Food and Agriculture Organization of the United Nations

## DEEP-SEA CARTILAGINOUS FISHES OF THE SOUTHEASTERN ATLANTIC OCEAN



# DEEP-SEA CARTILAGINOUS FISHES OF THE SOUTHEASTERN ATLANTIC OCEAN 

by

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## PREPARATION OF THIS DOCUMENT

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Its production follows the recommendations made during a workshop on "Deep-sea Species Identification" held in Rome in 2009 organized in response to the need for a strategy for the development of appropriate deep-sea species identification tools for fishery purposes, in particular, to address the broadened requirements for reporting on not only target species, but also associated species following recent international developments with respect to fisheries management guidance and biodiversity conservation. The workshop recommended that a series of identification guides be developed for certain vulnerable groups of species affected by bottom gear, with an initial focus on three of the most impacted groups: cartilaginous fishes, corals and sponges. As a starting point, in consideration of the extensive information available on cartilaginous fishes from other FAO guides and publications, it was decided to develop identification guides for deep-sea members of this group at a regional level, with the Indian Ocean chosen as the first region and for which a two-volumes catalogue and an identification guide were developed.

The present publication is dedicated to the identification of deep-sea cartilaginous fishes occurring in the Southeastern Atlantic Ocean (FAO Fishing Area 47) providing accounts for all orders, families, and genera and for fifty of the seventyeight species known to occur in the area. Moreover, fully illustrated keys to all taxa are included.

It is aimed at facilitating the species specific identification of deep-sea shark fishes occurring in the Southeastern Atlantic Ocean by fishery observers, crew members, scientists, fishery officers and the interested public.

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#### Abstract

This volume is a comprehensive, fully illustrated Catalogue of the Sharks, Batoid Fishes, and Chimaeras of the Southeastern Atlantic Ocean, encompassing FAO Fishing Area 47. The present volume includes 10 orders, 23 families, 45 genera, and 78 species of cartilaginous fishes occurring in the Southeastern Atlantic. It provides accounts for all orders, families, and genera and all keys to taxa are fully illustrated. A species representative account of each genus is also provided and includes: valid modern names and original citation of the species; synonyms; the English, French, and Spanish FAO names for the species: a lateral view 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, an extensive glossary, and a dedicated bibliography.


## ACKNOWLEDGEMENTS

A volume of this magnitude and scope could not be accomplished without the generous help of others and I wish to thank all of those who have been extremely helpful and generous with their time in responding to my numerous questions, providing data and information from their own research (some of it unpublished), and providing much needed literature. The generic and species accounts were improved immensely from the contribution of colleagues and friends. I wish to apologize beforehand if I have forgotten anybody, which will inevitably happen with a work of this magnitude, but I do thank you all for your help and assistance.

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## 1. INTRODUCTION

The present catalogue covers the deep-seachondrichthyans of the Southeastern Atlantic Ocean, FAO Fishing Area 47. The catalogue 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 little known species that may be of research, educational, and ecological importance. The catalogue is intended to be a comprehensive review of the shark-like fishes of the deep-sea Southeastern Atlantic Ocean 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 at sea, and the general public.

Biogeography of Region. The Southeastern Atlantic region encompasses FAO Fishing Area 47, and is bounded by a line beginning on the west African continental coast at $6^{\circ} 04^{\prime} 36^{\prime \prime}$ S latitude and $12^{\circ} 19^{\prime} 48^{\prime \prime} \mathrm{E}$ longitude, and extending in a northwesterly direction to a point intersecting at $12^{\circ} 00^{\prime} \mathrm{E}$ with the parallel $6^{\circ} 00^{\prime} \mathrm{S}$ and to the west along a parallel to $20^{\circ} 00^{\prime} \mathrm{W}$, and then due south along this meridian to the $50^{\circ} 00^{\prime} S$ parallel and due east along this parallel to $30^{\circ} 00^{\prime} \mathrm{E}$, and then due north to the African continental coast and in a westerly and northerly direction to the original point of departure (Figure 1 - Map of the Southeastern Atlantic Ocean FAO Area 47). FAO Area 47 includes the Benguela Large Marine Ecosystem, defined by the Benguela Current that runs the length of this region off the African continental coast. A small portion of FAO Area 47 also includes the Agulhas Current Large Marine Ecosystem extending from about Cape Point at $18^{\circ} 42^{\prime}$ E longitude and extending eastwards to the boundary of Area 51 at $30^{\circ} 00^{\prime} E$ (Ebert, 2013). The Southeastern Atlantic region is mostly a cool temperate regime, influenced by the broad north flowing Benguela Current that extends northwards from Cape Point, South Africa to about $15^{\circ} \mathrm{S}$, or at about Mossâmedes, Angola (Briggs, 1995), where it meets the tropical Angolan Current and veers offshore.

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 (2013), Ebert, Fowler and Compagno (2013), Ebert and Stehmann (2013), Ebert and Compagno (In press), and Ebert (2014) 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. The cohort Batoidea recognizes four orders, Torpediniformes, Pristiformes, Rajiformes, and Myliobatiformes, although the higher classification is still unresolved for this group. Nelson (2006) provided a table reflecting different concepts and comparing his own classification of the previous 3rd edition (Nelson, 1994) with those of Compagno (1999a, b) with six orders and 21 families, McEachran and Aschliman (2004) with four orders and 14 families, and finally his own concept of the 4th edition (Nelson, 2006) with four orders and 17 families. More recently Aschliman, Claeson and McEachran (2012) recognized 13 batoid families, and considered the skates to be comprised of a single family with nearly 300 species, while Naylor et al. (2012a, b) found support for retaining the family Arhynchobatidae as separate from the family Rajidae. Therefore, given this uncertainty as to the higher classification of the batoids, particularly the skates, the classification of Nelson (2006) is followed with the exception of retaining the skate family Arhynchobatidae (Fowler, 1934), resurrected by Compagno (1999a, b, 2005), and generally followed in most current literature. The Holocephali (chimaeras) are composed of a single living order Chimaeriformes. 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 sharks 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 hypotheses break down largely between traditional morphologists (Compagno, 1973, 1977, 1999a, b, 2001, 2005; Shirai, 1992a, 1996; de Carvalho, 1996) and newer molecular evidence (Douady et al., 2003; Naylor et al., 2005, 2012a, b; 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):

[^0]Southeastern Atlantic Ocean Biodiversity. The Southeastern Atlantic has a relatively low-diverse chondrichthyan fauna with 10 orders, 23 families, 45 genera, and at least 78 species being represented (Table 1). However, these numbers are likely an under-estimate since there are several undescribed species and a few species complexes under investigation that should eventually resolve the systematics of those species. Also, the deep-sea off Angola is not well studied and it is likely that additional species may be found to occur in this region. The Southeastern Atlantic deep-sea shark fauna is represented by 6 orders, 17 families, 30 genera, and at least 50 species (Table 1). The most species-rich group of deep-sea sharks are the Squaliformes with at least 32 species, representing about $64 \%$ of the deep-sea shark species in this region. Most are in the families Etmopteridae ( $\mathrm{n}=9$ ) and the Centrophoridae and Somniosidae with 6 species in each family. The Carcharhiniformes are represented by 10 species, 8 of which belong to the family Scyliorhinidae. All of the other shark orders only have four or fewer species representatives. The deep-sea batoid fauna is represented with 3 orders, 4 families, 10 genera, and at least 20 species (Table 1). The most specious group of deep-sea batoids are the skates (Rajiformes) that have two families (Arhynchobatidae and Rajidae), 8 genera and 18 species represented. The deep-sea chimaera fauna has representatives of two families (Chimaeridae and Rhinochimaeridae), and includes five genera, and at least 8 species.

| SEA Ocean <br> (FAO Area 47) | Sharks | Batoids | Chimaeras | Tot. |
| :---: | :---: | :---: | :---: | :---: |
| Orders | 6 | 3 | 1 | 10 |
| Families | 17 | 4 | 2 | 23 |
| Genera | 30 | 10 | 5 | 45 |
| Species | 50 | 20 | 8 | 78 |

Table 1. - The families, genera, and species represented within the deep-sea Southeastern Atlantic Ocean (SEA).

### 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), with 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. A difference in the present catalogue is that not all species accounts are dealt with in the same comprehensive detail. A list of all deep-sea species known to occur in the Southeastern Atlantic Ocean is presented for each family, with a representative species of each genus presented in detail and indicated by the presence of a shark, skate or chimaera icon beside its scientific name. For some genera, especially those where subgroups (e.g. Apristurus, Etmopterus) are recognized, an example of each species subgroup is presented in detail. In total, 50 of 78 species are presented in detail here.

The species specific information on the biology, conservation status, distribution, habitat, fisheries, and systematics of Southeastern Atlantic Ocean chondrichthyans was compiled from primary literature sources including, but not limited to,

Compagno (2001), Compagno, Ebert and Smale (1989), Compagno, Ebert and Cowley (1991), Compagno and Ebert (2007), Ebert et al. (2013), Kyne and Simpfendorfer (2010), and Ebert and Compagno (In press). Electronic sources were also of invaluable help and included, but were not limited to, the California Academy of Sciences Catalogue of Fishes (http://www.calacademy.org/research/ichthyology/catalog/ fishcatsearch.html) and IUCN Shark Specialist Group (http:// www.iucnredlist.org). A comprehensive bibliography of the literature, including primary, grey, and electronic sources is provided at the end of this volume.

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 Southeastern Atlantic deep-sea; common order Synonyms mainly from the Southeastern Atlantic deep-sea 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 deep-sea Southeastern 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 deep-sea Southeastern Atlantic Ocean genera in the family; family Synonyms with names mostly associated with the Southeastern Atlantic Ocean 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 deep-sea Southeastern 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 Southeastern Atlantic Ocean deep-sea 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 deep-sea Southeastern 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 Southeastern Atlantic Ocean deep-sea 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 as well as commonly used combinations that place a valid species in different genera.

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, 1984a, b, 2001; Ebert and Compagno, In press, Ebert, In preparation), and regional FAO Catalogues on the Sharks, Rays, and Chimaeras of the North Atlantic (Ebert and Stehmann, 2013), Eastern Central Atlantic (Compagno, 1981; Stehmann, 1981), Namibia (Bianchi et al., 1999), Western Central Atlantic (Compagno, 2002; Didier, 2002; McEachran and de Carvalho, 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 Area 47, or within the scope of the present Catalogue and do 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 (Cetorhinus) all have the Diagnostic Features section present only in the highest taxon covered.

Distribution. Geographic distributions for nearly all species are given by listing the countries off the coasts of or oceanographic features, e.g. seamounts and troughs, where the species occurs. In compiling distributional data and preparing maps it was noted that the distributions of many wide-ranging deep-sea 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 chondrichthyan faunas are poorly known for much of the world, and a number of deepsea 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. A few species (e.g. Cirrhigaleus asper, Carcharhinus altimus), only known from a single record from the eastern edge of Area 47, are mentioned in the order or family accounts, but not discussed further. The sixgill stingray, Hexatrygon bickelli, is known only from a couple of records off Port Elizabeth, South Africa, but since the type specimen for the family, genus and species was collected from there, it is included in detailed account.

Habitat. Habitat covers information on physical conditions where various species 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 deep-sea species are biologically well known, and several are known only from a very few specimens that have ever been observed.

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 chondrichthyans
researchers 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. I prefer and advocate as a standard method a direct measurement, in which the shark 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.

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 deep-sea sharks is often sketchy and combined for a number of species. Thus, catch statistics are generally
unavailable except 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 and are presented when available. Other aspects of human interaction are presented if available or known, although the average person rarely encounters most of these deep-sea sharks. 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) is provided. 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 basking shark have dozens of names. Wherever possible common local names are presented, especially for important wide-ranging species. 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 Area 47.

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 47 (Southeastern Atlantic Ocean)

### 1.2 Technical Terms and Measurements

### 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 $\uparrow$
$<$ 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
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
FL = FORK LENGTH
PCL = PRECAUDAL-FIN LENGTH
PD2 = PRE-SECOND DORSAL-FIN LENGTH
PD1 = PRE-FIRST DORSAL-FIN LENGTH
HDL $=$ HEAD LENGTH
PG1 = PREBRANCHIAL LENGTH
PSP = PRESPIRACULAR LENGTH
POB = PREORBITAL LENGTH
PP1 = PREPECTORAL-FIN LENGTH


Fig. 17 Main longitudinal measures
PRN = PRENARIAL LENGTH
POR = PREORAL LENGTH
EYL = EYE LENGTH
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
P1B = PECTORAL-FIN 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 Measurements of pectoral fin, gill slits, eye and snout

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
CTL = TERMINAL CAUDAL-FIN LOBE
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
D21 = 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
P2I = 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
ANP $=$ ANAL-FIN POSTERIOR MARGIN


Fig. 19 Measurements of caudal fin


Fig. 20 Measurements of dorsal, pelvic and anal fins


Fig. 21 Other common measurements (lateral view)

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

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

DAO $=$ SECOND DORSAL-FIN ORIGIN ANAL-FIN ORIGIN

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MOL = MOUTH LENGTH
CLO = CLASPER OUTER LENGTH
MOW = MOUTH WIDTH
CLI = CLASPER INNER LENGTH
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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e) DORSO-LATERAL VIEW
f) DORSAL VIEW

$$
\begin{aligned}
& \text { INO }=\text { INTERORBITAL SPACE } \\
& \text { SPL }=\text { SPIRACLE LENGTH } \\
& \text { ESL }=\text { EYE SPIRACLE SPACE } \\
& \text { HDW }=\text { HEAD WIDTH } \\
& \text { TRW }=\text { TRUNK WIDTH } \\
& \text { ABW }=\text { ABDOMEN WIDTH } \\
& \text { TAW }=\text { TAIL WIDTH } \\
& \text { CPW }=\text { CAUDAL-FIN PEDUNCLE WIDTH }
\end{aligned}
$$

Fig. 22 Other common measurements (ventral and dorsal view)

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



Fig. 23 Upper side of a typical skate (family Rajidae)


Fig. 24 Base of tail in stingrays (family Dasyatidae)



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


Fig. 29 Lateral line canals of the head of a typical Chimaera


PICTORIAL KEY OF DEEP-SEA SHARK ORDERS OCCURRING IN THE SOUTHEASTERN ATLANTIC OCEAN (not a cladogram)

Fig. 30 Higher classification of Sharks (Orders)


Fig. 31 Higher classification of Batoids and Chimaeras (Orders)

### 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 (1984a, 1988, 1999b) and a short glossary in Compagno, Ebert and Smale (1989). The main glossary 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.

Acute: Pointed or sharp at tip.
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 sacs 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.

Alar thorns: Enlarged hooked shaped spines on the outer pectoral fins of adult male skates.

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

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.

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 filament: The long, thin, whip-like structure that extends behind the end of the caudal fin in chimaeras.

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 dactyl: 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.

Common name: The informal or regional vernacular name of an organism; these names may change from region to region.

Concave: Curving inwards as opposed to convex (curving outwards).

Confluent: Joined together, without a space.
Continental shelf: The portion of the seabed surrounding the continents and islands from the shore-line to approximately 200 m depth.

Continental slope: The portion of the seabed that slopes steeply from the edge of the outer continental shelf down to the ocean floor; below approximately 200 m depth.

Convex: Arching or curving outwards as opposed to concave (see above).

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.

Deciduous: Usually referring to denticles that are easily rubbed off, especially common in Chimaeras.

Demersal: Living on the bottom.
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 close-set 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.

Disc: The fused unit of the head, snout, and pectoral fins and body on batoids; also referred to as the Pectoral disc.

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.

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

Endemic: A species 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.

Eye spots: Large eye-like pigment spots on the dorsal surface of some batoids; they are usually located on the dorsal surface of the pectoral fins.

Filament or Filamentous: A thread-like structure usually associated with the tail.

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.

Malar: Rows of thorn patches found only on adult males (in some skate species) along anterior margin of disc in front of the eyes.

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.

Nuchal thorns: One or more thorns on the nape of skates, located just behind the spiracles; some juvenile skates may have an enlarged nuchal thorn to aid in escaping the egg case, but this thorn disappears soon after birth while in some species this thorn may remain throughout the skate's life.

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 sacs 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.

Orbital thorns: Thorns around the eyes of some skate species.

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: A pair 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 cross-biased 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 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.

Rostral thorns: Thorns on the rostrum of some skate species.

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.

Scapular thorns: Thorns on the shoulder girdle of some skate species.

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.

Sexual dimorphism: Differences in physical shape or form usually found in skates.

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.

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, $66^{\circ} 30^{\prime} \mathrm{N}$.

Tenaculum: A unique reproductive organ found on adult male chimaera. The frontal tenaculum is located on the forehead and is curved with hook-like denticles and a knob
at the end. The pelvic tenaculum is located just in front of the pelvic fins. All these structures are used during courtship and copulation in chimaeras.

## 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-sacs 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.

## 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 Deep-sea Southeastern Atlantic Ocean Families: 2.
Synonyms: Part 1 Squali, Abtheilung 3: Müller and Henle, 1839: 80. Ordo Plagiostomi, Subordo Squalini, Sectio Proktopterides, Tribus Mononotopterini: Bleeker, 1859: xii. Order Squali, suborder Squali: Gill, 1862: 394, 396. Order Squali, suborder Galei: Gill, 1872: 23. Order Plagiostomi diplospondyli, suborder (equivalent rank) Palaeonotidani: Hasse, 1879: 35, tab. 2. Order Selachophichthyoidi: Garman, 1884b: 116; Garman, 1884c: 484; Jordan, 1923: 97; Whitley, 1940: 68. Order Pternodonta: Gill, 1884: 524. Order Opistarthri: Garman, 1884c: 484; Gill, 1893: 129. Group Cladodonti Garman, 1885a: 30. Group Notidani Garman, 1885a: 30. Order Selachii, suborder Asterospondyli: Woodward, 1889: 157. Order Diplospondyli: Jordan and Evermann, 1896: 15, 16; Fowler, 1941: 4; Smith, 1949: 37, 38. Order Euselachii, suborder Pleurotremata, Division Notidanoidei: Regan, 1906a: 722. Order Selachii, Group 1, suborder Notidani Goodrich, 1909: 139. Order Pleurotremata, suborder Notidanoidei: Engelhardt, 1913: 97. Order Notidani, suborder Opistharthri: Jordan, 1923: 97. Order Plagiostomi, suborder Notidaniformes: Lozano y Rey, 1928: 280. Order Hexanchea, suborder Hexanchida, superfamily Hexanchoidea: White, 1936: 4; White, 1937: 36, tab. 1; Whitley, 1940: 68. Order Euselachii, suborder Notidaniformes: Bertin, 1939: 8. Order Hexanchiformes: Berg, 1940 (1947): 136; Berg and Svetovidov, 1955: 63; Arambourg and Bertin, 1958: 2025; Patterson, 1967: 670; Lindberg, 1971: 8, 256; Rass and Lindberg, 1971: 303; Applegate, 1974: 743; Nelson, 1976: 32; Chu and Meng, 1979: 114, tab. 2; Compagno, 1973: 26; Nelson, 1984: 49; Compagno, 1984a: 13; Pfeil, 1983: 24; Gubanov, Kondyurin and Myagkov, 1986: 3, 44; Cappetta, 1987: 26, 44; Eschmeyer, 1990: 435; Shirai, 1992: 122; Nelson, 1994: 53; de Carvalho, 1996: 55; Shirai, 1996: 33; Eschmeyer, 2012. Order Selachii, Suborder Notidanoidea: Romer, 1945: 576; Bigelow and Schroeder, 1948: 77. Order Selachii, suborder Chlamydoselachoidea: Bigelow and Schroeder, 1948: 77, 93. Order Hexanchoidei: Schultz and Stern, 1948: 224. Order Hexanchiformes, suborder Chlamydoselachoidei: Berg and Svetovidov, 1955: 63; Patterson, 1967: 670; Compagno, 1973: 26; Cappetta, 1987: 26, 44; de Carvalho, 1996: 55. Order Hexanchiformes, suborder Hexanchoidei: Berg and Svetovidov, 1955: 64; Patterson, 1967: 670; Compagno, 1973: 26; Cappetta, 1987: 26, 44; de Carvalho, 1996: 55. Order Lamnida, suborder Hexanchida: Matsubara, 1955: 1-789. Order Lamnida, suborder Chlamydoselachina: Matsubara, 1955: 1-789. Order Pleurotrema, suborder Notidanoidea: Norman, 1966: 6. Order Selachii, suborder Hexanchoidea: Romer, 1966: 350. Order Chlamydoselachida, suborder Chlamydoselachina: Fowler, 1967a: 91. Order Hexanchida, suborder Hexanchina: Fowler, 1967a: 83. Order Chlamydoselachida: Glikman, 1967: 213; Fowler, 1967a: 91. Order Hexanchida: Glikman, 1967: 214; Fowler, 1967a: 82. Order Hexanchida, suborder Hexanchoidei: Glikman, 1967: 214. Order Selachii: Blot, 1969: 702-776. Order Pleurotremata, suborder Hexanchiformes: Budker and Whitehead, 1971: 5, tab. 2. Order Chlamydoselachiformes: Fowler, 1947: 8; Rass and Lindberg, 1971: 303; Applegate, 1974: 743; Pfeil, 1983: 24; Shirai, 1992: 122; Shirai, 1996: 33. Order Hexanchiformes, suborder Chlamydoselachoidea: Chu and Meng, 1979: 114, tab. 2. Order Hexanchiformes, suborder Hexanchoidea: Chu and Meng, 1979: 114, tab. 2. Order Galeomorpha, suborder Hexanchoidea: Carroll, 1988: 599.

FAO Name: 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 in 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 enlarged 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.

Distribution: Wide-ranging in all seas, but are only found inshore in temperate seas and in deep water in the tropics.
Habitat: These sharks occur 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 m ; some deepwater species common down to 1100 m . These sharks do not penetrate into fresh water rivers and lakes but can be found in estuaries that fluctuate seasonally in salinity.

Biology: Reproductive 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 members of this group, Hexanchus griseus and Notorynchus cepedianus 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, such as False Bay, South Africa, where the larger species are known to seasonally congregate.

The conservation status of the group varies by region from Data Deficient to Near Threatened depending on the species.
Local Names: Hexanchoid or Hexanchiform sharks, One-dorsaled sharks; Koei en Frilletjieshaaie (South Africa).
Remarks: The interrelationships of frilled and cow sharks were reassessed by Ebert and Compagno (In press) and built upon 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, 2012a, b), tend to support the chlamydoselachids and hexanchids 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 chlamydoselachids and hexanchids 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 three deep-sea species occur in the Southeastern Atlantic Ocean. The relatively shallow occurring Notorynchus cepedianus, although very common along the coast of South Africa and Namibia, is not discussed further here.

## Key to Deep-sea Southeastern Atlantic Ocean Families:

1a. Body elongated and eel-like. Head snakelike, with short snout and terminal mouth (Fig. 32a). Teeth tricuspidate in both jaws (Fig. 32b) family Chlamydoselachidae


Fig. 32 Chlamydoselachidae
1b. Body moderately stout and not eel-like. Head not snakelike, with moderate snout and subterminal mouth (Fig. 33a). Teeth cuspidate in upper jaw and compressed and comb-like in lower jaw (Fig. 33b).
family Hexanchidae


b) UPPER AND LOWER TEETH

Fig. 33 Hexanchidae

### 2.1.1 Family CHLAMYDOSELACHIDAE

Family: Chlamydoselachidae Garman, 1884a, Bull. Essex Inst., 16: 52 (p. 8 in separate).
Type genus: Chlamydoselachus Garman, 1884a.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Genera: 1.

Synonyms: Family Chlamidoselachidae Cervigón, 1960: 40. Erroneous spelling of Chlamydoselachidae Garman, 1884a.
FAO Names: En - Frilled sharks; $\mathbf{F r}$ - Requins à collerette; $\mathbf{S p}$ - 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 an 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 benthic, epibenthic, and occasionally epipelagic, and are often 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 a half years. Nothing is known about the age and growth of these sharks. The diet consists mainly of cephalopods, teleosts, and elasmobranchs, especially members of the families Squalidae and Scyliorhinidae.

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

The conservation status of Chlamydoselachus anguineus is Near Threatened globally due to concerns over expansion of deep-sea fisheries, especially in the Western North Pacific, while C. africana has been assessed as Data Deficient. These sharks are in general 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); Frilletjieshaaie (South Africa).
Remarks: A single genus, Chlamydoselachus.
Literature: Garman (1884a, b, c, d); Ebert (1990); Ebert and Compagno (2009, In press); Ebert (2013); Ebert, Fowler and Compagno (2013) Ebert and Stehmann (2013).

## List of Deep-sea Species Occurring in the Area:

Chlamydoselachus africana Ebert and Compagno, 2009
Chlamydoselachus anguineus Garman, 1884

## Chlamydoselachus Garman, 1884

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

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 2.

Synonyms: Genus Chlamydoselache Günther, 1887: 2. Emendation of Chlamydoselachus Garman, 1884a, and hence taking the same type species, Chlamydoselachus anguineus Garman, 1884a. 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, 1884a (cited six times as such).

Field Marks: Eel-like sharks with 6 gill slits, terminal mouth with tricuspid 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 (USA), 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 African frilled shark (C. africana) into a distinctly different species.

Southeastern Atlantic Ocean records of frilled sharks (Chlamydoselachus spp.) are patchy, and as such specimens should be carefully examined to determine the specific species involved. The frilled shark (C. anguineus) is known from North Atlantic waters, but records of this species from the Southeastern Atlantic Ocean should be carefully examined to determine whether it is C. anguineus or C. africana, the latter known from southern Angola, Namibia, and South African waters. Since both species are very similar morphologically, tissue samples should also be taken when possible for molecular study.

## Key to Deep-sea Southeastern Atlantic Ocean Species:

1a. Total vertebral centra 147, monospondylous-diplospondylous transition at $18^{\text {th }}$ vertebral segment just behind the posterior end of the pectoral fins. Spiral intestinal valve counts 26 to 28 . Head length 17.3 to $17.9 \%$ of total length.

Chlamydoselachus africana

1b. Total vertebral centra 160 to 171 , monospondylous-diplospondylous transition between the $72^{\text {nd }}$ and $75^{\text {th }}$ vertebral segment and occurs about over the pelvic fins. Spiral intestinal valve counts 35 to 49 . Head length 13.1 to $16.2 \%$ of total length.

## Chlamydoselachus africana Ebert and Compagno, 2009

Chlamydoselachus africana Ebert and Compagno, 2009, Zootaxa, 2173: 1-18, figs. 1-4, 5 (distribution map), 6, 7, tabs. 1-6. Holotype: South African Museum, SAM 31028, 1170 mm TL , immature female, off the Cunene River, Namibia, $19^{\circ}$ 59 'S, $11^{\circ} 48^{\prime} \mathrm{E}, 409 \mathrm{~m}$ deep, trawled by RV Benguela.

Synonyms: Chlamydoselachus anguineus Smith 1951, 87; Smith 1965, 511, Fig. 3b; Smith, 1967a: 105, pl. 19-23; Trunov, 1968, 137, fig. 3; Bass, D'Aubrey and Kistnasamy, 1975c, 16, text fig. 9, pl. 6; Domanevskij, 1975: 1117; Timokhin, 1980, 125; Allue et al., 1984, 124; Compagno, 1984a, 14, ill.; Bass, 1986, 47, Fig. 3.1; Lloris, 1986, 87, figs. 17-18; Compagno, Ebert and Smale, 1989, 19, pl. 2; Ebert, 1990, 30, Fig. 3.1, Tab. 2.1; Compagno, Ebert and Cowley, 1991, 51, Fig. 3a (distribution map).

Other Combinations: None.

FAO Name: En - African frilled shark.


Fig. 34 Chlamydoselachus africana
Field Marks: Externally, this slender, eel-like shark, with a compressed body behind the pectoral fins, sixgill openings, a terminal mouth, tricuspid teeth in both jaws, and a single dorsal fin, is morphologically very similar looking to the common frilled shark, but is smaller in size and with a proportionally longer head, greater head height and width, and proportionally longer pre-pectoral and pre-dorsal fin lengths. Colour is a dark chocolate brown, but with a thin membranous mucous covering the shark that upon being rinsed off after death reveals a dark grey body colour beneath the membrane.

Diagnostic Features: Body long, slender, eel-like, compressed behind the pelvic fins. Pectoral-pelvic space moderately long with a noticeable difference between males ( 23.0 to $24.1 \%$ ) and females ( 24.6 to $27.7 \%$ ) of total length. Head broad, flattened, wider than high, slightly convex; head length 17.4 to $17.9 \%$ of total length. Preoral snout length 0.1 times mouth width. Snout tip broadly rounded. Nostrils lateral, width 5.9 times in internarial width, 2.2 times in eye length, and 0.2 times in third gill opening length. Eyes large, rounded, length approximately 10.1 times in head length. Spiracle present or absent. Distance from snout tip to sixth gill opening 1.5 times in pectoral-pelvic space. Height of gill openings descending in length; first gill opening extends across throat; width of third gill opening about 2.4 times in head length and 4.3 times eye length. Mouth broadly rounded, large, distensible, length is about 0.9 times in mouth width; the width is about 2.7 times in head length, and 1.0 times head width at mouth corners. 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 24 to 30 upper jaw, 23 to 27 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 broad, rounded and low on body; pectoral-fin length 8.8 to $9.6 \%$ of total length, 1.0 times into anterior margin length; pectoral fins much smaller than pelvic fins; pectoral-fin origin is posterior to sixth gill opening. Pelvic fins large and broadly rounded; anterior and posterior margins convex; inner margin sexually dimorphic being in males somewhat longer than in females. Anal fin very large, broadly rounded, its height is 2.0 times dorsal-fin height, base length 1.7 times 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; fin height 2.3 to 2.7 times into base and 2.0 to 4.2 times inner margin. Dorsal fin set far back, about 62.6 to $64.5 \%$ of total length from snout tip, and low, only 1.9 times anal-fin height; anterior margin is rounded and convex with posterior margin; base is short, 0.5 times dorsal-caudal space, height 3.1 times in base, and inner margin 0.9 times in height and 3.1 in base. Caudal fin elongated, subtriangular, and without a subterminal lobe; length of dorsal-fin margin 2.6 times in precaudal length. Vertebral counts: total vertebral count 147 , precaudal vertebral count 94 , monospondylous vertebral count 18 . Spiral valve turns 26 to 28 . Moderate-sized, to at least 117 cm total length. Colour: in life varies from a dark chocolate brown to greyish, with a thin membranous mucous covering the shark that upon being rinsed off after death reveals a dark grey colour beneath the membrane. Colour after preservation varies from light brown to grey.

Distribution: Known only from Southern Africa off southern Angola, Namibia, and the west coast of South Africa, but likely extending around South Africa to off Durban in the Southwestern Indian Ocean. Records of frilled sharks from off South Africa are scarce, but they have been caught off Cape Town (Rob Leslie, Department Agriculture, Forestry and Fisheries, Cape Town, South Africa, pers. comm.), the Transkei coast, Eastern Cape Province, and off the KwaZulu-Natal coast, South Africa (Ebert and Compagno, 2009).

Habitat: A benthic, epibenthic, and possibly pelagic species on upper continental slopes at depths between 300 and 1400 m . One record of note is of an angler who supposedly caught a frilled shark off the Port Alfred Pier, in the Eastern Cape Province of South Africa (Smith, 1951). The specimen, unfortunately, was not retained by the angler and discarded before its identification could be confirmed. Margaret M. Smith (former Director, J.L.B. Smith Institute of Ichthyology, now the South African Institute for Aquatic Biodiversity) who knew the angler personally, considered him very reliable in fish identification (M.M. Smith pers. comm. to D.A. Ebert, December 1986). Since the continental shelf in that area is quite broad it would seem unlikely that this deepwater species would venture so far from its normal habitat, but perhaps this individual fish was ill or may have been disabled. Scuba divers in Japanese waters have videotaped what appears to have been a sick or dying frilled shark in relatively shallow water.

Hydrographic and substratum data are virtually unknown for the southern frilled shark, but data collected on one specimen from off southern Namibia indicated it was a low oxygen, high nutrient zone, with a soft bottom substratum (Ebert and Compagno, 2009). This appears to be consistent with other nominal records from off Japan and North Carolina, USA, where video footage has shown these sharks to be over soft bottom substrates.

Biology: Yolk-sac viviparous, with three young from a single litter being the only information available for


Fig. 35 Chlamydoselachus africana
$\square$ Known distribution litter size. Nothing else is known about the litter size, gestation time, or reproductive cycle of this species. Kukuev and Pavlov (2008) suggested that seamounts along the Mid-Atlantic Ridge may be areas where mating activity occurs due to possible concentrations of frilled sharks in this region, but whether these captures are of Chlamydoselachus africana or C. anguineus remains uncertain (see comments below).

Examination of southern frilled sharks, prior to preservation, of the jaws and buccal cavity reveals that they are highly distensible suggesting that these sharks are capable of ingesting quite large prey items. The inwardly projecting, needle sharp teeth further indicate that these are highly specialized predators. In addition, the abdomen is elongate and the stomach distensible, further indicating that these sharks are capable of ingesting fairly large prey. Given these morphological characteristics, e.g. elongated abdomen, anguiform tooth arrangement, terminal mouth, and highly distensible jaws, these sharks appear to have a rather specialized body arrangement reminiscent of gulper eels (Saccopharyngidae) or vivperfish (Chauliodontidae). Furthermore, these sharks are capable of swallowing relatively large prey items ranging from one-third to one-half their own body length in much the same way snakes are able to engulf larger prey items. Forensic examination of southern frilled shark prey items revealed them to consume primarily scyliorhinid (Apristurus and Galeus spp.) and squaloid sharks, some measuring $40 \%$ or more of the shark's total body length. Examination of frilled shark diet from the North Atlantic reveals them to have consumed mostly smaller sharks, mainly squaloids and scyliorhinids (Ebert, 1990; D.A. Ebert, pers. obs.).

Kukuev and Pavlov (2008) noted the catch of 34 frilled sharks in a single bottom trawl tow on the Mid-Atlantic Ridge from north of the Azores, and compared these to other frilled sharks captured from different regions from around the Atlantic Ocean. They suggested that the ratios of the dorsal and anal-fin bases were about equal in length for those specimens from the South Atlantic, including Southern Africa, while those from the North Atlantic had a shorter dorsal-fin base. Ebert (1990) commented that North Atlantic frilled sharks appear to differ slightly morphologically from Southern Atlantic frilled sharks, while Ebert and Compagno (2009) stated that Chlamydoselachus species from different regions revealed a high degree of proportional differences unique to each region.

Size: Maximum known total length 117 cm for an immature female; males mature at approximately 91.5 cm TL , with a maximum length of 99 cm . Size at birth unknown, but three near-term embryos from a single litter ranged in size from 40 to 45 cm total length.

Interest to Fisheries and Human Impact: Of no importance in the Southeastern Atlantic Ocean fisheries as it is occasionally taken as bycatch in bottom trawl and longline fisheries. There are no reported landings of this species.

The conservation status of this species is Data Deficient due to a lack of specimens and information on its general biology and population status.

