Eastern North Pacific, virtually nothing is known about its life history or movement patterns in the Eastern North Atlantic.

Literature: Ripley (1946); Olsen (1984); Compagno (1984, 1988); Wheeler (1978); Ferreira and Vooren (1991); Peres and Vooren (1991); Ellis, Pawson and Shackley (1996); Officer et al. (1995, 1996); Smith, Au, and Snow (1998); West and Stevens (2001); Ebert (2003); Walker et al. (2006); Cavanagh, Ellis, and Dulvy (2006); Gibson et al. (2008); Chabot and Allen (2009); Last and Stevens (2009); ICES (2010); Chabot and Nigenda (2011); Ebert (In preparation).

## Mustelus Linck, 1790

Genus: Mustelus Linck, 1790, Mag. Neueste Phys. Naturg. Gotha 6: 31.
Type species: Squalus mustelus Linnaeus, 1758 by suspension of the Rules by the International Commission on Zoological Nomenclature, Opinion 93, 1926.

## Number of Recognized North Atlantic Species: 3.

Synonyms: Genus Mustellus Fischer, 1813, Zoognosia Tab. Synopt. Illustr. Ed. III. 1: 78. Type species: Squalus mustelus Linnaeus, 1758 by subsequent designation of Jordan and Evermann, 1917, Stanford U. Pub., U. Ser., Gen. Fish. (1): 85. Subgenus Mustelus Cuvier, 1816 (Genus Squalus Linnaeus, 1758), Reg. Anim., ed. 1, 2: 28. Type species: Squalus mustelus Linnaeus, 1758 by monotypy and absolute tautonymy. Genus Galeus Leach, 1818, Mem. Wernerian Nat. Hist. Soc. Edinburgh, 2: 62. Type species: Galeus mustelus Leach, 1818 by monotypy, equals Squalus mustelus Linnaeus, 1758. A junior homonym of Galeus Rafinesque, 1809 (Scyliorhinidae) and Galeus Cuvier, 1816 (equals Galeorhinus Blainville, 1816). Genus Emissola Jarocki, 1822, Zoologia. 4: 448. Type species: Squalus mustelus Linnaeus, 1758 by subsequent designation of Hubbs, 1938, p. 11. Genus Myrmillo Gistel, 1848, Naturg. Thierr: 10. Substitute name for Mustelus Cuvier, 1816, and therefore taking the same type species, Squalus mustelus Linnaeus, 1758. Genus Pleuroacromylon Gill, 1863, Proc. Acad. Nat. Sci. Philadelphia 16: 148. Type species: Mustelus laevis Müller and Henle, 1841 by original designation, equals Squalus mustelus Linnaeus, 1758. Genus Cynias Gill, 1903, Proc. U.S. Natn. Mus. 26: 960. Type species: "Mustelus canis" of Jordan and Evermann, 1896, by original designation, a composite of Squalus canis Mitchill, 1815 and Mustelus asterias Cloquet, 1821. Genus Allomycter Guitart, 1972, Poeyana (99): 1. Type genus: Allomycter dissutus Guitart, 1972 by monotypy, probably equals Squalus canis Mitchill, 1815.

Field Marks: Usually slender houndsharks with long, parabolic-subangular snouts, dorsolateral eyes and strong subocular ridges, angular mouths, teeth formed into a pavement, with cusps and cusplets variably developed but usually obsolete or absent, medial teeth not differentiated from anterolaterals, and second dorsal fin nearly as large as first.

Diagnostic Features: Snout long and parabolic-subangular in dorsoventral view, preoral length less than 1.3 times mouth width. Eyes horizontally elongated or oval and dorsolateral, subocular ridges strong. Anterior nasal flaps rather elongated and lobate, well separated from each other and mouth; no nasoral grooves. Internarial width about 1.0 to 2.0 times nostril width. Mouth angular and moderately long. Labial furrows moderately long, uppers falling well behind level of upper symphysis. Teeth not bladelike and similar in both jaws, varying from somewhat compressed and with short erect cusps and cusplets to rounded, molariform, and without cusps and cusplets; medial teeth not differentiated from anteroposteriors. First dorsal fin moderately large, base less than $3 / 4$ of dorsal caudal-fin margin; origin over pectoral-fin inner margins or slightly behind their free rear tips, midbase about equidistant between pectoral and pelvic-fins bases or closer to pectoralfin bases. Second dorsal fin nearly as large as first, height about $2 / 3$ to $3 / 4$ as high as first. Anal fin considerably smaller than second dorsal fin. Ventral caudal-fin lobe hardly developed in young but varying from poorly developed to short and strong in adults; terminal lobe of caudal fin moderately long and about 2.3 to 3.0 times in dorsal caudal-fin margin. Vertebral counts: total vertebral counts 109 to 162, monospondylous precaudal vertebral counts 25 to 47, diplospondylous precaudal vertebral counts 23 to 66, precaudal vertebral counts 58 to 106. Spiral valve turn counts 7 to 10 . Development viviparous with or without a yolk-sac placenta. Size medium to large, adults 43 to 170 cm . Colour: depending on the species, some are relatively plain dorsally, while others have distinctive patterns of lighter or sometimes darker spots; fin edges may be lighter or darker; ventral surface is usually lighter.

Interest to Fisheries and Human Impact: Mustelus species are abundant temperate to tropical, inshore to offshore bottom sharks of continental and insular shelves and uppermost slopes that figure prominently in artisanal and commercial fisheries.

Local Names: Smoothhounds, Smooth hounds, Smooth dogfish, Gummy sharks, Gummys, Emissoles, Musolas, Tollos, Palombos, Cazones, Dog sharks.

Remarks: Members of the genus Mustelus are unusually difficult to separate from one another, particularly without the use of internal characters. Many of the morphological, morphometric and meristic characters that distinguish species partially overlap, and considerable variation occurs within species. Presently, there are 27 valid species recognized within this genus, and with three known to occur in the North Atlantic. The blackspotted smoothhound, Mustelus punctulatus, has variously been reported in some literature accounts as occurring in Area 27, just outside the Mediterranean, but this could not be confirmed here and as such this species is not considered further in the present work.

## Key to North Atlantic Species:

1a. Numerous small white spots on dorsal surface of body, particularly along lateral line (NOTE: These spots are often faint or sometimes absent)(Fig. 250a). Upper labial furrows considerably longer than lowers (Fig. 250b)

Mustelus asterias (NE Atlantic)

1b. Dorsal surface uniform grey or with a few dark spots (Figs. 251a, 252a). Upper labial furrows usually about as long or hardly longer than lowers (Figs. 251b, 252b) (noticeably longer in M. canis and to a lesser extent in M. mustelus)

2a. Internarial space broader, 2.7 to $3.6 \%$ of total length. Labial furrows somewhat longer, 1.6 to $2.7 \%$ of total length (Figs. 251b). Precaudal centra more numerous, 85 to 100 (Western Atlantic) . . . . . . . .

Mustelus canis (NW Atlantic)

2b. Internarial space narrower, 2.4 to $3.0 \%$ of total length. Labial furrows somewhat shorter, 1.4 to $2.0 \%$ of total length (Fig. 252b). Precaudal centra fewer, 70 to 93 (Eastern Atlantic, Mediterranean and Cape Coast of South Africa)

Mustelus mustelus (NE Atlantic)


Fig. 250 Mustelus asterias


Fig. 251 Mustelus canis


Fig. 252 Mustelus mustelus

## Mustelus asterias Cloquet, 1821

Mustelus asterias Cloquet, 1821, Emissole, in Dict. Sci. Nat. 14: 401. Holotype: none. Type locality not mentioned.
Synonyms: Squalus hinnulus Blainville, 1825, in Vieillot et al., Faune Francaise, Poiss., liv. 13-14: 83, pl. 20, fig. 2. Holotype: Adult male, $3^{\prime}$ long (specimen with measurements in text and figured), lost? Type locality: Mediterranean Sea. Mustellus stellatus Risso, 1826, Hist. nat. Princip. Prod. Europe Méred., Paris, Poissons, 3: 126. Types: ? Type locality not given, but based on Squalus hinnulus Blainville, 1825. Mustelus plebejus Bonaparte, 1834, Iconog. Fauna ltalica, 3, Pesci, fasc. 8, pl. 49, fig. 1. Types: ? Type locality: Italy. Mustelus equestris Bonaparte, 1834, Iconog. Fauna Italica, 3, Pesci, fasc. 8 (in part). Types: ? Type locality: Italy. Mustelus vulgaris Müller and Henle, 1839, Syst. Beschr. Plagiost., pt. 2: 64 (in part, apparently including several species, M. asterias, possibly M. mustelus, and species from the Red Sea, South Africa, Australia, and Japan; ibid., 1841, pt. 3: 190, pl. 27, fig. 1. Syntypes: Zoologisches Museum der Humboldt-Universität, Berlin, ZMHU (ZMB) 4502, 1039 mm stuffed female, Red Sea (also syntype of M. mosis), ZMHU 31649, 795 mm female (alcohol), no locality, ZMHU 31650, 125 mm fetus from Nice, France; ZMHU 31651, 98 mm fetus with no locality, according to Paepke and Schmidt (1988, Mitt. Zool. Mus. Berlin 64[1]: 170). Not M. vulgaris Cloquet, 1821, = Squalus mustelus Linnaeus, 1758. Squalus albomaculatus Plucar, 1846, Fischplatz Trieste: 7. Types: ? Type locality, Trieste, Italy. Squalus edentulus Chiereghini, in Doderlein, 1881, Man. Ittiolog. Mediterraneo (2), fasc. 1, Epibranchi, Elasmobranchii: 30. A manuscript name, listed in synonymy of M. plebejus Bonaparte, 1834.

Other Combinations: None.
FAO Names: En - Starry smooth-hound; Fr - Émissole tachetée; Sp - Musola dentuda.


Fig. 253 Mustelus asterias


UNDERSIDE OF HEAD


DERMAL DENTICLES

Field Marks: A large, white-spotted Mustelus with relatively narrow internarial space, buccopharyngial denticles covering almost entire oral cavity, unfringed dorsal fins, relatively small pectoral and pelvic fins, and 90 to 100 precaudal centra. It is the only white-spotted smoothhound in European waters, although these spots are often faint or even lacking.

Diagnostic Features: Body fairly slender. Head short, prepectoral length 13 to $17 \%$ of total length. Snout moderately long and bluntly angular in lateral view, preoral snout 5.4 to $7.2 \%$ of total length, preorbital snout 5.7 to $7.2 \%$ of total length. Internarial space fairly narrow, 2.0 to $2.6 \%$ of total length. Eyes large, eye length 1.6 to 2.2 times in preorbital snout and 2.5 to $4.1 \%$ of total length. Interorbital space relatively narrow, 3.4 to $4.5 \%$ of total length. Mouth relatively short, subequal or smaller than eye length, length 2.2 to $3.5 \%$ of total length. Upper labial furrows considerably longer than lowers, upper furrows 1.8 to $2.5 \%$ of total length. Teeth molariform and asymmetric, with cusp reduced to a low point, cusplets absent except in very young sharks. Buccopharyngial denticles covering entire palate and floor of mouth. Crowns of lateral trunk denticles broadly lanceolate, with longitudinal ridges extending at least half of their lengths. Pectoral fins moderate-sized, length of anterior margins 12 to $16 \%$ of total length, width of posterior margins 7.8 to $13 \%$ of total length. Pelvic-fin anterior margins 6.6 to $9.1 \%$ of total length. Interdorsal space 19 to $25 \%$ of total length. Trailing edges of dorsal fins denticulate, without bare ceratotrichia. Anal-fin height 2.4 to $3.9 \%$ of total length. Anal-caudal space usually greater than second dorsal-fin height, 6.8 to $11 \%$ of total length. Ventral caudal-fin lobe not falcate in adults. Vertebral counts: total vertebral counts 143 to 149 , monospondylous precaudal vertebral counts 36 to 40 , diplospondylous precaudal vertebral counts 49 to 61, precaudal vertebral counts 90 to 100. Development viviparous without yolk-sac placenta. Size large, adults 80 to 140 cm . Colour: grey or grey-brown above, light below, usually with numerous small white spots on sides and back, but without dark spots or dark bars.

Distribution: Eastern North Atlantic: British Isles and North Sea to Canary Islands, Mediterranean and Mauritania.

Habitat: A common inshore and offshore shark of the continental and insular shelves, on or near bottom at depths from the intertidal down to at least 100 m . Prefers sandy and gravelly bottoms. Juveniles often occur in bays and the outer reaches of large estuaries.

Biology: A viviparous species, without a yolk-sac placenta; number of young 6 to 18 per litter, with litter size increasing proportionally to maternal size. The gestation period is about 12 months. Young are born inshore in summer, and presumably mating occurs shortly afterwards. Eastern North Atlantic males and females mature at 4 to 5 years and at 6 years, respectively.
Primarily a crustacean feeder, that eats crabs, hermit crabs, lobsters and squat lobsters. Hermit crabs are eaten complete with the whelk shells they live in and sometimes with the commensal sea anemones that live on their shells.


Fig. 254 Mustelus asterias
Known distribution

Size: Maximum about 140 cm ; males maturing between 72 and 85 cm , females at about 83 to 91 cm . The size at maturity for males between Eastern North Atlantic and Mediterranean is similar. However, the size at maturity for females varies significantly between the Mediterranean female populations, which mature at a much larger total length ( 96 cm ), than the Eastern North Atlantic population. Size at birth about 28 to 32 cm .

Interest to Fisheries and Human Impact: Smoothhound sharks are caught by bottom trawls, gillnets and longline, and juveniles are also caught in beam trawls; utilized fresh and probably dried salted; also taken by shore anglers. Both smoothhound shark species are reported in fishery landings, being reported at a generic level or species level. Landed fish are separated on the basis of the presence (Mustelus asterias) or absence (M. mustelus) of spots; a characteristic that is not always reliable. However, population trends in northern Europe for the genus as a whole are stable or increasing. Readily kept in large public aquaria, and currently a popular and attractive display animal in England. In captivity it is quite active and swims near the bottom.

The conservation status is Least Concern since its population appears to be stable and possibly increasing in European Atlantic waters.

Local Names: Starry smoothhound, Stellate smoothhound, Smooth hound (English); Squale lentillat, Emissole tachetée (France); Musola estrellada (Spain); Gefleckter Hundshai (Germany); Stjernehaj (Denmark); Nordlig hundhaj (Sweden).

Literature: Lozano y Rey (1928); Springer (1938); Bigelow and Schroeder (1948); Tortonese (1956); Heemstra (1974); Wheeler (1978); Compagno (1988); Ellis, Pawson and Shackley (1996); Compagno, Dando, and Fowler (2005); Serena, Mancusi and Ellis (2006); Gibson et al. (2008); Farrell, Mariani, and Clarke (2009, 2010a, b); ICES (2010, 2012); Ebert (In preparation).

## Mustelus canis (Mitchill, 1815)

Squalus canis Mitchill, 1815, Trans. Lit. Philos. Soc. New York, 1: 486. Type locality: New York. Type specimens not preserved (Heemstra, 1997, Bull. Mar. Sci. 60[3]: 899).

Synonyms: ?Allomycter dissutus Guitart, 1972, Poeyana (99): 2, fig. 1. Holotype: 89 cm total length female, from off Matanzas, Cuba, in 366 m depth, not saved. See Compagno (1988). Mustelus canis insularis Heemstra, 1997, Bull. Mar. Sci. 60(3): 903, fig. 5. Holotype: U.S. National Museum of Natural History, USNM-208012, 111 cm total length adult female, 5 mi . NW of Cay Sal Island, Cay Sal Bank, Bahamas, 214 m.

Other Combinations: Mustelus mustelus (not Linnaeus, 1758), Galeorhinus laevis (not Linck, 1790).
FAO Names: En - Dusky smooth-hound; Fr - Émissole douce; Sp - Boca dulce.



UNDERSIDE OF HEAD


TEETH


DERMAL DENTICLES

Fig. 255 Mustelus canis

Field Marks: A usually unspotted, large Mustelus with a short head and snout, broad internarial, large eyes, narrow interorbital, upper labial furrows somewhat longer than lowers, low-crowned teeth with weak cusps, buccopharyngial denticles confined to extreme front of mouth, lateral trunk denticles usually lanceolate and with complete ridges, unfringed dorsal fins, 85 to 100 precaudal centra, and a non-falcate but moderately expanded ventral caudal-fin lobe.

Diagnostic Features: Body fairly slender. Head short, prepectoral length 17 to $21 \%$ of total length. Snout moderately long and bluntly angular in lateral view, preoral snout 5.5 to $8.1 \%$ of total length, preorbital snout 5.9 to $8.3 \%$ of total length. Internarial space broad, 2.7 to $3.7 \%$ of total length. Eyes fairly large, eye length 1.9 to 2.3 times in preorbital snout and 2.2 to $4.2 \%$ of total length. Interorbital space narrow, 3.6 to $4.6 \%$ of total length. Mouth fairly short, subequal to or slightly longer than eye length, length 2.3 to $3.5 \%$ of total length. Upper labial furrows slightly longer than lowers, upper furrows 1.6 to $2.7 \%$ of total length. Teeth molariform and asymmetric, with cusp reduced to a low point, cusplets absent except in very young sharks. Buccopharyngial denticles confined to tongue and anteriormost part of palate. Crowns of lateral trunk denticles lanceolate, with longitudinal ridges extending at least half their length, and often their entire length. Pectoral fins moderately large, length of anterior margins 11 to $16 \%$ of total length, width of posterior margins 8 to $14 \%$ of total length. Interdorsal space 16 to $23 \%$ of total length. Pelvic fins moderately large, anterior margin length 6.6 to $8.6 \%$ of total length. Trailing edges of dorsal fins denticulate, without bare ceratotrichia. First dorsal fin somewhat falcate, with a nearly vertical posterior margin, midbase closer to pectoral-fin bases than pelvic fins. Anal-fin height 2.5 to $4.5 \%$ of total length. Anal-caudal space greater or subequal to second dorsal-fin height, 6.3 to $9.2 \%$ of total length. Ventral caudal-fin lobe not falcate but somewhat expanded in adults. Vertebral counts: total vertebral counts 143 to 149 , monospondylous precaudal vertebral counts 34 to 42 , diplospondylous precaudal vertebral counts 48 to 60, precaudal vertebral counts 85 to 100 . Development viviparous with yolk-sac placenta. Size large, adults 82 to possibly 150 cm . Colour: uniform grey above, light below, no white or dark spots or dark bars, but newborn young with dusky-tipped dorsal and caudal fins.

Distribution: Endemic to Western Atlantic: Canada (Bay of Fundy), Atlantic east Coast of the USA (Maine, Massachusetts, New York, Rhode Island, New Jersey, Delaware, Virginia, Maryland, North and South Carolina, Georgia, east coast of Florida), Gulf of Mexico coast of the USA (Florida, Texas) and Mexico, Venezuela, Surinam, French Guiana, and southern Brazil (south of Rio de Janeiro), Uruguay (Rio de Janeiro) and northern Argentina (Mar de Plata) for typical subspecies (Mustelus canis canis). Replaced by subspecies by insular subspecies (M. c. insularis), from Bahamas, Bermuda Cuba, Jamaica, Grand Cayman, Puerto Rico, Nevis Island, Saint Eustatius, Cay Sal Bank, Barbados, Bimini, Bahamas Bank, Turtle Rocks, Picket Rock, Jamaica, Leeward Islands.

Habitat: A temperate and tropical, mostly bottom-dwelling shark of the continental and insular shelves and upper slopes, ranging from shallow inshore waters and the intertidal down to 808 m . The


Fig. 256 Mustelus canis subspecies Mustelus canis canis prefers continental inshore waters between the intertidal and the shoreline down to 200 m , with a few records on the uppermost slopes down to 360 m , and it is commonly taken in waters of less than 20 m deep off the temperate US East Coast, with many coming into enclosed bays and harbours, especially with mud or sandy bottoms. It is mostly found on the continental shelves between the intertidal and the shoreline down to 200 m , with a few records on the uppermost slopes down to 360 m . In the Caribbean the subspecies Mustelus canis insularis apparently avoids coral reefs and generally prefers rough rocky bottoms. The subspecies M. c. insularis inhabits deeper offshore water on the outer shelves and upper slopes at depths of 137 to 808 m , with most recorded below 200 m ; it has also been reported to occur in the midwater off Cuba.

Biology: Viviparous, with a yolk-sac placenta, the number of young per litter is 4 to 20 , averaging 9 ; litter size increases in relation to size of the female. The gestation period of smooth-hounds off New England is about 10 to 12 months, with mating in midsummer (July) and birth between early May and mid-July of the next year. Age at maturity is 2 to 3 years for males and 4 to 7 years for females. Males and females reach a maximum age of 10 and 16 years, respectively.

This shark is a specialist crustacean feeder, predating on larger crustaceans but also takes a variety of small bony fishes (teleosts) and other invertebrate prey. Crustacean prey includes swimming crabs (Portunidae), rock crabs (Cancridae),
spider crabs (Majidae), mantis shrimp (Squillidae), hermit crabs (Paguridae), shrimps (Crangonidae), and lobsters (Nephropidae); cancrid crabs and American lobsters (Homarus, Nephropidae) are important prey. Teleost prey includes menhaden (Clupeidae), codlike fishes (Gadidae), eel-pouts (Ophididae), stickleback (Gasterosteidae), sand lances (Ammodytidae), wrasses (Labridae), porgies or sea bream (Sparidae), sculpins (Cottidae), flatfish (Pleuronectiformes) including American soles (Achiridae) and righteye flounders (Paralichthyidae), and puffers (Tetraodontidae). Other food items include king crabs (Limulidae), squid (Loliginidae; squid may be taken in springtime in New England waters), gastropods (Melongenidae), bivalves (Solenidae) and polychaete worms. Garbage is occasionally found in the stomachs. Some have been found with quantities of eel-grass (Zostera) in their stomachs, but this may be incidentally taken in while the smoothhounds are capturing animal prey.

This is a very active shark, constantly patrolling the bottom for food, which can be located when hidden as when in sight, indicating use of other senses including olfactory and electrosense. In captivity they readily attack crabs and shake them vigorously sideways before devouring them, but rarely molest active bony fishes; sick, injured or dead fish are quickly devoured.

This shark appears to be divided into several discrete populations, with few or no members of this species occurring in the broad gaps between them (Bigelow and Schroeder, 1948, Heemstra, 1997). The best-known population is the possibly cold-adapted coastal form, which occurs from the Carolinas north along the US Atlantic Coast to New England and southern Canada. The species is uncommon south of North Carolina but is again common off Florida and turns up at many localities in the Gulf of Mexico, where it is sympatric with the inshore Mustelus norrisi and offshore M. sinusmexicanus. A distinct deep-water insular form (M. canis insularis) occurs off Bermuda, the Bahamas, and various Caribbean islands. Finally the species occurs in the Western South Atlantic off southern Brazil to Uruguay and Argentina.

Off the Atlantic coast of the USA the species is migratory, and responds to changes in water temperature by moving to the north and inshore during the summer, but retreats to the south and moves off shore during the winter. The species primarily winters in the area between southern North Carolina and Chesapeake Bay. In the springtime as the water warms up on the bottom to at least 6 to $7^{\circ} \mathrm{C}$ it moves northwards along the coast to New England, and southwards to South Carolina. As summer wanes smooth dogfish move offshore and withdraw centrally to their wintering area.

Size: Maximum 150 cm ; males maturing at about 82 to 86 cm and females maturing at about 90 to 102 cm . Size at birth between 34 to 39 cm .

Interest to Fisheries and Human Impact: Interest to fisheries considerable. Common to abundant where it occurs. Off southern New England and the Middle Atlantic States of the USA this is the second most abundant shark, although falling far short of the picked dogfish, Squalus acanthias, in numbers. Over the past decade an average of about 400 tonnes was landed annually in the United States (FAO landings statistics). This locally abundant shark, however, is fished primarily off Cuba, Venezuela, and Brazil, but no doubt is utilized elsewhere in the Caribbean. It is caught with bottom and floating longlines, gillnets, occasionally with bottom trawls, and utilized fresh and dried salted for human consumption.

Smooth-hounds are harmless to humans, except for competing with them for crustaceans, especially the valuable American lobster. One estimate quoted in Bigelow and Schroeder (1948) suggested that in Buzzard's Bay, Massachusetts at the turn of the century, these sharks annually ate 200,000 crabs, 60,000 lobsters, and 70,000 small fish. They are kept for public viewing in aquaria.

The conservation status of this species is considered Near Threatened.
Local Names: Smooth houndshark, Smooth dogfish, Smooth dog shark, Smooth-hound, Smooth hound, Hound, Gummy shark, Dogfish, Nurse shark, Smooth grayfish, Dog shark, Blue dog, Smooth dog, Grayfish (USA).

Remarks: This species is sometimes separated in two subspecies, Mustelus canis canis of the continental shelves and uppermost slopes from the Bay of Fundy, Canada to Uruguay, and M. c. insularis from deep water off islands in the northern Caribbean. However, these subspecies are extremely difficult to distinguish externally. According to Heemstra (1997), these two species can be separated by the following characteristics:
M. c. canis. First dorsal fin slightly higher, usually more than $10 \%$ total length in adults over 80 cm long. Terminal caudal lobe somewhat shorter, 4.6 to $7.0 \%$ total length. Monospondylous precaudal centra 34 to 39 (mean 36.5), precaudal centra 85 to 93 (mean 88.2). White margins on fins of juveniles indistinct.
M. c. insularis. First dorsal fin slightly lower, usually less than $10 \%$ total length in adults over 80 cm long. Terminal caudal lobe somewhat longer, 6.5 to $8.6 \%$ total length. Monospondylous precaudal centra 39 to 42 (mean 40.2), precaudal centra 94 to 100 (mean 96.7). White margins on fins of juveniles distinct.

Literature: Springer (1939); Bigelow and Schroeder (1948); Heemstra (1974, 1997); Compagno (1984, 1988); Gelsleichter, Musick and Nichols (1999); Conrath, Gelsleichter, and Musick (2002); Conrath and Musick (2002); Compagno, Dando, Fowler (2005); Conrath (2005); Ebert (In preparation).

## Mustelus mustelus (Linnaeus, 1758)

Squalus mustelus Linnaeus, 1758, Syst. Nat., ed. 10, 1: 235. Holotype unknown, type locality: "Habitat in Europa."
Synonyms: Mustelus laevis Linck, 1790, Mag. Neueste Phys. Naturg. Gotha 6: 31. Mustelus vulgaris Cloquet, 1821 (?), Emissole, in Dict. Sci. Nat. 14: 401. Holotype: No known types. Type locality not mentioned. Squalus laevis Blainville, 1825, in Vieillot et al., Faune Francaise, Poiss., liv. 13-14: 84. Holotype: Specimen one meter long mentioned, lost? Based on Risso's article in J. Phys. vol XCXI: 242, ? date which first distinguished this species. Type locality: Mediterranean Sea. Mustellus levis Risso, 1826, Hist. nat. Princip. Prod. Europe Méred., Paris, Poissons, 3: 127. Mustelus equestris Bonaparte, 1834 (in part), Iconog. Fauna Italica, 3, Pesci: fasc. 8, punt. 43, pl. 132 (fig 2). Mustelus vulgaris Müller and Henle, 1839, Syst. Beschr. Plagiost., pt. 2: 64 (in part, possibly including this species as well as M. asterias (see its account, above). Mustelus laevis Müller and Henle, 1841, Syst. Beschr. Plagiost., pt. 3: 190 (possibly including this species as well as $\boldsymbol{M}$. punctulatus, intended as a species for the "Galeus laevis" of Rondelet, 1554, the European spotless smooth-hound). Types? Müller and Henle (loc. cit.) mention two varieties under this species, a spotless Var. 1 and Var. 2 with dark spots. The latter could possibly be either M. mustelus or M. punctulatus.

Other Combinations: Mustelus canis (not Mitchill, 1815).
FAO Names: En - Smooth-hound; Fr - Émissole lisse; Sp - Musola.


Fig. 257 Mustelus mustelus
Field Marks: A usually unspotted, large Mustelus with a short head and snout, broad internarial, large eyes, narrow interorbital, upper labial furrows slightly longer than lowers, low-crowned molar-like teeth with weak cusps, buccopharyngial denticles confined to extreme front of mouth, lateral trunk denticles usually lanceolate and with complete ridges, unfringed dorsal fins, 70 to 93 precaudal centra, and a semifalcate ventral caudal lobe. It is the only smooth-hound with the above characters where it occurs.

Diagnostic Features: Body fairly slender. Head short, prepectoral length 17 to $21 \%$ of total length. Snout moderately long and bluntly angular in lateral view, preoral snout 5.3 to $7.4 \%$ of total length, preorbital snout 5.9 to $8.0 \%$ of total length. Internarial space broad, 2.4 to $3.0 \%$ of total length. Eyes fairly large, eye length about 1.9 to 2.8 times in preorbital snout and 2.3 to $4.0 \%$ of total length. Interorbital space narrow, 3.7 to $4.8 \%$ of total length. Mouth fairly short, length subequal to eye length and 2.2 to $3.5 \%$ of total length. Upper labial furrows usually slightly longer than lowers and 1.4 to $2.1 \%$ of total length. Teeth molariform and asymmetric, with cusp reduced to a low point, cusplets absent except in very young sharks. Buccopharyngial denticles confined to tongue tip and extreme anterior end of palate. Crowns of lateral trunk denticles lanceolate or weakly tricuspidate, with longitudinal ridges extending their entire length. Pectoral fins moderately large, length of anterior margins 13 to $17 \%$ of total length, width of posterior margins 8.2 to $14 \%$ of total length. Pelvic fins moderately large, anterior margin length 6.5 to $9.9 \%$ of total length. Interdorsal space 18 to $25 \%$ of total length. Trailing edges of dorsal fins denticulate, without bare ceratotrichia. First dorsal fin falcate, with posterior margin almost vertical, midbase closer to pectoral-fin bases than pelvic fins. Anal-fin height 2.4 to $4.3 \%$ of total length. Anal-caudal space greater than second dorsal -fin height and 6.3 to $8.8 \%$ of total length. Ventral caudal-fin lobe more or less falcate in adults. Vertebral counts: total vertebral counts 131 to 137 , monospondylous precaudal vertebral counts 25 to 32 , diplospondylous precaudal vertebral counts 40 to 66 ,
precaudal vertebral counts 70 to 93 . Development viviparous with yolk-sac placenta. Size large, adults 70 to at least 150 cm . Colour: uniform grey or grey-brown above, light below, no white spots or dark bars, some specimens with dark spots.

Distribution: Eastern Atlantic: distribution in the northern parts of the area unclear, as nominal records may be misidentified M. asterias. Reported from British Isles and France, and south to Spain, Portugal, Mediterranean, Morocco, Canary Islands, possibly Azores, Madeira, Angola, Namibia, South Africa (Northern and Western Cape). Southwestern Indian Ocean: South Africa (Eastern Cape and kwaZulu-Natal).

Habitat: A common to abundant shark, where it occurs, of the continental shelves and uppermost slopes, most commonly found in shallow water at depths from 5 to 50 m , but often in the intertidal and ranging to at least 350 m depth; sometimes in midwater but prefers to swim near the bottom.

Biology: Viviparous, with a yolk-sac placenta; number of young 4 to 15 per litter. Gestation period about 10 to 11 months. The age at maturity for females is 12 to 15 years and for males 6 to 9 years; maximum age for females and males is 24 and 17 years, respectively.


Fig. 258 Mustelus mustelus
$\square$ Known distribution $\square$ Possible distribution

Primarily a crustacean feeder that eats crabs, lobsters, squat lobsters, hermit crabs, and shrimps, but also cephalopods (including octopi) and bony fishes (including snake eels).

Size: Maximum 164 cm ; males maturing between 70 to 74 cm and reaching at least 110 cm ; females maturing at about 80 cm and reaching at least 164 cm . Size at birth about 39 cm .

Interest to Fisheries and Human Impact: Fisheries for Mustelus mustelus and M. asterias occurs in the Eastern North Atlantic, but both species are generally reported as mixed smoothhound sharks. Over the past decade ( 2000 to 2009) an average of more than 2300 tonnes was landed annually with a peak of 3419 tonnes being landed in 2009. Most of the reported landings were from France, which averaged 2148 tonnes annually over the past decade. Smaller landing amounts were reported by Portugal, Spain, and the United Kingdom. These sharks are commonly taken in bottom trawl and fixed bottom nets, with longline gear, and occasionally in pelagic trawls. It is utilized fresh and fresh-frozen for human consumption, also dried salted and smoked. Its liver is used for oil and carcasses for fishmeal.

The global conservation status of this species is considered Least Concern, but in the Eastern North Atlantic it is Data Deficient.

Local Names (several of the European names probably refer to Mustelus asterias and possibly to M. punctulatus): Smooth hound, Smoothhound shark, Smooth dogfish, Smooth dog shark, Gray hound fish, European dogfish, Hound, Sweet William, Skate-toothed shark (English); Murloch (Scotland); Stinkard (Ireland); Ci llyfn (Wales); Chien de mer, Doucette, L'amissole commune, Lentillat, Moutelle, Mustela de mar, Mustele vulgaire, Squale emissole, L'émissole lisse, Missola, Nissole, Pallouna (France); Glatt hai (Germany); Caella, Cazón, Musola, Musola pintada, Mustela, Janquerellas, Mozuela, Pique (Spain); Cacáo, Cacáo morraceiro, Cacâo pique, Pique, Galhudo (Portugal); Smooth hound (Azores); Canéja (Madeira Islands); Akula-liudoed (Russia); Caneja, Jaqueta, Jacueta, Tollo (Canaries).

Remarks: This species is very close to Mustelus canis of the Western Atlantic and has been sometimes confused with it, but according to Heemstra (1974), it differs in having somewhat shorter upper labial furrows, a narrower internarial, and fewer vertebrae.

Literature: Lozano y Rey (1928); Springer (1938); Bigelow and Schroeder (1948); Poll (1951); Tortonese (1956); Cadenat (1957); Quignard and Capapé (1972); Heemstra (1974); Wheeler (1978); Cadenat and Blache (1981); Smale and Compagno (1997); Goosen and Smale (1997); Serena et al. (2004); ICES (2010); Ebert (In preparation).

### 2.6.4 Family CARCHARHINIDAE

Family: Subfamily Carcharhininae Jordan and Evermann, 1896, Bull. U.S. Nat. Mus. (47), pt. 1: 28 (Family Galeidae).
Type genus: Carcharhinus Blainville, 1816.

## Number of Recognized North Atlantic Genera: 5.

FAO Names: En - Requiem sharks; Fr - Requins; Sp - Cazones picudos, Tiburones, Tintoreras.
Field Marks: Small to large sharks with round to horizontal eyes, internal nictitating eyelids, no nasoral grooves or barbels, usually no spiracles, a long, arched mouth that reaches past anterior ends of eyes, moderately long labial furrows, small to large, more or less bladelike teeth in both jaws, often broader in the upper jaw, two dorsal fins and an anal fin, the first dorsal fin moderate-sized to large and with its base well ahead of pelvic-fin bases, the second dorsal fin usually much smaller than first, precaudal pits present, caudal fin with a strong ventral lobe and lateral undulations on its dorsal margin, intestine with a scroll valve, and usually no striking colour patterns.

Diagnostic Features: Head without laterally expanded blades. Eyes circular, vertically oval, or horizontally oval, with lengths 1.5 times height or less. Nictitating eyelids internal. Spiracles usually absent (except for Galeocerdo; occasionally present in Loxodon, Negaprion and Triaenodon). Anterior nasal flaps varying from lobular and tube-shaped (Triaenodon) to vestigial, not barbel-like; Internarial width usually about 3 to 6 times nostril width (exceptionally 1.5 times it in Nasolamia). Labial furrows varying from moderately long and conspicuous to short and hidden when mouth is closed. Teeth small to large, with acute and narrow to moderately broad cusps, sometimes lateral cusplets, but with basal ledges and grooves low to absent; teeth variably differentiated in upper and lower jaws, uppers often more compressed and bladelike, lowers often more cuspidate and not compressed; posterior teeth not comblike; tooth rows 18 to 60 upper jaw, 18 to 56 lower jaw. Precaudal pits present. Pectoral fins with radials extending into distal web of fins. First dorsal fin moderate-sized to very large but not keel-like, much shorter than caudal fin; first dorsal-fin base ahead of pelvic-fin bases, varying from closer to pectoral-fin bases to closer to pelvic fins; midpoint of first dorsal-fin base always in front of pelvic-fin origins. Second dorsal fin usually smaller than first (Lamiopsis and Negaprion are exceptions). Ventral caudal-fin lobe strong, undulations or ripples present in dorsal caudal-fin margin. Vertebral centra with strong, wedge-shaped intermedial calcifications. Vertebral counts: total vertebral counts 96 to 244, precaudal vertebral counts 41 to 131. Valvular intestine with a scroll valve. Colour: variable, usually no distinctive colour pattern. Development usually placental viviparous (Galeocerdo with yolk-sac viviparity).

Distribution: Requiem sharks are found in all warm and temperate seas, and especially in the tropics.
Habitat: These are the dominant sharks in tropical waters, often both in variety and in abundance and biomass. Most species inhabit tropical continental coastal and offshore waters; several species prefer coral reefs and oceanic islands while a few species, including the blue, silky and oceanic whitetip sharks, are truly oceanic and epipelagic, and range far into the great ocean basins. A minority of species range into temperate waters; one of these, the blue shark (Prionace glauca) has one of the greatest geographic ranges of any elasmobranch (rivaled or exceeded only by the white shark and possibly the bluntnose sixgill shark) and any marine vertebrate. Few occur at any great depth, however, and only the bignose (Carcharhinus altimus) and night (Carcharhinus signatus) sharks occur off the upper continental slopes down to 600 m .

Biology: This is one of the largest and most important families of sharks, with many common and wide-ranging species. Most requiem sharks are marine, a few occur into freshwater rivers and lakes, usually ranging from close inshore to the outermost shelf edges near the bottom and the epipelagic zone, but none are truly specialized deepwater sharks, unlike many species of Squalidae and Scyliorhinidae. Although species in other families may enter river mouths and ascend rivers for a short distance, a few members of this family, particularly the bull shark (Carcharhinus leucas) but possibly also the little-known river sharks (Glyphis), apparently are the only living sharks that can live in fresh water for extended periods; the bull shark has a wide range in tropical and temperate rivers and lakes of the world. Requiem sharks are active, strong swimmers, occurring singly or in small to large schools. Some species are continually active, while others are capable of resting motionless for extended periods on the bottom. Many are more active at night or dawn and dusk than the daytime. At least some of the species have been shown to give specialized displays when confronted by divers or other sharks, which may be indicative of aggressive or defensive threat. Some species are relatively small, reaching about a meter long, but most requiem sharks are medium to large-sized, between 100 to 300 cm long, and one species, the tiger shark, is one of the biggest sharks and may reach 740 cm long. Except for the tiger shark, which exhibits yolk-sac viviparity, all species are viviparous with a yolk sac placenta, and have litters of young from 1 or 2 to 135 . All are voracious predators, feeding heavily on bony fishes, other sharks, rays, squid, octopi, cuttlefishes, crabs, lobsters, and shrimp, but also sea birds, turtles, sea snakes, marine mammals, gastropods, bivalves, carrion, and garbage. Smaller species tend to select for a narrow range of prey, but certain very large species, especially the tiger shark (Galeocerdo) are virtually omnivorous.

Interest to Fisheries and Human Impact: This is by far one of the most important shark families for fisheries globally, with various species figuring prominently in artisanal, commercial and sports fisheries. Most are utilized for human food, but also for the preparation of various subproducts, including fins for the oriental soupfin market, oil and Vitamin A from the liver, fishmeal, and leather products. Several species are the targeted by sports fishers, and two species, the blue and tiger
sharks, are listed as International Game Fish Association record species. This family contains more dangerous species than any other; several of the larger requiem sharks have attacked people and boats while a few species (particularly the bull and tiger sharks), are among the most dangerous living sharks. The danger to divers posed by these sharks is relatively small, however, several species are popular and attractive subjects for viewing underwater. Several species are popular in public aquaria as display animals. The conservation status ranges from those that are Data Deficient due to a lack of life history information, Least Concern since the have relatively high reproductive rates, to Vulnerable or Critically Endangered from overexploitation, or from habitat degradation and or modification.

Local Names: Requiem sharks, Gray or Grey sharks, Whaler sharks, Man-eating sharks (English); Chiens de mer (France); Serye akuly, Pilozubye akuly, Kun'i akuly (Russia).

Remarks: The arrangement of this family follows Compagno (1984, 1988) and Ebert (In preparation). The family has 12 genera and 57 species, with five genera and 15 species represented in the North Atlantic.

## Key to North Atlantic Genera:

1a. Upper labial furrows very long, extending to front of eyes (Fig. 259). Spiracles present and relatively large. Prominent lateral keels on caudal peduncle. Vertical black or dusky bars on lateral trunk, obscure or absent on adults.

Galeocerdo

1b. Upper labial furrows long to very short, not extending in front of eyes (Fig. 260). Spiracles usually absent. Lateral keels usually absent (except for weak ones in Prionace)

2a. Snout short, preoral length much less than mouth width (Fig. 261a). Upper and lower teeth with narrow, unserrated cusps (Fig. 261b).

Negaprion

2b. Snout longer, preoral length about equal to mouth width. Upper teeth with broad, triangular, serrated cusps, lowers with narrow, smooth cusps .

3a. Second dorsal-fin origin well behind anal-fin origin, usually over or slightly anterior to anal-fin insertion. Preanal ridges very long and prominent, subequal to or greater in length than anal-fin base. Anal-fin posterior margin straight or shallowly concave (Fig. 262) .

Rhizoprionodon

3b. Second dorsal-fin origin usually near anal-fin origin, in some species posterior to it, but usually well anterior to anal-fin insertion and midbase of anal fin. Posterior margin of anal fin deeply concave or deeply notched (Fig. 263). 4

4a. Papillose gillrakers present on gill arches. Weak lateral keels present on caudal peduncle. First dorsalfin base much closer to pelvic-fin bases than pectoral fins (Fig. 263). Colour brilliant dark blue above in life

Prionace

4b. No papillose gillrakers on gill arches. No lateral keels on caudal peduncle. First dorsal-fin base equidistant between pectoral and pelvic-fin bases or (usually) closer to pectoral fins (Fig. 264). Colour light to dark grey, grey-brown, brown, or grey-black above .

Carcharhinus

2


UNDERSIDE OF HEAD
Fig. 259 Galeocerdo

a) UNDERSIDE OF HEAD


UNDERSIDE OF HEAD
Fig. 260 Rhizoprionodon

b) UPPER TOOTH

Fig. 261 Negaprion


Fig. 262 Rhizopriodon


Fig. 263 Prionace


Fig. 264 Carcharhinus

## Carcharhinus Blainville, 1816

Genus: Subgenus Carcharhinus Blainville, 1816, Bull. Sci. Soc. Philomat. Paris, (8): 121 (Genus Squalus Linnaeus, 1758).

Type species: Carcharias melanopterus Quoy and Gaimard, 1824, under suspension of the Rules by the International Commission on Zoological Nomenclature, Opinion 723, 1965, Bull. Zool. Nomencl. 22: 32.

## Number of Recognized North Atlantic Species: 11.

Synonyms: Subgenus Carcharias Cuvier, 1816 (Genus Squalus Linnaeus, 1758), Reg. Anim., ed. 1, 2: 125, in part. Junior homonym of Genus Carcharias Rafinesque, 1810a (Odontaspididae), and rejected by the International Commission on Zoological Nomenclature, Option 723, 1965, Bull. Zool. Nomencl. 22: 33. Subgenus Carcharinus Cloquet, 1817 (Genus SqualusLinnaeus, 1758), Dict. Sci. Nat. 7:7. Incorrectspelling of CarcharhinusBlainville, 1816 and rejected by the International Commission on Zoological Nomenclature, Opinion 723, 1965, Bull. Zool. Nomencl. 22: 33. Subgenus Carcharias Risso, 1826 (Genus Squalus Linnaeus, 1758), Hist. nat. Princip. Prod. Europe Méred., Paris, Poissons: 119. Genus Carcharias Müller and Henle, 1839, Syst. Beschr. Plagiost., pt. 2: 27. Subgenus Aprion Müller and Henle, 1839 (Genus Carcharias Müller and Henle, 1839), Syst. Beschr. Plagiost., pt. 2: 31). Type species: Carcharias (Aprion) isodon Valenciennes, in Müller and Henle, 1839 through subsequent restriction by Gill, 1862a, Proc. Acad. Nat. Sci. Philadelphia, 1861: 59; and Gill, 1862b, Ann. Lyceum Nat. Hist. New York, 7(32): 401, 411. A junior homonym of Aprion Cuvier and Valenciennes, 1830 in Osteichthyes. Subgenus Hypoprion Müller and Henle, 1839 (Genus Carcharias Müller and Henle, 1839), Syst. Beschr. Plagiost., pt. 2: 34. Type species: Carcharias (Hypoprion) macloti Müller and Henle, 1839 by subsequent designation of Gill, 1862b, Ann. Lyceum Nat. Hist. New York, 7(32): 401. Subgenus Prionodon Müller and Henle, 1839 (Genus Carcharias Müller and Henle, 1839), Syst. Beschr. Plagiost., pt. 2: 35. Genus Carcharius Lowe, 1839, Proc. Zool. Soc. London 1839 (7): 90. Apparent error for Carcharias Cuvier, 1816, as name was subsequently used correctly as his Carcharias microps Lowe, 1840, Proc. Zool. Soc. London, 1840 (8): 38. Genus Galeolamna Owen, 1853, Descr. cat. osteol. ser. coll. Roy. Coll. Surgeons: 96. Type species: Galeolamna greyi Owen, 1853 by monotypy, possibly a junior synonym of Squalus obscurus Lesueur, 1818 or Carcharias (Prionodon) falciformis Bibron, 1839. Genus Aprionodon Gill, 1862a, Proc. Acad. Nat. Sci. Philadelphia, 1861: 59 (name only); Gill, 1862b, Ann. Lyceum Nat. Hist. New York, 7(32): 401, 411. Type species: Aprionodon punctatus Gill, 1862 by monotypy and subsequent designation of Gill, 1862b, Ann. Lyceum Nat. Hist. New York, 7(32): 401; a junior homonym of Carcharias (Aprion) isodon Valenciennes, in Müller and Henle, 1839. Genus Hypoprionodon Gill, 1862b, Ann. Lyceum Nat. Hist. New York, 7(32): 401, 409. Type species: Carcharias (Prionodon) hemiodon Valenciennes, in Müller and Henle, 1839 by original designation. Genus Eulamia Gill, 1862b, Ann. Lyceum Nat. Hist. New York, 7(32): 401, 410. Type species: Eulamia lamia Gill, 1862 by original designation, probably equals Carcharias (Prionodon) lamia Müller and Henle, 1839 and hence a junior synonym of Squalus maou Lesson, 1830. Genus Gymnorrhinus Hemprich and Ehrenberg, 1899, Symbol. Physic. Icones Ined., Zool:: pl. 7; p. 6 as Gymnorhinus (a junior homonym of Gymnorhinus Maximillian, 1841 in Aves), a probable text emendation by Hilgendorf in Hemprich and Ehrenberg. Fowler, 1941, Bull. U.S. Natn. Mus., (100) 13: 148 listed Carcharias (Prionodon) menisorrah Valenciennes, in Müller and Henle, 1839 as type of Gymnorhinus (and hence of Gymnorrhinus); this species was synonymized with Gymnorrhinus pharaonis Hemprich and Ehrenberg, 1899 by Hilgendorf in Hemprich and Ehrenberg. Hence the type species of Gymnorrhinus is considered to be G. pharaonis here. Genus Pterolamia Springer, 1950, Amer. Mus. Novit. (1451): 7. A junior homonym of Pterolamia Breuning, 1942 in Insecta, and rejected by the International Commission on Zoological Nomenclature, Opinion 723, 1965, Bull. Zool. Nomencl. 22: 33. Genus Pterolamiops Springer, 1951, Copeia, 1951 (3): 244. Type species: Squalus longimanus Poey, 1861 by original designation and as a replacement name for Pterolamia Springer, 1950.

Field Marks: Requiem sharks with small, wide-spaced nostrils, no spiracles, labial furrows confined to mouth corners, usually serrated upper teeth, no cusplets on lower teeth, no keels on caudal peduncle, transverse crescentic precaudal pits, first dorsal midbase closer to pectoral-fin bases than to pelvic fins or at most about equidistant between them, second dorsal fin less than half the height of first, second dorsal-fin origin usually about opposite anal-fin origin, anal fin with preanal ridges short to absent and with a deeply notched posterior margin.

Diagnostic Features: Body fairly slender to very stout. Head narrow to broad, flattened but not trowel-shaped; snout varying from narrowly parabolic or subangular to bluntly rounded or nearly truncate in dorsoventral view, very short to long, with preoral length varying from about equal to much greater than internarial space and from much less to considerably greater than mouth width; eyes small to large, without posterior notches; spiracles absent; no papillose gillrakers on internal gill openings; nostrils small, internarial space 3 to 6 times nostril width; anterior nasal flaps short, varying from vestigial to narrowly or broadly triangular, but not tubular; labial furrows short, essentially confined to mouth corners, with uppers about as long as lowers or shorter, ends of uppers falling far behind eyes; teeth highly variable, anteroposteriors similar or strongly differentiated in upper and lower jaws; uppers usually with more or less erect, broad to narrow cusps, variably developed cusplets or blades, and serrations usually present; lowers without cusplets but with variably oblique to erect cusps and with serrations and blades present or absent; cusps of lower teeth no prominently protruding when mouth is closed; tooth counts 24 to 37 upper jaw, 23 to 35 lower jaw, with most species not exceeding $33 / 33$. Interdorsal ridge variably absent, present and prominent, or sometimes vestigial; no dermal keels on caudal peduncle; upper precaudal pit transverse and crescentic. First dorsal-fin origin varying from over or slightly anterior to pectoral-fin insertions to slightly behind their rear tips, midbase usually closer to pectoral-fin bases than pelvic fins but sometimes equidistant between them, and free rear tip usually well in front of pelvic
fins but occasionally opposite their origins; second dorsal fin much smaller than first, height $2 / 5$ of first dorsal-fin height or less; its origin usually about opposite anal-fin origin but slightly anterior to it in some species and well behind it in others (but usually in front of anal-fin insertion); pectoral fins varying from moderately broad and semifalcate, to narrow and falcate or broad-tipped, their lengths from origin to free rear tip about $1 / 3$ to $2 / 3$ of pectoral anterior margins; pectoral-fin origins varying from about under 3rd to 5th gill slits; anal fin varying from considerably larger than second dorsal-fin to about as large, with preanal ridges very short or absent and a deeply notched posterior margin. Vertebral counts: total vertebral counts 96 to 244, precaudal vertebral counts 41 to 131 . Small to very large sharks, adults from below 100 to about 400 cm . Colour: variably grey, bronze, brownish above, without a colour pattern other than variable light or dark fin markings and lateral light stripes.

Local Names: Gray sharks, Grey sharks, Requiem sharks, Whaler sharks, Ground sharks (English).
Remarks: The genus consists of 33 species worldwide, of which 11 occur in the North Atlantic.

## Key to North Atlantic Species:

1a. Pectoral and first dorsal fins very broad distally and broadly rounded apically, only slightly tapering towards their apices. Most fin tips mottled white in adults, also black-tipped and with black dorsal saddle-marks on the caudal peduncle in juveniles (Fig. 265) . . . . Carcharhinus longimanus

1b. Pectoral and first dorsal fins tapering distally and usually pointed or narrowly rounded. Fins not mottled white, often black tipped but without black saddles on the caudal peduncle (Fig. 266) .

2a. Interdorsal ridge present (Fig. 266) . . . . . . . . 3
2b. Interdorsal ridge absent . . . . . . . . . . . . . . . .

3a. Snout very long, narrow and pointed, internarial space 1.7 to 1.9 in preoral snout (Fig. 267).

Carcharhinus signatus
3b. Snout shorter, narrowly to broadly rounded, internarial space usually less than 1.6 in preoral snout (Fig. 268) 4

4a. First dorsal-fin origin well behind pectoralfin free rear tips. Very coarse serrations or small cusplets on feet of upper anterolateral teeth. Inner margin of second dorsal fin very long, usually over twice fin height (down to 1.6 times it) (Fig. 269)

Carcharhinus falciformis
4b. First dorsal-fin origin over or anterior to pectoral-fin free rear tips. Serrations on feet of upper anterolateral teeth small and not very coarse. Inner margin of second dorsal fin shorter and generally less than twice fin height (up to 2.1 times it in C. obscurus)(Fig. 270). 5

5a. First dorsal-fin origin opposite or somewhat in front of pectoral-fin rear tips but closer to them than pectoral-fin insertions (Fig. 270)

Carcharhinus obscurus
5b. First dorsal-fin origin in front or over pectoralfin insertions or at least nearer to it than pectoralfin free rear tips (Fig. 271). 6


Fig. 265 C. Iongimanus


Fig. 266 C. signatus


UNDERSIDE OF HEAD
Fig. 267 C. signatus


UNDERSIDE OF HEAD
Fig. 268 C. falciformis


Fig. 269 C. falciformis


Fig. 270 C. obscurus

6a. Anterior nasal flaps usually low and inconspicuous. Distance from nostrils to mouth more than 2.4 times in mouth width (Fig. 278). Upper anterolateral teeth moderately high; upper anterolateral teeth usually in 14 rows. First dorsal fin very high, with height about half predorsal space. Interdorsal ridge low (Fig. 271)

## Carcharhinus plumbeus

6b. Anterior nasal flaps usually high and triangular. Distance from nostrils to mouth less than 2.4 times in mouth width (Fig. 273). Upper anterolateral teeth very high; upper anterolateral teeth usually in 15 rows. First dorsal fin lower, with height much less than half predorsal space. Interdorsal ridge high $\qquad$
7a. Snout very short and broadly rounded, internarial space usually less than preoral length (Fig. 274a). Upper anterolateral teeth with very broad, triangular cusps and straight to concave distal margins; lower anterolaterals with strongly arched roots (Fig. 274b)

## Carcharhinus leucas

7b. Snout longer and parabolic or wedge-shaped to pointed, internarial space equal or greater than preoral length (Fig. 275a). Upper anterolateral teeth with narrow cusps and strongly notched distal margins; lower anterolaterals with nearly transverse roots (Fig. 275b). . . . 8

8a. Only 11 rows of anteroposterior teeth; lower anterolateral teeth with mostly oblique cusps. Snout tip with a dusky or black blotch (Fig. 276)

## Carcharhinus acronotus

8b. Fourteen or more rows of upper anteroposterior teeth; lower anterolateral teeth with mostly erect cusps. Snout tip without a dark blotch

9a. Upper labial furrows noticeably elongated and prominent. Usually at least 16 rows of upper anteroposterior teeth. First dorsal fin lower, its height over 2.2 times in the interdorsal space; first dorsal-fin origin over or just behind pectoral-fin rear tips (Fig. 277) .

Carcharhinus brevipinna
9b. Upper labial furrows shorter and less noticeable. Usually 15 or fewer rows of upper anteroposterior teeth. First dorsal fin higher, its height 2.2 times or less in interdorsal space; first dorsal-fin origin over or just behind pectoral-fin insertions (Fig. 278)

10a. Teeth with smooth edges in both jaws, except for weakly and irregularly serrated upper teeth of adults
(Fig. 279)
Carcharhinus isodon
10b. Teeth with serrated edges in both jaws (Fig. 280)
Carcharhinus limbatus


Fig. 278 C. limbatus


LOWER TOOTH
Fig. 279 C. isodon


UPPER AND LOWER TOOTH
Fig. 280 C. limbatus

## Carcharhinus acronotus (Poey, 1860)

Squalus acronotus Poey, 1860, Mem. hist. nat. Cuba: 335, pl. 19, fig. 3-4. Holotype: Adult or adolescent male, 980 mm , extant? Type locality, Cuba.

Synonyms: Carcharias (Prionodon) remotus Valenciennes in Dumeril, 1865, Hist. Nat., Poiss. 1: 374. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN-A9661, stuffed mounted female, 1135 mm TL , specimen, Antilles, Pleé.

Other Combinations: None.
FAO Names: En - Blacknose shark; Fr - Requin nez noir; Sp - Tiburón amarillo.


Fig. 281 Carcharhinus acronotus
Field Marks: A small shark with moderately long rounded snout, fairly large eyes, a black spot on the underside of the snout tip, oblique-cusped serrated teeth in both jaws, upper teeth without cusplets, no interdorsal ridge, small pectoral fins, a small first dorsal fin with a short rear tip and a moderately large second dorsal fin with a short rear tip, and dusky to blackish markings on the second dorsal and upper caudal tip.

Diagnostic Features: Small, relatively slender sharks (up to about 140 cm ) with snout moderately long and rounded, internarial width 1.4 to 1.7 in preoral length. Eyes horizontally oval or circular and moderately large, length 1.6 to $1.7 \%$ total length in specimens over 80 cm long. Upper labial furrows short and inconspicuous. Hyomandibular line of pores just behind mouth corners not conspicuously enlarged. Gill slits short, 3rd 2.7 to $3.2 \% \mathrm{TL}$ and less than a third of first dorsal base. Upper teeth with moderately narrow, strongly serrated, strongly oblique cusps, and crown feet with slightly coarser serrations but no cusplets; lower teeth with slightly oblique serrated cusps and transverse roots; tooth counts usually 25 to 28 upper jaw and 23 to 25 lower jaw. No interdorsal ridge. Pectoral fins small, falcate, with narrowly rounded or pointed apices, length of anterior margins about $15 \% \mathrm{TL}$ in individuals above 80 cm long. First dorsal fin small and semifalcate, with pointed or narrowly rounded apex and posterior margin curving ventrally from fin apex; origin of first dorsal fin over pectoral-fin free rear tip; inner margin of first dorsal fin short, less than a third of dorsal-fin base. Second dorsal fin moderately large, height 2.6 to $2.9 \% \mathrm{TL}$, inner margin short and 1.1 to 1.3 times height; origin of second dorsal fin over or slightly behind anal-fin origin. Vertebral counts: total vertebral counts 161 to 181, precaudal vertebral counts 80 to 88 , caudal vertebral counts 81 to 94 . A moderate sized Carcharhinus species with a maximum length of about 137 cm . Colour: black or dusky tips present on second dorsal, dorsal caudal-fin lobe, and sometimes preventral edge of ventral caudal-fin lobe; underside of snout with a conspicuous dusky to black blotch.

Distribution: Endemic to Western Atlantic: USA (Virginia to Florida, Gulf of Mexico off Florida and Louisiana), Bahamas, Cuba, Virgin Islands, Puerto Rico, Antilles, Trinidad and Tobago, Honduras, Guyana, Venezuela, southern Brazil.

Habitat: A common coastal tropical and warm-temperate shark of the continental and insular shelves, mainly over sandy, shell and coral bottoms, depths 18 to 64 m .

Biology: Viviparous, with a yolk-sac placenta; number of young 3 to 6 per litter. Mating appears to take place in May and early June off South Carolina, U.S.A. Gestation appears to vary between locations as off South Carolina, it takes about 10 to 11 months, but only 8 months off northeastern Brazil. The reproductive cycle appears to be annual, although some have suggested it may be biennial. Birth occurs off South Carolina during late May and June while off southwestern Florida pregnant females occur from January to April, and most individuals are caught from March through November, indicating a local migration. Partition off northeastern Brazil appears to occur in mid to late summer (December and January).

Age at maturity appears to differ between regional populations. Maturity has been reported to occur in as little as 2 years, but age at fifty percent maturity has been estimated at about 4.3 years and 4.5 years in the western North Atlantic, but appears to be earlier in the Gulf of Mexico at 3.4 and 3.2 years for males and females, respectively. Maturity has been estimated to occur in as little as two years in other studies. The maximum estimated age ranges from 7.2 years for males up to about 19 years for females. The blacknose shark feeds on small fishes, including pinfish (Sparidae) and porcupine fish. This is a small harmless shark that is often preyed upon by larger shark species.

Size: Maximum length 137 cm ; males maturing between 97 and 110 cm ; females maturing at about 101 to 120 cm and reaching at least 137 cm . Size at birth between 31 and 50 cm .

Interest to Fisheries and Human Impact: Caught in large numbers mainly off the coastal waters of the southeastern


Fig. 282 Carcharhinus acronotus

- Known distribution United States and northeastern Brazil and Venezuela, but also caught elsewhere throughout its range. This species is taken by gill nets and longline gear, and in large numbers as bycatch in shrimp fisheries. Current stock assessment of this species in coastal U.S. waters indicates that its population is currently at about $25 \%$ of virgin levels from the 1950 s. Caught mainly on surface longlines and utilized dried salted for human consumption.

This species is kept in public aquaria where it has been observed to perform a "hunch" display, with back arched, caudal fin lowered and head raised when confronted by divers or newly introduced conspecifics. This is thought to be a possible threat display.

Its conservation status has been assessed as Near Threatened due to targeted fisheries, its inshore habitat, and continuing declines in its population along the Atlantic coast of the United States.

Local Names: Blacknose shark, Black-nosed shark, Tiburón nariznegra.
Literature: Bigelow and Schroeder (1948); Clark and von Schmidt (1965); Myrberg and Gruber (1974); Garrick (1982); Schwartz (1984, 1989); Carlson, Cortes, and Johnson (1999); Carlson, Palmer and Parsons (1999); Castro, Woodley, and Brudek (1999); Hazin, Oliverira, and Broadhurst (2002); Driggers et al. (2004a, b); Morgan et al. (2008); K. Parsons (pers. comm.).

## Carcharhinus altimus (Springer, 1950)

Eulamia altima Springer, 1950, Amer. Mus. Novit. (1451): 9. Holotype: U.S. National Museum of Natural History, USNM133828,52 " or $1321 \mathrm{~mm}(1225 \mathrm{~mm})$ immature female, partly skinned, from off Cosgrove Reef, Florida Keys at 197 m. Confirmation of holotype status and additional data from Howe and Springer (1993, Smiths. Contr. Zool. [540]: 3).

Synonyms: None.
Other Combinations: None.

FAO Names: En - Bignose shark; Fr - Requin babosse; Sp - Tiburón baboso.


Fig. 283 Carcharhinus altimus

Field Marks: A large, deep-benthic shark with a long rounded or bluntly pointed snout, prominent anterior nasal flaps, high, triangular, serrated teeth without cusplets in upper jaw, erect narrow-cusped serrated teeth in lower jaw, usually $15 / 14$ to 15 rows of anteroposterior teeth, a high interdorsal ridge, moderately high first dorsal fin, long, nearly straight pectoral fins, a moderately high second dorsal fin with a short rear tip and no conspicuous markings.

Diagnostic Features: Large, fairly slender sharks (up to about 280 cm ) with snout moderately long and bluntly pointed to rounded, internarial width 1.3 to 1.4 in preoral length. Eyes circular and moderately large, length 1.4 to $2.3 \%$ total length. Anterior nasal flaps rather high, triangular, and fairly broad. Upper labial furrows short and inconspicuous. Hyomandibular line of pores just behind mouth corners not conspicuously enlarged. Gill slits moderately long, third slit 3.1 to $3.9 \%$ total length and about a third of first dorsal base. Upper teeth with broad, strongly serrated, triangular, erect to slightly oblique, very high cusps that merge into the crown feet, the latter without coarse serrations or cusplets; lower teeth with erect, narrow serrated cusps and transverse roots; tooth counts for anteroposterior teeth varying from 29 to 34 upper jaw, and 29 to 31 lower jaw. A prominent interdorsal ridge present. Pectoral fins large, hardly falcate, with narrowly rounded or pointed narrow apices, length of anterior margins about 20 to $22 \%$ total length. First dorsal fin moderately large and falcate, with bluntly pointed apex and posterior margin curving ventrally from fin apex; origin of first dorsal fin over pectoral-fin insertion to about over midlength of pectoral-fin inner margins; inner margin of first dorsal fin moderately long, half dorsal-fin base or slightly less. Second dorsal fin large and high, height 2.8 to $3.4 \%$ total length, inner margin short and 1.1 to 1.4 times height; origin of second dorsal fin slightly anterior to anal-fin origin. Vertebral counts: total vertebral counts 194 to 206, precaudal vertebral counts 101 to 110. A large sized Carcharhinus species with a maximum length of about 300 cm . Colour: light grey above, sometimes bronzy, white below, with dusky fin tips (except for pelvic fins) but no conspicuous markings; white marking on flanks inconspicuous.

Distribution: Occurs in most warm temperate and tropical seas worldwide, but distribution is patchy. Western Atlantic: Virginia to Florida (U.S.A.), Bahamas, Cuba, Nicaragua, Costa Rica, and Venezuela. Eastern North Atlantic: unknown at the present time from Area 27, but does occur in the Mediterranean Sea and the Eastern Central Atlantic from off Senegal, Gambia, Sierra Leone, Ivory Coast and Ghana.

Habitat: A common, large, offshore, bottom-dwelling warm-temperate and tropical shark usually found in deeper water near the edge of continental and insular shelves and the uppermost slopes, at depths of 80 m or more down to at least 250 to 430 m . The young may occur in shallower water, up to 25 m depth. An large mostly a bottom dwelling shark, it is known to make forays to the surface especially at night. An individual, about 280 cm TL , was once caught in the daytime
at the surface in water over 130 m deep by a party boat trawling for marlin. This shark species appears to benthic species during the day, but at night actively migrates vertically as individuals have been at or near the surface in water depths of up to 1000 m .

Biology: Development viviparous with yolk-sac placenta; number of young per litter 3 to 15 . Mediterranean sharks give birth in August and September. Eats a variety of bony fishes, including lizardfish, croakers, batfish, soles, and other sharks including dogfish (Squalus), catsharks (Holohalaelurus), stingrays (Dasyatis), and cuttlefish.

Size: Maximum possibly about 300 cm ; mature males at about 190 cm with a maximum length of at least 267 cm ; mature females at 225 with a maximum length of at least 282 cm . Size at birth probably between 60 and 90 cm . A length-weight equation is given by Kohler, Casey and Turner (1995) for fork length $(\mathrm{FL}): \mathrm{Wt}(\mathrm{kg})=1.0160 \times 10^{-6} \mathrm{xFL}$ L.4613, $\mathrm{n}=38$ (both sexes), where FL $=0.8074 \mathrm{x}$ $T L+7.7694, n=10$.


Fig. 284 Carcharhinus altimus
Known distribution

Interest to Fisheries and Human Impact: Interest to fisheries localized. Apparently regularly taken in the Caribbean region on deep-set longlines (especially off Cuba, but also southern Florida), and there utilized for fishmeal, oil and shagreen. In some areas, bignose sharks are often mistaken for sandbar sharks that may have lead to under reporting of catches of this species. Although of large size, this species is probably not dangerous to people because of its deep-water habitat.

The conservation status of this species is Data Deficient due to its not being targeted in fisheries and the lack of biological information on it.

Local Names: Bignose shark, Bignosed shark, Knopp's shark, Réquiem babosse.
Literature: Springer (1950); Garrick (1982); Moreno (1982); Moreno and Hoyos (1983); Compagno (1984, 1988); Kohler, Casey and Turner (1995); Anderson and Stevens (1996); Crow, Lowe and Wetherbee (1996); Castro, Woodley, and Brudek (1999); Pillans et al. (2008); Last and Stevens (2009); Ebert (In preparation); K. Parsons (pers comm.).

## Carcharhinus brevipinna (Müller and Henle, 1839)

Carcharias (Prionodon) brevipinna Müller and Henle, 1839, Syst. Beschr. Plagiost. pt. 2: 31, pl. 9. Holotype: Rikjsmuseum van Natuurlkjke Histoire, Leiden, RMNH-2525, mounted skin of ca. 785 mm specimen, Java, according to Garrick (1982, NOAA Tech. Rep., Nat. Mar. Fish. Serv. Circ. (445): 47).

Synonyms: None.
Other Combinations: Carcharhinus maculipinnis (Poey, 1865).

FAO Names: En - Spinner shark; Fr - Requin tisserand; Sp - Tiburón aleta negra.


Fig. 285 Carcharhinus brevipinna
Field Marks: A large fairly slender shark with a long pointed snout, small eyes, unusually long (for a grey shark) upper labial furrows, narrow, mostly erect- and narrow-cusped serrated or partly serrated upper anterolateral teeth without cusplets, lower teeth with narrow, smooth-edged cusps, long gill slits, no interdorsal ridge, small pectoral fins, a small first dorsal fin with a short rear tip and a moderately large second dorsal fin with a short rear tip, and usually black tips on most fins in juveniles to adults.

Diagnostic Features: Large, slender to slightly stocky sharks (up to about 280 cm ) with snout long and pointed or narrowly rounded, internarial width 1.5 to 1.8 in preoral length. Eyes circular and fairly small, 1.1 to $2.0 \%$ total length. Anterior nasal flaps relatively low and inconspicuous. Upper labial furrows usually long and conspicuous, directed obliquely anterolaterally. Hyomandibular line of pores just behind mouth corners not conspicuously enlarged. Gill slits long, third 3.7 to $5.5 \%$ total length. Upper teeth with narrow, finely serrated, erect to slightly oblique, long cusps, and crown feet with fine serrations but no cusplets (serrations often irregular in young); lower teeth with erect, usually smooth-edged narrow cusps and transverse roots; tooth counts 32 to 37 upper jaw, 29 to 35 lower jaw. No interdorsal ridge. Pectoral fins falcate, with narrow, pointed or narrowly rounded tips; relatively small, about 14 to $16 \%$ total length in specimens above 100 cm and slightly smaller in young. First dorsal fin small and semi-falcate, with pointed or narrowly rounded apex and posterior margin curving ventrally from apex; origin of first dorsal fin usually over or slightly posterior to pectoral-fin free rear tip; inner margin of first dorsal fin short, a third of dorsal-fin base or slightly less. Second dorsal fin moderately large, height 1.8 to $2.6 \%$ total length, inner margin short and 1.4 to 1.9 times height; origin of second dorsal fin over or usually slightly behind anal-fin origin. Vertebral counts: total vertebral counts 155 to 185 , precaudal vertebral counts 84 to 96 . A large Carcharhinus species with a maximum length of about 278 cm . Colour: young plain-finned but large juveniles to adults with black tips usually present on pectoral fins, second dorsal fin, anal fin, and ventral caudal-fin lobe, and sometimes on pelvic fins, first dorsal fin and dorsal caudal-fin lobe. A white band on flanks, but often this is not conspicuous.

Distribution: Eastern Atlantic: Spain and possibly southern Portugal (Area 27), Mediterranean, Cape Verde islands, Senegal, Guinea and Sierra Leone, Togo, Nigeria, and Angola. Western Atlantic: Massachusetts to Florida (U.S.A.), Bahamas, Cuba, northern Gulf of Mexico, British Guiana, and southern Brazil. Elsewhere, wide spread throughout IndoWestern Pacific.

Habitat: A common coastal-pelagic shark of warm temperate and tropical seas, occurring from close inshore to offshore; most common in shallow water at a depth of less than 30 m , but ranging down to at least 75 m deep, from the surface to the bottom. The spinner shark is a schooling, active species like Carcharhinus limbatus, but more commonly leaps spinning out of the water. Off Florida and Louisiana in the Gulf of Mexico, USA these sharks are highly migratory, moving inshore in spring and summer for reproduction and feeding, but possibly moving southwards and into deeper water during the fall and winter.

Biology: Reproductive development is viviparous, with a yolk-sac placenta, the number of young 3 to 15 , with larger females carrying more young. Gestation is about 12 to 15 months with birth occurring in the spring to early summer in the Gulf of Mexico off Florida and Louisiana. In the Gulf of Mexico sharks adults remain in shallow water during the summer but retreat possibly southwards or into deeper water in the fall.
The growth rate for females in the first year is approximately 30 cm , but then decreases from 25 to 16 cm per year from 2 to 5 years, and from 14 to 8 cm between years 6 and 10. Males grow at a rate of 33 cm per year the first year, then decrease from 27 to 15 cm from years 2 to 5 and from 12 to 5 cm per year between 6 to 10 years. Age at maturity is 8 to 10 years for both sexes. The oldest estimated male and female are 19 and 17 years, respectively.
Primarily a fish-eater, with diet including ten-pounders (Elops), sardines and herring, anchovies, sea catfish, lizardfish, mullets, bluefish, tunas, bonito, croakers, jacks, mojarras, grunts, tongue-soles, stingrays, cuttlefish, squid and octopi. It


Fig. 286 Carcharhinus brevipinna
 frequently uses an unusual method of feeding on schools of small bony fishes that gives this shark its common name; it swims rapidly upwards through the schools with open mouth, spinning along its long axis and snapping in all directions, and then shoots out of the water after its feeding run. This species is associated with and probably feeds on migrating schools of scombrids and jacks. As with Carcharhinus limbatus, this species will congregate to eat trash fish dumped off shrimp trawlers, and no doubt participates in feeding frenzies like its smaller relative.

Size: Maximum length at least 278 cm ; males maturing at 159 to 203 cm and reaching at least 233 cm ; females maturing at 170 to 200 cm and reaching 278 cm . Size at birth about 60 to 75 cm .

Interest to Fisheries and Human Impact: This is one of the more common inshore to offshore coastal sharks taken in recreational and commercial fisheries from about North Carolina to Florida, although the species is more commonly caught in the Gulf of Mexico. This species is often misidentified with the blacktip shark (Carcharhinus limbatus). Its meat is utilized fresh and dried-salted for human consumption. Its hide and fins are also utilized, as is its liver for liver oil. Its dried jaws are probably marketed as curios.
In at least one instance this shark apparently attacked a bather; however, like its relative $\boldsymbol{C}$. limbatus it is probably not highly dangerous, but could be troublesome to divers when they are spearfishing. It has small, narrow-cusped teeth (smaller than in C. limbatus) that are clearly not adapted for feeding on large prey, and probably greatly prefers whole small fishes to mammalian prey. No catch limitations imposed by EU, but removal of fins and discarding of body is prohibited on EU vessels in all waters and non-EU vessels in EU waters (EU, 2012).

The spinner shark is similar in reproductive potential and habits to the blacktip shark, and its vulnerability to fisheries is also probably very similar to that of the blacktip. Therefore, its conservation status is considered to be Near Threatened.

Local Names: Large black-tipped shark, Large blacktip shark or Large blacktipped shark (Western Atlantic); Tiburón de aleta negra (Spain); Tubarão-tecelão (Portugal).

Remarks: This common and wide-ranging shark has often been confused with its somewhat smaller relative, Carcharhinus limbatus, in the past, but in addition various growth stages of this shark in different areas has often-lead researchers to consider it a separate species. The coloration and tooth serrations of this shark change markedly with growth, and these changes have resulted in much confusion in the literature (see Garrick, 1982, for a discussion of the taxonomy and nomenclature of this species).

Literature: Bigelow and Schroeder (1948); Poll (1951); Cadenat (1957); Springer (1960, 1963); Clark and von Schmidt (1965); Cadenat and Blache (1981); Branstetter (1982, 1987a); Garrick (1982); Branstetter in Whitehead et al. (1984); Compagno (1984, 1988); Burgess (2005); Carlson and Baremore (2005); ICES Report (2010); Ebert (In preparation); K. Parsons, T. Sutton (pers. comm.).

Carcharhinus falciformis (Müller and Henle, 1839)
Carcharias (Prionodon) falciformis Bibron, in Müller and Henle, 1839, Syst. Beschr. Plagiost. pt. 2: 47. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN-1134, 528 mm TL female embryo, Cuba, according to Garrick (1982, NOAA Tech. Rep., Nat. Mar. Fish. Serv. Circ. (445): 164).

Synonyms: ?Carcharius falcipinnis Lowe, 1839, Proc. Zool. Soc. London 1839 (7): 90. Type locality, Madeira Islands. No type material was mentioned but Lowe apparently examined more than one specimen for his original description. Günther (1870, Cat. Fish. British Mus. 8: 366) had synonymized it with Carcharhinus obscurus, which was followed by various authors. Garrick (1982, NOAA Tech. Rep., Nat. Mar. Fish. Serv. Circ. (445): 54, 162) noted that there is a stuffed specimen in the British Museum (Natural History), BMNH-1851.4.9.14 (specimen no. 840), ca. 950 mm male labeled as a probable syntype of Carcharhinus falcipinnis which is referable to $\boldsymbol{C}$. falciformis. The uncertain status of the specimen and vagueness of the original description led him to reject $\boldsymbol{C}$. falcipinnis as a species dubium. Carcharhinus floridanus Bigelow, Schroeder and Springer, 1943, Proc. New England Zool. Club 22: 69, pl. 13-14. Holotype: Museum of Comparative Zoology, Harvard, MCZ-35807, 2414 mm female, partly skinned, from Fort Pierce, Florida according to Garrick (1982, NOAA Tech. Rep., Nat. Mar. Fish. Serv. Circ. (445): 164).

FAO Names: En - Silky shark; Fr - Requin soyeux; Sp - Tiburón jaquetón.


Fig. 287 Carcharhinus falciformis
Field Marks: A large, dark, slim, oceanic shark with moderately long rounded snout, moderately large eyes, oblique-cusped serrated teeth in the upper jaw, upper teeth with basal cusplets or very strong serrations, usually $15 / 15$ rows of anteroposterior teeth, an interdorsal ridge, long narrow pectoral fins, a moderate-sized first dorsal fin with its origin behind the pectoral-fin rear tips, a low second dorsal fin with a greatly elongated inner margin and rear tips, and no conspicuous markings.

Diagnostic Features: Large, fairly slender sharks (up to about 330 cm ) with snout moderately long and rounded, internarial width 1.2 to 1.6 in preoral length. Eyes circular and moderately large, length 1.2 to $2.7 \%$ total length. Upper labial furrows short and inconspicuous. Hyomandibular line of pores just behind mouth corners not conspicuously enlarged. Gill slits moderate-sized, third 2.9 to $3.6 \%$ total length and less than $2 / 5$ of first dorsal base. Upper teeth with fairly narrow, strongly serrated, erect to moderately oblique cusps, well-delimited from crown feet, feet with heavy serrations or small cusplets; lower teeth with erect, narrow, smooth-edged cusps and transverse roots; tooth counts 31 to 37 upper jaw, 30 to 37 lower jaw. A narrow interdorsal ridge present. Pectoral fins large (especially in adults, shorter in young), narrowly falcate, with narrowly rounded or pointed apices, length of anterior margins about 14 to $22 \%$ total length. First dorsal fin moderate-sized and falcate, with narrowly to broadly rounded apex and posterior margin curving ventrally from fin apex; origin of first dorsal fin behind pectoral-fin free rear tips; inner margin of first dorsal fin long, about half dorsal-fin base or slightly more or less. Second dorsal fin very small and low, height 1.3 to $2.2 \%$ total length, inner margin long and 1.6 to 3.0 (usually over 2.0) times height; origin of second dorsal fin over or slightly behind anal-fin origin. Vertebral counts: total vertebral counts 199 to 215, precaudal vertebral counts 98 to 106. A very large Carcharhinus species with a maximum length of about 330 cm . Colour: dark grey or grey brown above, sometimes nearly blackish, white below; tips of fins other than first dorsal dusky but not black-tipped; an inconspicuous white band on flank.

Distribution: Oceanic and coastal, circumtropical. Eastern Atlantic: Madeira Islands, Atlantic Spain, and from Senegal to northern Angola. Western Atlantic: Massachusetts (U.S.A.) to southern Brazil, including Gulf of Mexico and Caribbean Sea, and Central Atlantic from St. Paul's Rocks.

Habitat: The silky shark is a common to abundant tropical oceanic epipelagic and offshore littoral shark that is commonest near the edge of continental and insular shelves but also occurs far from land in the open sea. It occasionally occurs inshore where the water is as shallow as 18 m but is usually found beyond the 200 m isobath in the epipelagic zone. In the open ocean it occurs from the surface down to at least 500 m . The silky shark is often found over deepwater reefs and near insular slopes. Water temperatures of $23^{\circ} \mathrm{C}$ and above have been recorded where it occurs.

Biology: Viviparous, with a yolk-sac placenta, the number of young ranges from 1 to 16 per litter, averaging 6 to 12 . Birth occurs after about 9 to 12 months


Fig. 288 Carcharhinus falciformis
$\square$ Known distribution $\square$ Possible distribution and it is thought that females undergo a year resting period between pregnancies. There does not appear to be a well defined birthing or mating season, but in the Gulf of Mexico may occur in the late spring and summer months. In the Western North Atlantic nursery areas for the young of this shark occur along the outer edge of the continental shelf and on oceanic banks in the Caribbean.
Age at maturity varies by region, but on average about 6 to 7 years for males and 7 to 9 years for females. The maximum estimated age is about 25 years.
Primarily a fish-eater, eating pelagic and inshore teleosts including sea catfish, mullet, mackerel, yellowfin tuna, albacore, and porcupine fish, but also squid, paper nautiluses, and pelagic crabs. These sharks are known to feed in large aggregations at times, especially when prey is abundant and concentrated. Silky sharks are often found in association with schools of tunas and groups of cetaceans, but it appears these sharks are feeding on the same prey items as the tunas and cetaceans rather than on them.
Population dynamics and structure are poorly known. The silky shark is much more abundant offshore near land than in the open ocean, unlike the blue shark (Prionace glauca) and the oceanic whitetip shark (Carcharhinus longimanus), which occur with it. It may be that this shark is less well-adapted to a true oceanic life than the whitetip and blue sharks, and that its greater activity is best supported in offshore areas close to land masses that have higher productivity of prey species than the open ocean. The sluggishness, opportunistic feeding habits, and long pectoral fins of the blue and whitetip sharks may be energy-saving adaptations for life in the open sea; the blue shark additionally has gill raker papillae that apparently adapt it to preying on small pelagic animals. Sketchy data shows no strong tendency for sexual segregation in the silky shark, but this may very well occur. There is size segregation, with young occurring on offshore nursery areas and adults seawards from them. This is one of the three commonest oceanic sharks, along with the blue and oceanic whitetip sharks, and one of the more abundant large marine organisms.
The movements and migration patterns of silky sharks is poorly known. A long-term tagging study in the Western North Atlantic shows that this shark can travel at estimated speeds of up to 60 km per day and can make long distance migrations, with one individual having travelled at least $1,339 \mathrm{~km}$. However, whether silky sharks utilize ocean basins in the way that blue sharks are now known to, remains largely unknown. Based on limited information neonates and young juveniles appear to live in nearshore nursery grounds often associated with snapper reef areas (Bonfil, 2008) for the first few years of life, but move into offshore waters as they grow and assume a pelagic life-style.
The silky shark is an active, quick moving, aggressive or bold shark, but defers to the more sluggish but stubbornly persistent oceanic whitetip shark when both species are present. When approached by divers individuals have been seen to perform a "hunch" display, with back arched, head raised and caudal fin lowered, possibly as a defensive threat display.