Local Names: Frilletjieshaai (Afrikaans).

Literature: Smith (1951, 1965, 1967a); Trunov (1968); Bass, D'Aubrey and Kistnasamy (1975c); Domanevskij (1975); Bass in Smith and Heemstra (1986); Lloris (1986); Compagno, Ebert, and Smale (1989); Ebert (1990); Compagno, Ebert and Cowley (1991); Kukuev and Pavlov (2008); Ebert and Compagno (2009, In press); Barnett et al. (2012); Ebert (2013); Ebert, Fowler and Compagno (2013); D.A. Ebert and L.J.V. Compagno (unpubl. data).

### 2.1.2 Family HEXANCHIDAE

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

Type genus: Hexanchus Rafinesque, 1810.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Genera: 2.

Synonyms: Subfamily Notidanini Bonaparte, 1838 (family Squalidae): 130. Type subgenus: Notidanus Cuvier, 1816, a junior synonym of Hexanchus Rafinesque, 1810. Family Notidanidae Owen, 1846: 51. Type subgenus: Notidanus Cuvier, 1816, a junior synonym of Hexanchus Rafinesque, 1810. Family Notidanoidae Gill, 1862: 404. Type subgenus: Notidanus Cuvier, 1816, a junior synonym of Hexanchus Rafinesque, 1810. Family Hexanchidae Gill, 1884: 618. Also subfamily Hexanchinae (family Hexanchidae) Fowler, 1947: 8. Type genus: Hexanchus Rafinesque, 1810. Family Heptranchidae Garman, 1913: 2. Type genus: Heptranchias Rafinesque, 1810. Family Hexeptranchidae Garman, 1913: 2, 14. Inadmissible since based on a combination of two type genera, Hexanchus Rafinesque, 1810 and Heptranchias Rafinesque, 1810. Family Heptranchidae Barnard, 1925: 20. Type genus: Heptranchias Rafinesque, 1810. Family Heptranchiidae McCulloch, 1929: 3. Subfamily Heptranchiinae (family Hexanchidae) Fowler, 1947: 8. Type genus: Heptranchias Rafinesque, 1810. Family Notorynchidae Shirai, 1992: 122. Type genus: Notorynchus Ayres, 1855.

FAO Names: En - Cow sharks; Fr - Requins grises; 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 rounded. 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 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 cow shark 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: Reproduction is yolk-sac viviparity with some species having relatively large litters of 13 to at least 108. The reproductive cycle, although poorly known, is annual or biannual for those species where some information is available. These are sluggish to active, strong swimming sharks usually occurring near the bottom. They 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.

Cow sharks may snap when captured and can inflict lacerations if carelessly handled; the two larger species (Hexanchus griseus and Notorynchus cepedianus) have been confirmed as biting divers in the sea. Diving with N. cepedianus and H. griseus in the sea has become a popular ecotourism attraction in some areas, especially in False Bay, Southern Africa. Although the paucity of confirmed attacks by cow sharks biting people suggests that they are often docile and inquisitive in their reactions to humans, large cow sharks should be treated with respect as with other big macropredatory sharks.

The conservation status of this family is poorly known. The smaller deep-sea 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 and Sevengill sharks, Sixgill and Sevengill cow sharks, Combtooth sharks (English); Koeihaaie (South Africa).

Remarks: Three living genera are currently recognized, Heptranchias, Hexanchus, and Notorynchus, of which two (Heptranchias and Hexanchus) occur in the deep-sea. The monotypic genus Notorynchus is mostly a coastal species, often occurring in bays and estuaries, and along the open coast usually at less than 200 m depth. This species will not be discussed here further.

Literature: Garman (1913); Daniel (1928); Fowler (1941, 1967a); Bigelow and Schroeder (1948); Springer and Waller (1969); Garrick and Paul (1971); Bass, D'Aubrey and Kistnasamy (1975c); Compagno (1984a); Ebert (1990); Shirai (1992a,b, 1996); de Carvalho (1996); Barnett et al. (2012); Ebert (2013); Ebert and Stehmann (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press).

## List of Deep-sea Species Occurring in the Area:

Hor Heptranchias perlo (Bonnaterre, 1788)
Hexanchus griseus (Bonnaterre, 1788)

Key to Deep-sea Southeastern Atlantic Ocean Genera:
1a. Six pairs of gill openings (Fig. 36)
Hexanchus

1b. Seven pairs of gill openings (Fig. 37) . . . . .
Heptranchias


Fig. 36 Hexanchus


Fig. 37 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 perlo Bonnaterre, 1788.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 1.

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, 1885b (in part): 537, 538; Garman, 1888: 58, 67, 68, 72, 82, pl. 14. Possible emendation of Heptranchias Rafinesque, 1810, and Heptanchus Müller and Henle, 1837a. No type species indicated.

Diagnostic Features: Head acutely pointed in dorsoventral view, compressed and rounded or vertically oval in section at eyes level. Eyes large. Seven paired gill openings. Mouth very narrow and angular-parabolic. Five rows of lower combshaped 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 vertebral counts 28 to 38 , caudal vertebral counts 60 to 67 . Intestinal valve count ranges from 18 to 22 . Maximum total length 139 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 shark.
Remarks: Following Garrick and Paul (1971), Bass, D'Aubrey and Kistnasamy (1975c), Ebert (1990, 2013), Ebert and Stehmann (2013), and Ebert, Fowler and Compagno (2013) 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 in 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, 1975c; 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 (2013). Heptrancus angio Costa, 1857: 5, pl. 13, 14, fig. 3. Existence of types uncertain. Type locality, Mediterranean Sea. Notidanus (Heptanchus) cinereus, var. pristiurus (var. aetatis) Bellotti, 1878: 60. Syntypes: Two, whereabouts unknown according to Eschmeyer (2013). Type locality, Mediterranean Sea. Heptranchias deani Jordan and Starks, 1901: 384. Holotype, Stanford University, Division of Systematic Biology, SU-12620, 954 mm TL adult (?) female, Misaki, Japan. Heptranchias dakini Whitley, 1931: 310. New name for Heptranchias perlo of McCulloch, 1911: 2, pl. 1, fig.1. Holotype as designated by Whitley is the female specimen figured by McCulloch, 1911, approximately 69 cm TL , one of seven specimens from off Cape Everard, Southeastern Australia, in 110-128 m depth. This is possibly Australian Museum, Sydney, AMS I. 10825 according to Paxton et al. (1989: 26) and Eschmeyer (2013), approximately 97 km South of Cape Everard, Victoria. Two other specimens (AMS I.10794-95) in the series are considered paratypes by Eschmeyer (2013).

Other Combinations: Heptanchus perlo (Bonnaterre, 1788), Heptanchus or Heptranchias cinereus (Gmelin, 1789).
FAO Names: En - Sharpnose sevengill shark; $\mathbf{F r}$ - Requin perlon; Sp - Cañabota bocadulce.


Fig. 38 Heptranchias perlo

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: Angola, north-central Namibia, and off South Africa (Western Cape, off Cape Agulhas), but not recorded from south-central Namibia or the west coast of South Africa. In the region also recorded off the Republic of Congo and likely Gabon. Elsewhere wide-ranging but somewhat patchily distributed the sharpnose sevengill shark is found in most tropical and warm temperate seas except for the Eastern Central and North Pacific Ocean.

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. Nothing known about their biology in the Southeastern Atlantic, but in the Mediterranean Sea and off Japan these sharks seem to be reproductively active throughout the entire year. Very little else is known about its reproductive biology.

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 lanternfishes (Myctophidae), lightfishes (Phosichthyidae), cods (Gadidae), lings (Phycidae), hake (Merluccidae), grenadiers (Macrouridae), roughies (Trachichthyidae), hairtails (Trichiuridae), jack mackerel (Trachurus, Carangidae), scorpionfish (Scorpaenidae), flatfish (Citharidae), 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). 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 139 cm ; reports of it reaching a total length of 214 cm or over 300 cm 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 the Southeastern Atlantic Ocean, but may be caught in small numbers off Northern Namibia and Angola as a bycatch of deepwater fisheries utilizing bottom trawls or bottom longlines. Used for human consumption, said to be good eating, and presumably for fishmeal. There is no data available on current and past catches, although species-specific catch data is desirable.

Although this shark is very active and will snap vigorously when captured there are no records of it having attacked divers. Its deepwater habitat likely precludes it from coming into contact with divers. It has been maintained occasionally in captivity at public aquariums in Japan.

Conservation status is considered Near Threatened due to suspected declines that may have occurred in places such as southern Mozambique, Taiwan, and portions of the Mediterranean Sea where deepwater demersal trawl fisheries for shrimp and bony fishes have been operational over the past few decades. There is no information available for the Southeastern Atlantic population of this species.

Local Names: Sharpnose sevengilled cow shark, Sharpnose sevengill shark, Skerpneus-sewekiefhaai (South Africa).

Literature: Pissarro and Sanches (1973); Bass, D'Aubrey and Kistnasamy (1975c); Tanaka and Mizue (1977a, b); Penrith (1978); Capapé (1980); Boeseman in Whitehead et al. (1984); Compagno (1984a); Lloris (1986); Compagno, Ebert, and Smale (1989); Ebert (1990); Compagno, Ebert and Cowley (1991); Frentzel-Beyme and Köster (2002); Paul and Fowler (2003); Braccini (2008); Barnett et al. (2012); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013); 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 Deep-sea Southeastern Atlantic Ocean Species: 1.

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, 1816 (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, 1816 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, 1816). Genus Hexancus Agassiz, 1846: 181; Agassiz, 1848: 522 (emended spelling of Hexanchus Rafinesque, 1810).

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 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 irregular brown spots; no black tips on fins.

Local Names: Sixgill sharks.
Remarks: Following Springer and Waller (1969), Bass, D'Aubrey and Kistnasamy (1975c), Compagno (1984a), Ebert (1990, 2013), Barnett et al. (2012), Ebert and Stehmann (2013), Ebert, Fowler and Compagno (2013), and Ebert and Compagno (In press), two living species are presently recognized here for this genus, Hexanchus griseus (Bonnaterre, 1788) and H. nakamurai Teng, 1962 (senior synonym of H. vitulus Springer and Waller, 1969). However, a recent molecular study (Naylor et al., 2012a) suggested that two species of the latter species might indeed exist; an Atlantic form (?H. vitulus) and an Indian Ocean form (?H. nakamurai). The issue is currently under investigation (Ebert, White, and Ho, 2013) by the present author (D.A. Ebert, unpubl. data). The smaller sixigill shark (H. nakamurai) is not known to occur in the Southeastern Atlantic region and will not be discussed here further. The larger sixgill shark species (H. griseus) appears to be a single wide-ranging species (Ebert, 2013; Ebert, Fowler and Compagno, 2013).

## 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: None.
Other Combinations: Notidanus griseus (Bonnaterre, 1788).

FAO Names: En - Bluntnose sixgill shark; Fr - Requin griset; Sp - Cañabota gris.


Fig. 40 Hexanchus griseus
Field Marks: A heavy-bodied, broad-headed sixgill shark with a ventral mouth with 6 rows of lower bladelike, combshaped teeth on each side, one dorsal fin, a 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 and 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 short and 4.3 to $5.4 \%$ of total length. 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-fin lobe poorly developed at all stages, postventral margin weakly concave to straight and not subdivided. Vertebral counts: total vertebral counts 118 to 148, monospondylous precaudal vertebral counts 41 to 52 , diplospondylous vertebral counts 18 to 30, precaudal vertebral counts 67 to 77, and caudal vertebral counts 50 to 77 . Intestinal valve counts 35 to 39 . A giant shark, with a maximum length of at least 482 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: Wide-ranging, one of the most common large deep-sea shark species, it occurs in boreal, temperate and tropical seas, possibly absent in the Arctic and Antarctic oceans. In the Southeastern Atlantic Ocean it occurs off the Republic of Congo, Angola, Namibia, and South Africa, also common around offshore seamounts and ridges extending to and including the Mid-Atlantic Ridge.

Habitat: This is a mostly deepwater benthic 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. It occurs at the surface in the tropics and close inshore near beaches, at the heads of submarine canyons, and in bays in cold temperate


Fig. 41 Hexanchus griseus
waters, but extending down to at least 2500 m on the upper continental slope. It may 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 deepwater 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 continental slope off southern Namibia, between 300 and 400 m , may be one such pupping area as neonate bluntnose sixgill sharks appear seasonally in this area and are taken as bycatch along with large adult females measuring in excess of 4 m total length (Ebert, 2002). Furthermore, Ebert (1990, 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, King and Saunders (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), marlins (Istiophoridae), dolphinfishes (Coryphaenidae), flounders (Pleuronectidae), gurnards (Triglidae) and anglers (Lophiidae); marine mammals including unspecified seals (probably phocids), South African fur seals (Arctocephalus pusillus pusillus, Otariidae), and dolphins (Delphinidae); carrion; gastropods, squids (Ommastrephidae and Loliginidae), crabs, and shrimps.

The diet of bluntnose sixgill sharks changes with growth as those below 120 cm feed primarily on cephalopods and secondarily on bony fishes, with very little chondrichthyan prey evident, while those 120 to 200 cm long feed primarily on cephalopods, bony fishes and chondrichthyans with small marine mammals comprising a small component. Large sixgills, those above 200 cm , feed primarily on marine mammals (South African 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 100 cm 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 behaviour.

Size: Maximum total length 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: 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.

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 Southeastern Atlantic.

Local Names: Sixgill shark, Six-gilled shark, Cow shark, Mud shark (English); Seskiefhaai (South Africa).
Remarks: The bluntnose sixgill shark is one of the most common and wide-ranging shark species worldwide, ranking alongside the picked or spiny 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.

Nominal regional names all appear to be referable to Hexanchus griseus based on the study by Ebert (1990) who examined available type material and collected morphological and meristic data from most geographic regions where this shark is known to occur.

Literature: Bigelow and Schroeder (1948); Smith (1949); Springer and Waller (1969); Bass, D'Aubrey and Kistnasamy (1975c); Smith (1975); Penrith (1978); Boeseman in Whitehead et al. (1984); Compagno (1984a); Ebert (1984, 1986a, b, 1990, 1994, 2002, 2003, 2013); Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); McFarlane, King and Saunders (2002); Cook and Compagno (2005); Barnett et al. (2012); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013); 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 Deep-sea Southeastern Atlantic Ocean Families: 7.

Synonyms: Part 1 Squali, Abtheilung [Division] 4: Müller and Henle, 1839, Syst. Besch. Plagiost. (2): 83. Ordo Plagiostomi, subordo Squalini, Sectio Aproctopterides: Bleeker, 1859: xii. Order Squali, suborder Galei: Gill, 1872: 23, 24. Order Plagiostomi Diplospondyli, suborder Plagiostomi Cyclospondyli, group 1. Laemargi: Hasse, 1879: 41. Order Plagiostomi Diplospondyli, suborder Plagiostomi Cyclospondyli, group 2. Spinacidae: Hasse, 1879. Order Plagiostomi Diplospondyli, suborder Plagiostomi Cyclospondyli, group 3. Echinorhini: Hasse, 1879: 41. Order Selachii, suborder Tectospondyli: Woodward, 1889: 30. Order Tectospondyli: Gill, 1893: 129. Order Cyclospondyli, suborder Cyclospondyli: Jordan and Evermann, 1896: 52, 53. Order Euselachii, suborder Pleurotremata, division Squaloidei: Regan, 1906a: 723. Order Selachii, group 2, division B, subdivision 2, suborder Squaliformes: Goodrich, 1909: 151. Order Plagiostoma, suborder Antacea, "group" Squaloidei: Garman, 1913: 11, 13. Order Pleurotremata, suborder Squaloidei: Engelhardt, 1913: 100. Order Tectospondyli, suborder Squaloidei: Jordan, 1923: 101. Order Plagiostomi, suborder Squaliformes or Esqualiformes: Lozano y Rey, 1928: 281. Order Squalea, suborder Squalida, superfamily Squaloidea: White, 1936: 5; White, 1937: 37, tab. 1. Order Euselachii, suborder Squaliformes: Bertin, 1939: 10. Order Squaliformes: Berg, 1940, Trudy Zool. Inst. Akad. Nauk SSSR, 5(2): 138 (for squaloids, pristiophoroids, and squatinoids); Berg and Svetovidov, 1955, Trudy Zool. Inst. Akad. Nauk SSSR, 20 : 68 (for squaloids and squatinoids); Arambourg and Bertin, 1958: 2041; Rass and Lindberg, 1971: 304; Lindberg, 1971: 259; Compagno, 1973: 26; Applegate, 1974: 743; Nelson, 1976: 38; Chu and Meng, 1979: 114, tab. 2; Pfeil, 1983: 24; Compagno, 1984a: 24; Nelson, 1984: 56; Gubanov, Kondyurin and Myagkov, 1986: 3, 168; Cappetta, 1987: 26, 50; Eschmeyer, 1990: 437; Shirai, 1992: 122; Nelson, 1994: 54; de Carvalho, 1996: 55; Shirai, 1996: 33; Eschmeyer, 1998. Order Squaliformes, Suborder Squaloidei: Berg, 1940: 138; Berg and Svetovidov, 1955: 68; Arambourg and Bertin, 1958: 2042; Lindberg, 1971: 259; Nelson, 1976: 38; Nelson, 1984: 56; de Carvalho, 1996. Order Tectospondyli, suborder Squaloidei, superfamily Squaloidea: Whitley, 1940: 69. Order Cyclospondyli Fowler, 1941: 4, 222; Smith, 1949: 37, 55. Order Selachii, suborder Squaloidea: Romer, 1945: 577; Bigelow and Schroeder, 1948: 77, 449; Romer, 1966: 350; Order Squaloidea, suborder Squaloidea: Schultz and Stern, 1948: 225. Order Lamnida, suborder Squalina: Matsubara, 1955: 1-789. Order Pleurotremata, suborder Squaloidea: Norman, 1966: 24. Order Squatiniformes, suborder Squaloidei: Glikman, 1967: 215. Order Squatiniformes, suborder Echinorhinoidei: Glikman, 1967: 215. Order Lamniformes, suborder Squaloidei: Patterson, 1967: 670. Order Squalida, suborder Squalina: Fowler, 1968: 203, 204. Order Squalida, suborder Squalina, superfamily Squalicae: Fowler, 1968: 203, 204. Order Euselachii, suborder Squaloidei: Blot, 1969: 702-776. Order Squalida, suborder Squalina, superfamily Echinorhinicae: Fowler, 1969a: 73. Order Pleurotremata, suborder Squaliformes: Budker and Whitehead, 1971: 6, tab. 2. Order Squaliformes, suborder Squaloidea: Chu and Meng, 1979: 114, tab. 2. Order Squaliformes, suborder Dalatioidea: Chu and Meng, 1979: 114, tab. 2. Order Squaliformes, suborder Echinorhinoidea: Chu and Meng, 1979: 114, tab. 2. Order Echinorhiniformes: Pfeil, 1983: 24; Shirai, 1992: 122; de Carvalho, 1996: 55; Shirai, 1996: 33. Order Dalatiformes: Shirai, 1992: 122; Shirai, 1996: 33. Order Centrophoriformes: Shirai, 1992: 122; Shirai, 1996: 33. Order Squalomorpha, suborder Squaloidea: Carroll, 1988: 599. Order Squaliformes, suborder Dalatioidei: de Carvalho, 1996: 55.

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 total 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.

Distribution: Circumglobal in tropical, temperate, cold boreal, polar and subantarctic marine waters. Most species occur in temperate and tropical seas and are most diverse in the Atlantic and Indo-West Pacific, and the least diverse in the Eastern Pacific. Some of the small to moderate-sized oceanic species, and certain slope or epibenthic species, are circumglobal or wide-ranging. Many smaller benthic species have more limited ranges, with centres of endemicity in the North Atlantic and Western Pacific.

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 the ice pack 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 sharks 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 saw-like 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 squaloids are small (less than 100 cm long), have relatively small fins, and seem to have very limited importance for the oriental soup-fin trade.

The conservation status for the majority of squaloids 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 fisheries.

Local Names: Dogfish sharks, Hondhaaie (South Africa).
Remarks: The arrangement of the order as restricted here follows Ebert, Fowler and Compagno (2013) in recognizing seven families in the order. All seven families are represented in the Southeastern Atlantic.

## Key to Deep-sea Southeastern Atlantic Ocean Families:

1a. First dorsal fin originating posterior to pelvicfin origins (Fig. 42). family Echinorhinidae

1b. First dorsal fin originating anterior to pelvicfin origins (Fig. 43). 2


Fig. 42 Echinorhinidae


Fig. 43 Oxynotidae

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. 44)

## family Squalidae

3b. Dorsal-fin spines, if present, with lateral grooves. Teeth dissimilar in upper and lower jaws. Upper precaudal pit absent from caudalfin base (Fig. 45); strong lateral caudal keels generally absent. Subterminal notch present on caudal fin

4a. Underside of body, flanks, and tail usually with more or less conspicuous black markings with light organs (photophores)(Fig. 45)
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. 46)

5b. Upper teeth relatively narrow and not bladelike, lowers high and wide (Fig. 47) . . . . . . . . . . 6

6a. Head moderately broad and somewhat flattened or conical. Snout flat and narrowly rounded to elongate-rounded in dorsoventral view. Both dorsal fins either with or without finspines (Fig. 48).
family Somniosidae

6b. Head narrow and rounded-conical; snout conical and narrowly rounded to elongaterounded in dorsoventral view. Most genera lack dorsal-fin spines, except for a small spine present on the first dorsal fin of Squaliolus (Fig. 49)
family Dalatiidae

### 2.2.1 Family ECHINORHINIDAE

Family: Echinorhinoidae Gill, 1862, Ann. Lyceum 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 Deep-sea Southeastern Atlantic Ocean Genera: 1.

Synonyms: None.
FAO Names: En - Bramble sharks; Fr - Squales boucles; Sp - Tiburones espinosos.
Field Marks: Short-nosed and flat-headed with a cylindrical, heavy-body. Short-tailed with no anal fin. Two small, spineless, posterior dorsal fins, the first behind the pelvic-fin origins, and covered with coarse spiky denticles or enlarged tack-like 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 a 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. Teeth of both jaws compressed, low-crowned, broad, bladelike, and forming a saw-like cutting edge, not arranged in a quincunx pattern but forming a single flat non-imbricated 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. Total tooth row counts 18 to 28 upper jaw, 18 to 27 lower jaw. 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-fin base. Pelvic-caudal space very short and less than half length of pelvic-fin bases. Caudal peduncle compressed, very short, and without lateral keels and precaudal pits. Body without photophores. Denticles large to enormous, sessile and not pedicellate. Denticle crowns flattened and leafshaped, but with a median cusp. Pectoral fins low, broadly rounded-angular and not falcate or leaf-shaped, anterior margins moderately large and about equal to or somewhat smaller than the prespiracular length, rear tips rounded and not elongated. 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. Vertebral counts: total vertebral counts 86 to 102, monospondylous vertebral counts 50 to 59 , precaudal vertebral counts 58 to 62 . Intestinal valve with 8 to 16 turns. Adults from 150 cm to over 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 deepwater species with a patchy 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 1100 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 sketchily 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 ( 326 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 unutilized bycatch of other fisheries, including those for other sharks, although targeted fisheries for bramble sharks have occurred off of Southwestern India and Namibia. They are taken by longline gear, deepset gillnets, and bottom trawls. No world or local fisheries records are available for these sharks.

The conservation status is poorly known, but depending on the species is Data Deficient or Near Threatened.
Local Names: Bramble sharks, Braamhaaie (South Africa).
Remarks: This family has a single living genus Echinorhinus with two valid species, although recent molecular evidence suggests that a third species may occur in the Northern Indian Ocean. 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, 1992, 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. Recent molecular studies have shown the family Echinorhinidae to be a sister taxon to a clade consisting of the Pristiophoriformes and Squatiniformes (Naylor et al., 2012a, b).

Literature: Garman (1913); Bigelow and Schroeder (1948, 1957); Garrick (1960a); Cadenat and Blache (1981); Compagno (1984a); Shirai (1992, 1996); Ebert (2003); Naylor et al. (2012a, b); Ebert (2013); Ebert and Stehmann (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press).

## List of Deep-sea Species Occurring in the Area:

## Echinorhinus brucus (Bonnaterre, 1788)

## 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 Deep-sea Southeastern Atlantic Ocean 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, 1837a. Subgenus Rubusqualus Whitley, 1931: 311 (genus Echinorhinus Blainville, 1816). Type species: Echinorhinus (Rubusqualus) mccoyi Whitley, 1931, by original designation. Genus Echynorhynus Nobre, 1935: 410. Apparent error for Echinorhinus Blainville, 1816.

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 (1973, In J. C. Hureau and T. Monod, eds., CLOFNAM. Check-list. fish. NE Atlantic Mediterranean, 1: 45) and Eschmeyer (2013). 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, 1825: 66-68, pl. XVI (fig. 1-2); Müller and Henle, 1841: 96; Duméril, 1865: 459-461, pl. XII (fig, 16-20); Bocage and Capello, 1866: 35; Günther, 1870: 428-429; Canestrini, 1872: 42; Döderlein, 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, 1908a: 42; Roule, 1912: 18, 25; Lozano y 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, 1816: 131; Risso, 1826: 136. Echinorhinus obesus Smith, 1849: (no pagination), pl. 1. Types: A 6 ' $61 / 2^{\prime \prime}(1995 \mathrm{~mm})$ TL specimen (with detailed measurements) is the only one specifically mentioned in the text. A specimen illustrated in PI. 4 may be an adult male. Type locality: Cape of Good Hope, South Africa, is the only locality mentioned in Smith's account. Smith's E. obesus was synonymised with Echinorhinus spinosus (Gmelin) by Gray (1851: 78), and by Günther (1870: 428); however, neither author mentions possible type material of this species in the British Museum (Natural History) although many other Smith specimens were deposited there. Echinorhinus (Rubusqualus) mccoyi Whitley, 1931: 311. New name for Echinorhinus spinosus of McCoy (1887: 165, pl. 144). Holotype is in National Museum, Melbourne, NMV 50760, ca $219 \mathrm{~cm}\left(7^{\prime} 2^{\prime \prime}\right)$ dry specimen, probably female, Portland, Victoria, Australia (Paxton et al., 1989: 34; Eschmeyer, 1998).

Other Combinations: Echinorhinus spinosus (Gmelin, 1788).
FAO Names: En - Bramble shark; Fr - Squale bouclé; Sp - Tiburón de clavos.


Fig. 50 Echinorhinus brucus


UNDERSIDE OF HEAD


UPPER AND LOWER TOOTH


DERMAL DENTICLES

Field Marks: A large, short-nosed and flat-headed, cylindrical, heavy-bodied shark, with two spineless dorsal fins, the origin of the first set far posterior, originating behind the pelvic-fin origins, no anal fin and 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 centimeter wide; some of these enlarged 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 with 12 to 16 turns. Maximum total length to about 326 cm . Colour: uniformly grey or brownish to black or grey-black, usually lighter ventrally; photophores absent.

Distribution: South Africa to southern Angola. Also recorded off Côte d'lvoire. Elsewhere, wide ranging but patchily distributed throughout the Atlantic, Western Indian, and Western Pacific Oceans, and in the Mediterranean Sea.

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 deepwater 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. On the cold-temperate west coast of South Africa and Namibia it may move close inshore up submarine canyons where it has been regularly caught by shore-side anglers on rod and reel, and by smallscale commercial fishers.

Biology: Yolk-sac viviparity, with the number of young per litter ranging from 10 to 52. It has been suggested that in Indian waters these sharks may breed in the spring months (Silas and Severaj, 1972), but a more recent study that examined over 5,300 individuals throughout the year found that pregnant females had embryos in different stages of development and concluded that there does not appear to be a defined breeding season in Indian waters (Akhilesh et al., 2013). Along the west coast of South Africa and Namibia there are anecdotal reports of this species moving inshore during the late winter and early spring seasons.


Fig. 51 Echinorhinus brucus

The diet of these sharks consists mostly of crustaceans and teleosts, but also includes cephalopods and elasmobranchs.

Size: Maximum total length is about 326 cm for females and 300 cm for males, although there is one record of this shark attaining 394 cm in Indian waters. Size at maturity varies, with females and males in Indian waters maturing at 189 cm and

187 cm , respectively. Elsewhere females have been found to mature at about 213 to 231 cm and males between 150 and 174 cm . Size at birth is between about 40 and 54 cm ; late term embryos with reabsorbed yolk-sacs between 35 and 42 cm were observed in Indian waters (Akhilesh et al., 2013).

Interest to Fisheries and Human Impact: Bramble sharks in most locations are taken as bycatch in deep-sea bottom fisheries, although there is little information available on the numbers landed except for a recent study in Indian waters where $17 \%$ of the bycaught sharks were of this species (Akhilesh et al., 2013). Starting in 2005, a targeted fishery for Centrophorus species off Southwestern India caught large numbers of bramble sharks as bycatch. The estimated catch of bramble sharks in this fishery declined from 132 mt to 49 mt between 2008 and 2011, but it is not clear if this decline was due to fishing effort or a decline in fishing due to lack of a market for these sharks. During the mid-19 ${ }^{\text {th }}$ century a small-scale targeted fishery for this species developed off Lüderitz, Namibia, for its liver oil. In South Africa the liver oil of this species is held in high value by traditional healers. The meat is of poor quality and other than use for liver oil it is not usually retained.

The conservation status of this species is Data Deficient.
Local Names: Braamhaai, Prickle shark, Bramble shark (South Africa).
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: Gilchrist (1902); Thompson (1914); Barnard (1925); Bigelow and Schroeder (1948, 1957); Smith (1965); Nair and Lal Mohan (1971); Silas and Selvaraj (1972); Bass, D'Aubrey and Kistnasamy (1976); Cadenat and Blache (1981); Compagno (1984a); McEachran and Branstetter, in Whitehead et al. (1984); Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); Hemida and Capapé (2002); Paul (2003b); Last and Stevens (2009); Akhilesh et al. (2013); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013); 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 Deep-sea Southeastern Atlantic Ocean Genera: 2.

Synonyms: Family Squalinidae Leach, 1818: 61. Type genus: Squalus Linnaeus, 1758. Family Squalidae Bonaparte, 1832: 99; Bonaparte, 1838: 206. Type genus: Squalus Linnaeus, 1758. Tribe Acantiana Gray, 1851: 69 (Family Squalidae). Type genus: Acanthias Risso, 1826. Possible error for Tribe Acanthiana? Family and subfamily Acanthias Hasse, 1879: 44, tab. 2. Type genus: Acanthias Risso, 1826. Subfamily Squalinae: 239 (family Squalidae). Type genus: Squalus Linnaeus, 1758.

FAO Names: En - Dogfish sharks; Fr - Squales; Sp - Galludos, Tollos.
Field Marks: Short-nosed sharks with cylindrical body and 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 and 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 space 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 saw-like cutting edge with deep, imbricated series. Teeth not arranged in a quincunx pattern, 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-fin base. Pelviccaudal 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 crossshaped 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 vertebral 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 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 the neonates and young of some species occupy a pelagic habitat and live well off the bottom in inshore and offshore continental waters. 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: 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 may be 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. Several squalid dogfishes are social, with some species apparently forming large to immense schools that are highly nomadic and migratory, moving locally and on regular yearly migrations. Others are suspected of being solitary or occurring in small aggregations at most.

Interest to Fisheries and Human Impact: Dogfishes are taken in target fisheries and are often an important bycatch in mixed 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, boiledmarinated, and as fish cakes. Other products prepared from dogfish include liver oil for vitamins (and potentially squalene), fishmeal, pet food, fertilizer and leather.

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, and do reasonably well in captivity.

The conservation status of the group ranges from Data Deficient to Vulnerable 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.
Remarks: The family consists of 2 genera, Squalus and Cirrhigaleus, which comprise 29 species. The Squalus is the more species-rich genera with 26 species, a number likely to increase. The taxonomic status of the Squalus species occurring in the Southeastern Atlantic is unresolved as of this writing two and possibly three species may represent different species. The genus Cirrhigaleus is only known from very few records of Cirrhigaleus asper from the Eastern Cape Province, South Africa. The genus is most common in the Southwestern Indian Ocean. Therefore, the genus and species are not further discussed here except for being listed as occurring in the area and in the key separating the genera Squalus and Cirrhigaleus. For a review of this genus and species from the Indian Ocean see Ebert (2013).

Literature: Garman (1913); Fowler (1941, 1968); Bigelow and Schroeder (1948, 1957); Garrick (1960c, 1961); Bass, D'Aubrey and Kistnasamy (1976), Compagno (1984a); Myagkov and Kondyurin (1986); Parin (1987); Muñoz-Chapuli and Ramos (1989a); Last and Stevens (2009); Ebert et al. (2010); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013); Ebert and Compagno (In press).

## List of Deep-sea Species Occurring in the Area:

Cirrhigaleus asper (Merrett, 1973)
Squalus acanthias Linnaeus, 1758
Squalus acutipinnis Regan, 1908
Squalus cf. blainville (Risso, 1826)
Squalus cf. mitsukurii Jordan and Snyder, in Jordan and Fowler, 1903

## Key to Deep-sea Southeastern Atlantic Ocean Genera:

1a. Anterior nasal flaps with very large, broad secondary lobes, expanded into a long or very short barbel (Fig. 52); upper precaudal pit weak or absent; second dorsal fin almost as large as first; postventral caudal-fin margin shallowly concave; denticles very large, body surface rough .

## Cirrhigaleus

1b. Anterior nasal flaps with secondary lobe small and narrow to absent (Fig. 53); upper precaudal pit strong; second dorsal fin much smaller than first; postventral caudal-fin margin deeply notched; denticles smaller, body surface smooth.

Squalus


Fig. 52 Cirrhigaleus

## 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 Deep-sea Southeastern Atlantic Ocean Species: 4.

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", = 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 tricuspidate and triridged flat leaf-shaped crowns; skin smooth. Free rear tips of pectoral fins narrowly rounded to acutely angular. Pelvic fins low and obtusely triangular, with anterior margins about a third to one-half length of pectoral-fins anterior margins. Second dorsal fin smaller than first dorsal fin and with base length about three-fourths of first dorsal-fin base; second dorsalfin origin usually behind free rear tips of pelvic fins, but occasionally over them. Caudal peduncle elongated and with dorsocaudal 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-fin lobe strong; postventral caudal-fin margin usually deeply concave in adults. Vertebral counts: total vertebral counts 93 to 127, monospondylous vertebral counts 35 to 51, precaudal vertebral counts 67 to 93 . 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). Of the 26 currently recognized species, 4 are considered deep-sea and occur in the Southeastern Atlantic Ocean. One species, Squalus acanthias, is not usually considered a deepsea species throughout most of its range, but off the west coast of South Africa and southern Namibia, this species occurs within a very narrow depth range, usually between 125 and 515 m deep. Given its strikingly different habitat preference and behaviour, the Southeastern Atlantic population may prove to be distinct from the North Atlantic S. acanthias population.