Size: Maximum about 330 cm ; males mature at about 210 to 220 cm and reaching 270 cm ; females maturing at 225 cm and reaching at least 330 cm . Size at birth is about 57 to 87 cm .
A length-weight curve for Cuban sharks is: $W T=0.8782 \times 10^{-5} \mathrm{TL}^{3.091}$ (Guitart, 1975).
A length-weight equation is given by Kohler, Casey and Turner (1995) for fork length ( FL ): $\mathrm{Wt}(\mathrm{kg})=1.5416 \times 10^{-5} \times \mathrm{KL}^{29221}$, $\mathrm{n}=85$ (both sexes), where $\mathrm{FL}=0.8388 \times \mathrm{TL}-2.6510, \mathrm{n}=15$.

Interest to Fisheries and Human Impact: In tropical offshore seas this is one of the most important shark species due to its abundance. It is regularly caught as a bycatch of offshore fisheries for large bony fishes, particularly those utilizing pelagic longlines, gillnets, and purse seines and either discarded intact or finned and discarded. However, species-specific statistics for this shark are generally not reported in such fisheries. The meat of the silky shark has been utilized fresh and dried-salted for human consumption, while hides have been processed for leather, fins have figured in the oriental shark fin trade, and its liver has been extracted for liver oil (which has a high vitamin A content in this species).
Silky shark are regarded as potentially dangerous to people, particularly because of its size and abundance offshore, although no confirmed attacks have been attributed to it. However, it is likely less dangerous than the larger, more aggressive and powerful oceanic whitetip shark (Carcharhinus longimanus) which has been confirmed in attacks on people. No catch limitations imposed by EU, but removal of fins and discarding of body is prohibited on EU vessels in all waters and non-EU vessels in EU waters (EU 2012a). Its retaining on board shall be prohibited in the ICCAT Convention Area (EU 2012a).

The conservation status of this shark is Near Threatened due to intense fishing pressure by pelagic fisheries and potential declines in its population.

Local Names: Tubarão-luzidio (Portugal); Tiburón lustroso (Spain)
Literature: Bigelow and Schroeder (1948); Cadenat (1957); Springer (1960, 1967); Garrick (1967b, 1982); Guitart (1975); Compagno (1984, 1988); Cadenat and Blache (1981); Branstetter (1987b); Bonfil et al. (1993); Kohler, Casey and Turner (1995, 1998); Bonfil et al. (2007); Bonfil (2008); Gibson et al. (2008); ICES (2010); Stevens (2010); EU. (2012a)

## Carcharhinus isodon (Müller and Henle, 1839)

Carcharias (Aprion) isodon Valenciennes, in Müller and Henle, 1839, Syst. Beschr. Plagiost. pt. 2: 32. Holotype: Museum National d'Histoire Naturelle, MNHN-1037, 631 mm immature male, New York, U.S.A., Western North Atlantic, according to Garrick (1985, NOAA Tech. Rep., Nat. Mar. Fish. Serv. (34): 11).

Synonyms: Aprionodon punctatus Gill, 1862a, Proc. Acad. Nat. Sci. Philadelphia, 1861: 59. Gill, 1862, Ann. Lyceum Nat. Hist. New York, 7(32): 401 (name). Gill, 1863, Proc. Acad. Nat. Sci. Philadelphia: 262.

Other Combinations: Aprionodon isodon (Valenciennes, in Müller and Henle, 1839).
FAO Names: En - Finetooth shark; Fr - Requin à petites dents; $\mathbf{S p}$ - Tiburón dentiliso.


Fig. 289 Carcharhinus isodon

Field Marks: A small shark with moderately long pointed snout, fairly large eyes, snout tip, very long gill slits about half length of dorsal-fin base, erect-cusped smooth or irregularly serrated teeth in both jaws, upper teeth without cusplets, no
interdorsal ridge, small pectoral fins, a small first dorsal fin with a short rear tip and a moderately large second dorsal fin with a short rear tip, characteristic dark bluish-grey upper surface in fresh specimens, and no prominent markings on fins.

Diagnostic Features: Moderate-sized, fairly slim sharks (possibly up to 200 cm , but most below 160 cm ) with snout fairly long and moderately pointed, internarial width 1.3 in preoral length. Eyes circular and moderately large, length 1.8 to $1.9 \%$ total length. Upper labial furrows short and inconspicuous. Hyomandibular line of pores just behind mouth corners not conspicuously enlarged. Gill slits very long, third 4.8 to $5.7 \%$ total length and about half of first dorsal base. Upper teeth with narrow, weakly serrated or smooth, erect to slightly oblique cusps, and crown feet with weak serrations or none and no cusplets; lower teeth with erect, smooth cusps and transverse roots; total tooth counts 27 to 32 upper jaw, 29 to 31 lower jaw. No interdorsal ridge. Pectoral fins small, falcate, with narrowly rounded or pointed apices, length of anterior margins about $13 \%$ in small individuals. First dorsal fin large and somewhat falcate, with pointed or narrowly rounded apex and posterior margin curving ventrally from fin apex; origin of first dorsal fin over or only slightly posterior to pectoralfin insertions; inner margin of first dorsal fin moderately short, about a third of dorsal-fin base. Second dorsal fin large and high, height 2.8 to $2.9 \%$ of total length, inner margin short and 1.4 times height; origin of second dorsal fin over or slightly posterior to anal-fin origin. Vertebral counts: total vertebral counts 163 to 166, precaudal vertebral counts 77 to 81 . A moderate sized Carcharhinus with a maximum length of at least 160 cm , possibly larger. Colour: plain, dark blue-grey above, white below; no conspicuous markings on fins; an inconspicuous white band on flank.

Distribution: Western Atlantic: United States (New York to the Atlantic coast of Florida and the Gulf of Mexico coast of Florida, Alabama, Mississippi and Texas); an old Cuban record is apparently erroneous, but it is definitely recorded (but rare) from Trinidad, Guyana and southern Brazil. Records of this species from the Eastern Atlantic off Senegal and Guinea-Bissau is most likely that of a different Carcharhinus species and not C. isodon (see below).

Habitat: A locally common, highly active migratory shark, most abundant off the warm-temperate and tropical Atlantic coast of the USA, where it moves northwards to live and breed close inshore off South Carolina and Georgia during the spring and summer when the surface water is warmer than $20^{\circ} \mathrm{C}$, and moves south to Florida in the fall when the surface water cools to below $20^{\circ} \mathrm{C}$ and where it winters in deeper water off central to south Florida or southwards. Peaks in abundance off the east coast of Florida are recorded in the late fall and


Fig. 290 Carcharhinus isodon
$\square$ Known distribution winter, and again in spring, with surface temperatures above $20^{\circ} \mathrm{C}$. A distinct 'run' or mass movement of this shark occurs past Daytona Beach, Florida, during the first week of April, as large schools or aggregations move northwards to Georgia and South Carolina. It is not known what the relationship is between the migratory, breeding east coast population and finetooth sharks that occur in the Gulf of Mexico and southwards. It generally occurs close inshore on the inner continental shelf from the intertidal and surf zone to about 20 m .

Biology: Viviparous, with a yolk-sac placenta and a litter size numbering 1 to 6 young, but averaging 2 to 4 per litter. Females give birth from May to mid-June. The female finetooth shark has a two-year reproductive cycle in the western North Atlantic, particularly off South Carolina, but in the northern Gulf of Mexico the reproductive cycle may be annual. In South Carolina waters the gestation period is about a year long and following birth the females are emaciated, with small livers, and appear to take a year to regain condition and develop the next batch of oocytes before they are ready to ovulate and mate (in the following May), and begin carrying young. In the northern Gulf of Mexico individuals appear to have both near-term pups and vitellogenic oocytes suggesting an annual cycle. This appears to be one of the few, if not only, examples of intraspecific divergence in the reproductive cycle of an elasmobranch within a discrete area.
Age at fifty percent has been estimated at 3.9 and 4.3 years for males and females, respectively, with the oldest individuals being aged at about 8 years for both sexes.
This species feeds primarily on small fish, particularly menhaden (Brevoortia tyrannus), but also spot (Leiostomus), Spanish mackerel (Scomberomorus), mullet (Mugilidae) and small Rhizoprionodon terraenovae; also shrimp (Penaeidae); most prey is less than 30 cm long.

Size: Maximum length possibly to 189 cm , although recent collections have not yielded adults above 161 cm ; males adult at about 133 cm and reaching at least 158 cm ; females maturing between 125 and 135 cm and reaching at least 165 cm . Size at birth 55 to 58 cm .
A length-weight curve (Castro, 1993) based on 93 individuals of both sexes is: $\mathrm{Wt}(\mathrm{kg})=\left(4.0834 \times 10^{9}\right) \mathrm{L}(\mathrm{mm})^{93.034069}$.
Interest to Fisheries and Human Impact: Mainly recreational anglers target this shark, although they are also taken as bycatch in demersal shrimp fisheries along the Atlantic and Gulf of Mexico coasts (U.S.A.). These sharks make up only a small portion of the small coastal shark complex that includes blacknose (Carcharhinus acronotus), Atlantic sharpnose (Rhizoprionodon terraenovae), and bonnethead (Sphyrna tiburo) sharks.

The conservation status is Least Concern for this species since its population appears to be relatively stable.
Local Names: Smoothtooth shark, Roundnose shark (USA).
Remarks: Old records of this species from tropical West Africa have not been confirmed, and it is possible that these were based on some other species, particularly Carcharhinus brevipinna but possibly also C. limbatus. Castro (1993) indicates that an old record of $\boldsymbol{C}$. isodon by Poey from Cuba may have been based on C. limbatus and Sphyrna lewini, as his reexamination of the tooth specimens on which the record is based suggested these species rather than $\boldsymbol{C}$. isodon. Also, $\boldsymbol{C}$. isodon has not been collected off Cuba in recent times.

Literature: Bigelow and Schroeder (1948); Baughman and Springer (1950); Clark and von Schmidt (1965); Cadenat and Blache (1981); Compagno (1984, 1988); Garrick (1985); Castro (1993); Castro, Woodley, and Brudek (1999); Carlson, Cortes, and Bethea (2003); Neer and Thompson (2004); Carlson, Kyne, and Valenti (2008); Driggers and Hoffmayer (2009).

## Carcharhinus leucas (Müller and Henle, 1839)

Carcharias (Prionodon) leucas Valenciennes, in Müller and Henle, 1839, Syst. Beschr. Plagiost. pt. 2: 42. Syntypes: Four stuffed specimens in Museum National d'Histoire Naturelle, Paris, of which two are extant according to Garrick (1982, NOAA Tech. Rep., Nat. Mar. Fish. Serv. Circ. (445): 82): MNHN-A9650, 1600 mm adult male, and MNHN-A9652, 1860+ mm female with broken tail, both from the Antilles.

Synonyms: None.
Other Combinations: Numerous.
FAO Names: En - Bull shark; Fr - Requin bouledogue; $\mathbf{S p}$ - Tiburón sarda.


Fig. 291 Carcharhinus leucas

Field Marks: A large, stout shark with very short, bluntly rounded snout, small eyes, broadly triangular serrated teeth in upper jaw, heavy but narrower cusped teeth with arched roots in lower jaw, upper teeth without cusplets, tooth counts usually 25 to 29 upper jaw, 25 to 29 lower jaw, no interdorsal ridge, large angular pectoral fins, a large triangular first dorsal fin with a short rear tip and a moderately large second dorsal fin with a short rear tip, fins with dusky tips but not strikingly marked.

Diagnostic Features: Large, stocky to very heavy-bodied sharks (stoutest as adults; up to about 340 cm ) with snout very short and bluntly and broadly rounded, internarial width 0.7 to 1.0 in preoral length. Eyes circular and small, length 0.8 to $1.8 \%$ total length. Upper labial furrows short and inconspicuous. Hyomandibular line of pores just behind mouth corners not conspicuously enlarged. Gill slits moderately long, third 3.1 to $4.1 \%$ total length but less than a third of first dorsal base. Upper teeth with very broad, triangular, strongly serrated, erect to slightly oblique cusps that merge smoothly with the coarsely serrated crown feet, but with no but no cusplets; lower teeth with erect to semioblique, broad serrated cusps and arched roots; total tooth counts 25 to 29 upper jaw, 25 to 29 lower jaw. No interdorsal ridge. Pectoral fins large and broad, triangular to semifalcate, with narrow, pointed apices, length of anterior margins about 18 to $21 \%$ total length. First dorsal fin large and broadly triangular or somewhat falcate, with pointed or sharply rounded apex and posterior margin curving ventrally or posterior-ventrally from fin apex; origin of first dorsal fin usually over or just behind pectoral-fin insertions but exceptionally nearer their free rear tips; inner margin of first dorsal fin short, less than a third dorsal-fin base or slightly less. Second dorsal fin large and high, height 3.2 to $4.5 \%$ total length, inner margin short and 0.7 to 1.1 times height; origin of second dorsal fin anterior to anal-fin origin. Vertebral counts: total vertebral counts 198 to 227, precaudal vertebral counts 101 to 103. A very large Carcharhinus species with a maximum length of 350 cm to possibly 400 cm . Colour: fin tips dusky, especially in young, but not strikingly marked; an inconspicuous white band on flank.

Distribution: Widespread along the continental coasts of all tropical and subtropical seas and travelling far up warm rivers and into freshwater lakes. Eastern Atlantic: the Azores, Morocco, Senegal, Gambia to Angola; found in Gambia River (Gambia) and Ogoue River (Gabon). Western Atlantic: Massachusetts to southern Brazil, including Gulf of Mexico, Caribbean Sea, and Bahamas; found in Mississippi and Atchafalaya Rivers (southern U.S.A.), Lake Nicaragua and San Juan River (Nicaragua), Lake Ysabel (Guatemala), Patula River (Honduras), Panama Canal (Panama), Amazon River (Brazil).

Habitat: A coastal, estuarine, riverine and lacustrine, tropical and subtropical shark usually found close inshore in marine habitats, in water less than 30 m deep and occasionally less than a meter deep, but ranging into deeper water close to shore down to at least 152 m depth. In marine habitats it commonly occurs in hyposaline and hypersaline lagoons and bays, river mouths, passages between


Fig. 292 Carcharhinus leucas
$\square$ Known distribution islands, close to wharves, and right off the surf line. It is often found in muddy areas with few other shark predators. It is the only wide-ranging shark that penetrates far into fresh water and apparently is able to exist there at length in tropical lakes and rivers, although it may not be able to maintain its entire life cycle in fresh water and does not have landlocked populations there. Apparently even newborn bull sharks are euryhaline, and juveniles commonly migrate into freshwater. In the Western Atlantic, there is a northwards movement of individuals along the US Atlantic coast during the summer from its tropical stronghold, but as the water-cools they retreat southwards.

Biology: Development viviparous, with a yolk-sac placenta, the number of young per litter 1 to 13 . Estuaries and river mouths are normally used for pupping grounds; some females may give birth to young in freshwater lakes such as Lake Nicaragua, but this is probably exceptional. In the Western Atlantic off Florida and the Gulf of Mexico mating occurs in the late spring and summer (June and July) and following a 10 to 12 gestation period the young are born in late spring or early summer the following year; off Nicaragua females may have young throughout the year, with a peak in spring and early summer. Females often have courtship scars, but males rarely have fighting scars.
Age at maturity estimates may vary slightly between regions, but for the northern Gulf of Mexico population males mature at about 14 to 15 years and females at about 18 years. Maximum age for this shark is about 21 to 32 years for males and 24 to 29 years for females, but with an estimated longevity of about 50 years for some populations. These sharks have
been maintained in captivity for over 20 years in public aquaria. Growth rates are relatively fast the first five years of life, averaging 15 to 20 cm per year, about 10 cm per year from 6 to 10 years, 5 to 7 cm per year for years 11 to 16 , and 4 to 5 cm per year once maturity is attained.
The bull shark has a broad and varied diet that includes bony fishes and elasmobranchs, with adults taking more elasmobranch prey than young, probably because of their size and habitat. Bony fishes that are eaten include garfish (Lepisosteus), tarpon, freshwater eels, snake eels, shad, menhaden and sardines, anchovies, milkfish, gonorhynchids, characins, sea catfish, needlefish, mullet, mackerel and Spanish mackerel, tuna, sea bass, perch and striped bass, cichlids, snappers, bluefish, jacks, snook, grunts, snappers, porgies, croakers, spadefish, eleotrid gobies, parrotfish, soles and flounders, gurnards, flatheads, and boxfish. This shark is an important predator on other elasmobranchs, particularly young sharks in inshore nursery grounds and stingrays, and takes bramble sharks, picked dogfish (Squalus acanthias), grey sharks (Carcharhinus), sharpnosed sharks (Rhizoprionodon), hammerheads, guitarfish, sawfish, skates, stingrays, butterfly rays, eagle rays, and devil rays (Mobula). Sea turtles, birds, dolphins (Delphinidae), whale offal, and terrestrial mammals in whole and part have been recorded. Invertebrate prey includes crabs, shrimp, hermit crabs, mantis shrimp, squid, sea snails, and sea urchins. Slaughterhouse offal and fish and other animals scavenged from fishing gear is readily taken; however, this shark is far less prone to swallow inedible garbage than the tiger shark, although such things are occasionally eaten.
Tagging studies on adult and juvenile bull sharks show that coastal inshore habitats, especially river and estuary systems with high freshwater inflow are critical habitat for these sharks. Bull sharks show a high degree of site fidelity with some coastal movements north and south along the US Atlantic coast and to the west and east in the northern Gulf of Mexico. These sharks travel an average of 5 to 6 km per day and spend most of their time in water less than 20 m deep where the water temperature is on average $26{ }^{\circ} \mathrm{C}$ or more. Given the coastal habitat preference by these sharks anthropogenic environmental degradation to their preferred habitat may have a substantive impact on its life history.

Size: Maximum about 340 cm , but unconfirmed reports up to 400 cm ; males maturing at 157 to 226 cm and reaching at least 299 cm ; females maturing between 180 and 230 cm and reaching at least 340 cm . Size at birth between 56 and 81 cm .

Interest to Fisheries and Human Impact: The bull shark is generally not targeted in North Atlantic fisheries due to it being less abundant relative to other species, but rather it is taken mostly as bycatch. It is caught mainly with longlines, hook-and-line gear and gillnets, and utilized fresh, fresh-frozen or smoked for human consumption; its hide is used for leather, its fins for shark-fin soup, and its liver for oil, which is extracted for vitamins (liver oil of this species is high in vitamin content). This is one of the most dangerous tropical shark species, and is certainly one of the three most dangerous sharks by numbers of attacks recorded on people (the other two being the great white and tiger sharks). As it is less distinctive than either of the other species, and as its genus, Carcharhinus, was until recently a taxonomic disaster, its contribution to the roster of shark attacks may be underemphasized in comparison to the great white and tiger sharks.

This species is probably the most dangerous living shark, especially in the tropics, because of its large size, massive jaws and proportionately very large teeth, abundance in the tropics, indiscriminate appetite and propensity to take largish prey, and close proximity to human activities in both fresh and salt water. It is less distinctive that the great white shark (Carcharodon carcharias) and tiger shark (Galeocerdo cuvier), with the number of attacks by it in the tropics likely underestimated. No catch limitations imposed by EU, but removal of fins and discarding of body is prohibited on EU vessels in all waters and non-EU vessels in EU waters (2012).

The conservation status has been regionally assessed as Near Threatened due to fishing and its occurrence in estuarine and freshwater river systems that are subject to habitat degradation and modification.

Local Names: Cub shark, Roundnose shark, Pigeye shark, Ground shark (North America); Bull shark (Azores).
Literature: Bigelow and Schroeder (1948); Cadenat (1957); Springer (1960, 1963); Garrick and Schultz (1963); Clark and von Schmidt (1965); Cadenat and Blache (1981); Garrick (1982); Compagno (1984, 1988); Snelson, Mulligan, and Williams (1984); Branstetter and Stiles (1987); Santos, Porteiro and Barreiros (1997); Castro, Woodley, and Brudek (1999); Ebert (2003, In preparation); Neer, Thompson, and Carlson (2005); Simpfendorfer and Burgess (2005); Gadig, Juliano, and Barreiros (2006); Heupel and Simpfendorfer (2008); Yeiser, Heupel, and Simpfendorfer (2008); Ortega et al. (2009); Brunnschweiler, Queiroz, and Sims (2010); Carlson et al. (2010); Heupel et al. (2010).

## Carcharhinus limbatus (Müller and Henle, 1839)

Carcharias (Prionodon) Iimbatus Valenciennes, in Müller and Henle, 1839, Syst. Beschr. Plagiost. pt. 2: 49, pl. 19 (teeth). Syntypes: Two specimens in the Museum National d'Histoire Naturelle, Paris, of which MNHN-3468, a 720 mm male (mounted skin) from Martinique, is extant according to Garrick (1982, NOAA Tech. Rep., Nat. Mar. Fish. Serv. Circ. (445): 31). The second syntype, about 843 mm , was apparently lost.

Synonyms: Carcharias microps Lowe, 1840, Proc. Zool. Soc. London, 1840 (8): 38. Holotype? One specimen about $8^{\prime} 5$ or $6^{\prime \prime}(260 \mathrm{~cm})$, from Madeira Islands, possibly not lodged as a type specimen according to Garrick (1982, NOAA Tech. Rep., Nat. Mar. Fish. Serv. Circ. (445): 30).

Other Combinations: None.
FAO Names: En - Blacktip shark; Fr - Requin bordé; Sp - Tiburón macuira.


Fig. 293 Carcharhinus limbatus
Field Marks: A large fairly stout shark with a long pointed snout, small eyes, narrow, mostly erect- and narrow-cusped serrated upper anterolateral teeth without cusplets, long gill slits, lower teeth with narrow, usually serrated cusps, no interdorsal ridge, moderately large pectoral fins, a large first dorsal fin with a short rear tip and a moderately large second dorsal fin with a short rear tip, and usually black tips on most fins in juveniles to adults.

Diagnostic Features: Large, fairly stocky sharks (up to about 260 cm ) with snout moderately long and moderately pointed, internarial width 1.3 to 1.7 in preoral length. Eyes circular and moderately large, length 1.2 to $2.2 \%$ total length. Anterior nasal flaps low, triangular, and not elongated. Upper labial furrows short and inconspicuous. Hyomandibular line of pores just behind mouth corners not conspicuously enlarged. Gill slits long, 3rd 3.8 to $4.9 \%$ total length but less than half first dorsal base. Upper teeth with narrow, strongly serrated, erect to slightly oblique high cusps, and crown feet with slightly coarser serrations but no cusplets; lower teeth with erect, narrow, serrated high cusps and transverse roots; tooth counts 29 to 35 upper jaw, 27 to 33 lower jaw. No interdorsal ridge. Pectoral fins moderately large, falcate, with narrowly rounded or pointed apices, length of anterior margins about 18 to $20 \%$ total length in individuals above 100 cm long. First dorsal fin large and falcate, with pointed or narrowly rounded apex and posterior margin curving ventrally from fin apex; origin of first dorsal fin usually over or slightly posterior to pectoral-fin insertions but exceptionally near the pectoral-fin free rear tips; inner margin of first dorsal fin short, about a third of dorsal-fin base. Second dorsal fin large and high, height 2.5 to $3.6 \%$ total length, inner margin short and 1.1 to 1.6 times height; origin of second dorsal fin over or slightly anterior to anal-fin origin. Vertebral counts: total vertebral counts 174 to 203, precaudal vertebral counts 88 to 102. A large Carcharhinus species with a maximum length of 255 cm . Colour: grey or grey-brown above, white below; black tips usually present on pectoral fins, second dorsal fin, and ventral caudal-fin lobe, and sometimes on pelvic and anal fins (anal fin usually plain), and black edges usually present on first dorsal-fin apex and dorsal caudal-fin lobe; adults in some areas may have plain or virtually plain fins. A conspicuous white band on flank.

Distribution: Widespread in all tropical and subtropical continental waters. Eastern Atlantic: absent from Area 27, but occurs in the Mediterranean, and to the south from off Madeira Islands, Canary Islands, and from Senegal to Zaire. Western Atlantic: Massachusetts to southern Brazil, including Gulf of Mexico and Caribbean.

Habitat: A common tropical and warmtemperate, inshore and offshore pelagic shark, found on or adjacent to the continental and insular shelves but not truly oceanic. Commonly occurs close inshore, off river mouths and in estuaries, in shallow muddy bays, in more saline parts of mangrove swamps, in island lagoons and along drop-offs on coral reefs as well as well offshore; rarely found deeper than 30 m . It can tolerate reduced salinities in estuaries and off river mouths, but does not penetrate far into freshwater.

Biology: Development viviparous, with a yolk-sac placenta; number of young 1 to 10 per litter, averaging 4 to 7 . Gestation


Fig. 294 Carcharhinus limbatus
Known distribution period is 10 to 12 months, with young being born in late spring or early summer, and mating and early growth of embryos occurring soon after this. Pregnant females move inshore to drop their young in nursery and pupping grounds. Maturity occurs at an age of 4 to 5 years for males and 6 to 7 years for females, with a maximum age of at least 12 years. Females are thought to produce young only in alternate years.
Primarily a fish-eater, but their diet also includes some cephalopods and crustaceans. Food includes a wide variety of bony fishes, including sardines, menhaden, herring and other clupeids, anchovies, ten-pounders (Elopidae), sea catfish, coronetfish, tongue-soles, threadfins, mullet, Spanish mackerel, jacks, groupers, snook, porgies, mojarras, emperors (Lethrinidae), grunts, slipjaws, butterfish, croakers, soles, tilapia, triggerfish, boxfish and porcupine fish, as well as small sharks such as smooth-hounds (Mustelus), sharpnosed sharks (Rhizoprionodon), the young of larger sharks (including dusky sharks), guitarfish, skates, butterfly rays, stingrays, eagle rays, squid, cuttlefish, octopi, crabs and lobsters. The high activity of this shark (aided perhaps by its relatively long gill slits) and its social behavior makes it subject to feeding frenzies when a highly concentrated food source, like the fish bycatch of a shrimp trawler being dumped overboard, is competed for by numbers of these sharks.
This is a very active, fast- swimming shark that often occurs in large schools at the surface. It leaps out of the water, and like the related spinner shark (Carcharhinus brevipinna), may rotate up to three times around its axis before dropping into the sea. It is a less common spinner and leaper than its relative, however. The leaping-spinning behavior of this shark is thought to be used while feeding on small schooling fishes; the sharks launch themselves vertically through the schools, spinning and snapping in all directions, and then breach the surface after their feeding run.

Size: Maximum 255 cm ; size at maturity varies between geographic regions with males maturing between 135 and 180 cm and reaching 226 to possibly 255 cm , and females maturing at about 120 and 190 cm and reaching 255 cm . Size at birth 38 to 72 cm .

Interest to Fisheries and Human Impact: A common and important species for recreational fisheries and more recently targeted by commercial fishers. The species if taken with longlines, by hook-and-line, fixed bottom nets, and bottom trawls (especially shrimp trawls). Utilized fresh, fresh-frozen, or dried salted for human consumption; hides for leather; liver oil for vitamins (oil high in vitamin content); and carcasses for fishmeal.
A few attacks on people have been attributed to this species, but it is likely that without a food stimulus or other special circumstances (like feeding stimuli provided by people that dangle their limbs in the water) that this species is of little hazard to people. Small individuals of this shark have approached divers, apparently out of 'curiosity', but circled them at a distance without closing. Blacktips commonly appear around spearfishing divers and will harass them, and can become very aggressive and actively belligerent when contending a speared catch with a diver. Therefore, they should be treated with respect in baited circumstances, as with many other large sharks. Its speed may make the blacktip a difficult opponent when it becomes aggressive, particularly when several sharks are about and they become hyperstimulated.

Conservation status is Near Threatened due its nearshore habitat and nursery areas that make it vulnerable habitat degradation.

Remarks: This species may actually represent a species-complex as current molecular studies indicate regional populations are quite distinct (G. Naylor, pers. comm.).

Local Names: Blacktip, Small blacktip or Blacktipped shark, Grey shark, Blackfin shark, Soupfin shark, Spotfin ground shark, Spinner shark.

Literature: Bigelow and Schroeder (1948); Springer (1960, 1963); Garrick and Schultz (1963); Clark and von Schmidt (1965); Garrick (1982); Cadenat and Blache (1981); Compagno (1984, 1988); Killam and Parsons (1990); Castro (1983, 1996); Santos, Porteiro, and Barreiros (1997); Castro, Woodley, and Brudek (1999); Heupel and Hueter (2001, 2002); Heupel and Simpfendorfer (2002); Ebert (2003, In preparation); Burgess and Branstetter (2005); Carlson, Sulikowski, and Baremore (2006); Barry et al. (2008); Last and Stevens (2009).

## Carcharhinus longimanus (Poey, 1861)

Squalus longimanus Poey, 1861, Mem. hist. nat. Cuba: 338, pl. 19, fig. 9-10. Holotype? 1640 mm male, Cuba (extant?) according to Garrick (1982, NOAA Tech. Rep., Nat. Mar. Fish. Serv. Circ. (445): 154). Garrick (ibid., 151) used this species rather than its senior synonym $\boldsymbol{S}$. ( $\boldsymbol{C}$.) maou because $\boldsymbol{S}$. Iongimanus was placed on the Official List of Specific Names in Zoology (Name no. 2059) by the International Commission on Zoological Nomenclature, Opinion 723 (1965, Bull. Zool. Nomencl. 22: 32).

Synonyms: Carcharias lamia Risso, 1826, Hist. nat. Princip. Prod. Europe Méred., Paris, Poissons, 119. Based on Squalus carcharias Risso, 1810, Ichthyol. Nice, Paris, 25. Junior homonym of Carcharias lamia Rafinesque, 1810a, $=$ Carcharodon carcharias (Lamnidae). Carcharias (Prionodon) lamia Müller and Henle, 1839, Syst. Beschr. Plagiost. pt. 2: 37, pl. 12 (new combination). Based on Carcharias lamia Risso, 1826. Junior homonym of Carcharias lamia Rafinesque, 1810a, = Carcharodon carcharias (Lamnidae).

Other Combinations: Pterolamiops Iongimanus (Poey, 1861).
FAO Names: En - Oceanic whitetip shark; Fr - Requin océanique; Sp - Tiburón oceánico.


Fig. 295 Carcharhinus longimanus

Field Marks: An unmistakable shark, with stocky build, short blunt snout, and long, broad, paddle-shaped pectoral fins and a high first dorsal fin, plus white tips and black markings on fins.

Diagnostic Features: Large, stocky shark (up to about 300 cm or more) with snout short and broadly rounded, internarial width 1.0 to 1.1 in preoral length. Eyes circular and small, length 0.9 to $2.5 \%$ total length. Upper labial furrows short and inconspicuous. Hyomandibular line of pores just behind mouth corners not conspicuously enlarged. Gill slits moderately long, third 3.1 to $4.1 \%$ total length and less than a third of first dorsal base. Upper teeth with very broad, triangular, strongly serrated, erect to slightly oblique cusps that merge into crown feet with slightly coarser serrations but no cusplets; lower teeth with erect to slightly oblique, stout serrated cusps and transverse or moderately arched roots; total tooth counts 27 to 32 upper jaw, 27 to 33 lower jaw. A low interdorsal ridge usually present. Pectoral fins very large, elongated, nearly straight, and distally expanded, with broadly rounded apices, length of anterior margins about 19 to $29 \%$ total length. First dorsal fin very large and distally expanded, not falcate, with a broadly rounded apex and posterior margin curving antero-ventrally and postero-ventrally from fin apex; origin of first dorsal fin just anterior to the pectoral-fin free rear tips; inner margin of first dorsal fin moderately long, half dorsal-fin base or somewhat less. Second dorsal fin large and high, height 2.7 to $3.9 \%$ total length, inner margin short and 1.0 to 1.1 times height; origin of second dorsal fin over or slightly anterior to anal-fin origin. Vertebral counts: total vertebral counts 228 to 244, precaudal vertebral counts 123 to 131. A large Carcharhinus species with a maximum length of 300 cm . Colour: grey-bronze above, white below; white mottling usually present on fins, particularly pectoral fins, first dorsal fin, pelvic fins, and caudal-fin tips; but young additionally with black blotches or tips on most fins, especially the pelvic, second dorsal, anal, and ventral caudal-fin lobes, as well as black saddles at second dorsal-fin insertion, upper caudal-fin origin, and sometimes between the dorsal fins, that fade in adults; an inconspicuous white band on flank.

Distribution: Worldwide, primarily oceanic in most tropical and warmtemperate waters. Eastern Atlantic: Madeira Islands, Portugal south to the Gulf of Guinea, southern Angola, and the west coast of South Africa, possibly Mediterranean Sea. One vagrant was stranded in Sweden, but generally absent from northern parts of area 27. Western Atlantic: Maine (U.S.A.) to Argentina, including Caribbean and Gulf of Mexico.

Habitat: A common, oceanic-epipelagic but occasionally coastal, tropical and warm-temperate shark, usually found far offshore in the open sea. It sometimes occurs in water as shallow as 37 m inshore, particularly off oceanic islands or in continental areas where the continental shelves are very narrow, but is generally found in water with the bottom below 184 m , from the surface to at least 152 m deep. Temperatures of waters in which it regularly occurs are 18 to $28^{\circ} \mathrm{C}$ and normally prefers water above $20^{\circ} \mathrm{C}$, although one was caught in water of $15^{\circ} \mathrm{C}$; it tends to withdraw from waters that are cooling below this, as in the Gulf of Mexico in winter.


Fig. 296 Carcharhinus longimanus
Known distribution $\square$ Possible distribution

Biology: Development viviparous, with a yolk-sac placenta; litter sizes 1 to 15 , averaging 5 or 6 , with larger females having larger litters. This shark apparently mates and gives birth in the early summer in the Western North Atlantic and has a gestation period of about 9 to 12 months. Although there is some evidence that females may give birth in the equatorial Atlantic during the spring and summer there does not appear to be a well-defined birthing or mating season as seen for other Carcharhinus species.
Maturity occurs between 4 and 7 years for both males and females. Rapid growth and an early maturity appear to play an important role in the survival strategy of this species. The maximum age is 11 to 13 years with a maximum estimated age of 22 years.
Feeds primarily on oceanic bony fishes and cephalopods, and occasionally stingrays (probably Pteroplatytrygon violacea), sea birds, turtles, marine gastropods, crustaceans, carrion from marine mammals, and garbage. It was seen feeding on a tight school of threadfins like a person eating an apple, by slowly taking bites out of the school. Divers have filmed them removing huge chunks out of dead whales and dolphins, which they readily do by biting and shaking to drive the teeth through the meat.

Size: Maximum possibly 350 to 395 cm for gigantic individuals, but most are below 300 cm ; males maturing at 168 to 198 cm and reaching at least 245 cm ; females maturing at about 175 to 200 cm and reaching at least 270 cm or more. Size at birth is from 55 to 77 cm in length.

Interest to Fisheries and Human Impact: This is a wide-ranging, common oceanic shark that is regularly caught with pelagic longlines, probably pelagic gillnets, also handlines and occasionally pelagic and even bottom trawls. It is utilized fresh, smoked and dried salted for human consumption, for hides, for fins (processed into the ingredients for shark-fin soup), and for liver oil (extracted for vitamins) and fishmeal. The population of this species has declined in some areas due to fishing. They are often retained for their fins, which bring a high value.
This is a dangerous species, responsible for several verified attacks on swimmers and boats. Divers have encountered it in the open ocean, and it has shown extreme persistence in investigating and circling them both in baited and unbaited situations, possibly as a prelude to biting. Because of its opportunistic feeding habits, heavy build, strong jaws and teeth, and stubborn inquisitiveness, this shark should be treated with care. Retaining on board, transhipping or landing any part or whole carcass of this species taken in any fishery in the ICCAT Convention Area shall be prohibited (2012).

The conservation status has been assessed as Vulnerable globally, but Critically Endangered in the Western North and Central Atlantic due to supposed sharp declines in its population.

Local Names: Whitetip shark, Whitetip oceanic shark, White-tipped shark (English), Requin océanique (French), Marracho, Tubarâo, Oceanic whitetip shark, Tubarão de pontas brancas (Azores, Portugal), Cazón (Spain).

Literature: Bigelow and Schroeder (1948); Springer (1950); Backus, Springer and Arnold (1956); Garrick and Schultz (1963); Garrick (1967b, 1982); Lineaweaver and Backus (1970); Guitart (1975); Compagno (1984, 1988); Cadenat and Blache (1981); Myrberg (1991); Santos, Porteiro, and Barreiros (1997); Seki et al. (1998); Ebert (2003, In preparation); Burgess et al. (2005a, b); Baum et al. (2006); Bonfil, Clarke, and Nakano (2008); Gibson et al. (2008); Stevens (2010).

## Carcharhinus obscurus (Lesueur, 1818)

Squalus obscurus Lesueur, 1818, J. Acad. Nat. Sci. Philadelphia 1(2): 223, pl. 9. No type material according to Garrick (1982, NOAA Tech. Rep., Nat. Mar. Fish. Serv. Circ. (445): 120, 122), type locality North America.

Synonyms: Prionodon obvelatus Valenciennes, in Webb and Berthelot, 1844, Ichthyologie Canarienne, in Hist. Nat. Isles Canaries, 2(2): 103, pl. 26. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN-3464, 760 mm female (mounted skin), Canary Islands according to Garrick (1982, NOAA Tech. Rep., Nat. Mar. Fish. Serv. Circ. (445): 122).

Other Combinations: None.
FAO Names: En - Dusky shark; Fr - Requin de sable; Sp - Tiburón arenero.


Fig. 297 Carcharhinus obscurus

Field Marks: A large grey shark with a fairly short broadly rounded snout, low anterior nasal flaps, fairly large eyes, broad, triangular, rather low, erect and semioblique-cusped serrated anterolateral teeth without cusplets in upper jaw, lower teeth erect and narrow-cusped, tooth counts usually 29 to 33 upper jaw, 27 to 32 lower jaw, a low interdorsal ridge, large, falcate pectoral fins, a moderate-sized first dorsal fin with a short rear tip and origin about opposite free rear tips of pectoral fins, a small, low second dorsal, and no conspicuous markings on fins.

Diagnostic Features: Very large, fairly slender sharks (up to at least 370 cm ) with snout short to moderately long and broadly rounded internarial width 1.0 to 1.4 in preoral length. Eyes circular and moderately large, length 1.0 to $2.1 \%$ total length. Anterior nasal flaps low and poorly developed. Upper labial furrows short and inconspicuous. Hyomandibular line of pores just behind mouth corners not conspicuously enlarged. Gill slits moderately long, third 2.7 to $4.0 \%$ total length and less than a third of first dorsal base. Upper teeth with broad, triangular, strongly serrated, rather low erect to slightly oblique cusps that smoothly merge into crown feet, which have slightly coarser serrations but no cusplets; lower teeth with erect, moderately broad, serrated cusps and transverse or sometimes arched roots; total tooth counts 29 to 33 upper jaw, 27 to 32 lower jaw. A low interdorsal ridge present. Pectoral fins large and falcate, with narrowly rounded or pointed apices, length of anterior margins about 17 to $22 \%$ total length. First dorsal fin moderate-sized and semifalcate, with pointed or narrowly rounded apex and posterior margin curving ventrally from fin apex; origin of first dorsal fin usually over or slightly anterior to the pectoral-fin free rear tips; inner margin of first dorsal fin moderately short, a third of dorsal-fin base or less. Second dorsal fin small and low, height 1.5 to $2.3 \%$ total length, inner margin fairly long and 1.6 to 2.1 times height; origin of second dorsal fin about over anal-fin origin. Vertebral counts: total vertebral counts 173 to 194, precaudal vertebral counts 86 to 97 . Colour: tips of most fins dusky but not black or white. An inconspicuous white band on flank.

Distribution: Eastern North Atlantic: possibly off Portugal, Spain, Morocco, and Madeira Islands, but definitely from the Canary and Cape Verde Islands, Senegal, and Sierra Leone. Records of this species from the Azores may be of the Galapagos shark (Carcharhinus galapagensis), assuming that species is distinct from C. obscurus (see Remarks section below). Western Atlantic: Southern Massachusetts and Georges Bank to Florida (U.S.A.), Bahamas, Cuba, northern Gulf of Mexico, and Nicaragua; southern Brazil. Elsewhere, worldwide in most tropical and warm-temperate seas.

Habitat: A common, coastal-pelagic, inshore and offshore warm-temperate to tropical shark species of continental and insular shelves and oceanic waters adjacent to them. Dusky sharks, depending on their life stage, occur from close inshore in the surf zone to well out to sea and from the surface to 400 $m$ depth. It does not prefer areas with reduced salinities and tends to avoid estuaries. Juveniles tend occupy a more coastal habitat, but as they grow and mature, they move offshore and take up a more oceanic habitat.


Fig. 298 Carcharhinus obscurus

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\square \text { Known distribution } \quad \square \text { Possible distribution }
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Biology: Development viviparous, with a yolk-sac placenta; number of young per litter 3 to 14. There does not appear to be a correlation between maternal size and litter size in this shark, unlike some other species of Carcharhinus. Birth may occur over a long time span of several months in a given region, and has been reported as occurring from late winter to summer. Pregnant female sharks caught off Florida in the winter have two size-classes of young, those from 43 to 70 cm and full or near full-term fetuses of 85 to 100 cm . These classes may indicate either a biannual staggered birth seasons with a gestation period of 8 or 9 months or a longer gestation period of about 16 months; either way females apparently mate in alternate years. Females move inshore to drop their young, and then depart the nursery area for an offshore habitat. Age at maturity varies regionally between populations from Australia, South Africa, and the Western North Atlantic, but is generally between 17 and 24 years for males, and about 21 years for Western North Atlantic females. The oldest age estimated for these sharks is at least 34 years and possibly more.
Dusky sharks eat a wide variety of prey, with reef, bottom, and pelagic bony fishes (teleosts) being their primary prey and elasmobranchs and crustaceans being the next most important prey; while other marine vertebrates and invertebrates can also be taken. Whale meat, sea turtles and occasional garbage is eaten, but unlike the bull shark (Carcharhinus leucas) and tiger
shark (Galeocerdo cuvier) mammalian carrion, oddities and garbage are apparently uncommon items in the diet of this shark. Young dusky sharks are readily preyed on by other species of large sharks, including sand tiger (Carcharias), great white shark (Carcharodon), shortfin mako (Isurus oxyrinchus), bull (Carcharhinus leucas), and tiger (Galeocerdo) sharks.

Size: Maximum size possibly over 400 cm ; males maturing at about 280 to 290 cm and reaching at least 340 cm ; females maturing between 257 and 300 cm and reaching at least 365 cm . Size at birth 69 to 100 cm .
A length-weight equation is given by Kohler, Casey and Turner (1995) for fork length (FL): Wt $(\mathrm{kg})=3.2415 \times 10^{-5} \times \mathrm{FL}^{2.7862}$, $\mathrm{n}=247$ (both sexes), where $\mathrm{FL}=0.8396 \times T L-3.1902, \mathrm{n}=148$.

Interest to Fisheries and Human Impact: A common offshore shark regularly caught with longlines, also hook-and-line and set bottom nets. This species is now protected in U.S. Atlantic waters and must be released immediately, with minimal injury and without being removed from the water if caught. It is utilized fresh, dried salted, frozen and smoked for human consumption, but in recent years its fins have become highly prized and as such they are often targeted in some regions specifically for their fins. No catch limitations imposed by EU, but removal of fins and discarding of body is prohibited on EU vessels in all waters and non-EU vessels in EU waters (2012). This species is protected in US Atlantic waters and must be released immediately (2012). Shark finning is prohibited in the USA.
Dusky sharks have on occasion been implicated in attacks on people, but little is known of their behavior in relation to divers, swimmers or surfers. Given the large adult size this shark attains, it should invite respect where it occurs. The young are readily kept in aquaria.

Dusky shark population declines in the Western North Atlantic were initially due to directed recreational fisheries targeting this species and from bycatch in commercial pelagic fisheries mainly targeting swordfish. This species was later the subject of targeted commercial fisheries in the 1980s, but after further dramatic declines in its population was listed as a protected species in U.S. Atlantic waters in 2000. Due to the severe decline in this species in the Western and Central Atlantic it has been assessed as Endangered in these regions. Globally, however, the dusky shark is considered Vulnerable; it is not a common species and is likely misidentified with other Carcharhinus species in the Eastern North Atlantic.

Local Names: Tiburón negrillo; Dusky shark, Dusky ground shark, Bay shark, Brown shark, Shovelnose (USA); Requin or Requiem de sable (French); Tiburón arenero (Spain); Tubarão-faqueta (Portugal).

Remarks: The dusky shark (Carcharhinus obscurus) is very closely related to the Galapagos shark (C. galapagensis), and difficult to distinguish from each other. Recent molecular studies have suggested that these two species may in fact be the one in the same, with one form being found far from landmasses (C. galapagensis) and the other (C. obscurus) occurring in association with continental shelves and upper slopes (G. Naylor, pers comm.). studies are currently ongoing to determine the relationship between these two species.

Literature: Bigelow and Schroeder (1948); Springer (1960, 1963); Clark and von Schmidt (1965); Garrick (1982); Compagno (1984, 1988); Cadenat and Blache (1981); Natanson, Casey, and Kohler (1995); Natanson and Kohler (1996); Govender and Birnie (1997); Santos, Porteiro, and Barreiros (1997); Castro, Woodley, and Brudek (1999); Gelsleichter, Musick and Nichols (1999); Ebert (2003); Compagno, Dando, and Fowler (2005); Musick et al. (2007a); Gibson et al. (2008); G. Naylor, pers comm.).

## Carcharhinus plumbeus (Nardo, 1827)

Squalus plumbeus Nardo, 1827, Isis 20(6): 477, 483. No specimens mentioned, Venice, Italy. See Garrick (1982, NOAA Tech. Rep., Nat. Mar. Fish. Serv. Circ. (445): 134-135) for the detailed rationale for using Carcharhinusplumbeusrather than C. milberti for this species.

Synonyms: Carcharias (Prionodon) milberti Valenciennes, in Müller and Henle, 1839, Syst. Beschr. Plagiost. pt. 2: 38, pl. 19 (teeth). Probable syntypes: Museum National d'Histoire Naturelle, Paris, MNHN-1142, 598 mm male, New York, Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, ZMB/ISZZ-4467, 510 mm male, Trieste, Italy, possibly Rikjsmuseum van Natuurlkjke Histoire, Leiden, RMNH-2555, 1540 mm female, Livorno, Italy according to Garrick (1982, NOAA Tech. Rep., Nat. Mar. Fish. Serv. Circ.(445): 141). Lectotype: MNHN-1142, designated by White et al. (1961, Bull. Zool. Nomencl. 18: 273-280). Carcharias ceruleus DeKay, 1842, Zool. New York (4), Fishes: 349, pl. 61, fig. 200. Holotype?: ca 635 mm specimen, possibly from New York, apparently not deposited in a collection according to Garrick (1982, NOAA Tech. Rep., Nat. Mar. Fish. Serv. Circ. (445): 135). Lamna caudata DeKay, 1842, Zool. New York (4), Fishes: 354, pl. 62, fig. 205, 205a, b. Holotype?: ca 2235 mm specimen from Rhode Island coast, apparently not deposited in a collection according to Garrick (1982, NOAA Tech. Rep., Nat. Mar. Fish. Serv. Circ. (445): 135). Carcharias obtusirostris Moreau, 1881, Hist. nat. poiss. France, 1: 332, text fig. 53-54. No identifiable specimens listed in the original account although Museum National d'Histoire Naturelle, Paris, MNHN-98-1227, a 420 mm male fetus, has been considered a type (see discussion in Garrick, 1982, NOAA Tech. Rep., Nat. Mar. Fish. Serv. Circ. (445): 136-137). Type locality France, Mediterranean Sea.

Other Combinations: Eulamia or Carcharhinus milberti (Valenciennes, in Müller and Henle, 1839).

FAO Names: En - Sandbar shark; Fr - Requin gris; Sp - Tiburón trozo.


Fig. 299 Carcharhinus plumbeus

Field Marks: A medium-sized grey shark with short rounded snout, an extremely tall triangular first dorsal fin with its origin over or anterior to the pectoral-fin insertions, broad- and high-cusped, triangular serrated upper teeth without cusplets, tooth counts usually 27 to 32 upper jaw, 25 to 32 lower jaw, an interdorsal ridge, large pectoral fins, a moderately large dorsal fin with a short rear tip, and no conspicuous markings on fins.

Diagnostic Features: Medium to large, fairly stocky sharks (up to about 240 cm but mostly smaller) with snout short and broadly rounded or broadly parabolic, internarial width 0.9 to 1.3 in preoral length. Eyes circular and moderately large, length 1.7 to $2.9 \%$ total length. Nostrils with very short, low, poorly developed anterior nasal flaps. Upper labial furrows short and inconspicuous. Hyomandibular line of pores just behind mouth corners not conspicuously enlarged. Gill slits short, third 2.4 to $3.6 \%$ total length and less than a third of first dorsal base. Upper teeth with broadly triangular, strongly serrated, semierect to slightly oblique cusps merging smoothly into crown feet with slightly coarser serrations but no cusplets; lower teeth with erect, narrow serrated cusps and transverse roots; total tooth counts 27 to 32 upper jaw, 25 to 32 lower jaw. A narrow interdorsal ridge present. Pectoral fins large, semifalcate, with narrowly rounded or pointed apices, length of anterior margins about 17 to $22 \%$ total length. First dorsal fin very large and semifalcate, with pointed or narrowly rounded apex and posterior margin curving ventrally from fin apex; origin of first dorsal fin over or slightly anterior to pectoral-fin insertions; inner margin of first dorsal fin moderately long, $2 / 5$ of dorsal-fin base or slightly less. Second dorsal fin moderately high, height 2.1 to $3.5 \%$ total length, inner margin short and 1.0 to 1.6 times height; origin of second dorsal fin over or slightly anterior to anal-fin origin. Vertebral counts: total vertebral counts 152 to 189 , precaudal vertebral counts 82 to 97 . Colour: grey-brown above, white below; tips and posterior edges of fins often dusky, but no conspicuous markings; an inconspicuous white band on flank.

Distribution: Eastern Atlantic: Portugal, Spain, Morocco, Senegal and to the Gulf of Guinea, and Zaire; possibly the Canary Islands and Madeira Islands. Also, found in the Mediterranean Sea. Western Atlantic: Southern Massachusetts to Florida, northern and western Gulf of Mexico, Bahamas, Cuba, Nicaragua, Costa Rica, Venezuela, southern Brazil. Elsewhere, worldwide in most tropical seas.

Habitat: An abundant, inshore and offshore, coastal-pelagic shark of temperate and tropical waters, found on continental and insular shelves and in deep water adjacent to them, and oceanic banks; common at bay mouths, in harbours, inside shallow muddy or sandy bays, and at river mouths, but tends to avoid sandy beaches and the surf zone, coral reefs and rough bottom, and the surface. Depths range from the intertidal in water barely deep enough to cover it to 280 m . Although common in inshore environments, it does not ascend rivers into fresh water. It favours the bottom, and normally is not
seen at the surface unless travelling in water so shallow that its large first dorsal fin comes out of the water.

Biology: Development viviparous, with a yolk-sac placenta; number of young 1 to 14 per litter, with 5 to 12 common. Litter size varies directly with size of the mother, and in populations with smaller adults the litter size averages smaller. The size of young at birth varies considerably among different allopatric populations of this shark, including adjacent ones in the Western Atlantic, as does the size attained by adults. In this shark as in many other carcharhinids the size range of adults is relatively narrow, indicating virtually determinate growth after maturity. The gestation period is estimated as 8 to 12 months, commonly 9 months off Florida. Females may give birth every other year at most. Young are born at a ratio of $1: 1$, but in the Western Atlantic off the US southeastern seaboard adult females far outnumber males by 5 or 6: 1. However, only about 17 to $27 \%$ of adult females are gravid, which may be a reflection of the apparent dearth of males but might be due to some other factor.


Fig. 300 Carcharhinus plumbeus In the Western North Atlantic pupping grounds are in temperate waters, in shallow bays and estuaries of the east-central USA, into which gravid females come to drop their young in summer (June to August). Off Senegal in the Eastern Atlantic young are born in April. Females are thought to be inhibited from feeding when they give birth and shortly afterwards, and leave the pupping grounds soon after giving birth. The young inhabit shallow coastal nursery grounds during the summer and move offshore into deeper, warmer water in winter. These nursery grounds are separate from the ordinary ranges of adults, except for females arriving to drop their young and shortly departing after doing so, which probably protects the young from cannibalism. Mating occurs in the spring and summer in various populations. Mating wounds are apparent on females during mating season.
Age at maturity for Western North Atlantic sandbar sharks appears to be between 15 and 16 years. Elsewhere, age at maturity varies between regional populations, ranging from 8 to 14 years for males and 7.5 to 16 years for females with a maximum age of 19 and 25 years for males and females, respectively.
The sandbar shark is primarily a predator on relatively small bottom fishes, with some molluscs and crustaceans taken. It does not consume garbage and mammalian carrion as a rule, unlike some other members of its genus. Evidence from fisheries indicates that very fresh fish bait is greatly preferred by these sharks to stale or even fresh-frozen fish, and fish greatly preferred to mammalian meat. These sharks feed by day and night, more actively at night. It is thought that this shark is far more successful in obtaining a regular supply of food than larger carcharhinids such as Galeocerdo cuvier, Carcharhinus leucas and C. obscurus, this is reflected in greater number of sandbar sharks with full or nearly full stomachs, and liver weight, which shows much less fluctuation in sandbar sharks than in the three larger species. Data from captive individuals suggests that digestion is relatively rapid, and prey is largely digested after two days.
This species has an annual migration cycle along the Western North Atlantic seaboard of the United States, heading south for the winter and north for the summer. Seasonal temperature changes apparently are a prime cause of these migrations, but they are strongly influenced by the pattern of currents and locally by upwelling. Although young on nursery grounds form mixed-sex schools, adults are usually segregated. When engaged in southwards migrations, males migrate earlier and deeper than females. Southward-migrating sharks often travel in large schools. Preferred temperatures range from 23 to $27^{\circ} \mathrm{C}$.

Size: Maximum possibly to 300 cm but otherwise to 239 cm or less for adults; males maturing at 131 to 178 cm and reaching 224 cm ; females maturing at 144 to 183 cm and reaching 234 cm . Size at birth 56 to 75 cm .
A length-weight equation is given by Kohler, Casey and Turner (1995) for fork length ( FL ): Wt( kg ) $=1.0885 \times 10^{-5} \times \mathrm{FL} \mathrm{L}^{3.0124}$, $n=1548$ (both sexes), where $F L=0.8175 \times T L+2.5675, n=123$.

Interest to Fisheries and Human Impact: This is an abundant inshore and offshore species where it occurs, and at one time formed an important of targeted shark fisheries in the Western North Atlantic. However, the species is now prohibited from being taken under the U.S. Fishery Management Plan for Atlantic sharks. Prohibited species must be released with minimum injury and without being removed from the water. Although the flesh is edible and highly desirable, its fins are now highly prized in many regions of the world. No catch limitations imposed by EU, but removal of fins and discarding of body is prohibited on EU vessels in all waters and non-EU vessels in EU waters (2012).

This species has never been implicated in attacks on people, and is thought to be not particularly dangerous because of its strong preference for live fish and invertebrate prey. It is a popular aquarium shark for public viewing, as it is hardy and spectacular.

The sandbar shark is considered Vulnerable because of its slow maturation and apparent regional population declines.
Local Names: Brown shark, Sandbar shark or Sand bar shark, White shark, Small blue shark, Milbert's (sandbar) shark, New York ground shark, Atlantic grey shark (English); Tauro, Tiburón gris, Tintorera, Tiburón de Milberto (Spain) Tubarão corre costa (Portugal).

Literature: Bigelow and Schroeder (1948); Springer (1960, 1967); Cadenat (1957); Wheeler (1962); Clark and von Schmidt (1965); Garrick (1982); Cadenat and Blache (1981); Casey, Pratt, Stillwell (1985); Casey and Natanson (1992); Stillwell and Kohler (1993); Sminkey and Musick (1995, 1996); Heist and Gold (1999); Castro, Woodley, and Brudek (1999); Brewster-Geisz and Miller (2000); Merson and Pratt (2001, 2007); Rechisky and Wetherbee (2003); Compagno, Dando, and Fowler (2005); McAuley et al. (2006); McElroy et al. (2006); Ellis and Musick (2007); Musick et al. (2007b); Portnoy, Piercy, Musick, Burguss, and Graves (2007); Conrath and Musick (2008, 2010); Gibson et al. (2008); Last and Stevens (2009); Andrews et al. (2011); Ebert (In preparation).

## Carcharhinus signatus (Poey, 1868)

Hypoprion signatus Poey, 1868, Repert. fis.-nat. Cuba, 2: 452, pl. 4, fig. 7-8. Holotype: A pair of jaws from Cuba (? extant), according to Garrick (1985, NOAA Tech. Rept. NMFS, (34): 20).

Synonyms: Hypoprion longirostris Poey, 1876, An. Soc. Espan. Hist. Nat. Madrid, 5: 394, pl. 9, fig. 8-9 (teeth). Holotype: 2266 mm male, Cuba (?extant) according to Garrick (1985, NOAA Tech. Rept. NMFS, (34): 20). Hypoprion bigelowi Cadenat, 1956, Bull. Inst. Francaise Afr. Noire, 18: 539, fig. 1-5. Holotype: Museum National d'Histoire Naturelle, MNHN-$55-4915,1590 \mathrm{~mm}$ female, between the limits of the coasts of French and Portuguese Guinea, West Africa, tropical Eastern Atlantic.

Other Combinations: None.
FAO Names: En - Night shark; Fr - Requin de nuit; Sp - Tiburón de noche.


Fig. 301 Carcharhinus signatus

Field Marks: A large shark with a long pointed snout, large eyes, oblique-cusped upper anterolateral teeth with smooth or weakly serrated cusps and strong cusplets, lower teeth with erect to semierect cusps but no cusplets, an interdorsal ridge, moderatesized pectoral fins, a small first dorsal with a moderately long rear tip and a low second dorsal fin with a long rear tip, and no conspicuous markings on fins.

Diagnostic Features: Large, fairly slender sharks (up to about 280 cm ) with snout very long and moderately pointed, internarial width 1.7 to 1.9 in preoral length. Eyes circular and moderately large, length 1.8 to $2.7 \%$ total length. Upper labial furrows short and inconspicuous. Hyomandibular line of pores just behind mouth corners not conspicuously enlarged. Gill slits short, third $2.5 \%$ total length and less than a third of first dorsal base. Upper teeth with narrow, smooth or irregularly serrated, oblique cusps, and crown feet with strong distal cusplets (young) or coarse proximal and distal serrations or weak cusplets (adults); lower teeth with erect, smooth cusps and transverse roots; tooth counts 31 to 34 upper jaw, 30 to 32 lower jaw. Interdorsal ridge present. Pectoral fins moderate-sized, slightly falcate, with narrowly to fairly broadly rounded apices; length of anterior margins about 17 to $18 \%$ total length in individuals of all sizes. First dorsal fin small and triangular, with pointed or narrowly rounded apex and posterior margin curving posteroventrally from fin apex; origin of first dorsal fin over the pectoral-fin free rear tips; inner margin of first dorsal fin moderately long, half of dorsal-fin base or slightly less. Second dorsal fin small and low, 1.7 to $2.1 \%$ total length, inner margin long and about 1.9 to 2.2 times height; origin of second dorsal fin over or slightly posterior to anal-fin origin. Vertebral counts: total vertebral counts 184 to 192, precaudal vertebral counts 101 to 104. A large Carcharhinus species with a maximum length of 280 cm . Colour: fins without conspicuous markings, sometimes small black spots scattered on body; an inconspicuous white band on flank.

Distribution: Eastern Atlantic: not known from Area 27, but occurs from Senegal to Ivory Coast, Ghana to Cameroon, Zaire, Angola, and Namibia. Western Atlantic: Delaware to Florida, Bahamas, Cuba, southern Brazil, and Argentina.

Habitat: A common deepwater coastal and semioceanic carcharhinid, occurring on or along the outer continental and insular shelves and off the upper slopes of the tropical and warm-temperate Atlantic. Prefers waters 50 to 100 m deep, but with considerable numbers reaching the surface and extending down to 200 m , and some occurring down to at least 600 m .

Biology: Viviparous, with a yolk-sac placenta, and with litters of 4 to 15 young. Age at maturity for males is about 8 years and for females it has been estimated at 10 years. Maximum age is at least 17 years and possibly up to 31 years. The night shark feeds mainly on small active bony fishes, including flying fish, scombrids, butterfishes, sea basses, squid, and shrimp. It is apparently a relatively quick, active shark.


Fig. 302 Carcharhinus signatus
Known distribution

The night shark is apparently a schooling species, uncommonly caught singly, but often in groups and is usually caught at night or dawn rather than the day, which indicates that it makes vertical migrations. Shows a seasonal variation in numbers off Cuba apparently as a result of geographic migrations. Recorded temperatures where it was caught off West Africa at depths of 90 to 285 m are 11 to $16{ }^{\circ} \mathrm{C}$; salinity 36 ppt ; oxygen $1.81 \mathrm{ml} / \mathrm{l}$ (Poll, 1951).

Size: Maximum about 280 cm ; females mature at about 180 to 205 cm , with pregnant females at 210 to 252 cm ; male sharks mature at over 190 cm with the largest about 215 cm . Size at birth about 60 cm .
A length-weight equation is given by Kohler, Casey and Turner (1995) for fork length ( FL ): $\mathrm{Wt}(\mathrm{kg})=2.9206 \times 10^{-6} \times \mathrm{FL}^{3.2473}$, $\mathrm{n}=124$ (both sexes), where $\mathrm{FL}=0.8390 \times T L+0.5026, \mathrm{n}=38$.

Interest to Fisheries and Human Impact: This species is prohibited from capture in U.S. Atlantic waters, but is still fished off Cuba and Brazil, with longlines but occasionally also pelagic trawls. The night shark is not known to be dangerous to people.

The conservation status of the night shark is Vulnerable due to intense fishing efforts throughout much of its range. It is a protected species, however, in U.S. waters.

Local Names: Night shark, Requiem de nuit, Tiburón nocturno, Tiburón jesuita.
Literature: Bigelow and Schroeder (1948); Poll (1951); Cadenat (1956); Guitart (1975); Cadenat and Blache (1981); Compagno (1984, 1988); Kohler, Casey and Turner (1995); Castro, Woodley, and Brudek (1999); Hazin et al. (2000); Santana and Lessa (2004); Compagno, Dando, and Fowler (2005); Santana, Lessa, and Carlson (2006).

Galeocerdo Müller and Henle, 1837a

Genus: Galeocerdo Müller and Henle, 1837a, Ber. K. preuss. Akad. wiss. Berlin, 2: 115; Müller and Henle, 1837b, Arch. Naturg. 3: 398.

Type species: Squalus arcticus Faber, 1829, by subsequent monotypy in Bonaparte, 1838, Nuov. Ann. Sci. Nat. Bologna, ser. 1, 2: 211.

## Number of Recognized North Atlantic Species: 1.

Synonyms: Genus Boreogaleus Gill, 1862b, Ann. Lyceum Nat. Hist. New York, 7(32): 402. Type species: Boreogaleus arcticus Gill, 1862 by original designation, equals Squalus arcticus Faber, 1829.

Field Marks: See the single species.
Diagnostic Features: Body fairly stout. Head broad and flat but not trowel-shaped; snout bluntly rounded or nearly truncate in dorsoventral view, very short, with preoral length about equal to internarial space and much less than mouth width; eyes fairly large, without posterior notches; large, slitilike spiracles present; no papillose gillrakers on internal gill openings; nostrils small, internarial space about 3 times the nostril width; anterior nasal flaps short, broadly triangular, and not tubular; labial furrows very long, with uppers over twice as long as lowers and nearly reaching anterior ends of eyes; teeth similar in upper and lower jaws, of characteristic cockscomb shape, with heavy, bent, oblique cusps, strong distal cusplets and prominent serrations but no blades; cusps of lower teeth not prominently protruding when mouth is closed; tooth counts 18 to 26 upper jaw, 18 to 25 lower jaw. Interdorsal ridge present and very prominent; low but prominent dermal keels present on caudal peduncle; upper precaudal pit transverse and crescentic. First dorsal-fin origin above pectoral-fin insertions or inner margins, its midbase closer to pectoral-fin bases than to pelvic fins, and free rear tip well in front of pelvic fins; second dorsal fin much smaller than first, its height about $2 / 5$ of first dorsal-fin height or less; its origin slightly anterior to anal-fin origin; pectoral fins moderately broad and semifalcate, pectoral-fins length from origin to free rear tips about $3 / 5$ to $2 / 3$ of their anterior margins; pectoral-fin origins under interspace between third and fourth gill slits; anal fin about as large as second dorsal fin, with short preanal ridges and a deeply notched posterior margin. Vertebral counts: total vertebral counts 216 to 234, precaudal vertebral counts 100 to 112 , caudal vertebral counts more than 117 to 126 . Gigantic sharks, up to 600 and possibly 740 cm . Colour: grey with a unique colour pattern of black spots and vertical bars on dorsal surface of body, bold in young but fading out in adults.

Local Names: Tiger sharks.

## Galeocerdo cuvier (Péron and Lesueur, 1822)

Squalus cuvier Peron and Lesueur, in Lesueur, 1822, J. Acad. Nat. Sci. Philadelphia 2: 351. Holotype: None. Type locality: Northwest coast of New Holland (Australia).

Synonyms: Squalus arcticus Faber, 1829, Nat. Fische Islands: 17. Type locality: Iceland. Galeocerdo tigrinus Müller and Henle, 1839, Syst. Beschr. Plagiost. pt. 2: 59, pl. 23. Syntypes: Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, a small specimen, and Museum National d'Histoire Naturelle, Paris, stuffed specimen.
Other Combinations: Galeocerdo arcticus (Faber, 1829).
FAO Names: En - Tiger shark; Fr - Requin tigre commun; Sp - Tintorera tigre.


Fig. 303 Galeocerdo cuvier


UNDERSIDE OF HEAD



UPPER AND LOWER TOOTH

Field Marks: A big-headed, very short and blunt-snouted, large-mouthed shark with a rather slender body behind the pectoral fins, long upper labial furrows that reach the eyes, large spiracles, cockscomb-shaped curved teeth with heavy serrations and distal cusplets, low keels on caudal peduncle, a slender caudal fin with an acutely pointed tip, and characteristic dark, vertical tiger-stripe markings, faded or obsolete in adults and possibly absent in specimens over 300 cm total length.

Diagnostic Features: See genus.
Distribution: Circumglobal in temperate and tropical seas. Eastern North Atlantic: vagrant reported from Iceland; an unconfirmed sighting from the English Channel; normally occurs further south, including the Azores, Morocco and Canary Islands, Senegal, Gambia, Guinea, lvory Coast and Ghana, but probably more wide-ranging in the area, from Morocco to Angola. Western Atlantic: Massachusetts, U.S.A. to Uruguay, including Gulf of Mexico and Caribbean islands.

Habitat: A common, very large, wideranging coastal-pelagic tropical and warm-temperate shark, with a wide tolerance for different marine habitats, on or adjacent to continental and insular shelves at depths from the surface and intertidal to possibly 140 m . It seems to prefer turbid areas in continental waters, large island groups or high volcanic islands where high runoff of fresh water may contribute to a high density of prey organisms. It often occurs in river estuaries, close inshore off wharves and jetties in harbors, and in coral atolls


Fig. 304 Galeocerdo cuvier and lagoons. It is also known to make excursions far offshore, in the open ocean, but is not considered to be a truly oceanic species like certain Carcharhinus. This is a common species in the Western North Atlantic seasonally following the Gulf Stream Current as far north as New England (U.S.A.), but in the Eastern North Atlantic this tropical to warm temperate shark is uncommon.

Biology: The only carcharhinid shark to exhibit yolk-sac viviparity, it is uncertain whether this condition is primitive in the tiger shark or due to loss of the vitelline placenta. The related Hemigaleidae, the apparent sister group of the Carcharhinidae, all have placental viviparity, suggesting that the condition in the tiger shark is secondary; a hypothesis supported by phylogenetic and molecular analysis. Tiger sharks have one of the larger litter sizes with between 10 and 82 young per litter. Pupping takes place in spring and early summer, usually from April to June in the Northern Hemisphere. The gestation period is from 12 to 16 months. In the Northern Hemisphere, mating may also occur in the spring. In the Western North Atlantic there does not appear to be a well-defined nursery area, but rather parturition takes place over a broad area from about $27^{\circ}$ to $35^{\circ} \mathrm{N}$ (Central Florida to North Carolina, U.S.A.), but appears most concentrated from $31^{\circ}$ to $33^{\circ} \mathrm{N}$ (along the Carolina's). Another area of dense abundance occurs in the northern Gulf of Mexico between $83^{\circ}$ and $88^{\circ} \mathrm{W}$ and $93^{\circ}$ and $95^{\circ} \mathrm{W}$; an area approximately from northern Florida to Texas, U.S.A. Birth occurs along coastal areas at depths of less than 100 m . Neonate and juvenile (age $1+$ years) tiger sharks appear to have a higher mortality rate, at 0.12 to 0.50 and 0.08 to
0.36 , respectively, in the Western North Atlantic than in the northern Gulf of Mexico where estimated mortality values range from 0.11 to 0.98 for neonates and from 0.08 to 0.57 for juveniles.
The tiger shark is one of the few shark species where age estimates have been validated. The age at maturity varies slightly between populations, but in general males mature between 7 to 10 years and females from 8 to 10 years; a study in the Western North Atlantic determined that males and females both mature at 10 years. The growth of young tiger sharks is quite rapid as they nearly double their size over the first year of life and then slowing to about 20 cm per year until they reach maturity, after which their growth slows to about 10 cm per year. Males live to at least 20 years and females to 22 years, but longevity estimates put their maximum ages at 27 to 37 years.
The tiger shark is the most omnivorous of sharks, consuming a wide variety of marine life as well as being somewhat of a 'garbage can with fins' in its taking of carrion and all manner of inedible objects. The tiger shark is a 'sea hyena', a potent predator-scavenger that opportunistically exploits its environment. It takes a wide variety of bony and elasmobranch fishes, marine reptiles more than any other shark species, frequently preys on sea turtles and is one of the most important predators on sea snakes. Sea birds are taken along with migrating land birds that fall into the water. Marine mammals taken by the tiger shark include sea lions, fur seals, monk seals, dolphins, possibly porpoises (Phocaenidae), and small baleen whales (probably taken as carrion); pinnipeds are apparently killed by the sharks, though cetaceans may be more readily taken as carrion. In one instance a tiger shark was observed to scavenge concurrently with a great white shark
(Carcharodon carcharias). Invertebrate prey, including octopi, squid, cuttlefish, spiny lobsters, crabs, horseshoe crabs, conchs and other marine gastropods, tunicates, and even jellyfish, is readily eaten, and tiger sharks have been found gorged with lobsters, horseshoe crabs and conchs. Carrion from terrestrial birds and mammals is commonly devoured. Apart from people definitely known to have been attacked and killed, and on occasion eaten by tiger sharks, some of the terrestrial vertebrates found in tiger shark stomachs were likely taken alive. The tiger shark is famed for swallowing an incredible variety of floating and bottom junk from human activity and natural sources, including leather, fabrics, pieces of coal and wood, seeds and other vegetable material, feathers, plastic bags, burlap bags, small barrels, cans, and pieces of metal to name, but a few of the oddities found in their stomachs on occasion.
Adults and subadult tiger sharks may be resident or semi-resident, with movement by some individuals into or out of an area seasonally while others appear to remain in an area year-round. Tiger sharks are capable of making long distance migrations over short time periods as demonstrated by one individual that traveled 3,330 miles in six months, and another that traveled 1,015 miles in 17 days for an average daily rate of 58 miles.

Size: Maximum size reputed to be about 740 cm , but this cannot be confirmed. Most tiger sharks are smaller than 500 cm , with only a few large females reaching over 550 cm . Males mature between 226 to 292 cm and reach at least 370 cm ; females mature between 250 to 350 cm and reach over 550 cm , though most do not exceed 430 cm ; one gigantic adult female caught off Indo-China in 1957 was reported as being 740 cm long and weighing 3110 kg (Fourmanoir, 1961). Size at birth is between 46 and 89 cm .
A length-weight equation is given by Kohler, Casey, and Turner (1995) for fork length ( FL ): $\mathrm{Wt}(\mathrm{kg})=2.5281 \times 10^{-6} \times \mathrm{FL}^{3.2603}$, $\mathrm{n}=187$ (both sexes), where $\mathrm{FL}=0.8761 \times \mathrm{TL}-13.3535, \mathrm{n}=44$.

Interest to Fisheries and Human Impact: The tiger shark is commonly caught in coastal and offshore fisheries with longlines, hook and line, and fixed bottom nets as well as other gear. It is one of the more common species caught in U.S. Atlantic and Gulf of Mexico coastal waters, but is managed under the U.S. Fisheries Management Program that was instituted in 1993 and as part of the Large Coastal Shark group which also includes the sandbar (Carcharhinus plumbeus) and blacktip (C. limbatus) sharks. This shark is fished by recreational anglers and caught with rod and reel; it is one of the sharks recognized as a big-game fish by the International Game Fish Association and is currently the second largest fish taken by rod and reel (the great white shark being the largest). Its meat is utilized fresh, fresh-frozen, dried-salted and smoked for human consumption, and its hide is of high quality for used as leather and other products. In recent years, its fins have become highly valued for use as shark-fin soup. No catch limitations imposed by EU, but removal of fins and discarding of body is prohibited on EU vessels in all waters and non-EU vessels in EU waters (2012). The tiger shark is one of the most dangerous sharks, with more confirmed attacks on divers and swimmers (including multiple attacks) and attacks on boats being recorded for this species than all other sharks except the great white shark. Because most shark attacks occur in the tropics, where this species and other potentially dangerous requiem sharks abound, this and other dangerous carcharhinids may actually be responsible for more attacks than the far more notorious white shark. On the other hand, the tiger shark is easier to recognize than most large grey sharks (Carcharhinus spp.) in the tropics, and may have more attacks correctly attributed to it than dangerous grey sharks.
The tiger shark can be inquisitive and sometimes aggressive underwater, and may approach humans closely. In more than one instance tiger sharks have attacked divers while they were spearfishing or attracting sharks to bait for photography, and had to be dissuaded by prompt defensive action. Divers should treat this shark with respect, however, because of its size, large teeth, broad prey spectrum (including marine mammals) and lack of reluctance in eating unusual items. The tiger shark has the worst reputation as a man-eater amongst tropical sharks.

The conservation status of the tiger shark has been assessed as Near Threatened as it faces a number of potential threats including those from target and bycatch fisheries, and in some areas of the world it is subject to targeted fishing in eradication programs from populated beaches with high human activity.

Local Names: Spotted shark (UK); Tubarâo tigre (Azores); Tigrisháfur (Iceland).

Literature: Bigelow and Schroeder (1948); Baughman and Springer (1950); Cadenat (1957); Springer (1960, 1963); Clark and von Schmidt (1965); Cadenat and Blache (1981); Compagno (1984, 1988); Branstetter, Musick, and Colvocoresses (1987); Kohler, Casey, and Turner (1995); Lowe et al. (1996); Santos, Porteiro, and Barreiros (1997); Natanson et al. (1999); Heithaus et al. (2001); Ebert (2003, In preparation); Simpfendorfer (2005); Musick and Ellis (2005); Lopez et al. (2006); Driggers et al. (2008); Gibson et al. (2008); Kneebone et al. (2008); Last and Stevens (2009); Meyer et al. (2009, 2010); Nakamura et al. (2011).

## Negaprion Whitley, 1940

Genus: Negaprion Whitley, 1940, Fish. Australia (1): 111.
Type species: Aprionodon acutidens queenslandicus Whitley, 1939, equals Negaprion queenslandicus Whitley, 1940, by original designation; probably junior synonym of Carcharias acutidens Rüppell, 1837.

## Number of Recognized North Atlantic Species: 1.

Synonyms: None.
Field Marks: Carcharhinids with the second dorsal fin about as large as first, very short, broadly rounded or angular snouts, usually no spiracles, labial furrows confined to mouth corners, narrow-cusped, largely smooth-edged upper teeth (serrations when present confined to upper tooth blades), no cusplets on any teeth, no keels on caudal peduncle, longitudinal precaudal pits, first dorsal-fin midbase closer to pelvic-fin bases than pectoral fins, anal fin with preanal ridges virtually absent and with a deeply notched posterior margin.

Diagnostic Features: Body stout. Head very broad and flattened but not trowel-shaped; snout broadly rounded or almost wedge-shaped in dorsoventral view and short, with preoral length subequal to internarial space and much less than mouth width; eyes small, without posterior notches; spiracles absent; no papillose gillrakers on internal gill openings; nostrils small, internarial space about 3 to 5 times the nostril width; anterior nasal flaps short, broadly triangular, but not tubular; labial furrows very short, essentially confined to mouth corners, with uppers shorter than lowers and with their ends falling far behind eyes; teeth strongly differentiated in upper and lower jaws; upper anteroposteriors with more or less erect, slender, narrow cusps, no cusplets, and serrations either absent or confined to crown feet; lowers without cusplets but with mostly erect, fairly long slightly hooked cusps and no serrations; cusps of lower teeth not protruding when mouth is closed; tooth counts 27 to 33 upper jaw, 27 to 33 lower jaw. Interdorsal ridge absent; no lateral keels on caudal peduncle; upper precaudal pit longitudinal and not crescentic. First dorsal-fin origin over or behind pectoral-fin free rear tips, its midbase considerably closer to pelvic-fin bases than pectoral fins and its free rear tip slightly anterior, over, or slightly posterior to pelvic-fin origins; second dorsal fin nearly or quite as large as first, its height $4 / 5$ or more of first dorsal-fin height, its origin about opposite or slightly anterior to anal-fin origin; pectoral fins broad and triangular or falcate, their lengths from origin to free rear tip over $2 / 3$ of pectoral-fin anterior margins; pectoral-fin origins under interspace between third and fourth gill slits; anal fin somewhat smaller than second dorsal fin, with preanal ridges hardly developed and a deeply notched posterior margin. Vertebral counts: total vertebral counts 197 to 229, precaudal vertebral counts 117 to 142, caudal vertebral counts 84. Large sharks, adults reaching over 300 cm . Colour: grey, yellow or brownish above, without a colour pattern.

Local Names: Lemon sharks, Sharp-tooth sharks.
Remarks: The genus Negaprion as currently recognized has only two living species, but some 11 nominal species, most of them Indo-West Pacific forms and all junior synonyms of $N$ acutidens, fall within this genus. Only one species, $N$ brevirostris, occurs in the North Atlantic.

## Negaprion brevirostris (Poey, 1868)

Hypoprion brevirostris Poey, 1868, Repert. fis.-nat. Cuba, 2: 451, pl 4, figs 5-6, 20. Type locality, Cuba.
Synonyms: None.
Other Combinations: Negaprion fronto (Jordan and Gilbert, 1883).

FAO Names: En - Lemon shark; Fr - Requin citron; Sp - Tiburón galano.


Fig. 305 Negaprion brevirostris
Field Marks: A big, stocky, short-nosed, pale yellow-brown shark with the second dorsal fin about as large as the first, and narrow, smooth-cusped teeth in both jaws.

Diagnostic Features: Dorsal, pectoral and pelvic fins usually weakly falcate. Serrations well-developed on blades of upper teeth in individuals 140 cm long and larger, and absent in small individuals 70 cm or less; tooth counts 30 to 33 upper jaw, 29 to 33 lower jaw. Vertebral counts: total vertebral counts 197 to 206. Colour: pale yellow brown above, becoming lighter ventrally.

Distribution: Western Atlantic: from New Jersey (U.S.A.) to southern Brazil, including Gulf of Mexico, Bahamas and Caribbean. Absent from the Eastern North Atlantic, but does occurs in tropical Eastern Atlantic from Senegal, Ivory Coast (probably wide-ranging off West Africa). Elsewhere, occurs in the Eastern Pacific from Mexico (Southern Baja California and Gulf of California) to Colombia and Ecuador.

Habitat: A common to abundant large coastal, inshore tropical shark of the continental and insular shelves, found from the surface and intertidal down to at least 92 m ; these sharks also occasionally venture into the open ocean, near or at the surface, apparently for purposes of migration. They commonly occur around coral keys, at mangrove fringes, around docks, on sand or coral mud bottoms, in saline creeks, in enclosed sounds or bays, and in river mouths and on occasion they may enter fresh water but do not penetrate far up tropical rivers as does Carcharhinus leucas. Neonates and large juveniles have a high degree of site fidelity often remaining tidal creeks and estuaries until they mature. Translocated neonates and juveniles have been shown to return to their original home range. Individuals occur singly or form loose aggregations of up to 20 individuals, with some segregation by size and sex. Off Florida adult lemon sharks may migrate southwards and into deeper water, at least in transit, at the onset of winter.

Biology: Development viviparous, with a yolk-sac placenta; number of young 4 to 17 per litter. In the Western Atlantic, mating and birth occurs in spring and summer, with a peak in spring. The gestation period is between 10 and 12 months. Off the west coast of Florida there is a seasonal increase in abundance of these sharks as males and nongravid females congregate to mate. Pregnant females enter shallow nursery areas and drop their young, which will remain in these nursery areas for considerable lengths of time. Age at maturity has been estimated at 11.6 years for males and 12.7 years for females, with a maximum estimated age of 27 years. Growth of tagged free-ranging sharks is approximately $1 / 4$ as great as those kept in captivity and given food to satiation, suggesting that availability of food is a limiting factor in the growth and ultimately reproduction of these sharks; as well as indicating that captive studies of the growth of sharks under ideal conditions may give an incorrect impression of what occurs in free-living sharks. Courtship behavior and copulation has occurred in captivity, and wild-caught adult female sharks have scars from bites delivered above the pelvic fins by courting adult males.
The lemon shark feeds primarily on fishes, but also takes crustaceans and molluscs. Prey taken includes sea catfishes, mullet, jacks, croakers, porcupine fishes, cowfish (Ostraciontidae), guitarfish, stingrays, eagle rays (Pteromylaeus), crabs, crayfish, occasional sea birds, barnacles, amphipods, and conchs. Juvenile lemon sharks will selectively forage for specific prey items, but will readily switch to more opportunistic prey when available.
The lemon shark shows definite site specificity especially in the young but to a lesser extent in adults, with a tendency in some individuals to return to the same favored place each day. Lemon sharks tend not to passively drift with a current while moving and have been observed swimming in a set course, which sometimes places them against or across a current during a change in tidal direction. Although this species favors shallow areas, it readily can move into deeper water; one was observed to move from a reef into the Gulf Stream current and travel 100 km before returning to the shallows. With growth the sharks expand their home ranges dramatically, although still favoring shallow areas. Young sharks range over a limited space of 6 to $8 \mathrm{~km}^{2}$ on eelgrass flats, lagoons, and other shallow areas but as they grow to subadults gradually expand their range to about $300 \mathrm{~km}^{2}$; adults additionally occupy offshore reefs and deeper water, especially for migrations, although they readily return to the shallows.
The Western Atlantic lemon shark population appears to be one continuous stock, with no distinct stocks, and with gene flow occurring throughout the region. There is no evidence however that the Eastern Central Pacific and Eastern Central Atlantic populations are part of the same stock as the Western Atlantic.

Size: Maximum about 340 cm ; males maturing at about 224 cm and reaching at least 279 cm ; females maturing at about 239 cm and reaching at least 285 cm . Size at birth 60 to 65 cm .

Interest to Fisheries and Human Impact: Acommon inshore shark widely caught where it occurs, on longlines and probably, gillnets, handlines, and other gear; meat utilized dried salted, smoked, and probably fresh frozen, hides for leather and other products, fins for shark-fin soup base, oil extracted from the liver for vitamins, and carcasses for fishmeal. Fished extensively in the Gulf of Mexico and Caribbean, and off Senegal.
The lemon shark has been involved in several unprovoked attacks on people and boats, often after being disturbed, hooked or harpooned. Although lemon sharks are apparently not aggressive to divers when undisturbed, they should be regarded as potentially dangerous because of their size, powerful jaws and large teeth, and tendency to defend themselves when disturbed. Baiting with fish underwater or spearfishing may result in close approaches by these sharks.

The conservation status of this species is considered Near Threatened due to fishing pressure and habitat degradation.
Local Names: Yellow shark, Tiburón, Tiburón amarillo, Requin limon, Tiburón limón.
Literature: Springer (1950, 1960, 1963); Bigelow and Schroeder (1948); Cadenat (1957); Clark and von Schmidt (1965); Cadenat and Blache (1981); Gruber (1981); Compagno (1984, 1988); Brown and Gruber (1988); Motta et al. (1997); Castro, Woodley, and Brudek (1999); Feldheim, Gruber, and Ashley (2001a, b, 2002); Barker et al. (2005); Edrén and Gruber (2005); Sundström (2005); Yeiser, Heupel, and Simpfendorfer (2008); Murchie et al. (2010); Newman, Handy, and Gruber (2010).

## Prionace Cantor, 1849

Genus: Subgenus Prionace Cantor, 1849 (Genus Carcharias Cuvier, 1816), J. Asiatic Soc. Bengal, 18(2): 1399.
Type species: Squalus glaucus Linnaeus, 1758 under suspension of the Rules by the International Commission on Zoological Nomenclature, Opinion 723 (1965, Bull. Zool. Nomencl. 22: 32).

## Recognized Number of North Atlantic Species: 1.

Synonyms: Genus Thalassorhinus Valenciennes, in Bonaparte, 1838, Nuov. Ann. Sci. Nat. Bologna, ser. 1, 2: 210. Type species: Thalassorhinus vulpecula Valenciennes, in Bonaparte, 1838, by monotypy; species listed by name only. Genus Thalassorhinus Valenciennes, in Müller and Henle, 1839, Syst. Beschr. Plagiost. pt. 2: 62. T vulpecula described; junior synonym of Squalus rondeletii Risso, 1810 and probably S. glaucus Linnaeus, 1758. Genus Cynocephalus Gill, 1862, Ann. Lyceum Nat. Hist. New York, 7(32): 401. Type species: Squalus glaucus Linnaeus, 1758 by original designation. Revival of the pre-Linnaean Cynocephalus Klein, 1742 and Klein in Anon., 1775-1781, rejected by the International Commission on Zoological Nomenclature, Opinion 89 (1925, Smithsonian Misc. Colln. 73: 27); and Cynocephalus Klein in Walbaum, 1792, rejected in Opinion 21 (1910, Smithsonian Publ. (1938): 51). Junior homonym of Cynocephalus Boddaert,

1768 (Cynocephalidae) and Cynocephalus Geoffroy and Cuvier, 1795 (Cercopithecidae) in Mammalia. Genus Thalassinus Moreau, 1881, Hist. nat. poiss. France, 1: 319. Type species: Thalassinus rondeletii Moreau, 1881 by monotypy, equals Squalus rondeletii Risso, 1810 and probably a junior synonym of S. glaucus Linnaeus, 1758. Genus Galeus Garman, 1913, Mem. Harvard Mus. Comp. Zool., 36: 4, 145. Type species: Squalus glaucus Linnaeus, 1758 by original designation). Revival of Galeus Valmont, 1768, rejected by the International Commission on Zoological Nomenclature, Opinion 89 (1925, Smithsonian Misc. Colln. 73: 27). Junior homonym of Galeus Rafinesque, 1809 (Scyliorhinidae), Galeus Cuvier, 1816 (= Galeorhinus Blainville, 1816; Triakidae), and Galeus Leach, 1818 (= Mustelus Linck, 1818; Triakidae).

Field Marks: See species account.
Diagnostic Features: Body rather slender. Head narrow, only moderately depressed, not trowel-shaped; snout narrowly parabolic in dorsoventral view, very long, with preoral length greater than internarial space and mouth width; eyes large, without posterior notches; spiracles absent; unique papillose gillrakers present on internal gill openings; nostrils small, internarial space about 2.5 to 3 times the nostril width; anterior nasal flaps very short and broadly triangular, not tubular; labial furrows very short with uppers shorter than lowers and with their ends falling far behind eyes; teeth well differentiated in upper and lower jaws; upper and anteroposteriors with broad, triangular, curved erect to oblique, serrated cusps but with no blades or cusplets (except in very young specimens); lowers with slender cusps, no blades or cusplets, and variable serrations; cusps of lower teeth not prominently protruding when mouth is closed; tooth counts 24 to 31 upper jaw, 24 to 34 lower jaw. Interdorsal ridge absent; low dermal keels present on caudal peduncle; upper precaudal pit transverse and crescentic. First dorsal-fin origin well behind pectoral-fin rear tips, its midbase much closer to pelvic fins than to pectoral-fin bases, and free rear tip slightly anterior to pelvic-fin origins; second dorsal fin much smaller than first, its height $1 / 2$ of first dorsal-fin height or less; its origin slightly posterior to anal-fin insertion; pectoral fins very narrow and somewhat falcate, pectoral-fin length from origin to free rear tip $1 / 2$ or less of pectoral anterior margin; pectoral-fin origins varying from under interspace between third and fourth gill slits to under fourth gill slits; anal fin slightly larger than second dorsal fin, with short preanal ridges and a deeply notched posterior margin. Vertebral counts: total vertebral counts 239 to 253, precaudal vertebral counts 142 to 150, and caudal vertebral counts 96 to 106. Large sharks, adults possibly reaching 400 cm or more. Colour: intense deep blue above, white below, without any distinctive colour patterns.
Local Names: Blue sharks, Akula planshchenosnaia (Russia).
Remarks: The complex nomenclatural and systematic history of this genus is discussed in detail in Bigelow and Schroeder (1948) and Compagno (1988). It is generally regarded as being monotypic, with a single, extremely wide-ranging species, the blue shark (Prionace glauca). The status of Thalassorhinus and its synonym Thalassinus is discussed in Compagno (1988).

## Prionace glauca (Linnaeus, 1758)

Squalus glaucus Linnaeus, 1758, Syst. Nat., ed. 10, 1: 235. Holotype, unknown, type locality: "Habitat in Oceano Europaeo."
Synonyms: ?Squalus rondeletii Risso, 1810, Ichthyol. Nice, Paris: 27. ?Squalus (Monopterhinus) Ciliaris Blainville, 1816, Bull. Sci. Soc. Philomat. Paris, (8): 121. Nomen nudum, probably based on Squalus ciliaris Bloch and Schneider, 1801. Squalus (Carcharhinus) caeruleus Blainville, 1825, in Vieillot et al., Faune Francaise, liv. 13-14: 90, pl. 25, fig. 1. Holotype: 4.5 ' female, lost? Type locality: Mediterranean Sea. Blainville suggested that this might be the same as the "Squale de Rondelet" of Risso, 1810. ?Galeus thalassinus Valenciennes, in Cuvier, 1835: 2. ? Thalassorhinus vulpecula Valenciennes, in Müller and Henle, 1839, Syst. Beschr. Plagiost. pt. 2: 62. Based on Carcharias rondeletii Risso, 1826 (and by synonymy Squalus rondeletii Risso, 1810), with no specimens listed, from the Atlantic and Mediterranean Sea.

Other Combinations: Thalassorhinus rondeletii Moreau, 1881; Glyphis glaucus Fowler, 1916.
FAO Names: En - Blue shark; Fr - Peau bleue; Sp - Tiburón azul.


Fig. 307 Prionace glauca


Field Marks: Dorsal colouration dark blue, bright blue on sides and abruptly white on the undersides, usually slender body, long snout, large eyes, gill raker papillae, long, narrow, pointed pectoral fins, short labial furrows, first dorsal fin on back but closer to the pectoral-fin bases than the pelvic fins, second dorsal fin less than a third size of first but about opposite it, a weak keel on the caudal peduncle, and a narrow-lobed caudal fin with a long ventral lobe.

Diagnostic Features: See genus.
Distribution: Oceanic and circumglobal intemperate and tropical waters (probably the widest ranging chondrichthyan). Eastern Atlantic: Norway to South Africa, Mediterranean. Western Atlantic: Newfoundland to Argentina.

Habitat: A wide-ranging, oceanicepipelagic and fringe-littoral shark, occurring from the surface to at least 350 m depth; deeper in warm temperate and subtropical waters. Although an offshore species it may venture inshore, especially at night, and often in areas with a narrow continental shelf or off oceanic islands. In temperate waters blue sharks occasionally venture to the edges of kelp forests or sufficiently far inshore to be caught in pound nets. The blue shark is often found in large aggregations, not tightly organized schools, and often close to or at the surface in temperate waters. It prefers relatively cool water between 7 and $16{ }^{\circ} \mathrm{C}$ but can tolerate water at $21^{\circ} \mathrm{C}$ or more; it ranges far into the tropics but shows tropical submergence and occurs at greater depths there.


Fig. 308 Prionace glauca
$\square$ Known distribution

Biology: Viviparous, with a yolk-sac placenta; number of young 4 to 135 per litter. The number of young varies considerably among females, more so than any other live bearing shark, and may be partially dependent on size of the female. The gestation period is 9 to 12 months with these sharks making extensive migrations throughout the North Atlantic and over the course of the year to specific areas for mating, pupping, nursery grounds, and for subadults. Courtship behavior and copulation has not been observed in the blue shark, but these apparently involve biting of females by males. Between adult and subadult sharks, this behavior is sufficiently consistent with sex that sharks in the field can be sexed accurately merely by the presence or absence of bite wounds or scars. The blue shark has an unusual morphological adaptation for this behavior; adolescent and mature females develop skin about three times as thick as males.
Age at maturity varies slightly between regions, but in general female blue sharks are immature at 0 to 4 years old and adult between 5 and 7 years. Males mature at about 4 to 5 years old. In the Western North Atlantic blue sharks mature in about 5 years, with males reaching a maximum age of 15 years and females a maximum age of 16 years. Unlike some other carcharhinids clasper growth in males is apparently a prolonged and gradual process that may take at least a year, making condition of claspers rather difficult to use for determining maturation of males. Females have a prolonged maturation phase in their 4th and 5th years during which time they become sexually active and copulate with males. Five year old females store sperm in their oviducal glands after mating season in late spring to early winter, and retain it for a
prolonged period while their ovaries and oviducts enlarge and become differentiated; in their 6th year, in the next spring, fertilization occurs and young are born in spring to early summer of their 7 th year. Some females may mature a year earlier than the majority or shift out of phase with them in having young out of the usual season. The maximum estimated age for these sharks is about 20 years. These are very rapidly growing sharks compared to most other carcharhinids for which information is available.
The blue shark feeds heavily on relatively small prey, especially bony fishes and squid, though other invertebrates, small sharks, and mammalian carrion is readily taken and seabirds occasionally are caught at the surface by these sharks. Much of the prey of the blue shark is pelagic, though bottom fishes and invertebrates figure in its diet also. Squid are a very important prey of these sharks; some species of squids form huge breeding aggregations, which are attended by blue sharks. Some sharks slowly ingest masses of squid almost like browsing herbivores, and leisurely swim forwards and sweep their heads and tails in broad arcs, catching squid at the corners of their mouths. Newly arrived and presumably hungry sharks may rapidly charge through dense schools of squid gulping down large masses. These sharks also feed on the undersides of dense schools, assuming a vertical posture and lunging upward into the school to take prey. With scattered or alert squid the sharks may attack in swift, fast turns and catch them in their mouth corners. Cuttlefish (Sepiidae), vampire squid (Vampyroteuthidae) and pelagic octopi are also taken by blue sharks, as well as sea snails (Gastropoda), slipper lobsters, shrimp, mantis shrimp and crabs (including swimming crabs). The papillose gill rakers of the blue shark, unique among the requiem sharks, may be very useful for preventing small prey like squid, red crabs or anchovies from slipping out the internal gill slits. On the other hand, these sharks proverbially gather in great numbers at a whale carcass and feast avidly on its blubber. Whale and porpoise blubber and meat have been recorded from blue shark stomachs. These sharks are also known to attack the cod-ends of trawls to remove the fish. Blue sharks have been seen biting at floating objects such as tin cans and boxes at the surface.
In the North Atlantic tagging and recapturing of individuals has shown a regular clockwise trans-Atlantic migration route with the current system. Sharks tagged off the USA have been recovered off Spain, in the Straits of Gibraltar, and in the equatorial north-central Atlantic, while sharks tagged in the Canary Islands have turned up off Cuba. Apparently the sharks ride the Gulf Stream to Europe, take various currents down the European and African coasts, and ride the Atlantic North Equatorial Current to the Caribbean region. There is considerable sexual segregation in populations, with females more abundant at higher latitudes than males. During the late summer, fall and winter months juveniles of both sexes, subadult females, and adult males move offshore into the Gulf Stream Current with some moving south to the Caribbean and South America. Other portions of the population, mainly juvenile and subadult females, most of which have recently mated, follow the current to the Eastern Atlantic. During the spring these sharks move back inshore from the Gulf Stream and northward along the continental shelf. It is during the summer months that large numbers of blue sharks are encountered from off southern New England to Nova Scotia, including the Georges and Grand Banks. Mature females are rare in the inshore waters of the Western North Atlantic. Conversely, the Eastern Central Atlantic blue shark population consists primarily of adult females, most of which are gravid, during the winter months in the area from about $27^{\circ}$ to $32^{\circ} \mathrm{N}$, approximately from the Canary Islands to the North African coast. At this same time, adult males occupy an area further to the north off the Portuguese and Spanish coasts, that also includes juveniles and subadult females that have move south from northern European waters. Adult males and females during the spring and summer months are found from $32^{\circ}$ to $35^{\circ} \mathrm{N}$ where it is believed that mating takes place. Subadult females migrate to the north during the spring and summer months where they are common off the English coast. After a 9 to 12 month gestation period, birth occurs in the early spring in nursery areas from the Bay of Biscay to off the Iberian Peninsula and near the Azores, and in the western Mediterranean. Newborns do not make extensive migrations and remain in the nursery area until they are about 2 to 3 years old and at a total length of about 130 cm .

Size: Maximum size 383 cm , although unconfirmed reports of larger individuals up to 480 to 650 cm are mentioned in the literature but have not been confirmed. Males maturing between 182 and 281 cm , and reaching at least 311 cm , females adolescent at 173 to 221 cm , adult at 221 and to at least 323 cm . Size at birth about 35 to 44 cm .
Length-weight curves for North Atlantic blue sharks include: Kohler, Casey and Turner (1995) for fork length (FL), Wt $(\mathrm{kg})=3.1841 \times 10^{-6} \times F L(\mathrm{~cm})^{3.1313}(\mathrm{n}=4529$, both sexes), where $\mathrm{FL}=0.8313 \times \mathrm{TL}+1.3908(\mathrm{n}=572$, Western North Atlantic).

Interest to Fisheries and Human Impact: This common oceanic shark is usually caught with pelagic longlines but also hook and lines, pelagic trawls, and even bottom trawls near coasts. It is utilized fresh, smoked, and dried salted for human consumption; its hides are used for leather; fins for shark-fin soup base; and also for fishmeal and liver oil. This shark is also considered a game fish and taken by sports anglers with rod and reel. No catch limitations imposed by EU, but removal of fins and discarding of body is prohibited on EU vessels in all waters and non-EU vessels in EU waters (2012). This shark has bitten boats and people on rare occasion, and should be treated with respect. Spearfishing divers have been harassed by these sharks, and have had to fend them off with spears to keep from being bitten. Sometimes these sharks will slowly circle divers, possibly out of curiosity, and sometimes for a quarter hour or more. The blue shark is not strongly aggressive under such circumstances of contact with people underwater, but on the other hand is not very timid.

One of the most prolific shark species, the blue shark is currently listed as Near Threatened. However, recent life history and demographic data suggests that this assessment is overly conservative and its conservation status should be reassessed.

Local Names: Blue shark, Great blue shark, Blue whaler, Rondelet's shark, Blue dog (English); Janequin (Canaries); Requin
bleu, Squale glaque, Pei can, Cagnot, Cagnot bleu, Le bleu, Le grand chien bleu, Peau bleu, Requin Tchi, Verdoun (France); Bhtyhaai blau, Wehaai, Blauwe haai (the Netherlands); Blaauwe haii (Belgium); Blauer hai (Germany); Morghi glas (Wales); Blaahai (Norway); Blåhaj (Sweden); Blauwe haai (the Netherlands); Bláhávur (Faroe Islands); Ca mari, Taburó, Tiburón, Tintorera (Spain); Quelha, Tintureira, Veletina (Portugal); Tintureira, Tubarão azul, Blue shark (Azores); Tintureira (Madeira Islands); Golubaya akula (Russia).

Remarks: See genus.
Literature: Bigelow and Schroeder (1948); Garrick and Schultz (1963); Stevens (1973, 1974, 1975, 1976, 1984, 2010); Clarke and Stevens (1974); Casey (1979); Pratt (1979); Compagno (1988); Cadenat and Blache (1981); Muñoz-Chápuli (1984); Vas (1990); Henderson, Flannery, and Dunne (2001); Ebert (2003, In preparation); McCord and Campana (2003); Nakano and Seki (2003); Skomal and Natanson (2003); Queiroz et al. (2005, 2010); Stevens (2005); Campana et al. (2006b, 2009); Aires-da-Silva and Gallucci (2007); Aires-da-Silva, Ferreira, and Pereira (2008); Aires-da-Silva, Hoey, and Gallucci (2008); Gibson et al. (2008); Hueter and Simpfendorfer (2008); Kohler and Turner (2008); Nakano and Stevens (2008); Aires-da-Silva et al. (2009); Last and Stevens (2009); Megalofonou, Damalas, and de Metrio (2009).

## Rhizoprionodon Whitley, 1929

Genus: Rhizoprionodon Whitley, 1929, Aust. Zool. 5: 354.
Type species: None.

## Number of Recognized North Atlantic Species: 1.

Synonyms: None.
Field Marks: Requiem sharks with long, parabolic or subangular snouts, small, wide-spaced nostrils, no spiracles, labial furrows varying from short and confined to mouth corners to rather long but falling behind eyes, fairly large eyes, obliqueand narrow-cusped small teeth in both jaws, these with distal blades and serrations variably present or absent but without cusplets, no keels on caudal peduncle, transverse crescentic precaudal pits, second dorsal fin $1 / 3$ height of first or less, second dorsal-fin origin far behind anal-fin origin and about opposite its insertion, anal fin with elongated preanal ridges and a straight or slightly concave posterior margin.

Diagnostic Features: Body fairly slender to moderately stout. Head fairly broad, only moderately depressed, not trowelshaped; snout narrowly to broadly parabolic or obtusely wedge-shaped in dorsoventral view, long, with preoral length greater than internarial space and mouth width; eyes rather large, without notches; spiracles absent; no papillose gillrakers on internal gill openings; nostrils small, internarial space about 3 to 5 times the nostril width; anterior nasal flaps very short, narrowly triangular, and not tubular; labial furrows short to rather long, with uppers shorter or longer than lowers falling far behind eyes; teeth similar in upper and lower jaws, anteroposteriors with slender oblique cusps and distal blades but no cusplets; serrations variably developed; cusps of lower teeth not prominently protruding when mouth is closed; tooth counts 23 to 31 upper jaw, 21 to 28 lower jaw. Interdorsal ridge absent or rudimentary; no dermal keels present on caudal peduncle; upper precaudal pit transverse and crescentic. First dorsal fin origin usually over pectoral-fin inner margins but sometimes slightly behind their rear tips, its midbase about equidistant between pectoral and pelvic-fin bases or closer to the pectoral fins, and free rear tip usually anterior to pelvic-fin origins but occasionally over them; second dorsal fin much smaller than first, its height $1 / 3$ first dorsal-fin height or less, its origin about over anal-fin insertion; pectoral fins moderately broad and triangular, slightly falcate, pectoral-fin length from origin to free rear tip $2 / 5$ to $4 / 5$ of pectoral-fin anterior margin; pectoral-fin origins varying from below 3rd to below 4th gill slits. First dorsal-fin origin usually over pectoral-fin inner margins but sometimes slightly behind their rear tips, midbase about equidistant between pectoral and pelvic-fin bases or closer to the pectoral fins, and free rear tip usually anterior to pelvic-fin origins but occasionally over them. Second dorsal fin much smaller than first, height $1 / 3$ first dorsal-fin height or less; origin about over anal-fin insertion. Anal fin considerably larger than second dorsal fin, with very long preanal ridges and a straight or slightly concave posterior margin. Vertebral counts: total vertebral counts 121 to 170, precaudal vertebral counts 55 to 91 , and caudal vertebral counts 62 to 85 . Small sharks, adults not exceeding 130 to 150 cm and most smaller than 100 cm . Colour: light grey, yellowish or brownish grey above, without a colour pattern.

Local Names: Sharpnose sharks.
Remarks: The arrangement of this genus follows Springer (1964) in most details, except that the subgenus Protozygaena is not recognized (see Compagno, 1988 for a discussion of the classification and nomenclature of Rhizoprionodon and Protozygaena). Most of the species in Rhizoprionodon were formerly placed in Scoliodon, but the latter name is restricted to the very distinct Indo-Western Pacific $\boldsymbol{S}$. laticaudus and $\boldsymbol{S}$. macrorhynchos.

## Rhizoprionodon terraenovae (Richardson, 1836)

Squalus (Carcharias) terrae-novae (Richardson, 1836), Fauna Boreall-Americana (3), Fish: 289. Holotype: None? Type Locality: Newfoundland.

Synonyms: None.
Other Combinations: None.
FAO Names: En - Atlantic sharpnose shark; Fr - Requin aiguille gussi; Sp - Cazón picudo atlántico.


Fig. 309 Rhizoprionodon terraenovae

Field Marks: A distinctive grey to grey-brown shark with small white spots dorsally, becoming lighter ventrally and with dusky fin tips.

Diagnostic Features: Prenarial snout 3.6 to $4.5 \%$ total length. Upper labial furrows long, 1.6 to $2.2 \%$ total length. Total count of enlarged hyomandibular pores on both sides of head just behind mouth angle usually over 16 ( 8 to 18 per side). Teeth serrate in adults; teeth not differentiated in males and females; tooth counts 24 to 27 upper jaw, 24 to 27 lower jaw. Pectoral anterior margin usually longer than first dorsal length from origin to free rear tip; a pressed pectoral apex reaching behind first third of first dorsal base. First dorsal-fin origin usually over or slightly in front of pectoral-fin free rear tips. Second dorsal-fin origin ranges from above anal-fin midbase to just in front of its insertion. Vertebral counts: total vertebral counts 126 to 144, precaudal vertebral counts 58 to 66 , precaudal vertebral counts 67 to 81 . Size moderate, with a maximum length of 110 cm . Colour: grey or grey brown, white below, large specimens with small light spots, pectorals with white margins, dorsal fins with dusky tips.

Distribution: Endemic to Western North Atlantic: Canada (New Brunswick), USA (New England to Virginia, North Carolina, South Carolina, Georgia, Florida, Gulf of Mexico coast off Alabama, Texas, Mississippi, Louisiana), and Mexico (Yucatan Peninsula) south to Honduras.

Habitat: A small, common to abundant, coastal warm-temperate to tropical shark of the Western Atlantic and Gulf of Mexico continental shelf, ranging from the intertidal to possibly 280 m deep, but usually in water less than 10 m deep. It often occurs close to the surf zone off sandy beaches, and also enclosed bays, sounds, harbours, and marine to brackish estuaries. It readily tolerates reduced salinities in estuaries and river mouths but does not penetrate far into fresh water. In the northern Gulf of Mexico it shows a regular inshore-offshore seasonal migration, retreating to deeper water with the onset of winter in October or November and returning inshore in spring, April and May. Adult males appear to be most common in nearshore shallow waters during the spring and fall months when water temperatures are between $20^{\circ}$ and $24^{\circ} \mathrm{C}$, but move offshore during the summer when the water temperature rises and the oxygen levels are drop.

Biology: Viviparous, with a yolk-sac placenta; number of young 1 to 8 per litter, most commonly 4 or 6 per litter, with the number of embryos increasing with size of the female; the sex ratio of near term fetuses is $1: 1$. Off Texas, Florida and North Carolina young are born in late spring and summer (June to August). In the Gulf of Mexico mating occurs in late spring to summer, midMay to mid-July, and are born in May or June after a 10 to 12 month gestation period. Gravid female sharks move into inshore waters to deposit their young, and in the northern Gulf of Mexico outnumber adult males by nearly 3:1. Age at maturity is between 2.4 and 3.5 years for males, and 2.8 to 3.9 years for females. Maximum age has been estimated at about 10 to 11 years. The age at maturity in the northern Gulf of Mexico population was found to have declined over a 20 -year period, from 2.3 years to 1.4 years between 1979 and 2001. Also, the size at maturity for males and females in this population appears to have decreased from 78.3


Fig. 310 Rhizoprionodon terraenovae
$\square$ Known distribution cm and 80.2 cm (1979 and 1980), respectively, to 72.6 and 75.8 cm (1998 and 2001), respectively. Reasons for the decline in size at maturity, age, and an increase in growth rates are uncertain, but may include anthropogenic influences or natural causes, or may be do to differences in scientific methodologies between studies.
Food of this shark is primarily small bony fishes (teleosts), both benthic and littoral, with small crustaceans as an important secondary food category; molluscs and elasmobranchs are relatively unimportant. The diet of these sharks can vary by location, habitat, and size, but these sharks are also opportunistic consuming prey items that may be locally abundant or available. In general, neonates tend to consume invertebrates, mostly crustaceans, in higher proportion than teleosts, but as they grow and mature these sharks feed mostly bony fishes and to a lesser degree on elasmobranchs.

Size: Maximum about 110 cm ; males maturing between 65 and 85 cm and reaching at least 105 cm , females maturing at 75 to 90 cm and reaching 110 cm . Size at birth about 29 to 37 cm .

Interest to Fisheries and Human Impact: A common inshore shark, fished in U.S. waters, sharpnosed sharks are taken in large numbers as bycatch in shrimp trawling fisheries. It has been estimated that the bycatch in the shrimp fishery in the Gulf of Mexico from 1972 to 1995 ranged from less than 50 tonnes to nearly 350 tonnes during this time period. This number roughly equally nearly 75,000 sharpnose sharks being caught in 1995 alone (Pellegrin, 1996; Scott et al., 1996). It is harmless to people. This is a fast growing species that reproduces annually, and despite being taken as bycatch and in targeted fisheries its population appear to be sustaining.

The conservation status of this shark is Least Concern due to its high reproductive rate.
Local Names: Sharpnosed shark, Sharp-nosed shark, Newfoundland shark.
Literature: Bigelow and Schroeder (1948); Baughman and Springer (1950); Springer (1964); Clark and von Schmidt (1965); Compagno (1984, 1988); Parsons (1983a, b, 1985); Branstetter (1987c); Castro and Wourms (1993); Pellegrin (1996); Scott et al. (1996); Castro, Woodley, and Brudek (1999); Gelsleichter, Musick and Nichols (1999); Carlson and Baremore (2003); Hoffmayer and Parsons (2003); Loefer and Sedberry (2003); Bethea, Buckel, and Carlson (2004); Cortés (2005a); Parsons and Hoffmayer (2005); Bethea et al. (2006); Parsons (2006); Carlson et al. (2008).

### 2.6.5 Family SPHYRNIDAE

Family: Sphyrnidae Gill, 1872, Smiths. Misc. Coll. (247): 24.
Type genus: Sphyrna Rafinesque, 1810a, Caratt. gen. sp. anim. piant. Sicilia, Palermo, pt. 1: 46, 60.

## Number of Recognized North Atlantic Genera: 1.

FAO Names: En - Hammerhead sharks; Fr - Requins marteau; Sp - Cornudas.
Field Marks: The hammer or mallet-shaped lateral expansions of the heads of these sharks are unique.
Diagnostic Features: Head with laterally expanded blades, shaped like a double-bitted ax or mallet in profile. Eyes circular or nearly so. Nictitating eyelids internal. Spiracles absent. Anterior nasal flaps short and triangular, not barbel-like; Internarial width usually about 7 to 14 times nostril width (but only 1.1 to 1.3 times it in Eusphyra, which has tremendously expanded nostrils). Labial furrows vestigial or absent. Teeth small to moderately large, more or less bladelike, with acute and narrow to moderately broad cusps, no lateral cusplets, and with basal ledges and grooves strong to absent; teeth weakly differentiated in upper and lower jaws; tooth rows 24 to 37 upper jaw, 25 to 37 lower jaw. Precaudal pits present. Pectoral fins with radials extending into distal web of fins. First dorsal fin moderate-sized to very large but not keel-like, much shorter than caudal fin; first dorsal-fin base ahead of pelvic-fin bases, varying from equidistant between pectoral and pelvic-fin bases to closer to pectoral-fin bases; midpoint of first dorsal-fin base always in front of pelvic-fin origins. Second dorsal fin much smaller than first. Ventral caudal-fin lobe strong, undulations or ripples present in dorsal caudal-fin margin. Vertebral centra with strong, wedge-shaped intermedial calcifications. Vertebral counts: total vertebral counts 116 to 206, precaudal vertebral counts 52 to 107, caudal vertebral counts 64 to 108. Valvular intestine with a scroll valve. Colour: light grey or brownish above, white below, no colour pattern.

Distribution: Circumglobal in all warm-temperate to tropical seas.
Habitat: The hammerheads are a small but common family of wide-ranging warm-temperate and tropical sharks found in continental and insular marine waters on or adjacent to the shelves but with none being truly oceanic. Hammerheads occur in estuaries but none penetrate freshwater to any extent. Depths where these sharks occur range from the surface, surf line and intertidal down to at least 275 m .

Biology: Hammerhead sharks are viviparous with a yolk-sac placenta, and have litters from as little as 2 up to 50 young per reproductive cycle; the gestation period appears to range from 7 to 12 months depending on the species. The age at maturity, depending on the species, ranges from only two years (Sphyrna tiburo) to 15 years ( $\boldsymbol{S}$. lewini) for those species where age estimates are available. The size range can vary from several relatively small species reaching no more than 92 to 150 cm , while others attain a maximum length of 400 cm and possibly 600 cm .
Hammerheads are versatile feeders that take a wide variety of bony fishes, elasmobranchs, cephalopods, crustaceans, and other prey; some habitually feed on other elasmobranchs, and one species ( $\boldsymbol{S}$. tiburo) has enlarged, almost Heterodontus-like posterior teeth as an adaptation to crushing invertebrate prey. Hammerheads have relatively small mouths and teeth, and none feed on marine mammals and other very large marine vertebrates. Hammerheads feed on a wide variety of bony fishes, other sharks (including batoids), cephalopods (squids, octopi and cuttlefish), gastropods, bivalves, and crustaceans (shrimp, mantis shrimp, brachyurid crabs, lobsters, barnacles and isopods), but don't feed on marine mammals or other very large marine vertebrates.
Hammerheads are very active swimmers, ranging from the surface to the bottom, and occur in all warm seas. Some of the species are social and several species occur in polarized schools, sometimes with hundreds of individuals.

Interest to Fisheries and Human Impact: Hammerheads are the subject of target and non-target fisheries worldwide. The larger species are important elements of tropical inshore and offshore fisheries, while the smaller species figure in local artisanal fisheries where they occur.

Several of the larger hammerhead species have occasionally bitten people, but observations by researchers and sports divers show that these sharks are not particularly aggressive in unbaited situations and tend to be wary of divers and swimmers except for spearfishers whose catch they may try to confiscate. Bonnethead sharks and scalloped hammerhead sharks have successfully been kept in captivity in large public aquaria.

The conservation status of several species within this group are considered Near Threatened, Vulnerable, or Endangered do to direct and indirect fishing pressures.

Local Names: Hammerhead sharks, Hammerheaded sharks, Hammerheads, Mullet sharks (English).
Remarks: Following Compagno (1988) and Compagno, Dando, and Fowler (2005), the family Sphyrnidae comprises of two genera, and eight species; one genus and four species occur in the North Atlantic.

Literature: Müller and Henle (1839); Dumeril (1865); Günther (1870); Garman (1913); Springer (1940); Fraser-Brunner (1950); Gilbert (1967a, b), Compagno (1984, 1988); Ebert (In preparation).

## Sphyrna Rafinesque, 1810a

Genus: Sphyrna Rafinesque, 1810a, Caratt. gen. sp. anim. piant. Sicilia, Palermo, pt. 1: 46, 60.
Type species: Squalus zygaena Linnaeus, 1758, by subsequent designation of Jordan and Gilbert, 1882: 26.

## Number of Recognized North Atlantic Species: 4

Synonyms: Genus Sphyrnias Rafinesque, 1815, Anal. Nat.: 93. nomen nudum, and perhaps error or emendation of Sphyrna Rafinesque, 1810a. Genus Sphyrichthys Thienemann, 1828, Lehrbuch Zool. 3: 408. Substitute for Sphyrna Rafinesque, 1809, and thereby taking the same type species, Squalus zygaena Linnaeus, 1758. Genus Platysqualus Swainson, 1839, Nat. Hist. Fish. Amphib. Rept., Monocard. Anim., 2: 318. Type species: Squalus tiburo Linnaeus, 1758 by monotypy. Genus Zygana Swainson, 1839, Nat. Hist. Fish. Amphib. Rept., Monocard. Anim., 2: 318. Apparent emendation of Zygaena Cuvier, 1816, and thereby taking the same type species, Squalus zygaena Linnaeus, 1758. Genus Sphyra van der Hoeven, 1858, Handboek Dierkun. 2, fishes: 68. Emendation of Sphyrna Rafinesque, 1809, and thereby taking the same type species, Squalus zygaena Linnaeus, 1758. Genus Cestracion Gill, 1862a, Proc. Acad. Nat. Sci. Philadelphia, 1861: 59 (name only); Gill, 1862b, Ann. Lyceum Nat. Hist. New York, 7(32): 403. Type species: Cestracion zygaena Gill, 1862b by original designation, equals Squalus zygaena Linnaeus, 1758.

Field Marks: Unmistakable sharks with moderate broad, spade, mallet or ax-shaped heads about a third to a sixth as wide as the shark's length.

Diagnostic Features: Head variably spade, mallet or ax-shaped in dorso-ventral view and moderately broad, width across head about 17 to $33 \%$ of total length; lateral blades of head broad, not wing-like. Nostrils short, their widths 7 to 14 in internarial width and less than half mouth width. No bumps along anterior margin of head. Upper precaudal pit transverse and crescentic. First dorsal-fin origin over or behind pectoral-fin insertions.

Local Names: Hammerhead sharks, Bonnet-headed sharks (English).
Remarks: The genus currently has seven recognized species worldwide, although there is growing molecular evidence that some of these species, for example Sphyrna lewini and S. tiburo, may represent species-complexes that may eventually prove to involve regionally distinctive separate species. Four species occur in the North Atlantic.

## Key to North Atlantic Species:

1a. Head shovel-shaped and narrow, its width $21 \%$ of total length or less (usually less). Anterior margin of head not notched (Fig. 311). Posterior teeth expanded as broad, molariform crushers.

## Sphyrna tiburo

1b. Head broader and more hammer- or ax-shaped, its width over $22 \%$ of total length. Anterior margin of head more or less notched, just medial to nostrils. Posterior teeth not expanded as molariform crushers2

2a. Anterior margin of head nearly straight in adults (Fig. 312). Prenarial grooves absent or hardly developed. Teeth strongly serrated at all sizes. Pelvic fins high and falcate. First dorsal fin markedly falcate. Second dorsal fin very high, with a short inner margin and deeply concave posterior margin

Sphyrna mokarran

2b. Anterior margin of head moderately convex in adults, strongly so in young (Fig. 313 \& 314). Prenarial grooves well-developed. Teeth smooth-edged in young, weakly serrate in adults. Pelvic fins low and not falcate, with nearly straight posterior edges. First dorsal fin usually semifalcate. Second dorsal fin low, with a long inner margin and deeply concave posterior margin 3


UNDERSIDE OF HEAD
Fig. 311 Sphyrna tiburo


UNDERSIDE OF HEAD
Fig. 312 Sphyrna mokarran

3a. No median indentation on anterior margin of head (Fig. 313). Free rear tip of second dorsal fin well ahead of upper caudal-fin origin. Anal-fin base about as large as second dorsal-fin base

Sphyrna zygaena

3b. A prominent median indentation on anterior margin of head (Fig. 314). Free rear tip of second dorsal fin nearly reaching upper caudal fin. Anal-fin base noticeably larger than that of second dorsal fin

Sphyrna lewini


UNDERSIDE OF HEAD
Fig. 313 Sphyrna zygaena


UNDERSIDE OF HEAD
Fig. 314 Sphyrna lewini

## Sphyrna lewini (Griffith and Smith, 1834)

Zygaena lewini Griffith and Smith, in Cuvier, Griffith and Smith, 1834, Animal kingdom, 1:640, pl. 60. Holotype: unknown. Type locality: South coast of New Holland (Australia). Etymology: Whitley (1940, Fishes of Australia: 121) notes: "The trivial name of this species honours John William Lewin (1770-1819), natural history painter and coroner in New South Wales in the early days. Some authors have wrongly spelt it leeuwini instead of lewini"

Synonyms: Sphyrna diplana Springer, 1941/40, Proc. Fla. Acad. Sci. 1940, 5: 46-52. Holotype: U.S. National Museum of Natural History, USNM-108451, 1735 mm male, from off Englewood, Florida, Dalton Sta. 819. Status of holotype from Howe and Springer (1993, Smiths. Contr. Zool. [540]: 6). ?Sphyrna couardi Cadenat, 1951, Inst. Francaise Afr. Noire, Init. Afr. (3), 99. Holotype: none known. Type locality, Senegal.

Other Combinations: None.
FAO Names: En - Scalloped hammerhead; Fr - Requin-marteau halicorne; Sp - Cornuda común.


UNDERSIDE OF HEAD
Fig. 315 Sphyrna lewini

Field Marks: A large hammerhead shark with a broad, narrow-bladed head, anterior margin of head very broadly arched in adults and with a prominent median indentation, teeth with moderately broad cusps and smooth to weakly serrated edges, moderately falcate first dorsal fin with origin over or behind pectoral-fin insertions and free rear tip in front of pelvic-fin origins, low second dorsal fin with weakly concave posterior margin, long posterior margin about twice fin height, and free rear tip nearly or quite reaching upper caudal-fin origin, non-falcate pelvic fins, a deeply notched posterior anal-fin margin, and dusky or black-tipped pectoral fins.

Diagnostic Features: Expanded prebranchial head hammer- or axe-shaped and very wide but longitudinally narrow, its width 24 to $30 \%$ of total length (mostly above $26 \%$ ), distance from tip of snout to rear insertions of posterior margins of expanded blades less than half width of head; anterior margin of head very broadly arched, with prominent medial and lateral indentations; posterior margins of head long, angled posterolaterally, and generally broader than mouth width. Welldeveloped prenarial grooves present anteromedial to nostrils. Preoral snout about $1 / 5$ to $1 / 3$ of head width. Rear of eyes slightly anterior to upper symphysis of mouth. Mouth rather broadly arched. Anterior teeth with moderately long stout to slender cusps, smooth or weakly serrated, posterior teeth mostly cuspidate and not keeled and molariform. Total tooth counts upper jaw 30 to 36 , lower jaw 30 to 35 . Pelvic fins not falcate, with straight or slightly concave posterior margins. First dorsal fin moderately falcate, origin above or slightly behind pectoral-fin insertions, free rear tip well anterior to pelvic-fin origins. Second dorsal fin low, less than anal-fin height, with a shallowly concave posterior margin; inner margin long, about twice fin height, and ending almost opposite upper caudal-fin origin. Anal fin larger than second dorsal fin and rather long, base 4.3 to $6.4 \%$ of total length, origin well ahead of second dorsal-fin origin, posterior margin shallowly concave to nearly straight. Vertebral counts: total vertebral counts 174 to 209, precaudal vertebral counts 89 to 96 , caudal vertebral counts 85 to 108 . A large hammerhead, to over 300 cm . Colour: grey-brown above, white below, with dusky to black pectoral fin tips.

Distribution: Essentially circumglobal in coastal warm temperate and tropical seas. Eastern Atlantic: Spain, Portugal, and the Azores. Western North Atlantic: New Jersey to Florida. This species is much more common in the warm temperate and tropical seas of the Central Eastern and Western Atlantic.

Habitat: A coastal-pelagic, semioceanic warm-temperate and tropical species occurring over continental and insular shelves and in deepwater adjacent to them, often approaching close inshore and entering enclosed bays and estuaries. Occurs from the intertidal and surface down to at least 275 m depth.

Biology: Viviparous, with a yolk-sac placenta, gestation is about 9 to 10 month with the number of young per litter ranging from 13 to 41 . The reproductive cycle is poorly defined, but may be annual. This warm temperate to tropical water shark is mostly a seasonal visitor in the Western North Atlantic typically following the warm summer currents, but


Fig. 316 Sphyrna lewini
$\square$ Known distribution retreating southwards in the late autumn and winter as these waters cool. Scalloped hammerheads segregate at different stages of their life cycle by sex and size. Adult females move inshore, into estuaries to give birth. Neonates are seasonally common in several South Carolina, U.S.A. estuaries, which also serve as nursery areas. These neonates will remain in the nursery areas for several months before moving out into open coastal waters. Scalloped hammerheads grow quite rapidly during the first five years of life, averaging 10 to 15 cm per year, but after that their growth rate slows to 5 to 10 cm per year. Since juveniles are prey items for several larger shark species, including larger members of their own species, their rapid early growth rate allows them to reach a size at which they are less vulnerable to predation. Males mature in about 10 years and females at about 15 years and reach a maximum age of approximately 35 years. The growth rate of scalloped hammerhead sharks in the Western North Atlantic appears to be slower than Pacific Ocean populations.
The scalloped hammerhead takes a wide variety of fish prey, but also invertebrates (especially cephalopods). Food items include sardines and herring, anchovies, ten-pounders (Elopidae), conger eels, milkfish, sea catfish, silversides, halfbeaks, mullet, lizardfish, barracuda, bluefish, Spanish mackerel, jacks, porgies, mojarras, cardinal fishes, goatfish, grunts, damselfishes, parrotfishes, wrasses, butterfly fishes, surgeonfish, gobies, flatfish, sharpnosed sharks (Rhizoprionodon), blacktip reef sharks, angel sharks, stingrays, squid, octopi, cuttlefishes, sea snails, shrimp, mantis shrimp, crabs, lobsters and isopods.

These sharks congregate offshore over seamounts and near islands, and show a considerable range of behaviours including lateral tilting of the body (possibly to enhance the shark's view of divers when approached from above and behind them); accelerated swimming variants with headshaking, thrusting the midsection while swimming rightside up or upside down, and corkscrew swimming with rotation around their longitudinal axes; hitting other hammerheads with their snouts; jaw opening; and clasper flexion. Some of these displays may involve aggression or courtship. Many females bear apparent courtship scars, but a smaller proportion of males have them too. The function of these schools is uncertain: reproduction is thought unlikely because of the presence of juveniles in the schools; defense unlikely because of the absence of possible predators on the hammerheads; and grouping for attaining a swimming advantage in the strong currents that are common in these places unlikely because the sharks school when currents are absent. Feeding advantages may occur for the sharks to cluster near food resources or even for social feeding, but so far this is hypothetical because the sharks have never been seen to feed in the daytime when observations can be made though they may do so at night.

Size: Maximum total length about 370, but possibly over 400 cm ; males mature at 140 to 165 cm and reach at least 295 cm ; females mature at about 212 to 250 cm and reach at least 370 cm . Size at birth 38 to 56 cm .
A length-weight equation for the Western North Atlantic is given by Kohler, Casey and Turner (1995) for fork length (FL): $\mathrm{Wt}(\mathrm{kg})=7.7745 \times 10^{-6} \times \mathrm{FL}^{3.0669}, \mathrm{n}=390$ (both sexes), where $\mathrm{FL}=0.7756 \times \mathrm{TL}-0.3132, \mathrm{n}=111$.

Interest to Fisheries and Human Impact: In the tropics which is one of the most abundant, and commonest, of the large hammerhead shark species and is frequently taken in target and non-target fisheries. However, in the temperate waters of the Eastern North Atlantic this shark, although landed on occasion as part of a complex of hammerhead shark species, is not very common. This species is very abundant in the Western North Atlantic, and is managed in U.S. waters by the Highly Migratory Species Fishery Management Plan, under the Large Coastal Shark complex. It is also frequently taken in recreational fisheries. Scalloped hammerhead sharks are caught with pelagic and fixed bottom longlines, bottom nets, and even bottom and pelagic trawls. The meat is utilized fresh, fresh-frozen, dried salted and smoked for human consumption. Although humans consume the meat, the fins in recent years have become a prized and valuable commodity, and are highly sought after.
The scalloped hammerhead should be considered dangerous to people do to its size, but verified attacks by it are difficult to confirm because until recently large hammerheads, particularly this species and Sphyrna zygaena, have been regularly confused with each other, and so several unprovoked and provoked attacks on swimmers and divers as well as a few boat attacks can only be attributed to 'hammerheads'. Under baited conditions these hammerheads will closely approach divers but usually lose interest and departed once they determined that the divers are not the source of the food odor.
Retaining on board, transhipping or landing any part or whole carcass of hammerhead sharks of the family Sphyrnidae (except for the Sphyrna tiburo) in association with fisheries in the ICCAT Convention Area shall be prohibited (EU 2012a).

The global conservation status of the scalloped hammerhead is considered to be Endangered do to direct and indirect fisheries.

Local Names: Scalloped hammerhead, Hammer-head shark, Hammerhead shark, Hammerhead, Bronze hammerhead, Scalloped hammerhead shark (English); Requin marteau halicorne (France); Tubarão-mona, Tubarão-martelo, Tubarão-martelo-recortado (Portugal).

Remarks: Molecular studies on Sphyrna lewini suggest that the Atlantic population may be distinctly different from the Pacific, and that a possible "cryptic" species may occur in this area.

Literature: Bigelow and Schroeder (1948); Garrick and Schultz (1963); Gilbert (1967a, b); Cadenat and Blache (1981); Compagno (1984, 1988); Quéro in Whitehead et al. (1984c); Branstetter (1987a); Santos, Porteiro and Barreiros (1997); Ebert (2003); Duncan et al. (2006); Able et al. (2007); Piercy et al. (2007); Ulrich et al. (2007); Baum et al. (2007b); Gibson et al. (2008); EU (2012a).

## Sphyrna mokarran (Rüppell, 1837)

Zygaena mokarran Rüppell, 1837, Neue Wirbelth. Fauna Abyssinien gehör., Fische rothen Meeres (1835-1838): 66, pl. 17, fig. 3. Lectotype: Naturmuseums Senckenberg, Frankfurt, SMB-3590, 2515 mm stuffed adult or adolescent male, Massaua, Red Sea, according to Klausewitz (1960, Senckenbergiana Biol. 41: 293).

Synonyms: Zigaena mokarran Rüppell, 1837
Other Combinations: None.

FAO Names: En - Great hammerhead; Fr - Grand requin-marteau; Sp - Cornuda gigante.


UNDERSIDE OF HEAD
Fig. 317 Sphyrna mokarran

Field Marks: An easily recognized large hammerhead with anterior margin of head nearly straight in adults and with a median indentation, strongly serrate teeth, strongly falcate first dorsal fin with rear tip in front of pelvic-fin origins, high second dorsal fin with strongly concave posterior margin and short inner margin, falcate pelvic fins, and a deeply notched posterior anal-fin margin.

Diagnostic Features: Expanded prebranchial head hammer- or ax-shaped and very wide but longitudinally narrow, its width 23 to $27 \%$ of total length (mostly above $23 \%$ ), distance from tip of snout to rear insertions of posterior margins of expanded blades less than half width of head; anterior margin of head very broadly arched in young but nearly straight in adults, with prominent medial and lateral indentations; posterior margins of head long, angled posterolaterally in young but transverse in adults, and about as broad as mouth width. Prenarial grooves absent or hardly developed. Preoral snout less than $1 / 3$ of head width. Rear of eyes anterior to upper symphysis of mouth. Mouth rather broadly arched. Anterior teeth with moderately long stout cusps, strongly serrated edges, posterior teeth mostly cuspidate and not keeled and molariform; total tooth row counts upper jaw 35 to 39 , lower jaw 34 to 38 . Pelvic fins strongly falcate, with strongly concave posterior margins. First dorsal fin strongly falcate, origin over or slightly behind pectoral-fin insertions, free rear tip well anterior to pelvic-fin origins. Second dorsal fin high, about equal to anal-fin height, with a strongly concave posterior margin; inner margin short, about equal to fin height, and ending well in front of upper caudal-fin origin. Anal fin about as large or larger than second dorsal fin and moderately long, base 5.6 to $7.3 \%$ of total length, origin well ahead of second dorsal-fin origin, posterior margin deeply notched. Vertebral counts: total vertebral counts 197 to 212, precaudal vertebral counts 93 to 98 , caudal vertebral count 108. A large to gigantic hammerhead, common to 300 cm and growing to more than 550 cm . Colour: grey-brown above, light below, without fin markings.

Distribution: Circumglobal in warm temperate and most tropical seas. Eastern Atlantic: Spain, Portugal, Mediterranean, Morocco, Senegal, and possibly off the Canary Islands, Gambia, and Guinea. Western Atlantic: international waters east of New Jersey, U.S.A. to Brazil, including Gulf of Mexico and Caribbean.

Habitat: A coastal-pelagic and semi-oceanic tropical hammerhead occurring close inshore and well offshore, over the continental shelves, island terraces, and in passes and lagoons of coral atolls, as well as over deep water near land; depths range from near the surface and in water about a meter deep to over 80 m . The great hammerhead often favours continental and insular coral reefs, but recent tracking studies have shown this shark will move quite far offshore, at least 500 km and off the continental shelf in one study.

Biology: Viviparous, with a yolk-sac placenta. Birth occurs after an 11 month gestation period with the number of young per litter ranges from 6 to 42 . Sex ratios of fetuses are approximately 1:1. Birth occurs in late spring or summer in the
northern hemisphere. The median age at maturity for Sphyrna mokarran is between 5 and 6 years, giving it a faster growth rate and an earlier age at maturity when compared to some other large Carcharhinus and Sphyrna species. In one study, females were estimated to live to a maximum age of at least 44 years and males to at least 42 years; these maximum age estimates correspond to a total length of about 400 cm for females and 380 cm for males.
The great hammerhead takes a variety of prey, but seems especially to favor stingrays and other batoids, groupers and sea catfishes. Its diet includes tarpon, sardines, sea catfishes, toadfish, porgies, grunts, jacks, croakers, groupers and other serranids, tonguesoles, boxfishes, porcupine fishes, smooth-hounds (Mustelus) and other sharks, guitarfish, skates, stingrays, cow-nosed rays, crabs and squid. This species seems not to be bothered by the poisonous spines of its stingray and catfish prey, and is sometimes found with stingray stings imbedded in its buccal cavity (one had about fifty stings


Fig. 318 Sphyrna mokarran
Known distribution Possible distribution in its mouth, throat and tongue). This and other large hammerheads were the first to reach newly baited sharklines in the Florida shark fishery, indicating a particularly keen olfactory sense.
This species apparently is nomadic and migratory, with some populations moving polewards following warm water currents. A tracking study in the Western North Atlantic found this species to make long distance migrations in a relatively short time, with one individual moving from the middle of the Florida Keys northward to 500 km off the New Jersey coast, a minimum distance of 1200 km in only 62 days. This shark appeared to follow the warm Gulf Stream Current during its northward movement.

Size: Maximum total length 550 to $610+\mathrm{cm}$, but adults of either sex over 400 cm are uncommon. Males mature at 234 to 269 cm , and grow at least 380 cm ; females mature at 250 to 300 cm and grow to at least 550 cm , possibly larger. Birth size is between 50 and 70 cm .

Interest to Fisheries and Human Impact: Interest to fisheries more limited than other large hammerheads, especially in the North Atlantic where this typically tropical hammerhead shark is relatively rare. It is listed by ICES (2010) as one of three large hammerhead sharks occasionally taken by Portuguese and Spanish commercial fisheries. In the Western North Atlantic this species is less common that $\boldsymbol{S}$. Iewini in pelagic and bottom longline observer catches. The meat is less desirable for human consumption than other hammerhead species, but the fins are of high quality and are extremely valuable in the shark fin trade. In U.S. Atlantic and Gulf of Mexico waters however shark finning is banned. Retaining on board, transhipping or landing any part or whole carcass of hammerhead sharks of the family Sphyrnidae (except for the Sphyrna tiburo) in association with fisheries in the ICCAT Convention Area shall be prohibited (EU 2012a).
This species is thought to be dangerous to people, but few if any confirmed attacks can be definitely attributed to it because of the difficulty in distinguishing the other large hammerhead species from each other. In unbaited situations these hammerheads have approached divers but generally behaved unaggressive. The size and rather broad food spectrum of the great hammerhead, plus the considerable number of attacks attributed to hammerheads in general, make it a shark to be treated with respect and caution.

The global conservation status of this species is considered Endangered due to fishing pressure.
Local Names: Great hammerhead, Great hammerhead shark, Squat-headed hammerhead shark, Hammerhead shark (English); Marieau millet, Poisson pantouflier, Sorosena (France); Cornuda, Guardia civil, El tiburón, Tiburón (Spain); Tubarão-martelo-gigante (Portugal).

Literature: Bigelow and Schroeder (1948); Cadenat (1957); Springer (1960, 1963); Clark and von Schmidt (1965); Gilbert (1967a, b); Carvallo (1967); Cadenat and Blache (1981); Compagno, Dando, Fowler (2005); Denham et al. (2007); ICES (2010); Piercy, Carlson, and Passerotti (2010); Passerotti et al. (2010); Hammerschlag et al. (2011); EU (2012a).

## Sphyrna tiburo (Linnaeus, 1758)

Squalus tiburo Linnaeus, 1758, Syst. Nat., ed. 10, 1:234. Holotype unknown, type locality: "Habitat in America."
Synonyms: Sphyrna vespertina Springer, 1940, Stanford Ichthyol. Bull. 1(5): 161. Holotype, Division of Systematic Biology, Stanford University, SU-11584, 810 mm female, type locality, Panama.

Other Combinations: None.

FAO Names: En - Bonnethead; Fr - Requin-marteau tiburo; Sp - Cornuda tiburo.


UNDERSIDE OF HEAD
Fig. 319 Sphyrna tiburo

Field Marks: A small hammerhead with a unique, very narrow, shovel-shaped head without indentations on its anterior edge, enlarged, molariform posterior teeth, first dorsal-fin rear tip in front of pelvic-fin origins, and shallowly concave posterior anal-fin margin.

Diagnostic Features: Expanded prebranchial head shovel-shaped and rather narrow but longitudinally wide, its width 18 to $25 \%$ of total length (mostly below $21 \%$ ), distance from tip of snout to rear insertions of posterior margins of expanded blades over half width of head; anterior margin of head broadly arched or somewhat angular, without indentations; posterior margins of head short, transverse or angled posterolaterally, and generally narrower than mouth width. Prenarial grooves not present anteromedial to nostrils. Preoral snout about $2 / 5$ of head width. Rear of eyes slightly anterior to about opposite upper symphysis of mouth. Mouth rather broadly arched. Anterior teeth with short stout cusps, not serrated, posterior teeth cuspless, keeled, somewhat expanded, and resembling the molariform teeth of Heterodontus spp. Total tooth counts upper jaw 25 to 28, lower jaw 25 to 27 . Pelvic fins not falciform, posterior margins straight or nearly so. First dorsal fin moderately falcate, origin over inner margins of pectoral fins and well behind their insertions, free rear tip usually somewhat anterior to pelvic-fin origins. Second dorsal fin moderately high, about as high as anal fin, with a strongly concave posterior margin; inner margin moderately long, less than twice fin height, and ending well ahead of upper caudal-fin origin. Anal fin larger than second dorsal fin and rather long, base 6.4 to $8.5 \%$ of total length, origin well in front of second dorsal-fin origin, posterior margin shallowly concave to nearly straight. Vertebral counts: total vertebral counts 142 to 173, precaudal vertebral counts 72 to 88 , caudal vertebral counts 70 to 87 . A small hammerhead, to about 150 cm . Colour: grey or greybrown above, light below, often with small dark spots on sides of body.

Distribution: Western Atlantic: Rhodes Island U.S.A. to southern Brazil, including Cuba and the Bahamas. Elsewhere, occurs in the Eastern Pacific from Southern California, USA to Ecuador.

Habitat: An abundant inshore, coastal, continental and insular shelf species, in shallow water over mud and sand bottoms, also on coral reefs; commonly found in estuaries, shallow bays and channels, at depths between 10 and 25 m but down to at least 80 m and into the surf zone and the intertidal.

Biology: Viviparous, with a yolk-sac placenta; number of young 4 to 16 per litter. Off Florida there may be a spring and fall mating season in the bonnethead, or alternatively mating the year round. Males mature in two years and females in about two and a half years. The growth rate for both sexes is about 20 cm per year during the first year of life, and about 10 cm per year for the second year for males and 5 cm in the third year, but slows considerably after that. Males live to a maximum age of about 6 to 8 years. Females conversely grow throughout their lives, but slowing progressively each subsequent year once mature. Females live to at least seven year, but may live for a maximum age of 12 years in some populations.
The bonnethead is primarily a crustacean feeder that eats crabs, shrimp, mantis shrimp, isopods, and even barnacles, but also bivalves, octopi and small fish.
A common small hammerhead shark found of tropical and warm temperate waters of the Western Hemisphere. Along the Atlantic coast of the USA it is a common summer visitor as far north as New England, but it apparently retreats southwards with decreasing water temperatures in fall and winter. Considerable sexual segregation occurs in this species, with adult females often predominating in the shallows during pupping season. This shark seldom appears alone, instead usually occurs in small groups of 3 to 15 individuals.

Size: Maximum total length about 150 cm ; males maturing between 52 and 75 cm and reaching at least 124 cm , females mature at 84 cm or less and reaching at least 130 cm . Size at birth about 35 to 40 cm .

Interest to Fisheries and Human Impact: Interest to fisheries limited. An abundant inshore shark, commonly taken by small-scale fisheries; caught with shrimp trawls, trammel nets, bottom longlines, and hook-and-line, and utilized fresh, fresh frozen, or dried salted for human consumption; also processed into fishmeal.

The conservation status is Least Concern due to its early age at maturity, relatively short life span, and generation time. It also has relatively large litters and the population appears to be relatively stable.

Local Names: Bonnethead, Bonnethead shark, Bonnet shark, Bonnet, Atlantic bonnet, Bonnetnose shark, Heartheaded shark, Shovelhead shark, Shovel-head shark, Shovelhead, Shovelnose shark (English).

Remarks: Sphyrna tiburo from the eastern Pacific has been described as a separate species (Sphyrna vespertina), and subsequently as a subspecies and later synonymized by most authors as a single species. Recent molecular studies however suggest that the Pacific form may in fact represent a different species.

Literature: Springer (1938); Bigelow and Schroeder (1948); Baughman and Springer (1950); Clark and von Schmidt (1965); Gilbert (1967a, b); Myrberg and Gruber (1974); Compagno (1984); Parsons (1993a, b); Cortés, Manire, and Hueter (1996); Carlson and Parsons (1997); Marquez-Farias et al. (1998); Ebert (2003, In preparation); Lombardi-Carlson et al. (2003); Cortés (2005b); Heupel et al. (2006); G. Naylor (pers. comm.).

## Sphyrna zygaena (Linnaeus, 1758)

Squalus zygaena Linnaeus, 1758, Syst. Nat., ed. 10, 1:234. Holotype unknown, type locality: "Habitat in Europa, America."
Synonyms: Squalus malleus Shaw and Nodder, 1796, Naturalist Misc., 8: 375, pl. 267 (ident. by ill., Mediterranean). Zygaena vulgaris Cloquet, 1830: 621, Dictionnaire des Sciences Naturelles, Mediterranean Sea, Arabian Sea, and Red Sea, whereabouts unknown. Based on Squalus zygaena Linnaeus, 1758. Zygaena subarcuata Storer, 1848: 71, Proc. Boston Soc. Nat. Hist., v. 3 (1848-1851).

Other Combinations: None.
FAO Names: En - Smooth hammerhead; Fr - Requin-marteau commun; Sp - Cornuda cruz.


Fig. 321 Sphyrna zygaena
Field Marks: An easily recognized large hammerhead with a broad, narrow-bladed head, anterior margin of head broadly arched in adults and without a median indentation at any stage, teeth with very broad cusps and smooth to weakly serrated edge, moderately falcate first dorsal fin with free rear tip in front of pelvic-fin origins, low second dorsal fin with weakly concave posterior margin and long inner margin about twice fin height, non-falcate pelvic fins, and a deeply notched posterior anal-fin margin.

Diagnostic Features: Expanded prebranchial head hammer- or ax-shaped and very wide but longitudinally narrow, its width 26 to $29 \%$ of total length (mostly above $26 \%$ ), distance from tip of snout to rear insertions of posterior margins of expanded blades less than half width of head; anterior margin of head very broadly arched, with prominent lateral indentations but no medial indentation; posterior margins of head long, angled posterolaterally, and generally broader than mouth width. Welldeveloped prenarial grooves present anteromedial to nostrils. Preoral snout about $1 / 5$ to less than $1 / 3$ of head width. Rear of eyes slightly behind upper symphysis of mouth. Mouth rather broadly arched. Anterior teeth with moderately long, very stout cusps and smooth or weakly serrated edges, posterior teeth mostly cuspidate and not keeled and molariform; total tooth counts upper jaw 29 to 32, lower jaw 25 to 31 . Pelvic fins not falcate, with straight or slightly concave posterior margins. First dorsal fin moderately falcate, origin over pectoral-fin insertions, free rear tip well anterior to pelvic-fin origins. Second dorsal fin low, less than anal-fin height, with a shallowly concave posterior margin; inner margin long, about twice fin height, and ending well in front of upper caudal-fin origin. Anal fin slightly larger than second dorsal fin and rather long, base 4.3 to $5.7 \%$ of total length, origin slightly ahead of second dorsal-fin origin, posterior margin deeply notched. Vertebral counts: total vertebral counts 193 to 206, precaudal vertebral counts 94 to 102, caudal vertebral counts 103 to 104. A large hammerhead, to over 300 cm . Colour: dark olive or dark grey-brown above, white below, undersides of pectoral fin tips dusky.

Distribution: Circumglobal in warm temperate and tropical seas. Eastern North Atlantic: very occasional vagrants off southwest British Isles and Atlantic coasts of France, Spain, Portugal and Mediterranean to Mauritania, Senegal, Cape Verde Islands, Guinea, Ivory Coast, and Angola. Western North Atlantic: Nova Scotia, Canada to Florida, U.S.A. and Virgin Islands.

Habitat: The most cool water tolerant member of the family, Sphyrna zygaena is rarely found in tropical waters. This large, active swimming coastal-pelagic and semi-oceanic hammerhead is found close inshore and in shallow water over continental and insular shelves to well offshore, at depths from the surface down to at least 200 m along the edge of the continental shelf.

Biology: Viviparous, with a yolk-sac placenta. The number of fetuses per litter is between 20 and 50 . The young are born in the spring and early summer after a 10 to 11 month gestation period. Maximum age has been estimated at 18 years.
Feeds on a variety of bony fishes, including herring and menhaden, sea catfishes, sea bass, Spanish mackerel, and porgies, and also small sharks, skates, stingrays, shrimp, crabs, barnacles, and squid and other cephalopods. Small sharks, skates and stingrays are especially favoured, and sharks are readily scavenged from nets and hooks.
An active, common, hammerhead, this species apparently occurs at or near the


Fig. 322 Sphyrna zygaena
$\square$ Known distribution surface in relatively shallow water, while Sphyrna mokarran and S. lewini range into deeper water. This hammerhead is the most tolerant of temperate waters, and has been thought to be amphitemperate in its distribution; however, it definitely occurs in the tropics where its range is spottily known at present due to probable confusion with the more abundant $\boldsymbol{S}$. lewini. In some localities it may form enormous migrating schools of young sharks 150 cm or less long. Despite it abundance in some regions very little is known of its behavior as compared to the more tropical Sphyrna lewini.

Size: Maximum total length about 370 to 400 cm ; adults maturing at about 210 to 240 cm ; males to at least 256 cm and females at least 304 cm . Birth size at 50 to 61 cm .

Interest to Fisheries and Human Impact: The smooth hammer head shark is taken in fisheries worldwide where it occurs, but do to misidentification with the more common scalloped hammerhead shark, landings for it are much more difficult to come by. Along the Atlantic coast of the U.S. it is far less common than the scalloped hammerhead by a ratio of about 10 to 1 , Sphyrna lewinito S. zygaena. In the Eastern North Atlantic it is recorded as part of the hammerhead shark complex, but with no species-specific catch data recorded. In the Western North Atlantic this species is managed as part of the Large Coastal Shark complex under the U.S. Highly Migratory Species Fishery Management Plan, but there are no specific management measures for this species. Retaining on board, transhipping or landing any part or whole carcass of hammerhead sharks of the family Sphyrnidae (except for the Sphyrna tiburo) in association with fisheries in the ICCAT Convention Area shall be prohibited (EU 2012a).
Although the meat is utilized as food for human consumption, the fins are of high quality and are highly prized. However, in U.S. waters finning is prohibited. This common to abundant species is usually caught with pelagic or bottom longlines, and by pelagic and bottom trawls. This species is regarded as being dangerous to people, though of the several attacks by large hammerheads only a few can be tentatively attributed to this species due to their occurrence in temperate waters.

The conservation status of the smooth hammerhead shark, like many of the hammerhead shark species, is Vulnerable do to steep declines in its population regionally.

Local Names: (many names almost certainly represent more than one species, especially $\boldsymbol{S}$. lewini, in tropical areas): Smooth hammerhead shark, Hammerheaded shark, True hammerhead shark, Common hammerhead or Hammerhead shark, Hammerhead, Round-headed hammerhead shark, Shovel-nose shark, Stizzle-nose or Strizzle-nose, Balance fish (UK, USA), Albalestre, Baratelle, Cagnole, Le squale marteau, Marteau, Peï jouziou (France), Gemeiner hammerhai, Meerschlägel, Schlägelfisch (Germany); Balansvich, Kuyshaay (Holland); Cornailla, Cornuda, Cornudilla, Cornuilla, Guardia civil, Llunada, Pez martillo, Pez martillo, Tailandano (Spain); Cornudo, Martelo (Portugal); Cornuda, Peixe martelo, Tubarâomartello, Smooth hammerhead (Azores); Cornuda (Madeira Islands).

Literature: Bigelow and Schroeder (1948); Garrick and Schultz (1963); Gilbert (1967a,b); Compagno (1984, 1988); Cadenat and Blache (1981); Quéro in Whitehead et al. (1984c); Ebert (2003, In preparation); Casper et al. (2005); Southhall and Sims (2005); Gibson et al. (2008); Last and Stevens (2009); Piercy, Carlson, and Passerotti (2010); EU (2012a).

## 3. SYSTEMATIC CATALOGUE - Subclass NEOSELACHII - Cohort BATOIDEA

### 3.1 Order TORPEDINIFORMES - Electric rays

Order: Order Hypotremi, Suborder Sarcura, (group) suborder Torpedinoidea: Gill, 1892, Natn. Acad. Sci. (U. S.) Mem. 6, 6: 130 (group ranked as infraorder or superfamily, exclusively for torpedinoids).

Number of Recognized North Atlantic Families: 1.
FAO Names: En - Electric rays; Fr - Torpilles; Sp - Tremolinas.
Field Marks: Body disc thick and flabby, oval to roundish. Snout short, truncate or rounded. Skin soft and loose, without armature by dermal denticles or their modifications. Tail section thick, caudal fin well developed, as well as 0 to 2 dorsal fins (except torpedinid genus Hypnos).

Diagnostic Features: Eyes small to obsolete, several deepwater species are blind. Powerful electric organs derived from branchial muscles visible as large bean-shaped contour at both sides of head.

Distribution: Circumglobally in Atlantic, Indian and Pacific Oceans.
Habitat: All are bottom dwellers on mostly soft sandy and muddy bottoms, a very few are known to swim pelagically even far offshore into the open ocean (e.g. Torpedo nobiliana). A few species live in deepwater habitat, but most species are found in tropical and subtropical shallow inshore and shelf waters and may be locally rather abundant; few species living also in cool and warm temperate latitudes.

Biology: Reproductive mode is yolk-sac viviparous, but very little else is known on the life cycle of most species. The diet consists of a variety of benthic invertebrates and for the larger species also teleost fishes. As electric rays are sluggish swimmers, they usually narcotise their prey by electric shocks to immobilize it prior to feeding.

Interest to Fisheries and Human Impact: Electric rays are unwanted bycatch in inshore and shelf bottom fisheries, and fishermen avoid them carefully fearing their powerful electric shock discharges, and hence discard them promptly, although the survival rate is unknown. Their flesh is flabby, watery and disliked for human consumption.

The conservation status of most species is uncertain and as such many are considered Data Deficient or Least Concern due to a lack of fisheries and poor knowledge of their life history and population status.

Local Names: None.
Remarks: The order as restricted here has two families recognized globally, of which one (Torpedinidae) occurs in the North Atlantic. Representatives of the second family, Narcinidae, do not occur within the geographical range of Areas 21 and 27. Some classifications recognize as many as four families within this order (Compagno, 2005).

Literature: Nelson (2006).

### 3.1.1 Family TORPEDINIDAE

Family: Subfamily Torpedinini Bonaparte, 1838, Nuov. Ann. Sci. Nat., Bologna, ser. 1, 2: 130 (Family Rajidae). Also as Family Torpedinoidae Gill, 1862, Ann. Lyceum Nat. Hist. New York, 7(32): 386.

Type Genus: Torpedo Houttuyn, 1764.

## Number of Recognized North Atlantic Genera: 1

FAO Names: En - Electric rays; Fr - Torpilles; Sp - Tremolinas.
Field Marks: Body disc heavy and of flabby consistency, more or less circular; pelvic fins unilobed and long; tail massive, with two large dorsal fins and well developed oval to paddle-shaped caudal fin. Skin soft and naked.

Diagnostic Features: Heavy-bodied rays of medium size (max. total length to about 180 cm , max. weight to about 90 kg , but most species less than 100 cm in length); consistency of body typically soft and flabby. Head and body greatly flattened dorso-ventrally; head, trunk and the broadly expanded pectoral fins forming a more or less circular disc. Pectoral fins very thick toward their margins, completely fused to sides of head, and expanded rearward to, or slightly beyond origin of the single-lobed pelvic fins. Anterior contour of disc conspicuously truncate or emarginate, snout extremely short. Rostral cartilage absent or reduced. Eyes and spiracles small and close-set on top of head; posterior margins of spiracles either smooth, or set with knobs or tentacles. Nostrils transverse and relatively large, closer to mouth than to snout edge; their
inner margins broadly expanded rearward and fused as a transverse nasal curtain, smooth free rear margin of which nearly overlaps upper jaw. Tail massive and shark-like, distinctly shorter than and marked off from body disc, with narrow dermal fold along either lower edge. Two relatively large, separated dorsal fins, the first larger than second and originating partly or entirely above pelvic-fin bases. Caudal fin large, subtriangular paddle-shaped. Mouth fairly small and distinctly arcuate, flanked by long longitudinal grooves; jaws extremely slender, labial cartilages absent; numerous small monocuspid teeth set in pavement pattern and forming bands along jaws. Skin very soft and often loose, completely naked without any dermal denticles, except in one Eastern Central Atlantic species. Two very well developed, powerful electric organs (their bean-like shape visible externally) flank the head along its entire length. Colour: above either plain dark, or variegated on various shades of brown with all kinds of light and dark patterns (coloured eye-spots, blotches, or marblings), underside white, often with dark bordering of disc and pelvic fins.

Distribution: Torpedinid electric rays inhabit tropical to temperate shelf waters circumglobally from inshore to about 100 m depth, but some have been reported from as deep as 350 m .

Habitat: Electric rays are usually rather inactive and are often buried on soft bottoms in sand or mud, and appear sluggish when swimming; a few species (e.g. Torpedo nobiliana) are highly migratory, with the adults swimming pelagically. Several species although may lie quietly on the bottom during the day, become quite active at night and will swim off the bottom in search of prey items.

Biology: All species are yolk-sac viviparous, but in addition adult females produce by villi and folds on their uterus walls a secretion commonly called "uterine milk", which the embryos take up, depending on their development stage, through their external gills, or through the ectoderm of the yolk-sac and its stalk. Electric rays feed mainly on bottom-living invertebrates and small fishes.

Interest to Fisheries and Human Impact: Although electric rays can be locally quite abundant in tropical and subtropical latitudes, there is no targeted fisheries for them or any use for human consumption; this is mainly due to the flabby consistency of their bodies and because a large part of the pectoral fins is occupied by the electric organs of gelatinous texture. Fishermen fear these rays because of their discharge of strong electric shocks, and tend to discard them.

The conservation status of these electric rays is poorly known due to a lack of life history data and information on population trends.
Local names: None.
Remarks: The family consists of two genera, Hypnos and Torpedo, and about 25 species, of which only the latter genus (Torpedo) is represented in the North Atlantic; the other genus Hypnos is an Australian endemic.

Literature: Nelson (2006).

## Torpedo Houttuyn, 1764

Genus: Torpedo Houttuyn, 1764, Nat. Hist. Dieren, Planten, Mineral. 1(6): 453-462.
Type Species: Raja torpedo Linnaeus, 1758 by absolute tautonomy as generally accepted.
Number of Recognized North Atlantic Species: 3.
Synonyms: None.
Diagnostic Features: See family and key to genera.
Remarks: The genus comprises two subgenera (Tetronarce and Torpedo), both represented in the North Atlantic, and about 24 species, plus two doubtful and several yet undescribed species. Three species are found in the North Atlantic.

Key to North Atlantic Subgenera and Species:
1a. Margins of spiracles smooth (Fig. 323) (subgenus Tetronarce); uniformly coloured above . . . . . . . . . . . . . . Torpedo nobiliana

1b. Margins of spiracles rimmed with knobs or tentacles (Fig. 324) (subgenus Torpedo); upper side with colour pattern 2


Fig. 323 Torpedo nobiliana

Margins of spiracles rimmed with knobs or tentacles


Fig. 324 Torpedo marmorata

2a. Brown above, with five (sometimes fewer) large eyespots with dark blue centre, encircled by orange inner and black outer ring (Fig. 325).

Torpedo torpedo

2b. Dorsal colouration variably mottled light on dark background (Fig. 326)

Torpedo marmorata


Fig. 325 Torpedo torpedo


Fig. 326 Torpedo marmorata

## Torpedo (Torpedo) marmorata Risso, 1810

Torpedo marmorata Risso, 1810, Ichthyol. Nice: 20-21, pl. III (Fig. 5). No type material.
Synonyms: None.
FAO Names: En - Marbled electric ray; Fr - Torpille marbrée; $\mathbf{S p}$ - Tremolina mármol.


Fig. 327 Torpedo (Torpedo) marmorata
Field marks: Front margin of more or less circular disc broadly truncate. Disc thick and fleshy to outer margins. Tail section stout and massive, with two separated dorsal fins, of which the first one only a little larger than the second one, and large, paddle-like caudal fin. Margin of spiracles rimmed with 6 to 8 tentacles of equal length. Upper side with constant pattern of light mottling or marbling on brown ground colour.


DETAIL OF EYE AND SPIRACLE

Diagnostic Features: Front margin of thick and fleshy disc broadly truncate, shape of disc subcircular to subquadrangular. Tail stout and massive, with long, unilobed pelvic fins attached to sides of its origin; two distinct dorsal fins, of which the first one only slightly larger than the second one; caudal fin large, paddle-like, with upper and lower lobes of about equal size. Margin of spiracles rimmed with 6 to 8 slender tentacles of about equal length (tentacles or knobs on spiracle margin are diagnostic feature of subgenus Torpedo), their tips as a rule almost meeting in centre of spiracle. Distance from origin of first dorsal fin to midpoint of caudal-fin rear margin just about one-third of ray's total length. Colour: variable above but usually light mottling or marbling on brown background; underside white to creamy-white.

Distribution: Eastern Atlantic: South Africa northward to Brittany and English Channel, also in entire Mediterranean, but not in Black Sea. Occasional vagrants in southern North Sea, to Kattegat where less common, also occurring along west coast of Scotland.

Habitat: Benthic on inner shelves on soft and stony bottom to about 40 m depth, rarely deeper to about 100 m .

Biology: Yolk-sac viviparous, with 5 to 32 young, the number of young increases with the size of the female; birth usually occurs from November to December in the Mediterranean after about 10 months gestation. Feeds on small benthic fish and also invertebrates.

Size: Maximum total length is about 60 cm .

Interest to Fisheries and Human Impact: Electric rays are not used for human consumption or other purposes, mainly due to the flabby consistence


Fig. 328 Torpedo (Torpedo) marmorata
 of their flesh and because a large proportion of the pectoral fins is not musculature but the huge electric organs. Taken as bycatch in bottom fisheries but usually discarded or retained for public aquaria. Fishermen should handle these rays carefully as they can discharge powerful electric shocks.

The conservation status of this poorly known electric ray is Data Deficient.
Local Names: Flekket el-rokke (Norway); Marmorierter Zitterrochen (Germany); Tremelga marmoreada (Portugal).
Remarks: A few otherwise typical looking specimens of this species may on occasion show some of the 6 to 8 tentacles around the spiracle margins to be shorter or even knob-like only, similar in appearance to other members of the subgenus Torpedo, various intermediate conditions have also been found occasionally.

Globally, this subgenus has about 13 recognized species, but only two are known to occur within the present study area.
Literature: Stehmann and Bürkel, Torpedinidae, in: Whitehead et al. (1984); Notarbartolo et al. (2003).

## Torpedo (Tetronarce) nobiliana Bonaparte, 1835

Torpedo nobiliana Bonaparte, 1835, Iconogr. Fauna ital.: fasc. XII, pta. 63, 2pp., 1 plate, 3 figs. At ANSP 23 syntypes, coll. Nos 426-439, 461-469.

Synonyms: None.
FAO Names: En - Electric ray; Fr - Torpille noire; Sp - Tremolina negra.


Fig. 329 Torpedo (Tetronarce) nobiliana

Field marks: Front margin of more or less circular disc broadly truncate. Tail section stout and massive, with two large, separated dorsal fins, of which the first one about twice as large as second one, and large, paddle-like caudal fin. Margins of spiracles smooth, without tentacles. Upper side mostly plain dark grey or purple-brown.

Diagnostic Features: Front margin of thick and fleshy disc broadly truncate, shape of disc subcircular to subquadrate. Tail stout and massive, with long pelvic fins attached to sides of its origin; dorsal fins distinct and large, the first one about twice the size of the second


DETAIL OF EYE AND SPIRACLE one; caudal fin large, paddle-like, with upper and lower lobes of about equal size. Spiracles with smooth margins, without tentacles or papillae (diagnostic feature of subgenus Tetronarce). Totally smooth on both surfaces, without dermal denticles or thorns. Colour: mostly plain dark violet-brown above, occasionally with indistinct darker dots and whitish spots; underside white to creamy-white, often with dusky margins to disc and pelvic fins.

Distribution: Eastern Atlantic: South Africa northward to Scotland, but rarely found in the North Sea; also occurring throughout the entire Mediterranean Sea, but not in the Black Sea. Western North Atlantic: Cuba and the Florida Keys (U.S.A.) northward to Nova Scotia (Canada). Worldwide, several nominal species referred to as Torpedosp. cf. nobiliana may in fact represent different species.

Habitat: Juveniles living mainly benthic on continental shelf soft bottoms from 10 to 150 m depth, with a few records deeper to 350 m (an extralimital record from off Morocco at 927 m depth (Iglésias, 2011). Adults may be pelagic or semi-pelagic, regularly swimming singly and reported migrating over long distances.

Biology: Yolk-sac viviparous, with up to 60 embryos depending on size of the female; gestation period probably about a year, with the young being released offshore. Juveniles feed mostly on smaller benthic fish and invertebrates, and adults mainly on fish that may be relatively large.

Size: An impressive, very large electric ray attaining about 180 cm total length.

Interest to Fisheries and Human Impact: Electric rays are not used for human consumption or other purposes, mainly due to the flabby consistence of their flesh and because a large proportion of the pectoral fins is not musculature but the huge electric organs. Taken as bycatch in bottom and pelagic fisheries but usually discarded. Fishermen should handle these rays carefully as they can discharge powerful electric shocks.