The taxonomic status of the other three southern African Squalus species ( $\boldsymbol{S}$. cf. blainville, $\boldsymbol{S}$. cf. megalops, and $\boldsymbol{S}$. cf. mitsukurii) is currently under investigation as they are likely not these species. Compagno, Ebert and Cowley (1991) suggested that the Southeastern Atlantic Ocean Squalus species occurring off the west coast of South Africa and Namibia should be critically examined to confirm their identification. More recent accounts of Southern Africa Squalus species (Ebert et al., 2010; Naylor et al., 2012a; Eschmeyer, 2013) consider the valid species name for Southern Africa shortnose spiny dogfish to be $\boldsymbol{S}$. acutipinnis Regan, 1908 rather than $\boldsymbol{S}$. cf. megalops, a name frequently seen in recent Southern Africa literature. This difference between the endemic Australian $S$. megalops and the southern African $\boldsymbol{S}$. cf. megalops has been confirmed by Naylor et al. (2012a) who found a significant difference between these two populations. Therefore, given these significant differences the Southern Africa shortnose spiny dogfish previously referred to as $\boldsymbol{S}$. megalops or $\boldsymbol{S}$. cf. megalops should in fact be referred to as $\boldsymbol{S}$. acutipinnis Regan, 1908. These findings now open up the question as to the status of S. cf. megalops populations from throughout the entire Eastern Atlantic; a study that is now under investigation (A. Verissimo and R. Leslie, pers. comm.).

The below key to Squalus species is provisional pending a review and resolution of the Eastern Atlantic S. cf. blainville, S. cf. megalops, and S. cf. mitsukurii complexes.

Key to Deep-sea Southeastern Atlantic Ocean Species (Provisional):


Fig. 54 Squalus acanthias


Fig. 55 Squalus acutipinnis


Fig. 56 Squalus acutipinnis 3


Fig. 57 Squalus cf. mitsukurii nostril longer than distance from inner edge of nostril to front of upper labial furrow (Fig. 57) . . . . 3

3a. First dorsal fin high and erect, about $75 \%$ of fin length, with first dorsal-fin spine about as long as fin base (Fig. 58); precaudal vertebral counts 90 to 96

Squalus cf. blainville


Fig. 58 Squalus cf. blainville

3b. First dorsal fin lower, about $67 \%$ of fin length or less, first dorsal-fin spine shorter than fin base (Fig. 59); precaudal vertebral counts 83 to 89

Squalus cf. mitsukurii


Fig. 59 Squalus cf. mitsukurii

## 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 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 (2013). Acanthias vulgaris Bleeker, 1860: 57 (Cape of Good Hope, skin from large specimen 670 lines long); Thompson, 1914: 149 (Cape seas, South Africa, in part?). Acanthias linnei Malm, 1877: 624. Apparently a replacement name for Squalus acanthias Linnaeus, 1758, as this name is listed in synonymy. Squalus acanthias africana Myagkov and Kondyurin, 1986: 560 (translated 1986: 5). Holotype: Zoological Museum of Moscow State University, no. P-15990, 125 mm TL female fetus taken from the uterus of a 72 cm TL female, $28^{\circ} \mathrm{S}, 17^{\circ} \mathrm{E}$, from "Wolffish Bay" (coordinates indicate Port Nolloth, South Africa rather than Walvis Bay, Namibia). Junior homonym of Squalus africana Gmelin, $1788=$ Poroderma africana (Scyliorhinidae).

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. 60 Squalus acanthias
Field Marks: A moderate-sized to very large dogfish, with a moderately long, narrow, angular or subangular snout, obliquecusped cutting teeth in both jaws, pectoral fins narrow and falcate or semifalcate, with straight to concave posterior margins, 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. 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 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 usually slightly nearer to snout tip than mouth. Anterior nasal flap with medial barbel 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-fin anterior margins. Pelvic-fin 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 $50 \%$ (but sometimes up to $70 \%$ ) 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 $33 \%$ 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 precaudal 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 total length. 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: Off the west coast of South Africa and Namibia, and possibly to southern Angola, but unconfirmed from this area. Elsewhere, antitropical with apparent isolated populations or subpopulations of uncertain taxonomic status; the Southeastern Atlantic population may be distinct.

Habitat: Contrary to its habitat preferences elsewhere, off the west coast of Southern Africa Squalus acanthias is an offshore species of the outer continental shelf and upper slope. Surveys conducted along the west coast of Southern Africa show this species to occur mostly between 125 and 515 m , a depth preference deeper than S. acutipinnis, but slightly shallower than $S$. cf. mitsukurii. It also occurs over a very narrow latitudinal range extending from about $28^{\circ} \mathrm{S}$, $15^{\circ} \mathrm{E}$ to $34^{\circ} \mathrm{S}, 17^{\circ} \mathrm{E}$. Off the west coast of Southern Africa it usually occurs on or near the bottom or in the midwater off the outer continental shelf.

Biology: Viviparous with a yolk sac, litters size for Southern Africa population between 2 and possibly 12, but may be higher in other, e.g. North Atlantic, populations. Very little else is know about the reproductive cycle of this species in southern African waters. The diet consists of bony fishes primarily myctophids and hake (Merluccius sp .).

Size: Maximum total length of Southeastern Atlantic Ocean individuals is about 92.5 cm for females and 78.1 cm for males; females mature at about 65 to 75 cm and males between 51 and 65 cm in length. Size at birth is uncertain for the Southeastern Atlantic population, but smallest freeswimming neonates were about 31 cm total length.


Fig. 61 Squalus acanthias
$\square$ Known distribution

Interest to Fisheries and Human Impact: In the Southeastern Atlantic it is caught occasionally in deep-sea bottom trawls, but the species is relatively uncommon compared to the other two more common species of Squalus, S. acutipinnis, and S. cf. mitsukurii.

Commonly caught in longline fisheries and utilized for its meat, fins, and high value liver oil.
The global conservation status of Squalus acanthias is Vulnerable, but the southern African population is considered Least Concern due to a lack of deep-sea fisheries.

Local names: Spiky jack, Penhaai or Pen haai, Doringhaai, Dogfish (South Africa and Namibia).
Remarks: The status of southern African Squalus acanthias should be closely examined as it exhibits several different meristic characteristics relative to the North Atlantic populations.

Literature: Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); Ebert, Compagno and Cowley (1992); Fordham et al. (2006); Ebert et al. (2010); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013); 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, 1837a.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Genera: 2.

Synonyms: Subfamily Centrophorus (family Acanthias) Hasse, 1879: tab. 2. Type genus: Centrophorus Müller and Henle, 1837a. Subfamily Deaniinae Compagno, 1973: 26 (family Squalidae). Type genus: Deania Jordan and Snyder, 1902.

FAO Names: En - Gulper sharks; Fr - Squale chagrins; Sp - Quelvachos.
Field Marks: Short to long-nosed, cylindrical to somewhat compressed sharks with 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-fin 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, no anal fin, and 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 saw-like 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-fin 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-fin 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 fin; 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-fin insertions, or pelvic-fin 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 vertebral counts 24 to 37 . Intestinal valve with 10 to 25 turns. Adults are small to moderatesized, between 43 to 170 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, seamounts and ridges. Gulper sharks are generally absent from very high latitudes, except Centrophorus squamosus that 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 Centrophorus species may be regional endemics.

Habitat: Members of the Centrophoridae 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. 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 deepwater sharks in temperate and tropical seas, but general biology, including behaviour, sociobiology and population biology 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 Western Indo-Pacific and Eastern North Atlantic, these sharks are commonly fished as part of targeted deepwater shark fisheries and also form an important bycatch of deepwater fisheries for bony fishes. Some species are regularly caught as discarded bycatch of fisheries for deepwater teleosts. They are caught with longlines, bottom trawls, and fixed bottom gillnets. 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 lifehistory parameters such as fecundity, life span, age at maturity, and gestation period.

Local Names: Gulper sharks, Birdbeak dogfish, Oil tankers.
Remarks: The current arrangement of the Centrophoridae is comprised of two genera, with 15 nominal species currently recognized. Both genera and 6 species have been reported from the Southeastern Atlantic Ocean.

Literature: Regan (1908a); Garman (1913); Bigelow and Schroeder (1948, 1957); Bass, D’Aubrey and Kistnasamy (1976); Cadenat and Blache (1981); Compagno (1984a, 1999); Muñoz-Chapuli and Ramos (1989b); Shirai (1996); Last and Stevens (2009); Kyne and Simpfendorfer (2010); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013); White et al. (2013); Ebert and Compagno (In press).

## List of Deep-sea Species Occurring in the Area:

Centrophorus granulosus (Bloch and Schneider, 1801)
Centrophorus squamosus (Bonnaterre, 1788)
Centrophorus cf. uyato (Rafinesque 1810)
Deania calcea (Lowe, 1839)
Deania profundorum (Smith and Radcliffe, 1912)
Deania quadrispinosa (McCulloch, 1915)

## Key to Deep-sea Southeastern Atlantic Ocean Genera:

1a. Preoral snout length less than distance from mouth to pectoral-fin origin (Fig. 62a); dermal denticles of back leaf-shaped with pedicels, or sessile with low ridges, and without erect pitchfork-shaped crowns (Fig. 62b). . . . . . . . . . . . . . . Centrophorus


Fig. 62 Centrophorus
1b. Preoral snout length greater than distance from mouth to pectoral-fin origin (Fig. 63a); dermal denticles of back with tall, slender pedicels and pitchfork-shaped crowns (Fig. 63b).

Deania

a) LATERAL VIEW
b) DERMAL DENTICLES

Fig. 63 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 $\boldsymbol{S}$. granulosus), but also noted that "Squalus squamosus, Bl. 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 S. squamosus, but Müller and Henle (1839, Syst. Beschr. Plagiost., pt. 2: 90) reversed their previous opinion and included $\boldsymbol{S}$. squamosus in Centrophorus.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 3.

Synonyms: Genus Lepidorhinus Bonaparte, 1838: 207. Type species: "Squalus Squamosus Brousson (-et? 1788), Lac. 1. X. 3." by monotypy, equals Squalus squamosus Bonnaterre, 1788. Genus Machephilus Johnson, 1867: 713. Type species: Machephilus Dumérilli Johnson, 1867, by original designation. Genus Atractophorus Gilchrist, 1922: 48. Type species: Atractophorus armatus Gilchrist, 1922, by monotypy. Genus Actractophorus Gilchrist, 1922: 48. Probable error for Atractophorus Gilchrist, 1922. Subgenus Gaboa Whitley, 1940: 146 (genus Centrophorus Müller and Henle, 1837a). Type species: Centrophorus harrissoni McCulloch, 1915, by original designation. Subgenus Somnispinax Whitley, 1940: 146 (genus Centrophorus Müller and Henle, 1837a). Type species: Centrophorus nilsoni Thompson, 1930, by original designation; a junior synonym of Squalus squamosus Bonnaterre, 1788. Subgenus Somnisphinax Neave, 1950: 252. Probable error for Somnispinax Whitley, 1940. Genus Encheiridiodon Smith, 1967b: 128. Type species: Encheiridiodon hendersoni Smith, 1967b, by original designation; a junior synonym of Squalus squamosus Bonnaterre, 1788. Genus Attractophorus Bass, D'Aubrey and Kistnasamy, 1976: 27. Apparent error for Atractophorus Gilchrist, 1922. Genus Encheridiodon Shiino, 1976: 11. Apparent error for Encheiridiodon Smith, 1967b. Genus Pseudocentrophorus Chu, Meng, and Liu, 1981: 100. Type species: Pseudocentrophorus isodon Chu, Meng, and Liu, 1981, by original designation.

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 rear tips more or less angular to attenuated, two dorsal fins each with a strong grooved spine, no anal fin, caudal fin with a strong subterminal notch, body coloration light grey or grey-brown to blackish grey, sometimes lighter below and 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-fin 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, blockshaped, 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 dorsalfin 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, monospondylous vertebral counts 49 to 64 , precaudal vertebral counts 77 to 92 . Intestinal valve with 10 to 30 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 Centrophorus has a complex and convoluted taxonomic history, in part because many researchers have had difficulty interpreting differences in denticles, fin spines, teeth, body and fin morphology within and between species that are related to growth and sexual dimorphism. Also, until recently researchers have tended to concentrate on the same few external characters without examining other characters that are less subject to growth and sexual changes. Poor or inadequate sampling of Centrophorus species from most localities where these deepwater sharks occur has exacerbated these problems.

The genus currently has 11 recognized species, but the taxonomic status of most Centrophorus species is very poor with most species having been inadequately described and with type material missing or in poor condition. At present, 3 nominal Centrophorus species have been reported from the Southeastern Atlantic Ocean.

The current key of species below is provisional and should be used with caution 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 the genus Centrophorus, including detailed examination of external morphological, anatomical and molecular characters is currently being carried out by the author and W.T. White (CSIRO, Hobart, Tasmania, Australia) and should resolve some of the current taxonomic issues within this group in the near future. This includes the confused systematics of Centrophorus species referred to as C. acus and C. niaukang, that are both now known to be junior synonyms of C. granulosus (White et al., 2013). The taxonomic status of Centrophorus cf. uyato is currently under investigation since this species, whose name originally referred to a Squalus species of unknown identification in the Mediterranean Sea, now appears to be more wide-ranging and may be in fact be a junior synonym of another species (W.T. White and D.A. Ebert, unpubl. data). The name Centrophorus cf. uyato is therefore retained here since it has been commonly used in referring to the smallest of the three known gulper shark species (Centrophorus spp.) that occur in this area. A resolution to the taxonomic nomenclature of this species is pending the outcome of an investigation by W.T. White and D.A. Ebert.

Key to Deep-sea Southeastern Atlantic Ocean Species (Provisional):
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. 64)

## 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. 65) 2

2a. A small species, with a maximum length of 110 cm and a moderately long pectoral-fin free rear tip; first dorsal fin slightly greater in height than second dorsal fin; first dorsal-fin relatively short, triangular in shape (Fig. 66) . .

Centrophorus cf. uyato
2b. A large species, with a maximum length of 170 cm and a moderately short pectoral-fin free rear tip; dorsal fins about equal in height; first dorsal-fin relatively long and low, not triangular in shape (Fig. 67)

Centrophorus granulosus
DERMAL DENTICLES


DERMAL DENTICLES
Fig. 65 C. granulosus

Fig. 64 C. squamosus


Fig. 66 Centrophorus cf. uyato


Fig. 67 Centrophorus granulosus

## 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 Atlantic Mediterranean, 1: 44) and Eschmeyer (2013).

Synonyms: Encheiridiodon hendersoni Smith, 1967b: 129, pls. 24-27. Holotype: J.L.B. Smith Institute of Ichthyology, RUSI-663, 1080 mm adult male, Port Elizabeth, Algoa Bay, South Africa, procured by a diver in shallow water ( $3-4 \mathrm{~m}$ ), possibly a discarded trawl catch. Catalog number from Eschmeyer (2013).

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; $\mathbf{S p}$ - Quelvacho negro.


Fig. 68 Centrophorus squamosus
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, 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 moderately long. Preoral length 0.8 to 1.3 times mouth width, 0.9 to 1.8 in space from mouth to pectoral-fin origins, and 0.6 to 0.9 times head width at mouth level. Snout broadly parabolic in dorsoventral view, broad to narrow and wedge-shaped in lateral profile, depth at mouth 1.2 to 2.3 times 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-fin insertion to second dorsal-fin 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 length; base length 11.9 to $21.6 \%$ of total length. Second dorsal fin height 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 precaudal vertebral counts 55 to 60 , precaudal vertebral counts 82 to 88 . Intestinal valve counts 12 to 14 . Size relatively large, adults 103 to 164 cm total length. 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: Namibia and South Africa (Western and Northern Cape Provinces), likely Angola, and northwards to European waters, but absent from the Mediterranean Sea. Also, occurs in the Indian, and Western and Southeastern Pacific Oceans.

Habitat: A large deepwater gulper shark of the continental slopes from 229 to 2359 m deep, but off the coast of Namibia and the west and south coasts of South Africa it occurs primarily in water 370 to 809 m deep, with most records between 400 to 660 m deep. Also found in the epipelagic or mesopelagic zone between the surface and 1250 m depth over water 1000 to over 3900 m deep, but it is uncertain if this species regularly occurs in oceanic waters. One was collected dead by a spearfisherman in water 3 to 4 m deep off the south coast of South Africa, but the species does not normally stray onto the continental shelves off Southern Africa and the specimen may have been a longline or trawl discard. A common species in some localities, but does not appear to be very common in the Southeastern Atlantic.

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 squids), and crustaceans (euphausiid and penaeid shrimps).

Size: Maximum total length about 164 cm . Males mature at about 100 to 110 cm , and adult females at 110 to 125 cm . Size at birth is from 30 to 40 cm .


Fig. 69 Centrophorus squamosus
Known distribution

Interest to Fisheries and Human Impact: Interest to fisheries limited in the Southeastern Atlantic where it is taken, as bycatch on occasion, but is not a common species in bycatch landings.

Conservation status is listed as Vulnerable globally, although regionally its status may vary from Data Deficient (Australia, New Zealand, and South Africa) to Endangered in the Eastern North Atlantic because of deepwater bycatch fisheries and targeted deep-shark fisheries.

Local Names: Grinner dogfish, Gryns-hondhaai (South Africa).
Remarks: The nomenclature and systematic status of this species is currently undergoing an extensive revision by the author and W.T. White (CSIRO, Hobart, Tasmania, Australia).

Literature: Bass, D'Aubrey and Kistnasamy (1976); Bass, Compagno and Heemstra in Smith and Heemstra (1986); Compagno, Ebert and Smale (1989); Muñoz-Chapuli and Ramos (1989b); Compagno, Ebert and Cowley (1991); Ebert, Compagno and Cowley (1992); White (2003); Bañón, Piñeiro and Casas (2008); Last and Stevens (2009); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013); White et al. (2013); Ebert and Compagno (In press); 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 Deep-sea Southeastern Atlantic Ocean 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. Genus Nasisqualus Smith and Radcliffe, in Smith, 1912: 681. Type species: Nasisqualus profundorum Smith and Radcliffe, in Smith, 1912, by original designation. Genus Deaniops Whitley, 1932: 326. Type species: Acanthidium quadrispinosum McCulloch, 1915, by original designation. Genus Daeniops Bigelow and Schroeder, 1957: 101. Apparently an error for Deaniops Whitley, 1932.

Field Marks: Deepwater sharks with an extremely long and 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 a strong subterminal notch, body colour 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-fin 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 more than 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, Birdbeaked dogfishes, Pylkop-hondhaai (South Africa).
Remarks: The genus currently has four species recognized, but there are several problems with the present arrangement, including identifying criteria for separation of Deania hystricosa from D. calcea other than larger denticles and often but not always a darker coloration; the former may be a junior synonymy of the latter species. Bigelow and Schroeder (1957) and Compagno (1984a) had synonymized D. rostrata (Garman, 1906) with D. eglantina or D. calcea, but Yano and Tanaka (1983) suggested that it was separable from D. calcea without giving details on how the two species differed. This problem needs to be further investigated. Although D. profundorum and D. quadrispinosa are readily separable from each other and from D. calcea or $\boldsymbol{D}$. hystricosa, it is necessary to critically compare adequate samples within all of the Deania species and across their very broad ranges to confirm the current arrangement. Dr. Sho Tanaka is currently revising the genus.

## Key to Deep-sea Southeastern Atlantic Ocean Species:

1a. A subcaudal keel on the lower surface of the caudal peduncle (Fig. 70)

Deania profundorum

1b. No subcaudal keel on the lower caudal peduncle


Fig. 70 Deania profundorum

2a. First dorsal fin rather high, angular, and short, distance from its spine origin to free rear tip about one-half to $2 / 3$ of distance from free rear tip to origin of second dorsal-fin spine (Fig. 71) .

Deania quadrispinosa

2b. First dorsal fin rather low, rounded, and long, distance from its spine origin to its free rear tip equal to or greater than distance from free rear tip to origin of second dorsal-fin spine (Fig. 72)

Deania calcea


Fig. 71 Deania quadrispinosa


Fig. 72 Deania calcea

## 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: Centrophorus crepidalbus Bocage and Capello, 1864: 262, fig. 2. No specimens were mentioned or type-designations made in Bocage and Capello's brief original description, which describes and illustrates an undoubted Deania but which may not be diagnostic to species. The figure has a short first dorsal fin as in D. quadrispinosum and D. profundorum (both of which occur in the Eastern South Atlantic), which could be significant although the figure's sketchiness is problematical. Bocage and Capello noted after the description of C. crepidalbus: "An Acanthidium calceus, Lowe?". This suggested that they doubted that C. crepidalbus was separable from D. calcea. Krefft and Tortonese (1973: 42) list British Museum (Natural History), BMNH 1867.7.23.1 as a possible syntype. Paepke and Schmidt (1988: 161) suggest that Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, ZMB-6471, a 720 mm female in alcohol, is a syntype based on unpublished correspondence in the archives of the Zoologisches Museum; these writers note that the type material of the species in the Museu Bocage may have been destroyed by fire. Eschmeyer (2013) lists the following three specimens as possible syntypes: BMNH 1867.7.23.1, Museum National d'Histoire Naturelle, Paris, MNHN 4801, and ZMB 6471. K. Yano (1991) has used this species as a senior synonym of $\boldsymbol{D}$. profundorum. Examination of one of these possible syntypes (BMNH 1867.7.23.1) indicates that it is apparently based on D. profundorum or a close relative, but the name may be unavailable because of its brief description and lack of specimen references including type designations. Acanthidium natalense Gilchrist, 1922: 49, pl. 7, fig. 2. Syntype: J.L.B. Smith Institute of Ichthyology, RUSI 2, Pickle station $152,30^{\circ} 9^{\prime} 45^{\prime \prime} \mathrm{S}, 30^{\circ} 58^{\prime} 02^{\prime \prime} \mathrm{E}$, SE of Durban, Natal, South Africa, 293 m , according to Eschmeyer (2013), who indicates that this is one of two syntypes of the species and the only one that was confirmed. Gilchrist (1922) did not indicate the number and size of specimens on which his description was based, though the brief description suggests but does not prove that it may have been based on a single individual. Deania elegans Springer, 1959: 31, fig. 1. Holotype: U. S. National Museum of Natural History, USNM-159603, 315 mm TL immature male, Delaware 58-1-tow 5, off Cape Fear, North Carolina, $34^{\circ} 40^{\prime} \mathrm{N}, 75^{\circ} 32^{\prime} \mathrm{W}, 366 \mathrm{~m}$. Status of holotype confirmed by Howe and Springer (1993: 7). Deania cremouxi Cadenat, 1960b: 312, fig. 1-16. Syntypes: in Museum National d'Histoire Naturelle, Paris, (221) MNHN 1965177 [ex IFAN 58-103], Senegal coast, 350-600 m depth according to Eschmeyer (2013).

Other Combinations: Acanthidium profundorum (Smith and Radcliffe, 1912), Deania calceus cremouxi Cadenat, 1960b, Deania natalensis (Gilchrist, 1922).

FAO Names: En - Arrowhead dogfish; Fr - Squale-savate lutin; Sp - Tollo flecha.


Fig. 73 Deania profundorum

Field Marks: Extremely long flat snout, compressed cutting teeth in both jaws, pitchfork-shaped small denticles that make 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 dorsalfin 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 total length. Colour: medium to dark grey or grey brown above and below, fins dusky.

Distribution: South Africa (Northern and Western Provinces), Namibia, and possibly Angola; northwards to the Republic of Congo, Gabon and Nigeria. Also recorded in the Eastern and Western Central Atlantic, North Atlantic, Western Indian (KwaZulu-Natal, South Africa) and Western Pacific Oceans.

Habitat: A little-known deepwater benthic dogfish of the upper continental and insular slopes found on or near the bottom at depths from 205 to 1785 m on the upper, middle and lower slopes. In the Southeastern Atlantic it occurs at 205 to 608 m, but most common between 400 and 500 m , while off the Canary Islands it has been caught at 600 to 1500 m and in the Western North Atlantic mostly between 412 and 617 m deep. 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 .

Interest to Fisheries and Human Impact: Interest to fisheries minimal. The species is infrequently encountered off the west coast of South Africa and Namibia, but when taken as bycatch they are usually caught in large numbers


Fig. 74 Deania profundorum
Known distribution suggesting they form large aggregating schools. Off Namibia and the west coast of South Africa these sharks will often also aggregate in large numbers with other Deania species, especially D. calcea. Utilized in some regions for liver oil and meat.

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

Local Names: Arrowhead dogfish, Pylkop-hondhaai (South Africa).
Remarks: The species name Deania crepidalbus (currently considered a junior synonym) is often seen in the literature for the Southeastern Atlantic region for $\boldsymbol{D}$. profundorum and it may eventually prove to be the proper species name as the genus Deania is currently being revised by S. Tanaka (Tokai University, Japan, pers. comm.).

Literature: Smith and Radcliffe in Smith (1912); Gilchrist (1922); Barnard (1925); Bigelow and Schroeder (1957); Cadenat (1960, 1961); Bass, D'Aubrey and Kistnasamy (1976); Cadenat and Blache (1981); Compagno (1984a); Compagno, Ebert and Smale (1989); Springer in Quero et al. (1990); Compagno, Ebert and Cowley (1991); Yano (1991); Ebert, Compagno and Cowley (1992); Bianchi et al. (1999); Ebert, McCormack and Samiengo (2009); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013); Ebert and Compagno (In press); D.A. Ebert (unpubl. data); P.C. Clerkin (pers. comm.).

### 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 Deep-sea Southeastern Atlantic Ocean Genera: 2.

Synonyms: Subfamily Spinacini Bonaparte, 1838: 206 (family Squalidae). Also as family Spinaces Müller and Henle, 1839 (1): 83; family Spinacidae Owen, 1846: 51; family Spinacoidae Gill, 1862: 404; and family Spinacida Schmarda, 1871: 309. Type genus: Spinax Cuvier, 1816. Subfamily Centroscyllium (family Acanthias) Hasse, 1879 (1): tab. 2. Type genus: Centroscyllium Müller and Henle, 1841.

FAO Names: En - Lantern sharks; Fr - Sagres lanterne; Sp - Tollos linternas.
Field Marks: Dwarf to moderate-sized sharks (usually less than 100 cm long and mostly below 80 cm long) with short to long snouts, cylindrical to slightly depressed bodies, 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) with a cusp and cusplets, except for Etmopterus sheikoi that has 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, no anal fin and 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 (except Trigonognathus) and not overlapping, with narrow erect or flexed conical cusps and often one to three pairs of conical cusplets (Centroscyllium and Etmopterus sheikoi); lower teeth either similar to upper teeth (Aculeola, Centroscyllium, Trigonognathus) 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 (Etmopterus sheikoi). 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-fin base but ranging from about 0.6 to several times its length; pelvic-caudal space elongated or short and equal to about twice pelvic-fin 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 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-fin spine usually much larger than the first dorsal-fin spine. First dorsal fin small, not falcate, with length usually less than prespiracular space (except Aculeola, in which it is longer than the prespiracular space); first dorsal-fin base over pectoral-pelvic 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 vertebral counts 7 to 27 , total precaudal vertebral counts 50 to 73 , caudal vertebral counts 18 to 31 . Intestinal valve with 4 to 19 turns. Adults dwarf to moderate-sized, from 16 to 107 cm total length but mostly below 80 cm total length. 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 ( $\boldsymbol{E}$. gracilispinis, $\boldsymbol{E}$. 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 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, Aksnes and Mallefet (2010), Claes et al. (2010, 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 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.

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 be protected and managed under existing regional governmental legislation, but imperfect monitoring of etmopterid bycatch and mortality from trawling makes conservation difficult even in protected areas.

Local Names: Lanternsharks or Lantern sharks (general).
Remarks: 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, 1908a); Garman (1913); Bigelow and Schroeder (1948, 1957); Bigelow, Schroeder and Springer (1953); Bass, D'Aubrey and Kistnasamy (1976); Cadenat and Blache (1981); Compagno (1984a); Yamakawa, Taniuchi and Nose (1986); Tachikawa, Taniuchi and Arai (1989); Shirai and Nakaya (1990a, b); Shirai (1992, 1996); Shirai and Tachikawa (1993); Schaaf-Da Silva and Ebert (2006); Claes and Mallefet (2008, 2010a, b); Claes, Aksnes and Mallefet (2010), Claes et al. (2010, 2011); Straube et al. (2010); Ebert, Compagno, and DeVries (2011); Straube, Kriwet and Schliewen (2011); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013); Ebert and Compagno (In press); D.A. Ebert (unpubl. data).

## List of Deep-sea Species Occurring in the Area:

Centroscyllium fabricii (Reinhardt, 1825)
Etmopterus bigelowi Shirai and Tachikawa, 1993
Etmopterus compagnoi Fricke and Koch, 1990
Etmopterus granulosus (Günther, 1880)
Etmopterus polli Bigelow, Schroeder and Springer, 1953
Etmopterus pusillus (Lowe, 1839)
Etmopterus sculptus Ebert, Compagno and DeVries, 2011
Etmopterus spinax (Linnaeus, 1758)
Etmopterus viator Straube, 2011

## Key to Deep-sea Southeastern Atlantic Ocean Genera:

1a. Lower teeth similar to uppers, not compressed and blade-like, and overlapping or abutting one another (Fig. 75). 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. 76). Mouth short, nearly straight and transverse

Etmopterus


Fig. 75 Centroscyllium

UPPER AND LOWER TOOTH

Fig. 76 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 Deep-sea Southeastern Atlantic Ocean Species: 1.

Synonyms: Genus Paracentroscyllium Alcock, 1889, Ann. Mag. Nat. Hist. (6), 4(23):379. Type species: Paracentroscyllium ornatum Alcock, 1889, by monotypy. Genus Centrocyllium Jordan and Fowler, 1903, Proc. U. S. Natn. Mus. 26 (1324): 635. Apparent misspelling for Centroscyllium in two places (species account and figure legend of $\boldsymbol{C}$. ritteri), but properly spelled elsewhere in their account.

Field Marks: Short to moderately long snout, comb-like teeth with cusps and cusplets in both jaws, dorsal-fin spines present and large and no anal fin. Colour greyish or blackish-brown.

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. 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). Vertebral counts: total vertebral counts 81 to 97, monospondylous vertebral counts 37 to 46 , diplospondylous vertebral counts 14 to 22 , total precaudal vertebral counts 54 to 67 , caudal vertebral counts 29 to 31 . Intestinal valve with 4 to 10 turns. Size small to moderate with adults to 84 cm , and possibly 107 cm total length. 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, with Centroscyllium fabricii (Reinhardt, 1825) as the only species known to occur in the Atlantic Ocean, and the other six members of the genus occurring 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 (2013).

Synonyms: None.

Other Combinations: None.
FAO Names: En - Black dogfish; Fr - Aiguillat noir; Sp - Tollo negro merga.


Fig. 77 Centroscyllium fabricii
Field Marks: Body moderately stout and compressed, 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, two dorsal fins with grooved spines, the first low and the second moderately high, first dorsal fin with a low subangular fin web and no anal fin. 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 40\% of 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 precaudal vertebral counts 43 to 46 . Intestinal valve counts 7 to 10 . Size moderate, with adults 84 to 107 cm total length. Colour: blackish brown above and below, without conspicuous black markings on ventral surface or sides of tail; fins without white markings.


Fig. 78 Centroscyllium fabricii

Distribution: West coast of Southern Africa from Quoin Point (South Africa) to at least the Cunene River (Angola). It also occurs in the Northeastern, Northwestern, Eastern Central and Western Central Atlantic. Southwestern Atlantic records from off Argentina (Beagle Channel) should be closely examined to determine whether this or a similar but different species occurs there.

Habitat: An abundant deepwater schooling shark of the outermost continental shelves and slopes at depths ranging from 180 to 2250 m , but mostly below 275 m . Off the west coast of Southern Africa it is most common below 700 m to at least 1016 m . It is one of the most commonly encountered deep-sea sharks recorded in surveys. At high latitudes in the North Atlantic it may move up to near the surface, especially during the winter and when darkest at night. Water temperatures at the bottom where these sharks are most commonly caught is 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. The species does not appear to have a defined reproductive season. Hermaphrodism has been observed in this species with individuals having both ovaries and testes.

Off the west coast of Southern Africa this shark feeds primarily on crustaceans, especially penaeid shrimps but also euphausiids and secondarily on cephalopods, lanternfish (Myctophidae, including Diaphus sp.), barracudinas (Paralepididae) and unidentified teleosts. Behavioral 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. The diet of this species in the North Atlantic consists primarily of teleosts (gadoids mackerel, myctophids), crustaceans (pelagic crustaceans and demersal decapod crabs), and cephalopods. 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 Macrouridae heads.

Very little is known about their behavior off Southern Africa, although they appear to form large schooling aggregations. In the North Atlantic this species exhibits strong evidence of segregation by sex and size within populations and of movements of schools into shallower waters 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 adults that occur mostly over 750 m . 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 westwards mostly males of all maturity stages and immature females occurred. No such similar segregation patterns have been observed to date for the southern African populations.

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 at least 84 cm , may reach 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: The species is commonly taken by bottom trawls, but is a discarded bycatch in Southern Africa. In the North Atlantic it is of limited fisheries interest as it is a retained bycatch mainly by French trawl fisheries operating in the Eastern North Atlantic.

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: Black dogfish.
Remarks: It is uncertain if discrete populations, or possibly different species, occur throughout the North and South Atlantic, but the population structure should be critically compared to determine if they comprise a single species.

Literature: Bigelow and Schroeder (1948, 1957); Bass, D'Aubrey and Kistnasamy (1976); Cadenat and Blache (1981); Compagno (1984a); Compagno, Ebert and Smale (1989); Springer in Quero et al. (1990); Compagno, Ebert and Cowley (1991); Ebert, Compagno and Cowley (1992); Yano (1995); Bianchi et al. (1999); Jakobsdóttir (2001); Ebert et al. (2009); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013); 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 Deep-sea Southeastern Atlantic Ocean Species: 8.

Synonyms: Genus or subgenus Spinax Cloquet, 1816, Dict. Sci. Nat., ed. 1 (2?), 1, suppl., 93 (not seen); Subgenus Spinax Cuvier, 1816, Reg. Anim., ed. 1, 2: 129 (genus Squalus Linnaeus, 1758). Type species: Squalus spinax by absolute tautonymy. Probably also subgenus Spinax Bosc 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, 1816 = 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, second dorsal fin and spine larger than first dorsal fin and spine and no anal fin.

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. Dorsalfin 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 51 to 73 , monospondylous vertebral counts 36 to 56 . Intestinal valve with 8 to 19 turns. Colour: variable, from blackish to tan above, often black below; fin webs varying from not much lighter than the bases to abruptly lighter; a semicircular or elongated patch of white skin on edge of upper eyelid in some species. 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.

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; Lanternhaaie (South Africa).
Remarks: This is one of the most speciose genera of sharks worldwide with 37 nominal species currently recognized, of which 8 species are currently recognized as occurring in the Southeastern Atlantic Ocean deep-sea. The genus has several species-complexes that will likely reveal additional species making it, along with the Apristurus, among the most speciesrich genera of sharks. The group appears to exhibit a high degree of endemism with several species having a restricted distributional range. The scientific names for several of these nominal species will likely change with improved taxonomic resolution of the group.