The conservation status of this common, but poorly known electric ray, and like most others in the family is Data Deficient.

Local Names: Svart el-rokke (Norway); Schwarzer Zitterrochen (Germany); Tremelga negra (Portugal).

Literature: Stehmann and Bürkel, Torpedinidae, in: Whitehead et al. (1984); Notarbatolo et al. (2004); Iglésias (2011).


Fig. 330 Torpedo (Tetronarce) nobiliana
Known distribution

## Torpedo (Torpedo) torpedo (Linnaeus, 1758)

Raja torpedo Linnaeus, 1758, Syst. Nat., ed. 10, 1: 231 (partim). No type material.
Synonyms: None.
FAO Names: En - Common torpedo; Fr - Torpille ocellée; $\mathbf{S p}$ - Tremolina comun.



DETAIL OF EYE AND SPIRACLE

Fig. 331 Torpedo (Torpedo) torpedo

Field Marks: Front margin of more or less circular disc broadly truncate. Tail section stout and massive, with two separated dorsal fins, of which the first one only a little larger than second one, and large, paddle-like caudal fin. Margins of spiracles rimmed with short tentacles or knob-like papillae of varying length. Upper side of disc patterned with regularly five, sometimes fewer, large, blue-centred eyespots (ocelli) encircled by black and orange-yellow rings.

Diagnostic Features: Front margin of thick and fleshy disc broadly truncate, shape of disc subcircular to subquadrangular. Tail stout and massive, with long pelvic fins attached to sides of its origin; two distinct dorsal fins, of which the first one only slightly larger than the second one; caudal fin large, paddle-like, with upper and lower lobes of about equal size. Margin of spiracles rimmed with short tentacles or knob-like papillae (tentacles or knobs on spiracle margin are diagnostic feature of subgenus Torpedo) of varying length. Distance from origin of first dorsal fin to midpoint of caudal-fin rear margin distinctly longer than one-third of ray's total length. Colour: plain dark or light brown above, at times indistinctly mottled, with regularly five, sometimes fewer, large, blue-centred eyespots (ocelli) encircled by black and orange-yellow rings; underside white to creamy-white.

Distribution: Eastern Atlantic: Angola northward to southern Bay of Biscay; found also throughout the entire Mediterranean Sea, more common along the North African coast, but not in Black Sea.

Habitat: Most common in tropical waters. Mainly a benthic species found in nearshore habitats and on soft bottoms, but also to about 70 m depth and occasionally deeper.

Biology: Yolk-sac viviparous, with litters of 3 to 21 young, depending on size of female, with birth occurring from March to September in the Mediterranean. The diet includes mostly small benthic fishes but also invertebrates.

Size: Maximum about 60 cm TL , but most commonly observed at 30 to 40 cm TL . Size at birth about 8 to 10 cm in length.

Interest to Fisheries and Human Impact: Electric rays are not used for human consumption or other purposes, mainly due to the flabby consistence of


Fig. 332 Torpedo (Torpedo) torpedo
$T$ Known distribution their flesh and because a large proportion of the pectoral fins is not musculature but the huge electric organs. Taken as bycatch in bottom fisheries but usually discarded. Fishermen should handle these rays carefully as they can discharge powerful electric shocks.

The conservation status is Data Deficient.
Local Names: Augenfleck-Zitterrochen (Germany); Tremelga de olhos (Portugal).
Remarks: This electric ray is the type species of genus Torpedo Houttuyn, 1764.
Literature: Stehmann and Bürkel, Torpedinidae, in: Whitehead et al. (1984); Serena, Notarbartolo and Ungaro (2003).

### 3.2 Order PRISTIFORMES - Sawfishes

Order: Order Hypotremi, Suborder Sarcura, (group) suborder Pristoidea: Gill, 1892, Natn. Acad. Sci. (U. S.) Mem. 6, 6:130 (group ranked as infraorder or superfamily, exclusively for pristoids).

## Number of Recognized North Atlantic Families: 1.

FAO Names: En - Sawfishes; Fr - Poissons-scie; Sp - Peces sierras.
Field Marks: Body elongated shark-like, although head depressed, but gill slits on underside of head. Snout extremely extended as a massive, long, flat blade with very solid, long transverse teeth of about equal size along each side; length of saw about one fourth of total length.

Diagnostic Features: Very large rays of up to 700 cm length. Barbels on saw absent. Two large, separated dorsal fins and a large, asymmetric caudal fin. Pectoral fins not extended forward to and not fused with sides of head, long-based but not much broadened. Pelvic fins widely separated from pectoral fins and originating below first dorsal fin. Eyes and spiracles semilaterally on top of head. Small jaw teeth numerous, arranged in pavement pattern and forming band along jaws. Entire saw, body, tail and fins covered "shark-like" with close-set, minute, flattened ovoid placoid scales; larger tubercular scales or thorns absent.

Distribution: Circumtropical in Atlantic, Indian and Pacific oceans.
Habitat: Primarily marine in shelf waters, but also entering brackish coastal waters and river estuaries, rarely in freshwater or ascending rivers.

Biology: Reproduction is yolk-sac viviparous, but relatively little else known about these batoids.
Interest to Fisheries and Human Impact: See family account below.
Local Names: None.
Remarks: Monotypic order with only family Pristidae. All sawfishes are endangered and listed by CITES since 2007 on Appendix I, except for Pristis microdon which is listed on Appendix II.

Literature: Nelson (2006).

### 3.2.1 Family PRISTIDAE

Family: Subfamily Pristidini Bonaparte, 1838, Nuov. Ann. Sci. Nat., Bologna, ser. 1, 2: 206 (Family Rajidae). Family ranking and correct suffix as Pristidae Owen, 1846, Lect. Comp. Anat. Phys. Vert. Animals, 1: 51.

Type Genus: Pristis Linck, 1790.

## Number of Recognized North Atlantic Genera: 1.

FAO Names: En - Sawfishes; Fr - Poissons-scie; Sp - Sierras.
Field Marks: See order Pristiformes above.
Diagnostic Features: See order Pristiformes above.
Distribution: Primarily marine in circumtropical shelf waters, but also entering brackish coastal waters and river estuaries, rarely in freshwater and ascending rivers.

Habitat: Living on or over soft bottom in shallow coastal waters, in brackish waters of river mouths and estuaries, rarely also entering freshwater.

Biology: Yolk-sac viviparous. Feeds mostly on benthic invertebrates and small schooling fish, and the saw-like rostrum is used for slashing through fish schools to dispense and injure individual fishes that are then consumed.

Interest to Fisheries and Human Impact: Mainly artisanal fisheries have badly affected the few stocks being limited geographically and by size. The flesh of the large shark-like sawfishes has been used by local populations for human consumption, the impressive saws sold well as tourist trophies. During recent years, the large shark-like fins were primarily cut off and sold to Asian dealers for high price. Target catch is meanwhile prohibited, since all species were listed in 2007 by CITES on Appendix I (only Pristis microdon on Appendix II), but these shallow living large sawfishes get easily entangled with their saws in any kind of static fishing gear commonly used in tropical and subtropical coastal waters.

Local Names: None.
Remarks: Of the two genera, only Pristis represented in North Atlantic.
Literature: Nelson (2006).

## Pristis Linck, 1790

Genus: Pristis Linck, 1790, Mag. Phys. Naturgesch. 6(3): 31
Type Species: Squalus pristis Linnaeus, $1758=$ Pristis pristis (Linnaeus, 1758) by absolute tautonymy.
Number of Recognized North Atlantic Species: 2.
Synonyms: None.
Diagnostic Features: See family above.

## Key to North Atlantic Species:

1a. 15 to 20 pairs of rostral teeth on saw (Fig. 333).
. . . . . . . . . . . . . . . . . . . . . . . . Pristis pristis


1b. 24 to 32 pairs of rostral teeth on saw (Fig. 334) .
Pristis pectinata


## Pristis pectinata Latham, 1794

Pristis pectinatus Latham, 1794, Trans. Linn. Soc. London, 2(25): 278-279, pI. XXVI (Fig. 2). No type material.
Synonyms: None.
FAO Names: En - Smalltooth sawfish; Fr - Poisson-scie tident; Sp - Peje-peine.


LATERAL VIEW
Fig. 335 Pristis pectinata


UNDERSIDE OF HEAD

Field Marks: About a quarter of total length is a broad, firm and heavy saw-like rostral blade extension, with 24 to 32 pairs of massive lateral teeth.

Diagnostic Features: Snout extremely elongated into a broad, firm and heavy saw-like rostral extension with 24 to 32 pairs of transverse, strong lateral teeth; the "saw" is about a quarter of its total length. Shark-like appearance, with long, massive tail section bearing two large, distinctly separated dorsal fins of equal size and a large, oval caudal fin without marked lower lobe; origin of first dorsal fin at the level of pelvic-fin origin; pectoral fins not much enlarged, their origin fused to posterior part of head and well behind level of mouth. Gill slits on underside of head. Nostrils separated from and well anterior of straight mouth. Colour: plain dark grey-brown on back and sides, underside whitish.

Distribution: Eastern North Atlantic: on the shelf off tropical and subtropical West Africa, northward to about Gibraltar; historical records from the Western Mediterranean are questionable. Western North Atlantic: historically, widespread from off New York (U.S.A.) to Uruguay and northern Argentina, but severe declines have been reported in several regions where it was formerly common (Adams et al., 2006). Reported also from the Western and Eastern Indian Ocean, but in the latter region this species may have been misidentified with other sawfish species.

Habitat: Living on or over soft bottom in shallow coastal waters, in brackish waters of river mouths and estuaries, also entering freshwater (e.g. Lake Nicaragua population now severely depleted).

Biology: Yolk-sac viviparous, females reported with 15 to 20 embryos born. The life span of this sawfish has been estimated at between 40 and 70 years


Fig. 336 Pristis pectinata
$\square$ Known distribution (Adams et al. 2006). Feeding on benthic invertebrates and small schooling fish, with the saw used for slashing into fish schools to dispense and injure individual fishes.

Size: Attains about 550 cm total length, with the saw being about a quarter of its total length; size at maturity about 320 cm in length. Size at birth from 70 to 80 cm .

Interest to Fisheries and Human Impact: Species-specific catch data from along the WestAfrican coast are not available, but probably not targeted due to its apparent rarity now in this area. Artisanal fisheries may take considerable numbers, since this species is easily taken in shallow waters and gets entangled in gillnets. The flesh can be used for human consumption dried or salted, but more profitable are the shark-like large dorsal and caudal fins, and the saws that are sold as trophies or souvenirs. Pristis pectinata is critically endangered and has been listed on Appendix I of CITES since 2007.

The conservation status is Critically Endangered.
Local Names: Grosser Sägerochen, Schmalzahn-Sägerochen (Germany).
Literature: Stehmann and Bürkel, Pristidae, in: Whitehead et al. (1984); Adams et al. (2006).

## Pristis pristis (Linnaeus, 1758)

Squalus pristis Linnaeus, 1758, Syst. Nat., ed. 10, 1: 235-236. No type material.
Synonyms: None.
FAO Names: En - Common sawfish; Fr - Poisson-scie commun; Sp - Sierra commún.


DORSAL VIEW


## UNDERSIDE OF HEAD

## Fig. 337 Pristis pristis

Field Marks: About a quarter of total length is a broad, firm and heavy saw-like rostral blade extension, with 15 to 20 pairs of massive lateral teeth.

Diagnostic Features: Snout extremely elongated into a broad, firm and heavy saw-like rostral extension with 15 to 20 pairs of transverse, strong lateral teeth; this "saw" about a quarter of total length. Shark-like appearance, with long, massive tail section bearing two large, distinctly separated dorsal fins of equal size and a large, oval caudal fin without marked lower lobe; origin of first dorsal fin somewhat anterior to pelvic-fin origin; pectoral fins not much enlarged, their origin fused to posterior part of head and well behind level of mouth. Gill slits on underside of head. Nostrils separated from and well anterior of straight mouth. Colour: plain ochre-greyish on back and sides, underside whitish.

Distribution: Eastern North Atlantic: tropical and subtropical West Africa, from Angola northward to off Portugal; records from Western Mediterranean are questionable, as this species, if it did once occur there, probably no longer occurs in this area.

Habitat: Living on or over soft bottom in shallow coastal waters, in brackish waters of river mouths and estuaries, also entering freshwater. Rare towards northern range limit, moderately more common along Central West Africa.

Biology: Yolk-sac viviparous, but no further information on its reproductive biology. Feeds on benthic invertebrates and small schooling fishes, with the saw used for slashing into fish schools to dispense and injure individual fishes.

Size: Attains about 450 to 500 cm total length, with the saw being about a quarter of this length

Interest to Fisheries and Human Impact: Catch data from along the West African coast are not available, but it is probably not targeted. Artisanal fisheries, however, may take considerable numbers as this species is easily taken in shallow waters or often gets entangled in gill nets. The flesh can be used for human consumption dried or


Fig. 338 Pristis pristis salted, but more profitable is the sharklike large dorsal and caudal fins, and the saws that are sold as marine curios.

Pristis pristis is Critically Endangered and listed on Appendix I of CITES since 2007.
Local Names: Ostatlantischer Sägerochen, Gewöhnlicher Sägerochen (Germany); Espadarte-Serra (Portugal).
Remarks: This sawfish is the type species of genus Pristis Linck, 1790.
Literature: Stehmann and Bürkel, Pristidae, in: Whitehead et al. (1984); Cook and Compagno (2005b).

### 3.3 Order RAJIFORMES - Skates

Order: Rajae: Müller \& Henle, 1841, Syst. Besch. Plagiost. [Part] 2, (3): 103 (group equivalent to order for batoids).

## Number of Recognized North Atlantic Families: 3.

FAO Names: En - Skates.
Field Marks: Guitarfishes (Rhinobatidae) have an elongated, shark-like appearance and size, but gill slits are on underside of head, and they are shark-like entirely and densely covered with small placoid scales; a long, massive tail section not distinct from the body and with two large separated dorsal fins and a large, unilobed caudal fin. Skates (Rajidae and Arhynchobatidae) have a completely dorsoventrally flattened body and greatly extended pectoral fins forming a disc; slender tail sharply distinct from the disc. Dorsal fins small, caudal fin rudimentary or absent; body and tail never completely covered by overlapping, very densely set placoid scales.

Diagnostic Features: Rhinobatidae: Only head and body with pectoral and pelvic fins dorsoventrally flattened to form a rather narrow and short body disc. Snout wedge-shaped, with a broad, solid rostral cartilage to snout tip. Pelvic fins unilobed. Rajidae and Arhynchobatidae: Shape of disc varying from almost circular to inverse heart-shaped and subrhombic, with snout ranging from very short and blunt to very elongated and pointed; snout either supported by a firm rostral cartilage extending to snout tip, or by forward extension of anterior pectoral radials and their basal skeletal elements almost to snout tip because of lacking, incomplete or very delicate rostral cartilage; tail from moderately slender in most species to very thin threat-like, usually not much longer than disc; two dorsal fins small, or absent, caudal fin rudimentary or absent; pelvic fins bilobed in majority of species; most species with a distinct upper side pattern of conspicuous thorns set in small patches on certain areas of head, and in longitudinal rows along back of trunk and tail; thorns on disc reduced in some genera, mostly so in arhynchobatid genus Bathyraja, mature males with a patch of malar thorns on cheeks, and across wing tips with a field of sharp, claw-like alar thorns being either retractable in dermal pockets, or permanently erect; very low powered electric organs along entire, or only part of tail length, which derived from lateral caudal musculature. Sizes range from pygmy to more than 200 cm total length. Colour: basic coloration and pattern extremely variable on both sides.

Distribution: Circumglobally in Atlantic, Indian and Pacific Oceans, including Arctic and Antarctic waters (except for Rhinobatidae).

Habitat: See family for Rhinobatidae. Here restricted to the far more numerous species of the families Rajidae and Arhynchobatidae: Skates live only in marine habitats, except for one uniquely endemic species found in estuarine waters, and in all oceans from tropical to polar latitudes and from shallow inshore waters down to the deep sea abyssal plains (to a depth over $4,000 \mathrm{~m}$ ). The majority of species are found demersally on subtropical to polar shelves and upper slopes, where locally rather abundant, a few large species mainly in deepwater are also benthopelagic and may migrate over long distances.

Biology: Most species of Rhinobatidae are viviparous with a yolk-sac, but some are suspected of being oviparous. All species of skates are oviparous producing relatively low numbers of eggs that are encapsulated in rather large, rectangular horny capsules with a pair of slender horns at both ends. The females deposit these egg capsules individually on the sea floor, where the embryos develop over many months to possibly years (depending on temperature of environment), until they hatch from capsules. The life span of these batoids may range from about 10 years to nearly 40 years or more. All species feed primarily on benthic invertebrates, but larger size species also feed on small fishes; some of the larger sized deepwater species are active hunters on larger benthopelagic fishes, including other chondrichthyans.

Interest to Fisheries and Human Impact: There is a long tradition in many European and Asian countries of fishing for skates on the shelves for human consumption. Modern trawler fisheries have overfished skate stocks in many places; catch quotas have been introduced slowly only in some areas, often only quite recently, because intensive fishing has led to severe depletion of stocks due to the slow growth, late maturity and low reproductive rate of skates. The same holds true for Guitarfishes with their more restricted shelf habitat in tropical and subtropical waters, where they are targeted in these days for their large dorsal fins in addition to their flesh that is used for human consumption.

Local Names: None.
Remarks: Nelson (2006) has combined four batoid families of very different morphological appearance - Rhinidae, Rhynchobatidae, Rhinobatidae, Rajidae - into a single order, the Rajiformes, following McEachran and Konstantinou (1996) and McEachran and Aschliman (2004), who considered two rhinid genera incertae sedis. Compagno (2005) placed Rhinidae and Rhynchobatidae in two suborders under Rajiformes. The order as currently restricted is composed of four families, more than 30 genera, and over 350 species. According to Aschliman et al. (2012) and Naylor et al. (2012), the Arhynchobatidae should be recognized as fifth family in this order. Three families occur in the North Atlantic.

Literature: McEachran and Konstantinou (1996); McEachran and Aschliman (2004); Compagno (2005); Nelson (2006); Aschliman et al. (2012); Naylor et al. (2012).

## Key to North Atlantic Families:

1a. Body rather shark-like, but gill slits on underside of head; with long, massive tail section bearing two large, widely separated dorsal fins and a large caudal fin; only head and body with pectoral and pelvic fins dorsoventrally flattened to form a rather narrow body disc. Snout wedge-shaped, with a broad, solid rostral cartilage to snout tip (Fig. 339)
family Rhinobatidae


Fig. 339 Rhinobatos
1b. Pectoral fins completely fused with sides of head and greatly flattened dorsoventrally to form a large disc. Tail distinctly marked off from body disc, slender rather and, if present, dorsal fin(s) and caudal fin very small to rudimentary (Fig. 340)

2a. Stiff rostral cartilage extended to snout tip; anterior pectoral-fin radials and their basal elements falling short of snout tip (can be checked by touch or against translucent light) (Fig. 340)
family Rajidae
2b. Flexible, delicate rostral cartilage extended to snout tip, or being incomplete to not reach rostral node in snout tip, or rostral cartilage largely or totally lacking; anterior pectoral-fin radials and their basal elements extended forward to close to, or being in touch with snout tip (can be checked by touch or against translucent light) (Fig. 341) . . . . family Arhynchobatidae


Fig. 340 Raja


After Whitehead et al. (1984)
Fig. 341 Bathyraja

### 3.3.1 Family RHINOBATIDAE

Family: Rhinobatidae Müller and Henle, 1837, Ber. K. preuss. Akad. wiss. Berlin, 2: 116. 1837, Arch. Naturg. 3: 399.
Type Genus: Rinobatos Linck, 1790.

## Number of Recognized North Atlantic Genera: 1.

FAO Names: En - Guitarfishes; Fr - Guitares; Sp - Guitarras.
Field Marks: Body rather shark-like, but gill slits on underside of head; with long, massive tail section not clearly marked off from body and bearing two large, separated dorsal fins and a large, unilobed caudal fin.

Diagnostic Features: Only head and body with pectoral and pelvic fins dorsoventrally flattened to form a rather narrow and short body disc. Snout wedge-shaped, with a broad, solid rostral cartilage to snout tip. Entire body and fins (like in sharks) densely covered with small placoid scales; dorsally, additional thornlets and thorns at orbits, between spiracles, on nape and shoulder and along midline of body and tail. Colour: above uniformly in shades of brown, with or without various light, dark or ocellar pattern components; underside usually white, but greyish fin margins and/or dark blotch on snout tip may occur.

Distribution: Tropical to warm temperate latitudes of all oceans, but not reported from the numerous islands of the Western Pacific.

Habitat: Guitarfishes are sluggish, bottom-living shark-like rays on sandy and muddy ground in shelf waters from inshore to about 110 m depth, also entering estuaries and freshwater.

Biology: Most species are yolk-sac viviparous, but some are suspected of being oviparous. Females produce litters of about 4 to 15 young once or twice a year. Guitarfishes feed on small fishes and all kinds of bottom-living invertebrates. They swim slowly over the bottom in shark-like mode by undulating their stout tails, rest often buried in the substrate.

Interest to Fisheries and Human Impact: Guitarfishes were locally and regionally rather abundant but have become overfished in many places. Their flesh is said to be of mediocre quality but was used by local people mostly dried salted. During recent years, guitarfishes were more intensively target fished, because Asian markets demanded their large dorsal fins. As a consequence and due mostly to a lack of management and conservation measures, many stocks have become much depleted.

Local names: None.
Remarks: Compagno (1999) introduced Glaucostegus as a subgenus of Rhinobatos without providing a rationale or specifying any diagnostic features. Furthermore, Compagno et al. (2005) elevated Glaucostegus to generic rank, again without specifying any rationale or specifying any diagnostic features. Since diagnostic characters are not available to distinguish these genera, both are kept here at the subgeneric level to avoid confusion.

Literature: McEachan and Capapé, Rhinobatidae, in: Whitehead et al. (1984); Compagno (1999); Compagno et al. (2005).

## Rhinobatos Linck, 1790

Genus: Rhinobatos Linck, 1790, Mag. Phys. Naturgesch. 6(3): 32.
Type Species: Raja rhinobatos Linnaeus, 1758 by absolute tautonomy.
Number of Recognized North Atlantic Species: 2.
Synonyms: None.
Diagnostic Features: See family above.
Remarks: This genus comprises about 45 species worldwide. The EU (2012) has prohibited the fishing for, retaining on board, transhipments or to land guitarfishes in and from throughout much of the ICES area (subareas I-XII).

## Key to North Atlantic Species:

1a. Rostral ridges widely separated throughout length, converging only a little at tip. Anterior nasal flap extended, reaching to level of inner corner of each nostril (Fig. 342).

Rhinobatos rhinobatos

1b. Rostral ridges very narrowly separated only. Anterior nasal flap not, or very little extended onto internasal space (Fig. 343). Mostly with a dark blotch on underside of snout.

Rhinobatos cemiculus


Fig. 342 Rhinobatos rhinobatos


Fig. 343 Rhinobatos cemiculus

## Rhinobatos (Glaucostegus) cemiculus Geoffroy Saint-Hilaire, 1817

Rhinobatus cemiculus E. Geoffroy Saint-Hilaire, 1817, Decr. Égypte, Poissons: pl. XXVII (Fig. 3); text description by I. Geoffroy Saint-Hilaire (1827), Decr. Égypte, Poissons, 1: 338. Holotype: MNHN No. 1966.

Synonyms: None
FAO Names: En - Blackchin guitarfish; Fr - Guitare de mer fouisseuse; Sp - Guitarra barbanegra.


Fig. 344 Rhinobatos (Glaucostegus) cemiculus
Field Marks: Shark-like appearance, with long, massive tail section bearing two large, widely separated dorsal fins and a large, oval caudal fin without marked lower lobe; only head and body with pectoral and pelvic fins dorsoventrally flattened to form a rather narrow body disc. Gill slits on underside of head. Brown above, white below but with blackish blotch on snout being more distinct in smaller specimens.

Diagnostic Features: Elongated snout wedge-shaped, with rostral ridges only narrowly separated, almost joining at snout tip. Anterior nasal lobes little extending inward, not reaching to inner corners of nostrils. Eye diameter 5.0 to 6.6 times eye and spiracle length combined, 3.0 to 3.7 times in preorbital snouth length. Spiracle with two well developed folds of about equal size. Thorns around inner margin of orbit, on shoulders and along midline of body and tail, only the latter distinct. Colour: brown above, without obvious markings, white below but with blackish blotch on snout which more distinct in smaller specimens.

Distribution: Eastern North Atlantic: West Africa from off Angola to off northern Portugal, and in the Mediterranean Sea.
Habitat: A moderately common guitarfish living on the bottom, partly buried into substrate, or slowly swimming over sandy and muddy bottom searching for prey. From shallow inshore brackish to marine waters to about 100 m depth in tropical and subtropical Eastern Atlantic.

Biology: Yolk-sac viviparous, with litters of 9 to 16 young being born a after gestation period of 4 to 6 months. This guitarfish may have one or two litters per year in some regions. Feeding on benthic invertebrates, mainly prawns, and small fish.

Size: Maximum length about 230 cm total length for females and 192 cm for males. Size at birth is about 34 cm total length.
Interest to Fisheries and Human Impact: The species is hardly found any more along the Iberian Peninsula. It has also disappeared in catches in the north-western Mediterranean but is still taken in good numbers along southern Mediterranean coasts. A reduction in the size of individuals and a strong decline in this species has been observed throughout its range off West Africa: e.g., off Senegal landings have decreased from $4,050 \mathrm{t}$ in 1998 to 821 t in 2005 (see Notarbartolo et al., 2007). Other specific catch data from along West Africa not available, but artisanal fisheries may take considerable numbers, as this species is easily taken in shallow waters by simple gear like handlines and bycatch in trawl fisheries for shrimps and prawns. Rhinobatos cemiculus appears to be the dominant species in batoid landings (up to 40\%) in several West African countries.

The flesh can be used for human consumption dried or salted, but more attractive are presumably the shark-like large dorsal and caudal fins.

The conservation status is Endangered.
Local Names: Schwarzkinn-Geigenrochen (Germany).

Remarks: Compagno (1999) revived Glaucostegus Bonaparte, 1846 from the synonymy of genus Rhinobatos as a subgenus of Rhinobatos without mentioning reasons and specifying diagnostic features. Compagno et al. (2005) elevated Glaucostegusto generic rank, again without mentioning reasons and specifying diagnostic features. As diagnostic characters thus not available to allow a proper key to these genera and users in the field the distinction between genera Rhinobatos and Glaucostegus, both were kept here at subgeneric status to avoid confusion.

Literature: McEachan and Capapé,


Fig. 345 Rhinobatos (Rhinobatos) cemiculus
$\square$ Known distribution

Rhinobatidae, in: Whitehead et al. (1984);
Compagno (1999); Compagno et al. (2005); Notarbartolo et al. (2007a).

## Rhinobatos (Rhinobatos) rhinobatos (Linnaeus, 1758)

Raja rhinobatos Linnaeus, 1758, Syst. Nat., ed. 10, 1: 232-233. No type material.
Synonyms: None.
FAO Names: En - Common guitarfish; Fr - Guitare de mer commune; $\mathbf{S p}$ - Guitarra común.


DORSAL VIEW

Fig. 346 Rhinobatos (Rhinobatos) rhinobatos


Field Marks: Shark-like appearance, with long, massive tail section bearing two large, widely separated dorsal fins and a large, oval caudal fin without marked lower lobe; only head and body with pectoral and pelvic fins dorsoventrally flattened to form a rather narrow body disc. Gill slits on underside of head. Khaki-brown above, underside white.

Diagnostic Features: Elongated snout wedge-shaped, with rostral ridges widely separated over their entire length, slightly converging only near snout tip. Anterior nasal lobes much extended inward to inner corners of nostrils. Eye diameter 4 to 5 times eye and spiracle length combined, 2.7 to 3.0 times in preorbital snouth length. Spiracle with two moderately large folds, of which the outer one more prominent. Small thorns around inner margin of orbit, on shoulders and along midline of body and tail. Colour: khaki-brown above, without obvious markings, underside white.

Distribution: Eastern North Atlantic: West Africa from off Angola to the southern Bay of Biscay, and in the Mediterranean Sea.

Habitat: A moderately common guitarfish living on the bottom, partly buried in the substrate, or slowly swimming over sandy and muddy bottoms searching for prey. Occurs from shallow inshore waters to about 180 m depth in the tropical and subtropical Eastern Atlantic.

Biology: Yolk-sac viviparous, with a gestation period of about four months, and with one or two litters per year of 4 to 10 young. Feeding on benthic invertebrates and small fish.

Size: Maximum total length about 140 to 160 cm . Males mature at about 75 cm and females at about 85 cm in length. Size at birth about 30 cm .

Interest to Fisheries and Human Impact: Rarely found nowadays along the Iberian Peninsula coast or in the Bay of Biscay; it also has disappeared from the north-western Mediterranean, but is still


Fig. 347 Rhinobatos (Rhinobatos) rhinobatos found in good numbers in the southern Mediterranean. Specific catch data from along the West African coast are not available, but it is probably not targeted in fisheries. However, artisanal fisheries may take considerable numbers, as this species is easily taken in shallow waters by simple gear like handlines, and as bycatch in shrimp-trawl fisheries. The flesh can be used for human consumption dried or salted, but more attractive presumably is the shark-like large dorsal and caudal fins for the fin market.

The conservation status is Endangered.
Local Names: Gewöhnlicher Geigenrochen (Germany); Viola (Portugal).
Remarks: This guitarfish is the type species of genus Rhinobatos Linnaeus, 1758. Compagno (1999) revived Glaucostegus Bonaparte, 1846 from the synonymy of genus Rhinobatos as a subgenus of Rhinobatos without giving any reasons and
specifying any diagnostic features. Later Compagno et al. (2005) also elevated Glaucostegus to generic rank, again without providing any reasons or specifying any diagnostic features. As diagnostic characters thus not available to allow a proper key to these genera and users in the field the distinction between genera Rhinobatos and Glaucostegus, both were kept here at subgeneric status to avoid confusion.

Literature: McEachan and Capapé, Rhinobatidae, in: Whitehead et al. (1984); Compagno (1999); Compagno et al. (2005); Notarbartolo et al. (2007b).

### 3.3.2 Family ARHYNCHOBATIDAE

Family: Subfamily Arhynchobatinae Fowler, 1934, Proc. Acad. Nat. Sci. Philad., 85: 240.
Type Genus: Arhynchobatis Waite, 1909.

## Number of Recognized North Atlantic Genera: 1.

FAO Names: En - Softnose skates.
Field Marks: Rostral cartilage flexible, delicate and extending to snout tip, or being incomplete to not reach rostral node in snout tip, or rostral cartilage largely or totally lacking; anterior pectoral fin radials and their basal elements extended forward to close to, or being in touch with snout tip. Snout skeleton characters can be checked by touch, or against strong light.

Diagnostic Features: The three species of the only genus Bathyraja occurring in the catalogue area grow to large size of about 200 cm total length and are heavy-bodied. Uncalcified, thin and flexible rostral cartilage continuous to snout tip, anteriormost pectoral radials and their basal elements extended almost to snout tip. Disc subrhombic, somewhat flabby and conspicuously massive. Snout moderately long, pointed and flexible. Tail solid, sharply marked off from disc, about as long as disc and gradually tapering to tip, with two small dorsal fins at rear and rudimentary upper caudal fin. Pelvic fins distinctly bilobed through deep incision in joint outer margin. Mature male claspers slender and very long to nearly first dorsal fin, with the glans short and only little widened; external glans clasper components relatively few and very similar for most species. Sharp, hooked male alar thorns permanently erect, not retractable into dermal pockets. Upper and lower disc may be totally covered by rough dermal denticles, or are partly or entirely smooth. Thorns on upper disc absent, only a median thorn row along tail, with or without thorns in interdorsal space. Colour: uniformly coloured above and below, only underside of disc may show irregular light blotches along midbody in dark-bellied species, or faint grey edging of disc and pelvic fins in light-bellied species.

Distribution: Worldwide in all oceans from continental shelves down the continental slopes to the deepsea abyssal plains. Absent in tropical shelf waters (Stehmann, 1986).

Habitat: Demersal from close inshore in cold temperate and boreal latitudes down the continental slopes and off far offshore islands and on submarine elevations to deepsea plains to more than $4,000 \mathrm{~m}$ depth.

Biology: Oviparous, with long embryonic development due to low temperatures of environment. Egg capsules rectangular, with two pairs of long horns at both ends. Some deepsea members of this genus are very long lived and do not mature until over 20 years in age. Diet includes various bottom living invertebrates and fishes.

Interest to Fisheries and Human Impact: Bathyraja skates are of medium to very large size ( 100 to 200 cm TL ) and rather abundant with many species on continental shelves and upper slopes primarily in two major centres of diversity, the North Pacific and Southwestern Atlantic, where they are targeted in intensive fisheries, or are a regular bycatch component in bottom trawl fisheries. Their stocks are partly in critical condition and require regulation of fishing effort. The majority of species are geographically widespread in deepwater, and these species are relatively safe still, but their population size is largely unknown. Intensified deepwater fisheries by bottom trawl and longlining may however eventually affect these deepwater skates.

Local names: None.
Remarks: Originally Group 1 (of 2) of the Rajoidei was established by McEachran and Miyake (1990), and later changed by McEachran et al. (1996) and by McEachran and Dunn (1998) to the subfamily Arhynchobatinae of the family Rajidae, such that the latter family finally was subdivided into the subfamilies Rajinae (with three tribes Amblyrajini, Gurgesiellini, Rajini) and Arhynchobatinae (with two tribes Arhynchobatini, Riorajini) of Rajidae. In parallel and later, Compagno (e.g. 1999, 2005) elevated in various taxonomic list appendices in books the subfamily Arhynchobatinae to family rank, but without providing any arguments or diagnosis, nor citing any specific references. Aschliman et al. (2012) and Naylor et al. (2012) have recently analysed the phylogenetic interrelationships within the Rajoidei and concluded, Arhynchobatidae is a monophyletic group and
a valid family comprising 11 genera. The genus Bathyraja of this family is the most diverse of all batoid fish genera, with more than 50 species described and named, plus a number of known but yet undescribed ones mainly in deep water.

Literature: Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Stehmann (1986); McEachran and Miyake (1990); McEachran et al. (1996); McEachran and Dunn (1998); Compagno (2005); Aschliman et al. (2012); Naylor et al. (2012).

## Bathyraja Ishiyama, 1958

Genus: Originally described by Ishiyama (1958) as subgenus of Breviraja Bigelow and Schroeder, 1948 - J. Shimonoseki Coll. Fish. 7 (2/3): 193-394; elevated to generic level by Ishiyama and Hubbs (1968) in context with a revision of genus Breviraja - Copeia 1968(2): 407-410.

Type Species: Raja isotrachys Günther, 1877 by original designation.
Number of Recognized North Atlantic Species: 3.
Synonyms: None.

## Diagnostic Features: See family.

Remarks: Globally more than 50 nominal valid species have been described and named, but with several additional mostly deepwater species remaining to be described; this genus is the most diverse of elasmobranchs. In the North Atlantic three species are known to occur.

## Key to North Atlantic Species:

1a. Underside ground colour as dark as upper side. Interdorsal thorns absent (Fig. 348)

Bathyraja richardsoni
1b. Upper and lower surfaces different in colour. Interdorsal thorns present (Fig. 349 \& 350) 2

2a. Upper side medium grey and almost completely covered with coarse dermal denticles, underside white with at most greyish margin to disc. Midrow on tail with 21 to 26 thorns (Fig. 349)

## Bathyraja spinicauda

2b. Upper side pale greyish-white and nearly devoid of dermal denticles, underside pale brown with a few light blotches. Midrow on tail with 16 to 21 thorns (Fig. 350).

Bathyraja pallida


Fig. 349 Bathyraja spinicauda


Fig. 348 Bathyraja richardsoni


Fig. 350 Bathyraja pallida

## Bathyraja pallida (Forster, 1967)

Breviraja pallida Forster, 1967, J. Mar. Biol. Ass. U.K., 47: 281-286. Holotype BMNH 1967.2.13.1; Paratype BMNH 1967.2.13.2.

Synonyms: None.
FAO Names: En - Pale ray.


Field Marks: No thorns on upper disc (except for alar thorn patches of mature males), only a median row of 16 to 21 blunt thorns along tail to first dorsal fin, and a thorn between dorsal fins. Upper and lower surfaces largely smooth. Upper side greyish to pale white, underside brown with irregular white patches along midbody.

Diagnostic Features: Adults with heavy body, trunk thick and massive. Disc subrhombic, with angular outer corners; front margins more (mature males) or less undulated; snout moderately long and pointed (angle about $80^{\circ}$ ), soft and flexible vertically. Tail shorter than body, gradually tapering to tip, with two small and separated dorsal fins at rear. Upper disc largely smooth, a patch of dermal denticles only halfway along anterior margin; tail prickly from its origin. Underside also largely smooth, with only loosely scattered dermal denticles on tail. Except for alar thorn patches across wing tips of mature males, no thorns on upper disc, only median row of 16 to 21 blunt thorns along tail to first dorsal fin, and usually a thorn between dorsal fins. Upper jaw tooth rows 25 to 31. Colour: upper surface greyish to pale white, underside brown, with irregular light blotches along midline of body.


SQUAMATION

Fig. 351 Bathyraja pallida

Distribution: Eastern North Atlantic: two type specimens found in deep water from the northern Bay of Biscay; only eight specimens have been taken since the original description, but no descriptive details published, except for one adult male from the Mid Atlantic Ridge at 2,568 $m$ depth (Orlov et al., 2006). Recently, Johnston et al. (2010) reported on five more specimens taken by Irish deepwater surveys in 2007 and 2008 in the deep Porcupine Seabight, but no further data and details were specified. The overall geographical range of the species is unclear, and it may eventually be found from further to the west and south of its current documented range.

Habitat: Benthic to semipelagic in deep water along lower continental slopes and on adjacent deepsea abyssal plains between about 1,879 and $2,950 \mathrm{~m}$ depth.

Biology: Oviparous, with embryos and young so far unknown; a half-formed intra-uterine egg-capsule was described by Stehmann and Merrett (2001). Size of egg capsules about 30 by 12 to 15 cm (excluding the horns). The large adults in deepwater are supposed to be rather active hunter for large prey such as fish and squids. The remains of the deepwater squid Todarodes sagittatus were found in stomach of a large female. Juveniles feed on polychaete worms, amphipods, isopods and
 copepods (Gordon and Duncan 1989).

Size: Attains at least about 160 cm total length (the first three specimens reported by Forster, 1967 and 1968).
Interest to Fisheries and Human Impact: As a deepwater species living at depths greater than current commercial deepwater fisheries operate, this skate is mainly taken as bycatch by deepwater trawlers and bottom longliners. Its wide distribution in deepwater may prevent much impact by fisheries, however the total population may not be very large, and recruitment and survival rate of the young may be rather low.

The conservation status is Least Concern.
Local Names: Heller Tiefenrochen (Germany).

Remarks: A little known, very rare deepwater skate, occasionally taken as bycatch in commercial fisheries, but not usually reported. Commercial vessels could greatly support future research, if they were to keep deep frozen at least small and half-grown specimens and forward these with precise locality data to national fishery institutes or Natural History Museums for further study.


Fig. 352 Bathyraja pallida
$\square$ Known distribution $\square$ Possible distribution

Literature: Forster (1967, 1968); Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Gordon and Duncan (1989); Stehmann and Merrett (2001); Orlov et al. (2006); Orlov (2007); Johnston et al. (2010).

Bathyraja richardsoni (Garrick, 1961)
Raja richardsoni Garrick, 1961, Trans. R. Soc. N.Z., 88(4): 743-748. Holotype V.U.W. 1898 (Cook Strait, New Zealand).

## Synonyms: None.

FAO Names: En - Richardson's ray; Fr - Raie de Richardson; Sp - Raya de Richardson.


Fig. 353 Bathyraja richardsoni

Field Marks: No thorns on upper disc (except for alar thorn patches of mature males), only a median row of 15 to 20 blunt thorns along tail to first dorsal fin, no thorns between close-set dorsal fins. Upper surface almost entirely set with coarse dermal denticles. Upper side usually dark brown-greyish, but intensity may vary; underside similar but always with irregular whitish markings along midbody, in pelvic region and on tail.

Diagnostic Features: Adults with heavy body, trunk thick and massive. Disc subrhombic; snout moderately long and pointed (angle about $90^{\circ}$ from larger juveniles onward), soft and flexible vertically; front margins distinctly undulated, outer corners angular. Tail shorter than body from larger juveniles onward, gradually tapering to tip, with two small, close-set dorsal fins at rear. Upper surface almost entirely set with dermal denticles, underside prickly to varying degrees, but dermal denticles mostly present on snout, body, abdomen and tail. Except for alar thorn patches across wing tips of mature males, no thorns on upper disc, only a median row of 15 to 20 blunt thorns along tail to first dorsal fin, and no thorn between close-set dorsal fins. Upper jaw tooth rows 21 to 39 . Colour: upper side usually dark brown-greyish, but intensity may vary; underside similar but always with irregular whitish markings along midbody, on pelvic region and tail.

Distribution: Eastern North Atlantic: Rockall Trough, west of Scotland and Ireland, northern Bay of Biscay. Western North Atlantic: off Labrador and Newfoundland. Recently a large number ( $n=151$ ) of specimens of this species were taken along the northern Mid-Atlantic Ridge (Orlov et al. 2006, details of 14 specimens). Interestingly, the holotype, a female, was taken from the Cook Strait, New Zealand, at $1,370 \mathrm{~m}$ depth. This species is unique among skates in having a very wide but patchy distribution.

Habitat: Benthic to benthopelagic in deepwater along lower continental slopes, on adjacent deep-sea abyssal plains and along submarine rises between mostly 1,370 and $2,550 \mathrm{~m}$ depth. Specimens in Western North Atlantic were found at 650 to $2,270 \mathrm{~m}$ on the Mid Atlantic Ridge at 526 to 2,951 m, and in Eastern North Atlantic at 1,219 to 2.542 m depth (Orlov et al. 2006).

Biology: Oviparous, with the first eggcapsules and embryos described by Stehmann and Merrett (2001); egg


Fig. 354 Bathyraja richardsoni
Known distribution capsules 20 to 21 cm length by 11 to 12 cm width (excluding the horns). Neonates have been found along the deep slope of the northern Bay of Biscay and within Rockall Trough (M. Stehmann, unpubl.), as well as on Mid Atlantic Ridge (Orlov et al., 2006). The large adults in deepwater are supposed to be rather active hunters for large prey as fishes and squids. A small amount of shrimps have also been observed in the stomachs (Templeman, 1973b).

Size: Attains at least 175 cm total length. Size at hatching is from 18.2 to 24.5 cm total length.
Interest to Fisheries and Human Impact: As a deepwater species, this skate will mainly be taken singly or in small numbers as a bycatch of deepwater trawlers and bottom longliners. Its very wide distribution in deep water may prevent much impact by fisheries, however the total population size and population dynamics are unknown. The proportion of catches that are retained for human consumption or discarded is largely unknown.

Conservation status is Least Concern.
Local Names: Richardsons Tiefenrochen (Germany).
Remarks: Johnston et al. (2010) reported from Irish deepwater surveys in the Porcupine Seabight three specimens in 2007, and another three in 2008, but total length, sex and depth were not specified. A United States expedition in 1986 near the Canary Islands caught specimens in very deepwater, which were preserved and deposited at AMNH New York; some of these typically dark coloured specimens, once surfaced, turned their colour to pale whitish even prior to preservation in formalin, and most did so after preservation (Norma F. Feinberg, formerly AMNH New York and member of the expedition team, pers. comm.). This observed peculiarity may lead to misidentification as Bathyraja pallida As very little is known of this rare
deepwater skate, commercial bycatches should be reported as species specific; also can commercial vessels help support research efforts, if they keep deep frozen at least small and half-grown specimens and forward these with precise locality data to national fishery institutes or Natural History Museums

Literature: Forster (1965, 1967); Templeman (1973a, b); Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Gordon and Duncan (1989); Stehmann and Merrett (2001); Orlov et al. (2006); Kulka, Orlov and Baker (2007); Johnston et al. (2010).

## Bathyraja spinicauda (Jensen, 1914)

Raja spinicauda Jensen, 1914, Mindeskr. Japetus Steenstrup Føds., 2(30): 30-32. Two syntype females ZMUC 352, 353 (Davis Strait).

Synonyms: None.
FAO Names: En - Spinetail ray; Fr - Raie à queue épineuse.


Fig. 355 Bathyraja spinicauda

Field Marks: No thorns on upper disc (except for alar thorn patches of mature males), only a median row of variably 12 to 29 (mean 21) blunt thorns along tail to first dorsal fin, and a thorn between dorsal fins. Upper surface entirely covered with coarse dermal denticles. Upper surfaces medium to light grey; underside white but with a more or less distinct grey margin from wing tips along posterior margin to axils of pectoral fins, as well as along outer margin of posterior pelvic-fin lobes, and grey blotches on root of tail.

Diagnostic Features: Adults with heavy body, trunk thick and massive. Snout moderately long and pointed, soft and flexible vertically. Front margins of subrhombic disc almost straight to weakly undulated, outer corners angular. Tail relatively short, with two small, usually separated dorsal fins at rear. Upper surface densely set with coarse dermal denticle; underside nearly smooth, only on tail may loosely scattered dermal denticles occur. Except for alar thorn patches across wing tips of mature males, no thorns on upper disc, only median row of mostly 21 to 26 blunt thorns along tail to first dorsal fin, and a thorn between dorsal fins. Colour: upper surfaces medium to light grey; underside white but with a more or less distinct grey margin from wing tips along posterior margin to axils of pectoral fins, as well as along outer margin of posterior pelvic-fin lobes, and grey blotches on root of tail.

Distribution: Eastern North Atlantic: Barents Sea and along East Greenland southward along Norway, around Iceland and along Iceland-Faroe-Shetland Ridge into Rockall Trough. Western North Atlantic: West Greenland across the Davis Strait to off Labrador, Newfoundland and southward to about George's Bank. Southern Indian Ocean records from near the Kerguelen Islands appear to be misidentification of another congener and require confirmation (Kulka et al., 2006).

Habitat: A moderately common benthic skate in Arctic and boreal latitudes in about 140 to 800 m depth in the Eastern North Atlantic, but to $1,650 \mathrm{~m}$ depth in the Western North Atlantic. Occurs along continental shelves down the slopes in deepwater with temperatures below $7.5^{\circ} \mathrm{C}$ (Kulka et al., 2007).

Biology: Oviparous, with large egg capsules measuring about 130 by 90 mm , excluding the horns. Egg cases are deposited on the bottom by females probably in summer, with embryonic


Fig. 356 Bathyraja spinicauda
Known distribution development taking an estimated 12 months, but may last longer in the Barents Sea from 3.5 to 4 years where the water temperature is from 0 to $5^{\circ} \mathrm{C}$ (Berestovskii 1994). Feeds on a variety of bottom dwelling invertebrates and fishes; juveniles mainly feed on invertebrates, while larger adult specimens feed primarily on fish.

Size: Attains a maximum length of about 170 to 180 cm . Size at hatching is about 21 cm total length.
Interest to Fisheries and Human Impact: A regular bycatch in bottom trawl and bottom longline fisheries at high latitudes in the North Atlantic. Large specimens are landed in small numbers.

The conservation status is Near Threatened globally, but is considered Vulnerable in the Western North Atlantic and Least Concern in the Eastern North Atlantic.

Local Names: Gråskate (Norway); Maríuskata (Iceland); Tornhalet rokke (Denmark and Greenland); DornschwanzTiefenrochen (Germany).

Literature: Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Berestovskii (1994); Kulka et al. (2006).

### 3.3.3 Family RAJIDAE

Family: Genus or Family Raia Blainville, 1816, Bull. Sci. Soc. Philomat. Paris, (8).
Type Genus: Raja Linnaeus, 1758.

## Number of Recognized North Atlantic Genera: 8.

FAO Names: En - Hardnose skates.
Field Marks: Rostral cartilage solid and stiff to snout tip, anterior pectoral-fin radials and their basal elements distinctly falling short of snout tip. Snout skeleton characters can be checked by touch, or against strong light.

Diagnostic Features: Species of the eight genera represented in the catalogue area range from pygmy size (to about 35 cm maximum total length) to very large size of more than 200 cm total length. Disc shape from almost circular to subrhombic or subquadrate, with snout very short and bluntly angled to very long and pointed. Tail solid, sharply marked off from disc, somewhat shorter than, about as long as, or a little longer than disc and gradually tapering to tip, with two small dorsal fins at rear and rudimentary upper caudal fin. Pelvic fins distinctly bilobed through deep incision in joint outer margin. Mature male claspers from very long to nearly first dorsal fin to rather short, about as long as one third tail length, and solid, with the glans elongated to at least one third of clasper length and widened; external glans clasper components relatively many and of characteristic, complex composition in each genus. Sharp, hooked male alar thorns not permanently erect, but retractable into dermal pockets. Upper and lower disc may be totally covered by rough dermal denticles, or are partly or entirely smooth. Thorns on upper disc always present, at least in juveniles, and arranged typically in pattern of orbital, nuchal, scapular and middorsal thorns along trunk and tail in at least one median row, but mostly also parallel thorns rows do occur and often lateral thorns along tail. Interdorsal thorns present or absent. Colour: ground colour and pattern very variable; shelf species mostly white-bellied and lively ornamented on upper disc with ground colour in shades of brown, light and dark dots and blotches in various arrangements, also with permanent eyespots in some species; deepwater species usually plain coloured dark or light above, underside white with dark edging and blotching, or dark with white markings, or totally dark.

Distribution: Worldwide in all oceans from inshore on shelf down the slopes to deepsea plains, also at distant offshore islands and on submarine elevations. Absent in shallow tropical shelf waters, but present in Arctic and Antarctic waters.

Habitat: Demersal from inner shelf from boreal and cold temperate to subtropical latitudes down the slopes of continents and far offshore islands and on submarine elevations to deepsea plains to more than $4,000 \mathrm{~m}$ depth. Larger deepwater species may be benthopelagic.

Biology: Oviparous, with embryonic development at least of a few months to possibly years depending on temperatures of environment. Egg capsule mostly rectangular, with two pairs of short or long horns at both ends. Feeds on all kinds of bottom living invertebrates and fishes.

Interest to Fisheries and Human Impact: Rajid skates have been abundant on continental shelves and upper slopes and have traditionally been fished for in European waters, where they are the subject of targeted fisheries and may be intensively fished in some areas, or are a regular bycatch component in bottom trawl fisheries. After World War II, fishing for and the utilization of skate wings for human consumption extended to other coastal areas around the world not only by coastal fisheries but also by development of long distance factory-freezer bottom trawl fisheries. Stocks for several North Atlantic species are considered overfished, and some large-bodied species extirpated from former range. Fisheries are now better regulated and some species cannot be landed in European waters. The deepwater species are often geographically widespread, and these species are still relatively safe, but their population size is largely unknown. Intensified deepwater fisheries by bottom trawl and longlining may however eventually affect the population of these deepwater skates.

Local names: Rays and skates in numerous, more or less specific combinations.
Remarks: Originally all skates were grouped in the family Rajidae with just one genus, Raja for all species, but over the past couple decades there have been considerable taxonomic changes. Other batoid families were split off, and remaining Rajidae were subdivided into several genera and subgenera of Raja. Most of these subgenera of Raja and other genera finally were elevated to generic rank by McEachran \& Dunn (1998). Presently, the family comprises 26 genera and nearly 250 species. Eight genera and at least 36 species occur in the North Atlantic.

Literature: Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); McEachran and Dunn (1998).

## Key to North Atlantic Genera:

1a. Snout very long and pointed, anterior disc margins deeply concave; a theoretical line from snout tip to pectoral wing tip not touching front margin of disc; internasal width usually less than $70 \%$ of the distance from one nostril to snout tip; thorns on disc usually absent, except for head thorns in small juveniles and alar thorns of mature males (Fig. 357).

1b. Snout moderately long to short, anterior disc margins somewhat convex, slightly concave or undulated; a theoretical line from snout tip to pectoral wing tip touching or cutting front margin of disc; internasal width usually more than $70 \%$ of the distance from one nostril to snout tip; thorns always present on disc, at least on head (Fig. 358)

2a. Underside of disc more or less dark, with mucus and sensory pores marked as black dots and/or dashes; sometimes hard to see in very dark-bellied species or under black mucus coverage, but pores also marked black on upper side and well visible on nape and snout (Fig. 359) . Dipturus

2b. Underside of disc white, with a broad blackish to grey margin around disc and pelvic fins; mucus and sensory pores not marked black (Fig. 360)

Rostroraja

3a. Upper disc and tail with dense coverage of fine or even velvet-like dermal denticles; underside of tail at least edged with, or totally covered with dermal denticles. Typically, median row thorns on tail dwindling in size rearward and totally disappearing in posterior third of tail length among dense dermal denticles a fair distance in front of first dorsal fin (Fig. 361 \& 362)

3b. Upper side of disc and tail totally or partly covered with coarse, less densely set dermal denticles; underside of tail usually smooth. Median row thorns on tail may show somewhat reduced size rearward, but are always set continuously to origin of first dorsal fin

4a. Pygmy size skates growing to maximum of 30 to 35 cm total length (very apparent by mature males of such small size), with tail distinctly longer than body (about $60 \%$ total length). Disc shape subrhombic to subcircular, with anterior margins strongly undulated in mature males. Snout short and bluntly angled (Fig. 361)

Neoraja


Fig. 357 Dipturus


Fig. 358 Leucoraja


Fig. 359 Dipturus
 black

Fig. 360 Rostroraja


Fig. 361 Neoraja

4b. Maximum size larger, to about 70 cm total length, males mature from about 50 cm total length on; tail length shorter, nearly equal to, or only little longer than body (less than $60 \%$ total length). Disc typically inverse heart-shaped, and anterior margins at most weakly undulated in mature males. Snout pointed and moderately elongated (Fig. 362) . . . . Malacoraja

5a. Disc shape subquadrate to subrhombic, outer corners angular. Tail length equal to, or somewhat shorter than body. Thorns on head set individually at orbits, on nape and shoulders; median row of distinct thorns from nape to first dorsal fin always present, may only be incomplete, or interrupted on back of trunk in large specimens, particularly in mature males (Fig. 363 \& 364)

5b. Disc shape subrhombic to subcircular, outer corners mostly rounded. Tail length equal to, but usually somewhat longer than body. Except in small juveniles, thorns on orbital rims set as continuous half-rings, and many thorns over nape and shoulder regions forming a triangle; median thorn row on trunk and tail either reduced or totally disappearing with growth, when parallel rows of large thorns become dominant, or median thorns persisting and flanked at least on tail by large parallel row thorns (Fig. 365). $\qquad$ 7

6a. Tail solid and shorter than body. Thorns conspicuously large, with high basal cones distinctly ribbed and on radiated basal plate (Fig. 363). Claspers of mature males massive, with club-shaped, widened glans

Amblyraja

6b. Tail more slender, its length equal to, or somewhat longer than body. Thorns not conspicuously large, of regular size, with smooth basal cones and usually long, recurved tip. Claspers of mature males rod-shaped, the glans not much widened and tapering to narrow tip (Fig. 364)

Raja

7a. Disc subcircular, with outer corners broadly rounded; snout short and bluntly angled (except for L. fullonica). Median row thorns on back of trunk and along tail becoming gradually reduced with growth to completely disappear in large adults, when simultaneously parallel row thorns grow larger and remain persistent (Fig. 365)

Leucoraja

7b. Disc subcircular (rarely) to subrhombic, with outer corners rounded to angular; snout either short and bluntly angled, or moderately elongated and pointed. Median row thorns on back of trunk and along tail persisting, but two or more parallel rows may become dominant with growth (Fig. 366)

Rajella


Fig. 362 Malacoraja


Fig. 363 Amblyraja


Fig. 364 Raja


Fig. 365 Leucoraja


Fig. 366 Rajella

## Amblyraja Malm, 1877

Genus: Amblyraja Malm, 1877, Göteborgs och Bohusläns Fauna: 607-608.
Type Species: Raja radiata Donovan, 1808 by subsequent designation of Jordan (1919).

## Number of Recognized North Atlantic Species: 3 .

Synonyms: Raja (Amblyraja), subgenus (Stehmann, 1970).
Field Marks: See Key to Genus above.
Diagnostic Features: Disc shape subquadrate to subrhombic, outer corners angular. Tail rather massive and somewhat shorter than body. Thorns on head set individually at orbits, on nape and shoulders; median row of relatively few conspicuously large thorns from nape to first dorsal fin always present; all thorns and thornlets with typically ribbed basal cone. Claspers of mature males massive, with club-shaped, widened glans. Colour: above plain medium to dark brown or greyish-brown, without patterning or with obscure dark blotching or with rather lively pattern of dark and light blotches and spots, but also plain whitish. Underside white, but in deepwater species only in young which become with growth increasingly dark blotched and finally almost totally dark, with only few white markings remaining along midbody.

Remarks: The genus comprises about 10 nominal species circumglobally, but the validity of some in deepwater is not finally clarified. Three species are recognized as occurring in the North Atlantic.

## Key to North Atlantic Species:

1a. Jaw teeth set in 52 to 66 largely parallel rows. Upper side dark grey to brown, but specimens of all sizes also found plain whitish; underside white with large dark markings only in young, larger specimens increasingly dark blotched to become nearly totally dark in adults with only few white markings left at mouth and along midbelly . . . . . . . . Amblyraja jenseni

1b. Less than 50 tooth rows. Colour above and below either similar to and developing with growth like in $\boldsymbol{A}$. jenseni, or upper side lively patterned and underside white

2a. Only 13 to 17 conspicuously large thorns in median row from anterior trunk to first dorsal fin. Entire upper disc very rough through the large thorns, many thornlets scattered over snout, pectoral wings and posterior pelvic-fin lobes, and coarse dermal denticles over most of disc and tail. Medium greyish-brown above, clouded with darker and few pale white blotches, also often with blackish dots arranged as rosettes; underside white, occasionally with small dark blotches and greyish disc margins (Fig. 367) . . Amblyraja radiata

2b. Median row of 25 to 32 thorns from anterior trunk to first dorsal fin. Upper disc rough through more or less loosely scattered thornlets and coarse dermal denticles, but less intensive as compared with A. radiata. Above dark grey or brown, occasionally with indistinct light spots and dark blotches; underside largely white only in juveniles, whereas dark blotches and speckling along midbody and along disc margins increasing with age and size to become predominantly dark on underside but with large white markings remaining on head, along midbody, longitudinally across pectoral fins, around cloaca and across pelvic fins (Fig. 368).


Fig. 367 Amblyraja radiata


Fig. 368 Amblyraja hyperborea

## Amblyraja hyperborea (Collett, 1879)

Raja hyperborea Collett, 1879, Forh. VidenskSelsk. Krist. 1878 (publ. 1879), 14: 7-12. Holotype ZMO 13134.
Synonyms: Raja (Amblyraja) hyperborea, subgenus (Stehmann, 1970)
FAO Names: En - Arctic skate; Fr - Raie arctique; Sp - Raya ártica.


Fig. 369 Amblyraja hyperborea

Field Marks: Disc subrhombic, with angular outer corners; tail short and solid. Snout short, bluntly angled, and stiff through stiff rostrum to snout tip. Thorns distinct, their bases typically ribbed and with stellate margin, as well as those of thornlets; entire upper disc rough through thorns, many thornlets scattered over snout and pectoral wings and coarse dermal denticles over most of disc and tail. Single thorns at orbits, on midline of nape and shoulder girdle, on shoulders, and a median, regular row of 25 to 32 (may be more in NW Atlantic) distinct thorns from anterior trunk to first dorsal fin; 0 to 2 thorns between dorsal fins depending on space of their separation. Underside smooth. Colour above dark grey or brown, occasionally with indistinct light spots and dark blotches; underside largely white only in juveniles, whereas dark speckling along midbody and along disc margins increasing with age and size with underside becoming predominantly dark.

Diagnostic Features: Body disc of large specimens thick and somewhat flabby. Disc subrhombic, with anterior margins strongly undulated in mature males, and angular outer corners; tail short and solid, with two small dorsal fins separated, or rarely confluent, at rear. Snout short, bluntly angled, and vertically not flexible due to stiff rostrum to snout tip. Upper thorns distinct, set in largely constant pattern of separate orbital and supraspiracular thorns, a single one each on midnape and mid-shoulder, 2 to 3 on each shoulder, and a very regular median row of 25 to 32 (may be more in NW Atlantic) thorns from anterior trunk to first dorsal fin; 0 to 2 thorns between dorsal fins, if these separated. All upper thorns large, their bases typically ribbed and with stellate margin, as well as those of thornlets; entire upper disc rough through large thorns, many thornlets scattered over snout and pectoral wings and coarse dermal denticles over most of disc and tail, but large specimens with almost bare centres of pectoral wings and bare sides of trunk; larger specimens may show rows of thornlets from anterior trunk onto anterior tail along each side of median thorn row; underside smooth. Tooth rows in upper jaw 35 to 48 , teeth of larger specimens long and pointed and set in parallel rows. Colour: above dark grey or brown, occasionally with indistinct light spots and dark blotches; underside largely white only in juveniles, whereas dark speckling along midbody and along disc margins increasing with age and size, so that underside becomes predominantly dark.

Distribution: North Atlantic: Arctic and subarctic waters of the North Atlantic, and southwards in the Eastern North Atlantic to the Faroe-Shetland-Scotland Ridge and occasionally in the northern Rockall Trough, and across to northern coast of Norway. Western North Atlantic along both sides of Greenland and across the Davis Strait to off Labrador, Newfoundland and the Grand Banks where it is rare. For extralimital records, see Remarks section below.

Habitat: A moderately common benthic and benthopelagic skate on and over various bottom substrates from the coastal waters in the high Arctic and somewhat deeper at Arctic and boreal latitudes down the slopes and on submarine elevations from 300 to $1,500 \mathrm{~m}$ depth (single records down to about $2,500 \mathrm{~m}$ ); largely restricted to Arctic water masses in temperatures from -1 to $+1.5^{\circ} \mathrm{C}$, but usually less than $+4^{\circ} \mathrm{C}$.

Biology: Oviparous, with egg capsules measuring 81 to 125 by 54 to 77 mm , excluding the horns; egg case size varies
 with size of the female, as well as number of capsules laid. Unlike its congener Amblyraja radiata, the surfaces of its egg case are not roughened by stiff fibres but are rather smooth in texture. Embryonic development may take many months in cold Arctic waters. Depending on its size, this skate feeds on a variety of benthic animals, including Arctic prawns, crabs and cephalopods, pelagic amphipods, with larger specimens also feeding on small Arctic bottom fish.

Size: Maximum length is about 100 cm , but specimens over 85 cm are rare and are usually found in deeper colder water. Females grow to a slightly larger size than males. The size at birth is about 16 to 18 cm total length.

Interest to Fisheries and Human Impact: Taken as bycatch in deepwater bottom trawls and by longlining, but they are mostly discarded, except for large specimens that may be landed. Due to its deepwater habitat in Arctic latitudes and under surface ice cover, fishery impact on this skate is limited. Dolgov et al. (2005a, b) reported the Arctic Skate as being the second most abundant species ( $3 \%$ in number in surveys and commercial bycatch) in the Barents Sea, but it also occurs regularly along the coasts of northern Norway and in the Norwegian Deep (Williams, 2008).

The conservation status of this skate is Least Concern.
Local Names: Arktischer Rochen, Eisrochen (Germany); Isskate (Norway); Skjótta skata (Iceland); Arktisk rokke (Denmark and Greenland).

Remarks: Various species of Amblyraja hyperborea-like habitus have been described from deepwater, Arctic and subantarctic latitudes from all oceans (badia, frerichsi, georgiana and a yet unidentified deepwater congener from around South Georgia, jenseni, reversa, robertsi, taaf). Stehmann (unpubl. data) collected over many years relevant information about all these nominal species, investigated type specimens, obtained radiographs, studied (if available) clasper morphology
and skeleton, and did dissections of scapulocoracoids in various museum collections. Stehmann presented preliminary results in an oral presentation at the 3rd Indo-Pacific Fish Conference 1989 in Wellington, New Zealand, where he demonstrated that significant species-specific differences between all these nominal species do not exist beyond what can be considered a (rather narrow) natural range of variation. Hence, there is strong indication, that A. hyperborea (as the oldest valid name) may well have a worldwide distribution in deep, cold waters. Last and Stevens (1994, 2009) and Kulka et al. (2007) have accepted Stehmann's hypothesis, in that they assigned specimens from deepwater off southern Australia and around New Zealand to A. hyperborea. However, genetic studies are still lacking to back, or disprove this conclusion, and adequate genetic samples will be very difficult to get from most of these very rare deepwater species.

Literature: Stehmann and Bürkel, Rajidae, in: Whitehead et al., (1984); Last and Stevens (1994, 2009); Dolgov et al. (2005a, b); Kulka et al. (2007); Williams (2008); Shark Trust (2009).

## Amblyraja jenseni (Bigelow and Schroeder, 1950)

Rajajenseni Bigelow and Schroeder, 1950, Bull. Mus. Comp. Zool. Harv., 103(7): 385-387, pl. 1. Holotype female USNM 35592.
Synonyms: None
FAO Names: En - Shortail skate; Fr - Raie à queue courte.


Fig. 371 Amblyraja jenseni

Field Marks: Disc subrhombic, outer corners angular, snout short, narrowly angled, and stiff through solid rostrum to snout tip; tail shorter than body. Thorns distinct, their base typically ribbed and with stellate margin; upper disc almost completely covered by coarse dermal denticles. A median, regular row of 20 to 31 distinct thorns from anterior trunk to first dorsal fin, no thorns in narrow interdorsal space. Externally, both Amblyraja hyperborea and $A$. jenseni are very closely related species and are very difficult to distinguish, and indeed the species-specific feature of $A$. jensenii is its much higher count of 52 to 66 tooth rows (vs 35 to 48 in A. hyperborea) - hence, one has to take a look in the mouth! Colour very variable, in general much alike A. hyperborea by being above dark grey or brown; however, young and also large specimens have been found being almost plain light brown to greyish-white above; this holds also true for underside colour, but mostly do dark markings exist around cloaca and on anterior pelvic fins, again like in A. hyperborea, and these markings tend to expand with growth and age over abdomen, and disc margins mostly darker.

Diagnostic Features: Body disc of large specimens thick and somewhat flabby. Disc subrhombic, with anterior margins strongly undulated in mature males, and angular outer corners; snout short, narrowly angled ( 85 to $103^{\circ}$ ), and stiff through solid rostrum to snout tip; tail short and solid rather, with two small, mostly close-set dorsal fins at rear. Upper disc almost completely covered by coarse dermal denticles, except for broadly smooth posterior disc and posterior pelvic fin margins and probably bare pectoral centres in adults. Thorns distinct and set in largely constant pattern, their base typically ribbed and with stellate margin, as well as those of thornlets; individual thorns in pre-and post-orbital and in supraspiracular position, a median nuchal and suprascapular one, respectively, 2 to 4 on each shoulder and 20 to 31 in regular median row from anterior trunk to first dorsal fin, and no thorn in narrow interdorsal space. Unlike Amblyraja hyperborea, less to no thornlets on snout (reduced with growth), on anterior disc margins and on pectoral wings, and no rows of thornlets along sides of trunk and onto anterior tail on either side of median thorn row. Many more, 52 to 66 tooth rows than A. hyperborea ( 35 to 48 only); teeth set in parallel rows, pointed in both sexes. Colour: rather variable, may depend on size and age and/or kind of bottom substrate, but in general very much alike $A$. hyperborea by being above dark grey or brown, but rarely showing indistinct light spots and dark blotches on disc and pelvic fins; but young and also large specimens have been found being almost plain light brown to greyish-white above; this holds also true for underside colour, but mostly do dark markings exist around cloaca and on anterior pelvic fins, again like in A. hyperborea, and these markings tend to expand with growth and age over abdomen and pectoral wings, but disc margins mostly darker, and nearly plain dark specimens do occur with only few white markings at mouth-nasal region and along midbody.

Distribution: Originally described from Western North Atlantic, where it occurs from off southern New England to Labrador, specimens have since been found also along northern Mid-Atlantic Ridge (Orlov et al. 2006) and in deep water along West Greenland, in Denmark Strait, around Iceland (Jónsson and Pálsson, 2006), and within Rockall Trough west of Scotland and in Porcupine Seabight west of Ireland.

Habitat: A moderately common species in deepwater in the northern Western North Atlantic, this benthic and benthopelagic skate is usually found over various bottom substrates in Arctic and boreal latitudes. It prefers a temperature range from 3.6 to $3.9^{\circ} \mathrm{C}$ and a depth range from 167 to $2,311 \mathrm{~m}$ in the Western North Atlantic, from 960 to 2,548 m along the Mid Atlantic Ridge, and in the northern Eastern North Atlantic from 1,800 to $2,190 \mathrm{~m}$ (Orlov et al. 2006).

Biology: Oviparous, egg capsules 123 by 76 mm (without horns, Kulka unpubl.) similar to but larger than those of


Fig. 372 Amblyraja jenseni
$\square$ Known distribution A. hyperborea Embryonic development also probably takes many months or possibly years in boreal and Arctic waters. Depending on size, this skate feeding on various kinds of benthic animals such as shrimps, crabs, cephalopods and small fishes.

Size: Maximum total length is 112 cm , but the maximum observed size differs by area and depth, with the largest specimens (up to 112 cm ) found in the Western North Atlantic and along the Mid-Atlantic-Ridge.

Interest to Fisheries and Human Impact: Taken occasionally as bycatch in deepwater bottom trawls and by longlines, but usually discarded; large specimens on occasion may be landed. Due to its deepwater habitat in high boreal and Arctic latitudes, impacts from fisheries are limited.

The conservation status is Least Concern.
Remarks: See remarks under Amblyraja hyperborea Johnston et al. (2010) reported four new records of this species in 2007 from the Irish deepwater surveys in the Porcupine Seabight and on another five specimens in 2008, but no information on the length, sex, or depth were specified.

Local Names: Jensensskata (Iceland); Jensens rokke (Denmark and Greenland); Jensens Rochen (Germany).
Literature: Jónsson and Pálsson (2006); Orlov et al. (2006); Kulka, Orlov and Baker (2008); Johnston et al. (2010).

## Amblyraja radiata (Donovan, 1808)

Raja radiata Donovan, 1808, Nat. Hist. Brit. Fish., 5: 2 unnumbered pages, pl. 114. No type material. Synonyms: Raja (Amblyraja) radiata, subgenus (Stehmann, 1970).

FAO Names: En - Starry ray; Fr - Raie radiée; $\mathbf{S p}$ - Raya radiante.


Fig. 373 Amblyraja radiata

Field Marks: Disc subrhombic, with anterior margins strongly undulated in mature males, and angular outer corners; tail short and solid. Snout short, bluntly angled and stiff through solid rostrum to snout tip. All upper thorns quite large, their bases typically ribbed and with stellate margin; entire upper disc very rough through large thorns, many thornlets scattered over snout and pectoral wings and coarse dermal denticles over most of disc and tail. Single thorns on head, nape, shoulder girdle and shoulders, and a median, regular row of 13 to 17 ( 9 to 34 off Canada, Kulka pers. comm.) large thorns from anterior trunk to first dorsal fin. Colour medium greyish-brown above, clouded with darker and few pale white blotches, also often with blackish dots arranged as rosettes; underside white, occasionally with small dark blotches and indistinct greyish disc margins.

Diagnostic Features: Disc subrhombic, with anterior margins strongly undulated in mature males, and angular outer corners; tail shorter than body and solid, with two small dorsal fins confluent, or rarely close-set, at rear. Snout short, bluntly angled, and vertically not flexible due to stiff solid rostrum to snout tip. Upper thorns conspicuously large, set in largely constant pattern of separate orbital and supraspiracular thorns, a single one each on mid-nape and mid-shoulder, 2


LATERAL AND UPPER VIEW OF A THORN to 3 on each shoulder, and a very regular median row of 13 to 17 ( 9 to 34 off Canada, Kulka pers. comm.) thorns from anterior trunk to first dorsal fin; rarely a thorn between dorsal fins, if these narrowly separated. All upper thorns quite large, their bases typically ribbed and with stellate margin; entire upper disc very rough through large thorns, many thornlets scattered over snout and pectoral wings and coarse dermal denticles over most of disc and tail; larger specimens may show a regular row of thornlets from anterior trunk to posterior tail along each side of median thorn row; underside smooth, except for some dermal denticles on snout. Claspers of mature males club-shaped, with marked, broad terminal region. Colour: medium greyishbrown above, clouded with darker and few pale white blotches, also often with blackish dots arranged as rosettes; underside white, occasionally with small dark blotches and indistinct greyish disc margins.

Distribution: Eastern North Atlantic: high Arctic latitudes, throughout the Barents Sea, Eastern Greenland, Iceland, and southward from Norway to the Western Baltic Sea (where it is rare), and throughout most of the North Sea, except for the southern most portion, around the British Isles and Ireland, to the southern limits of the English Channel and in the deeper portions of the northern Bay of Biscay. Western North Atlantic: Western Greenland across the Davis Strait, and southwards from Canada to off South Carolina, USA. Records of this species from off South Africa are now known to actually be of Amblyraja taaf (Compagno and Ebert, 2007).

Habitat: A very common benthic inshore coastal species at high latitudes, occurring from the continental shelves down to about $1,400 \mathrm{~m}$ depth, but mainly from 27 to 439 m . It is found on various bottom substrates in Arctic and boreal waters. This species prefers a water temperature range of -1.3 to $14^{\circ} \mathrm{C}$.


Fig. 374 Amblyraja radiata
$\square$ Known distribution

Biology: Oviparous, egg capsules 42 to 66 by 25 to 53 mm (up to 76 by 59 mm off Canada, Kulka pers. comm.), excluding horns, depending on size of female, as well as number of capsules laid. The young hatch after several months to possibly years of embryonic development; development time depends on the water temperature and latitude, with the maximum reported gestation time about 36 months in the White Sea (Berestovsky 1994). Egg case laying rate per female varies from 10 to 45 capsules annually. Egg capsules have a rough, coarse, sandpaper-like surface due short, stiff fibres. Size at sexual maturity varies by area. Depending on size, smaller skates feed on various benthic invertebrates including shrimps and crabs, but larger (maturing) skates feed on small bottom fishes such as sand eels and small gadoids.

Size: Maximum length about 110 cm , but maximum and maturity sizes varies by region; at lower latitudes and at moderate depths, 61 cm is the maximum length reported from the central North Sea, but in the Gulf of Maine and in deeper waters it is about 110 cm . Size at $50 \%$ maturity is 44 to 50 cm for males and 44 to 47 cm for females off western Greenland, but off the Grand Banks and Gulf of Maine $50 \%$ maturity is at about 87.5 cm for females and 86.5 cm for males. In the North Sea maturity is reached at 44 cm for both sexes. In very deep waters of 1000 m or more, males were still immature at 80 cm in length (M. Stehmann, unpubl.).The size at hatching is from 8 to 12 cm in length.

Interest to Fisheries and Human Impact: For a long time this skate was treated as an unwanted bycatch and discarded because of its relatively small size and the extreme roughness from its numerous big thorns and thornlets. However, as other traditional species of commercial interest became overfished, the Starry skate has become a target species in the NW Atlantic, where it attained a larger size, and catch regulations have become necessary in the Western North Atlantic due to stock declines (Kulka et al., 2004). Canadian catches within the 200 miles EEZ are exported to Europe, as well as catches from outside the NAFO Regulatory Area by Spain, Portugal and Russia. NAFO has implemented a TAC of 12,000 t for skates unspecified in Division 3LNO; thereof 2,000 t Canada, 7,556 t European Union, 2,000 t Russian Federation, and 444 t for other countries; a large proportion of this TAC is mostly Amblyraja radiata.
The United States National Marine Fisheries Service has forbidden possession and landing of any thorny skates within the Skate Management Unit ranging from Cape Hatteras (North Carolina) in the south, and northward to the U.S. Canadian border and eastward from the shore to the boundary of the EEZ (NOAA, 2011). As a species of the Order Rajiformes is subject to TAC regulations in EU waters and catches of this species should be reported separately (2012).
According to Dolgov et al. (2005a, b), A. radiata is by far the most dominant skate species in the Barents Sea and makes up to $96 \%$ in number and $92 \%$ of biomass in surveys and commercial bycatch of bottom trawl and longline fisheries. Williams et al. (2008) found $A$. radiata also was the most abundant skate species along the coasts of northern Norway.
It is still typically discarded in North Sea fisheries, although larger specimens may be landed occasionally (Silva, Ellis and Catchpole 2012), and although its abundance in the North Sea increased during the 1970s and 1980s, there has been a recent decline, but the causes of this are unknown, especially as this decline has occurred at a time of decreasing fishing effort.

The conservation status is Vulnerable globally, but Critically Endangered in U.S. waters.
Local Names: Sternrochen (Germany); Tindaskata (Iceland); Sterrog (The Netherlands); Raia repregada (Portugal); Kloskate (Norway); Tærbe (Denmark and Greenland); Thorny ray (Canada).

Remarks: $A$. radiata is the type species of genus Amblyraja Malm, 1877 by subsequent designation of Jordan (1919).
Literature: Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Berestovsky (1994); Kulka et al. (2004); Dolgov et al. (2005a, b); Williams et al. (2008); Shark Trust (2009); NOAA (2011); Silva, Ellis and Catchpole (2012).

## Dipturus Rafinesque, 1810

Genus: Dipturus Rafinesque, 1810, Caratt. Gen. Spec. Sicil.: 16.
Type Species: Raja batis Linnaeus, 1758 by original designation.
Number of Recognized North Atlantic Species: 5.
Synonyms: Raja (Dipturus) as subgenus (Stehmann, 1970).
Field Marks: See Diagnostic Features below.
Diagnostic Features: See also family and key to genera. Most striking external morphology characteristics are the usually long and pointed snout (internarial width less than $70 \%$ prenarial snout length), along with markedly concave anterior disc margins. Colour: underside is never white but either plain dark blackish-brown or sort of wishy-washy grey and brown, with constantly numerous mucus and sensory pores of irregular pattern marked as black dots and short streaks (often camouflaged through dark ground colour and/or blackish mucus coverage), as well as pores on upper side of head. Except for small juveniles, usually thorns on disc absent, and present only in a median row along tail to first dorsal fin, along with often strong lateral thorns on low edges of tail and sometimes parallel rows on tail.

Remarks: About 40 species are described and named from all oceans, but a few additional species are known but not yet described. Iglésias et al. (2009/2010) has demonstrated that Dipturus batis Linnaeus, 1758 is in fact a composite species and provisionally split it into the smaller $D$. sp. cf. flossada and the much larger $D$. sp. cf. intermedia (see Remarks under both species). As a consequence, the type species for the genus Dipturus is presently uncertain. The first author (Iglésias, op. cit.) is currently preparing a formal revision with full redescriptions of both species, and when this has been published, more characters may become available to distinguish between both than were presently available for the key below ( S . Iglésias, pers. comm.).

Other recent studies and publications strongly indicate a rather complex structure with several composite species among the Eastern North Atlantic and Mediterranean Sea Dipturus species. See Remarks under species accounts for additional discussion on $D$. sp. cf. flossada, $D$. sp. cf. intermedia, $D$. nidarosiensis, $D$. oxyrinchus and the Dipturus sp.

## Key to North Atlantic Species:

1a. Anterior pelvic-fin lobes very short, thumb-like blunt, distinctly shorter than posterior lobes

1b. Anterior pelvic-fin lobes conspicuously long and pointed, about as long as posterior lobes, or a little longer (Fig. 375).

Dipturus sp.
2a. Very large growing species with maximum total length exceeding 200 cm ; sexually mature from about 150 cm TL onward

2b. Moderately large growing species with maximum total length about 150 cm or less; sexually mature with about 100 cm total length, or less.

3a. Except for small juveniles with a few small orbital thorns, typically no thorns on upper disc (except for mature male alar thorn fields), but only a median row of 12 to 18 thorns along tail to first dorsal fin, and 1 to 2 thorns between dorsal fins. Colour dark olive-green above, with some pale spots, but large specimens becoming greyish-brown, with a more or less circular pseudo-ocellus formed on dark background by a concentration of pale spots and vermiculate streaks in most specimens; underside variable depending on individual size, but small specimens are dark and become increasingly paler with growth (Fig. 376)
. . . . . . . . . . . . . . . . . . . . . . . . . . Dipturus sp. cf. intermedia
3b. Small young not known, larger specimens without thorns on disc (except for mature male alar thorn fields), but only a median row of 40 to 50 small thorns along tail to first dorsal fin, and 1 to 3 thorns between dorsal fins. Colour above plain dark greyish-brown, underside somewhat darker plain brown but often covered by a thick, firm layer of black mucus (Fig. 377) $\qquad$ Dipturus nidarosiensis
4a. Snout very long and narrowly pointed, its preorbital length 5.5 to 7.0 times the interorbital distance. No thorns on upper disc, except for small preorbital thorns in young and alar thorn fields of mature males, only a median row of 4 to 11 thorns along tail to first dorsal fin, which more or less worn off in adults; 0 to 1 thorn between separate dorsal fins (Fig. 378).

Dipturus oxyrinchus
4b. Snout less elongated and more broadly pointed, its preorbital length at most 5.5 times, or less the interorbital distance

5a. Midrow on tail with only 12 to 18 thorns to first dorsal fin (Fig. 379).

Dipturus sp. cf. flossada (Eastern North Atlantic)
5b. Midrow on tail with 22 to 40 thorns to first dorsal fin, less than 20 only in small juveniles (Fig. 380)

Dipturus laevis (Western North Atlantic)


Fig. 376 Dipturus sp. cf. intermedia


Fig. 377 Dipturus nidarosiensis


Fig. 378 Dipturus oxyrinchus



Fig. 380 Dipturus laevis

## Dipturus sp. cf. flossada (Risso, 1826)

Dipturus sp. cf. flossada (Risso, 1826): new combination to partly replace Dipturus batis(Linnaeus, 1758) by Iglésias et al. (2009), published online by Wiley InterScience (www.interscience. wiley.com). DOI: 10.1002/aqc. 1083; print version published 2010 in Aquat. Conserv.: Mar. Freshwat. Ecosyst., 20: 319-333.

Synonyms: Dipturus batis (Linnaeus, 1758), partim.
FAO Names: En - Blue skate.


SQUAMATION



DETAIL OF LATERAL TAIL THORNS

Fig. 381 Dipturus sp. cf. flossada
Field Marks: Iris of eye pale yellowish. A large skate with broadly rhombic disc. Snout long and pointed. Tail solid, moderately long. Small young almost smooth on both surfaces, larger specimens becoming prickly on head and along anterior disc margins above and below. Small orbital thorns only in small young; larger specimens lack thorns on disc, only a median row of 12 to 18 thorns along tail to first dorsal fin, and often 1 to 2 small thorns ( 0 to 3 ) between dorsal fins. Specimens larger than 70 cm total length with strong thorns along lower edges of tail, their tips oriented at nearly
right angle transversally. Colour above brownish, with pale spots, with an oval eyespot on inner wings in most specimens consisting of a yellowish outer ring encircling a dark centre; underside variable depending on individual size, but small specimens are dark and become increasingly paler with growth. Sensory pores on both surfaces marked as black dots and streaks.

Diagnostic Features: Iris of eye pale yellowish (most reliable diagnostic feature externally). Disc broadly rhombic, wider than long, with acute outer corners and anterior margins deeply concave; a theoretical line from snout tip to outer wing tip does not even touch anterior disc margin. Snout long and pointed, the preorbital length in average 3 times, in any case less than 5.5 times the interorbital width. Tail rather solid and moderately long, gradually tapering to tip, with two equally small dorsal fins at rear separated by short interspace of much less than half a dorsal fin base length. Small young almost smooth on upper and lower surfaces, larger specimens becoming prickly on head and along anterior disc margins above and below, but pectoral-fin centres remain largely smooth especially in large males. Except for small young with a few orbital thorns, larger specimens without thorns on upper disc, except for malar thorn patches laterally on upper head level with eyes/spiracles and alar thorn fields across wing tips of mature males; only a median row of 12 to 18 thorns ( 12 to 31 found for all growth stages, but lost thorns not being replaced; S. Iglésias pers. comm.) along tail to first dorsal fin. Lateral thorns along lower tail edges of larger (usually $>70 \mathrm{~cm}$ total length, S . Iglésias, pers. comm.) specimens with tips oriented at nearly right angle transversally. Jaw teeth of immature and mature males and females with pointed cusp on narrow, roundish base, cusp longer in mature males. Colour: upper side brownish, with pale spots and in most specimens an oval eyespot on inner wings consisting of a yellowish outer ring encircling a dark centre; underside variable depending on individual size, but small specimens are dark and become increasingly paler with growth to end up almost white in large adults, with only head, scapular and inner pectoral regions remaining pale grey. Sensory pores on both surfaces marked as black dots and streaks.

Distribution: Eastern North Atlantic: Formerly as Dipturus batis widespread in European seas from East Greenland and Barents Sea southward along Norway into the North Sea, around the western United Kingdom and Ireland, along France, Spain and Portugal, and also off western North Africa, Madeira, and along the Mid-AtlanticRidge and into the Mediterranean. Due to overfishing in many places, the present range has been reduced to mainly around Iceland, along Norway to the northern North Sea, around the British Isles and west of Ireland, the Celtic Sea, with sporadic occurrences in other remaining areas. It may well turn out, although both species appear to live sympatrically throughout most of the original distribution area, northward into high Arctic latitudes the larger $D$. sp. cf. intermedia was and is predominant, whereas to the south the smaller $D$. sp. cf. flossada may be more common.

Habitat: Benthic to benthopelagic from coastal waters to about 600 m depth, mostly around 100 m (S. Iglésias, pers.


Fig. 382 Dipturus sp. cf. flossada comm.), since the development of deepwater fisheries found even down to $1,500 \mathrm{~m}$. Prefers soft bottom but also found on gravel and hard, rocky ground.

Biology: Oviparous, egg capsules large, with short horns and smooth surface, measuring about 120 to 180 mm in length (excluding horns). Biological knowledge of this species is uncertain due to previous confusion over the taxonomic separation of it and the closely related and sympatrically occurring Dipturus sp. cf. intermedia. Deposition of egg cases occurs in the spring and summer months, with embryonic development taking several months to possibly years at higher latitudes. Feeds on various kinds of benthic invertebrates, with larger specimens preferring fishes, including other skates (Rajidae).

Size: Maximum about 145 cm total length, a length much smaller than the closely related and sympatrically occurring congener $\boldsymbol{D}$. sp. cf. intermedia. Males and females mature at about 115 and 123 cm in length, respectively. Size at hatching from 21 to 29 cm total length, but the larger size may be referable to $D$. $\mathbf{s p}$. cf. intermedia, whereas hatching size of the present species may well be much smaller (S. Iglésias, pers. comm.).

Interest to Fisheries and Human Impact: Historically a heavily exploited species. Specimens being landed commercially in French ports appear to represent a mixture of at least three Eastern North Atlantic species of Dipturus, namely $D$. batis, D. nidarosiensis and D. oxyrinchus, and occasionally with Rostroraja alba intermingled. Landing registration was made in 10 French fishmarkets under the lump-term D. batis, and in two places under D. oxyrinchus. Landings were analysed during the period of July 2006 until October 2007, and comprised a total of 4,110 skates making up 14,081 tonnes by weight originating from 103 commercial fishing cruises of 41 different French vessels from a wide area, mostly in the Celtic Sea and around western Scotland and Ireland and at a depth range from the shelf to $1,500 \mathrm{~m}$ (Iglésias et al., 2009/2010).

Dipturus batis was listed by the IUCN Red List as Critically Endangered (Dulvy et al., 2006), but this assessment has not been updated for the two species: $D$. sp. cf. flossada and $D$. sp. cf. intermedia. The latter species is larger and so may be the more vulnerable of the two species. EU has prohibited to fish for, to retain on board, to tranship or to land $D$. batis in and from ICES subareas VI, VII, VIII, IX and X (2012). Accidentally caught specimens shall be promptly released. Future regulation measures will have to consider both species of the former $D$. batis.

Local Names: Skata (Iceland); Storskate (Norway); Slätrocka (Sweden); Glattrochen (Germany); Raia oirega, Airoga, Eiroga (Portugal); (however, unclear to which of both species under $\boldsymbol{D}$. batis local names are referred to).

Remarks: Iglésias et al. (2009) demonstrated that of 17 morphometric measurements being markedly different for D. sp. cf. flossada and D. sp. cf. intermedia 16 are allometric and change considerably with growth, if expressed as percentage of total length, with only interdorsal space being near-isometric and a constant difference of $1.2 \% \pm 0.4$ s.d. in the former and $2.4 \% \pm 0.5 \mathrm{~s}$. d . of total length in the latter species. However, the authors emphasized a few additional distinguishing features of external morphology such as ground colour, colour pattern, including mostly the presence of ocelli/pseuso-ocelli, colour of the iris (the best and consistent diagnostic feature), shape of the jaw, teeth base and size, as well as orientation of tip of lateral tail thorns allowing in combination correct field identification on board and at fish markets with rather high probability. The first author (Iglésias, op. cit.) currently is preparing a formal review of the taxonomic status of these morphologically similar Dipturus species with detailed redescriptions of both $D$. sp. cf. flossada and D. sp. cf. intermedia (Iglésias, pers. comm.).

Literature: Dulvy et al. (2006); Iglésias et al. (2009/2010); EU (2012).

## Dipturussp. cf. intermedia (Parnell, 1837)

Dipturus sp. cf. intermedia (Parnell, 1837), new combination to partly replace Dipturus batis (Linnaeus, 1758) by Iglésias et al. (2009), published online in Wiley InterScience (www.interscience.wiley.com). DOI: 10.1002/aqc.1083; print version published 2010 in Aquat. Conserv:: Mar. Freshwat. Ecosyst., 20: 319-333.

Synonyms: Dipturus batis (Linnaeus, 1758), partim.
FAO Names: En - Flapper skate.



Fig. 383 Dipturus sp. cf. intermedia

Field Marks: Iris of eye dark olive-green. A very large growing, heavy-bodied skate with broadly rhombic disc. Snout long and pointed. Solid tail with two small dorsal fins at rear separated by long interspace. Small young almost smooth on both surfaces, larger specimens becoming prickly on head and along anterior disc margins above and below. Small orbital thorns only in small young; larger specimens lack thorns on disc; a median row of 12 to 18 thorns only along tail to first dorsal fin, and mostly 1 to 2 thorns between dorsal fins. Larger specimens with strong thorns along lower edges of tail, with their tips distinctly inclined toward head. Colour dark olive-green above, with some pale spots, but large specimens becoming greyish-brown, with a more or less circular pseudo-ocellus formed on dark background by a concentration of pale spots and vermiculate streaks in most specimens; underside variable depending on individual size, but small specimens are dark and become increasingly paler with growth to end up greyish-white in large adults, with only head, scapular and inner pectoral regions remaining pale grey. Sensory pores on both surfaces marked as black dots and streaks.

Diagnostic Features: Iris of eye dark olive-green (most reliable diagnostic feature externally). Disc broadly rhombic, wider than long, with acute outer corners and anterior margins deeply concave; a theoretical line from snout tip to outer wing tip does not even touch anterior disc margin. Snout long and pointed but its proportion changing with growth from relatively long to shorter, preorbital length in average 3.2, but in any case less than 5.5 times the interorbital width. Tail rather solid, moderately long and gradually tapering to tip, with two equally small dorsal fins at rear separated by long interspace of about half a dorsal fin base length. Small young almost smooth on upper and lower surfaces, larger specimens becoming prickly on head and along anterior disc margins above and below, but pectoral centres remain largely smooth especially in large males. Small orbital thorns only in small young; larger specimens lacking thorns on disc, only a median row of 12 to 18 thorns ( 0 to 18 , mostly $15, \mathrm{~S}$. Iglésias, pers. comm.) along tail to first dorsal fin, and regularly 1 to 2 thorns ( 0 to 3, S. Iglésias, pers. comm.) between dorsal fins. Mature males showing field of alar thorns across each wing tip, but malar thorn patches are not developed. Larger specimens with strong thorns along lower edges of tail; tips of these thorns distinctly inclined toward head. Jaw teeth of immature and mature males and females with pointed cusp on narrow, or broadly transversally rhombic base, respectively. Colour: dark olive-green above, with some pale spots, but large specimens becoming greyish-brown, with a more or less circular pseudo-ocellus formed on dark background by a concentration of pale spots and vermiculate streaks in most specimens; underside variable depending on individual size, but small specimens are dark and become increasingly paler with growth to end up greyish-white in large adults, with only head, scapular and inner pectoral regions remaining pale grey. Sensory pores on both surfaces marked as black dots and streaks.

Distribution: Eastern North Atlantic: formerly as the widespread Dipturus batis in European seas from East Greenland and Barents Sea southward along Norway into the North Sea, around western United Kingdom and Ireland, along France, Spain and Portugal, and also offwestern North Africa, Madeira and in the Mediterranean. Due to overfishing in many places, the present range has been reduced to mainly around Iceland, along Norway to northern North Sea, around the western British Isles, and Celtic Sea, with rather sporadic occurrences in the remaining areas. It may well turn out, although both species appearto live sympatrically in mostofthe original distribution area, that northwards into high Arctic latitudes the larger $D$. sp. cf. intermedia was and is predominant, whereas to the south the smaller $D$. $\mathbf{s p}$. cf. flossada may be more common.

Habitat: Benthic to benthopelagic from coastal waters to about 600 m depth, mostly around 200 m , however since the development of deepwater fisheries it has been found down to $1,500 \mathrm{~m}$. Prefers soft bottom but also found on gravel and hard, rocky ground.

Biology: Oviparous, with very large egg cases measuring up to 250 by 150 mm in length and width, with short horns and a smooth surface. Egg cases are deposited in the spring and summer, with embryonic development taking several months to possibly years at high latitudes. The diet of this skate includes benthic invertebrates with larger individuals consuming more demersal fishes than smaller individuals.

Size: Maximum length to about 230 cm , but possibly up to 285 cm in length for females based on historical records; this species ranks as one of the largest, if not the largest, skate species in the world. Males and females mature at about 185 cm and 197 cm total length, respectively. The size at hatching uncertain due to confusion with Dipturus sp. cf. flossada but is likely from 21 to 29 cm .


Fig. 384 Dipturus sp. cf. intermedia
Known distribution $\square$ Possible distribution

Interest to Fisheries and Human Impact: Specimens landed commercially in French ports were found to represent a mixture of at least three Eastern North Atlantic species of Dipturus, namely D. batis, D. nidarosiensis and D. oxyrinchus, with Rostroraja alba occasionally intermingled. Landings registration was made in 10 French fishmarkets under the "lump-term" $\boldsymbol{D}$. batis and in two places under $\boldsymbol{D}$. oxyrinchus. Landings were analysed during the period July 2006 through October 2007, and found to comprise a total of 4,110 skates making up 14,081 tonnes by weight, and originated from 103 commercial fishing cruises by 41 different French vessels from a wide area, but mostly in the Celtic Sea and around western Scotland and Ireland and a depth range from the shelf to $1,500 \mathrm{~m}$.
EU has prohibited to fish for, to retain on board, to tranship or to land D. batis in and from ICES subareas VI, VII, VIII, IX and $X$ (2012). Accidentally caught specimens shall be promptly released. Future regulation measures will have to consider both species of the former $D$. batis.
Dipturus batis was listed by the IUCN Red List as Critically Endangered (Dulvy et al., 2006), but this assessment has not been updated for the two species: $\boldsymbol{D}$. sp. cf. flossada and $D$. sp. cf. intermedia. The latter species is larger and so may be the more vulnerable of the two species.

Local Names: Skata (Iceland); Storskate (Norway); Slätrocka (Sweden); Glattrochen (Germany); Raia oirega, Airoga, Eiroga (Portugal); (however, it is unclear to which or both species under $D$. batis the local names refer to).
Remarks: See remarks section above for comments on the separation of $D$. $\mathbf{s p}$. cf. flossada from $D$. $\mathbf{s p}$. cf. intermedia. A taxonomic review of this species is currently being undertaken (Iglésias, pers. comm.).

Raja batis Linnaeus, 1758 was designated by Rafinesque (1810) as type species of the genus Dipturus, based on Mediterranean specimens, however, the validity of D. batis (= R. batis) is an open question as to which of the Mediterranean species of Dipturus can be defined as genus type.
Literature: Dulvy et al. (2006); Iglésias et al. (2009/2010); EU (2012).

## Dipturus laevis (Mitchill, 1818)

Raja laevis Mitchill, 1818, American Monthly Magazine and Critical Review No. 6: 327. Holotype apparently lost according to CAS 'Catalog of Fishes'.

Synonyms: Raja laevis.

FAO Names: En - Barndoor skate; Fr - Grand raie; Sp - Raya grande.


Field Marks: Disc broadly rhombic, wider than long, with acute outer corners and anterior margins deeply concave. Snout long and pointed. Tail rather solid, moderately long. No thorns on upper disc, a few pre- and postorbital small thorns only in small young; a median row of 14 to 17 in small young, increasing with growth to 22 to 40 small thorns only along tail to first dorsal fin, and a thorn between dorsal fins. Colour above grey to brown, with pattern of more or less distinct pale spots with dark brown centre; underside dusky, darker at outer disc and pelvic-fin margins. Above and below, sensory and mucus pores marked as distinct black dots and streaks.

Diagnostic Features: Disc broadly rhombic, wider than long, with acute outer corners and anterior margins deeply concave, so that a theoretical line from snout tip to outer wing tip does not even touch the anterior disc margin. Snout long and pointed, its preorbital length less than, or at most 5 times the interorbital distance; snout angle 82 to $90^{\circ}$ in front of a line through spiracles. Tail rather solid, moderately long and gradually tapering to tip, with two equally small dorsal fins at rear separated by distinct interspace. Small young smooth on upper


Fig. 385 Dipturus laevis and lower surfaces. In larger specimens, upper wing centres largely smooth, especially in mature males, but snout tip, anterior disc margins, outer orbital and nape-shoulder regions, back and sides of trunk, as well as sides of tail more or less densely set with coarse dermal denticles; underside of larger males largely smooth, with few coarse prickles only on snout margins; in contrast, large females with dense prickles along snout sides, on interbranchial region and origin of pelvic fins. No thorns on upper disc, except for occasionally small thornlets on orbital rims and a few pre- and postorbital small thorns in small young; only a median row of 14 to 17 in small young, increasing with growth to 22 to 40 small thorns along tail to first dorsal fin, and a thorn between dorsal fins: a row of strong lateral thorns along low edges of tail becoming more distinct with growth from level of pelvic-fin tips to level of second dorsal fin. Tooth rows in upper jaw 30 to 40 , teeth set in pavement pattern in young and females, in parallel, somewhat separated rows of more pointed teeth in larger males. Colour: above grey to brown, with pattern of more or less distinct pale spots with dark brown centre and/or dark spots; often with a larger, elongated pseudo-eyespot blotch on inner pectoral fins level with outer corners; underside dusky, darker at outer disc and pelvic-fin margins. Above and below, mucus and sensory pores marked as distinct black dots and streaks.

Distribution: Western North Atlantic: its range was formerly thought to extend from Cape Hatteras, North Carolina, to only the southwestern portion of the Grand Banks, off Canada. However, recent data indicate that the barndoor skate extends exceptionally further north along the Labrador shelf edge and slope as far as $63^{\circ} \mathrm{N}$ in deep slope waters (Dulvy, 2003).

Habitat: Benthic and benthopelagic in shelf and slope waters at 10 to 788 m depth, most commonly at 10 to 145 m and at water temperature of 0.4 to $10.9^{\circ} \mathrm{C}$ but may occur up to $20^{\circ} \mathrm{C}$; recent data from the very nothern distribution limit has indicated unverified maximum depth at $1,400 \mathrm{~m}$ (Dulvy, 2003). Prefers sandy and gravelly ground, but in deeper water often also found on muddy bottom.

Biology: Oviparous, egg capsules very large and rectangular, about 124 to 132 mm length by 68 to 72 mm width, excluding horns. Females with fully formed egg capsules have been observed


Fig. 386 Dipturus laevis
Known distribution Possible distribution in December and January, suggesting that egg cases are laid in winter, with young hatching after about six months and in the early summertime. Egg production was estimated at 47 per year. At smaller size, barndoor skates feed on small benthic crustaceans, worms, gastropods, bivalves and squid, at larger size also all kinds of bottom or near-bottom fish are predominant from spiny dogfish, herring, butter fish to hake, haddock, cod and flatfishes.

Size: Maximum length about 153 cm and a weight of 20 kg . Females mature at about 96 to 105 cm , and males at about 100 cm in length (Sulak et al. 2009). Size at hatching uncertain, but the smallest free-swimming neonates reported were 18 to 19 cm in length.

Interest to Fisheries and Human Impact: Although never directly targeted, it was taken as bycatch in multispecies bottom trawl fisheries on the Georges Bank, Scotian Shelf, Grand Banks and Labrador Shelf and was also taken on longlines. Catch rates of barndoor skates in U.S. waters declined by 96 to $99 \%$ from the mid-1960s to the 1990s. After a dramatic deep in abundance, since the mid-1990s this skate became increasingly abundant again on Georges Bank and the Scotian shelf. In the U.S. the National Marine Fisheries Service has forbidden possession or landing of barndoor skates within the Skate Management Unit ranging from Cape Hatteras (North Carolina) in the south, northward to the U.S. Canadian border and eastward from the shore to the boundary of the EEZ (NOAA, 2011). As a species of the Family Rajidae is subject to TAC regulations in NAFO Divisions 3LNO (2012).

The conservation status is currently listed Endangered but is presently under review for probably downlisting
Local Names: Sharpnosed ray or skate (USA).
Remarks: The description of the barndoor skate of the Western North Atlantic was for a long time attributed to Mitchill (1817), but several authors have revised the year of the original reference to 1818; see references provided in CAS online 'Catalog of Fishes'.

Literature: Bigelow and Schroeder (1953); Dulvy (2003); Sulak et al. (2009); NOAA (2011).

## Dipturus nidarosiensis (Storm, 1881)

Raja nidarosiensis (Storm, 1881), K. norske Vidensk. Selsk. Skr. 1880 (publ. 1881), 4: 80-81. Syntype ZMO J6339, stuffed male; two further syntype females lost.

Synonyms: Raja nidrosiensis Collett, 1882, Raja (Dipturus) nidarosiensis subgenus (Stehmann 1970), also as R. nidrosiensis by authors referring to Collett (1882) and rarely to Collett (1879).

FAO Names: En - Norwegian skate; Fr - Pocheteau de Norvège; Sp - Raya noruega.


Field Marks: Disc broadly rhombic, wider than long, with acute outer corners and anterior margins deeply concave. Snout very long and pointed. Tail rather solid and relatively short. Upper disc largely smooth, prickly only on head and along anterior disc margins; in contrast, underside almost entirely covered with densely set, coarse dermal denticles. No thorns on upper disc, except for occasionally small thornlets on orbital rims; only a median row of 40 to 50 small thorns along tail to first dorsal fin, flanked at times by parallel rows in large females, and 1 to 3 small thorns between dorsal fins. Colour above plain dark greyishbrown, underside somewhat darker plain brown but often covered by a thick, firm layer of black mucus camouflaging the black marked dots and streaks of lateral line and sensory pores which also marked black dorsally.

Diagnostic Features: Disc broadly rhombic, with acute outer corners and anterior margins deeply concave, so that a theoretical line from snout tip to outer wing tip does not even touch anterior disc margin. Snout very long and pointed, its preorbital length less than, or at most 5 times the interorbital distance. Tail rather solid, relatively short and gradually tapering to tip, with two equally small dorsal fins at rear separated by distinct interspace. Upper disc


DORSAL VIEW
$\hat{\delta}$
SQUAMATION
Fig. 387 Dipturus nidarosiensis largely smooth, prickly only on head and along anterior disc margins; in contrast, underside almost entirely covered with densely set, very coarse dermal denticles. No thorns on upper disc, except for occasionally small thornlets on orbital rims and alar thorn fields of mature males; only a median row of 40 to 50 small thorns along tail to first dorsal fin, flanked at times by parallel rows in large females, and 1 to 3 small thorns between dorsal fins. Teeth in upper jaw in 41 to 44 rows, set in pavement in young and females, but in parallel rows in mature males. Colour: above plain dark greyish-brown, underside somewhat darker plain brown but often covered by a thick, firm layer of black mucus camouflaging the relatively few black marked dots and streaks of lateral line and sensory pores which also marked black dorsally.

Distribution: Eastern North Atlantic: deep fjords of central and southern Norway, along the slopes off southern Iceland, western Scotland (including Rockall Trough) and western Ireland. Nominal records from shelf edge of Celtic Sea, which may have been misidentifications of another congener; see Dipturus sp. below. Also, likely occurs along the Mid Atlantic Ridge and the Iceland-Faroe Ridge. Records from the deep slopes of the Bay of Biscay to off North Spain are currently under investigation (M. Stehmann, unpubl. data; see Remarks section below).

Habitat: Benthic and benthopelagic in boreal outer continental shelves and slope waters from about 200 m to more than $1,000 \mathrm{~m}$ depth on and over various kinds of bottom. Gordon and Duncan (1989) reported on 14 specimens (79 to 101 cm total length) from 11 trawl stations at 707 to 1235 m depth from the Hebridean Terrace slope.

Biology: Oviparous, egg capsules very large and rectangular, length about 180 to 260 by 92 to 113 mm width, excluding horns. Embryos and small young unknown. Feeds on various kinds of bottom fish and invertebrates; adults take also larger fish like Blue Whiting.

Size: Growing to at least 200 cm total length, but said to grow to 250 cm ; the second largest North Atlantic skate. Size at maturity and hatching are unknown.

Interest to Fisheries and Human Impact: A relatively rare deepwater skate taken as bycatch in deepwater bottom trawl and longline fisheries, occasionally landed but mostly discarded.


Fig. 388 Dipturus nidarosiensis
$\square$ Known distribution

The conservation status is Near Threatened.
Local Names: Black skate (England and Wales, Ireland); Drændaskata (Iceland); Schwarzbäuchiger Glattrochen (Germany); Svartskate (Norway).

Remarks: Cannas et al. (2010) reported D. nidarosiensis from the Western Mediterranean, based on 14 specimens ( 240 to 1482 mm total length, including a mature male) that were taken in the Sardinian Channel between 600 and $1,420 \mathrm{~m}$ depth; they presented molecular and morphological evidence on the specific identity in comparison with Eastern North Atlantic specimens of D. nidarosiensis, Eastern North Atlantic and Mediterranean D. oxyrinchus and with Eastern North Atlantic D. batis. The species name of the latter, D. batis, has been replaced by $D$. cf. flossada (the smaller species) and $D$. cf. intermedia (the much larger species) by Iglésias et al. (2009) - see species accounts in this catalogue. However, the juvenile male ( 240 mm total length), mature male ( 1180 mm total length) and largest female ( 1482 mm total length) of the Sardinian specimens, as illustrated by colour photographs in fig. 1 by Cannas et al. (2010), show a habitus quite different from northern Eastern North Atlantic D. nidarosiensis, of which these authors did not illustrate full view. A possible, yet undescribed black-bellied Dipturus sp. was taken off the mainland of Portugal and in the vicinity of the Gulf of Cadiz several years ago. Three specimens, two small juvenile females and a mature male, were given by IPIMAR Lisbon to $M$. Stehmann (unpubl. data) in order to clarify their identity; a larger mature female also collected at the time was unfortunately lost. The habitus of this Dipturus $\mathbf{s p}$. looks indeed very similar to the form that was reported by Cannas et al. (2010) from the Sardinian Channel, but both are unlike $D$. nidarosiensis from the northern Eastern North Atlantic. More detailed diagnostic features of the IPIMAR specimens are therefore given here under Dipturus $\mathbf{s p}$. in a separate species account. Adult size of the latter species and likewise the Sardinian D. nidarosiensis is however markedly smaller, a size at which northern Eastern North Atlantic D. nidarosiensis are just approaching sexual maturity.

Literature: Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Jónsson and Pálsson (2006); Stehmann (2007); Iglésias et al. (2009); Shark Trust (2009); Cannas et al. (2010).

## Dipturus oxyrinchus (Linnaeus, 1758)

Raja oxyrinchus Linnaeus, 1758, Syst. Nat., ed. 10, 1: 231. No type material.
Synonyms: Raja (Dipturus) oxyrinchus, as subgenus (Stehmann, 1970).

FAO Names: En - Longnosed skate; Fr - Pocheteau noir; Sp - Raya picuda.


COLORATION

Field Marks: Disc broadly rhombic, with acute outer corners and anterior margins deeply concave. Snout extremely long and pointed. Tail rather solid, about as long as body. Upper surface nearly smooth in young, becoming almost entirely spinulose in adults; development of dermal denticles the same on underside from young to adults. No thorns on upper disc, only a median row of 4 to 11 thorns along tail to first dorsal fin, which more or less worn off in adults; 0 to 1 thorn between separated dorsal fins; strong thorns along lower tail edge in adults. Colour above from light brown in young to dusky brown or grey in larger specimens, with more or less distinct pattern of light spots and black dots; underside light brown in young, dark brown to blue-grey in larger individuals; generally, mucous and sensory pores on both surfaces marked as black dots and streaks.

Diagnostic Features: Disc broadly rhombic, with acute outer corners and anterior margins deeply concave, so that a theoretical line from snout tip to outer wing tip does not even touch anterior disc margin. Snout extremely long and pointed, its preorbital length 5.5 to 7.0 times the interorbital distance. Tail rather solid and moderately long, gradually tapering to tip, with two equally small dorsal fins at rear separated by narrow interspace. Upper surface nearly smooth in young, becoming almost entirely spinulose in adults, but bare patches on pectoral-fin centres; development of dermal denticles the same on underside from young being nearly smooth, but underside gradually becoming spinulose with growth to almost entirely prickly in adults, except for bare pectoral-fin centres. No thorns on upper disc, except for small preorbital thorns in young and alar thorn fields of mature males, only a median row of 4 to 11 thorns along tail to first dorsal fin, which more or less worn off in adults; 0 to 1 thorn between separated dorsal fins; strong thorns developing with growth along lower tail edges. Teeth set in pavement pattern of maximum 40 rows in upper jaw. Colour: upper surface light brown in young, becoming gradually darker to dusky brown or grey in larger specimens, with more or less distinct pattern of light spots and black dots; underside light brown in young, dark brown to blue-grey in larger individuals; generally, mucus and sensory pores on both surfaces marked as black dots and streaks.

Distribution: Eastern North Atlantic: central Norway, Faroe Islands, Shetlands and northern North Sea southward along Atlantic shelf of European coasts to off Morocco, also at Canary Islands and Madeira; occurs also in the Mediterranean Sea but not in the Black Sea.

Habitat: Benthic on mainly soft mud and sand bottom but also found in loose rock areas and on gravel beds at 90 to 900 m depth, mostly around 200 m . Moderately rare.

Biology: Oviparous, egg capsules large and rectangular, 140 to 235 mm length (excluding horns) by 110 to 120 mm width. Egg case deposition occurs from the spring to early summer months. Embryos develop over several months and hatch at about 170 mm total length. Feeds on all kinds of bottom invertebrates, including cephalopods, crustaceans, and fishes; females appear to prefer cephalopods, and males crustaceans.


Fig. 390 Dipturus oxyrinchus
$\square$ Known distribution

Size: Maximum length to about 150 cm , but most usually found at a smaller size. Females reach maturity from 90 cm length, and males between 70 and 80 cm (in Mediterranean). Length at hatching is about 170 mm .

Interest to Fisheries and Human Impact: Still called a moderately common species in FNAM (1984), since the species as bycatch has been heavily exploited and its stocks have declined significantly. It was and is a bycatch species in bottom trawl and bottom longline fisheries, but is usually often discarded except for large specimens that were landed like other large regional Dipturus spp. As a species of the Order Rajiformes is subject to TAC regulations in EU waters (2012).

The conservation status of this skate is Near Threatened
Local Names: Spear-nosed skate, Snipers skate, Long-nosed Burton skate (England and Wales, Ireland); Spitzrochen (Germany); Langsnuitrog (The Netherlands); Raia dlugonosa, Raia bicuda (Portugal); Picón (Spain); Spisskate (Norway).

Remarks: In French landings often mixed with closely related species of Dipturus under D. batis, but see Remarks and comments on the latter under $\boldsymbol{D}$. sp. cf. flossada. S. Iglésias (2011 pers. comm.) indicated his recent findings, that D. oxyrinchus appears to be a composite species as well, just like $D$. batis, namely with one smaller form occurring in the North Eastern Atlantic and the Mediterranean Sea, and the larger other form under D. oxyrinchus only found in the North Eastern Atlantic. A recent publication by Griffiths et al. (2011), based on a comparative mitochondrial DNA analysis of D. oxyrinchus from the North Eastern Atlantic (Norway and Rockall Trough) and in the Mediterranean Sea from around the Balearic Islands, suggests that the Mediterranean stock may be genetically isolated since the last European glaciations maximum (i.e. since some 20,000 years) from stocks outside the Mediterranean Sea; indications of such stock differentiation, based on differences in maximum size and egg capsule size, had been noticed much earlier in the 1920s but were not further followed with detail studies.

Literature: Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Ungaro et al. (2007); Shark Trust (2009); Griffiths et al. (2011).

## Dipturus sp. Stehmann (in prep.)

Synonyms: probably Dipturus nidarosiensis (Storm, 1881), partim for Mediterranean records.
FAO Names: En - Black-bellied thin-tail skate.


Field Marks: Alarge deepwater skate with a rhombic disc broader than long, with anterior margins deeply concave and outer corners sharply angular. Snout long and pointed. Tail shorter than body and conspicuously slender, with a constriction in anterior half and becoming wider again in posterior half; two equal-size small dorsal fins at rear separated by long interspace, and postdorsal tail section long and with distinct upper caudal fold. Anterior pelvic-fin lobes conspicuously slender and long, nearly as long as (in large specimens) or even longer than posterior lobes (in small immature specimens). Colour above and below uniformly dark chocolatebrown, underside somewhat darker than upper side. Sensory and mucus pores on both surfaces marked as black dots and streaks but not very apparent due to dark ground colour of both surfaces. Small young and half-grown individuals lighter medium-brown on both sides, with fin margins dusky.

Diagnostic Features: See Field Marks above.


Fig. 391 Dipturus sp.

Distribution: Eastern North Atlantic: known only from a few specimens from the deep Gulf of Cadiz and possibly from the deep Rockall Trough and from the deep continental slope off Mauritania (M. Stehmann, unpubl. data).

Habitat: The first four specimens were taken by the Portuguese RV Capricornio' in 1117 m depth at $36^{\circ} 29.8^{\prime} \mathrm{N}$ and $08^{\circ} 08.0^{\prime}$ W off the Algarve, Gulf of Cadiz, with additional specimens from similar depth and even greater depth

Biology: Like other skates oviparous, but egg cases are unknown. Diet unknown but probably consisting of bottom invertebrates in small young and also fish in larger specimens. Nothing else is known of its biology.

Size: Maximum length 137 cm for an adult male, a somewhat larger female got lost. Largest immature female is a 44.1 cm specimen and a neonate female measuring 25.1 cm (umbilical scar still visible, and still with embryonic tail filament).

Interest to Fisheries and Human Impact: This deepwater species may be little affected by deepwater fisheries at this time other than as bycatch of bottom trawling and longlining, but future intensified deepwater fisheries may have a negative impact on the population.

Local Names: None.
Remarks: Gordon and Duncan (1989) reported on two Raja (Dipturus) sp. (69.5 and 82.4 cm TL ) taken at two stations at 991 to 1014 m depth within the Rockall Trough. Further examination of these Dipturussp. revealed them to bevery unlike D. nidarosiensis that was also taken within Rockall Trough by German (Stehmann, unpubl.), British (J.D.M.


Fig. 392 Dipturus sp. comm.) and Irish (G. Johnston, pers. comm.) deepwater surveys, as well as by British and Russian deepwater surveys off western North Africa (Merrett and Marshall 1981; Stehmann 1990; Stehmann 1995). All these records likely represent the present Dipturus $\mathbf{s p}$. and may eventually prove to be conspecific with the seeming D. nidarosiensis records from the Western Mediterranean by Cannas et al. (2010); see Remarks D. nidarosiensis.

Literature: Merrett and Marshall (1981); Gordon and Duncan (1989); Stehmann (1990); Stehmann (1995); Cannas et al. (2010).

## Leucoraja Malm, 1877

Genus: Leucoraja Malm, 1877, Göteborgs och Bohusläns Fauna: 609-610.
Type Species: Raja fullonica Linnaeus, 1758 by subsequent designation of Jordan (1919).
Number of Recognized North Atlantic Species: 6.
Synonyms: Raja (Leucoraja) as subgenus (Stehmann 1970).
Field Marks: See Diagnostic Features below.
Diagnostic Features: See also Family and key to genera. Disc subcircular, with outer corners broadly rounded; snout short and bluntly angled (except for Leucoraja fullonica). Tail length equal to, but usually somewhat longer than body. Median row thorns on back of trunk and along tail (only ones in small juveniles) becoming gradually reduced with growth to completely disappear in large adults, when simultaneously one or more parallel rows of thorns grow larger and remain persistent. Except in small juveniles, thorns on orbital rims set as continuous half-rings, and many thorns over nape and shoulder region forming a triangle. Most species live on shelf and at most upper slope, why they usually show rather light dorsal ground colour, along with lively colour pattern, and undersides are white.

Remarks: The genus comprises globally 13 to 15 described and named species, with a few more known but undescribed species. Six species are known to occur in the North Atlantic.

## Key to North Atlantic Species:

1a. Disc rhombic with rounded outer corners, snout moderately elongated, pronounced, rather pointed (angle about 90 to $110^{\circ}$ ). Usually a complete row of 8 distinct thorns on each orbital rim, but median ones may be reduced in large adults. No triangle of thorns over nape-shoulder region, but instead a median row of 3 to 9 thorns along nape and midshoulder. Larger specimens lack median thorns along trunk and with growth largely so also along tail; simultaneously and gradually a row of about 50 prominent thorns develops on either side of midline from posterior trunk to about first dorsal fin. Plain ashy-grey above, sometimes with inconspicuous darker bands across disc (may be more pronounced in juveniles)(Fig. 393).

Leucoraja fullonica (Eastern Atlantic)
1b. Disc subrhombic to mostly subcircular, snout short and bluntly angled ( $>110^{\circ}$ ). Many thorns set in a large triangle over nape-shoulder region, orbital thorns set in complete half-rings on each orbital rim. One or more parallel thorn rows from anterior trunk to beyond first dorsal fin becoming dominant with growth of specimens, when at the same time the median thorn row of juveniles becomes reduced to finally disappear. Upper side always with a more or less distinct colour pattern.

2a. Generally with a large circular eye-spot on each inner pectoral centre, which show yellowish spots on a blackish background and vermiculate stripes; some specimens show additional, smaller pairs of such eye-spots elsewhere on the pectoral fin. (Fig. 394)

Leucoraja naevus (Eastern Atlantic)
2b. Permanent eyespots as under 2a absent, but other constant pattern of few symmetrically distributed light spots or rosette-like concentrations of blackish dots shown, or just clouded dark and light and scattered with small dark spots, without or occasionally with pseudo-eyespot elements

3a. Constantly dorsal colour pattern elements present either in form of 4 to 6 pairs of circular creamy spots, each encircled dusky, or with large rosette-like blotches of dark spots around a central spot; in both cases such elements are arranged symmetrically on pectoral wings and on posterior pelvic-fin lobes

3b. Upper side patterned variably clouded dark and light and scattered with small dark spots, without or occasionally with pseudo-eyespot elements . . . 5 (two North West Atlantic species)

4a. A small species to about 45 cm total length, with disc rather inverse heart-shaped and tail about 1.5 times longer than body. Dorsal colour pattern of numerous small dark spots scattered over disc and pelvic fins in addition to large rosette-like blotches of dark spots around a central spot arranged symmetrically on pectoral wings and on posterior pelvic-fin lobes (Fig. 395). .

Leucoraja garmani (North West Atlantic)
4b. A rather large species to about 120 cm total length, with subrhombic disc shape and tail only a little longer than body. Dorsal surface light or reddish to dark brown with 4 to 6 pairs of small circular creamy spots, each encircled dusky, which are arranged symmetrically on the two pectoral fins and on posterior pelvic-fin lobes. High counts of 64 to 84 tooth rows in upper jaw. (Fig. 396)

Leucoraja circularis (Eastern Atlantic)


Fig. 394 Leucoraja naevus


Fig. 395 Leucoraja garmani


Fig. 396 Leucoraja circularis

5a. A small species to about 55 cm total length. Colour above greyish to dark brown, or clouded with light and dark brown; patterned with small dark spots, usually without pseudo-eyespots. Tooth rows in upper jaw 30 to 66 , in small juveniles (< 35 cm TL ) mostly less than 54 rows, in mature specimens never more than 66 rows (Fig. 397).

Leucoraja erinacea
(North West Atlantic)
5b. A rather large species to about 110 cm total length. Colour above light brown, usually with pattern of blackish spots in varying numbers; outer and posterior part of wings often with 1 to 4 larger, dark eyespot-like blotches edged light. Tooth rows in upper jaw 44 to 63 in juveniles less than 53 cm total length, and 90 to 110 rows when mature (Fig. 398) . . . . . Leucoraja ocellata (North West Atlantic)


Fig. 397 Leucoraja erinacea


Fig. 398 Leucoraja ocellata

## Leucoraja circularis (Couch, 1838)

Raja circularis Couch, 1838, Ann. Mag. Nat. Hist. (n.s.), 2: 71-73. No type material.
Synonyms: None.
FAO Names: En - Sandy ray; Fr - Raie circulaire; Sp - Raya falsa vela.


COLORATION


SQUAMATION

Field Marks: Disc subrhombic with rounded outer corners, short and bluntly angled snout, tip of which a little pronounced. Tail solid, a little longer than body. Typically, a complete row of distinct thorns on orbital rims and a large triangle of thorns over nape/shoulder region; juveniles with a median row of thorns from posterior to shoulder girdle to first dorsal fin; larger specimens with median row reduced on trunk and generally with a parallel thorn row on either side along trunk and tail to first dorsal fin (reduced on body in large adults), and another outer thorn row in anterior half of tail; altogether the impression of a broad band of heavy thorns along trunk and tail. Upper surface entirely spinulose; underside largely smooth. Colour above light to reddish-brown, with constant pattern of 4 to 6 pairs of creamy spots arranged symmetrically on each pectoral wing and on posterior pelvic-fin lobe; underside white, with pale greyish margin to disc and posterior pelvic-fin lobes.

Diagnostic Features: Disc subrhombic with broadly rounded outer corners, undulated anterior margins (strongly so in mature males), short, bluntly angled snout (> $110^{\circ}$ ), tip of which a little pronounced. Tail solid, a little longer than body, gradually tapering to its tip, with two small, close-set dorsal fins at rear. Typically, a complete row of about eight distinct thorns on each orbital rim and a large triangle of many thorns over nape/ shoulder region; only small juveniles with a median row of thorns from behind shoulder girdle to first dorsal fin; larger specimens with median row reduced on trunk and generally with a parallel row of heavy thorns on either side along trunk and tail to first dorsal fin (reduced on body in large adults), and with another outer thorn row in anterior half of tail, no thorn between close set dorsal fins; altogether the impression of a broad band of heavy thorns along trunk and tail. Upper surface entirely spinulose, sometimes bare areas in posterior half of disc of large adults; underside largely smooth, with dermal denticles only on snout and anterior disc margins, between gill slits and on abdomen. High counts of 64 to 84 tooth rows in upper jaw; bluntly pointed teeth set in pavement pattern in juveniles and females, but more pointed in mature males and close set in parallel rows.


OUTLINE OF FEMALE

Fig. 399 Leucoraja circularis Colour: upper side from light or reddish to dark brown, with a constant pattern of 4 to 6 pairs of circular creamy spots, each encircled dusky, arranged symmetrically on pectoral wings and on posterior pelvic lobes; underside white, with pale greyish margin to disc and posterior pelvic-fin lobes.

Distribution: Eastern North Atlantic: off northern Morocco and northward to Scotland, Iceland, Norway, and the northern North Sea and into Skaggerak; also in western Mediterranean.

Habitat: Demersal on sandy and muddy bottoms from the outer shelf and upper slope to 275 m depth; sometimes deeper to 800 m and occasional reports of specimens on inner continental shelf; the habitat is has shifted to deeper water, between 200 and 800 m depth, in the Mediterranean, as well as in Eastern North Atlantic (Ungaro et al., 2008).

Biology: Oviparous, egg capsules 82 to 94 mm in length by 46 to 53 mm in width (excluding horns), with smooth surfaces, and anterior pair of horns very elongated, about twice the length of posterior horns. Females deposit egg cases from about August to November, with the young hatching after several months of development. Very little else is known about the reproduction of this skate. Feeds on all kinds of benthic invertebrates, with larger specimens consuming a higher


Fig. 400 Leucoraja circularis
Known distribution proportion of small bony fishes.

Size: Maximum length about 120 cm , but mostly between 70 to 80 cm . Size at maturity and birth unknown.
Interest to Fisheries and Human Impact: Because it is a moderately rare offshore skate, it has not been subject to target fisheries, but it is taken as a bycatch in bottom trawls and on longlines when usually landed and used for human consumption. Intensive bottom trawling for other species has resulted in a decline in populations of Sandy ray. Current populations, although now typically offshore, are still within the range of regular commercial trawl and gillnet fisheries and will be affected further.

The conservation status of this skate is Vulnerable.
Local Names: Sandrochen (Germany); Leather Ray (England and Wales); Zandrog (The Netherlands); Raia de São Pedro (Portugal); Sandskate (Norway); Sandskata (Iceland).

Remarks: The common name 'sandy ray' is also used regionally for the more inshore small-eyed ray Raja microocellata, which can result in some confusion in terms of reported landings and captures.

Literature: Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Ungaro et al. (2008); Shark Trust (2009).

## Leucoraja erinacea (Mitchill, 1825)

Raja erinaceus Mitchill, 1825, Amer. J. Sci. Arts, 9: 290. Holotype said to have been sent to Paris (Bigelow and Schroeder 1953: footnote 148), but CAS Catalog of Fishes states 'no types known'.

Synonyms: None.
FAO Names: En - Little skate; Fr - Raie hérisson.


Field Marks: Disc subrhombic with rounded outer corners and short, bluntly angled snout. Tail moderately slender, a little longer than body. Typically, a complete row of thorns on orbital rims and a large triangle of many thorns over nape/ shoulder region; only small juveniles with a median row of thorns from posterior to shoulder girdle to first dorsal fin flanked by a parallel row of smaller thorns each side; larger specimens with median thorn row reduced or lacking on trunk and tail but with 2 to 4 parallel rows of strong thorns from behind shoulder girdle to level of first dorsal fin, so that larger specimens give the impression of a very broad band of heavy thorns along back of trunk and on tail. Upper side appearing very rough by thorns of the mentioned pattern, plus numerous thorns and thornlets scattered on snout, all over pectoral wings and on posterior pelvic-fin lobes; underside largely smooth. Tooth rows in upper jaw 30 to 66 in small juveniles (less than 35 cm total length), less than 54 rows in mature specimens and never more than 66 rows. Colour above greyish to dark brown, or clouded with light and dark brown; patterned with small dark spots, usually without pseudo-eyespots; underside white to light grey.


OUTLINE OF FEMALE
Fig. 401 Leucoraja erinacea

Diagnostic Features: Disc subrhombic with rounded outer corners, undulated anterior margins (strongly so in mature males) and short, bluntly angled snout ( 110 to $130^{\circ}$ ). Tail moderately slender, a little longer than body, with two small, confluent dorsal fins at rear. Typically, a complete row of thorns on orbital rims and a large triangle of many thorns over nape/shoulder region; only small juveniles with a median row of thorns from posterior to shoulder girdle to first dorsal fin flanked by a parallel row of smaller thorns each side; larger specimens with median thorn row reduced or lacking on trunk and tail but with 2 to 4 parallel rows of strong thorns from behind shoulder girdle to level of first dorsal fin and beyond, the outer rows with the smaller thorns; larger specimens give the impression of a very broad band of heavy thorns along back of trunk and on tail. Upper side appearing very rough by thorns of the mentioned pattern, plus numerous thorns and thornlets scattered on snout, all over pectoral wings and on posterior pelvic lobes; areas between thorns field and rows, however, smooth without dermal denticles, particularly so on rostral sides, outward along orbits to nape, interorbitally, on sides of trunk and along midline of trunk and tail; underside largely smooth, but with growth anterior disc margins from snout tip to level of mouth becoming prickly. Tooth rows in upper jaw 30 to 66 in small juveniles (less than 35 cm total length), less than 54 rows in mature specimens and never more than 66 rows. Colour: above greyish to dark brown, or clouded with light and dark brown; patterned with small dark spots, usually without pseudo-eyespots; underside white to light grey, occasionally some irregular dusky blotches on disc and tail, but sometimes underside of tail totally grey.

Beyond features given above, the only features to distinguish Leucoraja erinacea at all sizes from L. ocellata of corresponding size with some certainty are:
a) upper jaw tooth row counts: 30 to 66 rows in small $L$. erinacea, less than 54 rows in mature specimens, and never more than 66 rows, vs. 44 to 63 rows in immature L. ocellata less than 53 cm TL and usually 90 to 100 rows (maximum 110) in mature specimens more than 53 cm total length. See Table (from McEachran and Musick, 1973) for tooth row development and some overlap with growth by size groups.

|  | 9 to 16 cm | 16 to 21 cm | 21 to 35 cm | $>35 \mathrm{~cm}$ TL |
| :--- | :---: | :---: | :---: | :---: |
| L. erinacea | 30 to 48 | 36 to 53 | 43 to 52 | mostly $<54$ rows |
| L. ocellata | 44 to 55 | 50 to 60 | 58 to 70 | 63 or more rows |

b) absolute size in total length: specimens of $L$. erinacea and $L$. ocellata less than 9 cm total length can virtually not be distinguished by external features only. L. ocellata grows to about twice maximum total length of $L$. erinacea and attain sexual maturity at 53 to 58 cm total length in males, 65 to 73 cm total length in females, vs. about 39 cm total length in males and 40 to 48 cm total length in females of $L$. erinacea.

Distribution: Western North Atlantic: Scotian shelf, Gulf of Maine, Bay of Fundy, on Georges Bank and in general from the Grand Banks, Canada, southward to Cape Hatteras, USA, with the centre of abundance in U.S. waters. Reports from the Gulf of St. Lawrence and estuary are probably misidentified for juvenile L. ocellata.

Habitat: Benthic on sand and gravel bottom, less common on mud or rocky ground. Depth range 10 to 914 m , generally at less than 110 m , and most common at less than 25 m . Temperature range 1.2 to $21^{\circ} \mathrm{C}$, mostly found at less than $15^{\circ} \mathrm{C}$.

Biology: Oviparous, egg capsules very small, 55 to 63 mm in length by 34 to 45 mm in width (excluding horns), with anterior pair of slender horns much longer than posterior pair and longer than the egg case proper. Mating, production and deposition of egg cases appears to be year round without a defined season. Females produce from 28 to 33 egg cases per year. Embryos develop, depending on


Fig. 402 Leucoraja erinacea
$\square$ Known distribution water temperature, within 9 to 12 months until hatching at 9 to 10 cm in length. This small skate feeds on various kinds of small bottom invertebrates, mainly crustaceans, with a preference for Leptocheirus pinguis amphipods, but also takes small fish like Ammodytes and young of larger bony fish.

Size: Maximum length 54 cm , but most less than 48 cm , and a weight to 0.9 kg . Females reach sexual maturity at 40 to 48 cm , and males at about 39 cm in total length. The size at hatching is about 9 to 10 cm in length.

Interest to Fisheries and Human Impact: Although the most abundant skate in Western North Atlantic shelf waters and regularly taken in bottom trawls as bycatch, it is usually not kept and landed because of its very small size and thorniness. Bycatches of this skate are often used locally as bait for lobster traps. A year round reproductive cycle may prevent this skate from experiencing steep population declines as observed for other skate species, also this skate appears to have a good survival rate when discarded. Species of the family Rajidae are subject to TACs in NAFO Divisions 3LNO (2012).

The conservation status is Near Threatened.
Local Names: Common skate, Summer skate, Hedgehog skate, Tobacco box (USA and Canada).
Remarks: Occurring sympatrically with $L$. ocellata throughout most of its distributional range, these two species are difficult to distinguish (except for adult male L. erinacea that are notably smaller) when both species are less than 50 cm total length.

Literature: Bigelow and Schroeder (1953); McEachran and Musick, (1973); Sulikowski, Kulka and Gedamke (2008); Sulak et al. (2009).

## Leucoraja fullonica (Linnaeus, 1758)

Raja fullonica Linnaeus, 1758, Syst. Nat., ed. 10, 1: 231-232. No type material.
Synonyms: None.
FAO Names: En - Shagreen ray; Fr - Raie chardon; Sp - Raya cardadora.


Field Marks: Disc rhombic with rounded outer corners and pronounced, rather pointed snout. Tail solid, a little longer than body. Usually, a complete row of 8 distinct thorns on orbital rims, median ones may be reduced in large adults. Generally with a median row of 3 to 9 thorns on nape. A continuous median row of many moderately small thorns from anterior trunk to first dorsal fin only in young; these thorns becoming with growth totally reduced on trunk, and those along tail becoming smaller but often persist; with growth, a row of about 50 prominent thorns develops on either side of midline from posterior trunk to about first dorsal fin, no thorns between dorsal fins. Upper surface entirely set with dermal denticles, underside also prickly on large areas except for posterior two thirds of pectoral wings. Colour plain ashy-grey above, underside white with faint greyish margin of pectoral fins and posterior pelvic-fin lobes. Darker lines may be present on the dorsal surface, and these may be more pronounced on juveniles.

Diagnostic Features: Disc rhombic with rounded outer corners, undulated anterior margins (strongly so in mature males), pronounced, rather pointed snout (angle about 90 to $110^{\circ}$ ). Tail solid, a little longer than body, gradually tapering to its tip, with two small, close set dorsal fins at rear. Usually, a complete row of 8 distinct thorns on orbital rims, median ones may be reduced in large adults. Although this skate is the type species of genus Leucoraja, it lacks the triangle of thorns over
nape-shoulder region, instead shows a median row of 3 to 9 thorns on nape and midshoulder. Only smaller juveniles have a continuous median row of rather small thorns from anterior trunk to first dorsal fin, whereas larger specimens have these totally reduced on trunk and largely so also along tail. As individuals grow, they develop a row of about 50 prominent thorns on either side of midline from posterior trunk to about first dorsal fin; no thorns between dorsal fins. Upper surface entirely set with dermal denticles, with more or less bare wing centres only in large adults; underside also prickly on large areas except for posterior two thirds of pectoral wings. High counts of 58 to 68 tooth rows in upper jaw, pointed in both sexes and set in parallel rows in larger individuals. Colour: plain ashy-grey above, sometimes with inconspicuous darker bands across disc; underside white with faint greyish margin of pectorals and posterior pelvic-fin lobes, snout region may be dark in specimens.

Distribution: Eastern North Atlantic: off northern Morocco and Madeira and northward to Scotland and southern Iceland, along Norway into western Barents Sea, and in the northern North Sea and Skaggerak; also in western Mediterranean.

Habitat: Demersal on often rough ground on outer shelf and upper slope, occasionally on inner shelf, in relatively cold water in about 30 to 550 m depth; more abundant around 200 m line in northern waters, deeper in the south.


OUTLINE OF FEMALE
Fig. 403 Leucoraja fullonica

There are indications that habitat has shifted to outer shelf and upper slope depths, where this skate will still be within the range of regular bottom trawl fisheries and thus been affected further (Ellis et al., 2006).

Biology: Oviparous, egg capsules about 80 by 50 mm in length and width (excluding horns), anterior pair of horns much longer than the egg case proper and also as the posterior horns. Development of embryos takes several months until hatching. Further biological data are unavailable. Feeds on various benthic invertebrates, with larger individuals consuming bony fishes.

Size: Maximum length 120 cm , but most specimens usually 70 to 80 cm total length.
Interest to Fisheries and Human Impact: A moderately abundant species, this skate is mostly taken as bycatch in bottom trawl, gillnet and longline fisheries targeting other bony fish species. Larger bycatch specimens are usually landed for human consumption. Intensive bottom trawling for other species has resulted in steep declines of its population such that this skate is currently subject to TAC in EU waters.

The conservation status is Near Threatened.

Local Names: Chagrinrochen (Germany); Fuller's Ray, Rough Flapper, French Ray (England and Wales, Ireland); Kaardrog (The Netherlands); Náskata (Iceland); Raia pregada (Portugal); Nebbskate (Norway).

Remarks: L. fullonica is the type species of genus Leucoraja Malm, 1877.

Literature: Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Ellis


Fig. 404 Leucoraja fullonica et al. (2006b); Shark Trust (2009).

## Leucoraja garmani (Whitley, 1939)

Raja garmani Whitley, 1939, Aust. Zool., 9: 248. Lectotype: MCZ 915-S. Paralectotypes: MCZ 585-S (1), MCZ 51759 (1); USNM 43727 (1, or now 0).

Synonyms: Raja ornata Garman, 1881.
FAO Names: En - Freckled skate.


Field Marks: Disc inverse heart-shaped to subrhombic with rounded outer corners and short, bluntly angled snout. Tail moderately slender, longer than body. Typically, a complete row of thorns on orbital rims and a large triangle of many thorns over nape/shoulder region; broad band of thorn rows from behind shoulder girdle to first dorsal fin, consisting of 33 to 35 median thorns and 1 to 3 flanking, rather irregular parallel and lateral (on tail) rows developing with growth, and 1 to 2 thorns in interdorsal space. Upper side rough by thorns, thornlets and dermal denticles on head and around disc margins, only wing centres and sides of trunk smooth in larger specimens; underside smooth. Colour above grey to brown, with distinct pattern of nearly symmetrically arranged large rosette-like blotches of dark spots around a central spot over wings and posterior pelvic-fin lobes, plus narrow dark cross-bands along tail; numerous small dark spots scattered over disc and pelvic fins in addition to rosettes; underside white to pale yellowish.

Diagnostic Features: Disc inverse heart-shaped to subrhombic with rounded outer corners, undulated anterior margins (strongly so in mature males) and short and bluntly angled snout ( 112 to $115^{\circ}$ ). Tail gradually tapering to tip, about 1.5 times longer than body from snout tip to centre of cloaca, with two small, separated dorsal fins at rear. Beyond thorn pattern described under Field Marks, a row of small thorns along each rostral rim to snout tip, often thornlets and prickles on interorbital space; broad band of rough dermal denticles and thornlets from snout tip along anterior disc margins and around outer corner also along posterior disc margins, with a patch of thornlets, which stronger developed in mature females, on inner posterior pectoral fins. Centres of wings and sides of trunk largely smooth in
larger specimens. Dorsal fins separated, with 1 to 2 thorns in interspace. Underside smooth. Tooth rows 46 to 52 in upper, 42 to 50 in lower jaw; teeth set in dense pavement pattern in young and females, with blunt cusp, but more loosely and in nearly parallel rows set in mature males, and with blunt conical cusp. Colour: upper side greyish ochre to brown, freckled with pale dark or light spots, and typically distinctly marked with nearly symmetrically arranged large rosette-like blotches of dark spots around a central spot over wings and posterior pelvic-fin lobes, plus 6 to 8 narrow dark cross-bands along tail, with one through each dorsal-fin origin; underside white to pale yellowish, occasionally with greyish-brown blotches on disc and tail.

Distribution: Western North Atlantic: southern Florida northwards to southern New England, but not confirmed in Canadian waters.

Habitat: Benthic on mainly the outer continental shelf and upper slope at a depth range of 33 to 530 m , but mostly between 74 and 274 m , and with a temperature range of 5.3 to $15{ }^{\circ} \mathrm{C}$ (mostly 9 to $13^{\circ} \mathrm{C}$ ).

Biology: Oviparous, egg capsules very small. Embryos, depending on water temperature, may take from several months to a year or more to develop. Feeds on various benthic invertebrates and small fishes. Very little else is known about its biology.

Size: A small skate, with a maximum length of 57 cm . Size at maturity varies by region with males and females maturing between 33 and 44 cm north of Cape Hatteras, but south of this location maturity is attained between 25 and 32 cm . The size at hatching is about 8 to 9 cm , based on the smallest freeswimming specimens captured.


Fig. 406 Leucoraja garmani
$\square$ Known distribution $\square$ Possible distribution

Interest to Fisheries and Human Impact: A rather common skate in offshore waters along New England and farther south. Although regularly fished in the USA, mostly as bycatch, it is probably not much used due to its small size and thorniness.

The conservation status of this small skate is Least Concern.
Local Names: Rosetted skate, Leopard skate (USA).
Remarks: Given the different life histories of this skate it was previously considered two subspecies, Leucoraja garmani virginica north of Cape Hatteras, and L. g. caribbaea between the Cape and Dry Tortugas (McEachran, 1977). However, the current status of both subspecies, according to the 'Catalog of Fishes', has elevated them to species rank as L. caribbaea (McEachran, 1977), with its distribution only off Mexico, and L. virginica (McEachran, 1977) occurring off the U.S. east coast. Further molecular research may be necessary to determine the status of these two species.

Literature: Bigelow and Schroeder (1953); McEachran (1977); McEachran (2002); Gedamke (2008); Sulak et al. (2009); Eschmeyer and Fricke (2011).

## Leucoraja naevus (Müller and Henle, 1841)

Raja naevus Müller and Henle, 1841, Syst. Beschr. Plag.: 138. Syntypes MNHN 1306, 1332; RMNH 4237 (questionable syntype).

Synonyms: Raja (Leucoraja) naevus, subgenus (Stehmann 1970).
FAO Names: En - Cuckoo ray; Fr - Raie fleurie; Sp - Raya santiguesa.


Field Marks: Disc subcircular with rounded outer corners and short, bluntly angled snout, tip of which a little pronounced. Tail solid, a little longer than body. Typically, a complete row of distinct thorns on orbital rims and a large triangle of thorns over nape/ shoulder region; only juveniles with a median row of thorns from posterior to shoulder girdle to first dorsal fin; larger specimens with median row reduced on trunk and tail and generally with two parallel thorn rows on either side along tail to first dorsal fin, of which only the inner row usually continued onto back of trunk to shoulder region; altogether the impression of a broad band of heavy thorns along trunk and tail. Upper surface entirely spinulose, but wing centres often devoid of dermal denticles in adults; underside largely smooth. Colour above light grey to brown, constantly with a large roundish eye-spot on each inner pectoral centre consisting of blackish background ornamented with yellowish spots and vermiculate stripes; sometimes with more pairs of smaller eye-spots; underside white, with greyish margin to disc and posterior pelvic-fin lobes.


Fig. 407 Leucoraja naevus

Diagnostic Features: Disc subcircular with broadly rounded outer corners, undulated anterior margins (strongly so in mature males), short, bluntly angled snout ( 115 to $130^{\circ}$ ), tip of which a little pronounced. Tail solid, a little longer than body, gradually tapering to its tip, with two small, close-set dorsal fins at rear. Typically, a complete row of 9 to 13 distinct thorns on each orbital rim, median ones may be reduced in adults, and a large triangle of many thorns over nape/shoulder region. Only small juveniles with a median row of thorns from posterior to shoulder girdle to first dorsal
fin; larger specimens with median row reduced on trunk and tail and generally with two parallel rows of heavy thorns on either side along tail to first dorsal fin, of which only the inner row usually continued onto back of trunk to near shoulder region; no thorn between close set dorsal fins. Upper surface entirely spinulose, but often wing centres bare in large adults; underside largely smooth, with dermal denticles only on snout and anterior disc margins. Tooth rows in upper jaw 54 to 60, teeth pointed in both sexes. Colour: upper side ochre to greyish-brown, generally with a pair of large circular eye-spots on inner pectoral centres, which show on blackish background yellowish spots and vermiculate stripes; some specimens show additional, smaller pairs of such eye-spots; underside white, with greyish margin to disc and posterior pelvic-fin lobes.

Distribution: Eastern North Atlantic: off western North Africa to Ireland and Britain, including the northern and central North Sea, Skagerrak and Kattegat; also throughout Mediterranean. Uncommon in the southern North Sea and eastern English Channel.

Habitat: Demersal on sandy and course bottoms on the shelf from 30 to 200 m depth, but less abundant on the upper slope to 500 m ; most common between 50 and 200 m depth.

Biology: Oviparous, egg cases measure 50 to 70 mm in length by 30 to 50 mm in width (excluding horns), with weakly striated but smooth surfaces and the anterior pair of horns very elongated, about twice the length of posterior horns and longer than the egg case proper. Young hatch after about 8 months of embryonic development. Females deposit up to 100 egg cases over the course of a year since this skate does no have a defined


Fig. 408 Leucoraja naevus
 reproductive season. Age at maturity is estimated at 7.4 years for females, and at 6.8 years for males; longevity is about 12 years (Ellis et al., 2008). Juveniles feed on small crustaceans and polychaetes, adults mainly on bony fish, including sandeels (Ammodytidae), dragonets (Callionymidae) and gobies (Gobiidae).

Size: Maximum length 75 cm for females, and 68 cm for males. Size at maturity about 55 cm . Size at hatching from 9 to 10 cm length.

Interest to Fisheries and Human Impact: Although heavily fished, especially by the French fleet in the Bay of Biscay and Celtic Sea, it is also taken in large numbers as bycatch in other targeted fisheries. However, the population has remained relatively stable over the years due most likely to the comparably high reproductive rate per female and its year round reproductive cycle. As a species of the Order Rajiformes is subject to TAC regulations in EU waters and catches of this species should be reported separately (2012).

The global conservation status is Least Concern, but it is Near Threatened in the Mediterranean Sea.
Local Names: Kuckucksrochen (Germany); Grootoogrog (The Netherlands); Gjøkskate (Norway); Raia de dois olhos (Portugal).

Literature: Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Du Buit (1975, 1976a,b); Ellis, Pawson and Shackley (1996); Ellis et al. (2005); Ellis et al. (2005a); Ellis et al. (2008a); Shark Trust (2009); ICES (2010).

## Leucoraja ocellata (Mitchill, 1815)

Raja ocellata Mitchill, 1815, Trans. Lit. philos. Soc. N.Y., 1: 477. No type material available.
Synonyms: None.

FAO Names: En - Winter skate; Fr - Raie tachetée.


## COLORATION

SQUAMATION

Field Marks: Disc subrhombic with rounded outer corners and short, bluntly angled snout. Tail moderately slender, a little longer than body. Small juveniles with thorns along mid-snout on rostral ridges, on orbital rims, interorbitally, 3 to 4 on each shoulder and 12 to 16 thorns on midline of disc from nape to level of pectoral-fin axils, continued by 21 or more thorns along midline of tail to first dorsal fin; median row flanked by an irregular parallel row each side of slightly smaller thorns from behind pelvic girdle to aside dorsal fins; a third irregular thorn row along lower edge of median third of tail. With growth, thorns of middorsal row on disc and tail become reduced in size and get lost in large adults, as well as thorns on rostral ridges and on orbital rims decrease in number and size, whereas thorns on shoulders increase in size and number, and a thorny area develops on each inner, posterior pectoral fin; even larger or mature specimens show a band of 2 to 3 irregular thorn rows along either side of midline on trunk and tail to past the first dorsal fin, and thorns along lower edges of tail are the smallest. Upper side appearing very rough by thorns of the mentioned pattern, plus numerous thorns and thornlets scattered on snout, all over pectoral wings and on posterior pelvic-fin lobes; larger specimens, however, show largely bare areas from rostral sides, outward along eyes and spiracles to nape, on wing centres and along sides of trunk. Underside smooth only in small juveniles but with growth soon prickly on snout tip and along anterior disc margins to level of mouth and beyond in mature individuals. Tooth rows in upper jaw 44 to 63 in juveniles less than 53 cm total length and 90 to 110 rows when mature. Colour: above light brown, usually with pattern of blackish spots in varying numbers; outer and posterior part of wings often with 1 to 4 larger, dark eyespot-like blotches edged light; underside white, sometimes with irregular pale brown blotches of different size on posterior pectoral fins and along tail.

Diagnostic Features: Disc subrhombic with rounded outer corners, undulated anterior margins (strongly so in mature males) and short, bluntly angled snout ( 135 to $150^{\circ}$ ). Tail moderately slender, a little longer than body, with two small, confluent dorsal
fins at rear. Beyond features given under Field Marks, the only features to distinguish Leucoraja ocellata at all sizes from L. erinacea of corresponding size with some certainty are:
a) upper jaw tooth row counts: 44 to 63 rows in immature $L$. ocellata less than 53 cm total length and usually 90 to 100 rows (maximum 110) in mature specimens more than 53 cm total length, vs. 30 to 66 rows in small $L$. erinacea, less than 54 rows in mature specimens, and never more than 66 rows. See Table (from McEachran and Musick, 1973) for tooth row development and some overlap with growth by size groups.

|  | 9 to 16 cm | 16 to 21 cm | 21 to 35 cm | $>35 \mathrm{~cm}$ TL |
| :--- | :---: | :---: | :---: | :---: |
| L. ocellata | 44 to 55 | 50 to 60 | 58 to 70 | 63 or more rows |
| L. erinacea | 30 to 48 | 36 to 53 | 43 to 52 | mostly $<54$ rows |

b) absolute size in total length: specimens of $L$. ocellata and $L$. erinacea less than 9 cm total length can virtually not be distinguished by external features only. L. ocellata grows to about twice maximum total length of $L$. erinacea and attain sexual maturity at 53 to 58 cm total length in males, 65 to 73 cm total length in females, vs. about 39 cm TL in males and 40 to 48 cm total length in females of $L$. erinacea.

Distribution: Western North Atlantic: Labrador (rare) and off south-eastern Newfoundland, Gulf of St. Lawrence, Scotian Shelf, Gulf of Maine, Bay of Fundy and southward to the Carolinas (USA).

Habitat: Benthic on sand and gravel bottoms, less common on mud or rocky ground. Depth range from 10 to 723 m , but generally at less than 110 m , and most common from 37 to 90 m on the Scotian Shelf. The temperature ranges from -1.2 to $19^{\circ} \mathrm{C}$, but typically is from 9 to $15^{\circ} \mathrm{C}$ on the Scotian Shelf.

Biology: Oviparous, egg capsules 55 to 86 mm in length by 35 to 52 mm in width (excluding horns), with anterior pair of solid horns about 1.5 times longer than posterior pair and longer than the egg case proper. Mating, production and deposition of egg cases appear to occur year round without a defined season in most parts of its geographical range. Females produce between 18 and 35 egg capsules per cycle. Embryos develop, depending on water temperature, within 6 to 9 months until hatching at $11.2-12.7 \mathrm{~cm}$ in length


Fig. 410 Leucoraja ocellata
TI (Kulka, Sulikowski and Gedamke, 2004). Feeds on a variety of benthic invertebrates, mainly crustaceans, with larger individuals consuming squids and bony fishes.

Size: Maximum length to least 109 cm , but most common between 70 and 80 cm , and a weight to 3 kg . Females mature between 65 and 73 cm in length, and males at 53 to 58 cm total length, with the size at maturity increasing at higher latitudes.

Interest to Fisheries and Human Impact: Once one of the most abundant skates in the Western North Atlantic shelf waters and regularly taken in bottom trawls as bycatch, it became rapidly overfished, although it has a year round reproductive cycle. Prior to the establishment of a 200 nm Canadian EEZ, Eastern European trawlers fished it, until a directed Canadian fishery began in 1994, and the wings were exported mainly to Europe. Since the early 2000s, the fishery was totally closed on this species in Canadian waters.
The conservation status of this skate is Endangered.
Local Names: Big skate, Eyed skate (USA and Canada).
Remarks: The winter skate occurs sympatrically with L. erinacea throughout most of its distributional range, and it is especially difficult to distinguish both species when they are less than 50 cm in length, except for mature males of $L$. erinacea that are much smaller than L. ocellata.

Literature: Bigelow and Schroder (1953); McEachran and Musick (1973); Kulka, Sulikowski and Gedamke (2004); Sulak et al. (2009).

## Malacoraja Stehmann, 1970

Genus: Malacoraja Stehmann, 1970, Arch. FischWiss. 21(2): 151-152.
Type Species: Raja mollis Bigelow and Schroeder, 1950 by original designation = Malacoraja spinacidermis.
Number of Recognized North Atlantic Species: 3.
Synonyms: Raja (Malacoraja) Stehmann, 1970 as subgenus.
Field Marks: See Diagnostic Features below.
Diagnostic Features: Disc characteristically broadly inverse heart-shaped, with snout at most moderately long and pointed; anterior disc margins straight and also in mature males weakly undulated only. Tail length equal to, or only a little longer (less than $60 \% \mathrm{TL}$ ) than body. Upper disc with dense coverage of velvet-like dermal denticles, likewise but coarser on tail, underside of which at least edged with, or totally covered with dermal denticles. Typically, median row thorns on tail dwindling in size rearward and totally disappearing in posterior third of tail length among dense dermal denticles a fair distance in front of first dorsal fin. Upper side colour usually plain whitish, medium greyish-brown or dark grey to brown; underside plain whitish or dark brown blotched to become with growth almost totally dark.

Remarks: This genus comprises four species all of which occur in the Atlantic Ocean, and with three occurring in the North Atlantic.

## Key to North Atlantic Species:

1a. Upper side plain coloured from light greyish-brown in juveniles to increasingly dark greyish-brown with growth. On underside, tail always totally dark, but disc whitish in juveniles but becoming darker with growth to entirely dark, with a few white markings remaining in mouth-nasal region and along midbelly to cloaca (Fig. 411).

Malacoraja spinacidermis

1b. Upper side plain medium greyish-brown, with obscure dark and light mottling, or plain greyish- to limestone-white. Underside white, and tail never totally dark, at most occasionally dark blotched or dark only in posterior third 2

2a. Pale greyish-white on both surfaces, faint greyish spots may occur on posterior disc margins above and below, as well as dusky blotches on anterior pelvic-fin lobes above (Fig. 412)

Malacoraja kreffti

2b. Medium greyish-brown above, with rather obscure dark mottling and spots and sometimes pale blotches; small juveniles with 2 to 4 pale, dark edged cross-bars along tail fading with growth and totally disappearing from about half maximum size onward. Underside of disc and pelvic fins white, occasionally with a few small dusky spots on outer pectoral fins and snout; underside of tail either white, or irregularly dark blotched, or totally dark in posterior third (Fig. 413) . . . . . . . Malacoraja senta


Fig. 411 Malacoraja spinacidermis


Fig. 412 Malacoraja kreffti


## Malacoraja kreffti (Stehmann, 1977)

Raja (Malacoraja) kreffti Stehmann, 1977, Arch. FischWiss. 28(2/3): 77-93. Mature male holotype ISH 748-1974 = ZMH 25256 (Thiel et al. 2009).

Synonyms: None.
FAO Names: En - Krefft's ray; Fr - Raie de Krefft; Sp - Raya de Krefft.



SQUAMATION


Dorsal view


Ventral view

DETAIL OF TAIL
Illustrations by M. Stehmann
Fig. 414 Malacoraja kreffti
Field Marks: A relatively small deepwater skate. Disc inverse heart-shaped, broader than long, with rounded outer corners and moderately elongated, narrowly angled snout. Tail moderately slender, longer than body. Very typically, no thorns along back of trunk and tail behind shoulder girdle; just a few very small pre- and 1 to 2 postorbital thorns. Upper surface entirely spinulose with fine, close-set dermal denticles, which are coarser and hooked only on midline of body and tail. Underside smooth, except for prickly edges of tail. Colour plain greyish-white above and below.

Diagnostic Features: Disc evenly inverse heart-shaped, broader than long, with thin outer margins, rounded outer corners, almost straight anterior margins (weakly undulated in mature males); snout moderately elongated and pointed (angle 99 to $100^{\circ}$ in mature males, $115^{\circ}$ in mature females). Tail gradually tapering to tip, a little longer than body from snout tip to centre of cloaca, with two small confluent dorsal fins at rear and no thorn in between. The velvet-like, dense coverage with fine dermal denticles on upper wings is quite typical for this skate, with spinules on back of trunk and tail being coarser and hooked, and thorns are totally absent on snout and particularly posterior to shoulder girdle (except for malar and alar thorn patches of mature males) and on tail; at most a few very small thorns/thornlets in front of eyes and 1 to 2 behind. Underside of disc and pelvic fins smooth, only underside of tail with marginal bands of prickles over entire length or only partially, stronger prickly in large females than in males. Upper jaw teeth closely set in 59 to 66 rows, in pavement pattern and with blunt cusp in large females, whereas mature males show elongated, sharply pointed tooth cusp and pattern of close-set parallel rows. Colour: plain pale greyish-white above and below, side areas of rostrum semitransparent, with rostral cartilage thus clearly visible. Back of trunk and tail a little darker pale greyish, as well as prickly areas on underside of tail. Upper side of anterior pelvic-fin lobes either pale greyish, or with dusky blotches. Posterior disc margins above and below with scattered pale greyish spots.

Distribution: Eastern North Atlantic: off southwestern Iceland (Jónsson \& Pálsson, 2006), Rockall Trough (Stehmann, 1993), Porcupine Seabight (Dransfeld et al. 2007, Johnston et al. 2010), and the northern Mid-Atlantic Ridge; may also occur southwards along the Mid-Atlantic Ridge.

Habitat: Demersal in deepwater at 1,000 to $1,500 \mathrm{~m}$ depth, but may occur deeper.

Biology: Oviparous, but egg cases unknown at this time. Preferred prey unknown but probably includes benthic invertebrates such as crustaceans.

Size: A moderately small skate, with maximum length of about 60 cm . Males and females attain sexual maturity at about 50 cm in length. Small young and size at hatching unknown.

Interest to Fisheries and Human Impact: A rare deepwater skate only sporadically taken by deepwater fisheries as bycatch and most likely discarded except for a few specimens preserved for scientific reference collections.


Fig. 415 Malacoraja kreffti

The conservation status of this poorly known deepwater skate is Least Concern.
Remarks: Due to the rarity of this deepwater skate, specimens if taken should be preserved and forwarded to national research institutes for study.

Local Names: Bleikskata (Iceland); Kreffts Rochen (Germany).
Literature: Stehmann (1977); Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Stehmann (1993); Jónsson and Pálsson (2006); Dransfeld et al. (2007); Smale and Kulka (2007); Stehmann and Orlov (2007); Thiel et al. (2009); Johnston et al. (2010).

## Malacoraja senta (Garman, 1885)

## Raja senta Garman, 1885, Proc. U.S. natl. Mus., 8: 43. Syntype: USNM 21004, one specimen possibly lost?

Synonyms: None.
FAO Names: En - Smooth skate; Fr - Raie lisse américaine; Sp - Raya lisa norteamericana.


## Fig. 416 Malacoraja senta

Field Marks: A small skate. Disc inverse heart-shaped, broader than long, with rounded outer corners and moderately elongated, narrowly angled snout. Tail moderately slender, somewhat longer than body. Typically, median row thorns along trunk and onto tail becoming smaller rearward to totally disappear in posterior half or third of tail; orbital, median nuchal and shoulder thorns present. Parallel and lateral thorn rows absent on trunk and tail. Upper side of juveniles and larger females with dense coverage of fine, velvet-like dermal denticles, particularly so on entire tail and dorsal fins, and pectoral centres and trunk becoming largely smooth only in mature males; underside largely smooth, but underside of tail totally or marginally densely prickly (may be smooth only in mature males). Colour above medium greyish-brown, often patterned by many obscure dark spots, and with large areas aside rostral cartilage glassy translucent; small juveniles show two pale, dark-edged cross-bars on tail. Underside of disc and pelvic fins white, occasionally with a few small dusky spots on outer pectoral fins and snout; underside of tail either white, or irregularly dark blotched, or totally dark in posterior third.

Diagnostic Features: Disc evenly inverse heart-shaped, broader than long, with rounded outer corners, almost straight anterior margins (weakly undulated in mature males), and its outer margins very thin with pectoral-fin radials visible; snout moderately elongated and pointed (angle about $110^{\circ}$ ). Tail gradually tapering to tip, a little longer than body from snout tip to centre of cloaca, with two small confluent dorsal fins at rear. The velvet-like, dense coverage with fine dermal denticles on upper side (except for translucent side areas of rostrum) is quite typical for this skate, as well as the absence of thorns in posterior half or third of tail (except for small juveniles); underside largely smooth, but with growth fine prickles developing in narrow band only along anterior disc margins halfway from snout, and typically underside of tail totally and densely covered by dermal denticles, at least with dense marginal bands and only midline smooth; only maturing males may show smooth underside of tail. Generally no thorns on snout. Small juveniles with individual pre- and postorbital, supraspiracular, median nuchal and scapular thorns, as well as a continuous median rows of 30 to 40 thorns from behind shoulder girdle to first dorsal fin, but these median thorns becoming smaller along tail. Larger specimens with increased number of orbital thorns, often forming complete half-circle on orbital rims, median nuchal and shoulder thorns, and typically median row thorns dwindling in size rearward on tail to totally disappear in posterior half or one third of tail length within the very dense coverage with dermal denticles; mature males with a patch of malar thornlets opposite each eye and a field of hooked alar thorns across outer wing corners. Parallel and lateral thorn rows absent on trunk and tail. Upper jaw teeth with blunt cusp in juveniles and large females, closely set in pavement pattern of 38 to 40 rows, whereas mature males shows
elongated, sharply pointed tooth cusp and pattern of close-set parallel rows. Colour: medium greyish-brown above, with rather obscure dark mottling and spots and sometimes pale blotches; small juveniles with 2 to 4 pale, darkedged cross-bars along tail fading with growth and totally disappearing from about half maximum size onward. Underside of disc and pelvic fins white, occasionally with a few small dusky spots on outer pectoral fins and snout; underside of tail either white, or irregularly dark blotched, or totally dark in posterior third.

Distribution: Western North Atlantic: Strait off Belle Isle off Labrador, Gulf of St. Lawrence and St. Lawrence River, Flemish Cape, Grand Banks, Scotian Shelf, Bay of Fundy to Georges Bank; older records (Bigelow and Schroeder, 1953) from as far south as off New York and New Jersey (USA).

Habitat: Benthic on most kinds of bottom substrates, mainly on the outer continental shelf and upper slope at a depth range of 25 to $1,436 \mathrm{~m}$, but most commonly from 70 to 480 m , and at temperatures of -1.3 to $15.7{ }^{\circ} \mathrm{C}$; mostly at 2.5 to $10^{\circ} \mathrm{C}$.

Biology: Oviparous, egg capsules very small at 56 to 59 mm length by 38 to 45 mm width (excluding horns), dark brown to blackish when found deposited or empty, with smooth surfaces, of which one is flat and the other one strongly convex; the horns are thick and at least as long as the capsule proper. Embryos, depending on water temperature, may take


Fig. 417 Malacoraja senta several months to development until hatching at about 10 cm total length. Smallest specimens found were 8.3 to 8.7 cm in length. Fecundity estimated at about 100 egg capsules. Maturity is reached at between 8 and 10 years of age. Feeding on various kinds of small benthic invertebrates, and appears to be selective for small crustaceans; larger individuals consume bony fishes (Sulikowski et al., 2004).

Size: A small skate with a maximum length of 70 cm . Females reach sexual maturity at 41 to 54 cm in length, and males at about 49 to 57 cm . Size at hatching is between 8 and 10 cm .

Interest to Fisheries and Human Impact: A moderately common skate regularly taken as bycatch but probably not much used due to its small size and thin disc. U.S. NMFS has forbidden possession and landing of smooth skate from the Gulf of Maine Regulated Mesh Area (NOAA, 2011). Status presently reviewed by Canada.

The conservation status is Endangered.
Local Names: Smooth-tailed skate, Prickly skate, Raie lisse (USA and Canada).
Literature: Bigelow and Schroeder (1953); Sulikowski et al. (2004); Sulak et al. (2009); NOAA (2011).

## Malacoraja spinacidermis (Barnard, 1923)

Raja spinacidermis Barnard, 1923, Ann. S. Afr. Mus., 13: 440 . Holotype female ( 600 mm TL) transferred from SAM to BMNH coll. no. 1935.7.19.7.

Synonyms: Raja mollis Bigelow and Schroeder, 1950.