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 Deep-sea Southeastern Atlantic Ocean Species (Provisional):

1a. Skin smooth, denticles with low, flat, concave, sessile crowns atop low bases (Fig. 79)

1b. Skin with a fuzzy or rough texture, denticles with erect, thorn-like, cuspidate crowns, more or less elevated from their bases (Fig. 80).

2a. Nineteen to 24 rows of upper teeth. Upper tooth cusps stout and thick, lower tooth cusps become erect with growth. First dorsal fin more anterior, distance from pectoral-fin insertion to first dorsal-fin base three or more times in interdorsal space (Fig. 81). First dorsal-fin spine longer and stouter, equal or longer than first dorsal-fin base length. Forty-nine to 57 monospondylous centra. Sixteen to 19 intestinal valve turns

Etmopterus bigelowi
2b. Twenty-two to 31 rows of upper teeth. Upper tooth cusps slender, lower tooth cusps do not become erect with growth. First dorsal fin more posterior, distance from pectoral-fin insertion to first dorsal-fin base less than three times in interdorsal space (Fig. 82). First dorsalfin spine shorter and slenderer, equal or less than first dorsal-fin base length. Forty-six to 53 monospondylous centra. Ten to 13 intestinal valve turns

Etmopterus pusillus
3a. Denticles on dorsal surface of head arranged in linear rows, which extend to the flanks, caudal peduncle and caudal-fin base (Fig. 83) . . . . Etmopterus sculptus

3b. Denticles on dorsal surface of head not arranged in linear rows; flanks, caudal peduncle and caudal-fin base with or without linear rows of denticles

4a. Denticles on flanks, caudal peduncle, and caudalfin bases in regular longitudinal lines

4b. Denticles on sides of body randomly arranged, and not in regular longitudinal lines

5a. A very large Etmopterus species with a maximum length of 88 cm . Dermal denticles at base of dorsal fins minute, texture smooth to the touch. Flank marking not distinctive, if visible, anterior branch long, thin, and linear, posterior branch short (Fig. 84).

## Etmopterus granulosus

5b. A very small Etmopterus species with a maximum length of 24 cm (Fig. 85). Dermal denticles at base of dorsal fins bristle-like (Fig. 80), texture rough to the touch. Flank marking distinctive, anterior branch thick, long and curved, posterior branch thick, length similar to anterior branch

Etmopterus polli
6a. Coloration a uniform dark brown to brownish black above and below, without a rather abrupt transition from dorsal to ventral surface (Fig. 86)

## Etmopterus viator

6b. Coloration brown above, becoming dark to blackish below, transition from dorsal to ventral colour rather abrupt


DERMAL DENTICLES Dorsal view

Fig. 79 Etmopterus pusillus


DERMAL DENTICLES
Dorso-lateral view
Fig. 80 Etmopterus polli


Fig. 81 Etmopterus bigelowi


Fig. 82 Etmopterus pusillus
Denticles on dorsal surface of head arranged in linear rows


Fig. 83 Etmopterus sculptus


Fig. 84 Etmopterus granulosus


Fig. 85 Etmopterus polli


Fig. 86 Etmopterus viator

7a. Lateral flank markings, inconspicuous, broad or thin, extending anteriorly over or slightly beyond pelvicfin base and posteriorly to past second dorsal-fin base (Fig. 87)

Etmopterus compagnoi

7b. Lateral flank markings, inconspicuous, not thin, extending anteriorly over pelvic fin, but posteriorly, short, truncated not extending to second dorsal-fin base (Fig. 88)

Etmopterus spinax


Fig. 87 Etmopterus compagnoi


Fig. 88 Etmopterus spinax

## Etmopterus compagnoi Fricke and Koch, 1990

Etmopterus compagnoi Fricke and Koch, 1990, Stuttgarter Beit. Naturk. Ser. A (Biol.) (450): 2, figs. 1, 2a. Holotype: Staatliches Museum für Naturkunde, Stuttgart, SMNS 8999, 327 mm immature male, off Cape Town, South Africa, $34^{\circ}$ $41^{\prime} S, 18^{\circ} 37^{\prime} E$.

Synonyms: Not Etmopterus gracilispinis Krefft, 1968: 3, figs. 2, 3a, 4, 5a (off Uruguay). Etmopterus gracilispinis Karrer, 1973: 199 (South Africa, west of Cape Town, $33^{\circ} 54^{\prime} \mathrm{S}, 17^{\circ} 28^{\prime} \mathrm{E}, 440$ to 488 m ); Shcherbachev, Levitski and Portsev, 1978: 186 (South Africa, Agulhas Bank south of Plettenberg Bay, 1000 m); Compagno, 1984a: 76 (South Africa); Compagno, Ebert and Smale, 1989: 28, ill. (southern Namibia to Cape Agulhas, 479 to 923 m). Etmopterus spinax Gilchrist, 1922: 49 (RV Pickle \#42, $33^{\circ} 32.0^{\prime} \mathrm{S}, 17^{\circ} 10.3^{\prime} \mathrm{E}$, west of Cape Town, 763 m ); Barnard, 1925: 49 (off Cape Point, 763 m ); Fowler, 1936: 80 (South Africa, off Cape Point); Fowler, 1941: 251 (South Africa); Barnard, 1947: 20, pl. 3, fig. 5 (off Cape Point, South Africa); Smith, 1949: 59, fig. 51 (Cape Point, 732 m); Smith, 1965: 59, fig. 51 (Cape Point); Cadenat and Blache, 1981: 39 (South Africa); Compagno, 1984a: 85 (Cape Province, South Africa). Spinax spinax Norman, 1935: 37 (South Africa, southwest of Cape Town, $34^{\circ} 08^{\prime}$ S, $17^{\circ} 33^{\prime} \mathrm{E}, 402$ to ? 548 m). Etmopterus sp. Bass, Compagno and Heemstra, 1986: 57, fig. 5.16 (Southwestern Cape Province, Northern Natal). Etmopterus unicolor Compagno et al., 2005: 108, ill., PI. IV.

Other combinations: None.
FAO Name: En - Brown lanternshark.


Fig. 89 Etmopterus compagnoi
Field Marks: Body moderately stout, with a relatively short snout, upper teeth with less than 3 lateral paired cusplets, lower teeth compressed and knife-like, with a cusp and a blade, lateral trunk denticles small, slender, and conical, not forming a conspicuous line along body, dorsal fins with fin spines, first dorsal-fin spine smaller than second dorsal-fin spine, caudal fin relatively short and no anal fin. Colour brown above, underside grading to black with inconspicuous, elongated, broad to thin black markings above and behind the pelvic fins.

Diagnostic Features: Head broad and flat, not deep and conical; head relatively long 16 to $17.5 \%$ of total length; head width about 1.5 to 1.9 times in head length. Prespiracular length 1.1 to 1.5 times in head length. Snout broad and flattened, not bulbous; preoral length short between 8.4 and $10.2 \%$ of total length. Eyes moderately large, elongated. Gill openings width greater than spiracle length, width of third gill opening less than one-third eye length. Total tooth row counts unavailable;
upper teeth with less than three lateral cusplets, flanked by a central cusp. Body moderately firm, cylindrical, and stout; predorsal spine length about $33 \%$ of total length; interdorsal space greater than prespiracular length and prebranchial length. Pectoral fin moderately long, broadly rounded-subangular in shape. First dorsal-fin origin posterior to free rear tips of pectoral fins, base about equidistant from pectoral and pelvic-fin bases; first dorsal-fin spine stout, short, less than height of first dorsal-fin apex; spine origin about equidistant from snout tip and upper caudal-fin origin. Second dorsal fin much larger than first, about twice its area; apex rounded, posterior margin slightly concave; second dorsal-fin spine stout and moderately recurved. Vertebral counts: total vertebral counts 71 to 83 , monospondylous vertebral counts 37 to 45 , diplospondylous vertebral counts 14 to 19 , precaudal vertebral counts 53 to 60 , caudal vertebral counts 18 to 26. Intestinal valve counts not available. A large lantern shark, up to at least 68 cm total length or more. Colour: brown on dorsal surface, grading to black ventrally with inconspicuous lateral photomarks that may vary between individuals, some with thin relatively straight anterior branch extending over pelvic fins, and shorter relatively straight posterior branch extending past second dorsal-fin base, or with shorter anterior and posterior branches that are upswept giving it a "gull wing-like" appearance above and behind the pelvic fins; other black photomarkings along caudal fin and at its base. The original description of this species, based on a preserved specimen, states that the back is scattered with dark brown spots, but these dark brown spots appear to be absent in freshly caught specimens based on the examination of numerous specimens by the author.

Distribution: Southern Namibia to Cape Point, South Africa. Also found in the Southwestern Indian Ocean, from the Western Cape Province (Cape Peninsula) to the Eastern Cape Province (at least Port Alfred), South Africa.

Habitat: A poorly known lantern shark found on or near bottom at 383 to 1300 m , but mostly below 600 m . It has been caught in the epipelagic zone in the open ocean at 120 m depth over very deepwater. This species is broadly sympatric with Etmopterus granulosus.

Biology: Viviparous with yolk-sac, litters of 2 to 21, averaging 12, but little else known about its reproductive cycle. Diet includes small bony fishes, including myctophids, and cephalopods and penaeid shrimps.

Size: Maximum total length at least 68 cm ; males mature at about 55.5 cm ; females mature at about 62 cm . Size at birth about 17 to 22 cm , but smallest free-swimming individuals measured 22 to 25 cm in total length.

Interest to Fisheries and Human Impact: Interest to fisheries none, although the species is caught as bycatch in bottom trawl fisheries.

The conservation status of this species has been assessed as Data Deficient.


Fig. 90 Etmopterus compagnoi
Known distribution

Local Names: Compagno's lanternshark; Broadbanded lanternshark.

Remarks: This large sized lantern shark has a rather checkered taxonomic history. It was initially confused by early authors with the Eastern North Atlantic and Mediterranean Etmopterus spinax, a species that does occur off Angola, but subsequent authors considered it to be E. gracilispinis, a Southwestern Atlantic species. The present author and L.J.V. Compagno recognized it as being a distinctly different species based on a large number of specimens they collected during a series of survey cruises they participated on along the west coast of Southern Africa (Compagno, Ebert and Cowley, 1991). However, Fricke and Koch (1990) also recognized this species as being distinct and described it. Subsequent investigations by L.J.V. Compagno (Compagno et al., 2005) lead him to reconsider the validity of $\boldsymbol{E}$. compagnoi, whereby he reclassified it as $\boldsymbol{E}$. unicolor, a Japanese species that may also occur off Australia and New Zealand. Re-examination of southern African E. compagnoi material by the present author (D.A. Ebert), N. Straube, and R. Leslie (pers. comm. and unpubl. data) supports the separation of this species from $\boldsymbol{E}$. unicolor. Recent records of $\boldsymbol{E}$. spinax from off Angola should be carefully examined to confirm whether it is that species or may represent a range extension of E. compagnoi.

Literature: Compagno, Ebert and Smale (1989); Fricke and Koch (1990); Compagno, Ebert and Cowley (1991); Ebert, Compagno and Cowley (1992); Compagno et al. (2005); Ebert (2013); Ebert, Fowler and Compagno (2013); D.A. Ebert, R. Leslie, and N. Straube (unpubl. data).

## Etmopterus granulosus (Günther, 1880)

Spinax granulosus Günther, 1880, Rep. Sci. Res. Voy. H. M. S. Challenger, Zool., 1(6): 19, pl. 2C. Holotype: British Museum (Natural History), BMNH-1879.5.14.460, 256 mm TL adol. male, off Chile, Challenger Sta. 305A, $47^{\circ} 47^{\prime} \mathrm{S}$ to $47^{\circ} 48.5^{\prime} \mathrm{S}$, $74^{\circ} 47^{\prime} \mathrm{W}$ to $74^{\circ} 46^{\prime} \mathrm{W}, 220 \mathrm{~m}$.

Synonyms: None.
Other Combinations: None.
FAO Names: En - Southern lanternshark; Fr - Sagre long nez; Sp - Tollo negro narigón.


Fig. 91 Etmopterus granulosus
Field Marks: Body stocky, conspicuous lines of denticles on body, blade-like unicuspidate teeth in lower jaw and teeth with cusps and cusplets in upper jaw, two spined dorsal fins, no anal fin, conspicuous black markings on underside of body and tail, with tail marking short and not extending far posteriorly.

Diagnostic Features: Head shallow and flattened, not deep and conical; head relatively long, about 22 to $24 \%$ of total length and 2.3 times in snout-vent length; head width about 1.1 times preoral snout; head low, height $11 \%$ of total length. Prespiracular length 1.2 times spiracle-pectoral space. Snout broad and flattened, not bulbous; preoral length short and 9.5 to $11 \%$ of total length. Eyes narrow and elongated; upper eyelid apparently without a pale naked patch. Gill openings about as wide as spiracle; width of third gill opening less than one-third of eye length. Mouth relatively broad and 1.4 times eye length. Total tooth row counts upper jaw 27, lower jaw 28 (holotype); upper teeth with one or two pairs of cusplets, cusps expanded, about 2.5 times higher than adjacent cusplets; upper teeth of adolescent males with a cusp and a pair of long cusplets. Body moderately firm, cylindrical or slightly depressed, and moderately stout. Predorsal spine length about $35 \%$ of total length; interdorsal space slightly shorter than prebranchial length; pectoral-pelvic space about equal to head length in adolescent; snout tip to rear flank marking base $105 \%$ of snout tip to second dorsal-fin spine origin; dorso-caudal space about $9 \%$ of total length and about 2.1 in interdorsal space; pelvic-caudal space $16 \%$ of total length, about 1.5 times first dorsal fin length, 1.2 in interdorsal space, 0.8 of prebranchial length, slightly greater than prespiracular length, much shorter than head, and about 1.5 times in pectoralpelvic space. No rows of greatly enlarged denticles on flanks above pectoral fins; denticles largely absent from underside of snout except for lateral patches; denticles on head not in longitudinal rows, but in regular longitudinal rows on flanks, tail, and caudal base; denticles present on second dorsal fin, densely covering it; lateral trunk denticles short, robust, wide spaced, with moderately stout, high, curved conical crowns. Distal margins of fins not fringed with naked ceratotrichia. Pectoral fin small with anterior margin length about 9\% of total length, rounded-angular in shape. First dorsal-fin origin slightly in front of pectoral-fin free rear tips and over inner margins, base considerably closer to pectoral-fin bases than pelvic fins; first dorsal-fin spine stout, short, and lower than first dorsal-fin apex, origin nearer to snout tip than upper caudal-fin origin. Second dorsal fin much larger than first but less than twice its area, height $31 \%$ of second dorsal-fin length, apex more or less pointed, posterior margin broadly concave; second dorsal-fin spine stout and strongly recurved, but with its tip obliquely vertical in subadult. Dorsal caudal-fin margin slightly longer than head length. Vertebral counts: total vertebral counts 86 to 94 , precaudal vertebral counts 59 to 67, caudal vertebral counts 23 to 33 , monospondylous vertebral counts 46 to 53 . Intestinal valve counts 10 to 13 . Size large with adults to 88 cm total length. Colour: grey-brown on dorsal surface, underside of snout, branchial region and abdomen abruptly black, dorsal surface lighter in preservative, ventral surface conspicuously dark; fins light distally, no conspicuous dark bands at tip and through middle of caudal fin; apparently no small white pineal blotch on dorsal surface of head. No photolines on body although individual photophores are scattered on flanks. Suprapelvic photomark present anteriorly on pelvic-fin bases but not extending behind pelvic fins. Flank photomarks present; flank photomark base well behind second dorsal-fin spine; anterior branch of flank photomark long, slender and tapering posteriorly, much longer than posterior branch, posterior branch $27 \%$ of anterior branch; posterior branch of flank photomark short broad and extending slightly behind pelvic fins, not 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 very narrow, not enveloping ventral surface and not extending onto sides of caudal peduncle; caudal base photomark with a sharp-tipped, moderately elongated posterior branch about $4 \%$ of total length; oval central caudal photomark absent. Upper caudal photomark present, straight and short, and about 3\% of total length.

Distribution: In the Southeastern Atlantic it occurs from Orange River to Eastern Cape Province, South Africa, also possibly off Inaccessible Island, Tristan da Cunha Island group. Also found in the Southern Indian, Southern Pacific and Southwestern Atlantic Oceans. Wide-ranging in the Southern Ocean but records of large etmopterids from Southern Ocean islands and seamounts should be closely examined for this species.

Habitat: A large lantern shark from the upper continental and insular slopes, found on or near the bottom at depths of about 250 to 1500 m , commoner below 600 m . Recorded at 383 to 1300 m off South Africa, 830 to 1200 m off Australia, and about 250 to 1500 m off New Zealand. Where it occurs this species is typically very common.

Biology: Viviparous with a yolk-sac, with litter size of 9 to 16 off Australia and 6 to 15 off New Zealand. Wetherbee (1996) counted 7 to 30 large ovarian eggs (over 10 mm in diameter) and 9 to 15 large uterine eggs ( 40 to 55 mm in diameter) in each uterus and up to 39 in both uteri for New Zealand females, suggesting larger litters than indicated by fetal counts alone. New Zealand sharks may breed all year long, as there were mature males with semen-filled seminal vesicles and mature females with large ovarian and uterine eggs in July (winter) and October (late spring) off New Zealand (Wetherbee, 1996). Southeastern Atlantic population reproductive cycle little known, but neonates are quite common in the midwater, often several hundred meters off the bottom.

Age at maturity has been estimated at 30 years for females and 20 years for males, with a maximum age estimated for females and males of 57 and 48 years, respectively.

Off South Africa this shark feeds heavily on the large deepwater histioteuthid squid Histioteuthis miranda and is capable of dismembering individual squid much larger than it can swallow whole. It also eats the squid Todarodes angolensis (Ommastrephidae), unidentified octopuses, penaeid shrimp, unidentified decapod crustaceans, lanternfish (Myctophidae, including Diaphus sp.), barracudina (Paralepididae), deepwater eels (Synaphobranchidae), and other, unidentified teleosts (Ebert, Compagno and Cowley, 1992, and unpubl. data). Clark, King and McMillan (1989) found that off New Zealand this shark eats primarily bony fishes, cephalopods and decapod crustaceans (mostly unidentified), but also salps (Thaliacea), sponges (Porifera), and ribbonworms (Nemertina). Fish prey from New Zealand Etmopterus granulosus included oreo dories (Oreosomatidae), lanternfish (Myctophidae), hake (Merluccidae including hoki, Macruronus novaezelandiae), rattails (Macrouridae), Bathylagidae, and Idiacanthidae; cephalopod prey included octopods and squids (particularly Brachioteuthis sp.); and crustaceans included unidentified decapods, euphausiids, and mysids. Some of the prey fish found in New Zealand E. granulosus may have been scavenged from fisheries catches (oreo dories and Macruronus), but also suggested active feeding on small fishes (swallowed whole) and on larger fishes (eaten in bite-sized chunks).

Size: Maximum total length 88 cm ; size at maturity varies by region, but this may be an artefact of multiple species being involved. In general, males are adult at 46 to 68 cm and females are adult at 62 to 88 cm . Size at birth about 17 to 20 cm .

Interest to Fisheries and Human Impact: Interest to fisheries none at present, although taken as an incidental bycatch of trawl fisheries for deepwater hake (Merluccius paradoxus) fisheries off the west coast of South Africa, and probably caught in deepwater trawl fisheries for orange roughy (Hoplostethus atlanticus). This species is discarded from bottom trawl catches off South Africa.

Conservation status is Least Concern.
Local Names: None.
Remarks: A recent taxonomic study of this species has concluded that it appears to be a large, wide-ranging, Southern Hemisphere etmopterid species and not endemic to southern Patagonia as previously thought (N. Straube, pers. comm.). The New Zealand Etmopterus baxteri is a junior synonym of this species.

Literature: Günther (1880); Bass, D'Aubrey and Kistnasamy (1976); Clark, King and McMillan (1989); Compagno, Ebert and Smale (1989); Tachikawa, Taniuchi and Arai (1989); Compagno, Ebert and Cowley (1991); Ebert, Compagno and Cowley (1992); Wetherbee (1996); Yano (1997); Irvine, Stevens and Laurenson (2006); Kyne and Lamilla (2007); Last and Stevens (2009); Straube, Kriwet and Schliewen (2011); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press); P.C. Clerkin (pers. comm.); D.A. Ebert (unpubl. data).

## 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. 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 of the fishes of the north-eastern Atlantic and of the 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 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 BM (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: None.
Other Combinations: None.
FAO Names: En - Smooth lanternshark; Fr - Sagre nain; Sp - Tollo lucero liso.


Fig. 93 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 to $106 \%$ of snout tip to second dorsal-fin spine origin; dorso-caudal space 9 to $11 \%$ of total length, about 1.8 to 2.9 times 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 $80 \%$ 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 50 cm total length. 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-fin base photomark present, with anterior branch broad, partly enveloping ventral surface of caudal peduncle but not extending onto its sides; caudal-fin base photomark with elongated, blunt-tipped posterior branch over $7 \%$ of total length. No central caudal photomark. Upper caudal photomark present and straight.

Distribution: Angola, Namibia, and the west coast of South Africa. Elsewhere widespread, but scattered in the Atlantic, Indian and Western Pacific Oceans.

Habitat: A lantern shark 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 South Atlantic and Central North Pacific, at depths between the surface and 110 to 708 m over deepwater (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 in the Southeastern Atlantic 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 spp.), and lanternfish (Myctophidae, Diaphus spp.), and small squaloid sharks.


Fig. 94 Etmopterus pusillus
Known distribution

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 at 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 none in Southern Africa, but 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 the species level.

This species is listed as Least Concern given its widespread geographic and bathymetric distribution.
Local Names: None.

Remarks: Examination of regional Etmopterus 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 deep-sea ridges far from continental land masses (D.A. Ebert and J.D.S. Knuckey, unpubl. data).

Literature: Bigelow and Schroeder (1957); Cadenat and Blache (1981); Ebert, Compagno and Cowley (1992); Shirai and Tachikawa (1993); Coelho and Erzini (2005, 2007, 2008); Coelho, Tanaka and Compagno (2009); Last and Stevens (2009); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press); Ebert and Knuckey (unpubl. data).

## Etmopterus sculptus Ebert, Compagno and DeVries, 2011

Etmopterus sculptus Ebert, Compagno and DeVries, 2011, Copeia, 2011(3): 379, figs. 1-2, tab. 1. Holotype: South African Museum, SAM 37569, 442 mm TL, mature male, RV Africana cruise 060, mesopelagic survey, station A 6986060 01-02B, $33^{\circ} 22.9^{\prime} \mathrm{S}^{\prime} 17^{\circ} 29.1^{\prime} \mathrm{E}, 552 \mathrm{~m}, 04$ March 1988.

Synonyms: Etmopterus lucifer Gilchrist, 1922: 49. Barnard, 1925: 50. Smith, 1949: 59, fig. 52. Bigelow and Schroeder, 1957: 56. Smith 1965: 59, fig. 52. Bass, D’Aubrey and Kistnasamy, 1976: 25, figs. 17, 18c. Lleonart and Rucabado, 1984: 41. Allue et al., 1984: 126. Compagno, 1984a: 79. Lloris, 1986: 103, fig. 29. Turon et al., 1986: 65, 137, 173, 229, 295. Van der Elst and Vermeulen, 1986: 6. Spinax lucifer Norman, 1935: 37. Etmopterus brachyurus Bass, Compagno and Heemstra, 1986: 55, fig. 5.11. Compagno, Ebert and Smale, 1989: 30, ill. Compagno, Ebert and Cowley, 1991: 61. Ebert, Compagno and Cowley, 1992: 604. Compagno, 1999: 114. Etmopterus sp. Compagno et al., 2005: 95.

Other Combinations: None.
FAO Name: En - Sculpted lanternshark.


Fig. 95 Etmopterus sculptus

Field Marks: A moderately large lanternshark with non-overlapping, uniformly distributed dermal denticles giving it a sculpted textured appearance, well defined flank markings with anterior branch slightly longer than the posterior branch, upper teeth multicusped with a median spear-shaped cusp flanked by 2 to 3 lateral cusplets. Coloration dark grey brown above, black below with a well-defined narrow, elongated black flank marking above, in front of and behind pelvic fins.

Diagnostic Features: Head sub-conical, long, 19.0 to $21.8 \%$ of total length, slightly depressed, height 1.3 to 1.4 times in width. Snout moderately long, conical in lateral view, in dorsal view triangular-shaped becoming narrowly rounded at snout-tip. Eye elliptical, large, length 4.3 to 4.7 times in head length, 0.5 to 0.6 times eye width; eyes moderately spaced, inter-orbital space 1.1 to 1.2 times in head width. Spiracles small, crescent shaped. Nostrils large, oblique, length nearly equal to eye and internarial width; anterior nasal flap reasonably developed, triangular. Gill openings relatively small, narrow, slightly arched, size progressively decreasing posteriorly, height of first gill slit 1.3 to 1.5 times height of fifth gill opening, inter-gill length nearly equal to eye length. Mouth broad, length 0.2 times width, slightly curved, width 0.8 to 0.9 in preoral length. Teeth dissimilar in upper and lower jaw; upper teeth multicuspid in three functional series, functional teeth in lower jaw in single series, five to six series of replacement teeth in upper and lower jaw; multicuspid upper teeth small, perpendicular, with long, broad, spear-shaped median cusp flanked by 2 to 3 lateral cusplets on each side more than one half the length of the median cusp, innermost cusplet longest, decreasing in size distally; teeth in lower jaw fused into single row, unicuspid, bladelike, oblique, $30^{\circ}$ gradation. Tooth count in upper jaw 23 to 25 , lower jaw 36 to 43 . Body fusiform, trunk sub-cylindrical, moderately slender to somewhat robust. Dermal denticles on dorsal surface of body slender, moderately long, thorn-like, weakly curved, giving skin a jagged texture; denticles on ventral surface of snout, head, abdomen and tail straight, slightly curved, directed at an angle rearward, reduced in size, randomly arranged along ventral surface of body. Upper body surface covered by moderately spaced dermal denticles arranged in longitudinal rows, varying slightly in formation above, below mid-level of upper body; above mid-level, linear denticles diagonal, unidirectional, directed antero-ventrally along upper margin of snout to nostrils, directed postero-ventrally along upper margin of head, trunk, tail, and base of second dorsal fin; denticles on back in a single line flanking midline directed rearward to caudal axis; below mid-level, longitudinal dermal denticles on head, trunk and tail horizontal, directed rearward; transverse, curving upward posterior to pelvic fin towards
caudal axis. Area immediately behind dorsal, pectoral, and pelvic fins naked, without denticles. First dorsal fin small, prone, sub-triangular, insertion of base well forward of pelvic-fin origin; first dorsal-fin spine well behind pectoral-fin rear margin, short, slightly curved. Second dorsal fin conspicuously larger, more elevated than first dorsal fin; second dorsal-fin apex slightly sub-angular, posterior margin concave, free rear tip elongated; second dorsal-fin spine origin slightly behind insertion of pelvic fins, strongly curved towards fin apex, large, height about equal to fin height. Pectoral fins relatively large, base about two times into anterior margin length, angular at free rear tips, posterior margin somewhat straight edged. Caudal peduncle rounded, height about equal to width, tapering posteriorly, relatively long. Caudal fin moderately elongated, sub-terminal notch conspicuous, nearly sub-equal to head length, but conspicuously shorter than caudal peduncle. Vertebral counts: total vertebral counts 78 to 85 , monospondylous vertebral counts 41 to 46 , diplospondylous vertebral counts 16 to 19, precaudal vertebral counts 60 to 64 , caudal vertebral counts 18 to 21 . Intestinal valve counts 8 to 9 . Size moderate with adults to 52 cm total length. Colour: dark grey-brown above, ventral surface black with a narrow, elongated black margin above, in front of and behind pelvic fins. Upper caudal-fin lobe black, lower lobe and tips of fins whitish, not translucent. Photolines present on body distinct, intricate; head markings extending from ventral surface of head, starting just posterior to snout tip, expanding upward to level of nostrils, descending sharply below eye, extending slightly upwards towards mouth; discontinuous with belly marking at upper end of mouth; breaks in otherwise solid photophores just posterior to nostrils, ventrally at mid-level of eye; subtle luminescent markings visible in preserved specimens above, slightly behind eye. Dorsal surface of head bearing an elaborate photophore pattern, originating from three lines of photophores on back stretching from caudal-fin origin blending into a dark solid patch between spiracles, branching out into two distinct photophore lines extending to anterior margin of eyes, fused into a dense aggregation of photophores towards tip of snout. Belly marking connected to head behind lower half of mouth, extending dorsally below gill openings on lower base of pectoral fin creating a two-prong forked pattern, extending onto upper pectoral surface resembling a curved thorn; margin on pectoral-pelvic space clearly defined, line extending from rear margin of pectoral-fin base to pelvic-fin insertion; dark, slightly curved finger-like extension on upper pelvic-fin base less than half the length of pelvic-fin base with dark sub-angular extension on ventral surface. Flank markings well defined, consisting of both an anterior and posterior branch; anterior branch long, 8.4 to $11.1 \%$ of total length, slender, extending well beyond origin of pelvic-fin; posterior branch slightly shorter than anterior, 7.5 to $8.6 \%$ of total length, extending just anterior of distal free rear-tip of second dorsal fin; base of flank marking wide. Central caudal-fin marking is very distinct, narrowly ovoid, its length about twice that of flank marking base. Upper caudal-fin marking very narrow, its length about two times central caudal-fin marking.

Distribution: Namibia to southern Mozambique.
Habitat: A lantern shark from the upper continental slopes, on or near bottom at depths of 240 to 1023 m , mostly below 450 m .

Biology: Viviparous with yolk-sac, but little else known of its reproductive biology. Diet includes lanternfish (Myctophidae, including Diaphus sp. and Lampanyctodes hectoris) and lightfish (Phosichthyidae), but also cephalopods and crustaceans (including penaeid shrimp).

Size: Maximum total length about 53 cm ; adult females 45 to 53 cm long, adult males about 41 to 48 cm in length. Size at birth is from 15 to 17 cm total length.

Interest to Fisheries and Human Impact: Interest to fisheries none, although taken as bycatch in bottom trawl fisheries for hake (Merluccius spp.).

The conservation status of this species has not been assessed.

Local Names: None.
Remarks: This large, dark, rough, lantern shark with linear denticles from snout-tip to caudal-fin base has been previously confused with Etmopterus brachyurus and $\boldsymbol{E}$. lucifer in the southern African literature but is quite distinct from both of these species and from E. molleri. It is close to the apparently smaller dark lantern shark E. bullisi from the Western North Atlantic but differs in numerous proportional measurements, in higher tooth counts, and in photomark patterns.


Fig. 96 Etmopterus sculptus

Literature: Bass, D’Aubrey and Kistnasamy (1976); Compagno (1984a); Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); Ebert, Compagno and Cowley (1992); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press); D.A. Ebert (unpubl. data).

### 2.2.5 Family SOMNIOSIDAE

Family: Somniosidae Jordan, 1888, Man. Vert. Ani. Northern U.S., ed. 5: 15.
Type genus: Somniosus Lesueur, 1818.
Number of Recognized Deep-sea Southeastern Atlantic Ocean Genera: 5.
Synonyms: None.
FAO Names: En - Sleeper sharks; Fr - Laimargue dormeurs; Sp - Tiburones Tollos.
Field Marks: Short to long-nosed, cylindrical to somewhat compressed sharks with two dorsal fins with or without spines, the first with origin in front of pelvic-fin origins and usually opposite the pectoral-fin bases or pectoral-fin inner margins and exceptionally just behind the pectoral-fin free rear tips, the 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, no anal fin, caudal fin with a strong subterminal notch, no keels on the caudal peduncle, 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.

Diagnostic Features: Head moderately broad and somewhat flattened or conical. 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. 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 saw-like 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-fin 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, submarine peaks and ridges. The giant sleeper sharks of the genus Somniosus (subgenus Somniosus, S. antarcticus, S. microcephalus, and S. pacificus) are among the few non-batoid sharks 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 both the Eastern and Western Hemispheres. These sharks have very low diversity in the Eastern Pacific, with only the sleeper shark S. pacificus in the Eastern North Pacific and S. antarcticus and Centroselachus crepidater in the Eastern South Pacific off South America. Several of the species are wide-ranging in the Atlantic but the greatest known diversity of the family is in the IndoWest 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 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 most species are 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. The family has one apparently epipelagic species (Scymnodalatias albicauda) and one bottom-dwelling species that is semioceanic (Zameus squamulosus) and may occur in the epi- and mesopelagic zones of the open ocean.

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 Far East and 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 a high squalene content. In the Southeastern Atlantic they are caught on occasion as bycatch in bottom trawl fisheries.

Local Names: Sleeper sharks, Velvet dogfishes.
Remarks: The family is small, but rather diverse with seven genera and about seventeen species globally, of which six species occur within the area.

Literature: Müller and Henle (1839); Gray (1851); Duméril (1865); Günther (1870); Regan (1908a); Garman (1913); Bigelow and Schroeder (1948, 1957); Cadenat (1959a, b, c), Garrick (1959a, b, 1960b); Bass, D'Aubrey and Kistnasamy (1976); Cadenat and Blache (1981); Compagno (1984a, 2005); Taniuchi and Garrick (1986); Yano, Stevens and Compagno (2004); Last and Stevens (2009); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press); D.A. Ebert (unpubl. data).

## List of Deep-sea Species Occurring in the Area:

Centroscymnus coelolepis Bocage and Capello, 1864
Centroscymnus owstonii Garman, 1906
Scymnolachus crepidater (Bocage and Capello, 1864)
Somniosus antarcticus Whitley, 1939
Zameus squamulosus (Günther, 1877)

## Key to Deep-sea Southeastern Atlantic Ocean Genera:

1a. Dorsal-fin spines present, though sometimes short
and partly covered by skin (Fig. 97a) . . . . . . . . . . .

1b. Dorsal-fin spines absent4

2a. Snout greatly elongated, preoral length about equal to distance from mouth to pectoral-fin origins (Fig. 97b). Upper labial furrows greatly elongated, their lengths greater than distance between their anterior ends .

Centroselachus

2b. Snout shorter, preoral length much less than distance from mouth to pectoral-fin origins (Fig. 98a). Upper labial furrows shorter, their lengths less than distance between their anterior ends

3a. Lower teeth with relatively low, more or less oblique cusps (Fig. 98b)

Centroscymnus

3b. Lower teeth with relatively high, more or less erect cusps (Fig. 99)

Zameus


Fig. 97 Centroselachus

a) UNDERSIDE OF HEAD

b) LOWER TEETH

Fig. 98 Centroscymnus


Fig. 99 Zameus

4a. Lower teeth with high, erect cusps (Fig. 100a). Ventral caudal-fin margin half as long as dorsal caudalfin margin (Fig. 100b). Eyes horizontally elongated

Scymnodalatias

4b. Lower teeth with low, oblique cusps (Fig. 101a). Ventral caudal-fin margin about $2 / 3$ as long as dorsal caudal-fin margin (Fig. 101b). Eyes nearly circular . .