FAO Names: En - Soft skate; Fr - Raie peau hérissée; Sp - Raya piel áspera.


Field Marks: A relatively small deepwater skate. Disc inverse heart-shaped, broader than long, with rounded outer corners, and moderately elongated, narrowly angled snout. Tail moderately slender, a little longer than body. Very typically, no thorns along back of trunk and tail behind shoulder girdle; just 1 to 2 small pre- and postorbital, 1 small mid-nape and mid-shoulder thorn, and 1 to 2 small shoulder thorns in smaller specimens which may become reduced or get lost in adults. Entire upper surfaces densely covered with fine dermal denticles, velvet-like to touch, but underside smooth except for usually totally prickly tail. Colour above plain from light greyish-brown in smaller individuals to darker grey in adults, with semi-translucent areas flanking rostrum; underside white in small juveniles, with scattered grey speckles, but underside of tail always totally dark grey; larger specimens becoming increasingly dark on disc and pelvic fins to nearly match colour of underside of tail, but creamy-white patches remain medially.

Diagnostic Features: Disc evenly inverse heartshaped, broader than long, with very thin outer margins and almost straight anterior margins (weakly undulated in mature males); snout moderately elongated and pointed (angle about $115^{\circ}$ ). Tail gradually tapering to tip, a little longer than body from snout tip to centre of cloaca, with two small confluent dorsal fins at rear. The velvet-like, dense coverage with fine dermal denticles on upper side is quite typical for this skate, as well as the total absence of thorns on snout and particularly posterior to shoulder girdle and on tail (except for malar and alar thorn patches of mature males); only smaller juveniles have individual small thorns pre- and postorbitally, medially on nape and shoulder and on each shoulder, but these often becoming reduced with growth and may totally disappear. Underside of disc and pelvic fins smooth, except for narrow bands of fine spinules along anterior disc margins, whereas underside of tail always totally prickly. Upper jaw teeth with blunt cusp in juveniles and large females, closely set in pavement pattern of 54 to 60 rows, whereas mature males show elongated, sharply pointed tooth cusp and pattern of close-set parallel rows in median two fourths of jaws. Colour: plain light greyish-brown above at smaller size, darker grey to brown in adolescent and adult specimens, with semi-translucent areas flanking rostrum; underside of disc predominantly white only in smaller juveniles, with
some dark specks irregularly scattered, but underside of tail marked off totally dark brown-grey; with growth becoming predominantly as dark as underside of tail, with creamy-white patches remaining around mouth, interbranchially, at cloaca and in pectoral axils.

Distribution: Atlantic Ocean: off western North Africa (Stehmann 1995), Rockall Trough, Iceland-Faroe-Ridge, off South Iceland (Jónsson and Pálsson 2006), around southern Greenland (Nakaya, 1995) and across the Davis Strait to off the Grand Banks, Scotian slope and Georges Bank. Elsewhere, originally described from off South Africa, but also known from off Namibia (Ebert, Cowley, and Compagno 1991).

Habitat: Demersal in deepwater between 475 and $1,570 \mathrm{~m}$, usually deeper than $1,000 \mathrm{~m}$ depth, and adults may live deeper than $1,500 \mathrm{~m}$ and down to the abyssal plains.

Biology: Oviparous, egg cases small, partially described from South African specimens (Ebert, Compagno, and Cowley 2007). The diet of this skate includes crustaceans, mainly shrimps, and small benthic fishes.

Size: A moderately small skate, with


Fig. 419 Malacoraja spinacidermis
$\square$ Known distribution $\square$ Possible distribution a maximum length of about 71 cm TL. Size at maturity is about 59 cm for females, and 58 cm for males. Size at hatching uncertain, but the smallest freeswimming specimen was 12.7 cm in length (Ebert, Compagno, and Cowley 2007).

Interest to Fisheries and Human Impact: A rare deepwater skate only sporadically taken by deepwater fisheries as bycatch and discarded or preserved for scientific reference.

The conservation status is Least Concern.
Local Names: Roughskin skate, Prickled ray, Raie molle, Raie profonde (USA and Canada); Sjafnarskata (Iceland); Lådden rokke (Denmark and Greeland); Samthautrochen (Germany).

Remarks: Raja mollis Bigelow and Schroeder, 1950 (= M. spinacidermis) is the type species of the genus Malacoraja Stehmann, 1970. As so little is known of this rare deepwater skate, specimens taken should be preserved and forwarded to national research institutes.

Literature: Bigelow and Schroeder (1953); Hulley (1970); Hulley and Stehmann (1977); Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Ebert, Cowley, and Compagno (1991); Nakaya, Rajidae, in: Okamura et al. (1995); Stehmann (1995); Jónsson and Pálsson (2006); Ebert, Compagno, and Cowley (2007); Sulak et al. (2009).

## Neoraja McEachran and Compagno, 1982

Genus: Neoraja McEachran and Compagno, 1982, Bull. Mar. Sci. 32(2): 399-425.
Type Species: Breviraja caerulea Stehmann, 1976 by original designation.

## Number of Recognized North Atlantic Species: 3 .

Synonyms: Breviraja (partim), Neoraja (Neoraja) subgenus.

Field Marks: See Diagnostic Features section below.
Diagnostic Features: Skates of pygmy size growing to maximum 30 to 35 cm total length only - apparent in mature males of such small size. Disc shape subrhombic to subcircular, with anterior margins strongly undulated in mature males. Snout short and bluntly angled. Tail distinctly longer than body (about $60 \% \mathrm{TL}$ ). Upper disc and tail with dense coverage of fine dermal denticles; underside of tail at least edged with, or totally covered with dermal denticles. Typically, median row thorns on tail dwindling in size rearward and totally disappearing in posterior third of tail length among dense dermal denticles a fair distance in front of first dorsal fin. Nasobasal fenestrae absent in nasal capsules of cranium; rostral shaft continuous to rostral node, but abruptly narrowing in front of broad basal triangle, with very long rostral appendices extending rearward to level of basal triangle. Scapulocaracoid with large anterior fenestra not divided by anterior bridge, and with a single large postdorsal and postventral fenestra; scapulocoracoid displaying distinct sexual dimorphism: rectangular, with marked angular rear corner in females, whereas overall shape ovoid in males, with rear corner rounded and sloping diagonally to metacondyle. Accessory terminal 1 cartilage of clasper skeleton typically double U-shaped. Colour: light ochre to medium greyish-brown above and with apparent pattern of symmetrically arranged white and dark brown dots and spots, with underside white in only one species; remaining species plain dark or bluish on upper disc without any pattern, and underside largely to totally dark.

Remarks: The genus is comprised of five species, with three occurring in the Eastern North Atlantic; one species occurs just south of this catalogue's area in the Western North Atlantic.

## Key to North Atlantic Species:

1a. Upper disc conspicuously bluish, with back of trunk and tail marked off greyish-white, and tail with several faint dusky crossbars. Underside of disc and origin of pelvic fins centrally white, or largely blotched dark to nearly totally dark, but always a broad blackish margin around disc and to posterior pelvic-fin lobes; underside of tail marked off whitish at least in posterior half (Fig. 421)

Neoraja caerulea

1b. Upper disc plain greyish-brown, or ochre to medium greyishbrown with apparent pattern of few pale and more numerous dark brown spots and blotches, less so with growth, in symmetrical arrangement; back of trunk and tail of equal ground colour as disc, with either no crossbars at all on tail, or these very indistinct. Underside either plain medium dark, or predominantly white, with at most faint ochre margins to disc and pelvic fins, faint brownish blotches may occur centrally on disc and also on tail

2a. Disc subcircular, anterior margins strongly undulated in mature males. Upper side ochre to medium greyish-brown, with apparent pattern of few pale and more numerous dark brown spots and blotches, less so with growth, in symmetrical arrangement. Underside largely white, with at most faint brownish margin to disc and pelvic fins, but pale brown blotches may occur centrally on disc and also on tail (Fig. 422)

Neoraja iberica

2b. Disc inverse heart-shaped, with anterior margins also in mature males evenly convex and not undulated, snout rather narrowly angled and pointed. Upper side plain greyish-brown, without any pattern, and underside somewhat lighter plain greyish-brown (Fig. 423)

Neoraja sp.


Fig. 420 Neoraja caerulea


Fig. 421 Neoraja iberica


Fig. 422 Neoraja sp.

## Neoraja caerulea (Stehmann, 1976)

Breviraja caerulea Stehmann, 1976, Arch. FischWiss., 27(2): 97-114. Mature male holotype ex-ISH 90-1974a, now ZMH 24050; 11 paratypes both sexes ZMH 24043-24049, 24051-24052.

Synonyms: None.
FAO Names: En - Blue ray; Fr - Raie pygmeé azuré; Sp - Raya pigmea azul.


Fig. 423 Neoraja caerulea

Field Marks: A very small deepwater pygmy skate. Disc roundish, with outer corners broadly rounded. Snout extremely short and obtusely angled. Tail distinctly longer than body. Up to 12 small thorns on each orbital rim, 4 to 6 median thorns along nape and on midshoulder, 1 to 3 thorns on each shoulder. From short distance behind shoulder girdle, a somewhat irregular median row of 33 to 58 small thorns along trunk and tail but ending at about two thirds tail length distinctly before first dorsal fin. Upper side entirely and densely spinulose, underside smooth, except for marginal bands of prickles on tail. Colour of upper disc and pelvic fins violet-blue (fresh), sometimes clouded with greyish-brown; back of body and tail marked off light greyish, and tail with 6 to 9 dark cross-bars. Central disc and pelvic region below usually white, with some dark blotches on midbody, but broad blackish-brown margin around disc and to posterior pelvic-fin lobes; underside of tail light. Specimens with almost entirely dark underside do occur.

Diagnostic Features: Disc roundish, with outer corners broadly rounded and anterior margins convex to weakly undulated, but strongly undulated in mature males. Snout extremely short and obtuse (angle 131 to $145^{\circ}$ ), soft and flexible due to very delicate rostral shaft; often with short integumental filament at tip which best developed in mature males. Tail distinctly longer (about 60\% of total length) than distance snout tip to mid-cloaca, relatively slender and gradually tapering to tip; two small dorsal fins with confluent bases at very rear, postdorsal tail section extremely short. Upper side almost completely and densely covered with fine dermal denticles, even on pectoral centres of mature males; patches of 4 to 7 small thorns pre- and 2 to 5 postorbitally, usually not forming complete half-rings but separated by gap supraorbitally; 4 to 6 thorns medially along nape and midshoulder, of which 1 to 2 in suprascapular position, and 1 to 3 thorns on each shoulder; median row of 33 to 58 closely set thorns from some distance behind shoulder girdle becoming somewhat irregular on tail, where ending at about two thirds tail length far before first dorsal-fin origin and continued to first dorsal fin as a shallow median groove devoid of dermal denticles; sides of tail set with coarse, hooked dermal denticles. Underside smooth, only marginal, narrow bands of prickles along tail. Dentition with 47 to 55 rows of upper jaw teeth, which show blunt cusp in juveniles and larger females and are set in pavement pattern, whereas teeth of mature males with elongated and pointed cusp and set in parallel rows. Colour: upper disc and pelvic fins very apparent violet-blue (fresh), sometimes clouded with greyish-brown; back of body and tail marked off light greyish, and tail with 6 to 9 dark cross-bars; after preservation, the blue shade remains at least on head, sides of trunk and posterior pelvic-fin lobes. Irregular pale specks may occur along posterior disc margins. Colour and pattern of underside relatively variable; usually snout dark, mouth-nasal region and line of gill slits white, as well as centre of disc to pelvic-fin origin and tail; a very broad blackish-brown margin from outer disc corners along posterior margins and on posterior pelvic-fin lobes, much narrower along anterior disc margins; but dark blotching mostly occurring to varying extent on creamy-white midbody to the extreme of almost totally dark ventral side with only small white markings on head and midbody; tail always marked off lighter, even if blotched pale greyish or marbled with dark, but with subdorsal section white.

Distribution: Eastern North Atlantic: apparently regionally endemic to the slopes and adjacent banks along the Rockall Trough, west off Scotland and Ireland and Bay of Biscay. RodriguezCabello et al. (2011) reported on a range extension southward to deep water of the southern Bay of Biscay off Galicia.

Habitat: A pygmy skate with a very restricted distribution. Demersal in deepwater from 600 to 1260 m depth and at temperatures between 6.4 and $9.1^{\circ} \mathrm{C}$ (mostly 6.4 and $6.9^{\circ} \mathrm{C}$ ) and a salinity of 35.17 to 35.33 ppm , i.e. within the Eastern North Atlantic water mass, so that its maximum depth range is likely not much deeper than about 1300 m . Iglésias (2011) listed a mature male of 31.9 cm TL from 1479 to 1518 m depth taken southwest off Ireland in the Porcupine Seabight.

Biology: Oviparous, but egg capsules not described. The diet consists mostly of small benthic invertebrates, including polychaetes and amphipods. Little else is known of the biology of this pygmy skate.


Fig. 424 Neoraja caerulea
$\square$ Known distribution

Size: Maximum length about 30 to 35 cm . Maturity for males between 20 and 25 cm ; a male 19.6 cm was immature while one 27 cm was mature. Female size at maturity is uncertain at this time. Size at hatching not reported.

Interest to Fisheries and Human Impact: A rare deepwater pygmy skate sporadically taken on occasion by deepwater fisheries as bycatch, but discarded because of its very small size. As a species of the Order Rajiformes is subject to TAC regulations in EU waters (2012).

Although its conservation status is currently Data Deficient, its occurrence within deepwater fishing grounds combined with its apparent limited geographic distribution may make it vulnerable to fishing pressures.

Remarks: Johnston et al. (2010) reported several specimens captured from Irish deepwater surveys in the Porcupine Seabight, but did not provide any further information on the length, sex or depth. A very rare, poorly known, deepwater pygmy skate that if captured should be retained, preserved and deposited in national research institutes for further study.

Local Names: Blauer Zwergrochen (Germany); Raie bleue (France); Blauwe dwergrog (the Netherlands).
Literature: Stehmann (1976); Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Gordon and Duncan (1989); Séret and Stehmann (2004); Johnston et al. (2010); Iglésias (2011); Rodriguez-Cabello et al. (2011).

## Neoraja iberica Stehmann, Séret, Costa and Baro, 2008

Neoraja iberica Stehmann, Séret, Costa and Baro, 2008, Cybium 32(1): 51-71. Mature male holotype MB 4869. Totally 49 paratypes both sexes and all sizes at MB 4870-4878; MNCN 259.151-259.164; MNHN 2007-0013 - 0018, 2007-0124 -0125; TCWC 13204.01, 13205.01; ZMH 25427-25438.

Synonyms: None.
FAO Names: En - Iberian pygmy skate; Fr - Raie pygmeé ibérique; $\mathbf{S p}$ - Raia pigmea ibérica.



## SQUAMATION

## JUVENILE

Fig. 425 Neoraja iberica

Field Marks: A very small pygmy skate in moderately deep upper slope water. Disc inverse heart-shaped to subrhombic, broader than long, with outer corners broadly rounded. Snout extremely short and obtusely angled, with short, triangular projection at tip. Tail distinctly longer than body. Up to 13 small thorns on each orbital rim, 2 to 7 median thorns along nape and on midshoulder, 0 to 4 thorns on each shoulder. Distinct median thorns from anterior trunk onto tail with mostly 35 to 40 apparent thorns to about half or two thirds tail length but becoming very indistinct on posterior half of tail to first dorsal fin. Upper side entirely and densely covered with fine dermal denticles; underside smooth, except for narrow marginal bands of prickles on tail. Colour above ochre (mainly in small young) to medium greyish-brown or greyish in larger specimens; upper side ornamented with many dark brown spots and dots and frequently a few paired whitish spots in small and half-grown specimens, all often reduced in larger size specimens to few pairs of larger symmetrically placed brown, pale edged spots, plus 1 to 2 pairs of pale spots or dots; tail with 7 to 8 more or less distinct dark cross-bars or asymmetrically placed saddle blotches; underside of disc and tail white, at most pale greyish margin to pectoral-fin corners and posterior margins, and occasionally a cloud of merged pale brownish spots centrally on each pectoral wing.

Diagnostic Features: Disc inverse heart-shaped to subrhombic, broader than long, with outer corners broadly rounded and anterior margins convex to weakly undulated, but stronger undulated in mature males. Snout very short and obtuse (angle 119 to $145^{\circ}$ ), soft and flexible due to very delicate rostral shaft; usually with short, triangular integumental projection at tip. Tail distinctly longer (about 60\% of total length) than distance snout tip to mid-cloaca, slender and gradually tapering to tip; two small dorsal fins with mostly confluent bases at very rear. Upper side almost completely and densely covered with fine dermal denticles, even on pectoral centres of mature males; coarser spinules set often in rows along sides of trunk and particularly on sides of tail, where they are of nearly thornlet size and hooked. Patches of 2 to 8 , mostly 4 to 6 , small thorns pre- and 2 to 5 (mostly 2 to 4 ) postorbitally, usually not forming complete half-rings but separated by gap supraorbitally, and usually a pair of small conical interspiracular thorns; 2 to 7 (mostly 4) thorns medially along nape and midshoulder, of which 1 to 2 in suprascapular position, and 0 to 4 thorns on each shoulder; distinct median thorns set at equally short interspaces from anterior trunk to level of pectoral axils usually in rather regular line of 7 to 17 (mostly 10 to 15 ); this median row continued onto tail where becoming more irregular and thorns reduced in size to finally after half or two thirds of tail length disappear by becoming indistinguishable from dermal denticles on tail; in average, about 60 median thorns from posterior to shoulder girdle onto tail. Underside smooth, except for extreme edge of tail set with dermal denticles encroaching from sides of tail. Upper jaw teeth 40 to 52 rows; teeth of small young and females set in pavement pattern, whereas in mature males close-set in parallel rows in outer thirds of jaw but medially in pavement; individual teeth at all sizes and in both genders with rhombic base bearing a short conical cusp. Colour: upper side ground colour and pattern changing very apparent from small young to halfgrown and mature specimens. Small young dorsally ochre-brown, with lively pattern, including rostral area and eyeballs, to extreme edges of disc and posterior pelvic lobes of dark brown oval to circular dots and spots, of which several symmetrical pairs on inner parts of both pectorals are larger and pale edged; mostly two pairs of circular whitish spots are found on inner pectorals level with posterior nape (the larger) and level with posterior trunk (the smaller), and although fading
with growth these do often also remain in larger specimens; usually eight blackish-brown cross-bars or somewhat asymmetrically paired saddle blotches along tail more apparent in small specimens. Larger specimens turn to greyishbrown ground colour, with much reduced pattern of scattered dark dots and spots, and only one or a few pairs of the larger dark spots and eventually one or two pairs of the pale or whitish dots remain, or specimens may even appear nearly plain greyish-brown. The white underside of disc displays seemingly in smaller specimens with very thin disc margins dark spots and dots, which however are translucent from the dorsal pattern; the intensity of the broad greyish margin to outer disc corners and posterior margins, as well as that to posterior pelvic-fin lobes, varies but becomes indistinct rather in larger specimens; these also show rather regularly large clouds variously on inner ventral pectoral fins of more or less distinct medium brown spots merging to various degrees.

Distribution: Eastern North Atlantic: upper slope of the southern Iberian Peninsula within Bay of Cadiz only; an endemic pygmy skate with a very restricted distribution. RodriguezCabello et al. (2011) however reported on a mature male of 35 cm total length taken at 784 m depth in the southern Bay of Biscay off Galicia, which is a considerable range externsion northward.

Habitat: Demersal on upper slopes on fine sand, occasionally muddy-sand bottoms at depths of 270 to 670 m and a bottom temperature and salinity of approximately between 12.8 and $14^{\circ} \mathrm{C}$ and 36.18 and 37.20 psu, respectively. The latitudinal, longitudinal and depth distribution of this skate is sharply restricted by the water mass of the Mediterranean outflow into the Atlantic along the Bay of Cadiz slopes, but see new record above.

Biology: Oviparous, but egg capsules not yet reported. Nothing is known about the diet of this pygmy skate, but given its relatively small mouth it likely feeds on small benthic invertebrates.

Size: A pygmy skate with a maximum length 30 to 35 cm ; the largest reported female was 31.6 cm and the largest male 32.7 cm (but see new record above). Maturity is attained for males and females between 25 and 30 cm in length; an adolescent male was 27.8 cm while an adult male was 29.5 cm in length. Size at hatching small, with the smallest freeswimming neonate measured 5.5 cm in length.

Interest to Fisheries and Human Impact: Since this pygmy skate occurs within the depth range of commercial fisheries for fish and shrimps off the Portuguese Algarve and the Spanish Cadiz coasts, it is probably taken regularly as bycatch, but discarded because of its very small size.

The conservation status of this regional endemic pygmy skate is currently Data Deficient, but its population may be impacted due to deepwater fisheries occurring throughout its range.

Remarks: As so little is known of this pygmy skate, specimens taken should be preserved and forwarded to national research institutes for mainly biological investigations and population assessment.

Local Names: Raia pigméia ibérica (Portugal); Iberischer Zwergrochen (Germany).
Literature: Stehmann and Valenti (2008); Stehmann et al. (2008); Rodriguez-Cabello et al. (2011).

Neoraja sp. sensu Stehmann et al. (2008)
Synonyms: Raja fullonica (non Linnaeus) Vaillant (1888), Stehmann (1973); Breviraja spec. in Stehmann (1976, 1979); Breviraja sp. in Stehmann and Bürkel (1984).

FAO Names: None.


Fig. 427 Neoraja sp.

Field Marks: See Diagnostic Features below.
Diagnostic Features: A pygmy skate with disc evenly inverse heart-shaped, broader than long, outer corners broadly rounded and anterior margins convex and not undulated though the only record is a mature male. Snout extremely short and obtusely angled. Tail distinctly longer than body, slender, gradually tapering to tip and with two small, clearly separated dorsal fins at rear. Upper surface of disc and tail completely covered with fine dermal denticles, with stronger, hooked denticles on sides of tail; underside smooth. A row of 6 thorns along each orbital rim, 2 median thorns on nape, and a median row of about 50 smaller thorns from behind shoulder girdle onto tail but ending at two thirds tail length and far in front of first dorsal fin. Dorsal fins clearly separated, both with very short bases, conspicuous height but narrow surface; postdorsal tail section very long, about twice the length of combined dorsal-fin bases. Colour: uniformly brown above and below.

Distribution: A single mature male only taken by RV 'Travailleur' in 1882 on the slope off northern Spain at $43^{\circ} 47^{\prime} \mathrm{N}, 06^{\circ} \mathrm{W}$, i.e. in the southern Bay of Biscay, but its specific capture locality not absolutely confirmed.

Habitat: The only known record was taken at 614 m depth. The species probably lives in moderately deep water on the upper slope.

Biology: Probably oviparous like all congeners, but nothing else known.

Size: A pygmy skate, with the only known specimen a mature male measuring about 26 cm total length.

Interest to Fisheries and Human Impact: No information available, but it may be taken as bycatch in deepwater fisheries.

The conservation status ofthis undescribed pygmy skate has not been assessed.

Remarks: The only known specimen, a mature male, badly disintegrated and partly skeletonised, is deposited at the National Museum of Natural History in Paris under MNHN 83-149 and has been investigated by M. Stehmann (Unpubl. Data). The skeletonised clasper has features that undoubtedly assign it to the genus Neoraja (see Stehmann et al. 2008), but also this specimen has a number of distinguishing, specific characters separating it from its five named and valid congeners in the Western North and Eastern Atlantic.


Fig. 428 Neoraja sp. Vaillant (1888) originally described and illustrated it as Raja fullonica Linnaeus, 1758, but this specimen is clearly not that species. There are some doubts about the correct capture locality of the specimen. If it is correct and was taken within the southern Bay of Biscay at 614 m depth, it is surprising that no additional specimens have ever been discovered since the late $19^{\text {th }}$ century, although its depth is within the range of regular, intensive commercial fishery activities at least since the middle of the $20^{\text {th }}$ century. However, two of its congeners, $N$. caerulea and $N$. iberica, both of which occur at comparable depth ranges have only recently been discovered in these intensive deepwater fisheries, and it is possible that the small size of these skates has precluded them from being reported more frequently since they are usually discarded bycatch. Hence, there is an urgent need to alert fishermen along the north coast of Spain and in the southern Bay of Biscay to keep their eyes open for such pygmy skates and to retain, preserve and forward suspicious specimens to national research institutes for investigation; these skates should be relatively easy to recognize due to the "pygmy" size of mature males with fully developed claspers.

Local Names: None.
Literature: Vaillant (1888), Stehmann, Rajidae, in Hureau and Monod (1973); Stehmann (1976, 1979); Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Stehmann et al. (2008).

## Raja Linnaeus, 1758

Genus: Raja Linnaeus, 1758, Syst. Nat., ed. 10, 1: 232.
Type Species: Raja miraletus Linnaeus, 1758 by subsequent designation of Bonaparte (1838).

## Number of Recognized North Atlantic Species: 8.

Synonyms: Raja (Raja) Linnaeus, 1758 as subgenus (Stehmann 1970).
Field Marks: See Diagnostic Features below.
Diagnostic Features: Disc shape subquadrate to subrhombic, outer corners angular. Tail length equal to, or somewhat longer than body. Thorns on head set individually at orbits, on nape and shoulders; median row of distinct thorns from nape to first dorsal fin always present, may only become incomplete, or interrupted on back of trunk in large specimens, particularly in mature males. Thorns usually not conspicuously large, of regular size, with smooth basal cones and a long, recurved tip. Colour: ground colour above all shades of brown, always with lively ornamentation of dark and light spots and/or blotches, dark and/or light banding, dark spots forming circular pseudo-eyespots in some, or with permanent circular multi-coloured
eyespots. Underside white, but often with more or less intense dark margins to disc and posterior pelvic-fin lobes, also black spots in a few species on snout, belly, on pelvic fins and tail. The majority of species is found in the Eastern Atlantic and Mediterranean, only a few individual species in the Western North Atlantic and elsewhere.

Remarks: So far, 12 species assigned to the genus, based on detailed studies of all relevant characters, but there are about 15 more valid species also currently in Raja (sensu lato), which have not yet been fully studied or given a definitive generic assignment.

## Key to North Atlantic Species:

1a. Side areas of rostrum uncoloured and markedly translucent. Colour above light brown to greyish, with apparent pattern of numerous dark spots/blotches and short bars on disc of variable shape and size; the bars often a bit wavy and generally transverse centrally, but almost parallel to anterior and posterior disc margins in outer disc regions; irregular pale spots may also be scattered on disc; dark crossbars on tail. Individual small orbital and scapular thorns only in small juveniles, larger specimens with thornlets along orbital rims and as a patch on shoulders; a persisting continuous median rows of 33 to 39 small thorns from nape to first dorsal fin, thorns becoming smaller rearward on tail and rather inconspicuous among the very dense coverage of dermal denticles on tail. (Western North Atlantic species)(Fig. 429).

Raja eglanteria


Fig. 429 Raja eglanteria

1b. Side areas of rostrum coloured, may appear at most semitransparent pale but not glassy translucent; colour pattern different from 1a. Orbital and scapular thorns distinct and always set individually; median row of thorns from nape to first dorsal fin often interrupted on back of trunk in large specimens, particularly in mature males, and size of thorns not markedly reduced on tail 2

2a. Upper disc typically ornamented with long blackish or light bands running centrally across trunk and inner pectoral fins, but are oriented on outer pectorals almost parallel to anterior and posterior disc margins; additional light and/or dark blotches and spots may occur (Fig. 430 \& 431) 3

2b. Upper disc ornamented variably with black and/or light spots, partly arranged as pseudo-eyespots, or with circular multi-coloured eyespots, a few species with marbled pattern

3a. Upper side ochre to greyish brown, occasionally rather dark, typically patterned by several more or less undulated dark bands edged with white spots like pearl-strings; these bands centrally across trunk and inner pectoral fins but almost parallel to anterior and posterior disc margins on outer pectoral fins; also often intermingled with larger whitish spots with dark outer ring. Interorbital width equal to (young) or up to 1.7 times the diameter of orbit (Fig. 430).

Raja undulata
3b. Upper side mostly pale sandy brown, patterned with light blotches and often wavy bands, which centrally run across trunk and inner pectoral fins but almost parallel to anterior and posterior disc margins on outer pectoral fins and posterior pelvic-fin lobe margins; pale blotches also along sides of tail. Interorbital width conspicuously wide, 1.5 (young) or up to 2.7 times the diameter of the very small orbits (Fig. 431)

Raja microocellata


4a. Upper side ochre to reddish-brown, with many dark spots scattered on disc and posterior pelvic-fin lobes; an apparent large circular eyespot on each central inner pectoral fin (rarely smaller additional ones), with centre light blue, encircled by an inner dark blue and outer orange ring (Fig. 432)

Raja miraletus
4b. Upper side pattern variably different, without multi-coloured large eyespot, but smaller or larger pseudo-eyespots may occur formed by ring-like arrangement of dark spots, or ornamented with dark and light spots and blotches to even marbled appearance.

5a. Colour above dark brown with a constant pattern of irregular light spots forming broad undulating transverse bands, and narrower unspotted bands between; underside predominantly white, but grey on snout and broad blackish margin to disc from middle of anterior margin to pectoral-fin axils; tip of tail blackish, as well as tips of anterior pelvic-fin lobes, and a dark spots on middle of shoulder girdle and on snout tip (Fig. 433).

## Raja maderensis

5b. Dorsal colour pattern dark spotted to light and dark marbled; underside at most with greyish margin to white disc and posterior pelvic-fin lobe, and black spot markings at constant positions absent.

6a. Colour ochre to pale greyish-brown above, with apparent pattern of numerous small dark spots to extreme edges of disc and posterior pelvic-fin lobes; pale pseudo-eyespots of different sizes symmetrically scattered on disc, each encircled by black spots. Jaw teeth very small, set in very high count of 60 to 90 rows in upper jaw (Fig. 434)

Raja brachyura
6b. Tooth row count in upper jaw less than 60. Upper side ornamented with larger dark spots not extending to extreme disc margins, or with dark and light spots and/or blotches to even marbled appearance

7a. Small young totally smooth above, larger specimens partly spinulose, but centre and posterior part of wings almost smooth; underside largely smooth, only with narrow bands of spinules along anterior disc margins and prickly patches in gill region and on abdomen. Beyond regular thorn pattern, no additional thorns scattered on upper wings or on underside. Greyish to yellowish brown above, with typical pattern of numerous, relatively large blackish spots not extending to extreme margins of disc and posterior pelvic-fin lobes, and spots also along tail; frequently spots are more sparse and sometimes there may be a concentration of darker spots forming a ring around paler centre like an eyespot on posterior inner part of pectoral fins; intermingled pale spots may also occur. Distinct cross-bars on tail absent (Fig. 435)

Raja montagui
7b. Upper surface always entirely covered by rough dermal denticles from smallest young onward, underside wholly prickly in large females, in young and large males only on snout and along disc margins. Large adults often show additional large, so-called 'buckler' thorns scattered over wings above, which also occur in mainly large females on underside of disc. Upper side ground colour and pattern extremely variable; brown to grey in light to dark shades variegated with dark and light spots and blotches, often marbled or clouded, or showing pattern like eyespots, but plain coloured specimens also recorded; tail usually with light and dark crossbars (Fig. 436)

Raja clavata


Fig. 432 Raja miraletus


Fig. 433 Raja maderensis


Fig. 434 Raja brachyura


Fig. 436 Raja clavata

## Raja brachyura Lafont, 1873

## Raja brachyura Lafont, 1873, Act. Soc. Linn. Bordeaux (3), 28(8): 503-504. No type material.

Synonyms: Raja (Raja) brachyura, subgenus (Stehmann 1970).
FAO Names: En - Blonde ray; Fr - Raie lisse; Sp - Raya boca de rosa.


Field Marks: Snout short and bluntly angled, its tip a little pronounced. Tail about as long as body. Upper disc largely smooth only in small juveniles, larger specimens wholly covered with dermal denticles. Few orbital thorns separated; regular median row of 40 to 45 thorns from nape to first dorsal fin in young and large females, interrupted on back of trunk in large males. Upper jaw tooth rows 60 to 90 . Colour ochre to pale greyish-brown above, with apparent pattern of numerous small dark spots extended to the extreme edges of the disc and posterior pelvic-fin lobes; larger pale spots symmetrically scattered on disc, each encircled by black spots; underside white.

Diagnostic Features: Disc broadly subrhombic, with sharply acute outer corners and undulated anterior margins, more so in mature males. Snout, with tip a little pronounced, short and bluntly angled ( 124 to $134^{\circ}$, juveniles blunter). Tail about as long as body, solid and gradually tapering to tip, with two small, separated dorsal fins at rear. Upper disc largely smooth only in small juveniles, larger specimens entirely covered with dermal denticles. A few orbital


OUTLINE OF FEMALE
Fig. 437 Raja brachyura thorns separated pre- and postorbitally; a regular median row of 40 to 45 thorns from nape to first dorsal fin in young and large females, but interrupted on back of trunk in large males, so that a few median thorns on nape and the row along tail remain, and a thorn between dorsal fins; larger specimens develop a row of strong, hooked lateral thorns along either low edge of tail. Compared with most congeners, exceptionally high count of 60 to 90 tooth rows in upper jaw; teeth with sharp cusp in both sexes. Colour: upper side ochre to pale greyish brown, with constant
pattern of numerous small dark spots extending to the extreme edges of disc and posterior pelvic-fin lobes; several larger, circular pale spots symmetrically paired on both wings, and each encircled by close-set dark spots; underside white, at most a pale greyish margins to disc and posterior pelvic-fin lobes.

Distribution: Eastern North Atlantic: off Morocco, at Madeira, and northward to Atlantic seaboards of France, Ireland and United Kingdom, including the Shetlands, some reports from Norwegian waters. Patchy distribution in North Sea, occurring in the north and south of this area. Also present in western Mediterranean Sea.

Habitat: Demersal on sandy grounds, including around sand banks from inshore to upper slope, mostly shallower than 150 m depth, exceptionally as deep as 900 m . Predates on crustaceans (including shrimps and brachyuran crabs), with larger specimens becoming increasingly piscivorous, feeding on sandeels (Ammodytidae), dragonets (Callionymidae) and gobies (Gobiidae).

Biology: Oviparous, egg capsules rectangular, about 120 mm long and 80 mm wide (excluding horns), with broad lateral keels and smoothly striated surfaces, anterior horns about twice as long as posterior ones. Females produce


Fig. 438 Raja brachyura
Known distribution about 30 egg cases a year, that are laid from February to August; embryos hatch at 16 to 18 cm in length after seven months of development. Juveniles feed mainly on small crustaceans, but adults prefer cephalopods and small fish.

Size: Maximum length 120 cm , but most specimens between 40 and 100 cm in length. Maturity in males and females is between 80 and 90 cm in length. Size at hatching is from 16 to 18 cm total length.

Interest to Fisheries and Human Impact: Traditionally landed from multispecies fisheries, although may be targeted in areas of high local abundance, and used for human consumption. Due to its patchy distribution and limited biological knowledge, its status is uncertain, but it remains locally abundant in some areas and rare on other grounds. As a species of the Order Rajiformes is subject to TAC regulations in EU waters and catches of this species should be reported separately (2012).

The conservation status is Near Threatened.
Local Names: Roker (England and Wales, Ireland); Raia pontuada (Portugal); Blonde rog (The Netherlands); Prikkskate (Norway); Blondrochen (Germany).

Literature: Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Ellis, Pawson and Shackley (1996); Kaiser et al. (2004); Ellis et al. (2005); Ellis et al. (2005a); Ellis et al. (2008b); Shark Trust (2009); ICES (2010).

## Raja clavata Linnaeus, 1758

Raja clavataLinnaeus, 1758, Syst. Nat., ed. 10, 1: 232. No type material.
Synonyms: Raja (Raja) clavata, subgenus Stehmann 1970).
FAO Names: En - Thornback ray; Fr - Raie bouclée; Sp - Raya de clavos.


Fig. 439 Raja clavata

Field Marks: Snout short and bluntly angled, its tip a little pronounced. Tail about as long as body. Upper surface always entirely covered by rough dermal denticles from smallest young onward. Few orbital thorns separated; regular median row of 30 to 50 thorns from nape to first dorsal fin in young and large females, interrupted on back of trunk in large males. Especially large females may show on wings above and below additional large 'buckler' thorns with swollen base. Underside wholly prickly in large females, in young and large males only on snout and along disc margins. Colour above extremely variable; ground colour brown to grey in light to dark shades, with all sorts of patterning from extensive yellowish marbling to almost plain with only few light spots; tail usually with light and dark crossbars; underside white, margins of disc and posterior pelvic-fin lobes often grey.

Diagnostic Features: Disc broadly subrhombic, with sharply acute outer corners and straight to weakly undulated anterior margins, stronger undulated in mature males. Snout, with tip a little pronounced, short and bluntly angled ( 109 to $127^{\circ}$ ). Tail about as long as body, solid and gradually tapering to tip, with two small, separated dorsal fins at rear. Upper surface always entirely covered by rough dermal denticles from smallest young onward. A few orbital thorns separated pre- and postorbitally; a regular median row of 40 to 45 thorns from nape to first dorsal fin in young and large females, interrupted on back of trunk in large males, so that a few median thorns on nape and the row along tail remain, and 0 to 2 thorns between dorsal fins; larger specimens develop a row of strong, hooked lateral thorns along either low edge of tail; larger specimens, particularly large females, tend to develop large 'buckler' thorns with swollen base and sharp, curved tip, scattered on disc above and sometimes also below. Underside wholly prickly in large females, in young and large males only on snout and along disc margins. Occasional specimens with no thorns but with a spinulose dorsal surface have been reported. Upper jaw tooth rows 36 to 44; individual teeth blunt in juveniles and females and close set in pavement pattern, whereas teeth of mature males with elongated, sharply pointed cusp and set in parallel rows. Colour: ground colour and pattern above extremely variable, so that this skate may be called the 'chameleon' among congeners. Ground colour brown to grey in light to dark shades, variegated with dark and light spots and blotches, often marbled or clouded, or showing pattern like eye-spots, but plain coloured specimens also recorded; tail usually with light and dark crossbars; underside white, margins of disc and posterior pelvic-fin lobes often grey.

Distribution: Eastern North Atlantic: off Iceland and Norway (south of the Arctic Circle), North Sea, Western Baltic Sea (rare), southward all around Great Britain and Ireland, Bay of Biscay, along Iberian Peninsula; also in entire Mediterranean and western Black Sea; farther south along West Africa (but not in tropical latitudes) to South Africa and into southwestern Indian Ocean; most extreme geographical record is an individual from the southern tip of the Madagascar Ridge at Walter's Shoal in the open southwestern Indian Ocean (Stehmann, 1995b).

Habitat: A relatively common skate, demersal on a variety of substrates (mud, sand and coarse grounds) from close inshore shallow waters to the outer continental shelf and upper slope from 10 to 300 m depth.

Biology: Oviparous, egg capsules subquadrate, 50 to 90 mm long and 49 to 69 mm wide (excluding horns), with broad lateral keels and smoothly striated surfaces; both pairs of horns curving


Fig. 440 Raja clavata
$\square$ Known distribution inward, but anterior horns only somewhat longer than posterior ones. Development takes about five months after which time the young hatch from the egg case. The age at maturity for both sexes is about 7 to 8 years. This skate is known to strongly segregate by sex and size, and exhibits seasonal inshore migrations of adults for mating and depositing egg capsules at specific shallow nursery areas; juveniles mostly found inshore at less than 30 m depth. Estimates of ovarian fecundity (up to 150 eggs) are greater than observed from egg-laying in captive specimens ( $38-52$ egg cases). Large females may produce up to 150 egg cases per year that are laid in the spring off north-western Europe, and in the winter and spring in more southern areas such as the Mediterranean Sea. Juveniles feed mainly on small crustaceans, and adults on larger crustaceans and a variety of fish.

Size: Maximum length is 130 cm for females and 105 cm for males, but most specimens are less than about 105 cm total length. Females mature from 60 to 85 cm and males from 60 to 77 cm . Size at hatching is from 10 to 13 cm total length.

Interest to Fisheries and Human Impact: This species was at one time very common in most areas where it occurred and was a target species of commercial importance in many demersal fisheries, as well as a regular bycatch; however this skate has become depleted in some European localities. It has declined in the eastern and central North Sea, with most of the North Sea stock(s) concentrated in the south-western North Sea. This skate is known to be relatively sedentary, with results from a tagging study revealing that recaptured specimens had moved very little, no more than 40 nautical miles from the original tagging locality. Since this species is known to aggregate in certain places, targeted fisheries for it should be managed conservatively. As a species of the Order Rajiformes is subject to TAC regulations in EU waters and catches of this species should be reported separately (2012).

The conservation status is Near Threatened.
Local Names: Roker, Maiden ray, Hardback (England and Wales, Ireland); Nagelrochen (Germany); Piggskate (Norway); Stekelrog (The Netherlands); Dröfnuskata (Iceland); Raia lenga (Portugal).

Remarks: Raja clavata has a highly variable colour pattern and as such can often be misidentified with other species (e.g., Raja brachyura and $\boldsymbol{R}$. montagui) closely resembling it. Therefore, closely checking the external morphological features is advised to assure the correct identification of $\boldsymbol{R}$. clavata from these other similar species.
Records of this species from around Madeira and at the Azores may be referable to Raja maderensis (cp. Stehmann, 1971 and species account this catalogue) or a local Azorean form, subspecies, or species, respectively. Clarification on the status of the Azorean form is pending. Records of this species from southern Africa should also be investigated as it may be a different species.

Literature: Stehmann (1971); Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Stehmann (1995b); Ellis and Shackley (1995); Ellis, Pawson and Shackley (1996); Ellis (2005); Ellis et al. (2005); Ellis et al. (2005a); Hunter et al. (2005); Ellis et al. (2008); Shark Trust (2009); ICES (2010).

## Raja eglanteria Bosc, 1800

Raja eglanteria Bosc, 1800, in Lacepède 1800, Histoire naturelle des poissons. 2: 104, 109, PI. 4 (fig. 2). No type material.
Synonyms: None.
FAO Names: En - Clearnose skate; Fr - Raie blanc nez; Sp - Raya hialina.


COLORATION


SQUAMATION

Field Marks: Snout moderately long and rather narrowly angled. Upper surface always entirely covered by dermal denticles from smallest young onward; dorsal spinulation reduced to anterior third of disc in mature males only. Few pre- and postorbital thorns separated only in young, but more and smaller thorns forming continuous row on orbital rims of larger specimens; patches of small thorns on each shoulder. A regular continuous median row of 33 to 39 thorns ( 14 to 19 only in small young) from nape to first dorsal fin persisting at all sizes, and 1 to 3 thorns between dorsal fins; lateral row of strong thorns along either lower edge of tail from small young onward, larger specimens may develop also parallel thorn rows on tail. Underside largely smooth. Colour above light brown to greyish, with apparent pattern of numerous dark spots and bars on disc of variable shape and size; side areas of rostrum marked off translucent; underside white.

Diagnostic Features: Disc broadly subrhombic, with sharply acute outer corners and straight to weakly undulated anterior margins, more so in mature males. Snout moderately long and in larger specimens pointed (angle about $90^{\circ}$ ). Tail about as long as body, solid, depressed and gradually tapering to tip, with two small, separated dorsal fins at rear. Upper surface always entirely covered by dermal denticles from smallest young onward; dorsal spinulation reduced to anterior third of disc in mature males; few pre- and postorbital thorns separated only in young, but more and smaller thorns forming continuous row on orbital rims of larger specimens; patches of small thorns on each shoulder. A regular continuous median row of 33 to 39 thorns ( 14 to 19 only in small young) from nape to first dorsal fin persisting at all sizes, and 1 to 3 thorns between dorsal fins; lateral row of
strong thorns along either low edge of tail from small young onward, larger specimens may develop also parallel thorn rows on tail. Underside largely smooth only in small young, except for prickly snout tip; larger specimens with band of spinules also along anterior disc margins; large females additionally bear prickles in a patch in front of each pectoral axil and are spinulose on pelvic fins. Upper jaw tooth rows 46 to 54; teeth close set in pavement pattern in young and females and with low conical cusp, mature males show parallel rows of teeth rather, with longer and pointed cusp. Colour: above light brown to greyish, with apparent pattern of numerous dark spots and short bars on disc of variable shape and size; the bars often a bit wavy and generally transverse centrally, but almost parallel to anterior and posterior disc margins in outer disc regions; irregular pale spots may also be scattered on disc; dark crossbars on tail. Typically, side areas of rostrum marked off translucent. Underside white.


DORSAL VIEW
ㅇ

## OUTLINE OF FEMALE

Fig. 441 Raja eglanteria

Distribution: Western North Atlantic: northern and eastern Gulf of Mexico and from off northern Florida northward to the southern Georges Bank and Gulf of Maine (mainly in summer), but not confirmed from Canadian waters.

Habitat: Benthic on sandy and soft substrates from close inshore, including estuaries, and out to 330 m depth, but mainly shallower than 100 m depth. Temperature ranges from 5 to $27^{\circ} \mathrm{C}$, but most commonly between 9 and $20^{\circ} \mathrm{C}$. A summer visitor toward to the northern distributional limit, the more northern part of the population appears to migrate south and into deeper water in the autumn and reappears in the springtime as the coastal waters warm. Prefers inshore habitats at 10 to $21^{\circ} \mathrm{C}$ temperatures.

Biology: Oviparous, egg cases subquadrate, with coarsely striated surfaces, two pairs of horns of nearly equal length at both ends; capsule body proper (excluding horns) about 5.8 to 8.9 cm long by 3.8 and 5.7 cm wide. Mating in inshore waters during spring, when soon after egg capsules are laid; embryonic development takes at least three months until hatching of young at 13.5 to 14.4 cm length, but Florida hatchlings are slightly smaller at 13 cm . This skate feeds on small bottom invertebrates when young, but larger specimens feed on fish, squids, crabs and shrimps, locally and seasonally with preference for squid (Ha, Luer and Sulikowski, 2008).

Size: Maximum length 84 cm , but smaller size in southern portion of their range where they also mature at smaller size. Females attain sexual maturity at 59 to 65 cm , and males at 56 cm ; both sexes mature at a


Fig. 442 Raja eglanteria
Known distribution somewhat smaller size ( 49 to 58 cm total length) in the southern portion of their range and produce somewhat smaller egg cases. Size at hatching is about 13 to 15 cm .
Interest to Fisheries and Human Impact: Although commonly taken as bycatch they are mostly discarded and not retained.
The conservation status is Least Concern.
Local Names: None.
Literature: Bigelow and Schroeder (1953); Ha, Luer and Sulikowski (2008); Sulak et al. (2009).

## Raja maderensis Lowe, 1838

Raia maderensis Lowe, 1838, Trans. Zool. Soc. Lond., 2(3, art. 14): 195. Syntypes lost.
Synonyms: Raja (Raja) maderensis, subgenus (Stehmann 1971).
FAO Names: En - Madeiran ray; Fr - Raie de Madère; Sp - Raya de Madeira.


Fig. 443 Raja maderensis
Field Marks: Disc subrhombic, wider than long, with acute outer corners. Snout short and bluntly angled, its tip a little pronounced. Tail somewhat longer than body. Upper side at all sizes wholly prickly with densely set, coarse dermal denticles. Few orbital thorns separated; regular median row of 21 to 25 thorns from nape to first dorsal fin in young and large females, interrupted on back of trunk in large males; 2 to 3 thorns between dorsal fins, and strong lateral thorns along lower edges of tail. Underside almost entirely prickly. Colour above dark brown with a constant pattern of irregular light spots forming broad undulating transverse bands and narrower unspotted bands between; underside predominantly white, but grey on snout and broad blackish margin to disc from middle of anterior margin to pectoral-fin axils; tip of tail blackish, as well as tips of anterior pelvic-fin lobes, and a dark spot on middle of shoulder girdle and on snout tip.

Diagnostic Features: Disc subrhombic, wider than long, with anterior margins weakly to strongly (mature males) undulated and acute outer corners. Snout short and bluntly angled, its tip a little pronounced. Tail somewhat longer than body, solid
and gradually tapering to tip, with two small, separated dorsal fins at rear. Snout angled at 107 to $128^{\circ}$, narrower angled in mature males than in young and females. Obvious thorns on snout absent, 1 to 3 pre- and 1 to 2 small postorbital thorns, 1 to 3 close-set median thorns on nape, no thorns on shoulders (small one may be present in young) and on midshoulder; median row of 21 to 25 thorns usually from origin of tail to first dorsal fin, but 1 to 6 thorns may extend forward onto posterior trunk; 2 to 3 distinct interdorsal thorns; 7 to 12 strong thorns irregularly along lower edges of tail from pelvic-fin axils to midlength of tail. Back and sides of tail, dorsal and caudal fins as densely prickly as the disc. Tooth rows in upper jaw 39 to 49, individual teeth flat, with blunt cusp in juveniles and females and arranged in pavement pattern, whereas teeth of mature males bear elongated, pointed cusp and are arranged in parallel rows. Colour: coffee- to dark brown upper side, but side areas of rostrum translucent somewhat lighter, with a constant pattern of irregular light spots forming broad transverse bands across disc and posterior pelvic-fin lobes, with narrower unspotted bands between; no obvious crossbars on tail, only light spots along sides, which often arranged symmetrically, and on dorsal fins. Underside predominantly white, but prenasal snout area dusky grey, and from midlength of anterior margin a broad blackish margin to outer corners and along posterior margins, and a distinct, elongated blackish blotch at pectoral-fin axils; subdorsal tip of tail blackish, as also tips of anterior pelvic-fin lobes, whereas margin of posterior lobes only light greyish, and a blackish spot on middle of shoulder girdle and on snout tip.

Distribution: Eastern North Atlantic: originally described from off Madeira, it or a very similar looking species also occurs around the Azores Archipelago. It may also occur on submarine banks and rises, e.g. Great Meteor Bank. Similar looking specimens from off western North Africa and the Canary Islands were likely misidentifications with either Raja clavata or R. straeleni (Stehmann, 1971, 1973, 1990; Stehmann and Bürkel, 1984).

Habitat: Occurs benthic on hard and soft bottoms to about 150 m depth.

Biology: Oviparous, but egg capsules are not described, but are probably very similar in size and surface texture to those of Raja clavata. Feeds on all kinds of bottom animals.

Size: Maximum length 70 to 80 cm , with sexual maturity possibly occurring at 50 to 60 cm total length.

Interest to Fisheries and Human Impact: Very restricted local populations


Fig. 444 Raja maderensis
Known distribution
Possible distribution off Madeira and the Azores. A relatively common species around the Azores and taken as regular bycatch in bottom longline fisheries, but mostly discarded with a fair chance of survival; if landed for commercial use, the population may soon become subject to overfishing. As a species of the Order Rajiformes is subject to TAC regulations in EU waters (2012)

Conservation status is Data Deficient.
Local Names: Raia da Madeira (Portugal); Madeira-Rochen (Germany).
Remarks: This species appears to be another example of insular endemism, like Raja herwigi Krefft, off the Cape Verde Islands, but the geographic range of $\boldsymbol{R}$. maderensis is more extended from Madeira to the Azores and possibly to some submarine banks and seamounts between both archipelagos. It is possible that Raja clavata may have reached Madeira from off North West Africa, and settled there as a local, isolated population that over time has evolved into an endemic species with a specific and constant phenotype of colour pattern (Stehmann, 1971). This endemic form may have spread farther to the west to the Azores, settled there again as an isolated local population with an external appearance very close to the initial form at Madeira; however, Azorean specimens show a few constant differences especially in the ventral colour pattern, as compared with specimens from Madeira, but a detailed comparison of both separated populations is still pending. Presumably has the invasion of the Azores happened more recently than the one before to Madeira, so that Azorean R. maderensis may be seen as a species still in statu nascendi. Chevolot et al. (2006) concluded in their phylogeography of $\boldsymbol{R}$. clavata, based on analysis of five nuclear microsatelite loci and mitochondrial cytochrome $b$ sequences and samples from 20 locations all over Europe, the north-western Mediterranean, Black Sea and the Azores, that all these populations were $\boldsymbol{R}$. clavata with strong regional groupings; regarding phylogeographic distribution of $\boldsymbol{R}$. clavata, three regional groups were defined in the Mediterranean Basin, at the Azores and on the Atlantic continental shelf. These authors concluded, that after the Last Glacial Maximum (about 20,000 years ago) the recolonization by R. clavata of northern European waters and the North Sea originated
mainly from the population refugia around the Iberian Peninsula and at the Azores. However, samples of $\boldsymbol{R}$. clavata from the very northern European range (up to Iceland), the southern Mediterranean (along African coast), from off North West Africa, from Madeira and from the very southern range (around South Africa) of its distribution were not included in the latter study. This species was described in 1839, vol. 2 of the Trans. Zool. Soc. London that was published in various parts over several years until 1841, and part 3 with article 14 by Lowe appeared to have been published in 1839 (Stehmann, 1973). However, the Catalog of Fishes (Eschmeyer and Fricke, 2011) corrects the year of publication to 1838 , which is followed here.

Literature: Stehmann (1971, 1973, 1990); Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Chevolot et al. (2006); Stehmann (2008a); Eschmeyer and Fricke (2011).

## Raja microocellata Montagu, 1818

Raja microocellata Montagu, 1818, Mem. Wern. nat. Hist. Soc. Edinb., 2(28): 430-432. No type material.
Synonyms: None.
FAO Names: En - Small-eyed ray; Fr - Raie mêlée; Sp - Raya colorada.

COLORATION

Field Marks: Snout short and bluntly angled, its tip a little pronounced. Eyes conspicuously small, broad interorbital space. Upper side predominantly spinulose, but centres and posterior parts of wings almost smooth. Orbital thorns separated, regular median row of about 50 thorns from nape to first dorsal fin, reduced in size and number on back of trunk in adults; strong lateral thorns along each lower edge of tail, especially in large females; no thorn between close-set dorsal fins. Underside almost smooth in small juveniles, but head and centre of disc prickly in larger specimens. Colour above greyish or olive but mostly pale sandy brown, patterned with light blotches and bands arranged nearly parallel to disc margins; underside white.

Diagnostic Features: Disc broadly subrhombic, with acute outer corners and anterior margins weakly to strongly (mature males) undulated. Snout, with tip a little pronounced, short and bluntly angled (about $130^{\circ}$ ). Tail a little shorter than, to as long as body, solid and gradually tapering to tip, with two small, close-set dorsal fins at rear. Eyes conspicuously small, orbit length 1.5 (young) to 2.7


SQUAMATION


OUTLINE OF FEMALE

Fig. 445 Raja microocellata
times in broad interorbital width, which is equal to or greater than combined orbit + spiracle length. Upper side predominantly spinulose, but centres and posterior parts of wings almost smooth in larger specimens. 0 to 2 pre-and 0 to 3 postorbital thorns separated, with age and growth often worn flat or disappearing; three median nuchal thorns and a thorn on each shoulder only in young and getting lost in larger individuals showing a regular median row of about 50 thorns from anterior trunk to first dorsal fin, but these thorns often reduced in size and number of large specimens; parallel rows of smaller thorns may flank the median row on trunk, and strong lateral thorns along each lower edge of tail especially in large females; no thorn between close-set dorsal fins. Underside almost smooth in small juveniles, but head and centre of disc prickly in larger specimens. Tooth rows in upper jaw 44 to 52; individual teeth flat and with blunt cusp in young and females, set in pavement pattern, but middle rows in mature males closely parallel, with tooth cusp longer and sharper. Colour: upper side greyish or olive, but mostly pale sandy brown, patterned with light blotches and bands arranged nearly parallel to margins of disc and posterior pelvic-fin lobes, and pale blotches also along sides of tail; underside white, with pale greyish margins to disc and posterior pelvic-fin lobes.

Distribution: Eastern North Atlantic: from off Morocco northward to south-western British Isles, including English Channel, Bristol Channel and Ireland. Occasional individuals in Irish Sea and southern North Sea. Absent from the Mediterranean Sea.

Habitat: Demersal on sandy ground from inshore in tidal areas to about 100 mdepth , favouring sandy bays and sandbanks. Juveniles occur in very shallow water on sandy beaches, with larger specimens occurring further offshore.

Biology: Oviparous, egg capsules subrectangular, 55 to 99 mm in length by 35 to 60 mm in width (excluding horns), with smoothly striated surfaces; long filamentous horns, anterior pair longer than posterior one, and distinct lateral keels. Young hatch at about 10 to 13 cm total length after about seven months embryonic development; 54 to 61 egg capsules produced per reproductive cycle with most egg cases being laid between June and September. Sexual maturity attained at about 58 cm TL. In the English


Fig. 446 Raja microocellata
$\square$ Known distribution $\square$ Possible distribution Channel, ripe females gather during summer. Juveniles feed on small crustaceans, adults almost exclusively on bony fish, including sand eels (Ellis, 2006).

Size: Maximum length 91 cm , with sexual maturity attained at about 58 cm . Size at hatching is from 10 to 13 cm .
Interest to Fisheries and Human Impact: Regular bycatch in commercial trawl fisheries, landed from localities where abundant inshore; popular game fish for recreational anglers. As a species of the Order Rajiformes is subject to TAC regulations in EU waters and catches of this species should be reported separately (2012)

Conservation status is Near Threatened.
Local Names: Painted ray/Painted skate, Sandy ray/Sandy skate, Owl ray/Owl skate (England and Wales, Ireland); Kleinäugiger Rochen (Germany); Kleinoogrog (The Netherlands); Smáøyet skate (Norway); Raia zimbreira (Portugal).

Remarks: The regional use of the term sandy ray has resulted in some confusion with Leucoraja circularis.
Literature: Clark (1926); Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Rousset (1987, 1990); Ellis et al. (2005) Ellis et al. (2005a); Ellis (2006); Shark Trust (2009).

## Raja miraletus Linnaeus, 1758

Raja miraletus Linnaeus, 1758, Syst. Nat., ed. 10, 1: 231. No type material.
Synonyms: Raja (Raja) miraletus, subgenus (Stehmann 1970).
FAO Names: En - Brown ray; Fr - Raie miroir; Sp - Raya de espejos.


COLORATION

Field Marks: Colour above ochre to reddish-brown, with many dark spots scattered on disc and posterior pelvic-fin lobes; an apparent large circular eyespot on each central inner pectoral fins (rarely smaller additional ones), with centre light blue, encircled by an inner dark blue and outer orange ring. Underside white. Upper side almost smooth in adults. Orbital thorns separated, median thorns on nape, regular median row of about 14 to 18 thorns on tail to first dorsal fin; strong lateral thorns along each lower edge of tail, especially in large females; 2 thorns between dorsal fins. Underside smooth, snout prickly in mature males.

Diagnostic Features: Disc broadly subrhombic, with acute outer corners and anterior margins weakly to strongly (mature males) undulated. Snout, with tip a little pronounced, short and bluntly angled (99 to $106^{\circ}$, blunter in juveniles). Tail a little longer than body, solid and gradually tapering to tip, with two small, separated dorsal fins at rear. Upper side prickly only in young, almost smooth in adults. Two pre- and 2 to 3 postorbital thorns separated, 2 median nuchal thorns; thorns on shoulders, on midshoulder and medially on trunk may be present in young, but these get lost with growth, and only a few may remain on back of trunk, so that median row of 14 to 18 thorns mainly along tail to first dorsal fin, and 2 thorns in interdorsal space; strong lateral thorns along each lower edge of tail, large females often with an additional parallel thorn row on anterior half of tail. Underside smooth, snout prickly in mature males. Tooth rows in upper jaw 40 to 42, individual teeth in young and females flat, with blunt cusp and arranged in pavement pattern, with longer and pointed cusp in mature
males and in close-set parallel rows in median third of jaws. Colour: upper side ochre to reddish-brown, with many dark spots scattered on disc and posterior pelvic-fin lobes; an apparent large circular eyespot on each central inner pectoral fin (rarely smaller additional ones), with centre light blue, encircled by an inner dark blue and outer orange ring. Underside white.

Distribution: Eastern North Atlantic: from off Madeira and Morocco northward to northern continental Portugal and Spain; also in entire Mediterranean Sea and along West Africa to South Africa and around the Cape into the southwestern Indian Ocean.

Habitat: Demersal on soft bottom from shallow shelf to about 300 m depth, mainly at 50 to 150 m .

Biology: Oviparous, egg capsules subrectangular, 42 to 45.5 mm in length by 27 to 29 mm in width (excluding horns) (Bor, 2011), with smoothly striated surfaces, long filamentous horns, anterior pair longer than posterior one, and distinct lateral keels. Young hatch at about 10 to 11 cm total length (Mediterranean) after a few months of embryonic development. Age at sexual maturity is 2 to 3 years, with longevity of about 10 years (Mediterranean) (Smale et al., 2003). Females produce 40 to 72 egg


Fig. 448 Raja miraletus $\square$ Known distribution capsules per year (Bor, 2011). Feeds on all kinds of bottom invertebrates and small fish.

Size: Maximum about 60 cm total length, with females maturing at 39 to 44 cm , and males at 36 to 40 cm .
Interest to Fisheries and Human Impact: A rather common species, regularly landed along West Africa, and in the Mediterranean. As a species of the Order Rajiformes is subject to TAC regulation in EU waters (2012).

The conservation status of this relatively small skate is Least Concern.
Local Names: Spiegelrochen (Germany); Raia de quatro olhos (Portugal); Spiegelrog (The Netherlands).
Remarks: Raja miraletus is the type species of genus Raja Linnaeus, 1758. Despite the widespread distribution, relatively little is known of its biology from West African and South African populations, although the population in this latter location may be that of a different species (Ebert, Compagno, and Cowley 2007). However, McEachran et al. (1989), after a study of samples from the Mediterranean, all along West Africa, and from off South Africa, concluded * $\boldsymbol{R}$. miraletus is considered a polymorphic species of at least three parapatrically or allopatrically distributed populations in the Mediterranean, off West Africa and South Africa. Thus, no taxonomic recognition of the populations is recommended". These authors also confirmed in agreement with Wallace (1967) and Hulley (1969), that the South African R. ocellifera Regan, 1906 is synonymous with $\boldsymbol{R}$. miraletus.

Literature: Clark (1926); Wallace (1967); Hulley (1969); Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); McEachran et al. (1989); Smale et al. (2003); Ebert, Compagno, and Cowley (2007); Bor (2011).

## Raja montagui Fowler, 1910

Raja montagui Fowler, 1910, Proc. Acad. nat. Sci. Philad., 62: 468. No type material.
Synonyms: Raja (Raja) montagui, subgenus (Stehmann 1970).
FAO Names: En - Spotted ray; Fr - Raie douce; Sp - Raya pintada.


Field Marks: Colour above greyish to yellowish brown; disc and posterior pelvic-fin lobes usually scattered with numerous blackish spots not extending to extreme margins, and spots also on tail; frequently a concentration of dark spots forming a ring around paler centre like an eye-spot on posterior inner part of pectoral fins; spots can be reduced in number or faint in some specimens; underside white, with greyish margins to disc and posterior pelvic-fin lobes. Snout short and bluntly angled, its tip a little pronounced. Upper side almost smooth in young, more spinulose in larger specimens, but with centre and posterior part of wings almost smooth. Orbital thorns separated; regular median row of 20 to 50 usually persisting thorns from nape to first dorsal fin; 1 to 2 thorns between dorsal fins. Underside largely smooth.

Diagnostic Features: Disc broadly subrhombic, wider than long, with acute outer corners and anterior margins weakly to strongly (mature males) undulated. Snout, with tip a little pronounced, short and bluntly angled (108 to $123^{\circ}$ ). Tail a little longer than body, solid and gradually tapering to tip, with two small separated


OUTLINE OF FEMALE
Fig. 449 Raja montagui dorsal fins at rear. Small young totally smooth, larger specimens partly spinulose, but centre and posterior part of wings almost smooth. 2 to 3 pre- and 2 to 3 postorbital thorns separated, 2 median nuchal thorns in young increase to 4 or more in larger specimens, and a thorn on each shoulder only in young; regular median row of 20 to 30 thorns in young, 40 to 50 in large specimens from behind shoulder girdle to first dorsal fin, and 1 to 2 thorns between dorsal fins; median thorns mostly persisting with growth, but may become irregularly spaced with less thorns on back of trunk; lateral thorn row along lower edges of tail mainly in young, but often persisting more or less completely in large adults. Underside largely smooth, only with narrow bands of spinules along anterior disc margins and prickly patches in gill region and on abdomen. Tooth rows in upper
jaw 38 to 60; individual teeth flat and with blunt cusp in young and females, set in pavement pattern, but with tooth cusp longer and sharper in mature males and in close-set parallel rows. Colour: greyish to yellowish brown above, with typical pattern of numerous, relatively large blackish spots not extending to extreme margins of disc and posterior pelvic-fin lobes, and spots also on tail; frequently a concentration of dark spots forming a ring around paler centre like an eyespot on posterior inner part of pectoral fins; pale spots may also occur; underside white, with greyish margins to disc and posterior pelvic-fin lobes.

Distribution: Eastern North Atlantic: from off Morocco northward to around Ireland and Great Britain, also in North Sea and occasionally Western Baltic Sea; found also in Mediterranean Sea.

Habitat: Demersal on soft substrate on shelf at 30 to 150 m depth, rarely as deep as 530 m .

Biology: Oviparous, egg capsules subrectangular, 53 to 78 mm in length by 30 to 50 mm in width (excluding horns), with smoothly striated surfaces, no distinct lateral keels, and a pair of solid horns at both ends, of which the anterior pair somewhat longer. Young hatch at about 8 to 10 cm total length after 5 to 6 months of embryonic development. Females deposit 60 to 70 egg capsules during the summer. Young feed on small crustaceans, but larger specimens feed on larger crustaceans and small bony fish (Ellis et al. 2007; Shark Trust (2009).

Size: Maximum about 80 cm total length


Fig. 450 Raja montagui
Known distribution with males maturing at about 40 cm .

Interest to Fisheries and Human Impact: Regular bycatch of commercial trawl fisheries, large specimens marketed. Despite fishing pressure throughout its range, this skate appears to be less affected due to its relatively small size and high fecundity. As a species of the Order Rajiformes is subject to TAC regulations in EU waters and catches of this species should be reported separately (2012).

Conservation status is Least Concern.
Local Names: Homelyn ray/Homelyn skate, Spotted homelyn ray/Spotted homelyn skate, Roker (England and Wales, Ireland); Fleckrochen, Gefleckter Rochen (Germany); Raia manchada (Portugal); Gevlekte Rog (The Netherlands); Flekkskate (Norway).

Literature: Clark (1926); Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Ellis, Pawson and Shackley (1996); Ellis et al. (2005); Ellis et al. (2005a) Ellis et al. (2007); Shark Trust (2009).

## Raja undulata Lacepède, 1802

Raja undulata Lacepède, 1802, Hist. Nat. Poissons, 4: 670. No type material.
Synonyms: None.

FAO Names: En - Undulate ray; Fr - Raie brunette; Sp - Raya mosaica.


Field Marks: Colour above ochre to greyish brown, typically patterned by several more or less undulated dark bands edged with white spots like pearl-strings, also often with larger whitish spots intermingled; underside white, with often greyish margins to disc and posterior pelvic-fin lobes, end of tail sometimes greyish-brown. Orbital thorns separated; 2 to 8 median thorns on nape; regular median row of 20 to 55 usually persisting thorns from behind shoulder girdle to first dorsal fin; 0 to 2 interdorsal thorns; sometimes lateral and parallel thorn rows on tail in adults. Underside largely smooth.

Diagnostic Features: Disc broadly subrhombic, with moderately acute outer corners and anterior margins weakly to strongly (mature males) undulated. Snout, with tip a little pronounced, short and bluntly angled ( 90 to $150^{\circ}$, blunter in juveniles). Tail about as long as body, solid and gradually tapering to tip, with two small, separated dorsal fins at rear. Upper side largely spinulose, with larger bare areas centrally and posteriorly on disc and on posterior pelvic-fin lobes. 0 to 2 pre- and 0 to 2 postorbital thorns separated; 2 to 8 median thorns sometimes a bit irregular along nape, and 0 to 3 thorns on each shoulder, 1 on midshoulder; regular median row of 20 to 55 usually persisting


Fig. 451 Raja undulata thorns from behind shoulder girdle to first dorsal fin, sometimes becoming irregular in number and interspaces on back of trunk in adults; 0 to 2 interdorsal thorns; sometimes lateral and parallel thorn rows on tail especially in adult females. Underside largely smooth, but snout and front margins of disc, sometimes also underside of tail prickly. Upper jaw tooth rows 40 to 50 , individual teeth close-set in pavement pattern, rather flat and with blunt cusp, but more pointed cusp in middle series'. Colour: upper side ochre to greyish brown, occasionally rather dark, typically patterned by several more or less undulated dark bands edged with white spots like pearl-strings, also often with larger whitish spots intermingled; underside white, with often greyish margins to disc and posterior pelvic-fin lobes, end of tail sometimes greyish-brown.

Distribution: Eastern North Atlantic: patchy distribution in eastern North Atlantic, ranging from off Morocco and northward to south-west Ireland and southern England; also in the Western Mediterranean mainly along African coastline, and along the West African coastline, to off Mauritania and Senegal.

Habitat: Demersal on soft and coarse substrate on the shelf to 150 m , but mostly in waters less than 100 m deep, and juveniles shallower. Locally common in certain areas, including the English Channel, and elsewhere in the eastern North Atlantic it is often found in inshore areas associated with outer estuaries, rias and lagoons.

Biology: Oviparous, egg cases subrectangular, 70 to 90 mm in length by 45 to 60 mm in width (excluding horns), with smoothly striated surfaces, no distinct lateral keels and a pair of solid horns at both ends, of which the anterior pair somewhat longer. Young hatch at about 14 cm total length after several months of embryonic development. In the northern part of their distribution, females deposit egg capsules from March to September. Feeding on various benthic invertebrates and fishes, with the young mostly feeding on small crustaceans, and larger specimens mainly on large crustaceans and fish.


Fig. 452 Raja undulata
$\square$ Known distribution $\square$ Possible distribution

Size: Maximum length at least 114 cm and possibly to 120 cm , with females maturing at about 75 cm and males at 73 cm . Size at hatching is about 14 cm total length. (Shark Trust 2009).

Interest to Fisheries and Human Impact: This little-known species has a patchy and potentially fragmented distribution. The EU since 2009 has prohibited to fish for, to retain on board, to tranship or to land Raja undulata in and from ICES subareas VI, VII, VIII, IX and X (2012).

The conservation status is Endangered.
Local Names: Painted ray/Painted skate (England and Wales, Ireland); Golfrog (The Netherlands); Perlrochen, WellenlinienRochen (Germany); Bølgeskate (Norway); Raia curva (Portugal).

Literature: Clark (1926); Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Coelho \& Erini (2002, 2006); Coelho et al. (2003); Moura et al. (2007, 2008); Shark Trust (2009); Ellis et al. (2012).

## Rajella Stehmann, 1970

Genus: Rajella Stehmann, 1970, Arch. FischWiss. 21(2): 151.
Type Species: Raja fyllae Lütken, 1888 by original designation.
Number of Recognized North Atlantic Species: 6.
Synonyms: Raja (Rajella), as subgenus (Stehmann, 1970).
Field Marks: See Diagnostic Features below.
Diagnostic Features: Disc subcircular (rarely) to subrhombic, with outer corners rounded to angular; snout either short and bluntly angled, or moderately elongated and pointed. Median row thorns on back of trunk and along tail persisting, but two or more parallel rows may become dominant with growth. Except in small juveniles, thorns on orbital rims mostly set in continuous half-rings, and mostly many thorns over nape and shoulder regions forming a triangle. The majority of species
lives in deepwater on continental and insular slopes down to deepsea plains and at submarine elevations. Colour: mostly uniformly dark or light according to deepwater habitat.

Remarks: The genus currently has 17 nominal species described with several additional species awaiting formal description. The genus is most diverse in the Atlantic, but with species occurring in the eastern South Pacific, Indian Ocean, and Australia. Six species occur in the North Atlantic.

## Key to North Atlantic Species:

1a. Small species to about 55 cm total length only. Shape of disc subcircular, with broadly rounded outer corners; tail conspicuously longer (to 1.5 times) than body. Upper side appearing very rough through coverage with coarse dermal denticles, thornlets scattered on head and wings, and a broad band of heavy thorns from nape-shoulder region along back of trunk and onto tail to dorsal fins. 2

1b. Larger size species growing to more than 55 cm total length. Shape of disc may change in some from small juveniles to adults, but at larger size is usually subrhombic; snout moderately extended and rather pointed. Tail at most a little longer to somewhat shorter than disc. Upper disc less rough, rarely with additional thornlets scattered over disc, dermal denticles mostly not covering entire disc, and several rows of thorns primarily on tail

3

2a. Disc roundish, somewhat broader than long. Snout very short and very blunt (angle 115 to $156^{\circ}$ ), its tip a little pronounced. Colour above quite variable from ashy-grey to dark brown, usually lively patterned in various ways from dark and/or pale clouded to spotted dark and light, tail often with dark cross-bars; underside mostly largely white, with dark blotching on head, belly and tail, and dark margins around disc and to posterior pelvic-fin lobes, but sometimes ventrally predominantly dark specimens occur, but few white markings always left (Fig. 453)

Rajella fyllae


Fig. 454 Rajella bigelowi

3a. Colour plain dark greyish-brown above; disc below predominantly white but with broad dark margins from outer corners along posterior margins and also at posterior pelvic-fin lobes; underside of tail marked off plain dark, or with broad median dark stripe, or with brownish median specks.

4

3b. Uniformly greyish-white to white above and below in large adults. Transitional colour morphs do occur, from dorsally plain dark greyish-brown in small young to medium brownish in half-grown and adult specimens, but adults mostly greyish-white. Likewise on underside transition of colour, with small young dark brown, but always large white markings on head, midbody and inner pectoral fins, and the underside of tail with white median stripe, and posterior third of tail white; larger juveniles with largely white disc and pelvic fins below, but margins dark brown, and brown blotches may variously occur on midbody, posterior pectoral fins and on pelvic fins, and underside of tail totally dark with at most some pale mottling. Large adults plain whitish below 5

4a. Underside of disc only with broadly dark edged posterior margins, no additional constant dark markings. Underside of tail either plain dark, or mottled with white posteriorly, but always subdorsal end of tail plain white. Median row of 20 to 32 thorns from behind shoulder girdle to only some distance in front of first dorsal fin, and up to 60 larger thorns flanking median row on tail in young, but in larger specimens extending forward onto back of trunk (Fig. 455).

Rajella dissimilis

4b. Underside of disc with a pair of large oval to bean-shaped brown blotches flanking cloaca, tips of anterior pelvic-fin lobes with brown spots; underside of tail mostly with dark median stripe, or at least an irregular double row of brownish specks medially along anterior half or nearly entire tail. A regular row of 39 to 44 close-set large thorns with sharp, recurved tip from shoulder girdle to first dorsal fin; no parallel thorns rows on trunk and tail, but a regular row of 50 to 60 close-set strong, hooked thornlets along each lower edge of tail persisting from smallest young onward (Fig. 456a \& 456b).

Rajella lintea

5a. Continuous half-rings of about 7 orbital thorns; median row of about 21 thorns from posterior trunk onto tail but ending some distance in front of first dorsal fin; median row flanked by two somewhat irregular parallel rows of many smaller thorns from anterior trunk to first dorsal fin, and small thorns along lower edges of tail. Limy-white on both surfaces, but dorsal fins dusky, and ventrally irregular small dark spots on posterior disc margins, pelvic fins, claspers and on tail (Fig. 457)

Rajella kukujevi (characteristics only based on mature male holotype, females and younger stages may appear somewhat different).

5b. A few orbital thorns always separated, regular median row of 31 to 41 large thorns from behind shoulder girdle to first dorsal fin; parallel and lateral rows of large thorns absent on trunk and tail, but larger specimens with a parallel row of thornlets (smaller than median ones) only on anterior half of tail. Large adults plain greyish-white above and below, but gradual transitions from small young to half-grown and adult specimens are found with respect to disc shape, as well as colour and patterning of both surfaces as indicated under 3b (Fig. 458)

Rajella bathyphila


Fig. 455 Rajella dissimilis

b) DETAIL OF TAIL

Fig. 456 Rajella lintea


Fig. 458 Rajella bathyphila

## Rajella bathyphila (Holt and Byrne, 1908)

Raja bathyphila Holt and Byrne, 1908, Fish. Irel. Sci. Invest. 1906 (publ. 1908), 5: 51-53. Holotype BMNH 1912.3.1.108.
Synonyms: None.


Field Marks: Shape of disc, snouth length and angle, and proportional tail length changing considerably with growth: tail longer than body in young (less than 50 cm TL ) and slender, more solid and finally shorter than body in large specimens, gradually tapering to tip, with two small confluent dorsal fins at rear. Upper disc entirely and densely covered with coarse dermal denticles; underside smooth, except for prickly tail edges to varying extent. No thorns on snout, a few orbital thorns always separated, 2 to 3 median nuchal thorns, 1 on midshoulder and 3 on each shoulder; a regular median row of 31 to 41 large thorns from behind shoulder girdle to first dorsal fin; parallel and lateral rows of large thorns absent on trunk and tail, but larger specimens with a parallel row of thornlets (smaller than median ones) only on anterior half of tail. Colour above plain dark greyish-brown in young, medium brownish in half-grown and adult specimens, but adults mostly greyish-white; colour and pattern below also changing considerably with growth, in that young show dark underside with few white markings along midbody which extend with growth, but dark margins to disc and pelvic fins, and adults become finally plain greyish-white. Gradual transitions between small young, half-grown and adult specimens are found with respect to shape, as well as colour of both surfaces and patterning below.


SQUAMATION
Fig. 459 Rajella bathyphila

Diagnostic Features: Disc inverse heart-shaped in young, with broadly rounded outer corners, snout short and bluntly angled; tail longer ( 1.2 to 1.4 times) than body in young, but from size larger than 50 cm total length gradually becoming less long and finally in adults shorter than body. Disc broadly subrhombic from half-grown specimens onward (over 50 cm total length), with increasingly acute outer corners, snout becoming more elongated and narrowly angled; snout angle 87 to $118^{\circ}$, but only in specimens over 50 cm total length less than $100^{\circ}$. Upper disc entirely and densely covered with coarse dermal denticles, pectoral centres becoming smooth only in mature males; posterior pelvic-fin lobes prickly centrally, and back and sides of tail densely set with coarse, often hooked spinules. Underside smooth, except for prickly tail edges to varying extent. Generally, only one pair of large pre- and postorbital thorns, occasionally a second pair of smaller postorbital and a pair of interspiracular thorns; 1 to 3 small thorns may additionally occur on shoulder girdle between the thorn triangle on each shoulder and the midshoulder thorn, but generally a nape-shoulder triangle of many thorns not obvious; only small juveniles may have just 31 to 32 median thorns, from larger young onward 33 to 41 median thorns, of which 6 to 8 (mostly 7 to 8 ) on back of trunk from behind shoulder girdle to level of pectoral-fin axils, which in large adults may be reduced in size. Upper jaw tooth rows 34 to 50 , mostly

outline of female
Fig. 460 Rajella bathyphila over 40; individual teeth flat and with blunt cusp in juveniles and larger females, arranged in pavement pattern, but in mature males with sharply pointed cusp and arranged in close-set parallel rows. Colour: changing remarkably from small young to adults on both surfaces. Plain dark greyish-brown above in young, medium brownish in half-grown and adult specimens, but adults mostly greyish-white. Colour and pattern below likewise changing considerably with growth: disc predominantly dark brown in small young, but always with large white markings on head and midbody and inner pectoral fins, at mouth-nasal region and on snout; underside of tail with white median stripe, posterior third of tail white. Larger juveniles with predominantly white disc and pelvic fins below, but margins dark brown, and brown blotches may variously occur on midbody, posterior pectoral fins and on pelvic fins, with underside of tail totally dark with at most some pale mottling. Large adults plain white below, only claspers and tail of mature males may be a little darker.

Distribution: Eastern North Atlantic: Greenland (Nakaya 1995), Denmark Strait and Rockall Trough (where it is common) and North West Africa off Rio de Oro (to about $20^{\circ} \mathrm{N}, 17^{\circ} \mathrm{W}$ )(Stehmann 1995). Western North Atlantic: northern Labrador Sea to Flemish Cape, Grand Banks and Georges Bank (Sulak et al. 2009).

Habitat: The species is probably widespread across the entire North Atlantic in deepwater, along continental slopes and at submarine elevations, although it is known mainly from sporadic records and depending on local deepwater fishery activities. It is rare in research trawling surveys in deepwater. A demersal species usually found on various kinds of bottom types from 600 to $2,300 \mathrm{~m}$ deep, but mostly deeper than $1,400 \mathrm{~m}$ and within a temperature range of 2.5 to $4^{\circ} \mathrm{C}$.

Biology: Oviparous, egg capsule subrectangular, withroughfibroussurfaces, about 87 mm in length by 52 mm in width (excluding horns), with narrow lateral keels


Fig. 461 Rajella bathyphila
$\square$ Known distribution
Possible distribution and a pair of slender horns at both ends. Reproductive biology and cycle are not known, although young hatch after several months of embryonic development, which may be longer depending on the water temperature, and colder waters likely slow development and growth. Neonates probably feeding on small benthic invertebrates while larger individuals feed on larger invertebrates and eventually fish (Gordon and Duncan 1989).

Size: Maximum length about 95 cm , with maturity attained at about 65 to 75 cm length. A male 61.7 cm was immature while another of 74 cm was fully mature. Size at hatching is about 12 cm .

Interest to Fisheries and Human Impact: Occasional taken as bycatch in local commercial deepwater bottom trawl fisheries at depths over $1,000 \mathrm{~m}$, e.g. at Flemish Cape in the Western North and within the Rockall Trough in Eastern North Atlantic. Only larger specimens kept and landed, e.g. in France, smaller ones discarded. The presumably wide distribution mainly at lower slope depths likely protects the species from target exploitation.

The conservation status is Least Concern.
Local Names: Tiefwasserrochen (Germany); Djúpskata (Iceland); Dybhavsrokke (Denmark and Greenland).
Remarks: A very poorly known deep-water skate with only a few verified records from the northern Rockall Trough at 1,260 to $1,870 \mathrm{~m}$ deep, and Porcupine Seabight (Johnston et al. 2010) from 511 to 1550 m deep. If specimens are caught in future surveys or as bycatch they should be retained and forwarded to national research institutes for future study.