Somniosus

a) LOWER TEETH

b) CAUDAL FIN

Fig. 100 Scymnodalatias


Fig. 101 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 Deep-sea Southeastern Atlantic Ocean 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, small fin spines present on both dorsal fins though sometimes inconspicuous (Centroscymnus owstonii), pectoral fins with broadly rounded free rear tips, no anal fin and caudal fin with a strong subterminal notch. Colour generally greyish or blackish-brown.

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-fin 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 main differences separating Centroscymnus and Scymnodon, two very similar genera, by previous authors stem from divergent views on the relative importance of lower tooth shape as opposed to dermal denticle morphology as the primary criteria separating these two genera. Compagno (1984a) commented that the separation of this genus from Scymnodon was unsatisfactory with the criteria in current usage at the time, but hesitated to merge them pending further work on the problem. Subsequently, Taniuchi and Garrick (1986) clarified the situation somewhat by re-examining these primary characters and concluded that those species with "Scymnodon" denticles (ringens, plunketi, ichiharai, and macracanthus) lacked ridges on the juvenile denticles, but these were replaced by fully ridged denticles in adults. Those species with "Centroscymnus" denticles (coelolepis, owstonii, and crepidater) by contrast had partly ridged juvenile denticles, but are replaced by denticles in which the ridging is progressively reduced with growth. These authors further went on to note that the cusp height to root height values, although not as well defined, could be used as a subjective means to separate these genera. However, among the aforementioned species they examined, $\boldsymbol{S}$. ringens had a significantly higher cusp height to root height ratio (124\%) than the other seven species they considered which ranged from 14 to $74 \%$. Taniuchi and Garrick (1986) stated that if Scymnodon were only to include S. ringens, as there is clearly a defined demarcation between it and the other species, and the others remained in Centroscymnus it would agree with Compagno (1984a). Compagno (1999b) somewhat followed this generic framework, except left ichiharai within Scymnodon, but later and without explanation (Compagno, 2005) moved ichiharai to Zameus and resurrected the genera Centroselachus (crepidater)
and Proscymnodon (macracanthus and plunketi) leaving coelolepis and owstonii as the only species within the genus Centroscymnus. The arrangement of this genus and its separation from the genus Scymnodon follows Ebert (2013), Ebert, Fowler and Compagno (2013), and Ebert and Compagno (In press), but acknowledges that further work, particularly at the molecular level, will help further clarify the status of this group.

## Key to Deep-sea Southeastern Atlantic Ocean 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. 102). Abdomen without lateral ridges; intestinal valve with 16 to 21 turns .
. . . . . . . . . . . . . . . . . . Centroscymnus coelolepis
1b. Snout moderately long, preoral length about as long as distance from mouth to first gill slits, and about equal to mouth width (Fig. 103). Abdomen with lateral ridges; intestinal valve with 11 to 15 turns

Centroscymnus owstonii


Fig. 102 C. coelolepis


Fig. 103 C. owstonii

## 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: ?Centroscymnus fuscus Gilchrist and von Bonde, 1924, Rep. Fish. Mar. Biol. Surv. Un. S. Africa, (3): 2. Holotype: 1100 mm TL, probably lost, $32^{\circ} 3^{\prime} 00^{\prime \prime} \mathrm{S}, 16^{\circ} 2^{\prime} 00^{\prime \prime} \mathrm{E}$, off St. Helena Bay, Western Cape, South Africa, 658 m . This species was tentatively synonymized with Centrophorus squamosus by Hulley (1971, Ann. S. African Mus. 57(11): 265270) and Bass, D'Aubrey and Kistnasamy (1976, S. African Ass. Mar. Biol. Res., Oceanogr. Res. Inst., Invest. Rep. (45): 27) but details of its original description suggests that it may have been based on Centroscymnus coelolepis, which is common off the west coast of South Africa below 600 m (Compagno, Ebert and Smale, 1989; Compagno, Ebert and Cowley, 1991) and has been taken in the area and at the depth where the type of C. fuscus was collected. In contrast Centrophorus squamosus is rare south of central Namibia. 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, $40^{\circ} 00^{\prime} \mathrm{N}, 68^{\circ} 52^{\prime} \mathrm{W}$, off Georges Bank, 769-878 m. Centroscymnus macrops Chu, Hu and Li, in Chu et al., 1982, Ocean. Limn. Sinica, 13(1): 305, 310, fig. 4. Holotype: South China Sea Fisheries Research Institute, no. O0150, 792 mm female, $19^{\circ} 24^{\prime} \mathrm{N}, 114^{\circ} 15.4^{\prime} \mathrm{E}$, South China Sea, 964 m .
Other combinations: None.
FAO Names: En - Portuguese dogfish; Fr - Pailona commun; Sp - Pailona.


Fig. 104 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 very 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 this 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-fin 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: South Africa (Eastern and Western Cape provinces), Namibia, and Angola. Elsewhere, wideranging in the Atlantic, Indian Ocean and Western Pacific.

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 , with a depth range of 128 to 3675 m . Bottom water temperatures where this species has been captured ranges 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 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 spp.) this shark will core flesh out of live cetaceans, deep-diving pinnipeds, and possibly large drifffishes (Nomeidae).

Size: Maximum total length about 122 cm ; males mature at 72 to 100 cm ; females mature at 92 to 110 cm . Size at birth about 23 to 35 cm ; smallest free swimming individual was 34 cm total length.


Fig. 105 Centroscymnus coelolepis
Known distribution

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. This species is not targeted in the Southeastern Atlantic Ocean, but is taken incidentally as bycatch. It is utilized for fishmeal, dried salted for human consumption, and for its squalene-rich liver oil. In Australian waters it is discarded because of the high mercury content in its flesh.

Conservation status is Near Threatened globally.
Local Names: Portugese shark (English).
Literature: Bigelow and Schroeder (1948, 1957); Cadenat and Blache (1981); Yano and Tanaka (1983, 1987, 1988); Compagno (1984a); Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); Ebert, Compagno and Cowley (1992); Clarke, Connolly and Bracken (2001); Stevens and Correia (2003); Verissimo, Gordo and Figueiredo (2003); Bañón, Piñeiro and Casas (2006); Last and Stevens (2009); Kyne and Simpfendorfer (2010); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013); Ebert and Compagno (In press); D.A. Ebert (unpubl. data).

## Centroscymnus owstonii Garman, 1906

Centroscymnus owstoni 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.

## Other combinations: None.

FAO Names: En - Roughskin dogfish; Fr - Pailona rapeux; Sp - Sapata lija.


Fig. 106 Centroscymnus owstonii
Field Marks: Body fairly stocky that does not taper abruptly from pectoral region, moderately long snout, lanceolate upper teeth and bladelike lower teeth with short, oblique cusps, large lateral trunk denticles with mostly smooth, circular, cuspidate and acuspidate crowns in adults and subadults and dorsal fins with fin spines buried in the fins or with tips slightly protruding, 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 first 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-fin 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 to 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 total length. Colour: light grey or brown to dark brown or black, without any conspicuous markings.

Distribution: Namibia, and South Africa. Also found in the Eastern Central Atlantic, Western Atlantic, Western Indian, Western Pacific and Eastern South Pacific Oceans.

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 fishes and cephalopods. As far as known it does not appear to remove core flesh from live cetaceans, deepdiving 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: Of no interest to fisheries in Southern Africa, it is mostly a discarded bycatch. It is not considered very common in the region, but this may be due to misidentification with Centroscymnus coelolepis or Centroselachus crepidater.

The conservation status of this species is currently listed as Least Concern.

Local Names: Rough dogfish, Shortnose velvet dogfish.
Remarks: Examination of material of Eastern Atlantic Centroscymnus cryptacanthus, including the holotype, indicated that the covered fin spine that primarily separates C. cryptacanthus from C. owstonii may be variably covered or uncovered (Ebert and Compagno, In press). This was previously observed by Hernández et al. (1998), who after examining many specimens of what they termed C. cryptacanthus, suggested that the dorsal fin character used by Compagno (1984a)


Fig. 107 Centroscymnus owstonii
$\square$ Known distribution to separate C. cryptacanthus from C. owstonii were variable and probably indicated one species. Furthermore, radiography of specimens from the Western North Atlantic, Eastern Atlantic, and the Western Pacific revealed similar vertebral counts in all the material examined. In addition, all these specimens appear very similar in external morphology.

Regan (1906b) published his C. cryptacanthus in December 1906, but there is no indication in his account that he'd seen Garman's (1906) description of C. owstonii published in January 1906.

Literature: Garman (1906, 1913); Regan (1906b); Bigelow and Schroeder (1957); Garrick (1959a); Krefft (1968); Cadenat and Blache (1981); Yano and Tanaka (1983, 1987, 1988); Compagno (1984a); Paul (2003a); Gibson et al. (2008); Last and Stevens (2009); Last and Stevens (2009); Kyne and Simpfendorfer (2010); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press); D.A. Ebert (unpubl. data).

## Centroselachus Garman, 1913

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 Deep-sea Southeastern Atlantic Ocean 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-fin 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.

Local Names: Longnose Velvet Dogfishes.

## 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: Centroscymnus crepidater Bass, D'Aubrey and Kistnasamy, 1976: 33, fig. 25; Bass, Compagno and Heemstra, 1986: 52, fig. 5.6; Compagno 1984a: 56, ill.; Compagno, Ebert and Smale, 1989: 32, ill.; Compagno, Ebert and Cowley, 1991: 58; Ebert, Compagno and Cowley 1992: 604.

Other combinations: None.
FAO Names: En - Longnose velvet dogfish; $\mathbf{F r}$ - Pailona à long nez; $\mathbf{S p}$ - Sapata negra.


Fig. 108 Centroselachus crepidater
Field Marks: Body fairly slender that does not taper abruptly from pectoral region, very long snout, greatly elongated labial furrows that nearly encircle mouth, lanceolate upper teeth and bladelike lower teeth with moderately long, oblique cusps, moderately large lateral trunk denticles with partly smooth, oval, cuspidate crowns in adults and subadults, dorsal fins with very small fin spines. Colour a uniform black or blackish brown.

Diagnostic Features: See genus Centroselachus.
Distribution: Namibia and west coast of South Africa. Elsewhere, wide-ranging in the Eastern Atlantic and Indo-Pacific.
Habitat: A little-known but common deepwater dogfish found on the upper continental and insular slopes on or near the bottom at depths of 200 to 1500 m .

Biology: 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), crustaceans 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, but not utilized in the Southeastern Atlantic.

Conservation status for this species is Least Concern due to its wide, but patchy distribution and apparent population increases in some regions.

Local Names: None.
Remarks: The possible synonymy of Centrophorus rossi Alcock, 1898 with this species was discussed by Bigelow and Schroeder (1957) and Garrick (1959a), both of whom recognize $\boldsymbol{C}$. rossi because of its supposedly longer head. Compagno (1984a) noted that the holotype of $\boldsymbol{C}$. rossi in the Zoological Survey of India, Calcutta, ZSI F 225/1 (233 mm female possibly newborn) had a head length $29.6 \%$ of total length, that fell in the range reported for Centroscymnus crepidater by Cadenat and Blache (1981), 21.3 to $29.7 \%$ of total length. As the specimen apparently had no other characters that distinguish it from C. crepidater, Centrophorus rossi was synonymized with C. crepidater by Compagno (1984a) and is followed here. The holotype of $\boldsymbol{C}$. rossi is not the only record of this species from the Western Indian Ocean, as records of Centroscymnus owstonii from the Aldabra Island group by Forster et al. (1970) were based on C. crepidater (Bass, Compagno and Heemstra in Smith and Heemstra, 1986) and Shcherbachev (1987) found the species on the Madagascar range of seamounts. In fact, this species is rather common at depth along the southern Madagascar range of seamounts ( P . Clerkin, Moss Landing Marine Laboratories, pers. comm.).


Fig. 109 Centroselachus crepidater

Literature: Bigelow and Schroeder (1948, 1957); Compagno (1984a); Bass, Compagno and Heemstra (1986); Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); Ebert, Compagno and Cowley (1992); Stevens (2003a); Irvine, Stevens and Laurenson (2006); Last and Stevens (2009); Kyne and Simpfendorfer (2010); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press); D.A. Ebert (unpubl. data); (P. Clerkin, Moss Landing Marine Laboratories, unpubl. data).

## Scymnodalatias Garrick, 1956

Genus: Scymnodalatias Garrick, 1956, Trans. Roy. Soc. New Zealand, 83(3): 564.
Type species: Scymnodon sherwoodi Archey, 1921, by original designation.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 1.

Synonyms: None.
Field Marks: Snout broadly rounded, elongated, somewhat flattened, not bulbous, mouth long and broadly arched, eyes horizontally elongated, upper teeth smaller 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 which 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, dark brown to mottled grey above, lighter below, fins with or without conspicuous fin markings or prominent light edges and light blotches on caudal-fin 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 a 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, tricuspidate and tri-ridged 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 rear tip 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 111 cm total length. Colour: dark brown or mottled greyish 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: This genus is very close to the genus Scymnodon, as suggested by the original placement of Scymnodon (=Scymnodalatis) sherwoodi in it own genus by Archey (1921) based on a specimen found stranded on a beach on the east coast of the South Island, New Zealand. Garrick (1956) later in a detailed revision erected a new genus (Scymnodalatias) separating it from other squaloid genera. In addition to lacking fin spines, this genus differs from Scymnodon in having the first dorsal fin slightly more posterior on the back; see Garrick (1956) and Taniuchi and Garrick (1986) for a detailed discussion of this genus and comparison to other closely related genera.

## Scymnodalatias albicauda Taniuchi and Garrick, 1986

Scymnodalatias albicauda Taniuchi and Garrick, 1986, Japanese J. Ichthyol. 33(2): 120, fig. 1-2. Holotype: University Museum, University of Tokyo, FUMT P-197, 914 mm female, Southeastern Indian Ocean between Kerguelen Islands and Cape Leeuwen, Western Australia, ca. $45^{\circ} \mathrm{S}, 92^{\circ} \mathrm{E}, 150-200 \mathrm{~m}$ on longline near surface in water ca. 1400-1800 $m$ deep.

Synonyms: None.
Other combinations: None.
FAO Names: En - Whitetail dogfish; $\mathbf{F r}$ - Squale grogneur à queue blanche; $\mathbf{S p}$ - Bruja cola blanca.


Fig. 110 Scymnodalatias albicauda
Field Marks: Short, broadly rounded snout, eyes horizontally elongated, and a long broadly arched mouth, upper teeth small, narrow with acutely erect cusps, lowers large blade-like smooth-edged, imbricate, with high, erect cusps, two spineless dorsal fins, second dorsal fin slightly larger than the first, pectoral fins elongated, upper caudal-fin margin nearly twice the length of the lower caudal-fin margin, colour a dark brown to mottled grey above, lighter below, with conspicuous white blotches on the caudal-fin base.

Diagnostic Features: Head length 17.8 to $18.9 \%$ and preorbital snout 4.2 to $4.6 \%$ of total length. Upper teeth with straight slender cusps; cusps of lower teeth erect or slightly oblique, cusp covering part of root and with small distal blade; tooth row counts 57 to $62 / 35$, upper rows more numerous than lowers, ratio 1.3:1. Predorsal length less than half or 41.0 to $44.7 \%$ of total length. Pectoral fins elongated and leaf-shaped, with angular and acute apices, anterior margins 17.2 to $18.6 \%$ of total length. First dorsal-fin free rear tip far anterior to pelvic-fin origins by over dorsal-fin base length. Second dorsalfin 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: total vertebral counts 82 to 84 , precaudal vertebral counts 57 to 61, monospondylous vertebral counts 43 to 44 . A moderate sized shark that reaches 111 cm total length. Colour: dark brown or mottled greyish above, lighter brownish grey below, fins with whitish grey margins, conspicuous white blotches on caudal-fin base and web except for dark terminal lobe.

Distribution: Known from only a few scattered records including the Southeastern Atlantic (southwest of South Africa).

Habitat: Oceanic in the epipelagic zone, where it is a rare catch on tuna longlines from 0 to approximately 200+ m in water approximately 1400 to 4000 m deep, also off a submarine ridge at 512 m near the bottom. It may be mesopelagic or bathypelagic as suggested by its dark body coloration, and could rise to near the surface at night, but this is speculative.

Biology: Viviparous with a yolk sac. A pregnant female from the South Atlantic had a litter of 59 near-term foetuses, which is higher than any other squaloid (with the possible exception of the large Somniosus spp.) and surpassed by few other sharks; it is not certain if any additional foetuses had been lost during capture. A second specimen from New Zealand waters had 36 embryos (A. Stewart, Te Papa Museum, pers. comm.).

Size: Maximum total length 111 cm ; females are adult at 74 to 111 cm long. Size at birth uncertain, but near-term foetuses with moderately large yolk sacs were 15.7 to 19.2 cm total length.

Interest to Fisheries and Human Impact: An incidental and rare bycatch of tuna longliners, utilization not recorded.

The conservation status of this poorly known species is Data Deficient.


Fig. 111 Scymnodalatias albicauda
$\square$ Known distribution $\square$ Possible distribution

Local Names: None.
Literature: Taniuchi and Garrick (1986); Kukuyev and Konovalenko (1988); Last and Stevens (1994, 2009); Nakaya and Nakano (1995); Duffy (2003); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press); Andrew 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 Deep-sea Southeastern Atlantic Ocean Species: 1.

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, 1816. Genus Laemargus Müller and Henle, 1837a, Ber. K. preuss. Akad. wiss. Berlin, 2: 116; Müller and Henle, 1837b, 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, 1816), 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. Genus Heteroscymnus Tanaka, 1912, Fig. Descr. Fish. Japan, 6: 102. Type species: Heteroscymnus longus Tanaka, 1912, by original designation. 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, 1826) and S. bauchotae Quéro, 1976, included in it.

Field Marks: Short to moderately long snout, 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, no fin spines on dorsal fins, no anal fin, caudal fin somewhat paddle-shaped, with a long lower lobe, size moderately 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-fin 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 counts 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 one species occurring in the Southeastern Atlantic Ocean.

## Somniosus antarcticus Whitley, 1939

Somniosus antarcticus Whitley, 1939, Aust. Zool. 9(3): 242. Macquarie Island. Based on the Somniosus sp. of Waite (1916, Australas. Antarct. Exped., 1911-1914, Sci. Rept. C, vol. 3(1): 51, fig. 10), a 249 cm shark apparently of this genus.

Synonyms: Somniosus microcephalus Bass, D'Aubrey and Kistnasamy (1976): 43; Duhamel and Hureau (1982): 73; Compagno (1984a): 103, ill.; Duhamel and Compagno (1985): 209; Gushchin et al. (1986): 514; Compagno, Ebert and Smale (1989): 32, ill.; Compagno (1990): 84, fig. 2. Somniosus cf. microcephalus Compagno, Ebert and Cowley (1991): 66.

## Other Combinations: Somniosus pacificus, Somniosus microcephalus.

FAO Names: En - Southern sleeper shark; Fr - Laimargue de l'Antarctique; Sp - Tollo meridional dormilón.


Fig. 112 Somniosus antarcticus
Field Marks: Heavy cylindrical body, short, rounded snout, upper teeth lanceolate, lower teeth with short, low, strongly oblique cusps and high, narrow roots, small precaudal fins, two spineless, equal-sized dorsal fins, 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 anal fin, no keels on base of caudal fin and long ventral caudal-fin lobe.

Diagnostic Features: Snout short and broadly rounded. Head moderately long, length from snout to pectoral fins $23 \%$ of total length in a specimen of 299 cm total length. Cusps of lower teeth short and low, strongly oblique, roots very high. Total tooth counts upper jaw 37 to 48 , lower jaw 49 to 59. 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-fin bases than pectoral-fin 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 pelvicfin 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 36 to 38, precaudal vertebral counts 30 to 31 . Spiral valve turn counts: 36 to 41 (mode = 39). Size large, exceeding 400 cm total length. Colour: uniformly grey to blackish, without conspicuous light or dark fin edges.

Distribution: Namibia and South Africa (Cape Columbine). Also widely distributed in the Southern Pacific, Indian and Western Atlantic Oceans.

Habitat: An abundant littoral and epibenthic shark of the continental and insular shelves and upper slopes down to at least 1440 m . In the Southern Hemisphere it is found in deep water ( 677 m ) off South Africa, in 245 to 370 m depth off Kerguelen Island, and off Macquarie Island between 300 to 1440 m . Water temperatures of places inhabited by these sharks range from 0.6 to $12{ }^{\circ} \mathrm{C}$.

Biology: Viviparous with a yolk sac, but litter sizes mostly unknown. Diet consists of fishes, pinnipeds, cetaceans, and especially cephalopods where they appear to target giant squid (Mesonychoteuthis hamiltoni). Much like the other giant members of this genus these sharks consume fast-swimming prey, but whether it is taken as carrion or alive is unknown.

Size: Maximum total length to at least 456 cm , but possibly 600 cm or more; males adult at about 400 cm and females at about 435 cm . Size at birth about 40 cm .

Interest to Fisheries and Human Impact: Taken as non-utilized bycatch of trawl and longline fisheries for hake, Patagonian toothfish (Dissostichus eleginoides, Nototheniidae), and other bottom fishes throughout most of its range.

The conservation status is Data Deficient.


Fig. 113 Somniosus antarcticus
Known distribution

Local Names: Blimp shark (South Africa).
Remarks: Somniosus antarcticus was named by Whitley (1939) based on a sketch and descriptive data from a Somniosus specimen found dead on a beach at Macquarie Island in the Antarctic. The specimen itself was not preserved, but teeth and skin samples were saved; however, it is uncertain whether these samples still exist. The descriptive data and sketch definitely indicate that the specimen represented a member of the subgenus Somniosus closest to $\boldsymbol{S}$. microcephalus, but these are sufficiently generalized to prohibit the differentiation of $\boldsymbol{S}$. antarcticus from $\boldsymbol{S}$. microcephalus. As with certain other sharks, Whitley apparently named $\boldsymbol{S}$. antarcticus primarily because of its Southern Hemisphere locality. However comparison of large Southern Oceans Somniosus to the two Northern Hemisphere forms have revealed that this species is indeed valid and could be separated by morphometric characteristics, and meristics including tooth, vertebral, and spiral valve turn counts (Yano, Stevens and Compagno, 2004). A molecular study (Murray et al., 2008) on the three large Somniosus species confirm the separation of S. microcepahlus from S. pacificus, but the genetic structure within the S. antarcticus-S. pacificus clade was more ambiguous and showed little to no variation. Furthermore, molecular examination using mtDNA and nuclear markers is required to determine the species status of $\boldsymbol{S}$. antarcticus and $\boldsymbol{S}$. pacificus.

Literature: Whitley (1939); Bigelow and Schroeder (1948); Bass, D'Aubrey and Kistnasamy (1976); Duhamel and Hureau (1982); Compagno (1984a); Stevens (2003c); Yano, Stevens and Compagno (2004, 2007); Murray et al. (2008); Ebert (2013); Ebert, Fowler and Compagno (2013); 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 Deep-sea Southeastern Atlantic Ocean 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, knifelike, fin spine preceding each dorsal fin, pectoral fins small, leaf-shaped to rounded, caudal fin with strong subterminal notch and short lower lobe, colour 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, with a 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 tricuspidate 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. Vertebral counts: total vertebral counts 93 to 105, precaudal vertebral counts 66 to 76 , monospondylous vertebral counts 50 to 57 . Spiral valve turns: 12 to 16 . Small to moderate sized 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 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: Scymnodon obscurus Bass, D'Aubrey and Kistnasamy, 1976: 35; Compagno 1984a: 98, ill. Centroscymnus obscurus Bass, Compagno and Heemstra, 1986: 53, fig. 5.7. Scymnodon squamulosus Compagno, Ebert and Smale, 1989: 32, ill.; Compagno, Ebert and Cowley, 1991: 66; Ebert, Compagno and Cowley, 1992: 607.

Other combinations: None.
FAO Names: En - Velvet dogfish; Fr - Squale-grogneur velouté; Sp - Bruja terciopelo.


Fig. 114 Zameus squamulosus
Field Marks: A small slender bodied shark, with a low flat head, fairly long snout, short narrow mouth, nearly transverse, postoral grooves much longer than the short upper labial furrows, small lanceolate teeth without cusplets in upper jaw and
large high, knife-cusped cutting teeth in lower jaw, a small fin spine preceding each dorsal fin, no anal fin, caudal fin with strong subterminal notch and short lower lobe. Colour uniformly black to dark brownish.

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 leaf-shaped; 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: Namibia and west coast of South Africa. Elsewhere, occurs throughout the Atlantic, Indian, and Pacific Oceans.

Habitat: A poorly known epipelagic and oceanic deepwater shark usually 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.

Biology: Viviparous with a yolk sac, litter of 3 to 10, but little else known about their reproductive cycle. 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 Scymnodon 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 somniosid is of limited fisheries interest. It is caught incidentally by bottom trawls and by bottom and pelagic longline gear. There is no species-specific information on the numbers of these sharks that are caught as bycatch, but it is likely low since they do not seem to be abundant where they are known to occur. Also caught infrequently by tuna longliners in the epipelagic zone.


Fig. 115 Zameus squamulosus
Known distribution

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 dogfish shark.

Local Names: None.
Remarks: The Eastern North Atlantic Scymnodon obscurus and the Japanese Scymnodon (=Zameus) squamulosus were considered to be separable by the presence (S. obscurus) or absence (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. obscurus and S. (=Z.) squamulosus 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 $\boldsymbol{Z}$. squamulosus.

Literature: Bigelow and Schroeder (1957); Bass, D’Aubrey and Kistnasamy (1976); Yano and Tanaka (1984); Taniuchi and Garrick (1986); Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); Ebert, Compagno and Cowley (1992); Burgess and Chin (2006); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press); D.A. Ebert (unpubl. data).

### 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 Deep-sea Southeastern Atlantic Ocean Genera: 1.

Synonyms: Subfamily Centrinae Swainson, 1838: 143, 155; Emended spelling as Subfamily Centrininae Swainson, 1839: 191, 314 (Family Squalidae). Also Hasse, 1879: tab. 2 as Subfamily Centrina, Family Acanthias. Type genus: Centrina Cuvier, 1816.

FAO Names: En - Rough sharks; Fr - Centrines; Sp - Cerdos marinos.
Field Marks: Unmistakable compressed, rough-skinned small to moderately large 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 rounded-angular 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 into 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 saw-like 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 crosssection, abdomen with strong lateral ridges. Interdorsal space short and variably less than or somewhat larger than length of first dorsal 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 auxiliary 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 95 , 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 are mostly regional endemics scattered throughout the Eastern Atlantic, including the Mediterranean, Western Central Atlantic, Western Pacific, Eastern Indian Ocean off Southern Australia and possibly the Southwestern Indian Ocean off Mozambique.

Habitat: Oxynotids are temperate to tropical, poorly known, deepwater bottom sharks of distinctive and bizarre 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 relatively 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, sipunculids 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 $\boldsymbol{O x y n o t u s}$ 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. At least one species ( $\boldsymbol{O}$. centrina) is reported to occur in the area, but only known from a very few specimens.

Literature: Garman (1913); Norman (1932); Bigelow and Schroeder (1957); Cadenat and Blache (1981); Compagno (1984a); Yano and Murofushi (1985); Yano and Matsuura (2002); Capapė (2008); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press).

## List of Deep-sea Species Occurring in the Area:

Oxynotus centrina (Linnaeus, 1758)

## 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 Deep-sea Southeastern Atlantic Ocean Species: 1.

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, 1816, 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 $(1816,1829)$ 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 (1862), Duméril (1865), Regan (1906a), and Garman (1913).

## Oxynotus centrina (Linnaeus, 1758)

Squalus centrina Linnaeus, 1758, Syst. Nat., ed. 10, 1: 233. Holotype unknown (see also Eschmeyer, 2013). Type locality: "Habitat in mari Mediterraneo".

Synonyms: Oxynotus shubnikovi Myagkov, in Gubanov, Kondyurin, and Myagkov, 1986: 171, fig. 59"be". Holotype: EMGEY P 11505, 20 cm ?, $17^{\circ} 48^{\prime} \mathrm{S}, 11^{\circ} 36^{\prime} \mathrm{E}$, southwest of the Cunene River mouth, Northern Namibia. Oxynotus sp. Bass, D'Aubrey and Kistnasamy, 1976: 8, fig. 5.
Other Combinations: None.

FAO Names: En - Angular roughshark; Fr - Centrine commune; Sp - Cerdo marino.


Fig. 116 Oxynotus centrina
Field Marks: Short, blunt snout, 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, high, sail-like dorsal fins with spines, first dorsal-fin spine inclined forwards, and no anal fin. 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, smoothedged 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, sharp-edged, 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-fin spine 2.6 to 2.8 times 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 times in first dorsal-fin spine height, second dorsal-fin anterior margin from spine to apex 0.6 to 0.8 times in second dorsal-fin spine height. Second dorsalfin base 1.5 to 1.8 times in interdorsal space, second dorsalfin 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 total length. 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: South Africa (Western Cape), Namibia and Angola and northwards to the Eastern Central and North Atlantic, including the Mediterranean Sea.


Fig. 117 Oxynotus centrina
Known distribution

Habitat: A rare to uncommon bottom shark of the continental shelves and upper slope at depths of 50 to 777 m , mostly below 100 m . Found mostly on coral, 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. Virtually, nothing known in the Southeastern Atlantic where it is extremely rare, but in the Mediterranean mating is reported to occur in February with parturition possibly occurring three to 12 months later. Birth appears to occur in the spring. The liver weight as a percent of body weight (hepatosomatic index) is 16 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 (Raja sp.) was found the stomach of one individual.

Size: Maximum total length about 150 cm , but most individuals less than 100 cm long. Females mature 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 at 52 and 58 cm in length (Poll, 1951). Males mature at about 60 cm total length. Size at birth is 21 to 24 cm .

Interest to Fisheries and Human Impact: Interest to fisheries in the Southeastern Atlantic none.
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: Flatiron shark, Angular rough shark, Strykysterhaai (South Africa).
Remarks: Oxynotus centrina or a similar species reported from off Southern Africa (Angola to South Africa) has been described as a different species, Oxynotus shubnikovi, based largely on the latter species having a shorter interdorsal space. However, comparison of southern African and Eastern North Atlantic O. centrina specimens revealed this characteristic to be variable. Therefore, lacking any other characteristics to separate the southern African Oxynotus from the Eastern North Atlantic and Mediterranean forms, $\boldsymbol{O}$. shubnikovi 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: Barnard (1949); Poll (1951); Capapé (1975); Bass, D’Aubrey and Kistnasamy (1976); Compagno (1984a); Yano and Murofushi (1985); Bass, Compagno and Heemstra in Smith and Heemstra (1986); Lloris (1986); Myagkov in Gubanov, Kondyurin, and Myagkov (1986); Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); Bianchi et al. (1999); Capapé, Seck and Quignard (1999); Barrull and Mate (2001); Yano and Matsuura (2002); Megalofonou and Damalas (2004); Bradaï et al. (2007); Capapé (2008); Ebert (2013); Ebert, Fowler and Compagno (2013); 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 Deep-sea Southeastern Atlantic Ocean Genera: 4.

Synonyms: Subfamily Scymnini Bonaparte, 1838: 207 (Family Squalidae). Type genus: Scymnus Cuvier, 1816. Family Scymni Müller and Henle, 1839: 91. Type genus: Scymnus Cuvier, 1816. Family Scymnorhinidae Gill, in Goode and Bean, 1896: 6. Type genus: Scymnorhinus Bonaparte, 1846. Family Isistidae Garman, 1899: 32. Type genus: Isistius Gill, 1865. Subfamily Euprotomicrinae (Family Dalatiidae) Shirai, 1992: 122. Type genus: Euprotomicrus Gill, 1865.

FAO Name: En - Kitefin sharks.
Field Marks: Short to moderately long-nosed, usually cylindrical or somewhat compressed (Euprotomicroides) sharks with 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 to pectoralfin bases to far behind the pectoral fins and somewhat anterior to pelvic-fin origins, the second dorsal fin not falcate and with its origin usually opposite to pelvic-fin bases or inner margins, but exceptionally slightly anterior to the pelvic-fin origins (Euprotomicroides), no anal fin, 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 saw-like 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 pelvicfin 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 vertebral 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: An almost circumglobal range in most temperate to tropical seas, but most species distribution sketchily to poorly known, particularly for the oceanic species, which may reflect uneven and inadequate sampling and patchy distributions.

Habitat: The Dalatiidae include species that represent at least two ecomorphotypes (Compagno, 1990), 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 gillnets; 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 migrators 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 6 to 16 young, but virtually nothing is known about their life cycle or age and growth. 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 hook-like 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 night lights 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 is 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 with which 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.

Local Names: Kitefin sharks, Black sharks (English).
Remarks: The family Dalatiidae is comprised of seven genera, five of which are monotypic genera, and ten species worldwide. Several of these genera (Euprotomicroides, Euprotomicrus, Heteroscymnoides, Isistius, and possibly Mollisquama) are considered to be oceanic. The geographic and bathymetric ranges are poorly known for all species within this family.

Four genera and species occur in the deep waters of the Southeastern Atlantic Ocean.
Literature: Müller and Henle (1839); Gray (1851); Bleeker (1859); Gill (1862); Duméril (1865); Günther (1870); Regan (1908a); Garman (1913); Bigelow and Schroeder (1948, 1957); Hubbs and McHugh (1951); Hubbs, Iwai and Matsubara (1967); Bass, D'Aubrey and Kistnasamy (1976); Compagno (1984a); Last and Stevens (2009); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press).

## List of Deep-sea Species Occurring in the Area:

Euprotomicroides zantedeschia Hulley and Penrith, 1966
Euprotomicrus bispinatus (Quoy and Gaimard, 1824)
Heteroscymnoides marleyi Fowler, 1934
Isistius brasiliensis (Quoy and Gaimard, 1824)

## Key to Deep-sea Southeastern Atlantic Ocean Genera:

1a. Gill openings increasing in width posteriorly, the fifth very wide. Pectoral-fin inner margin and free rear tip greatly expanded and lobate. Second dorsal-fin origin anterior to pelvic-fin origins. Cloaca greatly expanded as a luminous gland, with yellow papillae within it (Fig. 118).

## Euprotomicroides

1b. Gill openings of uniform or near-uniform width. Pectoral-fin inner margin and free rear tip not greatly expanded and lobate. Second dorsalfin origin posterior to pelvic-fin origins. Cloaca not expanded as a luminous gland, without papillae .

2a. First dorsal-fin insertion about over pelvic-fin origins (Fig. 119). Cusps of lower teeth covering the entire crown foot, without a convex accessory blade separated from the cusp by a notch . . Isistius

2b. First dorsal-fin insertion well anterior to pelvicfin origins (Fig. 120 \& 121). Cusps of lower teeth covering part of the crown foot, with a convex distal blade separated from the cusp by a notch

3a. Second dorsal-fin base as long as first dorsalfin base or shorter. Upper caudal-fin lobe not shortened, not paddle-shaped (Fig. 120) . . . . .

Heteroscymnoides
3b. Second dorsal-fin base at least twice as long as first dorsal-fin base. Upper caudal-fin lobe shortened, caudal paddle-shaped (Fig. 121) . .

Euprotomicrus


Fig. 118 Euprotomicroides


Fig. 119 Isistius
Second dorsal-fin base as


Fig. 120 Heteroscymnoides
Second dorsal-fin base twice as long as first dorsal-fin base


Fig. 121 Euprotomicrus

## Euprotomicroides Hulley and Penrith, 1966

Genus: Euprotomicroides Hulley and Penrith, 1966, Bull. Mar. Sci. 16(2): 222.
Type species: Euprotomicroides zantedeschia Hulley and Penrith, 1966, by original designation (new genus and species formula).

## Number of Recognized Species: 1.

Synonyms: None.
Diagnostic Features: Anterior nasal flaps very short, not expanded into barbels; snout moderately long, compressed and conical, length about $2 / 5$ of head length and less than distance from mouth to pectoral-fin origins; gill openings increasing in size from front to back, fifth over twice length of first; lips thick, fringed, but not suctorial; teeth strongly different in upper and lower jaws, uppers small, with narrow, acute, erect cusps and no cusplets, not bladelike, lowers much larger, bladelike, interlocked, with a high, broad, nearly erect cusp and distal blade, edges not serrated; tooth rows 29 upper jaw, 34 lower jaw. Both dorsal fins spineless; first dorsal-fin origin well behind free rear tips of pectoral fins, insertion about equidistant between pectoral and pelvic-fin bases and well ahead of pelvic-fin origins; second dorsal fin somewhat larger than first, base less than 1.5 times length of first dorsal-fin base; origin of second dorsal fin well ahead of pelvic-fin origins; pectoral fins with greatly expanded, broadly lobate free rear tips and inner margins, much as in chimaeras; caudal fin asymmetrical, not paddle-shaped, upper lobe long, lower lobe moderately long subterminal notch well-developed. No precaudal pits or lateral keels on caudal peduncle, but with a midventral keel. Dermal denticles flat and block-like, not pedicellate, no posterior cusps on flat, depressed crowns. Cloaca greatly expanded and modified as a luminous gland with secretory papillae. Vertebral counts and spiral valve turn counts not available. Colour: blackish brown with conspicuous light fin margins.

Local Names: Taillight sharks.
Remarks: A specimen of this genus (only the third known) was recently collected (22 August 2008) by a trawler in the South Pacific ( $34^{\circ} \mathrm{S}, 94^{\circ} \mathrm{W}$ ) and may represent a new species within the genus as this most recent specimen differs morphologically from Euprotomicroides zantedeschia.

## Euprotomicroides zantedeschia Hulley and Penrith, 1966

Euprotomicroides zantedeschia Hulley and Penrith, 1966, Bull. Mar. Sci. 16(2): 222, fig. 1-4. Holotype: South African Museum, SAM-23577, 176 mm TL immature male, west of Cape Town, 458-641 m.

Synonyms: None.
Other combinations: None.
FAO Names: En - Taillight shark; Fr - Squale à queue claire; $\mathbf{S p}$ - Tollo rabo claro.


Fig. 122 Euprotomicroides zantedeschia
Field Marks: Conical, moderately long, blunt, compressed snout, needle-like upper teeth and bladelike lowers, compressed body, gill slits increasing greatly in size from front to back, lobate, chimaera-like pectoral fins, midventral keel on caudal peduncle, no dorsal-fin spines, no anal fin, asymmetrical caudal fin, cloacal gland, dark colour with conspicuous light fin margins.

Diagnostic Features: See genus.
Distribution: West of Cape Town, South Africa. Recorded also east of Uruguay.

Habitat: A little-known, extraordinarily specialized, oceanic dwarf shark, known only from two specimens. One was caught offshore on the continental slope in a bottom trawl (holotype), but a second specimen was captured near the surface ( 0 to 25 m deep) far offshore in the epipelagic zone (Krefft, 1980).

Biology: Mode of reproduction unknown, probably viviparous with a yolk-sac and with few young. The cloaca of this shark is greatly expanded into a gland with internal villi that secrete a blue luminous substance ( $M$. Stehmann, pers. comm.). The broadly lobate, muscularbased pectoral fins, situated on the compressed body in a position similar to the pectoral fins of chimaeras, suggest that pectoral propulsion or at least pectoral hovering is important in this shark. Food unknown; the powerful jaws and sharp lower teeth suggest that this species can capture and dismember relatively large prey.

Size: Maximum total length about 42 cm ; an adult male was 41.6 cm long; the 17.6 cm holotype was originally recorded as an adult male, but turned out to be an immature female.

Interest to Fisheries and Human Impact: Interest to fisheries none.

The conservation status of this species is Data Deficient.
Local Names: None.


Fig. 123 Euprotomicroides zantedeschia

Literature: Hulley and Penrith (1966); Bass, D’Aubrey and Kistnasamy (1976); Krefft (1980); Compagno (1984a); Stehmann and Krefft (1988); Compagno, Ebert and Smale (1989); Kyne and Burgess (2009); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press); M. Stehmann (pers. comm.).

## Euprotomicrus Gill, 1865

Genus: Euprotomicrus Gill, 1865 (listed 1864), Proc. Acad. Nat. Sci. Philadelphia: 264, ftn. 4.
Type species: Scymnus labordii "Müller and Henle", 1839, by monotypy, equals Scymnus bispinatus Quoy and Gaimard, 1824.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 1.

Synonyms: None.
Field Marks: See species.
Diagnostic Features: Snout moderately long, bulbously conical, length about $2 / 5$ of head length and less than distance from mouth to pectoral-fin origins. Anterior nasal flaps very short, not expanded into barbels. Gill openings very small, uniformly broad. Lips thin, not fringed, pleated or suctorial. Teeth strongly different in upper and lower jaws, uppers small, with narrow, acute, erect cusps and no cusplets, not bladelike, lowers much larger, bladelike, interlocked, with a high, broad, nearly erect cusp and distal blade, edges not serrated; tooth rows 19 to 21 upper jaw, 19 to 23 lower jaw. Both dorsal fins spineless; first dorsal-fin origin far behind free rear tips of pectoral fins, insertion well ahead of pelvic-fin origins but much closer to pelvicfin bases than pectoral fins; second dorsal fin much larger than first, with its base about 4 times as long as base of tiny first dorsal fin. Origin of second dorsal fin over rear end of pelvic-fin bases. Pectoral fins with short, broadly rounded free rear tips and inner margins, not expanded and acute or lobate. Caudal fin nearly symmetrical, paddle-shaped, with short, strong upper lobe and long lower lobe; subterminal notch well-developed. 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 60 to 70, monospondylous vertebral counts 31 to 32 , precaudal diplospondylous vertebral counts 15 to 20 , total precaudal vertebral counts 46 to 52 , caudal vertebral counts 11 to 19 . Intestinal valve turn counts 12 to 13 . Colour: blackish with conspicuously light-edged fins.

Local Names: Pygmy sharks.

## Euprotomicrus bispinatus (Quoy and Gaimard, 1824)

Scymnus bispinatus Quoy and Gaimard, 1824, Zoologie, Poissons, in L. de Freycinet, Voyage aut. monde corv. S.M. l’Uranie et La Physicienne, 1817-1820: 197, pl. 44, figs. 1, 2. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN-1216, 196 mm male, Mauritius, Indian Ocean.

Synonyms: None.
Other combinations: None.
FAO Names: En - Pygmy shark; Fr - Squale pygmée; Sp - Tollo pigmeo.


Fig. 124 Euprotomicrus bispinatus
Field Marks: Small size, bulbous snout, cylindrical body, no dorsal-fin spines, tiny flag-like first dorsal fin, this over abdomen and closer to pelvic fins than pectoral fins and well behind pectoral fins, second dorsal-fin base about four times larger than first, no anal fin, blackish colour with conspicuous light-edged fins.

Diagnostic Features: See genus.
Distribution: West of the Cape of Good Hope, South Africa. Elsewhere, oceanic and amphitemperate, scattered throughout most ocean basins.

Habitat: The pygmy shark is an epipelagic, mesopelagic, and perhaps bathypelagic inhabitant of the central water masses of the North and South Pacific, South Atlantic, and Southern Indian Ocean, at water depths from 1829 to 9938 m . It occurs at or near the surface at night and apparently descends to at least midwater depths, to probably well below 300 m during the day; sand grains in the stomach of one specimen suggests that it may have been feeding on the bottom, presumably below 1800 m depth. All known specimens have been caught at the surface at night while none have been taken in midwater trawls at night or during the day. This also suggests that the diel vertical migrations of this little shark are enormous, at least 1500 m or more each way to put it below the normal range of midwater trawl hauls in the day. In human terms this would be roughly equivalent to someone climbing at least 11 km up and down each day.

Biology: Development viviparous with a yolk sac and with 8 young per litter. This shark eats deepwater squid and bony fishes, including hatchetfishes, lanternfishes, and lightfishes, with some crustaceans, but apparently does not take prey as relatively large as the squid taken by Isistius brasiliensis. Its jaws are moderately strong but far weaker than those of Isistius and Dalatias, and there is no evidence that the pygmy shark cuts plugs of flesh from fishes and other animals. Its lips are apparently not suctorial.


Fig. 125 Euprotomicrus bispinatus
Known distribution

Size: Maximum total length 27 cm ; males mature between 17 to 19 cm and reach 22 cm , females mature between 22 and 23 cm and reach 27 cm . Size at birth greater than 6 cm and less than or about 10 cm .

Interest to Fisheries and Human Impact: Interest to fisheries none.

The conservation status of this shark is Data Deficient.
Local Names: Leiche, Slime shark, Pygmy shark, Dwerghaai (South Africa).
Remarks: Pygmy sharks possess luminescent organs on their ventral surfaces that may serve to camouflage them from predators when they are at the surface. These organs may also play an important role in feeding and social recognition.

Literature: Hubbs and McHugh (1951); Bigelow and Schroeder (1957); Hubbs, Iwai and Matsubara (1967); Bass, D’Aubrey and Kistnasamy (1976); Seigel (1978); Cadenat and Blache (1981); Compagno (1984a); Last and Stevens (1994, 2009); Suda et al. (1999); Ebert (2003); Burgess (2006a); Last and Stevens (2009); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press).

## Heteroscymnoides Fowler, 1934

Genus: Heteroscymnoides Fowler, 1934, Proc. Acad. Nat. Sci. Philadelphia, 85: 239.
Type species: Heteroscymnoides marleyi Fowler, 1934, by original designation.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 1.

Synonyms: Genus Heteroscymnodes Fowler, 1969a, Quart. J. Taiwan Mus. 22(1-2): 70. Apparent typographical error for Heteroscymnoides.

Field Marks: See species.
Diagnostic Features: Anterior nasal flaps very short, not expanded into barbels. Snout very long, bulbously conical, length almost half head length and about equal to distance from mouth to pectoral-fin origins. Gill openings very small, uniformly wide. Lips thin, not fringed, pleated or suctorial. Teeth strongly different in upper and lower jaws, uppers small, with narrow, acute, erect cusps and no cusplets, not bladelike, lowers much larger, bladelike, interlocked, with a high, moderately broad, semi-erect cusp and distal blade, edges not serrated; tooth rows 22 upper jaw, 23 lower jaw. Both dorsal fins spineless. First dorsal-fin well forward, origin over pectoral-fin bases, insertion far ahead of pelvic-fin origins and much closer to pectoral-fin bases than pelvic fins. Second dorsal fin slightly larger than first but with base about equal to first dorsal-fin base. Origin of second dorsal fin over midbase of pelvic fins. Pectoral fins with short, narrowly rounded free rear tips and inner margins, not expanded and acute or lobate. Caudal fin semi-symmetrical, almost paddle-shaped, with moderately long upper lobe and well-developed lower lobe, subterminal notch strong. No precaudal pits, lateral or midventral keels on caudal peduncle. Dermal denticles flat but with pedicels, with lanceolate, ridged, wedge-shaped, monocuspidate crowns. Cloaca normal, not expanded as a luminous gland. Vertebral counts: total vertebral count 70, precaudal vertebral count 52. Colour: brown with conspicuous light and dark banded fin margins.

Local Names: Longnose pygmy sharks.

## Heteroscymnoides marleyi Fowler, 1934

Heteroscymnoides marleyi Fowler, 1934, Proc. Acad. Nat. Sci. Philadelphia, 85: 240, fig. 4. Holotype: Academy of Natural Sciences, Philadelphia, ANSP-53046, 128 mm newborn female, Durban coast at Point Ocean Beach, Natal.

Synonyms: None.
Other combinations: None.
FAO Names: En - Longnose pygmy shark; Fr - Squale mignon; Sp - Tollo pigmeo trompudo.


Fig. 126 Heteroscymnoides marleyi

Field Marks: Small size, bulbous elongated snout, no dorsal-fin spines, first dorsal fin far forward, with origin over pectoral-fin bases, second dorsal fin only slightly larger than first, no anal fin, dark brown colour with light-edged fins.

Diagnostic Features: See genus.
Distribution: Possibly circumglobal in cold subantarctic waters of the Southern Hemisphere (Stehmann, Kukuev and Konovalenko, 1999), but currently only known from six specimens from four widely dispersed locations. In the Southeastern Atlantic it was caught near the Walvis Ridge ( $30^{\circ} 4.0^{\prime} \mathrm{S}$, $5^{\circ} 22.0^{\prime} \mathrm{E}, 0$ to 502 m in water over 4000 m deep) and over the Walvis Ridge ( $35^{\circ} 53$ to $51^{\prime} \mathrm{S}, 2^{\circ} 32$ to $35^{\prime} \mathrm{E}$ at 280 to 300 m in water over 830 m deep). Also recorded in the Southwestern Indian Ocean (Durban, KwaZulu-Natal, South Africa) and Southeastern Pacific Ocean.


UNDERSIDE OF HEAD

Habitat: A dwarf oceanic shark. The holotype was found on a beach in a subtropical area (KwaZulu-Natal, South Africa), but additional specimens have been collected in the open ocean in the epipelagic zone in cold southern waters, in the South Atlantic and Eastern South Pacific between the surface and 502 m in water over 830 to over 4000 m deep (Krefft, 1980; Stehmann, Kukuev and Konovalenko, 1999). The Walvis Ridge and Selkirk Island specimens were found in cold current systems (Benguela and Humboldt Currents respectively).

Biology: A rare species (known from six individuals), with biology poorly known. Reproductive mode is unknown but likely yolk-sac viviparous and possibly with few young as suggested by the large size of a presumably neonate female ( 12.8 cm ) compared with an adult female ( 33.3 cm ). Food habits unknown, but presumably pelagic fish and invertebrates.

Size: Maximum total length 36.5 cm . Adult males (two) were 36.0 and 36.5 cm . Of the two larger females reported, Krefft's (1980) 28.5 cm female was not examined for maturity but Stehmann, Kukuev and Konovalenko (1999) indicated that a 33.3 cm female was an adult. The 12.8 cm female holotype was immature and had an umbilical scar, indicating it was close to the size at birth.

Interest to Fisheries and Human Impact: Interest to fisheries none; catches by fisheries unknown at present.

Conservation status of this poorly known species is Least Concern.


Fig. 127 Heteroscymnoides marleyi

Local Names: Longnose pygmy shark.
Literature: Fowler (1934, 1941); Bigelow and Schroeder (1948, 1957); Bass, D’Aubrey and Kistnasamy (1976); Krefft (1980); Compagno (1984a); Stehmann, Kukuev and Konovalenko (1999); Burgess (2006b); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press).

## 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 (2013).

Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 1.
Synonyms: Genus Leius Kner, 1864, Anz. Akad. Wiss. Wien, 1: 186; Kner, 1864, Ann. Mag. Nat. Hist., 3, ser. 15: 185-187; Kner, 1865, 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, 2013, Cat. Gen. Fish., who indicates type by monotypy.

Field Marks: Small size, cigar-shaped body with long abdomen and short tail, short, bulbous snout, suctorial lips, large to huge, triangular-cusped lower teeth without blades, small, spineless, nearly equal-sized dorsal fins far posterior on back, caudal fin with short to long ventral lobe and no anal fin.

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-fin 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 brasiliensis (Cuvier, In Quoy and Gaimard, 1824)

Scymnus brasiliensis Cuvier, in Quoy and Gaimard, 1824, Zoologie, Poissons, in L. de Freycinet, Voyage aut. monde corv. S.M. I'Uranie et La Physicienne, 1817-1820: 198. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN-A.7787, 140 mm total length, female, off Brazil.

Synonyms: None.
Other combinations: None.
FAO Names: En - Cookiecutter shark; Fr - Squalelet féroce; $\mathbf{S p}$ - Tollo cigarro.


Fig. 128 Isistius brasiliensis
Field Marks: Small sized sharks with cigar-shaped body, short, bulbous snout, suctorial lips, small, triangular-cusped lower teeth without blades and in 25 to 31 rows, spineless dorsal fins far posterior on back, no anal fin, nearly symmetrical caudal fin with long ventral lobe and a prominent dark collar-marking over branchial region.

Diagnostic Features: Snout moderately short, about length of eye. Eyes anterior on head but sufficiently far back to lack an extensive anterior binocular field. Teeth in upper jaw 30 to 37, lower jaw 25 to 31; lowers moderately large. Interdorsal space over twice first dorsal-fin base, space between second dorsal-fin insertion and upper caudal-fin origin over twice second dorsal-fin base. Pectoral fins subquadrate, pelvic fins larger than dorsal fins. Second dorsal-fin height about equal to first. Caudal fin large and nearly symmetrical, with a long ventral caudal-fin lobe over $2 / 3$ length of dorsal caudal-fin margin. Vertebral counts: total vertebral counts 81 to 89 , precaudal vertebral counts 60 to 66 , caudal vertebral counts 20 to 24 . Intestinal valve turn counts 8 to 10 . A small shark with a maximum total length of about 56 cm . Colour: pale brown above, becoming lighter below, with a conspicuous dark collar-like marking around the gill region; fins dark, but with pale to translucent edges.

Distribution: Recorded off southern Angola and South Africa, including Ascension Island. Elsewhere, known from scattered records throughout the Atlantic, Indian, and Pacific Oceans.

Habitat: A wide-ranging tropical oceanic shark, epipelagic to bathypelagic in distribution. It is caught at night, sometimes at the surface, but usually below it at depths between 85 to 3500 m , however its preferred depth range and maximum depth are uncertain. Apart from those captured at the surface specimens are generally taken in midwater nets fished over a wide depth range, and it is difficult to tell at what depth these sharks were captured. This shark is thought to be a vertical migrator on a diel cycle, coming to the surface and to the level of midwater trawl hauls at night and presumably dropping below this during the daytime as few if any of these sharks have been taken during the daytime. This implies a long vertical distance travelled, in excess of 2000 to 3000 m up and down in the ocean basins. These sharks are often caught near islands; this may imply an inshore pupping ground or merely the distribution of large potential victims. The cookiecutter shark may be capable of living in water of lower oxygen content than Euprotomicrus bispinatus or Squaliolus spp., but this is hypothetical.

Biology: Viviparous with a yolk sac, 6 or 12 large eggs have been found in ovaries and a 46.5 cm pregnant female had nine near-term foetuses, but little else is known about their reproductive biology.


Fig. 129 Isistius brasiliensis
Known distribution

This shark has very powerful jaws and large teeth. It feeds on free-living deepwater prey, including squid with bodies almost as large as itself, gonostomatid fishes, and crustaceans, but is also a facultative ectoparasite on larger marine organisms. It has highly specialized suctorial lips and a strongly modified pharynx that allows it to attach to the sides of large bony fishes such as marlin, tuna, albacore, wahoo, and dolphinfish, as well as phocid seals, dolphins and other cetaceans (including the melon-headed whale, Peponocephala electra) and even the megamouth shark (Megachasma pelagios), deep-sea stingray (Plesiobatis daviesi) and sixgill stingray (Hexatrygon bickelli). Off Brazil in the Santos area Isistius spp. (including this species and I. plutodus) bit swordfish (Xiphias), snake mackerel (Ruvettus and Lepidocybium), marlin and sailfish (Tetrapturus and Istiophorus), yellowfin tuna and albacore (Thunnus albacares and T. alalunga), dolphinfish (Coryphaena hippurus), bramids (Brama brama) and bigeye thresher (Alopias superciliosus). The shark drives its razor-sharp saw-like lower dentition into the skin and flesh of its victim, twists about to cut out a conical plug of flesh, then pulls free with the plug cradled by its scooplike lower jaw and held by the hook-like upper teeth. This method of feeding leaves 'crater wounds' on victims, which were long thought to be caused by bacteria or invertebrate parasites, until Jones (1971) connected them to the cookiecutter or cigar shark. It has been hypothesized that the strong luminescence shown by this shark may serve to lure in other predators to attack it, with the result that the shark attacks or parasitizes them instead. It has been suggested (Widder, 1998) that the dark collar marking of this shark, banded by luminescent areas on the head and abdomen, specifically serves as a lure to attract upwardlooking pelagic predators, which are killed and eaten or 'cored'. Incomplete crater wounds often show that the cookiecutter shark attacked its victim's head on, perhaps after they attacked it. Aggregations of these sharks may appear as schools of prey fishes to large pelagic fishes such as tuna or swordfish, which proves to be an unwelcome surprise as the fishes are in turn bitten by the cookiecutters.

The small paired fins, long body cavity and enormous, oily liver of this shark point to its being neutrally buoyant and not dependent on forward motion and its fins for dynamic lift. The liver and body cavity is proportionately much larger than in Euprotomicrus bispinatus or Squaliolus spp., and much more oil is present in its body cavity and gut. This may be an adaptation for greater depths than those attained by the other species, but may also compensate for its more highly calcified skeleton, which in turn may be necessary for supporting its activities in taking larger prey and gouging flesh from large animals. It can be quite quick and active when caught and can nip its captors if they are unwary.

This shark has luminous organs that cover the entire lower surface of its trunk with the exception of its fins and the dark collar marking. It is reported as glowing a bright, ghastly green.

An unusual habit of this shark, perhaps related to maintaining sufficient calcium levels in its body for its relatively well-calcified skeleton and replacing its massive dentition, is swallowing and possibly digesting its own lower teeth as they are replaced and become loose in entire series.

Size: Maximum total length about 56 cm ; males mature at about 31 to 37 cm and reach at least 42 cm , females mature between 38 and 44 cm and reach at least 56 cm . Size at birth between 14 to 15 cm .

Interest to Fisheries and Human Impact: Of little interest to fisheries because of its small size and low abundance, but reportedly captured by bottom trawls and used for fishmeal in the Eastern Atlantic. It has been also caught in experimental pelagic gillnets targeting pelagic ommastrephid squid in the North Pacific. Isistius brasiliensis might be of slight negative interest to fisheries because the species gouges plugs of flesh from commercially important fishes, which may increase their mortality rate, but this is uncertain. Also, extensively damaged or scarred fishes are of less valuable than undamaged ones.

Unusual non-edible and non-living victims of this shark include nuclear submarines of the U.S. Navy, which have had rubber sonar domes bitten by I. brasiliensis. Despite its rather vampire-like mode of feeding, it is not of much concern to people because of its small size and oceanic habitat preferences. The chances of it biting a swimmer or diver are remote though possible. There is at least one confirmed attack by this shark on an open ocean swimmer off the Hawaiian Island of Maui. The attack occurred at night while an open ocean swimmer was attempting to cross 30 -mile Alenuihaha Channel from the Big Island to Maui. There are other anecdotal accounts of swimmers, including a swimmer off a ship in mid-ocean, being nipped by dwarf sharks.

Conservation status is Least Concern, but may be of some concern regionally due to its presence as bycatch in fisheries targeting large bony fishes and squid.

Local Names: Cigar shark, Collared dogfish.
Literature: Bigelow and Schroeder (1948, 1957); Strasburg (1963); Garrick and Springer (1964); Parin (1966); Hubbs, Iwai and Matsubara (1967); Jones (1971); Cadenat and Blache (1981); Compagno (1984a); Jahn and Haedrich (1987); Gasparini and Sazima (1996); Widder (1998); Gadig and Gomes (2002); Ebert (2003); Stevens (2003b); Last and Stevens (2009); Papastamatiou et al. (2010); Honebrink et al. (2011); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press).

### 2.3 Order PRISTIOPHORIFORMES - Sawsharks

Order: Order Pristiophoriformes White, 1936, emendation of Order Squalea, Suborder Squalida, Super family Pristiophoridea White, 1936, Amer. Mus. Novit. (837): 5; White, 1937, Bull. Amer. Mus. Nat. Hist. 74: 37, tab. 1.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Families: 1.

Synonyms: Part 1 Squali, Abtheilung 3: Müller and Henle, 1839, Syst. Besch. Plagiost. (2): 83. Ordo Plagiostomi, Subordo Squalini, Sectio Aproctopterides: Bleeker, 1859, Acta Soc. Sci. Indo-Neerl. 6: xii. Order Squali, Suborder Squali: Gill, 1862, Ann. Lyc. Nat. Hist. N.Y. 7: 367, 394, 396. Order Squali, Suborder Galei: Gill, 1872 Smithsonian Misc. Colln. (247): 23, 24. Suborder Plagiostomi Tectospondyli, Group 1 Squalorajae: Hasse, 1879, Nat. Syst. Elasmobr. (1): 44. Order Selachii, Suborder Tectospondyli: Woodward, 1889, Cat. fossil fish. BM(NH) (1): 30. Order Asterospondyli: Gill, 1893, Natn. Acad. Sci. (U.S.) Mem. 6, 6: 130 (pristiophorids placed with 'galeoid' sharks). Order Euselachii, Suborder Pleurotremata, Division Squaloidei: Regan, 1906a, Proc. Zool. Soc. London (1906): 723. Order Selachii, Group 2, Division B, Subdivision 2, Suborder Squaliformes: Goodrich, 1909, In R. Lankester, ed., A treatise on Zoology (9), Vertebrata Craniata: 151. Order Pleurotremata, Suborder Squaloidei: Engelhardt, 1913, Abh. math.-phys. Klasse K. Bayer. Akad. Wiss., Suppl., Beitr. Naturg. Ostasiens, 4: 100. Order Squatinae: Fowler, 1941, Bull. U. S. Natn. Mus. (100) 13: 4, 279. Order Plagiostoma, Suborder Antacea, "Group" Squaloidei: Garman, 1913, Mem. Mus. Comp. Zool. Harvard 36: 11, 13. Order Euselachii, Suborder Galei, Series Galeoidei: Jordan, 1923, Stanford Univ. Publ., Univ. Ser., Biol. Sci., 3: 100, 101. Order Euselachii, Suborder Squaliformes: Bertin, 1939, Bull. Inst. Oceanogr. Monaco (775): 10. Order Squaliformes, Suborder Squaloidei: Berg, 1940, Trudy Zool. Inst. Akad. Nauk SSSR, 5(2): 138; Arambourg and Bertin, 1958, In P.-P. Grasse, ed., Traité de Zoologie, 13: 2010-2067; Nelson, 1976, Fishes of the world: 38. Order Pristiophori, Superfamily Pristiophoroidea: Whitley, 1940, Fishes Australia. Part I. Aust. Zool. Handbook: 69. Order Selachii, Suborder Squaloidea: Romer, 1945, Vert. Paleont. (ed. 2): 577; Romer, 1966, Vert. Paleont. (ed. 3): 350. Order Selachii, Suborder Pristiophoroidea: Bigelow and Schroeder, 1948, Mem. Sears Fnd. Mar. Res. (1) 1: 77, 532. Order Squaloidea, Suborder Squaloidea: Schultz and Stern, 1948, ways of fishes: 225. Order Pristiophorae: Smith, 1949, Sea fishes Southern Africa: 37, 61. Order Pristiophoriformes: Berg and Svetovidov, 1955, Trudy Zool. Inst. Akad. Nauk SSSR, 20: 70; Patterson, 1967, in W.B. Harland et al., Geol. Soc. London, Spec. Pub. 2: 672; Lindberg, 1971, Fishes of the world (trans. 1974): 8, 260; Rass and Lindberg, 1971, J. Ichthyol. (trans. Voprosy Ikhtiologii) 11(3): 304; Compagno, 1973, J. Linn. Soc.(Zool.), 53 suppl. 1: 26; Applegate, 1974, J. Mar. Biol. Ass. India, 14(2): 743; Chu and Meng, 1979, Monogr. Fish. China, Sci. Tech. Press, Shanghai: 114, tab. 2; Compagno, 1984a, FAO Fish. Synops. (125) 4(1): 130; Pfeil, 1983, Palaeo Ichthyologica, 1: 24; Cappetta, 1987, Handb. Paleoichthyol. 3B: 26, 64; Eschmeyer, 1990, Cat. gen. Recent fish.: 437; Shirai, 1992, Squalean phylogeny, Hokkaido U. Press, Sapporo, 122; Nelson, 1994, Fishes of the world, ed. 3: 57; de Carvalho, 1996, in Stiassny et al., Interrelationships fishes: 55; Shirai, 1996, in Stiassny et al., Interrelationships fishes: 34. Order Lamnida, Suborder Pristiophorina: Matsubara, 1955, Fish morphology hierarchy, (1): 1-789. Order Pleurotremata, Suborder Squaloidea: Norman, 1966, draft syn. Recent fishes: 24. Order Squatiniformes, Suborder Pristiophoroidei: Glikman, 1967, in Y.A. Orlov, ed., Fundamentals Paleontology, 11: 217. Order Euselachii, Suborder Squaloidei: Blot, 1969, in J. Piveteau, ed. Traité de Paleontologie. 2: 702-776. Order Pristiophorida, Suborder Pristiophorina, Superfamily Pristiophoricae: Fowler, 1969a, Q. J. Taiwan Mus. 22(1-2): 80. Order Pleurotremata, Suborder Squaliformes: Budker and Whitehead, 1971, Life of sharks: 6, tab. 2. Order Pristiophoriformes, Suborder Pristiophoroidea: Chu and Meng, 1979, Monogr. Fish. China, Sci. Tech. Press, Shanghai: 114, tab. 2. Order Squaliformes, Suborder Pristiophoroidei: Nelson, 1984, Fishes of the world, ed. 2: 58. Order Squalomorpha, Suborder Squaloidea: Carroll, 1988, Vertebrate paleont. evolut.: 599.

Field Marks: Small (to 150 cm long) slender sharks with long, flat snouts bearing lateral and ventral sawteeth and ventral barbels, 5 or 6 lateral gill openings, two spineless dorsal fins and no anal fin.

Diagnostic Features: Head greatly depressed and somewhat expanded laterally. Snout greatly depressed, laterally expanded, and elongated, with close-set lateral and ventral sawteeth and a pair of long string-like rostral barbels on the ventral surface anterior to the nostrils. Eyes dorsolateral on head, without nictitating lower eyelids, secondary lower eyelids, or subocular pouches; upper eyelids not fused to eyeball. Spiracles large and set just behind at level of eyes. Five or six paired gill openings present on sides of head, with the posteriormost in front of pectoral-fin origins. Nostrils longitudinal on snout, without barbels, nasoral grooves or circumnarial grooves; nostrils separate from mouth, anterior nasal flaps short and not reaching mouth. Mouth small, subterminal, broadly arched and short, extending slightly behind eyes. Labial furrows greatly reduced but present on both jaws. Teeth weakly 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; teeth with orthodont histological structure. Trunk cylindrical, not flattened and ray-like. Caudal peduncle with long thick lateral dermal ridges. Dermal denticles covering entire body, not enlarged as thorns or spines. Pectoral fins moderately large, not expanded and ray-like, without triangular anterior lobes that cover the gill openings. Pectoral girdle (scapulocoracoid) high, U-shaped, without a medial joint, and with superscapulae directed posterodorsally and not contacting vertebral column. Pectoral fin skeleton tribasal, with propterygium not excluded from contact with radials and metapterygium without a proximal segment; pectoral fins aplesodic, with radials not extending into fin webs; radial counts 21 to 27 with mostly 2 or 3 segments. Pelvic fins small, with vent continuous with their inner margins. Claspers with siphons in the abdomen at the pelvic-fin bases but without clasper sacs; clasper glans lacking a pseudosiphon but with a cover rhipidion, rhipidion and clasper spine; dorsal and ventral marginals of clasper skeleton strong but not rolled into a
tube for the clasper canal. Two spineless dorsal fins present, with origin of first over abdomen and well in front of pelvic-fin bases. Anal fin absent. Caudal fin with a long dorsal lobe and no ventral lobe; vertebral axis slightly elevated into the dorsal caudal-fin lobe (heterocercal caudal fin). Vertebral counts: total vertebral counts 132 to 157, precaudal vertebral counts 90 to 108, monospondylous vertebral counts 42 to 55 . Intestinal valve of conicospiral type, with 6 to 10 turns. Colour: brown to brownish-grey, light grey, or pale yellow above, lighter below; some species with blotches or stripes on rostrum. Reproductive mode yolk-sac viviparity.

Distribution, Habitat, Biology, Interest to Fisheries and Human Impact: See family Pristiophoridae.

Local Names: Sawsharks, Saaghaaie (South Africa).

Remarks: The Pristiophoriformes are a highly derived, small group of sharks that are transitional between more conventional sharks and the batoids, but which have many unique characteristics related to their unusual feeding mechanism. It is likely that the pristiophorids are the immediate sister group of batoids (Shirai, 1992, 1996, de Carvalho, 1996) but should rank as a separate order Pristiophoriformes with the single family Pristiophoridae following Whitley (1940) and many subsequent writers.

### 2.3.1 Family PRISTIOPHORIDAE

Family: Family Pristiophoroidei Bleeker, 1859, Act. Soc. Sci. Indo-Neerl. 6: xii. Type genus: Pristiophorus Müller and Henle, 1837a.

Type genus: Pliotrema Regan, 1906c.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Genera: 1.

Synonyms: Family Pliotremidae Jordan, 1923: 101. Emended as Subfamily Pliotrematinae Fowler, 1947: 13 (Family Pristiophoridae). Probably independently proposed as Family Pliotremidae by Gubanov, Kondyurin, and Myagkov, 1986: 223.

FAO Names: En - Saw sharks; Fr - Requins scie; Sp - Tiburones sierra.
Field marks: See order.
Diagnostic Features: See order.
Distribution: The Pristiophoridae have a sporadic and disjunct distribution in the Western North Atlantic, Eastern South Atlantic, Indian Ocean, and the Western Pacific.

Habitat: Sawsharks are temperate and tropical benthic and epibenthic inhabitants of the continental and insular shelves and upper slopes from close inshore to about 952 m . Some temperate-water sawsharks occur in shallow bays and estuaries near the intertidal and also on offshore sand and gravel banks down to the upper continental slopes. Tropical species occur on the upper continental and insular slopes.

Some sawsharks are or were common where they occur, and are found in large schools or feeding aggregations. The behavior of sawsharks is poorly known. At least one species shows segregation by depth within populations, with adults in deeper water than young.