Literature: Clark (1926: 47 partim as Raja lintea); Bigelow and Schroeder (1953); Stehmann, in: Tortonese and Hureau (1979) (CLOFNAM Suppl. 1978); Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Gordon and Duncan (1989); Stehmann (1995); Nakaya, Rajidae, in: Okamura et al. (Eds 1995); Stehmann (2008b); Sulak et al. (2009); Johnston et al. (2010).

## Rajella bigelowi (Stehmann, 1978)

Raja (Rajella) bigelowi Stehmann, 1978, Arch. FischWiss., 29(1/2): 26-35, 52-57. Holotype USNM 218284, 14 paratypes USNM 35584, 35591, 38210, 148269, 148276, 218273a, b, 218285, MOM uncatalogued, ISH 969-1973, 970-1973a+b, 1481974, ex $\operatorname{GMNH}(Z)$ 1977-170-11 transferred to BMNH as 1979.7.24.4.

Synonyms: Raja ackleyi (nec Garman, 1881) Roule (1912: 20); Raja bathyphila (nec Holt and Byrne, 1908) Bigelow and Schroeder (1953: 159-165); Bigelow and Schroeder (1954): 52-54; Stehmann (1970, partim); Stehmann (1971: 1; Stehmann (1973: 66 partim); McEachran and Stehmann (1977: 20-25).

FAO Names: En - Bigelow's ray.



Fig. 462 Rajella bigelowi
Field Marks: A small deepwater species. Disc narrowly roundish to subrhombic, hardly wider than long, with broadly rounded outer corners, snout short and mostly bluntly angled. Tail conspicuously longer than body ( 1.5 times). Upper surface entirely spinulose, only in mature males pectoral centres more or less bare. Generally a patch of distinct thorns on mid-snout; only small juveniles with orbital, nape, shoulder and midshoulder thorns separate, whereas larger specimens generally show a complete half-ring of orbital thorns and a large triangle of about 10 to 20 prominent thorns on napeshoulder region; median row of 26 to 33 thorns from behind shoulder girdle to first dorsal fin, flanked from larger young on by 1 to 2 irregular parallel rows of about 30 thorns on posterior trunk and tail. Underside smooth, except for marginal bands of prickles along tail. Except for half-grown specimens being often totally limy-white, colour above uniformly dusky grey, but generally with back of trunk and tail lighter to even limy-white; underside of disc and pelvic fins generally plain dark brown, darker than upper side, but the tail always marked off distinctly lighter.

Diagnostic Features: Disc narrowly roundish to subrhombic, hardly wider than long, with broadly rounded outer corners, snout short and mostly bluntly angled ( 102 to $122^{\circ}$, only in mature males more pointed with about $90^{\circ}$ ), anterior margins weakly undulated, stronger so in mature males. Tail conspicuously longer than body ( 1.5 times), gradually tapering to tip, with two small, confluent dorsal fins at rear. Narrow lateral tail folds only along posterior fourth of tail length. Dorsal dermal denticles relatively coarser and more loosely scattered in small young than in larger specimens; pelvic fins and male claspers smooth above, except for central patch of prickles on posterior pelvic-fin lobes. Snout thorns of thornlet size rather in early young, but these always larger than surrounding dermal denticles. Early young only with prominent separated thorns on head: a pair each in pre-, postand interspiracular position; 2 median thorns on nape, 2 to 3 thorns on each shoulder and 1 midshoulder thorn; larger specimens with complete half-rings of orbital thorns and a triangle of 10-20 thorns over nape-shoulder region; 26 to 33 (mostly less than 30) median thorns from behind shoulder girdle to first dorsal fin becoming smaller rearward, 4 to 8 (mostly 4 to 6 ) of these on back of trunk to level of pectoral-fin axils; except for very small young, 1 to 2 irregular parallel rows of up to 30 prominent thorns (becoming larger with growth than median ones) along tail, which in large specimens extend forward to posterior trunk. Lateral thorns along lower tail edges absent, but dermal denticles on sides of tail becoming with growth very coarse and hooked. Underside devoid of dermal denticles, only tail with broad marginal prickly bands over up to three fourths tail length, but a narrow median stripe remains more or less smooth, whereas totally smooth underside of tail only in small juveniles and mature males. Upper jaw tooth rows 34 to 44; individual teeth with blunt conical cusp set in pavement pattern in young and larger females, whereas teeth of mature males in close-set parallel rows and bearing slender pointed cusp in mid-third but shorter triangular cusp in outer thirds of jaw. Colour: upper and lower side without any patterning; typically, back of trunk and tail above marked off lighter from dark brown (young) to ashy to light grey (adults) disc and pelvic fins, except for half-grown specimens being limy white with only dorsal and caudal fins grey; below, disc and pelvic fins are darker than upper side, but underside of tail marked off lighter.

Distribution: Eastern North Atlantic: Greenland (Nakaya 1995), Iceland (Jónsson and Pálsson 2006), Rockall Trough, Porcupine Seabight, Bay of Biscay and off North West Africa from off Mauritania, Rio de Oro and Guinea (Conakry) (Stehmann 1995). Also, known from a single record from off the Azores. Western North Atlantic: southern Baffin Bay and Davis Strait southward to Grand Banks, Flemish Cape, Scotian slope, Georges Bank (Sulak et al. 2009); a few records as far south as off Florida and in north-eastern Gulf of Mexico. Also, found along the Mid-Atlantic Ridge (Orlov, Cotton and Byrkjedal 2006). Presumably this is a widespread species across the North Atlantic in deep water.

Habitat: Demersal on various kinds of bottom substrate from 650 to $2,200 \mathrm{~m}$ depth, mostly deeper than $1,500 \mathrm{~m}$ and within a temperature range of 2.5 to $4^{\circ} \mathrm{C}$; a yet unpublished record by the British RV 'Challenger' from the outer Porcupine Seabight at $4,156 \mathrm{~m}$ depth appears to be the deepest known record of a rajoid skate.

Biology: Oviparous, egg capsule not yet known. Virtually nothing known of the life history of this species. Its diet is poorly known, but it does include small benthic invertebrates mostly consisting of crustaceans (Gordon and Duncan 1989).

Size: Maximum length to about 55 cm . Size at maturity uncertain, but possibly between 40 and 45 cm in length; a Western North Atlantic male 43.4 cm in length was mature, while another 44.4 cm long was immature. Smallest known free-swimming specimen was 11.7 cm in length (USNM 148269 ).

Interest to Fisheries and Human Impact: Occasionally taken as bycatch in local deep-water commercial bottom trawl fisheries at depths of over $1,400 \mathrm{~m}$, but it is usually discarded because of its small size and thorniness. The presumably wide distribution in mainly lower slope depth protects so far the species from target exploitation and eventual overfishing.

The conservation status is Least Concern.


Fig. 463 Rajella bigelowi
$\square$ Known distribution

Local Names: Bigelow's Rochen (Germany); Bláskata (Iceland).
Remarks: As very little yet known of this small skate's biology and its distribution, specimens when caught should be preserved and be forwarded to national research institutes.

Literature: Bigelow and Schroeder (1953 as Raja bathyphila; 1954); Stehmann, in: Tortonese and Hureau (1979); Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Gordon and Duncan (1989); Stehmann (1995); Nakaya, Rajidae, in. Okamura et al. (1995); Jónsson and Pálsson (2006); Orlov, Cotton and Byrkjedal (2006); Orlov et al. (2008); Sulak et al. (2009); Johnston et al. (2010).

## Rajella dissimilis (Hulley, 1970)

Raja dissimilis Hulley, 1970, Ann. S. Afr. Mus., 55(4): 199-203. Holotype, adult male ( 640 mm TL ) ISH 46-1967a, now ZMH 22258; 2 paratype females ( $425,501 \mathrm{~mm} \mathrm{TL}$ ) ISH 46-1967b+c, now ZMH 22259.
Synonyms: Raja (Rajella) dissimilis, subgenus assignment by Hulley (1972).
FAO Names: En - Ghost skate.


COLORATION


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Field Marks: Disc inverse heart-shaped (young) to subrhombic in larger specimens, outer corners broadly rounded; snout moderately short and narrowly pointed. Tail somewhat longer than body. Upper disc densely covered with fine dermal denticles in young and larger females, but pectoral centres largely smooth in larger males. Small young may show individual thorns on head, but larger specimens with half-ring of thorns on orbital rims and a loose triangle of thorns over nape shoulder region; median row of 20 to 32 distinct thorns from behind shoulder along trunk and tail becoming much smaller on posterior tail and disappearing some distance anterior to first dorsal fin (except for small young); up to 60 larger thorns flanking median row on tail in young, and in larger specimens extending onto back of trunk. Underside smooth, but edges of tail may be prickly anteriorly. Colour plain dark greyish-brown above; disc below predominantly white but with broad dark margins from outer corners along posterior margins into pectoral-fin axils, as well as margin of posterior pelvicfin lobes; underside of tail marked off plain dark, may be mottled with white posteriorly, but subdorsal end of tail always plain white.

Diagnostic Features: Disc inverse heart-shaped (young) to subrhombic in larger specimens, with anterior margins weakly undulated in young and females, stronger so in mature males, outer corners broadly rounded. Snout moderately short and pointed at 85 to


SQUAMATION
Fig. 464 Rajella dissimilis $98^{\circ}$, narrower pointed in mature males. Tail somewhat longer ( 1.2 to 1.3 times) than body, rather solid, gradually tapering to tip, with two small confluent dorsal fins at rear. A few small thorns on snout only in juveniles, none in larger specimens; 1 to 8 pre-, 0 to 4 supra-, 1 to 5 postorbital thorns mostly as continuous halfrings, but supraorbital gap may occur, and a pair of supra- and interspiracular thorns; 1 to 4 median thorns on nape, 1 to 2 on midshoulder and 0 to 3 on each shoulder separated mainly in young; larger specimens with a loose triangle of up to 16 thorns over nape-shoulder region, in that lateral nuchal thorns are added with growth and a few between those on outer shoulders and midshoulder. Median row of 20 to 32 thorns from behind shoulder girdle to first dorsal fin only continuous in young, but in larger specimens these thorns becoming smaller and more widely spaced on back of trunk and on posterior tail to finally become indistinguishable some distance before first dorsal fin from regular spinules on back of tail. Smaller and half-grown specimens have the median thorn row flanked by 13 to 25 hooked thorns in parallel rows on anterior tail or to level of dorsal fins; large specimens show up to 50 to 60 parallel thorns of much larger size than median ones, in that parallel thorns extend to anterior trunk and also beyond first dorsal fin. Smaller specimens with upper disc almost completely and densely set with fine spinules, including eyeballs, but pelvic fins smooth, whereas back and sides of tail densely prickly, as well as dorsal and caudal fins; underside smooth, only marginal spinules in anterior third of tail. In larger females eyeballs smooth and spinules looser set on head, as well as on back of trunk and tail. Large males nearly smooth above on pectoral centres, pelvic fins, back of trunk and tail; fine spinules loosely scattered only on head, but a broad stripe of fine prickles along posterior three fourths of anterior disc margins curving at outer corners to run as narrow stripe also along posterior margins to pectoral-fin axils parallel to broadly smooth outer posterior disc margins; sides of tail remain densely spinulose in large specimens, which have underside totally smooth. Upper jaw tooth rows 33 to 41, individual teeth flat and with short conical cusp in young and females, rows set in pavement pattern; teeth sharply pointed in mature males and set in parallel rows. Colour: the species is characterised by uniformly dark upper side, with only tip of anterior pelvic-fin lobes whitish, and dusky dorsal and caudal fins; typically underside of disc white to pale light, with outer corners and posterior margins broadly edged more less dark greyish-brown, as well as posterior pelvic-fin lobes, but white anterior pelvic-fin lobe at most with some dark specks at tip and along posterior edge; underside of tail sharply marked off by being plain dark greyish-brown over most of its length, but pale speckles may occur in posterior third, and typically tail end from below first dorsal fin white with only extreme tail end dusky.

Distribution: Eastern Atlantic: previously known only from off southern Africa (Namibia and South Africa, Compagno et al. 1991) and off North West Africa (Rio de Oro, Stehmann 1995a), this species has recently been found to occur as far north as the Rockall Trough area at depths of over 1,000 m (M. Stehmann, unpubl. data).

Habitat: Benthic on various kinds of bottom types from 420 to $1,000 \mathrm{~m}$ depth off western South Africa and Namibia; mostly around $1,000 \mathrm{~m}$; records from off North West Africa from 1,200 to $1,640 \mathrm{~m}$ depth, and records further north from Rockall Trough area also deeper than $1,000 \mathrm{~m}$.

Biology: Oviparous, egg capsules measuring 8 cm in length excluding the horns, with a smooth surface and no prominent striations, anterior and posterior aprons are of similar size, and the lateral edges have a very narrow keel (Ebert et al. 2007). Very little else is known of the reproductive biology of this skate. The diet consists of crustaceans, including euphasiids, cephalopods, and small teleost fishes (Ebert et al. 1991).

Size: Maximum total length is at least 82.3 cm for a female and 79 cm for a male. Size at maturity for females is about 60 cm , and for males between 52 and 65 cm . The smallest free-swimming individual was 13 cm long (Ebert et al. 2007).

Interest to Fisheries and Human Impact: Occasionally taken as bycatch in commercial deepwater bottom trawl fisheries at depths over 700 m from off South Africa, Namibia, and in the Rockall Trough. They are generally discarded as being too small, but in the North Atlantic larger specimens may be kept and landed, e.g. in France.

The conservation status is Least Concern.

Local Names: Geister-Tiefwasserrochen (Germany).

Remarks: This skate, once considered to be very rare, is not uncommon at depth throughout much of its range in deeper water, usually below a depth of 700 m . Ebert, Compagno, and Cowley (2007) reported on 85 additional specimens from off South Africa.

Literature: Hulley (1970, 1972); Ebert, Cowley, and Compagno (1991); Stehmann (1995a); Smale (2004); Compagno and Ebert (2007); Ebert, Compagno, and Cowley (2007).


Fig. 465 Rajella dissimilis
$\square$ I Known distribution

## Rajella fyllae (Lütken, 1888)

Raja fyllae Lütken, 1888, Vidensk. Meddr. Dansk naturh. Foren. 1887 (publ. 1888): 1-4. Holotype ZMUC No. 1.
Synonyms: Breviraja marklei McEachran and Miyake, 1987; Raja (Rajella) fyllae, subgenus (Stehmann, 1970).
FAO Names: En - Round ray; Fr - Raie ronde; Sp - Raya redonda.



OUTLINE OF FEMALE

Fig. 466 Rajella fyllae
Field Marks: Disc roundish, broader than long, with greatly rounded outer corners and undulated anterior margins, stronger so in mature males. Snout very short and very blunt, its tip a little pronounced. Tail conspicuously longer than body. Entire upper side very rough with coarse prickles and many thornlets concentrated on head and posterior disc, only in mature males pectoral centres smooth. Orbital thorns forming complete inner half-rings of 5 to 9 thorns on orbital rims in larger specimens, which also show a large triangle of many thorns over nape and shoulder area; from small juveniles onward, a median row of thorns from behind shoulder girdle to first dorsal fin, flanked by with growth an increasing number of parallel rows of larger thorns along back and sides of trunk and tail, so that a broad band of many thorns runs from nape down onto tail. Underside smooth. Colour above quite variable from ash-grey to dark brown, usually lively patterned in various ways from clouded dark and/or pale to spotted dark and light, tail often with dark cross-bars; underside from largely white, with dark blotching on head, belly and tail and dark margins around disc and to posterior pelvic-fin lobes, to sometimes predominantly dark specimens with only few white markings left.

Diagnostic Features: Disc roundish, a little broader than long, with greatly rounded outer corners and undulated anterior margins, stronger so in mature males. Snout very short and very blunt (angle 115 to $156^{\circ}$ ), its tip a little pronounced. Tail conspicuously longer than body (about $60 \%$ of total length), rather solid, gradually tapering to tip and with two small confluent dorsal fins at rear. Entire upper side very rough with prickles and many thornlets concentrated on head and posterior disc, only in mature males pectoral centres smooth. Orbital thorns separate only in small young but forming complete inner half-rings of 5 to 9 thorns on orbital rims in larger specimens, which also show a large triangle of many thorns over nape and shoulder area; from small juveniles onward, but becoming indistinct with growth, a median row of thorns from behind shoulder girdle to first dorsal fin, flanked by with growth an increasing number of parallel rows of larger thorns along back and sides of trunk and tail, so that a broad band of many thorn rows runs from nape down onto tail. Underside largely smooth. Tooth rows in upper jaw 30-38; individual teeth blunt in juveniles and females, with short conical cusp and arranged in pavement pattern; teeth with longer, sharply pointed cusp closely set in parallel rows in mature males. Colour: ground colour above quite variable from ash-grey to dark brown, usually lively patterned in various ways from clouded dark and/or pale to spotted dark and light, tail often with dark cross-bars; locally, specimens do occur with large pale marking on snout, interorbitally, on mid-disc and at pectoral-fin axils; underside from largely white, with dark blotching on head, belly and tail, and dark margins around disc and to posterior pelvic-fin lobes, to sometimes predominantly dark specimens with only few white markings left.

Distribution: North Atlantic: across the entire northern North Atlantic from Arctic latitudes southward to about $45^{\circ} \mathrm{N}$ in the Eastern North Atlantic, off the western British Isles and Ireland and northern Bay of Biscay, and to about $40^{\circ} \mathrm{N}$ in the Western North Atlantic, off Nova Scotia, in Gulf of Maine (rare) and on outer Georges Bank (Sulak et al. 2009).

Habitat: A rather common species, demersal on soft substrate from about 170 m depth to 800 m , exceptionally to about $2,000 \mathrm{~m}$ and within temperature range of 1 to $7^{\circ} \mathrm{C}$.

Biology: Oviparous, egg cases very small, rectangular, 38 to 42 mm in length by 24 to 26 mm in width (excluding horns), with smoothly striated surfaces and narrow lateral keels, two pairs of slender, filamentous horns, with anterior pair not much longer than posterior pair. Size at sexual maturity is dependent on water temperature and/or latitude of habitat. Due to the rather coldwater habitat, embryonic development may take several months to possibly years until hatching at about 7 cm total length. This small skate species feeds mainly on small crustaceans, including amphipods and mysids.

Size: Maximum length to about 55 cm . Females and males mature at about 45 to 50 cm . Size at hatching about 7 cm .

Interest to Fisheries and Human Impact: A regular bycatch of commercial bottom trawl fisheries in Arctic and subarctic waters, but usually discarded because of its small size and thorniness. Dolgov et al. (2005a, b) reported Rajella fyllae as being the third most abundant skate species in the Barents Sea (2\% in number in surveys and commercial bycatch). Currently subject to TACs in EU waters and in NAFO Divisions 3LNO (2012).

Conservation status is Least Concern.
Local Names: Sandy skate (England and Wales, Ireland); Pólskata (Iceland); Rundskate (Norway); Fyllas rokke (Denmark and Greenland); Fyllarochen (Germany); Klingruskøta (Faroe Islands); Rundrocka (Sweden).

Remarks: $\boldsymbol{R}$.fyllae is the type species of


Fig. 467 Rajella fyllae
$\square$ Known distribution genus Rajella Stehmann, 1970.

Literature: Clark (1926); Bigelow and Schroeder (1953); Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Dolgov et al. (2005a, b); Kulka et al. (2008); Sulak et al. (2009); Shark Trust (2009).

## Rajella kukujevi (Dolganov, 1985)

Raja (Rajella) kukujevi Dolganov, 1985, Zool. Zhurnal, 64(2): 304-307. Holotype mature male ZIN 46195.
Synonyms: None.
FAO Names: En - Mid-Atlantic skate.


Field Marks: Disc subrhombic (adults) and somewhat wider than long, with anterior margins only weakly undulated even in mature males, outer corners broadly rounded; snout moderately short, narrowly pointed (angle about $90^{\circ}$ ) and its tip pronounced; tail somewhat longer than body, rather solid, gradually tapering to tip, with two small close-set dorsal fins at rear. Upper side largely smooth (mature male), rough prickly only at midlength of anterior margins. Thorns on snout absent; half-ring of about 7 thorns on orbital rims; 2 large median plus a few small lateral thorns on nape, a distinct thorn on midshoulder and 1 on each shoulder; median row of about 21 thorns from posterior trunk onto tail but ending some distance in front of first dorsal fin; no interdorsal thorns; median row flanked by a somewhat irregular parallel row of many smaller thorns from anterior trunk to first dorsal fin, and small thorns along lower edges of tail. Underside smooth. Tooth rows in upper jaw 43, 42 in lower jaw; individual teeth with sharp, pointed cusp. Colour plain limy-white on both surfaces, but dorsal fins dusky, and ventrally irregular small dark spots on posterior disc margins, pelvic fins, claspers and on tail.

Diagnostic Features: As so far no other descriptive information is available of this species than the brief original description by Dolganov (1985) of the 79 cm total length adult male holotype, no further details of variation in diagnostic features can be given here.


Fig. 468 Rajella kukujevi

Distribution: Eastern North Atlantic: Faraday Seamount, Mid-Atlantic Ridge, Faroe Islands, within the Rockall Trough area, northern Bay of Biscay and off northern Spain, and possibly as far south as off western North Africa.

Habitat: Demersal in deep water of lower continental slopes and submarine elevations to about 1200 m depth.

Biology: Oviparous, but nothing else known of its reproductive biology or diet.

Size: Maximum length is from 79 to 84 cm (Iglésias, 2011) for mature males, but nothing else known on size at maturity.

Interest to Fisheries and Human Impact: Possibly taken as bycatch in deepwater bottom trawl fisheries in the Rockall Trough area by French vessels, which occasionally land large specimens.

The conservation status of this poorly known deepwater skate is Data Deficient.

Local Names: Kukujevs Rochen (Germany).

Remarks: Few additional specimens have been caught off western North Africa (Merrett and Marshall 1981 as Raja sp.; Stehmann, 1990 as Raja


Fig. 469 Rajella kukujevi
(Rajella) sp. 2), in the Rockall Trough (Stehmann unpubl. data), and Johnston et al. (2010) reported on two specimens from Porcupine Seabight at 1,496 and 732 m depth. Recently, Rodríguez-Cabello et al. (2012) reported on two more specimens taken at Le Danois Bank (about $44^{\circ} \mathrm{N}, 04-05^{\circ} \mathrm{W}$ ) in the Cantabrian Sea at 1171 to 1238 m depth. Nothing is known of this skate's biology and distribution, and as such specimens when caught should be retained and preserved for further study in national research institutes.

Literature: Merrett and Marshall (1981); Dolganov (1985); Stehmann, Rajidae, in: Quero et al. (1990); Orlov (2008); Johnston et al. (2010); Iglésias (2011); Rodríguez-Cabello et al. (2012).

## Rajella lintea (Fries, 1839)

Raja lintea Fries, 1839, K. svenska VetenskAkad. Handl. 1838 (publ. 1839): 154-157. Holotype stuffed female NRMS 206a, but probably lost.
Synonyms: Dipturus linteus (Fries, 1839), as reallocated by McEachran and Miyake (1990, Appendix).
FAO Names: En - Sailray; Fr - Raie voile; Sp - Raya vela.


Field Marks: Upper side uniformly greyish-brown; underside largely white but constantly with greyish-brown markings, such as broad margin from outer disc corners along posterior margins and at posterior pelvicfin lobe margins, a blotch on each anterior pelvic-fin lobe tip, paired oval blotches flanking cloaca, and underside of tail mostly with dark median stripe, or at least an irregular double row of brownish specks medially along anterior half or nearly entire tail. A continuous median row of 38 to 51 distinct, close-set thorns from nape to first dorsal fin, and a row of 50 to 60 strong, hooked thornlets along each lower edge of tail.

Diagnostic Features: Disc subrhombic, broader than long, with straight to slightly convex anterior margins in juveniles and females, but strongly undulated margins in mature males; outer corners narrowly rounded in young and half-grown specimens, becoming angular rather in mature specimens; snout moderately elongated, more so in large specimens, with tip somewhat pronounced, and snout angled at about 90 to $100^{\circ}$ in young, at less than $90^{\circ}$ in large specimens. Tail solid, broadly triangular in cross-section, with two small confluent or closeset dorsal fins at rear and postdorsal tail section very short; lateral tail folds distinct only in posterior third or half, anteriorly a low ridge from pelvic axils on; tail a little longer than body in young, but about $50 \%$ of total length in larger individuals. Upper disc, including eyeballs, wholly and loosely set with coarse dermal denticles, but pelvic fins smooth, and sides of tail very densely covered with fine prickles except narrowly smooth back of tail along the course of median thorn row; both dorsal


Fig. 470 Rajella lintea fins prickly; underside of disc, pelvic fins and tail smooth, occasionally only a few embedded dermal denticles near snout tip. About 10 distinct thornlets in irregular double row on anterior half of rostrum in smaller specimens, increasing to about 40 thornlets in large ones; orbital thorns separated at smaller size, with one big inner and one small outer preorbital thorn, a small one supraorbitally, a large one postorbitally, 1 to 2 small or large ones in supraspiracular and constantly a pair of conical thorns more inward in interspiracular position; large specimens show in addition a patch of thornlets pre- and postorbitally, 2 to 4 large median nuchal thorns, first one smaller, followed by 1 to 2 large suprascapular thorns, and mostly three thorns on each shoulder, with inner one the biggest; a regular row of 39 to 44 close-set large thorns with sharp, recurved tip from shoulder girdle to first dorsal fin, of which 9 to 11 (mostly 10 ) on back of trunk to level of pectoral-fin axils; no thorn between dorsal fins, even if these separated by small interspace; median thorn row persisting from
smallest young onward, but tips become abraded in fully grown specimens on trunk and in anterior half of tail, and the basal cones tend to split up by radiated cracks. A regular row of 50 to 60 strong, hooked thornlets along each lower edge of tail persisting from smallest young onward. Mature males with an elongated field of strong malar thorns and thornlets at anterior disc margins from level of half snout length to the begin of the elongated alar thorn field across wing tips, consisting of three longitudinal and 29 to 31 transverse rows of sharp, claw-like thorns which erectile from individual dermal pockets. Jaw teeth set in 41 to 50 rows in pavement pattern in juveniles and females, in close-set parallel rows in mature males; teeth with conical, short, bluntly pointed cusp in juveniles and females, with sharp, longer pointed cusp in mature males. Monospondylous trunk vertebrae 34 to 35 , diplospondylous tail vertebrae to origin of first dorsal fin 68 to 72; pectoral-fin radials 82 to 84; pelvic-fin radials $1+22$ to 24 . Colour: upper side uniformly, rather dark greyish-brown, eyeballs dusky-bluish; edges of disc, pelvic fins and dorsal fins narrowly edged creamy-white. Underside largely creamy-white, but with constant brownish colour markings, namely broad more or less dark margin from wing tips to pectoral-fin axils and to posterior pelvic-fin lobes, a dark blotch on tip of anterior pelvic-fin lobe, a pair of large, oval to bean-shaped blotches flanking cloaca, and a broad dark median stripe along entire tail, edges of which are creamy; variation on underside of tail does occur, that instead of median dark stripe an irregular double row of brownish specks medially along anterior half or nearly entire tail.

Distribution: Eastern North Atlantic: Barents Sea, Norway to Skagerrak, northern North Sea, off Iceland and along the Iceland-Faroe-Ridge to northern Rockall Trough, and Greenland. Western North Atlantic: western Greenland across the Davis Strait to Baffin Bay to the Flemish Cape and eastern Grand Banks (Sulak et al. 2009).

Habitat: Demersal on various kinds of bottom substrate at 150 to 650 m depth, occasionally deeper, but mostly around 250 m at bottom temperatures of 3.3 to $6.0^{\circ} \mathrm{C}$. Appears to live deeper in the Western North Atlantic to about $1,500 \mathrm{~m}$.

Biology: Oviparous, egg capsules rectangular, about 10.7 cm in length by 7.7 cm in width (excluding horns), with two pairs of horns at both ends. Given the coldwater habitat, embryonic development once the egg cases are deposited may take many months to possibly years until hatching. The smallest known free-living specimen (a female neonate 15.9 cm total length, still had an embryonic tail filament


Fig. 471 Rajella lintea
Known distribution present when captured) was caught at about $54^{\circ} \mathrm{N}, 53^{\circ} \mathrm{W}$ and at a depth of 461 m , and with at a bottom water temperature of $4.5^{\circ} \mathrm{C}$ in Canadian waters (J. Treberg, pers. comm.). Very little else is know about the biology of this skate. The diet consists of demersal invertebrates with larger individuals consuming teleost fishes.

Size: Maximum length to at least 125 cm (mature male), but size at maturity unknown. The size at birth is uncertain, but the smallest known free-swimming neonate measured 15.9 cm in length.

Interest to Fisheries and Human Impact: This species mostly occurs below the depth range of most commercial fisheries, except for some of the more intensified deepwater trawling fleets. It is taken as bycatch only, and large specimens may be landed for human consumption. As very little is known of its biology, reproduction and nursery areas in boreal to cold temperate latitudes, bycatch rates should be carefully monitored. As a species of the Order Rajiformes is subject to TACs regulation in EU waters (2012).

The conservation status is Least Concern.
Local names: Pale ray (USA); Hvitskate (Norway); Hvidrokke (Denmark and Greenland); Hvítaskata (Iceland); Hvítaskøta (Faroe Islands); Weissrochen (Germany); Raia nevoeira (Portugal).

Remarks: After the changed generic assignment to Dipturus by McEachran and Miyake (1990), Stehmann (2012) has reinvestigated the species with a complementary redescription of the species, including for the first time a mature male's relevant clasper characters, and will present evidence for its generic reassignment to the genus Rajella.

Literature: Stehmann and Bürkel, Rajidae, in. Whitehead et al. (1984); McEachran and Miyake (1990); Kulka, Orlov and Stenberg (2006); Sulak et al. (2009); Stehmann (2012).

## Rostroraja Hulley, 1972

Genus: Rostroraja Hulley, 1972, Ann. S. Afr. Mus., 60(1): 77.
Type Species: Raja alba Lacepède, 1803 by original designation.
Number of Recognized North Atlantic Species: 1.
Synonyms: Raja (Rostroraja) Hulley, 1972 as subgenus.
Field Marks: See Diagnostic Features below.
Diagnostic Features: Very similar in size and shape to species of the genus Dipturus, but differing markedly from the latter in that underside of the disc is white, with only blackish or grey margins to disc and posterior pelvic-fin lobes, and in that sensory and mucus pores on both surfaces are inconspicuous because not marked black.

Remarks: This genus is monotypic.

## Rostroraja alba (Lacepède, 1803)

Raja alba Lacepède, 1803, Hist. Nat. Poissons, 5: 661-663. No type material.
Synonyms: Raja marginata Lacepède, 1803, Raja (Rostroraja) alba, as subgenus (Hulley 1972).
FAO Names: En - White skate; Fr - Raie blanche; Sp - Raya bramante.


Field Marks: Snout very long and pointed, its tip distinctly pronounced. Upper disc smooth only in small juveniles, but with growth increasingly prickly. Juveniles only with a distinct thorn in front of and behind eyes, more but smaller orbital thorns develop with growth. No other thorns on disc; a median row of 10 to 30 thorns along tail to first dorsal fin, and 0 to 2 thorns in interdorsal space; usually a row of strong lateral thorns along either lower edge of tail. Underside largely smooth only in juveniles, larger specimen becoming spinulose all over, including the tail. Colour above reddish brown in juveniles, greyishblue in larger specimens, usually with pattern of numerous pale spots; underside white but with dark margins to disc and posterior pelvic-fin lobes, and underside of tail dusky. Neither above, nor below are sensory and mucus pores marked black.

Diagnostic Features: Broadly rhombic disc about 1.5 times wider than long, outer corners acute, anterior margins undulated and overall deeply concave. Snout very long and pointed (angle about $105^{\circ}$ ), the tip marked off distinctly pronounced; preorbital snout length 2.5 to 3.2 times the interorbital distance. Tail somewhat shorter than body, broad and depressed, gradually tapering to tip, with two small dorsal fins at rear separated by narrow space. Disc above almost smooth only in small juveniles, but prickles on snout and along anterior margins; with growth becoming largely spinulose, with only centres of pectoral fins more or less smooth. Only small juveniles with a pre-and postorbital thorn, but with growth more and smaller thorns develop on orbital rims. Except for patches of malar and alar thorns of mature males, no other
thorns on disc; a median row of 10 to 16 (juveniles) and up to 16 to 30 (adults) thorns along tail to first dorsal fin, and 0 to 2 thorns in space between dorsal fins; a row of 7 to 17 (juveniles), up to 17 to 29 (adults) strong thorns along either lower edge of tail. Underside of disc almost smooth in juveniles bearing prickles only on snout and front margins, but larger specimens becoming largely spinulose, including the tail, with only outer pectoral fins smooth. Upper jaw tooth rows 40 to 48, teeth in median third with elongated, pointed cusp. Colour: reddishbrown above in juveniles, greyish-blue in larger specimens, with usually more or less distinct pattern of numerous pale spots; underside white but with distinct dark margins to disc and posterior pelvic-fin lobes in juveniles, but margins fading to various degree with growth, and underside of tail dusky. Black markings of sensory and mucus pores absent above and below, unlike similar looking species of genus Dipturus.

Distribution: Eastern Atlantic: southwestern Great Britain and Ireland southward along the European coasts, also in the Western Mediterranean, and along West Africa to South Africa and into the south-western Indian Ocean.

Habitat: Demersal on the continental shelf and upper slope from shallow waters to 400 m , occasionally to 500 m depth on sand and loose rocky substrate.


SQUAMATION
Fig. 472 Rostroraja alba

Biology: Oviparous, egg capsules large and subquadrate, 160 to 200 mm in length and 130 to 150 mm in width (excluding horns); horns rather thick and curving inward, anterior pair longer than posterior pair; surface structured by prominent longitudinal ridges. Females, said to produce 55 to 156 egg cases annually, with embryos developing and hatching after about 15 months. This is a relatively voracious predator consuming a variety of benthic invertebrates including crustaceans and cephalopods, but larger individuals primarily consume teleost fishes, and other chondrichthyans including catsharks and other skates (Ebert, Cowley, and Compagno 1991).

Size: Maximum length 240 cm , with females maturing at about 195 cm and males at 152 to 170 cm in South African waters (Ebert, Compagno, and Cowley 2007); in European and Mediterranean waters females at about 130 cm , males at about 120 cm length (Shark Trust 2009). Size at hatching about 30 cm in length.

Interest to Fisheries and Human Impact: Due to its large size and thick pectoral fins, this species was targeted in northern European waters until local stocks were drastically depleted. Subsequently landed as bycatch. The collapse of a directed long-line fishery off Brittany in the 1960s highlights the vulnerability of this skate. The species is listed in Appendix 3 of the Bern convention (Convention on the Conservation of European Wildlife and Natural Habitats); Appendix 3 of this convention requires 'regulation of species populations to keep them out of danger'. The Barcelona Convention also lists this species for the Protection of the Mediterranean Sea; this


Fig. 473 Rostroraja alba convention concerns specially protected areas and biological diversity within the Mediterranean Sea and lists the white skate on the Annex III, whose exploitation is regulated. It is prohibited by EU (2012) to fish for, to retain on board, to tranship or to land Rostroraja alba in and from ICES subareas VI, VII, VIII, IX and X.

The conservation status is Endangered globally, and Critically Endangered in the Eastern North Atlantic.
Local Names: Bottlenose skate, Bordered skate, Spearnose skate, White-bellied skate, Burton skate (England and Wales, Ireland); Burton-skate (Norway); Saumrochen (Germany); Raia tairoga (Portugal); Spidsrokke (Denmark).

Remarks: Rostroraja alba is the type species of the monotypic genus Rostroraja Hulley, 1970.
Literature: Stehmann and Bürkel, Rajidae, in: Whitehead et al. (1984); Smith and Heemstra (1988); Ebert, Cowley, and Compagno (1991); Dulvy et al. (2006); Rogers and Ellis (2000); Compagno and Ebert (2007); Ebert, Compagno, and Cowley (2007); Shark Trust (2009); Ellis et al. (2010); EU (2012).

### 3.4 Order MYLIOBATIFORMES - Stingrays

Order: Order Plagiostoma, Suborder Platosomia, "Group" Myloidei: Garman, 1913 (in part), Mem. Mus. Comp. Zool. Harvard 36: 258, 259 (group corresponding to infraorder or superfamily, and containing the Families Myliobatidae and Rhinopteridae. Essentially a separate group for the eagle and cownose rays).

## Number of Recognized North Atlantic Families: 3.

FAO Names: En - Stingrays.
Field Marks: Batoids with enlarged, expanded pectoral fins completely fused to the head and trunk (except for Myliobatidae) and forming a subrhombic to diamond-shaped, or broadly lozenge-shaped disc; a single dorsal fin that is variably present or absent, one or more serrated spines or stingers on the upper tail base, and an extremely short or very long and slender whip-like tail.

Diagnostic Features: Disc subrhombic to diamond-shape and no more than 1.3 times as wide as long, with long whiplike tail (Dasyatidae), pectoral fins completely fused with sides of head, eyes and spiracles on top of head; or extremely broadly lozenge-shaped, more than 2 times as wide as long, with extremely short tail being no longer than one fourth of disc length (Gymnuridae), pectoral fins completely fused with sides of head, with eyes and spiracles on top of head; or disc broadly lozenge-shaped, more than 2 times wider than long, with wing-like pointed pectoral fins and with whip-like tail being at least two times longer than disc, and further with pectoral fins not completely fused with sides of head, which elevated above pectoral-fin level and with eyes and spiracles on sides of head. Majority of species with a small dorsal fin on tail base, behind which one or more long, serrated spines present on tail. Small jaw teeth set in pavement pattern and forming bands along jaws (Dasyatidae, Gymnuridae), or jaw teeth in only 7 to 9 rows of very thick and massive teeth forming a grinding plate in each jaw, with teeth of median row being much wider than long and larger than teeth of adjacent rows (Myliobatidae). Colour: demersal species in shallow water (Dasyatidae, Gymnuridae) usually show substrate-like brown to olive or grey ground colour, and many display colour pattern on upper disc, whereas underside is white; bentho- and semipelagic species (Myliobatidae) are mostly uniformly coloured above in more or less dark brown to grey shades, but undersides are white.

Distribution: Worldwide in mostly shallow to inshore coastal waters of tropical to warm temperate latitudes, also in brackish and partly freshwater estuaries and river mouths.

Habitat: Most species are demersal, but some myliobatids are also semipelagic. One species (Pteroplatytrygon violacea) is pelagic.

Biology: All species are yolk-sac viviparous, with most species having relatively small litters, with many species having only one or two young per litter. The diet of these batoids includes various demersal and benthic invertebrates, and small fishes; the myliobatids have specialized dentition of thick grinding plates of a few tooth rows, with massive jaw muscles for crushing hard-shelled bivalves and crustaceans.

Interest to Fisheries and Human Impact: These rays have traditionally been caught by artisanal fisheries and used for human consumption dried and salted (wings) by local populations in tropical coastal areas. More recently, they are being taken in large numbers by trawl fisheries, often as bycatch in fisheries targeting other bony fish species, and processed for their flesh, for fishmeal and for animal food. Local and regional populations of these rays have thus become much depleted in many places and are in urgent need of fishery regulations and conservation measures.

Local Names: Butterfly rays, Eagle rays, Cownose rays, Devil rays, Mantas (English); Raies pastenagues (French); Rayas pastinacas (Spanish).

Remarks: The order has 10 families, with several subfamilies, of which 3 families are represented in the North Atlantic. The family Rhinopteridae (Cownose rays) is included in the family Myliobatidae as a subfamily Rhinopterinae. See preface to batoid fishes for discussion on classification.

## Key to North Atlantic Families:

1a. Disc subrhombic to diamond-shaped, at most 1.3 times as broad as long. Tail very slender to whip-like, much longer than disc width. Dorsal fin absent, one or more serrated long spines on anterior tail (Fig. 474)
family Dasyatidae


Fig. 474 Dasyatis

1b. Disc broadly rhombic or lozenge-shaped, about two times as broad as long. Tail thin to whip-like, either longer than disc width, or extremely short, i.e. shorter even than disc length. Dorsal fin on tail base and one or more long serrated spines directly behind mostly present, lacking only in a few species . . 2

2a. Disc lozenge-shaped, extremely broad, much wider than long. Pectoral fins completely fused with sides of head, which not marked off from disc. Tail extremely short, only about one fourth of disc length, with one or more long serrated spines near base but without dorsal fin. Eyes and spiracles on top of head. Numerous small jaw teeth set in about 100 to 140 transverse rows forming tooth bands along jaws (Fig. 475) . family Gymnuridae

2b. Disc broadly lozenge-shaped, much wider than long. Head marked off from disc, pectoral fins not evenly and completely fused with sides of elevated head; eyes and spiracles on sides of head. Tail at least two times longer than disc, whip-like posterior to base with a small dorsal fin and one or more long serrated spines directly behind it. Large jaw teeth in 7 to 9 rows, those of median row 3 to 9 times as broad as long and much wider than teeth of adjacent rows; teeth flat and massive, forming grinding plates in both jaws (Fig. 476). . . . . . . . . . . . . family Myliobatidae (with two subfamilies Myliobatinae and Rhinopterinae)


Fig. 475 Gymnura


Fig. 476 Myliobatis

### 3.4. 1 Family DASYATIDAE

Family: Dasyatidae Jordan, 1888, Man. Vert. Eastern U.S., ed. 5: 15.
Type Genus: Dasyatis Rafinesque, 1810.

## Number of Recognized North Atlantic Genera: 2.

FAO Names: En - Stingrays; Fr - Pastenagues; Sp - Pastinacas.
Field Marks: Stingrays with a long whip-like tail, no caudal or dorsal fins, and with one or more toxic serrated spines at tail base.
Diagnostic Features: Disc at most 1.3 times as broad as long, of rhombic, oval, subtriangular or subcircular shape. Pectoral fins fused with sides of head over its entire length. Snout obtuse to moderately pointed, from very short to moderately pronounced. Eyes and spiracles on top of head. Several fleshy papillae on floor of mouth. Small teeth in pavement pattern in many rows forming bands along jaws. Nasal curtain distinctly fringed. Dorsal and caudal fins absent on tail. Tail distinctly marked off from body disc, moderately slender to whip-like, usually much longer than disc; one or more long, serrated spines on tail base. Some species with longitudinal fold and/or ridge on upper and/or lower side of tail behind spine. Upper side either naked, or set to varying degrees with dermal denticles, thornlets and tubercular thorns. Stingrays of varying size, disc width from 30 cm to more than 200 cm . Colour: upper side mostly uniform grey to dark brown, with darker or paler markings in several species; underside generally white, but dark outer margins or irregular markings may occur; whip-like tail section behind spine usually blackish.

Distribution: Worldwide mainly in tropical and subtropical continental shelf waters from very inshore to little more than 100 m depth, but also in brackish and freshwater of estuaries and around river mouths.

Habitat: Demersal (except for the only pelagic species Pteroplatytrygon violacea), with most species living in relatively shallow shelf waters, usually found inshore, in lagoons, river mouths and especially in mangrove-lined habitats.

Biology: All species are yolk-sac viviparous. These stingrays feed on benthic invertebrates that they often dig out of the soft bottom substrate by vigorously flapping their wings and blowing a strong water stream from their mouth; some species also feed on small fishes.

Interest to Fisheries and Human Impact: Globally, many species are important in regional or artisanal fisheries, especially where they are abundant in tropical and subtropical areas. In the North Atlantic these batoids are generally not very abundant. Where they are fished, the stocks for many of these stingrays have become depleted. The flesh of the wings is well esteemed for human consumption (dried, salted, smoked); other parts and whole specimens also used for fishmeal and fish oil mainly on board of larger vessels operating offshore.

Local Names: None.
Remarks: The family comprises totally six genera, and more than 80 species, with several undescribed species. The genera and species of this family are most diverse in tropical shelf waters. Two genera and three species occur in the North Atlantic.

Literature: Bigelow and Schroeder (1953); McEachran and Capapé, Dasyatidae, in: Whitehead et al. (1984).

## Key to North Atlantic Genera:

1a. Upper and lower disc plain dark coloured. Disc shape almost triangular to rearward narrowly trapezoid, with entire anterior contour forming an even arc of great radius, snout not marked off and very short. Underside of tail with a distinct, very elongate cutaneous fold extending beyond tail sting for one half to three quarters of tail length; dorsal tail fold rudimentary or absent. Floor of mouth with 10 to 12 fleshy papillae (Fig. 477). . . Pteroplatytrygon


Fig. 477 Pteroplatytrygon
1b. Upper disc coloured plain greyish to olive-brown, underside white with at most darker margins. Disc subrhombic to diamondshaped, snout somewhat produced and bluntly angled. Short and deep cutaneous folds from level of tail sting on back and underside of tail, or a somewhat more elongated fold only on underside. Floor of mouth with 5 to 6 fleshy papillae (Fig. 478)


Fig. 478 Dasyatis

## Dasyatis Rafinesque, 1810

Genus: Dasyatis Rafinesque, 1810, Caratt. Gen. Spec. Sicil.: 16.
Type Species: Dasyatis ujo Rafinesque, 1810 = Raja pastinaca Linnaeus, 1758 by monotypy.

## Number of Recognized North Atlantic Species: 2.

Synonyms: None.
Field Marks: Stingrays with a ventral finfold height less than the tail height above it.
Diagnostic Features: See Family and Key to Genera above.
Remarks: The genus comprises about 40 to 45 species worldwide, but only two occur in the North Atlantic.

## Key to North Atlantic Species:

1a. Upper disc smooth, or with sparsely scattered dermal denticles on wings; widely spaced small thorns only in median row from nape to root of tail, few thorns on shoulders of large specimens may occur. A relatively short, but deep membranous fold on back and underside of tail from level of tail spine (Fig. 479)

Dasyatis pastinaca


Fig. 479 Dasyatis pastinaca
1b. Upper disc in larger specimens with large tubercles, thorns or bucklers irregularly from nape along midline, extending onto central and posterior wings in large specimens; thorns and large thornlets also along back and sides of tail; underside of tail smooth at origin to level of spine tip, thereafter thorny. A relatively long and deep membranous fold along underside of tail, but no fold or ridge above (Fig. 480).

Dasyatis centroura


Fig. 480 Dasyatis centroura

## Dasyatis centroura (Mitchill, 1815)

Raja centroura Mitchill, 1815, Trans. Lit. Phil. Soc. N.Y., 1(5): 479. No type material.
Synonyms: None.
FAO Names: En - Roughtail stingray; Fr - Pastenague des îles; Sp - Rayalátigo isleña.
Field Marks: Disc diamond-shaped, snout short and bluntly angled; undamaged tail 2.4 to 2.6 times the body length, with one or more long serrated spines on base. Upper disc in larger specimens with large tubercle thorns or bucklers irregularly from nape along midline and extending onto central and posterior wings in large specimens; underside of tail also thorny posterior to level of spine tip.

Diagnostic Features: Disc diamond-shaped, snout short and bluntly angled ( 130 to $140^{\circ}$ ); anterior disc margins straight to weakly convex and outer corners acutely angled; pelvic fins unilobed subquadrate; tail undamaged 2.4 to 2.6 times the body length, solid at origin and bearing a massive, long serrated spine (sometimes two or more), behind which the tail becomes abruptly thinner like a long whip-lash; originating at level of tail spine, a relatively long and deep membranous fold along underside of tail, but no fold or ridge above. Floor of mouth with 5 to 6 fleshy papillae. Disc of larger specimens above set with large tubercle thorns or bucklers irregularly from nape along midline and extending onto central and posterior wings; thorns and large thornlets also along back and sides of tail; underside of tail smooth at origin to level of spine tip, thereafter thorny. Teeth flat and set in pavement. Tail spine(s) with about 40 serration teeth each side in distal two thirds of spine length. Colour: above olive-brown, underside almost white, but tail blackish posterior to spine.

Distribution: Eastern North Atlantic: from off Morocco, Canary Islands and Madeira northward to southern Bay of Biscay, also in the Mediterranean, but not in the Black Sea; also along the coast of West Africa southward to about Angola. Western North Atlantic: from about Georges Bank southward to off Florida and into the eastern Gulf of Mexico; also along South America, often found off southern Brazil, Uruguay and north Argentina.

Habitat: Demersal on sandy and muddy bottoms from shallow inshore waters, where most common, to about 274 m depth.

Biology: Yolk-sac viviparous, a gestation period of about 4 months with birth occurring in the autumn and early winter. Litters range from 2 to 6 young. These rays feed on various kinds of benthic invertebrates, with preference for crabs, molluscs and also locally abundant squids, but they rarely feed on fishes.

Size: Maximum disc width 260 cm at 290 kg weight, but usually 100 to 130 cm disc width. Maturity occurs in females at 140 to 160 cm disc width and at 130 to 150 cm disc width for males in the Western North Atlantic, but at a much smaller size, 66 to 100 cm for females and 80 cm disc width for males, in the Mediterranean. Size at birth for Western Atlantic specimens is from 34 to 36 cm disc width, but is smaller at 8 to 13 cm in the Mediterranean.

Interest to Fisheries and Human Impact: Usually bycatch in trawl, longline, trammelnet and rod and line fisheries, but usually discarded; in Mediterranean and African waters, where they are locally common, these rays are often retained and their wings used for human consumption smoked or dried salted.

Conservation status is Least Concern globally, but Near Threatened in the Mediterranean and South Western Atlantic.
Local Names: Dornenschwanz-Stechrochen (Germany); Uge de Cardas (Portugal).

Remarks: Populations in the Eastern Atlantic and off Uruguay may represent different species (Struhsaker 1969, McEachran and Fechhelm 1998). The status of a single questionable record from India is likely a different species (Rosa et al., 2007).

Literature: Bigelow and Schroeder (1953); Struhsaker (1969); McEachran and Capapé, Dasyatidae, in: Whitehead et al. (1984); McEachran and Fechhelm (1998); Rosa et al. (2007).


Fig. 482 Dasyatis centroura $\square$ Known distribution

## Dasyatis pastinaca(Linnaeus, 1758)

Raja pastinaca Linnaeus, 1758, Syst. Nat., ed. 10, 1: 232. No type material.
Synonyms: ?Dasyatis tortonesei Capapé, 1975.
FAO Names: En - Common stingray; Fr - Pastenague commune; $\mathbf{S p}$ - Raya látigo común.
Field Marks: Disc diamond-shaped, with outer corners a rounded angle ( $90^{\circ}$ ); snout very short and very bluntly angled; tail (if undamaged) 1.3 to 1.5 times the body length, with a massive, long serrated spine (sometimes two or more) on base, behind which the tail thin like a long whip-lash; originating at level of tail spine, a relatively short but deep membranous fold on back and underside of tail. Large specimens with scattered dermal denticles on upper disc and median thorns on tail base; underside smooth. Colour plain greyish, olive or brown above, underside white but with broad greyish-brown margins to disc and pelvic fins, whiplash tail section also dark.

Diagnostic Features: Disc diamond-shaped, with anterior margins straight to weakly convex and outer corners a rounded angle $\left(90^{\circ}\right)$; snout very short, its preorbital length less than the interorbital space, and very bluntly angled; pelvic fins subquadrate single lobes; undamaged tail 1.3 to 1.5 times the body length, solid at origin and bearing a massive, up to 12 cm long serrated spine (sometimes two or more), behind which the tail becomes abruptly thinner like a long whiplash; originating at level of tail spine, a relatively short but deep membranous fold on back and underside of tail. Floor of mouth with 5 bulbose papillae. Upper disc may show very loosely


Fig. 483 Dasyatis pastinaca
scattered dermal denticles in large specimens and large, narrow-based thorns medially on origin of tail; underside smooth. Upper jaw tooth rows 28 to 43, teeth flat and set in pavement. Colour: above plain greyish, olive or brown, underside white but with broad greyish-brown margins to disc and pelvic fins, and except for white mid-origin tail also dark.

Distribution: Eastern North Atlantic: Azores, Madeira, Canary and Cape Verde Islands, off Morocco and northward along the European coasts to the British Isles, southern Norway and North Sea and Western Baltic Sea (rare); also throughout the Mediterranean and Black Sea; this or a similar species occurs southward along the West African coast to Angola.

Habitat: Demersal on mostly sandy and muddy bottoms, including river estuaries and brackish water, from inshore to about 200 m , but mostly 60 m or less in depth; locally common in subtropical habitats.

Biology: Yolk-sac viviparous with a gestation period of about 4 months until birth. Litters range from 4 to 9 young. These stingrays feed mainly on demersal invertebrates such as crustaceans, but also on small molluscs and fishes.

Size: Maximum total length about 250 cm , including undamaged whiplash tail; maximum disc width 60 cm ,


Fig. 484 Dasyatis pastinaca
$\square$ Known distribution
but commonly less than 50 cm . Females mature at about 28 to 38 cm and males at 26 to 32 cm disc width in the Mediterranean. Size at birth about 8 cm disc width.

Interest to Fisheries and Human Impact: Usually bycatch in trawl, longline, trammelnet and rod and line fisheries, when often discarded; in Mediterranean and African waters, where locally common, often retained and wings used for human consumption smoked or dried salted. The preference for shallow water habitat makes this stingray vulnerable to mostly intensive small-scale coastal fisheries.

Conservation status is Data Deficient globally, but Near Threatened in northern North Eastern Atlantic where it appears to have become more infrequent in the Bay of Biscay.

Local Names: Pilskate (Norway); Gewöhnlicher Stechrochen (Germany); Uge (Portugal).
Remarks: This stingray is the type species of the genus Dasyatis Rafinesque, 1810.
Literature: McEachran and Capapé, Dasyatidae, in: Whitehead et al. (1984); Serena et al. (2003); Shark Trust (2009).

## Pteroplatytrygon Fowler, 1910

Genus: Pteroplatytrygon Fowler, 1910, Proc. Acad. Nat. Sci. Philad. 62: 474.
Type species: Trygon violacea Bonaparte, 1832 by monotypy.
Number of Recognized North Atlantic Species: 1.
Synonyms: Dasyatis violacea (Bonaparte, 1832).
Diagnostic Features: See family and key to subfamilies and genera above.

## Pteroplatytrygon violacea (Bonaparte, 1832)

Trygon violacea Bonaparte, 1832, Iconogr. Fauna Ital., fasc. I, pta 6:2pp. Two syntypes ANSP 385, 386.
Synonyms: Dasyatis violacea (Bonaparte, 1832).
FAO Names: En - Violet stingray; Fr - Pastenague violette; Sp - Raya látigo violeta.
Field Marks: Disc almost triangular, with anterior margins forming an even arc; snout very short and bluntly rounded; outer corners acute. Undamaged tail 2.5 to 3.0 times as long as body, with long, serrated spine on base, behind which tail like a thin whip-lash; a long and distinct membranous fold on underside of tail posterior to spine. Larger specimens with scattered dermal denticles on upper disc and median row of small thorns from nape to tail spine origin; underside smooth. Colour above plain dark purple, underside similarly dark.

Diagnostic Features: Disc shape nearly triangular or trapezoid due to convex anterior margins forming an almost even arc, with very short snout broadly rounded (angle 158 to $169^{\circ}$ ) and tip not produced, outer corners acute and long posterior margins slightly convex to nearly straight; axis of maximum disc width extremely far anterior level with anterior nape; pelvic fins unilobed and subquadrate; tail (if undamaged) 2.5 to 3.0 times as long as body, rather solid in anterior third to large, serrated tail spine, but thereafter becoming abruptly thinner


Fig. 485 Pteroplatytrygon violacea like a long whip-lash; below extension of tail spine, a long and distinct membranous fold along half or two thirds of underside of tail, and sometimes a ridge above posterior to spine. Upper disc of larger specimens covered with scattered dermal denticles; median row of small thorns from nape to origin of tail spine; underside smooth. Floor of mouth with 10 to 12 broad-based fleshy papillae. Upper jaw tooth rows 28 to 34 , teeth set in dense pavement pattern, in adults with low acute cusp. Colour: above plain dark purple to bluish-green, underside slightly lighter also greyish-purple to greenish-blue.

Distribution: Worldwide in circumtropical to temperate waters. Eastern North Atlantic: Vagrants reported from around the British Isles, but more common in warmer oceanic waters from Bay of Biscay southwards to South Africa (Shark Trust 2009); also throughout the Mediterranean. Western North Atlantic: Grand Banks and Flemish Cape to Cape Hatteras, and from off Texas (USA) in the northern Gulf of Mexico and at the Lesser Antilles (McEachran and Fechhelm 1998).

Habitat: Unique among stingrays, this species lives a pelagic and oceanic lifestyle, occurring from over the edge of continental and insular shelves into the open ocean usually in the upper 100 m depth, but occasionally down to 240 m over very deepwater.

Biology: Yolk-sac viviparous, with a gestation period of 2 to 4 months and litters of 4 to 13 . Sexual maturity is attained at three years for females and two years for males. Longevity about 10 years (Baum et al, 2007a). Feeds on all kinds of pelagic invertebrates (like crustaceans, jellyfish, squids) and small fish.

Size: Maximum total length (if tail undamaged) 160 cm , or 80 cm disc width. Size at maturity varies by latitude and temperature, but in general females mature between 40 and 50 cm disc width and males at 35 to 40 cm disc width. Size at birth ranges from 14 to 24 cm disc width.

Interest to Fisheries and Human

Impact: Frequent bycatch in pelagic longline, drift net and purse seine fisheries targeting oceanic bony fishes like tuna and swordfish. Usually discarded, but retained and utilised in some areas (e.g. Indonesia).
The population of this stingray appears to be rather stable, and regionally may even be increasing due to the wide distribution of oceanic individuals and the relatively high fecundity.

The conservation status of this species is Least Concern.

Local Names: Blue stingray, Guiler's stingray, Violet stingray (England, Ireland); Violetter Stechrochen, Pelagischer Stechrochen (Germany); Pilrokke (Denmark); Uge-violeta (Portugal); Violett Spjutrocka (Sweden).

Remarks: The only dasyatid stingray known to exclusively inhabit a pelagic and oceanic environment.

Literature: McEachran and Capapé,


Fig. 486 Pteroplatytrygon violacea

Dasyatidae, in: Whitehead et al. (1984); McEachran and Fechhelm (1998); Baum et al. (2007a); Ellis (2007); Shark Trust (2009).

### 3.4.2 Family GYMNURIDAE

Family: Subfamily Gymnurinae Fowler, 1934 (Family Dasyatiidae), Proc. Acad. Nat. Sci. Philad., 85: 241.
Type Genus: Gymnura van Hasselt, 1823.

## Number of Recognized North Atlantic Genera: 1.

FAO Names: En - Butterfly rays; Fr - Pastenagues ailees; Sp - Raya-mariposas.
Field Marks: Large stingrays, with disc width much broader than long, to more than 200 cm . Tail extremely short, only about one fourth of disc length, with one or more long serrated spines near base in most species but without dorsal fin in most, caudal fin absent.

Diagnostic Features: Disc lozenge-shaped, extremely broad, much wider than long. Snout very short and extremely bluntly angled. Pectoral fins completely fused with sides of head, which not marked off from disc. Eyes and spiracles on top of head, with tentacles on spiracle margin in some species. Fleshy papillae on floor of mouth absent. Numerous small jaw teeth set in about 100 to 140 transverse rows forming tooth bands along jaws. Both sides of disc naked in most species, but may become more or less prickly above in large specimens of some. Colour: upper side greyish, olive-brown to dark brown, often in mixed shades; ground colour frequently speckled or marbled with darker and/or paler spots and blotches; underside of disc usually white, often with a brownish or rusty cast, sometimes with narrow dark margins. Tail dark above, light below, often with light and dark crossbars above and on sides.

Distribution: Cosmopolitan in tropical to warm temperate seas in mainly inshore shelf waters.
Habitat: Usually on sandy and muddy bottoms in shallow coastal waters, also in lagoons, estuaries and river mouths.
Biology: Yolk-sac viviparous, but little else known of its biology. Feeding on various kinds of benthic invertebrates and small fishes.

Interest to Fisheries and Human Impact: Although not rare locally, butterfly rays appear to be less abundant than dasyatid stingrays and are less frequently marketed than the latter. Their flesh (wings) appears to be as good as that
of dasyatids and is consumed smoked and dried salted. As most of the butterfly rays are easily taken by various fishing methods of artisanal fishery, their stocks have become depleted in many places.

Local Names: None.
Literature: McEachran and Capapé, Dasyatidae, in: Whitehead et al. (1984).

## Gymnura van Hasselt, 1823

Genus: Gymnura van Hasselt, 1823, Alg. Konst- Letter-bode Haarlem, 1823: 316.
Type species: Raja micrura Schneider, 1801 (in Bloch and Schneider, 1801) by monotypy.

## Number of Recognized North Atlantic Species: 1.

Synonyms: Pteroplatea Müller and Henle, 1841.
Diagnostic Features: See family and key to genera.
Local Names: None.
Remarks: The family has one genus and about 13 nominal species of which one species occurs in the North Atlantic.

## Gymnura altavela (Linnaeus, 1758)

Raja altavela Linnaeus, 1758, Syst. Nat., ed. 10, 1:232. No type material.
Synonyms: Pteroplatea altavela of authors.
FAO Names: En - Spiny butterfly ray; Fr - Raie-papillon épineuse; Sp - Raya mariposa.


Fig. 487 Gymnura altavela

Field Marks: Disc very broadly lozenge-shaped, twice as wide as long; snout very short and blunt. Thin tail extremely short, only one fourth of disc length, with long serrated spine on base. A slender tentacle on each spiracle's inner margin directed backward. Larger specimens with thornlets scattered over upper disc, underside smooth. Ground colour above dark-, greyish- or reddish-brown, often with dark or light spots or blotches, sometimes marbled and with pale-edged pseudo-eyespots; underside white.

Diagnostic Features: Disc transversally lozenge-shaped, about twice as wide as long, with anterior margins almost straight, sharply acute outer corners (less than $90^{\circ}$ ) and slightly convex posterior margins; snout short, very bluntly angled (about $135^{\circ}$ ); pelvic fins unilobed; tail very short, about one fourth of disc length, with one or more serrated, long spines near base; dorsal fin absent. A slender tentacle on inner spiracle margin pointing backward. Upper surface smooth only in young, covered with scattered thornlets in larger specimens, underside smooth. Upper jaw teeth in 98 to 138 rows, number increasing with growth; individual teeth of both sexes and all sizes with 1 to 2 distinct pointed cusps, set in dense pavement arrangement. Colour: above dark brown, or greyish- to reddish-brown, often patterned with small dark or light spots or blotches, sometimes sort of marbled pattern or also with pale-edged eye-spots; tail often with light and dark crossbars; underside white.

Distribution: Eastern North Atlantic: from off Morocco and Madeira northward to northern Portugal and Spain, also throughout the Mediterranean Sea and Black Sea; southward along the West African coast to Angola, also off the Canary Islands. Western North Atlantic: from off Massachusetts southward through the Caribbean Sea and along the South American coast to the mouth of La Plata and off northern Argentina.

Habitat: Benthic on sandy and muddy bottoms from shallow inshore waters to about 69 m depth, 10 m to 150 m depth off south Brazil (Vooren et al. 2007).

Biology: Yolk-sac viviparous, with a gestation period of about 4 to 9 months, after which 1 to 8 young are born. Feeds mainly on fish, crustaceans and molluscs.

Size: Maximum disc width about 200 cm in the Western North Atlantic, but may be up to 400 cm in the Eastern Atlantic off West Africa, although this width is probably erroneous. Size at maturity


Fig. 488 Gymnura altavela
$\square$ Known distribution between 100 and 150 cm disc width, but maturity size may differ between Eastern and Western North Atlantic populations. The size at birth is 38 to 44 cm .

Interest to Fisheries and Human Impact: Mostly taken as bycatch in beach seine, handline, coastal trawl and line fisheries, often discarded, but the wings are used fresh and dried-salted locally along the African Mediterranean coast and along West Africa.

The global conservation status is Vulnerable, but in United States waters it is Least Concern. However, in the Mediterranean and South Western Atlantic it is considered Critically Endangered (Vooren et al. 2007).

Local Names: Stachel-Schmetterlingsrochen (Germany); Uge-Manta (Portugal).
Literature: Bigelow and Schroeder (1953); McEachran and Capapé, Gymnuridae, in: Whitehead et al. (1984); Vooren et al. (2007).

### 3.4.3 Family MYLIOBATIDAE

Family: Subfamily Myliobatini Bonaparte, 1838, Nuov. Ann. Sci. Nat., Bologna, ser. 1, 2.
Type Genus: Myliobatis Cuvier, 1817.

## Number of Recognized North Atlantic Genera: 4.

FAO Names: En - Eagle rays; Fr - Aigles de mer; Sp - Aguilas de mar.
Field Marks: See key to subfamilies and genera below.
Diagnostic Features: See key to subfamilies and genera below.
Distribution: Worldwide in tropical and subtropical to warm temperate waters.
Habitat: Partly demersal to benthopelagic on/over soft shelf substrates (subfamily Myliobatinae and Rhinopterinae), partly pelagic near surface over shelves and in open oceans (Mobulinae).

Biology: All species are yolk-sac viviparous. Eagle rays feed on a variety of benthic invertebrates with a preference for hard-shelled molluscs and crustaceans (Myliobatinae, Rhinopterinae), or are filter feeders on plankton (Mobulinae).

Interest to Fisheries and Human Impact: Most species are regular bycatch components in bottom and pelagic trawls and longline fisheries and are used (wings) for human consumption. Several species are considered endangered due to the combined effects of intensive fisheries and low reproductive rates.

Local Names: None.
Remarks: The family is comprised of three subfamilies, seven genera, and about 37 species. The subfamily Myliobatinae has four genera and about 20 species, the subfamily Rhinopterinae has a single genus and about seven species, and the subfamily Mobulinae has two genera and about 10 species. All three subfamilies, five genera, and six species occur in the North Atlantic.

Literature: Nelson (2006).

## Key to North Atlantic Subfamilies and Genera:

1a. Huge rays of several metres wing span. Disc broadly lozenge-shaped, much wider than long. Head very broad. Anterior section of pectoral fins separated from wings and extended forward to form a pair of cephalic fins extending beyond front of head. Tail long and whip-like, with a small dorsal fin on base, with or without one or more long serrated stings behind. Gills modified to function also as a filter-apparatus, ventral gill slits very long

2 (Subfamily Mobulinae)
1b. Large rays of 1.5 to 3.5 metres wingspan. Disc broadly lozenge-shaped, wider than long. Narrow head marked off from body disc. Anterior section of pectoral fins separated from wings and extended forward to join in front of head to form a distinct uni- or bilobed subrostral lobe. Mouth on underside of head; jaws with massive flat tooth plates consisting of only 7 to 9 rows, median teeth of which are rectangular, much wider than long and much larger than teeth of adjacent lateral rows. Tail much longer than disc and whip-like, with a small dorsal fin on its base and one or more long, serrated spines directly behind. Gill slits shorter

2a. Very broad mouth terminal on head between cephalic-fin bases (Fig. 489). Manta


Fig. 489 Manta proper

2b. Very broad mouth on lower surface of head (Fig. 490)

## Mobula

3a. Short subrostral lobe deeply notched medially, appearing bilobed, on deeper level than anterior pectoral fins proper, and radials of subrostral lobe and pectoral fin are separated by a short gap (Fig. 491)

Rhinoptera (Subfamily Rhinopterinae)

3b. Longer subrostral lobe protruding from front of head, either bluntly rounded, or narrowly rounded to a pointed tip; subrostral lobe level with anterior margin of pectoral fins

4 (Subfamily Myliobatinae)

4a. Dorsal fin originating behind pelvic fin tips. Anterior pectoral fin radials continued forward under eye to join as distinct ridge with subrostral lobe, which relatively short and obtuse. Snout bluntly rounded (Fig. 492)

Myliobatis

4b. Dorsal fin originating in front of pelvic fin tips. Anterior pectoral fin radials discontinuous under eye, subrostral lobe separate by a gap and long, a little pointed in front; snout more pointed (Fig. 493)

Pteromylaeus


Fig. 490 Mobula


Fig. 491 Rhinoptera


Fig. 492 Myliobatis


Fig. 493 Pteromylaeus

## Myliobatis Cuvier, 1817

Genus: Myliobatis Cuvier, 1817, Règne anim. 2: 137.
Type species: Raja aquila Linnaeus, 1758 by subsequent designation of Bonaparte (1838).
Number of Recognized North Atlantic Species: 1.
Synonyms: None.
Field Marks: See family and key to subfamilies and genera above.
Diagnostic Features: See family and key to subfamilies and genera above.
Local Names: None.
Remarks: The genus has about 11 nominal species worldwide, but only one occurs in the North Atlantic.

## Myliobatis aquila (Linnaeus, 1758)

Raja aquila Linnaeus, 1758, Syst. Nat., ed. 10, 1: 232. No type material.
Synonyms: None.
FAO Names: En - Common eagle ray; Fr - Aigle commun; Sp - Aguila marina.


Fig. 494 Myliobatis aquila
Field Marks: Disc transversally lozenge-shaped, about twice as wide as long. Undamaged tail 2 to 2.5 times longer than disc, with a single, small dorsal fin on base a short distance posterior to pelvic fins, and a long, serrated spine originating directly behind dorsal fin, after which the tail abruptly thinner like a whip-lash. Snout short and bluntly rounded, but anterior head to level of posterior eyes marked off from disc as a broad, obtuse projection. Colour above from uniformly dusky bronze to almost blackish; underside white with brownish margins to disc and pelvic fins.

Diagnostic Features: Disc transversally lozenge-shaped, about twice as wide as long, with long anterior margins straight to weakly convex, sharply angled outer corners and shorter, concave posterior margins; head elevated from disc, with eyes and spiracles on sides, and forehead evenly sloping


LATERAL VIEW OF HEAD down to subrostral lobe; snout short and bluntly rounded, but anterior head to level of posterior eyes marked off from disc as a broad, obtuse projection, which is formed by a subrostral lobe of anterior pectoral-fin radials continuous below eyes and spiracles as a distinct ridge with remainder of pectoral fins. Pelvic fins subquadrate unilobed. Tail, if undamaged, 2 to 2.5 times longer than disc, with a single, small dorsal fin on base a short distance posterior to pelvic fins, and a long, serrated spine originating directly behind dorsal fin; thereafter, the tail abruptly thinner like a whip-lash. Upper disc smooth, at most with asperities or small tubercles along midline; underside smooth. Usually seven rows of flat, thick teeth in each jaw forming very massive grinding plates, teeth in middle row of upper jaw 4 to 6 times as broad as long. Colour: above from uniformly dusky bronze to almost blackish; underside white with brownish margins to disc and pelvic fins, and underside of tail whitish at origin to about spine tip but dark in posterior whip-lash part.

Distribution: Eastern North Atlantic: from off Morocco and Madeira, also the Azores, and northward to the southern and western coasts of the British Isles, including the English Channel and south-western North Sea where it is an occasional vagrant (Shark Trust 2009). Also, found throughout the Mediterranean Sea, but not in the Black Sea. Elsewhere found along the West African coast to South Africa and the south-western Indian Ocean north to Kenya.

Habitat: Benthopelagic and semi- to epipelagic in tropical to warm temperate coastal waters to 60 m depth, sometimes also farther offshore. Prefers shallow bays, lagoons and estuaries.

Biology: Yolk-sac viviparous, with lifehistory parameters appearing to vary regionally, but not well studied in most regions. Litters of 3 to 7 are born after a 6 to 8 month gestation period. Feeds mostly on hard-shelled bottom invertebrates such as crabs and molluscs but also on demersal worms; because they occur in small groups, eagle rays can become quite destructive to natural or cultured beds of bivalves.

Size: Maximum total length to 260 cm (if tail undamaged), with a disc width of about 150 cm (Mediterranean), but most are usually smaller; maximum 79 cm disc width reported for South African specimens (Holtzhausen et al. 2005). Maturity is attained at about 60 cm disc width in females and at about 40 cm in males in the Mediterranean.


Fig. 495 Myliobatis aquila
Known distribution $\square$ Possible distribution

Interest to Fisheries and Human Impact: Regular bycatch in mixed species fisheries where they are locally common. The schooling behaviour of this eagle ray means that large numbers could be fished out in one haul, and fishermen are known to target aggregations of these rays off western Africa. The wings are said to be good eating, and along the African coast they are regularly used for human consumption.

The conservation status of this common, but poorly known eagle ray is Data Deficient globally, but in the Mediterranean Sea it is Near Threatened.

Local Names: Bull ray, Sea Eagle, Whip-ray, Toad fish (England, |reland); Gewöhnlicher Adlerrochen, Alantischer Adlerrochen (Germany); Ratão-Aguia (Portugal); Ørneskate (Norway).

Remarks: This eagle ray is the type species of genus Myliobatis Cuvier, 1817. Populations in European and South African waters may be different species, and further studies are required (Holtzhausen et al. 2005).

Literature: McEachran and Capapé, Myliobatidae, in: Whitehead et al. (1984); Holtzhausen, et al. (2005); Shark Trust (2009).

## Pteromylaeus Garman, 1913

Genus: Pteromylaeus Garman, 1913, Mem. Mus. Comp. Zool. Harv. 36: 428, 437-438.
Type species: Myliobatis asperrimus Jordan and Evermann, 1898 by subsequent designation of Jordan (1920) = Pteromylaeus asperrimus (Jordan and Evermann, 1898).

Number of Recognized North Atlantic Species: 1.
Synonyms: None.
Diagnostic Features: See family and key to subfamilies and genera above.
Local Names: None.
Remarks: The genus has two nominal species worldwide, but only one occurs in the North Atlantic.

## Pteromylaeus bovinus (Geoffroy Saint-Hilaire, 1817)

Myliobatis bovina E. Geoffroy Saint-Hilaire, 1817, Descr. Égypte, Poissons: pl. XXVI (Fig. 1); text description: I. Geoffroy Saint-Hilaire (1827), Descr. Égypte, Poissons: 336. No type material.

Synonyms: None.
FAO Names: En - Bull ray; Fr - Aigle vachette; Sp - Chucho vaca.


Fig. 496 Pteromylaeus bovinus
Field Marks: Disc transversally lozenge-shaped, about twice as wide as long. Undamaged tail about twice as long as disc, with a single, small dorsal fin on base originating far anterior to pelvic fins posterior margins, and with a long, serrated spine directly behind dorsal fin, after which the tail becomes rapidly thinner like a whip-lash. Snout short but pronounced as a subrostral lobe that is narrowly rounded to a pointed tip. Colour of disc above plain brown in adults, but with 7 to 8 pale transverse streaks in juveniles; underside whitish.

Diagnostic Features: Disc transversally lozenge-shaped, about twice as wide as long, with long anterior margins strongly convex, falcate outer corners and strongly concave, somewhat undulated posterior margins; head elevated from disc, with eyes and spiracles on sides of head, forehead of which steeply sloping to subrostral lobe; snout short


LATERAL VIEW OF HEAD but pronounced as narrowly rounded to pointed tip formed by subrostral lobe of pectoral-fin radials being separated at sides of head from remainder of pectoral fins; pelvic fins subquadrate unilobed. Tail, if undamaged, about twice as long as disc, with a single, small dorsal fin on base originating far anterior to pelvic fins posterior margins, and a long, serrated spine originating directly behind dorsal fin; thereafter, the tail becoming rapidly thinner like a whip-lash. Skin smooth above and below. Usually seven rows of flat thick teeth in each jaw forming very massive grinding plates, teeth in middle row of upper jaw 6 to 8 times as broad as long. Colour: disc above plain brown in adults, but with 7 to 8 pale transverse streaks in juveniles; underside whitish, with wing tips more or less reddish-brown, the whip-lash tail dark.

Distribution: Eastern North Atlantic: from off Morocco and Madeira, but not at Azores, northward along the Iberian Peninsula to the southern Bay of Biscay. Also found throughout the Mediterranean Sea, but not in the Black Sea. Elsewhere, southward along the West African coast to off South Africa, where it is rare in the coldwater upwelling region off Namibia and the Western Cape region, but more common in the south-western Indian Ocean north to Zanzibar.

Habitat: Bentho- and semi- to epipelagic in tropical to warm temperate coastal waters between surf zone and moderate depth of 30 m , sometimes also farther offshore. It tolerates greatly reduced salinities and also occurs in shallow bays, lagoons and estuaries.

Biology: Yolk-sac viviparous, with litters of up to 8 young being born after a 5 to 6 months gestation period off North West Africa, but off South Africa the gestation may be up to one year with 3 to 4 young per litter (Wintner 2006). The reproductive parameters may


Fig. 497 Pteromylaeus bovinus

Known distribution differ greatly between regions. Feeds mostly on hard-shelled bottom invertebrates like crabs and molluscs but also on demersal worms; because living in small groups, these rays can become destructive to natural or cultured beds of bivalves.

Size: Maximum disc width is to about 175 cm when weighting more than 80 kg , but most are usually smaller. Maturity is attained at 90 to 100 cm disc width for females and at 83 to 100 cm for males, but off South Africa this size may be larger with females maturing at over 100 cm disc width and males at 95 cm (Wintner 2006). Size at birth off North West Africa is about 25 to 27 cm disc width with the smallest free swimming individual measuring 35.5 cm . Off South Africa newborns are larger at about 50 cm disc width (Wintner 2006).

Interest to Fisheries and Human Impact: Regular bycatch in mixed species fisheries, locally common. Wings are said to be good eating, and along African coasts they are regularly used for human consumption.

The conservation status is Data Deficient.
Local Names: Entenschnabelrochen (Germany); Ratão-Bispo (Portugal); Duckbill (England).
Literature: McEachran and Capapé, Myliobatidae, in: Whitehead et al. (1984); Wintner (2006); Shark Trust (2009).

## Rhinoptera Cuvier, 1829

Genus: Rhinoptera Cuvier, 1829, Règne anim. (ed. 2) 2: 401.
Type species: Myliobatis marginata E. Geoffroy St.-Hilaire, 1817 by subsequent designation of Bonaparte (1838).
Number of Recognized North Atlantic Species: 2.
Synonyms: None.
Diagnostic Features: See family and key to subfamilies and genera above.

## Local Names: None.

Remarks: The genus has seven nominal species, possibly up to 11, worldwide, but only two occur in the North Atlantic.

## Key to North Atlantic Species:

1a. Usually seven rows of flat, thick teeth in each jaw; teeth in middle row of upper jaw about twice broader than those in directly adjacent lateral rows, but 3 to 5 times as wide as those of more outer series; occasionally six or eight tooth rows in one jaw or the other. Colour above plain lighter or darker brownish, sometimes with yellowish or golden tinge; underside white or creamy-white, but more or less brownish at wing tips; some specimens marked above and below with many narrow obscure dark lines or bands radiating outward from disc centre (Fig. 498) . Rhinoptera bonasus

1b. Usually nine rows of flat, rectangular thick teeth in upper, seven in lower jaw; teeth in middle row of upper jaw at most three times as broad as long, teeth in next adjacent row either side about the same and in any case broader than small pentagonal teeth in outer rows either side; occasionally more than nine upper jaw tooth rows. Colour above uniformly greenish-brown to bronze; underside whitish, with disc margins and wing tips darker, tail dark (Fig. 499)

Rhinoptera marginata


UPPER JAW
Fig. 498 Rhinoptera bonasus


UPPER AND LOWER JAW
Fig. 499 Rhinoptera marginata

## Rhinoptera bonasus (Mitchill, 1815)

Raja bonasus Mitchill, 1815, Trans. Lit. philos. Soc. New York, 1: 479. No type material.
Synonyms: None.
FAO Names: En - Cownose ray; Fr - Mourine américaine; Sp - Mancha.


Fig. 500 Rhinoptera bonasus

Field Marks: Disc transversally lozenge-shaped, about twice as wide as long, with sharply angled outer corners. Head elevated from disc, with eyes and spiracles on sides of head; snout short, with short subrostral lobe deeply notched medially, thus appearing bilobed; radials of subrostral lobe and pectoral fin are separated by a short gap. Undamaged tail nearly three times longer than disc, with a single, small dorsal fin on base and one or more long, serrated spines originating directly behind dorsal fin; thereafter, tail abruptly thinner like a whip-lash. Usually seven rows of flat, thick teeth in each jaw forming pavement of very massive grinding plates; teeth in middle row of upper jaw about twice broader than those in directly adjacent lateral rows, but 3 to 5 times as wide as those of more outer series'; occasionally six or eight tooth rows in one jaw or the other. Colour above plain lighter or darker brownish; underside white or creamy-white, brownish at wing tips; some specimens marked above and below with


LATERAL VIEW OF HEAD many narrow obscure dark lines or bands.

Diagnostic Features: Disc transversally lozenge-shaped, about twice as wide as long, with anterior margins straight to weakly convex, sharply angled outer corners and deeply concave posterior margins; head elevated from disc, with eyes and spiracles on sides of head; snout short, with forehead bulbous and medially concave; short subrostral lobe deeply notched medially, thus appearing bilobed, and on deeper level than anterior pectoral fins proper, and radials of subrostral lobe and pectoral fin are separated by a short gap. Pelvic fins subquadrate unilobed. Tail, if undamaged, nearly three times longer than disc, with a single, small dorsal fin on base situated entirely anterior to level of pelvic fins posterior margins; one or more long, serrated spines originating directly behind dorsal fin; thereafter, the tail becoming rapidly thinner like a whip-lash. Skin smooth on upper and lower surfaces. Usually seven rows of flat, thick teeth in each jaw forming pavement of very massive grinding plates; teeth in middle row of upper jaw about twice broader than those in directly adjacent lateral rows, but 3 to 5 times as wide as those of more outer series'; occasionally six or eight tooth rows in one jaw or the other. Colour: above plain lighter or darker brownish, sometimes with yellowish or golden tinge; underside white or creamy-white, but more or less brownish at wing tips; some specimens marked above and below with many narrow obscure dark lines or bands radiating outward from disc centre.

Distribution: Western Atlantic: from off southern New England (Cape Cod, USA) to off southern Brazil, including the Gulf of Mexico, Cuba and other scattered Caribbean localities.

Habitat: Bentho- and semi- to epipelagic in tropical to warm temperate coastal waters to 60 m depth, prefers shallow bays, lagoons and estuaries. Often occurring in small schools, but sometimes gathering in giant schools of thousands of individuals during seasonal migrations when invading larger bays (e.g. Chesapeake Bay) and inlets.