Biology: Sawsharks exhibit yolk-sac viviparity, with litters of 7 to 17 young. Apparently sawshark fetuses gain nutrients primarily from their large yolk sacs, which are resorbed just before birth. The large lateral rostral teeth erupt before birth in sawsharks, but to prevent injury to the mother these large teeth lie flat against the rostrum in fetuses until after birth. Smaller teeth either erupt between the large ones after birth (some Pristiophorus species) or erupt along with the larger teeth before birth but are covered by them (Pliotrema).

Feeding habits of sawsharks are poorly known, but known prey include small fishes, crustaceans and squid. The long rostral barbels may have taste, touch or other sensors, that these sharks trail along the bottom like those of sturgeons (Acipenseridae) and catfish (Siluriformes) to locate prey, while the long, delicate rostrum has a lateral line and ampullal sensors for vibrationsensing and electrolocation, similar to the snout of paddlefish (Polyodontidae). The lateral and ventral rostral teeth, flat snout and head, enlarged occipital condyles, and specialized cervical vertebrae of sawsharks are evident modifications that allow these sharks to use their rostra as feeding devices to kill or capture prey and possibly stir up bottom sediments to rouse prey organisms, and possibly to defend themselves. Unlike the batoid sawfishes (Pristidae), feeding behavior using the rostral saw has not been observed, probably because sawsharks have been seldom kept in captivity and without much success (unlike sawfishes) and have not been studied underwater where they occur. The short jaws, small mouths and long oral and gill cavities of sawsharks suggest that they can suddenly suck prey into their mouths. Unlike sawfishes (Pristidae), sawshark
teeth are not strongly anchored in the snout, and are easily pulled out. The needle-pointed, sharp-edged lateral teeth, hooked ventral teeth set at a right angle to the lateral teeth, and the tendency of the rostral teeth to easily snag on various objects suggest that the saw may have a snaring or jigging action with prey. They may be able to hook the arms and tentacles of cephalopods, and the legs and antennae of crustaceans, as well as the bodies of small, soft fishes. Pristiophorus sawteeth are smooth-edged, but Pliotrema additionally has mesially directed barbs on its larger sawteeth that enhance adhesion.

Size: Sawsharks are small and slender, little-known sharks with a maximum total length of about 137 to 153 cm but with a few species possibly not exceeding 70 cm . Size at birth from 28 to 35 cm in total length.

Interest to Fisheries and Human Impact: Demersal gillnets and trawl fisheries take sawsharks as a relatively small landed bycatch off Southern Australia, where they are marketed fresh for human consumption. They are also taken and used in the Western North Pacific to some extent, but details are sketchy. Sawsharks are caught in bottom trawl fisheries off South Africa and Southern Mozambique, but are discarded.

Sawsharks are harmless to people, unlike large sawfishes (Pristidae) that have occasionally struck and even killed bathers in the shallows and can be a hazard to fishers when caught in nets and on line gear. The rostral teeth of sawsharks are extremely sharp though apparently non-toxic, and should be handled with due care to prevent minor puncture wounds on one's limbs.

The conservation status of sawsharks is mostly Data Deficient or Least Concern where some life history information is available. However, the highly 'adhesive' rostrum of sawsharks suggests that, as with sawfishes, they may be highly vulnerable to net gear (particularly gillnets) because their saws can easily get caught in such gear. Some species have restricted areal and bathymetric distributions, including possible habitat restrictions, and could have problems with intensive fisheries that are operating where they occur. Unfortunately sawsharks are poorly known biologically, and have attracted little attention because of their minor significance or lack of importance to fisheries or other human activities.

Local Names: Sawsharks, Saw sharks (English), Saaghaaie (South Africa).
Remarks: The family is comprised of two genera and seven species; a single genus and one species just barely occur in the Southeastern Atlantic Ocean, with a few scattered records from around Cape Town, South Africa.

The arrangement of genera and species in this family follows Ebert (2013) and Ebert, Fowler and Compagno (2013).
Literature: Günther (1870); Garman (1913); Fowler (1941, 1969); Springer and Bullis (1960); Last and Stevens (2009); Ebert and Cailliet (2011); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press).

## List of Deep-sea Species Occurring in the Area:

Pliotrema warreni Regan, 1906

## Pliotrema Regan, 1906

Genus: Pliotrema Regan, 1906c, Ann. Natal Mus., 1(1): 1.
Type species: Pliotrema warreni Regan, 1906b, by monotypy.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 1.

Synonyms: Genus Poliotrema Séret, 1987: 1. Genus Piliotrema Bass, D'Aubrey and Kistnasamy, 1975c: 58, Tab. 10. Both are typographical errors.

Diagnostic Features: Barbels more posteriorly situated on snout than in Pristiophorus, prebarbel snout length 64 to $67 \%$ of preoral length. Larger rostral sawteeth with 2 to 8 mesially-directed barbs on their posterior edges. Six paired gill slits. Teeth with transverse ridges on basal ledges. Most teeth with basal ledges notched and with a prominent rounded mesolabial peg. Lateral trunk denticles very widely spaced and only semi-imbricated in large specimens, usually separated by distances greater than their crown lengths. Six gill arches, with hypobranchials 2 to 5 present, hypobranchial 4 enlarged and reflexed distally; basibranchial copula with deep anterior concavities for hypobranchials 4 and 5 , with lateral wings for articulation of ceratobranchial 6 , and with a joint on its posterior pointed tip. Vertebral counts: total vertebral counts 146 to 157, precaudal vertebral counts 101 to 108 , monospondylous vertebral counts 48 to 53 . Intestinal valve with 7 to 8 turns. Colour: olive brown above, lighter below; no prominent markings.

Local Names: Sixgill sawsharks, Seskief-saaghaai (South Africa).

## Pliotrema warreni Regan, 1906

Pliotrema warreni Regan, 1906c, Ann. Natal Mus., 1(1): 1, pl. 1. Syntypes: British Museum (Natural History), two specimens each about 750 mm total length, one from "the coast of Natal" (KwaZulu-Natal) at about 73 m depth and apparently received from Dr. E. Warren of the Natal Government Museum (Pietermaritzburg, South Africa); and one from False Bay, Western Cape, South Africa received from Dr. J.D.F. Gilchrist of the University of Cape Town. BMNH-1905.6.8.9 includes one syntype ( 800 mm long according to Springer and Bullis, 1960, Bull. Mar. Sci. Gulf Caribb., 10(2): 249) or both. Fowler (1941, Bull. U. S. Natn. Mus., (100) 13: 283) and Eschmeyer (2013) list the type locality of the first syntype as "Bird Island, Natal, South Africa". This is questionable as Bird Island in KwaZulu-Natal is inside Lake St. Lucia (where sawfish, not sawsharks, were found). There is also Bird Island in Algoa Bay, Eastern Cape (off which the sixgill sawshark has been collected), which is a more likely locality if the specimen didn't come from KwaZulu-Natal.

Synonyms: None.
Other Combinations: Pristiophorus cirratus (Latham, 1794).
FAO Names: En - Sixgill sawshark; Fr - Requin scie flutien; Sp - Tiburón sierra del Cabo.


Fig. 130 Pliotrema warreni
Field Marks: Small slender sharks with six pairs of gill openings, saw-like snout with barbels and barbed sawteeth, two spineless dorsal fins, and no anal fin.

Diagnostic Features: As for genus.
Distribution: Known only from South Africa, from Table Bay and False Bay (Southeastern Atlantic), Western Cape Province, eastwards to Cape Agulhas (Southwestern Indian Ocean), to central and northern KwaZulu-Natal, and Southern Mozambique and possibly Southeastern Madagascar. Intensive trawling by the RV Africana during the last three decades between 40 to 500 meters along the west, southwest, and southeast coasts of South Africa suggests that this species normally does not occur along the cold-temperate west coast of South Africa northwards from the Cape Town area, which is influenced by the cold Benguela Current flowing southwards along the coast, but rather the population appears to be concentrated on the Agulhas Bank.

Habitat: A benthic and epibenthic offshore shark mostly found on the Agulhas Bank, but its range extends northwards along the east coast to KwaZulu-Natal, South Africa. It occurs on outer continental shelves and upper slopes in warm-temperate and subtropical waters of Southern Africa at depths of 37 to 200 m , but has been recorded to at least 500 m . Distribution off the Southern Cape coast of South Africa is bimodal, with most records between 20 to $21^{\circ} \mathrm{E}$ longitude on the outer continental shelf of the Western Cape off Cape Agulhas and Cape Infanta ( 60 to 160 m , mostly from 70 to 140 m ); and between 25 to $27^{\circ} \mathrm{E}$ longitude on the continental shelf and uppermost slope of the Eastern Cape from Algoa Bay to Port Alfred ( 70 to 290 m , mostly from 80 to 120 m ). There are few intermediate records between the two areas, and no records from the deeper slope below 300 m on the Cape coast. The distribution of this shark in Cape waters suggests a restricted habitat (possibly related to feeding?). Off central KwaZulu-Natal it ranges from 73 to 430 m , with most catches below 110 m . It has been taken at 360 m off Delagoa Bay.

Biology: Yolk-sac vivparous, with 5 to 17 young per litter. Adults are partially segregated by depth from young, which occur in shallower water. Females with term fetuses, neonates or small juveniles have been collected in the Eastern Cape (vicinity of Algoa

Bay) and off KwaZulu-Natal, suggesting pupping grounds there. Larger individuals including adult males are wider ranging, and have been collected from the Western Cape, South Africa, to Southern Mozambique. The behavior of this shark is poorly known.

The sixgill sawshark eats small fish (including Champsodon), crustaceans and squid. Larger individuals may have light parallel cuts and scratches suggestive of combat scars and apparently inflicted by both the oral and rostral teeth of other sawsharks. A live specimen removed from a trawl was observed to swing its head and rostrum violently and quickly from side to side when held just behind the pectoral fins. Predators of the sixgill sawshark are poorly known, but one specimen was found in the stomach of a tiger shark caught off KwaZulu-Natal, South Africa.

Size: Maximum total length at least 136 cm ; males mature at about 83 cm and reach at least 112 cm ; females immature at 68 to 87 cm , mature at about 110 cm and reach at least 136 cm . Size at birth between 35 to 37 cm , with free-living specimens at 35 cm and term fetuses up to 37 cm .

Interest to Fisheries and Human Impact: Taken by bottom trawlers as a bycatch of demersal fisheries off South Africa, but not utilized as far as is known and discarded. It probably is not common enough to warrant marketing from bycatch, much less a targeted fishery. It apparently has not been kept in captivity.


Fig. 131 Pliotrema warreni
Known distribution

The conservation status of the sixgill sawshark is Near Threatened, but should be closely monitored because it is a southern African endemic with a relatively restricted geographic, bathymetric, and habitat range. The sixgill sawshark should be monitored for decreases in abundance as intensive offshore trawl fisheries occur throughout its known range.

Local Names: Sixgill sawshark, Seskief-saaghaai, Saagbek (South Africa).
Remarks: Thompson (1914) listed the Australian Pristiophorus cirratus from Cape Province, South Africa, and noted that Dr. Boulenger of the British Museum (Natural History) had identified a specimen of this species from False Bay. Barnard (1925) thought that the presence of $\boldsymbol{P}$. cirratus in South African waters was doubtful, and that Prof. Gilchrist (pers. comm. in Barnard, 1925, p. 53) of the University of Cape Town had suggested that the False Bay specimen possibly was a Pliotrema warreni of which Boulenger had either overlooked the sixth gill slit or regarded it as an individual aberration. Fowler (1941) listed the South African record of Pristiophorus cirratus without comment while Smith (1949) recognized it but noted that it had only been collected once off South Africa. Bass, D'Aubrey and Kistnasamy (1975c) agreed with Gilchrist and Barnard's (1925) opinion on Boulenger's record not being valid. They suggested that as no more records of Pristiophorus had showed up in southern African waters in fifty years despite extensive collecting it was likely that Pristiophorus was confined to the central Indo-West Pacific, and that Pliotrema warreni was the only sawshark in the Southwestern Indian Ocean. Bass and Heemstra in Smith and Heemstra (1986) noted that Boulenger's False Bay specimen was one of the syntypes of Regan's $\boldsymbol{P}$. warreni, and hence confirmed Gilchrist's and Barnard's suggestion. Survey data from the RV Africana suggests that the only sawshark normally present in Cape waters between Cape Agulhas and Port Alfred is P. warreni.

Literature: Regan (1906a, c); Thompson (1914); Barnard (1925); Fowler (1941); Smith (1949); Bass, D'Aubrey and Kistnasamy (1975c); Compagno (1984a); Bass and Heemstra in Smith and Heemstra (1986); Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); Fowler (2004a); Ebert and Cailliet (2011); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press); J.J. Bizzarro, L.J.V. Compagno, D.A. Ebert, and R. Leslie, unpubl. data.

### 2.4 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 Deep-sea Southeastern Atlantic Ocean Families: 1.

Synonyms: [Part] 1 Squali, Abtheilung [Division] 3: Müller and Henle, 1839: 83. Ordo Plagiostomi, Subordo Squalini, Sectio Aproctopterides: Bleeker, 1859: xii. Order Squali, Suborder Rhinae: Gill, 1862: 395, 397; Gill, 1872: 23. Order Plagiostomi Diplospondyli, Suborder Plagiostomi Tectospondyli, Group 1 Squalorajae: Hasse, 1879: 44. [group] Rhinae Garman, 1885: 30. Order Selachii, Suborder Tectospondyli: Woodward, 1889: 30. Order Asterospondyli, Suborder Rhinae: Gill, 1893: 129. Order Cyclospondyli, Suborder Tectospondyli: Jordan and Evermann, 1896: 53, 58. Order Euselachii, Suborder Pleurotremata, Division Squaloidei: Regan, 1906a: 723. Order Selachii, Group 2, Division B, Subdivision 2, Suborder Rajiformes, Tribe 1: Goodrich, 1909, In R. Lankester, ed.: 155. Order Pleurotremata, Suborder Squaloidei: Engelhardt, 1913: 100. Order Plagiostoma, Suborder Antacea, "Group" Rhinoidei: Garman, 1913: 11, 13. Order Plagiostomi, Suborder Rhiniformes or Riniformes: Lozano y Rey, 1928: 280. Order Squalea, Suborder Rhinida, Superfamily Rhinoidea: White, 1936: 5; White, 1937: 37, tab. 1. Order Euselachii, Suborder Squatiniformes: Bertin, 1939: 10. Order Squaliformes, Suborder Squatinoidei: Berg, 1940: 138; Berg and Svetovidov, 1955: 68; Arambourg and Bertin, 1958, In P.-P. Grasse, ed.: 2044; Nelson, 1984: 59. Order Squatinoidei, Superfamily Squatinoidea: Whitley, 1940: 69. Order Squatinae: Fowler, 1941: 4, 279; Smith, 1949: 37, 60. Order Selachii, Suborder Squaloidea: Romer, 1945: 577; Romer, 1966: 350. Order Selachii, Suborder Squatinoidea: Bigelow and Schroeder, 1948: 77, 532. Order Squaloidea, Suborder Squatinoidea: Schultz and Stern, 1948: 225. Order Lamnida, Suborder Squatinina: Matsubara, 1955: 1-789. Order Pleurotremata, Suborder Squaloidea: Norman, 1966: 24. Order Squatinida, Suborder Squatinoidei: Glikman, 1967, in Y. A. Orlov, ed.: 217. Order Lamniformes, Suborder Squatinoidei: Patterson, 1967, in W.B. Harland et al.: 672. Order Euselachii, Suborder Squatinoidei: Blot, 1969, in J. Piveteau, ed: 702-776. Order Squalida, Suborder Squatinina: Fowler, 1969a: 74. Order Pleurotremata, Suborder Squaliformes: Budker and Whitehead, 1971: 6, tab. 2. Order Squaliformes, Suborder Squatinoidei: Lindberg, 1971: 8, 260; Nelson, 1976: 40. Order Squatiniformes: Rass and Lindberg, 1971: 304; Compagno, 1973: 27; Applegate, 1974: 743; Chu and Meng, 1979: 114, tab. 2; Compagno, 1984a: 138; Cappetta, 1987: 26, 68; Eschmeyer, 1990: 437; Shirai, 1992: 122; Nelson, 1994: 56; de Carvalho, 1996, in Stiassny et al.: 55; Shirai, 1996, in Stiassny et al.: 34; Eschmeyer, 2013. Order Squatiniformes, Suborder Squatinoidea: Chu and Meng, 1979: 114, tab. 2. Order Squalomorpha, Suborder Squatinoidea: Carroll, 1988: 599.

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 counts: total vertebral counts 119 to 146 , monospondylous vertebral counts 43 to 52 , diplospondylous 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 brown, reddish brown, or tan above, usually lighter below; most species have some saddles spots, or blotches on dorsal surface.

Distribution, Biology, Size, Interest to Fisheries and Human Impact: See family Squatinidae.
Local Names: Angel sharks, Angelsharks (English), Engelhaai (South Africa).
Remarks: The Squatiniformes or angel sharks are a small but bizarre and highly distinctive group of raylike sharks that have usually been recognized as a discrete taxon at the genus, family, and higher level. The order consists of a single family and a monotypic genus, with about 20 valid species recognized worldwide.

### 2.4.1 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 Duméril, 1806.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Genera: 1.

Synonyms: Family Rhinoidae Gill, 1862: 396, 408; also Family Rhinidae Garman, 1913: 11, 13, 248. Not "Gruppe" Rhinae Müller and Henle, 1841: 110; or Tribe Rhinae Gray, 1851: 91; type genus Rhina Bloch and Schneider, 1801 (a batoid).

FAO Names: En - Angelsharks, Sand devils; Fr - Anges de mer; Sp - Angelotes, Peces ángel.
Field Marks: See order.
Diagnostic Features: See order.
Distribution: Angel sharks are found primarily in continental waters, in the Eastern North and South Pacific, Western North and South Atlantic, Eastern Atlantic, extreme Southwestern and Southeastern Indian Ocean, temperate Western North and South Pacific, but are not known from most 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 species where some information is available appear to have an annual cycle with birth usually occurring in the spring and summer months. Most angel sharks are of moderate size, 120 to 160 cm , but at least one European species 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, trap-like 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. In the last decade, 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. 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 Near Threatened or higher for most species, with some species assessed as Critically Endangered. In those areas where fisheries for angel sharks have occurred, the fishery usually collapses within a few years.

Local Names: Angel sharks, Angelsharks, Monkfishes (English), Engelhaai (South Africa).
Remarks: A single genus, with about 20 nominal valid species worldwide. A single deep-sea species occurs in the Southeastern Atlantic Ocean.

Literature: Regan (1908b); Garman (1913); Fowler (1941, 1969); Compagno (1973, 1977, 1984a); Capapé and Roux (1980); Shirai (1992a, c, 1996); de Carvalho (1996); Walsh and Ebert (2007); Last and Stevens (2009); Walsh, Ebert and Compagno (2011); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press).

## List of Deep-sea Species Occurring in the Area:

Squatina aculeata Duméril, in Cuvier, 1829

## Squatina Duméril, 1806

Genus: Squatina Duméril, 1806, Zool. Analyt.: 102. No species. Genus Squatina Duméril 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), who also noted that Duméril applied the species name angelus to Squatina in 1806, with $\boldsymbol{S}$. angelus an unneeded substitute for $\boldsymbol{S}$. squatina. If correct this shifts the type allocation from Risso to Duméril. 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 Deep-sea Southeastern Atlantic Ocean Species: 1.

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 order.
Remarks: The genus is relatively sketchily known in the Southeastern Atlantic Ocean.

## Squatina aculeata Duméril, in Cuvier, 1829

Squatina aculeata Duméril, in Cuvier, 1829, Reg. Anim., ed. 2, 2: 394, ftn. 2. Holotype: Museum National d'Histoire Naturelle, Paris, MNHN-1218, 410 mm female, Marseille, France, Mediterranean Sea (Bertin, 1939: 77).

Synonyms: Squatina fimbriata Müller and Henle, 1839: 101, pl. 35. Syntypes: Anatomical Museum of Berlin, two young specimens, possibly lost, from the Mediterranean Sea. Paepke and Schmidt (1988: 161) could not locate these specimens in the collections of the Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin.
Other combinations: Rhina aculeata (Duméril, 1829).
FAO Names: En - Sawback angelshark; Fr - Ange de mer épineux; Sp - Angelote espinudo.


Fig. 132 Squatina aculeata

Field Marks: An angel shark with heavy middorsal and head spines, a concave interorbital space, heavily fringed nasal barbels and anterior nasal flaps, and no ocelli on body.

Diagnostic Features: Interorbital space concave. Head width about 3.3 to 3.6 times in precaudal length. Head length to notch about 3.8 to 4.6 times in precaudal length and 1.1 times in head width. Lateral head fold relatively high, with 2 or 3 prominent triangular lobes on each side. Eye length 2.5 to 3.0 times in interorbital space; preorbital length greater than eye length; eye-spiracle space less than 1.5 times eye length. Spiracle width subequal to or less than eye length; spiracles with 13 or 14 pseudobranchial folds; interspiracular space subequal to interorbital space. Nasal barbels fanlike, with expanded tips and strong lobate fringes; posterior edges and tips of anterior nasal flaps strongly fringed and tips multilobate; posterior nasal flaps greatly enlarged,


UNDERSIDE OF HEAD strongly fringed. Ratio of nostril width to internarial width not known. Exposed upper lip between bases of anterior nasal flaps forming a narrow high, rounded arch in frontal view. Tooth row counts 19 to 24 upper jaw, 19 to 23 lower jaw. Body relatively slender, width at pectoral-fin insertions about 0.7 to 1.0 times head length to upper notch and 5.4 to 6.0 times in precaudal tail. Tail length from pelvic-fin insertions to upper caudal-fin origin 0.8 to 1.1 times trunk from pectoral-fin origins to pelvic-fin insertions. Large thorns present on snout, on interorbital, and just behind eyes in front of spiracles; a single row of large thorns present on midline of back and tail from head to dorsal fins, on interdorsal space, and on postdorsal space, sometimes doubled. Dorsal denticles not closely spaced, surface coarsely granular; denticles pyramidal, not hooked and with three anterior ridges. Presence of enlarged thorns on anterior margins of paired fins uncertain in adult males. Underside of body largely naked except for anterior margins of pectoral and pelvic fins, underside of tail, and preventral margin of caudal fin. Pectoral fins long and low in young, higher in adults, angle of pectoral apex obtuse, slightly greater than a right angle. Pectoral-fin anterior margins slightly convex anteriorly, forming a weak anterior shoulder, apices narrowly subangular, posterior margin broadly concave or nearly straight, rear tips usually narrowly subangular, inner margins broadly convex and rounded. Distance from anterior tip of pectoral fin to insertion about $60 \%$ of maximum pectoral-fin length from anterior tip to free rear tip; maximum pectoral-fin length about 29 to $32 \%$ 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 about opposite pelvic-fin free rear tips; first dorsal-fin base about 1.5 to 1.6 times in interdorsal space, 2.0 times in postdorsal space. Postventral caudal-fin margin oblique. Vertebral counts: total vertebral count 146 , precaudal vertebral count 113 , monospondylous precaudal vertebral count 52 , diplospondylous precaudal vertebral count 61. Intestinal valve count not available. A large angel shark reaching about 188 cm total length. Colour: dull grey or light brown dorsally, pale below; small irregular white spots without dark edges sparsely scattered on dorsal surface, no white nuchal spot; small dark brownish spots scattered more or less regularly on back, large dark blotches on head, back, fin bases and tail; no ocelli on back; pectoral and pelvic fin webs without white anterior and posterior margins; dorsal fin bases and webs paler than body, with irregular dark spots; caudal fin with dark base, dorsal and preventral margins, web dark and irregularly speckled with light and dark spots.

Distribution: Namibia and southern Angola to Gabon, Nigeria, Equatorial Guinea, Senegal, Mauritania, Western Sahara, Morocco and Western Mediterranean.

Habitat: An offshore angel shark of the outer continental shelf and uppermost slope of the warm-temperate and tropical Eastern Atlantic, on or near the bottom at depths of 30 to 500 m . It apparently prefers muddy bottom.

Biology: Viviparous with a yolk-sac, with both ovaries functional. Gestation is about 12 months, but possibly with a biennial reproductive cycle. Ovarian fecundity ranges from 12 to 22 , but uterine fecundity is lower at 8 to 12 . Litter sizes, according to one study, show a positive correlation with the size of the female. Diet in the Mediterranean Sea includes small sharks, herring (Clupeidae), jacks (Trachurus, Carangidae), picarels (Centracanthidae), flatish (Citharus linguatula, Citharidae) sole (Solea solea, Soleidae), cuttlefish (Sepia officinalis), and crustaceans including shrimp, including manis shrimp, and crabs (Alpheus dentipes, A. ruber, Penaeus kerathurus, Squilla mantis, Parapenaeus longirostris, Dorippe lanata, Goneplax rhomboides, Macropipus


Fig. 133 Squatina aculeata

Size: Maximum total length reported to 188 cm ; males confirmed to at least 152 cm and females to 175 cm total length. Males mature at about 120 cm and females at about 137 cm . Size at birth 30 to 35 cm .

Interest to Fisheries and Human Impact: Interest to fisheries limited. Caught primarily in bottom trawls, but also in fixed bottom nets, on line gear, and even in pelagic trawls. Utilized dried-salted and fresh for human consumption; oil and hides for leather also taken. No species-specific catch data is available for this species; it is caught off Tunisia and possibly is a component of catches in other Mediterranean countries including those that report angel sharks (France, Malta, Albania, Turkey). Angel sharks are fished off the Atlantic coast of Africa but with little information being available. Angel shark catches off Namibia are substantial and have ranged from 20 to 253 tonnes during the 1990s, but species-specific information is lacking.

The conservation status of this species is Critically Endangered due to intense bottom trawling within its range.
Local names: Spiny angelshark, Monkfish, Sawback angel shark.
Remarks: This distinctive angelshark has sometimes been confused with Squatina oculata and S. squatina but is clearly separable from these species. Its nasal barbels and anterior nasal flaps are heavily fringed as in the four species of Australian angel sharks and the Taiwanese S. tergocellatoides.

Literature: Müller and Henle (1839); Garman (1913); Cadenat (1950, 1957); Poll (1951); Blache, Cadenat and Stauch (1970); Maurin and Bonnet (1970); Kreff in Hureau and Monod (1973a); Capapé (1975); Roux (1977); Penrith (1978); Capapé and Roux (1980); Compagno (1984a); Roux in Whitehead et al. (1984); Springer (1990); Bianchi et al. (1999); Capapé et al. (2005); Morey et al. (2007); Ebert, Fowler and Compagno (2013); Ebert and Compagno (In press).

### 2.5 Order LAMNIFORMES - Mackerel sharks

Order: Lamniformes Garman, 1885, Bull. Mus. Comp. Zool. Harvard, 12(1): 30 (emendation by Compagno 1984a of "group" Lamnae Garman, 1885).

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Families: 4.

Synonyms: Part 1 Squali, Abtheilung 2: Müller and Henle, 1838: 27; Müller and Henle, 1839: 27. Part 1 Squali, Abtheilung 2, Unterabtheilung 3: Müller and Henle, 1839: 66. Ordo Plagiostomi, Subordo Squalini, Sectio Proktopterides, Tribus Dinotopterini: Bleeker, 1859: xi. Order Squali, Suborder Squali: Gill, 1862: 394, 396. Order Squali, Suborder Galei: Gill, 1872: 22, 23. Order Plagiostomi diplospondyli, Suborder Plagiostomi asterospondyli, Group 2 Scylliolamnidae: Hasse, 1879: 51. Order Selachii, Suborder Asterospondyli: Woodward, 1889: 157. Order Asterospondyli: Gill, 1893: 130; Fowler, 1941: 4, 13; Smith, 1949: 37, 39. Order Asterospondyli, Suborder Galei: Jordan and Evermann, 1896: 19, 21. Order Euselachii, Suborder Pleurotremata, Division Galeoidei: Regan, 1906a: 723. Order Selachii, Group 2, Division B, Subdivision 1, Suborder Scylliodei: Goodrich, 1909: 148. Order Pleurotremata, Suborder Galeoidei: Engelhardt, 1913: 97. Order Plagiostoma, Suborder Antacea, Group Carcharoidei: Garman, 1913: 10, 11. Order Plagiostoma, Suborder Antacea, Group Isuroidei: Garman, 1913: 10, 12. Order Euselachii, Suborder Galei, Series Lamnoidei: Jordan, 1923: 99. Order Plagiostomi, Suborder Galeiformes: Lozano y Rey, 1928: 280. Order Galea, Suborder Isurida, Superfamily Odontaspoidea: White, 1936: 4; White, 1937: 36, tab. 1. Order Galea, Suborder, Isurida, Superfamily Isuroidea: White, 1936: 4; White, 1937: 36, tab. 1. Order Euselachii, Suborder Lamniformes: Berg, 1940: 137; Berg and Svetovidov, 1955: 65; Patterson, 1967: 670; Rass and Lindberg, 1971: 303; Lindberg, 1971: 8, 257; Compagno, 1973: 28; Applegate, 1974: 743; Nelson, 1976: 33; Compagno, 1984a: 212; Nelson, 1984: 51; Gubanov, Kondyurin and Myagkov, 1986: 3, 49; Cappetta, 1987: 26, 85; Compagno, 1988: 382; Eschmeyer, 1990: 435; Nelson, 1994: 51; de Carvalho, 1996: 55; Shirai, 1996: 32; Eschmeyer, 1998. Order Lamniformes, Suborder Lamnoidei: Berg, 1940: 137; Berg and Svetovidov, 1955: 65; Patterson, 1967: 670; Lindberg, 1971: 8, 257; Nelson, 1976: 33; Nelson, 1984: 51; Nelson, 2006: 57. Order Euselachii, Suborder Galei, Superfamily Odontaspoidea: Whitley, 1940: 68. Order Euselachii, Suborder Galei, Superfamily Isuroidea: Whitley, 1940: 68. Order Selachii, Suborder Galeoidea: Romer, 1945: 576; Bigelow and Schroeder, 1948: 77, 95; Romer, 1966: 350. Order Lamnoidea, Suborder Galeoidea: Schultz and Stern, 1948: 224. Order Lamnida, Suborder Lamnina: Matsubara, 1955: 1-789. Order Galeiformes, Suborder Isuroidea: Arambourg and Bertin, 1958: 2029. Order Pleutrema, Suborder Galeoidea: Norman, 1966: 7. Order Carchariida, Suborder Carchariina, Superfamily Carchariicae: Fowler, 1967a: 92, 140. Order Carchariida, Suborder Carchariina, Superfamily Lamnicae: Fowler, 1967a: 92, 104. Order Squatinida, Suborder Squaloidei: Glikman, 1967: 215. Superorder Lamnae, Order Odontaspidida: Glikman, 1967: 229, 230. Order Odontaspidida, Superfamily Odontaspidoidea: Glikman, 1967: 230. Order Odontaspidida, Superfamily Isuroidea: Glikman, 1967: 232. Order Odontaspidida, Superfamily Scapanorhynchoidea: Glikman, 1967: 233. Order Euselachii, Suborder Galeoidei: Blot, 1969: 702-776. Order Pleurotremata, Suborder Galeiformes: Budker and Whitehead, 1971: 5, tab. 2. Order Carcharhiniformes: Rass and Lindberg, 1971: 303; Gubanov, Kondyurin and Myagkov, 1986: 3, 61. Order Isuriformes: Chu and Meng, 1979: 114, tab. 2. Order Isuriformes, Suborder Carchariodea: Chu and Meng, 1979: 114, tab. 2. Order Isuriformes, Suborder Isuroidea; Chu and Meng, 1979: 114, tab. 2. Order Isuriformes, Suborder Cetorhinoidea: Chu and Meng, 1979: 114, tab. 2. Order Isuriformes, Suborder Alopioidea: Chu and Meng, 1979: 114, tab. 2. Order Galeomorpha, Suborder Lamnoidea: Carroll, 1988: 599.

FAO Name: En - Mackerel sharks.
Field Marks: The external appearance of each of the several members of this group appears to be unique and unrelated, but they share a number of features including a short to moderately long pointed snout, eyes usually lateral on the head (except dorsolateral on Carcharias), eyes without a nictitating membrane, spiracles if present 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 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 five 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 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 count 55 to 356 . Intestinal valve of conicospiral type, with 18 to 55 turns. Size small, from less than 1 m in length, to gigantic, up to 10 m 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.

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 depth 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 (oopghagy) 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 some areas of the world since their populations have declined from previous fisheries exploitation.

Several species, particularly the white shark (Carcharodon carcharias), are 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 great white shark and shortfin mako shark, among other lamnoids, have become popular ecotourist attractions for thrill seeking cage divers. The sandtiger 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 outgrow 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 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 Least Concern or Data Deficient due to a lack of information on their populations and basic biological information.

Local Names: Mackerel sharks, Haringhaaie (South Africa).
Remarks: The present account is modified from, and follows Compagno (1984a, 2001) in recognizing seven families, of which five are considered to inhabit the deep-sea; four deep-sea families occur in the Southeastern Atlantic. See Compagno (2001) for detailed discussion of the order.

## Key to Deep-sea Southeastern Atlantic Ocean Families:

1a. Snout extremely elongated, flat, and blade-like (Fig. 134). Precaudal pits and ventral lobe absent . .

## family Mitsukurinidae

1b. Snout short to moderately long, but not greatly elongated or blade-like, and broadly rounded. Precaudal pits and ventral caudal-fin lobe present.


Fig. 134 Mitsukurina owstoni

2a. Caudal fin about as long as trunk of body (Fig.
135). . . . . . . . . . . . . . . . . . . family Alopiidae


Fig. 135 Alopias superciliosus


Fig. 136 Cetorhinus maximus


Fig. 137 Pseudocarcharias kamoharai

### 2.5.1 Family MITSUKURINIDAE

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

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Genera: 1.

Synonyms: Family Scapanorhynchidae White, 1936: 4. Type genus: Scapanorhynchus Woodward, 1889, a Cretaceous fossil genus.

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 vertebral caudal counts 66 to 69 . Intestinal valve of ring type with 18 to 23 turns. Size large, with adults at least 550 to 620 cm total 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 (1984a, 2001). The family has a single genus and species, which occurs in all major oceans.

Literature: Compagno (1984a, 2001); Ebert (2003); Yano, Stevens and Compagno (2007); Last and Stevens (2009); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013).

## List of Deep-sea Species Occurring in the Area:

Mitsukurina owstoni Jordan, 1898

## 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 Deep-sea Southeastern Atlantic Ocean 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 (2013).

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 (2013). Scapanorhynchus jordani Hussakof, 1909: 257, text-figs., pl. 44. Syntypes (2): American Museum of Natural History, AMNH-00004SW, jaws, model on display from 1300 mm female; 1155 mm female, formerly in the Zoological Department at Columbia University. Scapanorhynchus dofleini Engelhardt, 1912: 644. Holotype: Zoologischen Staatssammlung München, 2100 mm female, Mayegawa, Sagami Sea, Japan. Locality of Holotype unknown according to Eschmeyer (2013). Scapanorhynchus mitsukurii White, 1937: 29 (error for Mitsukurina owstoni Jordan, 1898), Japan. Mitsukurina nasutus Albuquerque, 1954-56, Port. Acta. Boil., ser. B, 5: 82-83, fig. 47.