Biology: Yolk-sac viviparous, with the gestation period varying depending on the latitude of occurrence, but may be up to one year. The litter size usually one, but records of 2 to 6 young have been reported (Barker 2006). Feeds mostly on hard-shelled bottom invertebrates like crabs and molluscs, and when occurring in schools, cownose rays can become destructive to natural or cultured beds of bivalves. Stirring up prey from the bottom by heavily flapping their wings.


Fig. 501 Rhinoptera bonasus
$\square$ Known distribution

Size: Disc width variable depending on the latitude and region of occurrence, but a maximum width of 107 cm has been reported, with an average of about 90 cm or smaller most common. Maturity is reached at a disc width of 65 to 80 cm , but differs between regions. The size at birth is 25 to 40 cm disc width (McEachran and Fechhelm 1998, Barker 2006).

Interest to Fisheries and Human Impact: Regular bycatch in mixed species fisheries, locally common. The schooling behaviour in shallow water makes this species particularly vulnerable to target fisheries, and off southern Brazil it has nearly disappeared (Barker 2006). Except locally, of no commercial importance for human consumption, but fishermen in
the USA recently began considering target fishery for offering wing flesh as a speciality and at the same time fighting these rays and their destructive effect on bivalve cultures.

The conservation status of the cownose ray is Near Threatened.
Local Names: Cowfish, Skeete (USA); Cara De Vaca, Gavilan Mancha, Gavilan Manchado, Mancha, Raya gavilán (Spanish).
Remarks: The taxonomic status of the South American nominal species Rhinoptera brasiliensis Müller and Henle, 1841 has not been fully clarified as to whether it is distinct from $\boldsymbol{R}$. bonasus, since the only distinguishing characteristic appears to be the usually higher count of mostly nine or more tooth rows in $\boldsymbol{R}$. brasiliensis. Specimens of both species were found with varying numbers of tooth rows with some as low as seven. Bigelow and Schroeder (1953) provide a discussion on the status of these two species.

Literature: Bigelow and Schroeder (1953); McEachran and Fechhelm (1998); Barker (2006).

## Rhinoptera marginata (Geoffroy Saint-Hilaire, 1817)

Myliobatis marginata E. Geoffroy Saint-Hilaire, 1817, Descr. Égypte, Poissons: pl. XXV (Figs 3-4); text description: I. Geoffroy Saint-Hilaire (1827), Descr. Égypte, Poissons, 1: 334. Holotype MNHN 2605, two paratypes MNHN A8714, A7954.

Synonyms: Rhinoptera peli Bleeker, 1863.
FAO Names: En - Lusitanian cownose ray; Fr - Mourine lusitanienne; Sp - Gavilán lusitánico.


Fig. 502 Rhinoptera marginata

Field Marks: Disc transversally lozenge-shaped, about twice as wide as long, with sharply angled outer corners. Head elevated from disc, with eyes and spiracles on sides of head; snout short, with short subrostral lobe deeply notched medially, thus appearing bilobed; radials of subrostral lobe and pectoral fin are separated by a short gap. Undamaged tail nearly three times longer than disc, with a single, small dorsal fin on base and one or more long, serrated spines originating directly behind dorsal fin; thereafter, tail abruptly thinner like a whip-lash. Usually nine rows of flat, rectangular thick teeth in upper, seven in lower jaw forming pavement of very massive grinding plates; teeth in middle row of upper jaw at most three times as broad as long, teeth in next adjacent row either side about the same. Colour above uniformly greenish brown to bronze; underside whitish, with disc margins and wing tips darker, tail dark.


LATERAL VIEW OF HEAD

Diagnostic Features: Disc transversally lozenge-shaped, about twice as wide as long, with anterior margins straight to weakly convex, sharply angled outer corners and deeply concave posterior margins; head elevated from disc, with eyes and spiracles on sides of head; snout short, with forehead bulbous and medially concave; short subrostral lobe deeply notched medially, thus appearing bilobed, and on deeper level than anterior pectoral fins proper, and radials of subrostral lobe and pectoral fin are separated by a short gap. Pelvic fins subrectangular unilobed, longer than wide. Tail, if undamaged, nearly three times longer than disc, with a single, small dorsal fin on base situated entirely anterior to level of pelvic fins posterior margins; one or more long, serrated spines originating directly behind dorsal fin; thereafter, the tail becoming rapidly thinner like a whip-lash. Skin smooth on upper and lower surfaces, but large specimens may show some prickles above along midbody. Usually nine rows of flat, rectangular thick teeth in upper, seven in lower jaw forming pavement of very massive grinding plates; teeth in middle row of upper jaw at most three times as broad as long, teeth in next adjacent row either side about the same and in any case broader than small pentagonal teeth in outer rows either side; occasionally more than nine upper jaw tooth rows. Colour: above uniformly greenish brown to bronze; underside whitish, with disc margins and wing tips darker, tail dark.

Distribution: Eastern Atlantic: tropical and subtropical Eastern Atlantic from about the Gulf of Guinea northward to off southern Iberian Peninsula; also throughout the Mediterranean Sea where it is rare, but not in the Black Sea.

Habitat: Bentho- and semi- to epipelagic in tropical to warm temperate coastal waters mostly to only 30 m but occasionally to 60 m depth, and even 100 m in the Mediterranean. Prefers shallow bays, lagoons and estuaries. Often occurring in groups.

Biology: Yolk-sac viviparous, with a gestation period of up to one year, but further details on the reproductive biology, including size at sexual maturity are not really known. Data from Mauritania indicate sexual maturity for males at 77 cm and females at 80 cm disc width, and possibly only one young born per litter (Notarbartolo et al. 2006). Feeds mostly on hard-shelled bottom invertebrates like crabs and molluscs, and when occurring in schools, these cownose rays can become destructive to natural or cultured beds of bivalves. Sometimes feeds by stirring up prey from the bottom by heavily flapping their wings.


Fig. 503 Rhinoptera marginata
$\square$ Known distribution

Size: Maximum disc width from 150 to 200 cm , but most often found at smaller sizes of 65 to 75 cm disc width.
Interest to Fisheries and Human Impact: Regular bycatch in mixed species fisheries, locally common. The schooling behaviour in shallow water makes this species particularly vulnerable to target fisheries. Of little commercial importance for human consumption, except locally along north-west Africa, where it is marketed dried salted and smoked.

The conservation status of this poorly known ray is Near Threatened.
Local Names: Gaviāo do mar (Portuguese); Mourine échancrée; Ndiaouratt, Toumboulann, Rutj runtj (West Africa); Gewöhnlicher Kuhnasenrochen (Germany).

Remarks: This cownose ray is the type species of the genus Rhinoptera Cuvier, 1829.
Literature: Stehmann, Batoid Fishes, in Fischer et al. (1981); McEachran and Capapé, Rhinopteridae, in Whitehead et al. (1984); McEachran and Séret, Rhinopteridae, in Quero et al. (1990); Notarbartolo et al. (2006).

## Manta Bancroft, 1828

Genus: Manta Bancroft, 1828, Zool. J. 4: 454.
Type species: Manta americana Bancroft, 1828 by monotypy, = Manta birostris by so far common agreement.
Number of Recognized North Atlantic Species: 1.
Synonyms: See Bigelow and Schroeder (1953), and McEachran and Séret, Mobulidae, in: Quero et al. (1990) for detailed list of generic synonyms.

Diagnostic Features: See family and key to subfamilies and genera above.
Local Names: None.
Remarks: The genus has two nominal species worldwide, but only one occurs in the North Atlantic.

## Manta birostris (Walbaum, 1792)

Raja birostris Donndorff, 1798, Zool. Beitr., 3: 876. No type material.

## Synonyms: None.

FAO Names: En - Giant manta; Fr - Mante géante; Sp - Manta gigante


Fig. 504 Manta birostris

Field Marks: Very broad mouth terminal on front of head between the large forward directed cephalic fins. Tail short and whiplash-like, shorter than disc width, with a small dorsal fin on tail base and with a prominent hard, rounded ridge or knob in the position of a tail spine that is absent. Upper disc colour plain brownto blackish, with pale orwhite markings in certain areas; underside largely white but with dark posterior wings margins; occasionally, specimens with both surfaces almost totally blackish or white do occur.


FRONTAL VIEW OF HEAD

Diagnostic Features: Disc very broadly lozengeshaped, 2.0 to 2.3 times as wide as long, with anterior margins straight to weakly concave, outer corners sharply acute, and posterior margins distinctly concave; head very broad, marked off from body disc from level of spiracles onward; head elevated above level of pectoral wings, with eyes and spiracles on sides; anterior parts of pectoral fins separated from pectoral wings to form two long, vertically oriented cephalic fins; very broad mouth terminal on front of head between the cephalic fins. Pelvic fins subrectangular and unilobed. Tail short and whiplash-like, shorter than disc width, with a small dorsal fin on tail base level with inner pelvic-fin margins, without a long serrated tail spine behind dorsal fin but with a prominent hard, rounded ridge or knob in the same position, sometimes with tip of embedded spine sticking out. Numerous minute, flattened jaw teeth arranged in dense pavement pattern of about 220 to 250 transverse rows forming tooth band on median three fourths of lower jaw only; upper jaw without teeth but with two irregular bands of enlarged dermal denticles extending along upper jaw as wide as lower jaw tooth band. Prominent dermal denticles with bifid cusp scattered on both surfaces along sagittally oriented ridges in the skin, also on tail, dorsal fin and outer sides of cephalic fins. Colour: disc and tail above, as well as outer surface of cephalic fins plain reddish- or olive-brown to blackish; specimens show often an irregular white patch on each shoulder, sometimes crossed by series of dark spots; some individuals may show a pair of pale whitish bands on each wing, or a large white, triangular patch on posterior disc in addition to anterior markings; underside of disc and tail and inner surface of cephalic fins mostly white, but mouth surrounded by a more or less dark band, and posterior wing margins as a huge V very broadly black- or grey-edged; abdomen may be irregularly blotched grey to black. On both surfaces almost entirely blackish, and in contrast also whitish (very rare) morphotypes do occur.

Distribution: Circumglobally in most tropical and subtropical seas, but also sometimes occurs in temperate waters. Eastern North Atlantic: only confirmed from the Azorean Archipelago in Area 27, but found off the West African coast. Western North Atlantic: Georges Bank where it occurs seasonally as a summer visitor and southwards to the Caribbean.

Habitat: An epi- to benthopelagic species usually found over or near continental and insular shelves within areas with productive coastlines due to upwelling, but also found in the open sea far offshore and near the surface, particularly at offshore pinnacles and seamounts. Often leaping partly or entirely from the water, when returning to the water with a big splash audible over long distance. Often found in groups at certain places, where specimens gather for feeding, mating or being cleaned of parasites. A highly migratory species that travels long distances seasonally.

Biology: Yolk-sac viviparous, with only a single young being born, on rare


Fig. 505 Manta birostris occasions may be two per litter. The newborns are 120 to 140 cm disc width and weight 10 to 15 kg after a gestation period of 10 to 14 months. Longevity is over 20 years. Mantas are filter feeders depending on rich concentrations of plankton (mainly crustaceans but also small fish), sieving their food with their huge gill filter basket out of large amounts of water directed with aid of the cephalic fins into their huge mouth gape.

Size: Maximum disc width over 700 cm and a weight of over two tons, but most are usually found at smaller sizes of 430 to 460 cm disc width. Females and males mature at a disc width of 400 to 450 cm and 350 to 400 cm , respectively. The size at birth is 120 to 140 cm disc width.

Interest to Fisheries and Human Impact: Traditionally a more or less regular bycatch in pelagic fisheries with purse seines, trawls, driftnets and longlines, as well as by coastal fisheries for local subsistence. Nowadays targeted in many places for their huge wings used for human consumption fresh, salted, or smoked, but also for extracting wing cartilages and gill filaments for Asian markets; often processed for fish meal, and the large livers for fish oil. Quite a number of regional and local populations have shown a drastic reduction (Marshall et al. 2006).
The conservation status is Near Threatened.
Local Names: Giant manta ray, Pacific manta ray, Devilfish, Chevron manta, Pelagic manta, Oceanic manta, Manta.
Remarks: In parts of the distributional area, mainly in the Indo-Pacific, this species co-occurs sympatrically with the recently resurrected, but smaller Manta alfredi (Kreff, 1868) (Marshall et al. 2009).

Literature: Bigelow and Schroeder (1953); Stehmann, Batoid Fishes, in: Fischer et al. (1981); Marshall et al. (2006); Marshall et al. (2009).

## Mobula Rafinesque, 1810

Genus: Mobula Rafinesque, 1810, Indice Ittiol. Sicil. 1810: 48, 61.
Type species: Mobula auriculata Rafinesque, 1810 by monotypy = Mobular mobular Bonnaterre, 1788.
Number of Recognized North Atlantic Species: 1.
Synonyms: Numerous generic synonyms, see Bigelow and Schroeder (1953); McEachran and Séret, Mobulidae, in: Quèro et al. (1990).

Diagnostic Features: See family and key to subfamilies and genera above.
Local Names: None.
Remarks: The genus has nine nominal species worldwide, but only one occurs in the North Atlantic.

## Mobula mobular(Bonnaterre, 1788)

Raia mobular Bonnaterre, 1788, Tabl. encycl. méth. .... Ichth.: 5. No type material.
Synonyms: None.
FAO Names: En - Devil fish; Fr - Mante; Sp - Manta mobula.


Fig. 506 Mobula mobular

Field Marks: Broad mouth on underside of head between origins of cephalic fins. Tail long and whiplash-like, if undamaged about as long as disc width, with a small dorsal fin on tail base, and with one or more long serrated tail spines behind dorsal fin. Colour of upper disc plain brown to bluish-black, sometimes with a blackish collar across head; underside white, but dark spots and blotches may occur.

Diagnostic Features: Disc very broadly lozenge-shaped, 2.0 to 2.3 times as wide as long, with anterior margins straight to weakly concave, outer corners sharply acute, and posterior margins deeply convex; head very broad, marked off from body disc from level of spiracles onward; head elevated above level of pectoral wings, with eyes and spiracles on sides; anterior parts of pectoral fins separated from pectoral wings to form two long, thin, vertically oriented cephalic fins. Broad mouth on underside of head between origins of cephalic fins. Pelvic fins subrectangular and unilobed, their posterior margin hardly projecting behind margin of pectoral inner tips. Tail long and whiplash-like, if undamaged about as long as disc width, with a small dorsal fin on tail base level with inner pelvic fin margins, and with one or more long serrated tail spines behind dorsal fin. Numerous minute, flattened jaw teeth arranged in dense pavement pattern of about 150 to 160 transverse rows forming tooth band on median three fourths of both jaws. Both surfaces of disc and tail covered with rough dermal denticles, more densely so below. Colour: plain brown to bluish-black above, sometimes with blackish collar across head; underside white, but dark spots and blotches may occur; tail behind spine blackish above and below.

Distribution: Eastern North Atlantic: tropical and subtropical latitudes from off Senegal, Canary Islands, Azores and Madeira and occasionally to the temperate waters of northern Spain and Bay of Biscay; single record of a stranded individual from the British Isles (Shark Trust 2009); also in the Mediterranean Sea, but not in the Black Sea.

Habitat: This epi- to benthopelagic ray usually found over or near continental and insular shelves with highly productive coastlines due to upwellings, but also found in the open sea far offshore and near the surface. Often found in pairs and in small groups. Migrating close to the surface over long distances offshore into the open sea.

Biology: Yolk-sac viviparous, giving birth to only one young of about 160 cm disc width and 35 kg weight after a gestation period of up to 25 months. Mobulas are filter feeders depending on rich concentrations of plankton (mainly crustaceans but also small fish), sieving their food with their huge gill filter basket


Fig. 507 Mobula mobular
 out of large amounts of water directed with aid of the cephalic fins into their huge mouth gapes. Little else is know of their general biology.

Size: Maximum disc width to 520 cm , but usually found at smaller sizes.
Interest to Fisheries and Human Impact: More or less regularly accidental bycatch in pelagic fisheries with purse seines, trawls, driftnets and longlines and mostly discarded; often landed along Mediterranean coast of Africa and along West Africa, where the wings are used for human consumption fresh, dried-salted and smoked.

The conservation status is Endangered, although a ban on pelagic driftnet use in the Mediterranean is thought to have eased pressure on this devil ray (Notarbartolo et al. 2006).

Local Names: Giant Devil Ray, Devil Ray, Horny Ray (England, Ireland); Atlantischer Teufelsrochen (Germany); Jamanta, Diabo-do-mar (Azores, Portugal).

Remarks: This devil ray is the type species of genus Mobula Rafinesque, 1810.
Literature: McEachran and Capape, Mobulidae, in: Whitehead et al. (1984); Notarbartolo, Serena and Mancusi (2006); Shark Trust (2009).

## 4. SYSTEMATIC CATALOGUE - Subclass HOLOCEPHALI

### 4.1 Order CHIMAERIFORMES - Ghost sharks, Silver sharks, Ratfish, Chimaeras

Order: Chimaeriformes Patterson, 1965, Philos. Trans. R. Soc. Lond. B Biol. Sci. 249: 101-219.
Number of Recognized North Atlantic Families: 2.
FAO Names: En - Chimaeras; Fr - Chimères; Sp - Quimeras.
Field Marks: Body elongated and tapering rearwards to a filamentous tail, head very large, a prominent first dorsal-fin spine preceding a large, erect triangular dorsal fin, second dorsal fin low and elongated, broad pectoral fins, and noticeable open lateral line canals on head and trunk. Colour variable from silvery to grey, brown, reddish, or black with lighter or darker shades of each; prominent spots or stripes may be present on some species.

Diagnostic Features: Body more or less compressed, elongate, tapering posteriorly from large head to slender filamentous tail. Snout either short and rounded conically, elongate and spear-like, or with hoe-like proboscis. Eyes relatively large, and in life bright green. Nostrils large, located in front of mouth, connected with outer corner of mouth by a deep groove covered by lateral lobe of upper lip. Mouth ventrally located on head, anterior to eye level, transverse and small. Teeth plate-like, paired, with two pairs on upper jaw, a single pair on lower; plates with more or less conspicuous ridges and bumps on surface. Gill openings anterior to pectoral fins, one on each side and covered by a fleshy operculum. Spiracles absent. Skin smooth, often deciduous. Lateral line canals well developed, especially on head. Pectoral and pelvic fins broad, roughly triangular-shaped, and well developed. First dorsal fin triangular, erect, usually much higher than second, and preceded by an elongate, smooth or serrated edged spine; fin spine may or may not reach apex of first dorsal fin. Second dorsal fin separated from first, elongated, and much lower in height than first; margin of second relatively straight to undulating distally, terminating anterior to upper caudal-fin lobe. Anal fin absent or present; if present, small, low, and distinctly separated from caudal fin by a deep notch. Caudal fin lanceolate, with upper and lower lobes nearly equal in height, dorsal lobe margin with or without tubercules; lower lobe without tubercules; whip-like tail filament variably present of absent. Sexual dimorphism strong, males (adults only) with bulbous, denticulate frontal tenaculum set in pouch atop head. Pre-pelvic tenaculum blade-like with or without large denticles along the medial edge, retractable into pouches anterior to the pelvic fins. Claspers may be slender and rod-like in some, bifurcate in others, or with some being tripartite. Adult size small, 60 cm to relatively large at 150 cm total length or possibly more. Colour: uniform pale to whitish, silvery, brown, grey, or black; some species lighter or darker ventrally; depending on the species some may or may not exhibit striking patterns of spots and stripes.

Distribution: Circumglobal in all oceans except Antarctic waters. The North Atlantic has the second highest diversity of these fishes following the Western Indo-Pacific region. The family Chimaeridae tends to exhibit a high degree of endemism with some species having very restricted ranges while members of the family Rhinochimaeridae generally have a broader, but widely scattered distribution; both these families are represented in the North Atlantic. The family Callorhinchidae is restricted to the Southern Hemisphere.

Habitat: Chimaeroids are mostly deepwater inhabitants occupying outer continental shelves, slopes, seamounts, offshore island chains, and underwater ridges from depths 500 m to greater than 2500 m . A few species occur in relatively shallow coastal waters. They occur on both soft bottom and rocky reef habitats, some in areas of relatively high vertical relief.

Biology: Reproduction is oviparous, but for most species, very little else is known about their reproductive cycle, fecundity, or age and growth. There have been some limited diet studies that suggest they consume mostly benthic invertebrates including polychaetes, amphipods, molluscs, including bivalves, gastropods, and cephalopods, crustaceans, brittle stars, and small benthic fishes. The behavior of most chimaeroids is poorly known although it is well known that some species will form large aggregations, segregated by size and sex, while some species will occupy different habitats depending on the stage in life.

Interest to Fisheries and Human Impact: A few species, mostly the callorhinchids, are targeted in commercial fisheries, but most species are taken as bycatch and either discarded at sea or retained for market.

The conservation status of most species is either Data Deficient or Least Concern due to their deepwater habitat and lack of information on their abundance, life history, and population trend.

Local Names: None.
Remarks: The families Chimaeridae and Rhinochimaeridae are represented in the North Atlantic, with four genera and eight species. The present arrangement of the Chimaeriformes, families, and genera follows recent revisions by Didier (1995, 2004) and Didier, Kemper, and Ebert (2012).

Literature: Garman (1901, 1908, 1911); Bigelow and Schroeder (1953, 1954); Krefft in Hureau and Monod (1973b, c); Stehmann and Bürkel in Whitehead et al. (1984); Didier (1995, 2002, 2004); McEachran in Collette and Klein-MacPhee (2002); Nelson (2006); Last and Stevens (2009); Ebert and Winton (2010); Didier, Kemper, and Ebert (2012).

## Key to North Atlantic Families:

1a. Snout short and blunt (Fig. 508).
family Chimaeridae

1b. Snout elongated and tapering
(Fig. 509).
family Rhinochimaeridae


Fig. 508 Chimaera


Fig. 509 Rhinochimaera

### 4.1.1 Family CHIMAERIDAE

Family: Chimaeridae Bonaparte, 1831, Giornale Arcadico di Scienze, 49: 1-77.
Type genus: Chimaera Linnaeus, 1758.
Number of Recognized North Atlantic Genera: 2.
FAO Names: En - Shortnose chimaeras.
Field Marks: Small to large bodied chimaeras, with large heads, body tapering posteriorly to a filamentous whiplike tail. Snout fleshy, short, conical, and pointed at tip. First dorsal fin triangular, preceded with prominent fin spine. Anal fin variably absent or present. Body colour uniformly dark or light brown, grey, black, with spotting or lateral stripes in some species.

Diagnostic Features: Body elongate, compressed, tapering from large head to a filamentous tail. Snout short, conical, fleshy, bluntly pointed at tip. Eyes large, bright green in life. Skin smooth, often deciduous, flaking off in patches during and after capture. Nostrils large, located in front of mouth. Gills, one opening on each side, located anterior to pectoral fins, and covered by a fleshy operculum. Spiracles absent. Mouth small, ventral on head, connected by nostrils by deep grooves. Teeth nonreplaceable, in the form of three paired tooth plates; two pairs on upper jaw, one pair on lower jaw. Tooth plates robust with patches of dense hypermineralized tissue that appears as ridges and bumps on the surface. Lateral line canals appear as open grooves on head and flanks of body; canals on snout widening with regularly spaced expanded dilations. Pectoral and pelvic fins broad with delicate external fin webs supported by cartilaginous rays (ceratotrichia). First dorsal fin triangular, erect, preceded by an elongate, serrated spine. Second dorsal fin separated from first, elongated, and much lower in height than first; margin of second relatively straight to undulating distally, terminating before upper caudal-fin lobe. Anal fin, depending on the genera, absent or present; if present, small, low, and distinctly separated from caudal fin by a deep notch. Caudal fin lanceolate, with upper and lower lobes nearly equal in height, and terminating with a whiplike tail filament of variable length. Sexual dimorphism strong, mature males with bulbous, denticulate frontal tenaculum set in pouch atop the head anterior to eyes. Pre-pelvic tenaculum blade-like with large denticles along the medial edge, hidden in pouches anterior to the pelvic fins. Claspers bifurcate or tripartite with fleshy, denticulate tips. Size variable, ranging from 60 to 150 cm total length. Colour: uniform brown, grey, or black, but with some species exhibiting striking patterns of spots and stripes.

Distribution: The Chimaeridae have an almost circumglobal range in arctic and cold temperate to tropical seas, although most species, especially in lower latitudes, occur in very deepwater. This is the most species-rich family of chimaeras with most species being regional endemics. The only areas they appear not to occur is in Antarctic and northern most Arctic waters.

Habitat: Members of the Chimaeridae generally inhabit deepwater, usually at depths greater than 200 m , with some species known to well over 2500 m deep. They occupy a wide range of benthic habitats from soft muddy or sandy bottoms to cobble and rocky reefs, sometimes in association with high vertical relief.

Biology: Reproductive mode is oviparous, but little is know about their fecundity or reproductive cycle. Females lay pairs of spindle-shaped egg cases that are deposited on the bottom. Embryological studies indicate that development may take as long as 9 to 12 months.
Attempts to age these chimaeras have met with mixed results, but with the age not being validated for any of these species. Very little is known of their diet except where information is available they tend to feed on a variety of benthic invertebrates and small fishes.

Interest to Fisheries and Human Impact: Fisheries for chimaeras are poorly known with catches perhaps the least reported among any chondrichthyan group. In the North Atlantic, most shortnose chimaerids occur too deep and are not caught in sufficient numbers to warrant a targeted fishery, but are often retained as bycatch. The only shortnose chimaera species for which landings have been reported in the North Atlantic is Chimaera monstrosa.

The conservation status of most members of this family are Data Deficient or Least Concern, but some species, including Chimaera monstrosa and Hydrolagus mirabilis, are considered Near Threatened due to current or potential fisheries that may impact their populations.

Local Names: Ratfishes, Rabbitfishes, Ghostsharks, Silver sharks.
Remarks: The current arrangement of this family follows Didier, Kemper, and Ebert (2012) in recognizing two genera and 36 species. The separation of the genera Chimaera and Hydrolagus has been subject to much debate as they are morphologically very similar with the primary difference being the presence (Chimaera spp.) or absence (Hydrolagus spp.) of an anal fin. Both genera, comprising five species are known to occur in the North Atlantic. During the final stages of this project a sixth species was described from the Eastern North Atlantic. See Remarks section under genus account below.

Literature: Garman (1901, 1908, 1911); Bigelow and Schroeder (1953); Krefft in Hureau and Monod (1973b); Stehmann and Bürkel in Whitehead et al. (1984); Didier (1995); Nelson (2006); Gibson et al. (2008); Ebert and Winton (2010); Didier, Kemper, and Ebert (2012).

Key to North Atlantic Genera:
1a. Anal fin present (Fig. 510)
Chimaera

1b. Anal fin absent (Fig. 511).
Hydrolagus


Fig. 510 Chimaera


Fig. 511 Hydrolagus

## Chimaera Linnaeus, 1758

Genus: Chimaera Linnaeus, 1758, Syst. Nat., ed. 10, 1: 236.
Type species: Chimaera monstrosa Linnaeus, 1758, by subsequent designation of Jordan and Gilbert, 1883, 54.

## Number of Recognized North Atlantic Species: 1.

Synonyms: Genus Chimera Rafinesque, Ann. Nature, 1815: 92; emended spelling for Chimaera Linnaeus, 1758, by ref. to Linnaeus. Genus Chimaira Duméril, Mem. Acad. Sci. France, 1856, 27(1): 155; emended spelling for Chimaera Linnaeus 1758, by ref. to Linnaeus. Doubtful synonym Genus Callorhynchus Gronovius, 1772: 49. Type and only described species: Callorhynchus americanus.

Field Marks: Blunt-snouted chimaera with dorsal-fin spine attached to first one-third to one-half of dorsal fin, the upper half unattached, second dorsal-fin height even along its length, never indented, and anal fin separated from the anterior margin of the ventral caudal fin by a deep notch.

Diagnostic Features: See Field Marks above.

## Local Names: None.

Remarks: The genus contains 14 species worldwide with one recognized from the North Atlantic (but see Remarks under Family Chimaeridae), and several other different species occurring in the eastern and western Central Atlantic. It would not be unexpected if one of these other species were to eventually be reported from Areas 21 and 27.

As this catalogue was being completed a new Chimaera species, C. opalescens Luchetti, Iglesias, and Sellos, 2011, was described from the Eastern North Atlantic ranging from the slope west of the British Isles to France, between $48^{\circ}$ and $57^{\circ} \mathrm{N}$, and at a depth of 900 to 1400 m . The new species apparently differs from C. monstrosa, the only previously recognized Chimaera species in the Eastern North Atlantic, primarily by morphological differences in the claspers and genetically.

## Chimaera monstrosa Linnaeus, 1758

Chimaera monstrosa Linnaeus, 1758, Syst. Nat., ed. 10, 1: 236. ('Habitat in mari Atlantico). No type material.
Synonyms: Chimaera argentea Ascanius, 1772, Icon. Rer. Nat., 2: 6, pI XV. No type material, west coast of Norway. Chimaera borealis, Shaw, 1804, General Zool., 5 pt. II: 365-368, pI. CLVII. No type material (new name for C. monstrosa), northern ocean. Chimaera mediterranea Risso, 1826, Hist. nat. Europe merid., 3: 168-169. No type material, off Nice. Chimaera cristata Faber, 1829, Naturgesh. Fishe Islands: 45. No type material, Iceland. Chimaera arctica Gistel, 1848, Naturgesh. Thierreichs, 8: 103. No type material (new name for C. monstrosa only), northern seas. Chimaera dubia Osorio, 1909, Mems. Mus. Bocage, 1: 31-33, pl. III (fig. 1). Holotype: MB no. T 111 (141), off Nazaré.

Other Combinations: None.
FAO Names: En - Rabbit fish; Fr - Chimère commune; Sp - Quimera.


Fig. 512 Chimaera monstrosa

Field Marks: A reddish-brown body coloration with light mottling and longitudinal stripes on dorsal side of trunk, extending onto paired and median fins; pelvic claspers long and slender, divided for more than the distal one-third their length; distal edge of pelvic fins straight, not rounded.

Diagnostic Features: Body elongate, slender, tapering from head to whiplike tail filament; caudal filament length 44 to $160 \%$ of total body length. Head large, snout somewhat conical, gently pointed. Eyes large, 25 to $51 \%$ head length. Lateral line canals on head appear as open grooves, canals on the snout characterized by wide dilations. Preopercular and oral lateral line canals branch together at their junction with the infraorbital canal. On rare occasions a variation of this pattern is seen in which the oral and preopercular canals share a tiny common branch. Pectoral fins narrow and triangular in shape, reach to, and just beyond, origin of pelvic fin; pelvic fin squared along its distal edge. Pelvic claspers long, slender, divided distally for nearly one-half their length; long, fleshy tips covered with a shagreen of denticles. First dorsal fin high, triangular, with a short fin-base, fin preceded by a keeled spine, strongly serrate along the posterior edge of the distal tip; spine tip when depressed reaches beyond distal tip of the first dorsal fin. Second dorsal fin long and continuous to upper caudal fin, relatively even along its length, slightly sloping posteriorly; anterior height 4 to $7 \%$ body length, posterior height 3 to $6 \%$; lighter at the base with dark edge along distal margin. Anal fin short, low, and distinctly separate from lanceolate-shaped caudal fin. Caudal fin dorsal and ventral lobes nearly equal in height. Colour: an even reddish-brown mottled with pale splotches and stripes dorsally on the head, along the trunk, and onto the base of the fins, ventral surface an even pale gray-brown. Pectoral and pelvic-fin distal margins with distinctly dark edges in preserved specimens.

Distribution: Eastern North Atlantic: southern Arctic (about $80^{\circ} \mathrm{N}$ latitude), southeastern Greenland, Norway and Iceland southwards to the Azores and Morocco (about $30^{\circ} \mathrm{N}$ latitude). Mediterranean Sea, but rare in the eastern part. Records of this species from the Western Atlantic (Area 31) and southern Africa are apparently of different species.

Habitat: A common benthopelagic inhabitant along the upper continental slope usually from 200 to 700 m , occasionally to 1000 m or more, maximum depth recorded for this species is 1663 m . It usually occurs on mud or soft bottom substrate. Bottom temperature where this species has been caught ranges from 4.7 to $8^{\circ} \mathrm{C}$.

Biology: Oviparous, with egg deposition occurring mostly during the spring and summer. The neonates hatch after a 9 to 12 month incubation period. Egg cases slender, tadpole-shaped, tapering posteriorly to a pointed filamentous tip, with lateral flanges; capsule texture smooth. Nothing is known of early development. Age at maturity has provisionally
been estimated at 13.4 years for males and 11.2 years for females; maximum estimated age for males is 30 years and 26 years for females. The diet consists primarily of benthic invertebrates.

Chimaera monstrosa appears to aggregate, possibly by age and sex, in large to very large groups like many other Chimaera species. Nothing is known of its population structure, but it has been suggested that the Mediterranean population may be distinct from the North Sea population.

Size: Maximum total length, with intact filament may be up to 100 cm , with a body length of less than 50 cm . Maturity is attained at about 40 cm body length (about 70 cm total length) for both sexes. Size at birth unknown.

Interest to Fisheries and Human Impact: This is perhaps the most commonly caught chimaera in the Eastern North Atlantic in bottom trawl fisheries. It is largely taken as bycatch


Fig. 513 Chimaera monstrosa
$\square$ Known distribution and is either discarded or retained for market. Bycatch discard estimates indicate that this species may represent 13 to $15 \%$ of discarded biomass by deepsea trawlers operating off the West Coast of Ireland.

The conservation status of this Chimaera species is Near Threatened due to suspected, but unconfirmed, declines in its population from deepwater bottom trawl fisheries. More information is required to confirm the population status of this species.

Local Names: Seeratte (German); Havmus (Denmark, Norway); Geirnyt (Iceland); Ratazana (Portugal).
Remarks: It was long believed that this species ranged as far south as the west coast of South Africa, but a recent taxonomic examination of North Atlantic and South Africa material revealed the latter to represent a new species (Chimaera notafricana) endemic to southern Africa. Also, records of this species from the Western North Atlantic require further investigation as this may represent a different species from true C. monstrosa A second Chimaera species from the Western Central Atlantic, from off the Bahamas and formerly referred to C. monstrosa, was recently described as a new species, $\boldsymbol{C}$. bahamaensis. Given the recent description of another similar monstrosa-like species (C. opalescens) from the Eastern North Atlantic, it may be that this once monotypic, wide-ranging species may in fact represent a species complex.

Literature: Newell and Roper (1935); Bigelow and Schroeder (1953); Kreff in Hureau and Monod (1973b); MacPherson (1980b); Mauchline and Gordon (1983); Stehmann and Bürkel in Whitehead et al. (1984); Santos, Porteiro, and Barreiros (1997); Calis et al. (2005); Moura et al. (2004); Moura et al. (2005a); Serena (2005); Ross and Quattrini (2007); Dagit, Hareide, and Clò (2007); Gibson et al. (2008); ICES (2010); Kemper et al. (2010a, b); Didier, Kemper, and Ebert (2012); Luchetti, Iglesias, and Sellos (2011).

## Hydrolagus Gill, 1862

Genus: Hydrolagus Gill, 1862, Proc. Acad. Nat. Sci. Philad., 14: 331.
Type species: Chimaera colliei Lay and Bennett, 1839, off Monterey, California, USA, by monotypy.

## Number of Recognized North Atlantic Species: 4.

Synonyms: Subgenus Bathyalopex Collett, Forh. VidenskSelsk. Krist., 1904(9): 5. Type: Chimaera (Bathyalopex) mirabilis Collett, by monotypy) as a subgenus to Chimaera. Faroe Channel and Faroe Bank, 720 to 1200 m .

FAO Names: En - Ratfishes.
Field Marks: Blunt-snouted chimaera with a dorsal fin spine either attached to first dorsal fin entire length or free for distal one-half to one-third its length, second dorsal fin even in height along its length, or with deep indentation separating the fin into anterior and posterior portions, and no deep notch separating an anal fin from the ventral caudal fin.

Diagnostic Features: See Field Marks above.
Local Names: None.
Remarks: Worldwide there are 22 species recognized within this genus, with four species known from the present areas.

## Key to North Atlantic Species:

1a. Small-bodied, slender fish, some adults almost dwarflike; second dorsal-fin margin concave; body colour pale, brown, tan, or silvery-gray (Fig. 514)

Hydrolagus mirabilis


Fig. 514 Hydrolagus mirabilis
1b. Large-bodied fish, adults sometimes massive; second dorsal-fin margin straight; body colour dark black, purplish, blue, or gray

2a. Caudal dorsal-fin height greater than caudal ventral fin height; eye diameter more than 5 times in head length; body colour dark black or purplish black (Fig. 515) . . .

Hydrolagus affinis

2b. Caudal dorsal-fin height less than or equal to caudal ventral fin height; eye diameter less than 5 times in head length; body colour pale white, greyish, light brown or light reddish-brown. . 3


Fig. 515 Hydrolagus affinis


Fig. 516 Hydrolagus pallidus


Fig. 517 Hydrolagus Iusitanicus

## Hydrolagus affinis (de Brito Capello, 1868)

Chimaera affinis de Brito Capello, 1868, J. Sci. Math. Phys. Nat., Lisboa, 1(4): 314-315, 320, pl. III, fig. 1. Holotype: MB no. T115, off Setubal, Portugal. Holotype: lost in museum fire.

Synonyms: Hydrolagus plumbea Gill, 1878, Bull. Phil. Soc. Wash., 2: 182. Holotype: possibly lost?, southeast of La Have Bank, Nova Scotia, Canada. Chimaera abbreviata Gill, 1883, Proc. U.S. Nat. Mus., 6: 254. Psychichthys affinis Jordan, Evermann, and Clark, 1930, Rep. U.S. Comm. Fish. (1928), 2:33 (listed as Cape Cod to Portugal). Bathyalopex abbreviatus Jordan, Evermann, and Clark, 1930, Rep. U.S. Comm. Fish. (1928), 2: 33 (listed by ref. to Gill 1883). Bathyalopex plumbeus Jordan, Evermann, and Clark, 1930, Rep. U.S. Comm. Fish. (1928), 2: 33 (listed). Chimaera monstrosa Vladykov and McKenzie, 1935, Proc. N.S. Inst. Sci., 19: 52 (listed, Nova Scotia Banks), not Chimaera monstrosa Linnaeus, 1758.

Other Combinations: None.

FAO Names: En - Smalleyed rabbitfish.


Fig. 518 Hydrolagus affinis

Field Marks: A very large Hydrolagus with the oral and preopercular lateral lines sharing a short, common branch, first dorsal-fin spine not exceeding fin height, second dorsal-fin height relatively even along entire fin length, and a short (less than body length) tail filament. Colour a uniform dark brown to black.

Diagnostic Features: Body very stout, tapering from large head to relatively short whiplike filamentous tail; caudal filament ends in a blunt tip, its length ranges from 17 to $89 \%$ of body length. Snout bluntly pointed. Eyes large, 16 to $25 \%$ head length. Lateral line canals on head appear as open grooves, canals on the snout characterized by wide dilations. Preopercular and oral canals share a short common branch from the infraorbital canal; in rare cases branching together from the infraorbital canal. Skin rubbery, not deciduous, usually remains mostly intact. Pectoral fins broadly triangular, reaching to pelvic-fin base when laid back. Pelvic fins squared along distal edge and rounded ventrally. Males with robust frontal tenaculum with smooth, curved dorsal surface bulbous rounded tip, denticles do not extend on dorsal surface. Pre-pelvic tenaculum with at least five large denticles along medial edge. Pelvic claspers stout with bulbous fleshy tips covered by a shagreen of denticles; divided for the distal one-third of their length, reaching just to distal edge of pelvic fin. Males without postanal pads, females with large postanal pads. First dorsal fin high and triangular, with short fin-base; fin preceded by a stout spine, smooth along its anterior edge with two rows of serrations along the posterior edge for the distal one-third to onehalf spine length; spine tip just reaches to origin of second dorsal fin when depressed. Second dorsal fin long, continuous to upper caudal-fin lobe, and relatively even ( 3 to $9 \%$ body length) in height along its length. Caudal-fin dorsal and ventral lobes are rounded and nearly even in height; dorsal lobe slightly taller ( 3 to $4 \%$ body length) than lower lobe ( 2 to $4 \%$ ); insertion of ventral caudal lobe posterior to insertion of dorsal caudal lobe. Colour: uniformly dark brown to purplish black, pale along ventral edge of tail and around mouth. Pectoral and pelvic fins are evenly coloured, dark brown to purplish black. In some specimens the dorsal parts of the trunk and the base of the second dorsal fin may be slightly mottled.

Distribution: Widespread in the North Atlantic. Eastern North Atlantic: southwestern Greenland to Iceland and southwards to Portugal, the Azores and the Canary Islands. Western North Atlantic: south of Toms Canyon (off the New Jersey coast, USA), to the Gulf of Maine to off Sable Island and southeastern Grand Bank, Canada. Also, known from the Mid-Atlantic Ridge.

Habitat: This little known chimaera species inhabits deepwater continental


Fig. 519 Hydrolagus affinis
Known distribution
slopes, seamounts, ridges, and abyssal plains in the North Atlantic. It is found from 300 m to at least 2410 m depth, but is most common below 1000 m . Bottom temperature where these chimaeras have been captured ranged from 3.6 to $5.9^{\circ} \mathrm{C}$, and a salinity range of 34.94 to $35.13 \%$.

Biology: Nothing known of its reproductive biology. The diet of this chimaera species includes benthic invertebrates and small fishes. Hydrolagus affinis is apparently common around the Lucky Strike hydrothermal vent site along the northern Mid-Atlantic Ridge where they were found to consume the vent mussel Bathymodiolus spp.

Size: Maximum total length with intact filamentous tail about 147 cm ( 96 cm body length); maximum female total length at least 125 cm , total body length 86 cm ; male total length uncertain, but largest total body length 88.5 cm . Minimum size at maturity is attained in males at 66 cm body length and in females at 68.5 cm body length. Size at birth uncertain, but the smallest free-swimming individual was 32 cm total length ( 14 cm body length).

Interest to Fisheries and Human Impact: This chimaera is of no commercial importance, but is occasionally taken as bycatch in deepwater bottom trawl fisheries. At one time these, and likely other deepsea chimaeras, were taken in abundance in the halibut fishery that operated in the eastern part of the Gulf of Maine and off Nova Scotia, but with the collapse of that fishery few specimens of Hydrolagus affinis have been caught. In recent years, with developing deepsea bottom trawl and longline fisheries in the Eastern North Atlantic it is likely that this species may appear as bycatch in these fisheries.

The conservation status of this chimaera is Least Concern due to its relatively deepwater habitat, wide geographic range, and the lack of deepwater fisheries throughout much of its range. However, if deepsea fisheries continue to develop the conservation status of this species may need to be revisited.

Local Names: Atlantic chimaera, Deepwater chimaera (English); Småøjet havmus (Denmark, Greenland).
Remarks: Examination of the holotypes of Chimaera abbreviata and C. plumbea by Dr. Dominique Didier (pers. comm. to D.A. Ebert, June 2011) confirm these nominal species are junior synonyms of Hydrolagus affinis.

Literature: Bigelow and Schroeder (1953, 1954); Krefft in Hureau and Monod (1973b); Stehmann and Bürkel in Whitehead et al. (1984); Scott and Scott (1988); Hardy and Stehmann (1990); Marques and Porteiro (2000); McEachran in Collette and Klein-MacPhee (2002); Moore et al. (2003); Møller et al. (2004, 2010); Dagit and Clarke (2007a); Gibson et al. (2008); Didier, Kemper, and Ebert (2012).

## Hydrolagus Iusitanicus Moura, Figueiredo, Bordalo-Machado, Almeida, and Gordo, 2005

Hydrolagus Iusitanicus Moura, Figueiredo, Bordalo-Machado, Almeida, and Gordo, 2005, J. Fish Biol. 67: 742, figs. 1-4, tab. 1. Holotype: Museu Nacional de Historia Natural, Museu Bocage, MB-4666, mature male 944 mm precaudal length; 'Meireles Novo', 14.II. $2003,36^{\circ} 35^{\prime} \mathrm{N}, 8^{\circ} 35^{\prime} \mathrm{W}$. Type locality: on the continental slope of southern Portugal at the Algarve, 1600 m depth.
Synonyms: None.
Other Combinations: None.
FAO Names: En - Portuguese rabbitfish.


Fig. 520 Hydrolagus lusitanicus

Field Marks: A very large Hydrolagus with a relatively small eye, less than five times in head length, a pectoral-fin length more than 1.9 times its width. In life the colour is a uniform light to reddish brown.

Diagnostic Features: Body stout, tapering from large head to very short filamentous tail; caudal filament missing in all known specimens. Snout short and bluntly pointed. Eyes large and oval. Lateral line canals on head appear as open grooves. Preopercular and oral canals appear either separately or from a common branch on suborbital canal. Pectoral fins broad, triangular, and very large, with posterior margins rounded, when depressed extend to, or beyond, pelvic-fin base. Pelvic fins triangular, broad, posterior margin slightly concave. Males with robust, curved, bulbous frontal tenaculum with enlarged hooks directed posteriorly on the anteroposterior surface. Pre-pelvic tenaculum with five to eight enlarged hooks on outer edge. Pelvic claspers stout with bulbous fleshy tips covered by small denticles. Females with anal pad present. First dorsal fin high, triangular, and slightly concave along posterior margin; fin preceded by a stout spine attached to anterior margin of dorsal fin, with serrations along the posterior surface; spine lacking grooves; spine height about equal to first dorsal-fin height. Second dorsal fin continuous, relatively straight, about equal in height. Caudal-fin lobes rounded, ventral lobe originates anterior to dorsal caudal-fin lobe. Colour: in life a uniform rose to light brown with a few smaller irregular light and dark spots; point of snout and region between the eye and the pectoral fin whitish; fins violet blue.

Distribution: Eastern North Atlantic: Portugal from the Figueira da Foz (northern Portugal, $40^{\circ} 07^{\prime} \mathrm{N}, 9^{\circ} 45^{\prime} \mathrm{W}$ ) to the Algarve (southern Portugal $36^{\circ}$ $35 \mathrm{~N}, 8^{\circ} 35^{\prime} \mathrm{W}$ ).

Habitat: A little known chimaera (only known from 22 specimens) from very deep water, at least 1600 m deep, from the Portuguese continental slope between the Algarve and from off Figueira da Foz.

Biology: Oviparous, but nothing else known of its reproductive biology or diet.

Size: Maximum precaudal length 117.7 cm ; precaudal length of known males is 81.5 to 95.4 cm , with adulthood at 94.4 cm ; female precaudal length 98.6 to 117.7 cm , but size at maturity not reported. Size at birth unknown.

Interest to Fisheries and Human Impact: The species appears likely to be taken as bycatch in Portuguese


Fig. 521 Hydrolagus lusitanicus
Known distribution longline fisheries targeting black scabbard fish (Aphanopus carbo), with other deepwater elasmobranchs, but this has not been confirmed since they are likely to be discarded at sea.

The conservation status of this deepwater chimaera is Data Deficient due to a lack of information on this species.

## Local Names: Coelho (Portugal).

Remarks: This large, deepwater, chimaera should be closely examined and compared with Hydrolagus affinis and possibly H. pallidus as all three of these species are very closely related morphologically and appear to overlap in their body proportions, depth and habitat distribution.

Literature: Moura et al. (2005b); Gibson et al. (2008); Valenti and Couzens (2008); Didier, Kemper, and Ebert (2012).

## Hydrolagus mirabilis (Collett, 1904)

Chimaera (Bathyalopex) mirabilis Collett, 1904, Forh. VidenskSelsk. Krist.,(9): 5-6. Holotype: Lost? Lectotype: ZMO no. J 133, 150 km NW of Hebrides, 1100 m . Designated by Pethon, 1969: 3.

Synonyms: Chimaera mirabilis Holt and Byrne, 1910, 5: 11-17, pl. II, fig 2a.

## Other Combinations: None.

FAO Names: En - Large-eyed rabbitfish; Fr - Chimère à gros yeux; $\mathbf{S p}$ - Quimera ojón.


Fig. 522 Hydrolagus mirabilis

Field Marks: A very small Hydrolagus with the oral and preopecular lateral lines sharing a common branch, second dorsal fin concave, and a very long whip-like filamentous tail. Colour is a uniform light to dark brown or greyish, with darker fin edges.

Diagnostic Features: Body very short, stout, rapidly tapering behind pelvic fins to very long, slender, narrow whiplike filamentous tail; caudal filament length about $75 \%$ body length. Snout short, conical, and bluntly pointed. Eyes ovalshaped, relatively large, about $35 \%$ of head length. Gill openings noticeably smaller than in other similar chimaeroid species. Preopercular and oral lateral line canals share a common branch. Skin deciduous, smooth. Pectoral fins broadly rounded, reaching beyond pelvic-fin origins when laid back. Pelvic fins stoutly rounded along base. Adult males with small frontal tenaculum, curved dorsal surface, a rounded bulbous tip, and adorned with small denticles that do not overlap dorsal surface of tenaculum. Pelvic tenacula small, divided about one-half their length, with fleshy bulbous tips covered in an extremely fine shagreen of denticles; not reaching beyond the distal margin of the pelvic fins. First dorsal fin high, with a short fin-base; fin preceded by a slender fin spine that reaches to or slightly beyond the first dorsal-fin tip; posterior spine edges not strongly serrated; spine extends well beyond the origin of second dorsal fin when depressed. Interdorsal fin space very small, first and second dorsal fins joined by a fleshy ridge of skin. Second dorsal fin long, continuous to upper caudal-fin lobe; height less than one-third first dorsal-fin height; second dorsal fin with distinct concave dorsal margin, nearly separating fin into anterior and posterior portions, about mid-distance on fin. Colour: uniform pale to dark brown with darker grey-brown or blackish fin edges; second dorsal fin with light coloured band at base with a dark distal edge.

Distribution: Eastern North Atlantic: Iceland to the Irish Atlantic slope off Ireland, Scotland, the Hebrides, to northern Spain, and likely continuous to off the northwest African coast. It has recently been reported from off Namibia. Western North Atlantic: Flemish Cap to the Grand Banks, and in the northern Gulf of Mexico, it has also been reported from off northern South America as far south as Suriname. Given the widespread capture records of this species it may be widespread throughout the northern and central Atlantic at depth.

Habitat: A poorly known chimaera with a depth range of 450 to 1933 m , but generally occurring below 800 m . Possibly occurs over muddy or rocky reef habitat.

Biology: Oviparous, but nothing else known of it reproductive biology. Egg case rounded anteriorly, acutely pointed at tip, tapering posteriorly to an elongated filament; length about 13 cm . The diet of this chimaera includes benthic invertebrates such as echinoids, scyphozoans, and tunicates, and small bony fishes including roundnose grenadier, Coryphaenoides rupestris.

Size: Maximum total length to 80 cm (about 35 cm body length). Size at birth uncertain, but smallest free-swimming neonate measured 18.2 cm total length ( 6.7 cm body length).

Interest to Fisheries and Human Impact: Occasionally taken as bycatch, but not very common and usually only in very deepwater trawl fisheries.

The conservation status is currently Near Threatened due to concerns over expanding deepwater fisheries in the Eastern North Atlantic. However, given its apparent widespread, although patchy, distribution it is not likely to be impacted to the extent of other regions.

Local Names: Kurznasenchimäre (Germany); Storøjet havmus (Denmark); Digurnefur (Iceland).

Literature: Krefft in Hureau and Monod (1973b); Mauchline and Gordon (1983); Stehmann and Bürkel in Whitehead et al. (1984); McEachran and Fechhelm (1998); Didier (2002); Dagit, Compagno, and Clarke (2007); González, Teruel, Lopez, and Paz (2007); Gibson et al. (2008); Didier, Kemper, and Ebert (2012).


Fig. 523 Hydrolagus mirabilis
$\square$ Known distribution $\square$ Possible distribution

Hydrolagus pallidus Hardy and Stehmann, 1990
Hydrolagus pallidus Hardy and Stehmann, 1990, Arch. FischWiss. 40(3): 229, figs. 1-4, tabs 1, 3. Holotype: Institut für Seefischerei, Hamburg, ISH 33/81, male 1110 mm total length, 740 mm body length; FRV "Walther Herwig" sta. 574/81, 27.IX. 1981; Type locality: northeastern Atlantic, $61^{\circ} 06.2^{\prime}-07.2^{\prime} \mathrm{N}, 11^{\circ} 26.4^{\prime}-20.2^{\prime} \mathrm{W}, 1220 \mathrm{~m}$, bottom temperature $5.81^{\circ} \mathrm{C}$, bottom salinity $35.09 \%$. Collector: M. Stehmann.

Synonyms: Hydrolagus sp. Stehmann and Bürkel, 1984: 215.
Other Combinations: None.
FAO Names: En - Pale chimaera.


Fig. 524 Hydrolagus pallidus

Field Marks: A very large Hydrolagus with the oral and preopercular lateral line canals either sharing a short common branch or branching together, dorsal-fin spine about equal in height to first dorsal fin, and a very short filamentous tail. Colour is a uniform pale grey to white.

Diagnostic Features: Body large, very stout, tapering from large head to short filamentous tail; caudal filament very short with blunt tip. Snout short, bluntly pointed. Eyes relatively small, oval shaped. Lateral line canals on head appear as open grooves, canals on the snout characterized by wide dilations. Preopercular and oral canals either share a short common branch or branch together from the infraorbital canal. Skin not deciduous, typically remains intact. Pectoral fins short, broadly triangular, reaching to pelvic-fin base when laid back. Pelvic fins concave along distal edge and pointed ventrally. Male frontal tenaculum robust, bulbous with numerous sharp, curved hooks on rounded ventral and anterodorsal surfaces; denticles extending onto dorsal surface. Pre-pelvic tenaculum with at least five to six large denticles along medial edge. Pelvic claspers stout with bulbous fleshy tips covered by a shagreen of denticles; divided for the distal one-third of their length, reaching just to distal edge of pelvic fin. Males without postanal pads, females with large postanal pads. First dorsal fin high, triangular, a short fin-base, and a slightly concave posterior margin; fin preceded by a stout spine, about equal to dorsal-fin height, anterior edge smooth, posterior edge smooth in adults, weakly serrated in juveniles. Second dorsal fin long, continuous to upper caudal-fin lobe, and relatively even in height or slightly sloping posteriorly along its length. Caudal fin dorsal and ventral lobes are rounded; dorsal lobe slightly shorter or equal to lower lobe; insertion of ventral caudal lobe posterior to insertion of dorsal caudal lobe. Colour: uniformly pale grey to white, some small scattered darker spots mostly on ventral surface and fins. Juveniles a somewhat darker greyish-brown, but as these chimaeras mature they become lighter, with adults being a pale white.

Distribution: Eastern North Atlantic: southern Bay of Biscay to western Scotland within the Rockall Trough ( $44^{\circ}$ to $59^{\circ} \mathrm{N}$ ), Iceland, Greenland and the Mid-Atlantic Ridge, including the Azores. Western North Atlantic: seamounts off New England, USA; the Bear Seamount ( $39^{\circ} 54^{\prime} \mathrm{N}, 67^{\circ} 26^{\prime} \mathrm{W}$ ) and Welker Seamount ( $40^{\circ} 05^{\prime} \mathrm{N}, 68^{\circ} 30^{\prime} \mathrm{W}$ ). A record of this species from off Chile may in fact be that of another species.

Habitat: This apparently widespread species occurs along deepwater slopes, troughs, and seamounts at a depth range of 1188 to 2075 m , but possibly deeper to 2500 m or more. Bottom temperatures where this chimaera has been captured generally range from 4.4 to $7.0^{\circ} \mathrm{C}$, with an average salinity of about $35.1 \%$.

Biology: Oviparous, but nothing else known of its life history. Its diet may include benthic invertebrates.

Size: Maximum total length at least


Fig. 525 Hydrolagus pallidus 137.6 cm for females and for males at least 136 cm (body lengths not available); a female of 128.5 cm total length had a 91 cm body length and 111.1 cm total length male had a body length of 74 cm body length. Size at maturity is 73 cm and 77 cm body lengths for males and females, respectively. Size at birth unknown, the smallest free-swimming individual was a 68 cm total length ( 42 cm body length) male.

Interest to Fisheries and Human Impact: This species may be taken as bycatch on occasion in deepwater bottom trawl and longline fisheries. However, its abundance as far as known is low and it may occur to considerable depths beyond current deepwater fisheries.

The conservation status of this deepwater chimaera is considered Least Concern. Its deepwater habitat likely serves as a refuge from most commercial fishing operations.

Local Names: Bleg havmus (Denmark and Greenland).

Remarks: This species may be more common, but is recognized as Hydrolagus affinis, a congener with whom it overlaps in its distribution. Also, a comparison and re-evaluation of this species should be undertaken to better distinguish it from H. affinis and $\boldsymbol{H}$. lusitanicus since other than colour and some very subtle morphological differences all three species are very similar in appearance.

Literature: Stehmann and Bürkel in Whitehead et al. (1984); Hardy and Stehmann (1990); Santos, Porteiro, and Barreiros (1997); Moore et al. (2003); Møller et al. (2010); Dagit and Clarke (2007b); Gibson et al. (2008); Didier, Kemper, and Ebert (2012); Iglesias (2011).

### 4.12 Family RHINOCHIMAERIDAE

Family: Rhinochimaeridae Garman, 1901, Proc. New England Zool. Club, 2: 75-77.
Type genus: Rhinochimaera Garman, 1901.
Number of Recognized North Atlantic Genera: 2.
FAO Names: En - Longnose chimaeras.
Field Marks: Medium to large bodied chimaeras with elongated bodies tapering posteriorly to filamentous tail. Snout very long, distinctively spear-shaped, and flexible. First dorsal fin preceded by prominent fin spine. Anal fin, depending on the genus, may be present or absent. Body uniformly pale to dark brown or blackish with fin edges darker in some species.

Diagnostic Features: Body elongate, somewhat compressed, tapering from large head to elongated filamentous tail. Snout fleshy, very elongate and spear-like, flexible, extending anterior to head and tapering to a blunt point. Eyes large and prominent, bright green in life. Skin smooth, often deciduous, flaking off in patches during and after capture. Gill openings, one on each side covered by a fleshy operculum, and located anterior to pectoral fins. Spiracles absent. Mouth small, ventral on head, connected to nostrils by deep grooves. Teeth non-replaceable, in the form of three paired tooth plates; two pairs on upper jaw, one pair on lower jaw. Tooth plates typically robust with patches of dense hypermineralized tissue that appears as ridges and bumps on the surface. Lateral line canals appear as open grooves on the head and sides of body. Pectoral and pelvic fins somewhat ovoid in shape, broad with delicate external fin webs supported by cartilaginous rays (ceratotrichia). First dorsal fin triangular, erect, preceded by an elongate, smooth or serrated spine. Second dorsal fin separated from first, long, relatively low, with distal margin straight to slightly undulating. Anal fin present or absent. Caudal fin lanceolate, dorsal lobe with or without tubercules along margin; lower lobe without tubercules; whip-like tail filament present or absent. Sexual dimorphism strong, adult males with bulbous, denticulate frontal tenaculum that can retract into pouch atop head and anterior to eyes. Pre-pelvic tenacula blade-like, retractable into hidden pouch anterior to each pelvic fin; tenaculum medial margin with large denticles. Claspers slender, rod-like with small fleshy denticulate tip. Size ranging from 65 to 130 cm total length. Colour: uniform pale to greyish or brownish, often lighter or white ventrally, fins darker in some species, and without distinct pattern of spots or stripes. Neonates and very small juveniles may be paler in colour, darker around the opercular flap, and with very dark brown or black fins.

Distribution: The Rhinochimaeridae has a circumglobal distribution with most members being wide-ranging although many species have a patchy or scattered distribution.

Habitat: Very little is known about the habitat preference of longnose chimaeras. They tend occur over muddy or soft bottoms, although this may be an artifact of sampling methods Usually occurring in very deepwater from over 1000 m , but with several species occurring to 3000 m .

Biology: Virtually nothing known about their reproductive biology or life history. Maturity is attained by about 40 cm body length in some species. Females lay egg cases in pairs; egg cases are tadpole-like, with broad, fan-like lateral flanges with numerous transverse ridges. Their diet is little known, but they appear to feed on small benthic invertebrates and fishes.

Interest to Fisheries and Human Impact: Longnose chimaeras are of minimal fishery interest and are mostly taken as bycatch in bottom trawl fisheries and may be utilized for fishmeal or other fish products.

The conservation status of most longnose chimaeras is Data Deficient or Least Concern due to their patchy distribution, deepwater habitat, and lack of commercial fisheries. However, more information is needed on the abundance, life history, and population trends of this poorly known group.

Local Names: Spookfishes.
Remarks: The above family account is modified, and updated, after Didier (1995, 2002, 2004) and Didier, Kemper, and Ebert (2012) and recognizes three genera and at least eight described species. Two genera and three species are known to occur in Areas 21 and 27.

Literature: Garman (1901); Bigelow and Schroeder (1953, 1954); Kreff in Hureau and Monod (1973c); Stehmann and Bürkel in Whitehead et al. (1984); Didier (2002, 2004); Nelson (2006); Gibson et al. (2008); Last and Stevens (2009); Ebert and Winton (2010); Didier, Kemper, and Ebert (2012); D.A. Didier and D.A. Ebert (unpubl. data).

## Key to North Atlantic Genera:

1a. Lateral head profile convex; mouth located slightly anterior to eyes; tooth plates with raised hypermineralized tritors on the surface; dorsal-fin lobe caudal margin without tubercles (Fig. 526)

Harriotta


Fig. 526 Harriotta
1b. Lateral head profile straight; mouth located well in front of eyes; tooth plates smooth, lacking raised hypermineralized tritors on the surface; dorsal-fin lobe caudal margin with tubercles (Fig. 527)

Rhinochimaera


Fig. 527 Rhinochimaera

## Harriotta Goode and Bean, 1895

Genus: Harriotta Goode and Bean, 1895, Spec. Bull. U.S. Natl. Mus. Washington, D.C., 17: 471. Harriotta Goode and Bean, 1886, Proc. Biol. Soc. Wash., 3: 104 (nomen nudum), "a long-rostrated chimaeroid fish" without further description and without species named.

Type species: Harriotta raleighana Goode and Bean, 1895, by monotypy.
Number of Recognized North Atlantic Species: 2.
Synonyms: None.
FAO Names: En - Longnose chimaeras; $\operatorname{Fr}$ - Chimères spatules; $\mathbf{S p}$ - Quimeras-trompudo.
Field Marks: Longnose chimaera with elongated snout, fleshy at base, and tapering to a fine point at the tip, distal tip of snout curved upwards, more so in adult male which also have a series of small rounded knobs dorsally, caudal fin rounded with elongate filament, upper and lower lobes almost equal in height with the upper lobe slightly taller, upper lobe margin without tubercles, and no anal fin present.

Diagnostic Features: See Key to Genera and Field Marks above.
Local Names: None.
Remarks: This genus has two wide-ranging, but spottily distributed species, both of which occur in the North Atlantic. These are very poorly known chimaeras if encountered should be retained for detailed examination.

## Key to North Atlantic Species:

1a. Eye relatively small; dorsal-fin spine noticeably curved, significantly shorter than height of first dorsal fin (Fig. 528)

Harriotta haeckeli


Fig. 528 Harriotta haeckeli

1b. Eye relatively large; dorsal-fin spine nearly straight, equal to or longer than height of first dorsal fin (Fig. 529) . . . . . . . . . Harriotta raleighana


## Harriotta haeckeli Karrer, 1972

Harriotta haeckeli Karrer, 1972, Mitteilungen aus dem Zoologischen Museum in Berlin, 48(1): 210, fig. 3. Holotype: ZMB 22591, immature male, 496 mm TL. Type locality: North Atlantic, $63^{\circ} 21^{\prime} \mathrm{N}, 57^{\circ} 00^{\circ} \mathrm{W}, 1970$ to 2020 m .

Synonyms: None.
Other Combinations: None.
FAO Names: En - Smallspine spookfish.


Fig. 530 Harriotta haeckeli
Field Marks: A small longnose chimaera with a broad, moderately short, conical snout, eye diameter relatively small, dorsal fin and spine short, noticeably curved, spine height less than first dorsal-fin height, pectoral fins short and broadly rounded, and a caudal fin lacking tubercules on upper edge, and a short terminal tail filament. Colour is a uniform light brown above, darker below and with a pale dorsal-fin spine.

Diagnostic Features: Body tapering posteriorly from large head. Snout relatively short, wide at base, tapering distally; snout relatively straight not curving upwards at tip. Eyes ovoid, diameter very small, about four times in distance between eye and dorsal-fin spine. Head canals relatively wide spaced; trunk lateral line canal straight, not wavy; nasal canal on ventral side of trunk not expanded laterally at distal end and not joining rostral canal. Pectoral fins large, broadly rounded, not reaching past origin of second dorsal or to origin of pelvic fin. Pelvic fins broadly rounded. First dorsal fin very small, height only slightly great than second dorsal fin; fin spine very short, less than height of first dorsal fin; spine slightly recurved. Interdorsal space very small, when laid back first dorsal and fin spine do not reach origin of second dorsal fin. Second dorsal-fin base short, length relatively even in height, except rounded at ends. Upper lobe of caudal fin greater than lower lobe; space between second dorsal and upper caudal lobe very short; tubercules lacking on dorsal margin. Tail filament very short. Colour: uniform light brown above, darker ventrally; dorsal fin spine light to white; fin edges much darker, pelvic fins blackish.

Distribution: Eastern North Atlantic: very patchy, confirmed only from southern Greenland. Eastern Central Atlantic: Canary Islands and possibly off northwestern Africa. Western North Atlantic: Davis Strait (between Canada and Greenland) to Hudson Canyon, Virginia (USA).

Habitat: Virtually unknown, of the few records of this species it has been captured on deep slopes and troughs from 1114 to 2603 m deep.

Biology: Oviparous, but nothing else known of its life history.

Size: Maximum length without tail filament at least 72 cm ; males mature at about 45 cm total length ( 20 cm body length); female maturity at about 60 cm total length (about 25 cm body length). Size at birth is unknown.


Fig. 531 Harriotta haeckeli

Known distribution

Interest to Fisheries and Human Impact: This rare chimaeroid is occasionally taken, as bycatch in deepwater fisheries, but is just as likely to be taken on occasion on deepwater surveys.

The conservation status is Data Deficient due to it being known from only a very few specimens, its widely scattered, but spotty distribution and deepwater habitat.

Local Names: Langsnudet havmus (Denmark, Greenland).
Remarks: Bigelow and Schroeder (1953) described two small juveniles as Harriotta raleighana, but in fact Karrer (1972) recognized these as $\boldsymbol{H}$. haeckeli in her description of this new species. Both species appear to overlap in some portions of their distribution, therefore care should be taken to examine other Harriotta species when encountered. A similar situation occurs among the Rhinochimaera with $\boldsymbol{R}$. africana having long been misidentified as either $\boldsymbol{R}$. atlantica or R. pacifica (see genus discussion for Rhinochimaera below).

Literature: Bigelow and Schroeder (1953); Karrer (1972, 1973); Stehmann and Bürkel in Whitehead et al. (1984); McEachran in Collette and Klein-MacPhee (2002); Moore et al. (2003); Møller et al. (2004, 2010); Dagit (2006a); Gibson et al. (2008); Last and Stevens (2009); Didier, Kemper, and Ebert (2012).

## Harriotta raleighana Goode and Bean, 1895

Harriotta raleighana Goode and Bean, 1895, Proc. U.S. Nat. Mus., 17(1014): 472, pl. 19, figs 1-2. Lectotype (Syntype): USNM 35520, Albatross station 2210, female, 100 mm TL. Type Locality: Northwest Atlantic, Gulf Stream, New Jersey, USA, ( $39^{\circ} 37^{\prime} \mathrm{N}, 71^{\circ} 18^{\prime} \mathrm{W}$ ), 1812 m . Collected 21 August 1884. Goode and Bean (1895) based their description on four specimens, but without designating a holotype, therefore making them syntypes. However, according to Eschmeyer (2011) a lectotype was establish in Jordan and Evermann (1900) from the caption to plate 19, p. 3234, "Fishes of North and Middle America."

Synonyms: None.
Other Combinations: None.
FAO Names: En - Narrownose chimaera; Fr - Chimère de Raleigh; Sp - Quimera de Raleigh.


Fig. 532 Harriotta raleighana
Field Marks: A small-bodied rhinochimaerid with a moderately long, spear-like snout, broader at base and tapering to a narrow tip, eyes moderate-sized, pectoral fins short and broad, and a caudal fin with no tubercules on upper edge, and a long terminal tail filament. Colour is a uniform dark brown.

Diagnostic Features: Snout wide at base, moderately long, slightly flattened, tapering to a fine point with knobby protuberances at distal end; sometimes curves upwards. Eyes large, ovoid. Head oral and preopercular canals separated by a relatively wide space; trunk lateral line canal straight, not wavy; nasal canal on ventral side of trunk expanded laterally at its distal end and joins rostral canal. Pectoral fins large, reaching past origin of second dorsal to near origin of pelvic fin (about $4 / 5$ distance). Pelvic fins rounded in shape. Frontal tenaculum is small and slender with a pronounced curve and distal bulb bearing numerous spiny denticles. Pre-pelvic tenaculum with six stout spines along medial edge. Pelvic claspers in mature males are rod-like with a small fleshy denticulate tip. First dorsal fin relatively small, with a spine height about equal to or slightly greater in length to height of first dorsal fin; keeled and weakly serrate along distal one-half. Interdorsal space small, when laid back first dorsal and fin spine reach origin of second dorsal fin. Second dorsal fin gently slopes anteriorly and posteriorly but relatively even in height. Caudal fin with short filament. Colour: uniform dark brown; fin edges much darker, pelvic fins blackish.

Distribution: Circumglobal, but patchily distributed, most commonly found in the Atlantic. Eastern North Atlantic: Southeast Greenland, Iceland, Rockall Trough to off United Kingdom, and possibly to Bay of Biscay, but not confirmed. Records from the Canary Islands and from northwestern Africa may instead be Harriotta haeckeli. Western North Atlantic: the Carolinas, USA, to La Have Bank, Nova Scotia, Canada, but distribution most likely continuous to Greenland and to the Eastern North Atlantic.

Habitat: Poorly known deepwater longnose chimaera with a depth range of 380 to 2600 m , although an unconfirmed Indian Ocean record was from only 100 m depth. It has been observed at depth by remote operated vehicles over soft mud and gravelly bottom substrates and on occasion in association with other deepwater chimaeras (Hydrolagus $\mathbf{s p p}$.). There appears to be an ontogenetic shift between 300 and 1000 m depth with large individuals occurring deeper than smaller individuals.


Fig. 533 Harriotta raleighana

Biology: Oviparous, but little else known of it reproductive biology. Egg cases small, about 16 cm in length, strongly convex, more so on one side than the other, lateral flanges thin, with narrow transverse ridges numbering more than 50 rows on each side; capsule dark in colour, but lighter on flanges. Diet little known, but includes a variety of polychaetes, molluscs, and other small benthic invertebrates and teleosts. Smaller H. raleighana feed mainly on polychaetes, gastropods, and small crustaceans, but the diet of larger individuals shifts more to crustaceans.

Size: Maximum total length about 120 cm ( 70 cm precaudal length); males mature at about 25 to 30 cm body length and females at about 30 cm body length. Size at birth about 10 to 13 cm precaudal length.

Interest to Fisheries and Human Impact: There is no targeted fishery for this species, but it is likely taken as bycatch on occasion.

The conservation status is Least Concern since it appears to be one of the few chimaeroids with a wide geographic distribution and occurs at depths below where most fisheries occur.

Local Names: Bentnose rabbitfish, Bigspine spookfish, Longnose chimaera, Long-nosed chimaera, Longnosed chimaera (English); Peje Rata (Spanish); Smalnæset havmus (Denmark, Greenland); Langnefur (Iceland); Nevhavmús (Faroe Islands).

Remarks: This wide-ranging longnose chimaera is occasionally mistaken with H. haeckeli, another wide-ranging member of this genus.

Literature: Goode and Bean (1895); Bigelow and Schroeder (1953, 1954); Krefft in Hureau and Monod (1973c); Mauchline and Gordon (1983); Stehmann and Bürkel in Whitehead et al. (1984); Scott and Scott (1988); Compagno, Ebert, and Smale (1989); Compagno, Stehmann, and Ebert (1990); Compagno, Ebert, and Cowley (1991); McEachran in Collette and Klein-MacPhee (2002); Moore et al. (2003); Møller et al. (2004, 2010); Dagit (2006b); Gibson et al. (2008); James et al. (2009); Last and Stevens (2009); Dunn et al. (2010); Didier, Kemper, and Ebert (2012); D.A. Ebert (unpubl. data).

## Rhinochimaera Garman, 1901

Genus: Rhinochimaera Garman, 1901, by original designation, Proc. New Engl. Zool. Club, 2: 75-76.
Type species: Harriotta [sic] pacifica Mitsukuri, 1895, Kurikama, near Misaki, Sagami, by original designation.

## Number of Recognized North Atlantic Species: 1.

Synonyms: None.
FAO Names: En - Knife-nosed chimaeras; Fr - Chimères-couteau; Sp - Quimeras-navaja.
Field Marks: Longnose chimaera with elongated, fleshy snout, evenly tapering along its length to a fine blunt point, distal tip straight, without a series of small rounded knobs on adult males, caudal-fin lower lobe at least three times length of upper lobe, margin of upper caudal-fin lobe with row of tubercles, and no anal fin present.

Diagnostic Features: See Key to Genera and Field Marks above.
Local Names: None.
Remarks: Three species are recognized within this genus, of which one occurs within the present area. The paddlenose spookfish (Rhinochimaera africana) may eventually be found to occur in the North Atlantic since it has a rather wide, but spotty distribution and is known to occurs in the southeastern Atlantic.

## Rhinochimaera atlantica Holt and Byrne, 1909

Rhinochimaera atlantica Holt and Byrne, 1909, Ann. Mag. Nat. Hist., (8)3 v.15: 279, Holotype (unique): BMNH 1910.9.17.4, Type locality: Atlantic slope off southwest Ireland, $50^{\circ} 31^{\prime} \mathrm{N}, 11^{\circ} 31^{\prime} \mathrm{W}, 1225$ to 1410 m . The species was later illustrated and described in more detail by Holt and Byrne, 1910: 18, pls. 3, 4, figs. 4, 5.

Synonyms: Harriotta atlantica Meyer, 1951: 116-117, fig 1.
Other Combinations: None.
FAO Names: En - Straightnose rabbitfish; Fr - Chimère à nex mou; Sp - Narigón sierra.


Fig. 534 Rhinochimaera atlantica

Field Marks: A large bodied Rhinochimaera with a narrow, conical snout, subtriangular and fleshy at the base, tapering to a narrow distal tip, eyes moderate size, length of eye not less than $5 \%$ body length (range 5 to $10 \%$ body length) and caudal fin with a distal caudal filament. Colour a uniform pale to light brown or greyish-brown with darker fins, ventral side of snout and oronasal region white.

Diagnostic Features: Snout very long, straight, attenuated, subtriangular at base; snout base to mid-length fleshy, tapering to a narrow, bluntly pointed tip; distal tip of snout without knobs; snout length 50 to $87 \%$ body length (body length 50 to $66 \%$ in adults, 54 to $87 \%$ in juveniles). Oronasal region with prominent antero-ventral protuberance at snout base; mouth anterior to eye. Tooth plates thin, smooth, dark grey to blackish in colour with thin, blade-like cutting edges, not formed as crushing plates. Eyes moderate in size, 5 to $10 \%$ body length ( 5 to $8 \%$ in adults, 5 to $10 \%$ in juveniles). Preopercular and oral lateral line canals branch separately from the infraorbital canal below the eye. Pectoral fins ovoid and elongate, more narrow and long rather than triangular and broad shaped. Pelvic fins ovoid, sometimes squared along the distal edge, with anterior and posterior edges somewhat rounded. Adult males with short frontal tenaculum, flat, not deeply curved, and with a distal fleshy bulb with numerous small denticles. Pre-pelvic tenaculum spatulate with five strong denticles along the medial edge. Pelvic claspers simple, rod-like structures with a small, fleshy bulbous tip in which there are small pointed denticles; pelvic claspers just reach the distal edge of the pelvic fin. First dorsal fin triangular in shape, with concave posterior edge and a long fleshy base extending beyond the fin tip when depressed, but not connecting to second dorsal fin; fin preceded by fin spine that extends beyond first dorsal-fin height; fin spine connected to first dorsal fin along its posterior edge and when depressed together they form a deep groove; spine when depressed reaches one-half way to the origin of the second dorsal fin; spine keeled anteriorly with small serrations on distal one-third of the posterior edge;
large adult specimens posterior serrations may become reduced or worn away. Second dorsal fin elongate, separated from both first dorsal and dorsal caudal fins by a space; dorsal edge is gently rounded, sloping at anterior and posterior ends, reaching maximum height in the centre; height of second dorsal fin ranges 3 to $7 \%$ body length, and 7 to $16 \%$ second dorsal-fin base. Dorsal caudal fin very narrow, appears as thick fleshy ridge on dorsal surface of tail. In adults paired caudal tubercles are present along the distal edge of the dorsal caudal fin, most pronounced in males, but evident in adult females; tubercle counts range from 36 to 60 . Ventral caudal fin tallest anteriorly, tapering posteriorly, giving the caudal fin a somewhat heterocercal appearance externally. Tail elongate ending in a firm, whip-like caudal filament, sometimes broken, but if intact filament can range in length from $4 \%$ to $32 \%$ body length. Colour: uniform pale brown or greyish-brown to white, somewhat darker dorsally and lighter ventrally, leading edges of pectoral fins, ventral caudal, and second dorsal fin tend to be darker; mouth region white below oral folds with white colour extending onto the snout that is white ventrally with darker coloration dorsally. After preservation fins darker, often appearing dark brown or purplish.

Distribution: Eastern North Atlantic: southeast Greenland, Iceland to the Irish Atlantic slope off Ireland, Scotland, the Hebrides, and Bay of Biscay, and likely continuous to off the northwest African coast since it is known from off Mauritania, Senegal, and Gambia. It also occurs from off Namibia and South Africa. Western North Atlantic: Nova Scotia, Canada to Virginia, USA, also from the Gulf of Mexico and off Suriname and French Guiana.

Habitat: A little known, but somewhat common, at depth, longnose chimaera that occurs from about 400 to at least 1500 m . It appears to occur mostly on soft-bottom habitat.

Biology: Oviparous, but nothing else known of its reproductive biology or feeding habits. This species appears to aggregate in large numbers, often grouping by size, sex, and maturity status.

Size: Maximum length about 140 cm (precaudal length about 90 cm ). Adult


Fig. 535 Rhinochimaera atlantica
$\square$ Known distribution males at 107 cm total length ( 81.3 cm precaudal length, 47.3 cm body length), adolescent at $105.5 \mathrm{~cm}(80.3 \mathrm{~cm}, 47.7 \mathrm{~cm})$, maximum length at least 112.7 cm ( $82.3 \mathrm{~cm}, 46.6 \mathrm{~cm}$ ). Females adult at $127.4 \mathrm{~cm}(99.0 \mathrm{~cm}, 59.0 \mathrm{~cm})$, adolescent at $99.4 \mathrm{~cm}(75.0 \mathrm{~cm})$, maximum length at least 140 cm . Size at birth about 15 cm total length.

Interest to Fisheries and Human Impact: The straightnose rabbitfish is not landed commercially and does not appear to be of any significant fishery importance at this time. It is likely taken as bycatch in deepwater fisheries, but is most likely discarded at sea.

The conservation status of this poorly known longnose chimaera is Least Concern due to its widespread biogeography, deepwater habitat, and lack of directed commercial fisheries.

Local Names: Atlantic longnose chimaera, Spearnose chimaera, Straightnose rabbitfish, Broadnose chimaera, Knifenose chimaera (English); Chimère Nez Lance (French); Narigón sierra (Spanish); Spydnæset havmus (Denmark, Greenland).

Remarks: The differences between this species and Rhinochimaera pacifica is based exclusively on the number of caudal tubercules, a character that overlaps these two species. It will likely take molecular studies to resolve this issue. Another wide-ranging Rhinochimaera, $\boldsymbol{R}$. africana, is known from the southeastern Atlantic, but may eventually be found to occur in the North Atlantic. This latter species ( $\boldsymbol{R}$. africana) was previously misidentified as $\boldsymbol{R}$. atlantica or $\boldsymbol{R}$. pacifica.

Literature: Holt and Byrne (1909, 1910); Bigelow and Schroeder (1953, 1954); Krefft inHureau and Monod (1973c); Stehmann and Bürkel in Whitehead et al. (1984); Scott and Scott (1988); Compagno, Ebert, and Smale (1989); Compagno, Stehmann, and Ebert (1990); McEachran in Collette and Klein-MacPhee (2002); Didier (2002); Moore et al. (2003); Møller et al. (2004, 2010); Dagit and Compagno (2006); Gibson et al. (2008); Didier, Kemper, and Ebert (2012); D.A. Ebert (unpubl. data).

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## 6. INDEX OF SCIENTIFIC AND VERNACULAR NAMES

## Explanation of the System

Italics : Valid scientific names (double entry by genera and species)
Italics : Synonyms and misidentifications (double entry by genera and species)
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ROMAN : Names of classes, subclasses, cohorts, superorders and orders.
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This volume is a comprehensive, fully illustrated Catalogue of the Sharks, Batoid Fishes, and Chimaeras of the North Atlantic, encompassing FAO Fishing Areas 21 and 27. The present volume includes 11 orders, 32 families, 66 genera, and 148 species of cartilaginous fishes occurring in the North Atlantic. The Catalogue includes a section on standard measurements for a shark, batoid, and chimaera, with associated terms. It provides accounts for all orders, families, and genera and all keys to taxa are fully illustrated. Information under each species account includes: valid modern names and original citation of the species; synonyms; the English, French, and Spanish FAO names for the species; a lateral view for sharks and chimaeras, dorsal and often also ventral view for batoids, and often other useful illustrations; field marks; diagnostic features; distribution, including a GIS map; habitat; biology; size; interest to fisheries and human impact; local names when available; a remarks sections; and literature. The volume is fully indexed and also includes sections on terminology and measurements including an extensive glossary, a list of species by FAO Statistical Areas, and a dedicated bibliography.


[^0]:    Yano, K. 1995. Reproductive biology of the black dogfish, Centroscyllium fabricii, collected from waters off western Greenland. J. Mar. Biol. Assoc. UK, 75: 285-310.