Other Combinations: Scapanorhynchus owstoni (Jordan, 1898): Bass, D'Aubrey and Kistnasamy 1975b: 18, fig. 8, pl. 7.
FAO Names: En - Goblin shark; Fr - Requin lutin; Sp - Tiburón duende.


Fig. 138 Mitsukurina owstoni


UNDERSIDE OF HEAD


UPPER AND LOWER TEETH

Field Marks: A distinctive, unmistakable shark with its soft flabby body, elongated, flattened, bladelike snout, relatively small eyes, highly protrusible jaws, long and narrow teeth with a single cusp, two spineless dorsal fins, similar in size and about equal to the large rounded anal fin, second dorsal fin originating posterior to the pelvic fins, colour in life a spectacular pinkish-white to white with bluish fins.

Diagnostic Features: As for family Mitsukurinidae.
Distribution: Only a single confirmed record from the Southeastern Atlantic, from west of Cape Town, South Africa (Western Cape Province). Elsewhere, wideranging, with records in all major oceans, but patchily distributed.

Habitat: The goblin shark is a poorly known deep-sea 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 Japanese waters subadults are most common between 100 and 350 m depth 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 behaviour. The only confirmed record from the Southeastern Atlantic was from west of Cape Town and was caught by a bottom trawl at 549 m .

Biology: Virtually nothing is known about the biology of these sharks, although like all other lamnoids 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


Fig. 139 Mitsukurina owstoni
$\square$ Known distribution 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 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 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 free-swimming 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 soft-bodied 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.

The goblin shark has been kept in public aquaria where it was observed swimming 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 subadults suggesting that adults occur outside the depth range where most fisheries take place.

Local Names: Kabouterhaai (South Africa).
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 1500 and 4000 USD depending on the size and quality of the jaws.

Literature: Jordan (1898); Bean (1905); Garman (1913); Compagno, Ebert and Smale (1989); Duffy (1997); Compagno (2001); Parsons, Ingram and Havard (2002); Ebert (2003); Duffy, Ebert and Stenberg (2004); Yano, Stevens and Compagno (2007); Last and Stevens (2009); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013); D.A. Ebert (unpubl. data).

### 2.5.2 Family PSEUDOCARCHARIIDAE

Family: Pseudocarchariidae Compagno, 1973, J. Linn. Soc. (Zool.), 53, suppl. 1: 28.
Type genus: Pseudocarcharias Cadenat, 1963.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Genera: 1.

Synonyms: Family Pseudocarcharinidae Shirai, 1996: 34. Probable error for Pseudocarchariidae.
FAO Names: En - Crocodile sharks; Fr - Requins crocodile; Sp - Tiburones cocodrilo.
Field Marks: See species account below.
Diagnostic Features: Head much shorter than trunk. Snout moderately long, pointed and bulbously conical, not greatly elongated or flattened and blade-like. Eyes very large, length 3.6 to $4.9 \%$ of precaudal length. Gill openings moderately long, length of first 5.4 to $8.2 \%$ of precaudal length, extending onto dorsal surface of head; all gill openings in front of pectoral-fin bases; no gill rakers on internal gill slits. Mouth large, parabolic, ventral on head; jaws strongly protrusible to almost opposite snout tip but not greatly distensible laterally. Teeth large, the anteriors narrow and awl-like, the laterals more compressed and blade-like; tooth counts 26 to 29 upper jaw, 21 to 26 lower jaw; two rows of enlarged anterior teeth on each side of upper jaw, the uppers separated from the smaller upper lateral teeth by a row of small intermediate teeth; three rows of lower anteriors on each side, the first two rows enlarged but the third about as large as laterals; symphysials absent. Trunk cylindrical and slender. Caudal peduncle slightly depressed and with low lateral keels and upper and lower crescentic precaudal pits present. Dermal denticles small and smooth, with flat crowns, small ridges and cusps, and with cusps directed posteriorly on lateral denticles. Pectoral fins small, short, and broad, much shorter than head in adults. Pelvic fins large, somewhat smaller than pectoral and first dorsal fins. First dorsal fin small, low, and angular. Second dorsal fin smaller than first, but larger than anal fin; second dorsal fin with a broad non-pivoting base but anal fin pivotable. Caudal fin not lunate, dorsal lobe moderately long but less than half as long as rest of shark, ventral lobe short but strong. Vertebral counts: total vertebral counts 146 to 158 , precaudal vertebral counts 80 to 88 , caudal vertebral counts 60 to 71 . Intestinal valve ring type with 24 to 27 turns. Size small with adults to 122 cm total length. Colour: grey to grey-brown above, lighter below, and with lighter fin edges.

Distribution: Wide-ranging in all major tropical and subtropical oceans.
Habitat: See species account.
Biology: See species account.

Interest to Fisheries and Human Impact: See species account.
Local Names: Crocodile sharks, Krokodilhaaie (South Africa).
Literature: Compagno (1984a, 2001); Last and Stevens (2009); Ebert (2013); Ebert, Fowler and Compagno (2013).
List of Deep-sea Species Occurring in the Area:
Pseudocarcharias kamoharai (Matsubara, 1936)

## Pseudocarcharias Cadenat, 1963

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

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

Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 1.
Synonyms: None.
Field Marks: See species account below.
Diagnostic Features: See family Pseudocarchariidae above.
Local Names: Crocodile sharks.

## Pseudocarcharias kamoharai (Matsubara, 1936)

Carcharias kamoharai Matsubara, 1936, Zool. Mag. Tokyo, 48(7): 380. Holotype: Imperial Fisheries Institute, Japan, Kyoto University, Department of Fisheries, Faculty of Agriculture, Japan (housed at Maizuru, Japan) FAKU, Fish Spec. 1823, 735 mm male, Koti Fish Market, Koti, Japan, apparently lost according to Eschmeyer (2013).

Synonyms: Carcharias yangi Teng, 1959: 1, fig. 1. Holotype; Taiwan Fisheries Research Institute, TFRI 2895, 1000 mm total length, adult male, Su-ao fish market, from off Su-ao, Taiwan (Province of China). Pseudocarcharias pelagicus Cadenat, 1963: 529, figs. 1-5. Holotype: Museum National d'Historie Naturelle, Paris, MNHN 1963-1, 975 mm adult male, off the Guinea coast, West Africa.

Other Combinations: Odontaspis kamoharai (Matsubara, 1936).
FAO Names: En - Crocodile shark; Fr - Requin crocodile; Sp - Tiburón cocodrilo.


Fig. 140 Pseudocarcharias kamoharai

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

Diagnostic Features: As for Family Pseudocarchariidae above.
Distribution: Circumtropical. In the Southeastern Atlantic Ocean recorded off Angola and South Africa (Western Cape, vicinity of Cape Town and the Cape Peninsula, based mostly on a few strandings).

Habitat: An uncommon to locally abundant oceanic, epipelagic, and possibly mesopelagic shark, usually found offshore and far from land, but sometimes occurs inshore and near the bottom at depths from the surface to at least 590 m . Its bicoloured countershading colour pattern, lack of an expanded iris and prominent green or yellow retinal reflection, and frequent occurrence in pelagic longline catches suggest that it primarily inhabits the epipelagic zone. There are several stranding records in the Cape Town (South Africa) area that suggest upwelling of cold water may stun and possibly kill these sharks on occasion.

Biology: Viviparous with uterine cannibalism; the young have yolk sacs at 3 to 4 cm long, but reabsorb them and subsist on the eggs and possibly smaller embryos. Litter size is usually four, two per uterus with one male and female per uterus; up to nine fertilized eggs per uterus have been recorded. There does not appear to be any seasonality to their reproductive cycle as pregnant females are found year-round.

The diet is not well known, but appears to include midwater bony fishes and cephalopods.

Size: Maximum total length about 122 cm ; males adult at 74 to 81 cm , largest male 110 cm ; females adult at 87 to 98 cm , largest female 122 cm . Size at birth about 41 cm .


Fig. 141 Pseudocarcharias kamoharai
$\square$ Known distribution $\square$ Possible distribution

Interest to Fisheries and Human Impact: Interest to fisheries none, it is usually taken as bycatch in longline and trawl fisheries. The small size and poor quality of its flesh makes this a relatively undesirable species for human consumption.

The crocodile shark has been listed as Near Threatened.
Local Names: Grootoog-skeurtandhaai, Krokodilhaaie (South Africa).
Remarks: The above account is modified after Compagno (2001).
Literature: Matsubara (1936); Teng (1959); Cadenat (1963); Chen (1963); D'Aubrey (1964a, b); Merrett (1965); Abe et al. (1969); Abe (1973); Compagno (1973, 1984a, 2001); Bass, D'Aubrey and Kistnasamy (1975b); Compagno, Ebert and Smale (1989); Compagno and Musick (2005); Last and Stevens (2009); Oliveira et al. (2010); Fricke, Kulbicki and Wantiez (2011); Dai et al. (2012); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013).

### 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 Deep-sea Southeastern Atlantic Ocean Genera: 1.

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

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 moderately large to extremely large, diameter 1.8 to $4.3 \%$ of precaudal length; nictitating membrane absent. Spiracles present, but small, pore-like. Gill openings relatively short, first opening 3.1 to $5.2 \%$ of 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 or absent. Teeth small, blade-like, with a single erect cusp; depending on species cusplets may or may not be 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 in 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 723 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 shark 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 an important fisheries because their meat is of high quality for human consumption and the long fins are highly desirable in the shark-fin trade. However, despite their being a common bycatch component in drift gillnets 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: Threshers, Sambokhaaie (South Africa).
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 common thresher shark (Alopias vulpinus) and the pelagic thresher shark (A. pelagicus). The other group includes the bigeye thresher shark (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 (A. pelagicus and A. vulpinus) of which generally occur from nearshore to offshore waters and usually inhabit a more pelagic environment, while one species (A. superciliosus) generally occurs in much deeper water than the others. The family, genus, and species accounts are modified and updated from Compagno (1984a, 2001).

Literature: Bigelow and Schroeder (1948); Gruber and Compagno (1981); Compagno (1984a, 2001); Quéro in Whitehead et al. (1984); Ebert (2003); Last and Stevens (2009); Compagno, Ebert, and Smale (2013); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013).

## List of Deep-sea Species Occurring in the Area:

## 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 Deep-sea Southeastern Atlantic Ocean Species: 1.

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 an 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.

## Alopias superciliosus Lowe, 1841

Alopecias superciliosus Lowe, 1841, (Jan.), Proc. Zool. Soc. London, 1840(8): 39. Also Lowe, 1849, Trans., Zool. Soc. London, 3(1): 18 (sometimes dated 1839). Holotype unknown (Compagno, 2001), type locality Madeira, Eastern Atlantic.

Synonyms: Alopias profundus Nakamura, 1935: 2, pl. 1, fig. 1, pl. 2. Syntypes: three large specimens, 332, 352, and 366 cm total length, a large female illustrated and of uncertain size (Nakamura, 1935, pl. 1, fig. 1); also, a 72 cm total length foetus, presumably the same as illustrated (Nakamura, 1935, pl. 2); all specimens from So-au fish market, Taiwan (Province of China). Whereabouts of syntypes unknown according to Compagno (2001); syntypes may possibly have never been accessioned into a research collection.

Other Combinations: None.
FAO Names: En - Bigeye thresher; Fr - Renard à gros yeux; $\mathbf{S p}$ - Zorro ojón.


Fig. 142 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, 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 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 counts 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 counts 43 to 45 . Maximum total length about 484 cm . 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: Recorded off Angola with a few records from off the Western Cape Province, South Africa. Also recorded from Guinea to Sierra Leone and northwards, including the Mediterranean Sea. Elsewhere, found worldwide in all major oceans.

Habitat: Bigeye thresher sharks 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, migrating at night to within 10 and 100 m from the surface where the water temperature warms to between 20 and $26^{\circ} \mathrm{C}$.

Biology: Viviparous with a 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 benthic 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


Fig. 143 Alopias superciliosus
$\square$ Known distribution $\square$ Possible distribution enabling these sharks to hunt by searching for silhouettes of potential prey items above them.

The bigeye thresher, as well as the other members of this genus and the family Lamnidae is able to maintain its 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 between 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.

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 high levels of largely unmanaged and unreported mortality from targeted and non-targeted fisheries.

Local Names: Bigeyed thresher, Grootoog-sambokhaai (South Africa).
Literature: Bigelow and Schroeder (1948); Bass, D'Aubrey and Kistnasamy (1975b); Gruber and Compagno (1981); Gilmore (1983, 1993); Compagno (1984a, 2001); Compagno, Ebert and Smale (1989); Chen, Liu and Chang (1997); Liu, Chiang and Chen (1998); Ebert (2003); Weng and Block (2004); Amorim et al. (2009); Last and Stevens (2009); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013).

### 2.5.4 Family CETORHINIDAE

Family: Subfamily Cetorhinidae Gill, 1862, 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 Deep-sea Southeastern Atlantic Ocean Genera: 1.

Synonyms: Group Selachina Günther, 1870 (Family Lamnidae): 389, 394. Emended to Family Selachidae Günther, 1870, by Poey, 1875: 85. Also Subfamily Selache (Family Lamna) Hasse, 1879: tab. 2. Type genus: Subgenus Selache Cuvier, 1816 (Genus Squalus Linnaeus, 1758). Family Halsydridae Whitley, 1934: 196. Type genus: Halsydrus Neill, 1809a, b.

FAO Names: En - Basking sharks; $\mathbf{F r}$ - Requins pélerin; Sp - Peregrinos.
Field Marks: See species account below.
Diagnostic Features: Body fusiform, stout, and firm, not flabby; body stoutest from about pectoral fins 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 to 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 an 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 crescent-shaped, 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 10 m and possibly to 12 m 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: Coastal and pelagic oceanic, 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 transequatorial migrations.

Biology: See species account below.
Interest to Fisheries and Human Impact: See species account below.
Local Names: Basking sharks, Koesterhaaie (South Africa).
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 in all major oceans.
Literature: Bigelow and Schroeder (1948); Compagno (1984a, 2001); Ebert (2003); Last and Stevens (2009); Ebert (2013); Ebert and Stehmann (2013).

## List of Deep-sea Species Occurring in the Area:

Cotorhinus maximus (Gunnerus, 1765)

## 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 (1862, 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 Deep-sea Southeastern Atlantic Ocean 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 10 m TL from the New Jersey coast, not saved. Squalus rashleighanus Couch, 1838: 51. Type locality, Cornwall. Types? Polyprosopus macer Couch, 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. 144 Cetorhinus maximus


UNDERSIDE OF HEAD


UPPER TEETH

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: Circumglobal. South Africa, Namibia, and likely Angola.

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 depth 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 depth off Brazil, while another individual followed the $5^{\circ} \mathrm{C}$ thermocline at 750 to 1000 m depth off the Bahamas. In the Eastern Pacific, one shark tagged off San Diego, California (USA), travelled over 2500 km to just off the northeastern Hawaiian Islands in eight months. The shark remained at depth, mostly below 300 m , following a cooler water thermocline during this time.

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 areas. Previous age estimates for


Fig. 145 Cetorhinus maximus
 this species are now known to be erroneous as vertebral bands are associated with growth and not age.

These filter-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 2000 tons of water over their 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 2.5 m juvenile was once found in a sperm whale stomach in the Azores.

Basking sharks are now known to make extensive transoceanic and trans-equatorial movements in the Atlantic and Pacific often moving thousands of kilometers. 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. Similarly, a shark tagged off California travelled 2500 km to just off the Hawaiian Islands, suggesting that these sharks may utilize entire ocean basins during their life cycle. Information on this species in the Southeastern Atlantic Ocean is scant, as it does not appear to be very common, with very few confirmed records.

Size: Maximum total length about 10 to 12 m ; males mature at about 4 to 5 m and females at about 8 to 9 m TL. Size at birth about 1.5 to 2 m total length; smallest free-swimming individual measured 1.7 m in length.

Interest to Fisheries and Human Impact: Of little importance in the Southeastern Atlantic Ocean as this species does not appear to be very common. Elsewhere, these sharks have been fished historically in the North Atlantic since at least 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. Since 2003, basking sharks have been largely protected by most nation states with only bycatch landings allowed for in some regions.

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. In 2002, the basking shark was listed by the Convention on International Trade in Endangered Species (CITES) on Appendix II.

Local Names: Koesterhaai (South Africa).
Literature: Matthews (1950, 1962); Matthews and Parker (1950a, b); Parker and Stott (1965); Compagno (1984a, 2001); Compagno, Ebert and Smale (1989); Izawa and Shibata (1993); Harvey-Clark et al. (1999); Ebert (2003); Skomal, Wood and Caloyianis (2004); Fowler (2005); Southall et al. (2005); Hoelzel et al. (2006); Gore et al. (2008); Natanson et al. (2008); Last and Stevens (2009); Skomal et al. (2009); Ebert (2013); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013).

### 2.6 Order CARCHARHINIFORMES - Ground Sharks

Order: Carcharhiniformes Compagno, 1973, J. Linn. Soc. (Zool.) London, 53, suppl. 1.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Families: 3.

Synonyms: [Part] 1 Squali, Abtheilung [Division] 1: Müller and Henle, 1838, Syst. Besch. Plagiost. (1): 3 (division 1 equivalent to suborder for scyliorhinids and most orectoloboids, Squali equivalent to order for all living sharks). [Part] 1 Squali, Abtheilung [Division] 2: Müller and Henle, 1838 (in part), Syst. Besch. Plagiost. (1): 27; Müller and Henle, 1839 (in part), Syst. Besch. Plagiost. (2): 27 (division 2 equivalent to suborder for most carcharhinoids, all lamnoids, heterodontoids, and the family Rhincodontidae, Squali equivalent to order for all living sharks). [Part] 1 Squali, Abtheilung [Division] 2, Unterabtheilung [Subdivision] 1: Müller and Henle, 1838 (in part), Syst. Besch. Plagiost. (1): 27; Müller and Henle, 1839 (in part), Syst. Besch. Plagiost. (2): 27 (subdivision 1 equivalent to superfamily for carcharhinids and sphyrnids). [Part] 1 Squali, Abtheilung [Division] 2, Unterabtheilung [Subdivision] 2: Müller and Henle, 1839, Syst. Besch. Plagiost. (2): 57 (subdivision 2 equivalent to superfamily for some carcharhinids and triakids). Ordo Plagiostomi, Subordo Squalini, Sectio Proktopterides, Tribus Dinotopterini: Bleeker, 1859, Acta Soc. Sci. Indo-Neerl. 6: xi (tribus and sectio of equivalent rank to superfamily and infraorder, tribe for heterodontoids, lamnoids, carcharhinoids, orectoloboids, and hybodonts, section for all sharks with anal fins, suborder for all sharks, order for all elasmobranchs). Order Squali, Suborder Squali: Gill, 1862 (in part), Ann. Lyc. Nat. Hist. N. Y. 7: 394, 396 (suborder for all sharks except squatinids, order for all sharks). Order Squali, Suborder Galei: Gill, 1872 (in part), Smithsonian Misc. Colln. (247): 22, 23 (order for all sharks, suborder for all sharks except squatinids). Order Plagiostomi diplospondyli, Suborder Plagiostomi asterospondyli, Group 1 Scyllia: Hasse, 1879 (in part), Nat. Syst. Elasmobr. (1): 52 (suborder for 'galeoid' sharks and heterodontoids, group ranked as infraorder or superfamily and including most carcharhinoids and family 'Cheiloscyllium' = Hemiscylliidae). Order Selachii, Suborder Asterospondyli: Woodward, 1889 (in part), Cat. fossil fish. $\mathrm{BM}(\mathrm{NH})$ (1): 157 (suborder for hexanchoids, cochliodonts, heterodontoids, hybodonts, palaeospinacids, lamnoids, orectoloboids, and carcharhinoids, order for other living elasmobranchs, psammodonts, petalodonts, and pristodonts). Order Asterospondyli: Gill, 1893 (in part), Natn. Acad. Sci. (U. S.) Mem. 6, 6: 130 (carcharhinoids in unnamed suborder [Galei?] with other 'galeoid' sharks and pristiophorids in apposition to suborder for squatinoids); Fowler, 1941 (in part), Bull. U. S. Natn. Mus. (100) 13: 4, 13 (group for heterodontoids and 'galeoids'); Smith, 1949 (in part), Sea fishes Southern Africa: 37, 39 (group for "typical sharks" including heterodontoids and 'galeoids'). Order Asterospondyli, Suborder Galei: Jordan and Evermann, 1896 (in part), Bull. US Nat. Mus. 47(1): 19, 21 (order for heterodontoids and 'galeoid' sharks, suborder for 'galeoids'). Order Euselachii, Suborder Pleurotremata, Division Galeoidei Regan, 1906a (in part), Proc. Zool. Soc. London (1906): 723 (division ranking as infraorder or superfamily for all 'galeoid' sharks including lamnoids, orectoloboids, and carcharhinoids). Order Selachii, Group 2, Division B, Subdivision 1, Suborder Scylliodei Goodrich, 1909 (in part), In R. Lankester, ed., A treatise on Zoology (9), Vertebrata Craniata: 148 (subdivision and suborder for 'galeoid' sharks). Order Pleurotremata, Suborder Galeoidei: Engelhardt, 1913 (in part), Abh. math.-phys. Klasse K. Bayer. Akad. Wiss., Suppl., Beitr. Naturg. Ostasiens, 4: 97 (suborder for 'galeoid' sharks: carcharhinoids, lamnoids, and orectoloboids). Order Plagiostoma, Suborder Antacea, "Group" Carcharinoidei: Garman, 1913 (in part), Mem. Mus. Comp. Zool. Harvard 36: 11, 12 (group corresponding to infraorder or superfamily, and including the carcharhinoid families Carcharinidae [= Carcharhinidae in large part], Cestracionidae [= Sphyrnidae] and Galeorhinidae [= Triakidae in large part]). Order Plagiostoma, Suborder Antacea, "Group" Catuloidei: Garman, 1913 (in part), Mem. Mus. Comp. Zool. Harvard 36: 11, 12 (group corresponding to infraorder or superfamily, and including the carcharhinoid families and including the carcharhinoid families Catulidae [= Scyliorhinidae] and Pseudotriakidae as well as all orectoloboids except the whale shark). Order Euselachii, Suborder Galei, [Series] Scyllioidei: Jordan, 1923 (in part), Stanford Univ. Publ., Univ. Ser., Biol. Sci., 3: 97 (group for scyliorhinids and orectoloboids). Order Euselachii, Suborder Galei, Series Galeoidei: Jordan, 1923 (in part), Stanford Univ. Publ., Univ. Ser., Biol. Sci., 3: 100, 101 (group for triakids, higher carcharhinids, and pristiophoroids). Order Plagiostomi, Suborder Galeiformes: Lozano y Rey, 1928 (in part), Fauna Iberica. Peces. Vol. 1: 280 (suborder for 'galeoid' sharks: lamnoids, orectoloboids, and carcharhinoids). Order Galea, Suborder Carcharinida, Superfamily Catuloidea: White, 1936, Amer. Mus. Novit. (837): 4; White, 1937, Bull. Amer. Mus. Nat. Hist. 74: 37, tab. 1 (superfamily includes scyliorhinids, proscylliids and pseudotriakids, suborder all carcharhinoids, and order for all 'galeoid' sharks). Order Galea, Suborder Carcharinida, Superfamily Carcharinoidea: White, 1936, Amer. Mus. Novit. (837): 4; White, 1937, Bull. Amer. Mus. Nat. Hist. 74: 37, tab. 1 (superfamily includes triakids, hemigaleids, carcharhinids and sphyrnids, suborder all carcharhinoids, and order for all 'galeoid' sharks). Order Euselachii, Suborder Lamniformes: Bertin, 1939 (in part), Bull. Inst. Oceanogr. Monaco (775): 9 (suborder for lamnoids + pseudotriakids, order for all living elasmobranchs). Order Euselachii, Suborder Scylliformes: Bertin, 1939 (in part), Bull. Inst. Oceanogr. Monaco (775): 9 (suborder for scyliorhinids, proscylliids and orectoloboids, order for all living elasmobranchs). Order Euselachii, Suborder Musteliformes: Bertin, 1939 (in part), Bull. Inst. Oceanogr. Monaco (775): 9 (suborder for triakids, hemigaleids, proscylliids, carcharhinids, and sphyrnids, order for all living elasmobranchs). Order Lamniformes, Suborder Scyliorhinoidei: Berg, 1940, Trudy Zool. Inst. Akad. Nauk SSSR, 5(2): 137 (suborder exclusively for carcharhinoids, order also for lamnoids and orectoloboids); Berg and Svetovidov, 1955 (in part), Trudy Zool. Inst. Akad. Nauk SSSR, 20: 66; Patterson, 1967, in W. B. Harland et al., Geol. Soc. London, Spec. Pub. 2: 671 (suborder exclusively for carcharhinoids, order also includes squaloids, squatinoids, lamnoids, orectoloboids, squalicoracids, protospinacids, and orthacodontids); Lindberg, 1971, Fishes of the world (trans. 1974): 8, 258 (suborder exclusively for carcharhinoids, order also for lamnoids and orectoloboids); Nelson, 1976 (in part), Fishes of the world: 33 (suborder exclusively for carcharhinoids, order for 'galeoid' sharks including lamnoids and orectoloboids); Nelson, 1984, Fishes of the world, ed. 2: 53. Order Euselachii, Suborder Galei, Superfamily Scyllioidea: Whitley, 1940, Fishes Australia. Part I. Aust. Zool. Handbook: 68 (scyliorhinids). Order Euselachii, Suborder Galei, Superfamily Galeoidei: Whitley, 1940, Fishes Australia. Part I. Aust. Zool. Handbook: 68 (triakids and higher carcharhinoids). Order Selachii, Suborder Galeoidea: Romer,

1945 (in part), Vert. Paleont. (ed. 2): 576 (suborder for lamnoids, orectoloboids, and carcharhinoids, order for all living sharks and protospinacids, hybodonts, coronodonts, and edestoids); Bigelow and Schroeder, 1948 (in part), Mem. Sears Fnd. Mar. Res. (1) 1:77, 95 (suborder for lamnoids, orectoloboids, and carcharhinoids, order for all living sharks); Romer, 1966 (in part), Vert. Paleont. (ed. 3): 350 (suborder for lamnoids, orectoloboids, carcharhinoids, and orthacodonts, order for all living sharks and protospinacids, ptychodonts, hybodonts, coronodonts, and edestoids). Order Lamnoidea, Suborder Scyliorhinoidea: Schultz and Stern, 1948 (in part), Ways of Fishes: 224 (suborder exclusively for carcharhinoids, order also including lamnoids and orectoloboids). Order Lamnida, Suborder Lamnina: Matsubara, 1955 (in part), Fish morphology hierarchy, (1): 1-789 (suborder for lamnoids, orectoloboids, and carcharhinoids, order for all living sharks). Order Galeiformes, Suborder Carcharhinoidei: Arambourg and Bertin, 1958, In P.-P. Grasse, ed, Traité de Zoologie, 13: 2037 (suborder exclusively for carcharhinoids, order also for orectoloboids and lamnoids). Order Pleurotrema, Suborder Galeoidea: Norman, 1966 (in part), draft syn. Recent fishes: 7 (suborder for lamnoids, orectoloboids, and carcharhinoids, order for all living sharks). Order Carcharhinida: Glikman, 1967 (in part), in Y. A. Orlov, ed., Fundamentals Paleontology, 11: 222 (for carcharhinoids and palaeospinacids). Order Carchariida, Suborder Galeorhinina, Superfamily Galeorhinicae: Fowler, 1967b, Q. J. Taiwan Mus. $20(3-4)$ : 342, 360 (superfamily for triakids, hemigaleids and proscylliids, suborder for all carcharhinoids, order for 'galeoids'). Order Carchariida, Suborder Galeorhinina, Superfamily Scyliorhinicae: Fowler, 1967b, Q. J. Taiwan Mus. 20(3-4): 343 (superfamily for scyliorhinids). Order Carchariida, Suborder Galeorhinina, Superfamily Pseudotriakicae: Fowler, 1968, Q. J. Taiwan Mus. 21(3-4): 197 (superfamily for pseudotriakids). Order Carchariida, Suborder Galeorhinina, Superfamily Sphyrnicae: Fowler, 1968, Q. J. Taiwan Mus. 21(3-4): 197 (superfamily for sphyrnids). Order Euselachii, Suborder Galeoidei: Blot, 1969 (in part), in J. Piveteau, ed. Traité de Paleontologie. 2: 702-776 (suborder for lamnoids, orectoloboids, and carcharhinoids, order for all living sharks except hexanchoids and heterodontoids). Order Pleurotremata, Suborder Galeiformes: Budker and Whitehead, 1971 (in part), life of sharks: 5, tab. 2 (suborder for lamnoids, orectoloboids and carcharhinoids, order for all living sharks). Order Carcharhiniformes: Rass and Lindberg, 1971 (in part), 1971, J. Ichthyol. (Trans. Voprosy Ikhtiologii) 11(3): 304 (includes orectoloboids, carcharhinoids, and the lamnoid family Cetorhinidae); Compagno, 1973, J. Linn. Soc. (Zool.) London, 53, suppl. 1: 28 (exclusively for all carcharhinoids); Applegate, 1974, J. Mar. Biol. Ass. India, 14(2): 743 (exclusively for all carcharhinoids); Chu and Meng, 1979, Monogr. Fish. China, Sci. Tech. Press, Shanghai: 114, tab. 2 (exclusively for carcharhinoids); Compagno, 1984b, FAO Fish. Synops. (125)4(2): 251; Gubanov, Kondyurin and Myagkov, 1986 (in part), Sharks World Ocean: 3, 61 (for orectoloboids, carcharhinoids, and the lamnoid families Cetorhinidae and Megachasmidae); Cappetta, 1987, Handb. Paleoichthyol. 3B: 27, 111 (exclusively for carcharhinoids); Compagno, 1988, Sharks Order Carcharhiniformes: 87 (exclusively for carcharhinoids); Eschmeyer, 1990, Cat. gen. Recent fish.: 436 (exclusively for carcharhinoids); Nelson, 1994, Fishes of the world, ed. 3: 48; de Carvalho, 1996, in Stiassny et al., Interrelationships fishes: 55 (exclusively for carcharhinoids); Shirai, 1996, in Stiassny et al., Interrelationships fishes: 33 (exclusively for carcharhinoids); Eschmeyer, 1998, Cat. Fish. Order Carcharhiniformes, Suborder Carcharhinoidea: Chu and Meng, 1979, Monogr. Fish. China, Sci. Tech. Press, Shanghai: 114, tab. 2 (suborder for Family Carcharhinidae). Order Carcharhiniformes, Suborder Scyliorhinoidea: Chu and Meng, 1979, Monogr. Fish. China, Sci. Tech. Press, Shanghai: 114, tab. 2 (suborder for Family Scyliorhinidae). Order Carcharhiniformes, Suborder Sphyrnoidea: Chu and Meng, 1979, Monogr. Fish. China, Sci. Tech. Press, Shanghai: 114, tab. 2 (suborder for Family Sphyrnidae). Order Carcharhiniformes, Suborder Triakoidea: Chu and Meng, 1979, Monogr. Fish. China, Sci. Tech. Press, Shanghai: 114, tab. 2 (suborder for Family Triakidae). Order Galeomorpha, Suborder Carcharhinoidea: Carroll, 1988, Vertebrate paleont. evolut.: 599 (suborder exclusively for carcharhinoids, order also for palaeospinacids, hexanchoids, orectoloboids, lamnoids, and heterodontoids).

FAO Name: 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-fin 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, 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.

Distribution: Circumglobal from cold temperate to tropical seas, with representatives of three of eight families inhabiting the Southeastern Atlantic Ocean deep-sea.

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 the 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 having a more limited geographic range. They exhibit a variety of reproductive strategies 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 directly by the mother. One family (Pseudotriakidae) exhibits oophagy. 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 bycatch. 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 (Carcharhinus longimanus), and tiger shark (Galeocerdo cuvier) are among the species that have been implicated in shark attacks mostly in tropical and open ocean environments.

Local Names: None.
Remarks: The present account follows Compagno (1984b, 1988, 2005) and Ebert, Fowler and Compagno (2013) in recognizing eight families of which three families (Scyliorhinidae, Carcharhinidae and Pseudotriakidae) have representative species occurring in the Southeastern Atlantic Ocean deep-sea. See Compagno (1988) for detailed discussion of this order.

The family Carcharhinidae has 12 genera and 57 species, but only the bignose shark, Carcharhinus altimus, is considered truly a deepwater shark within this genus. There is one record of it having been caught off Port Alfred, Eastern Cape Province, South Africa, but except for this record, the species is more common in the Indian Ocean and has not been reported from elsewhere in the Southeastern Atlantic. The night shark, C. signatus, is also somewhat of a deepish water shark, occurring down to at least 600 m , and although rare does occur in the area, but this shark mostly occurs on the outer continental shelf between 50 and 200 m deep and is therefore not considered truly a deepwater shark. Since the only deep-sea representative of the family Carcharhinidae is known from only a single record in the extreme edge of this area, the family and species will not be discussed further. See Ebert (2013) for more information on this family and species in the Indian Ocean.

## Key to Deep-sea Southeastern Atlantic Ocean Families:

1a. First dorsal-fin base opposite or behind pelvic-fin bases (Fig. 146) . . . . . . . . . . family Scyliorhinidae

1b. First dorsal-fin base in front of pelvic-fin bases 2


Fig. 146 Scyliorhinus


2b. Precaudal pits absent. Dorsal caudal-fin margin not undulated. Labial furrows very short or absent. Snout bell-shaped in dorso-ventral profile, with a deep groove in front of eye. First dorsal fin elongated (Fig. 148)
family Pseudotriakidae


Fig. 148 Pseudotriakis

### 2.6.1 Family SCYLIORHINIDAE

Family: Scylliorhinoidae Gill, 1862, 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 Deep-sea Southeastern Atlantic Ocean Genera: 4.

Synonyms: Family Scyllia or Scyllium Müller and Henle, 1838a, Mag. Nat. Hist., n. ser., 2: 34; 1838, Syst. Beschr. Plagiost., pt. 1: 3 Type genus: Scyllium Cuvier, 1816, junior synonym of Scyliorhinus Blainville, 1816. Subfamily Scyllini Bonaparte, 1838, Nuov. Ann. Sci. Nat., Bologna, ser. 1, 2: 130 (Family Squalidae). Type genus: Scyllium Cuvier, 1816, junior synonym of Scyliorhinus Blainville, 1816. Family Pentanchidae Smith and Radcliffe, in Smith, 1912, Proc. U.S. Natn. Mus. 41(1872): 489. Type genus: Pentanchus Smith and Radcliffe, in Smith, 1912. Family Catulidae Garman, 1913, Mem. Harvard Mus. Comp. Zool., 36: 68. Type genus: Catulus Garman, 1913, equals Catulus Valmont, 1768, rejected by the International Commission on Zoological Nomenclature (Opinion 89, 1925, Smithsonian Misc. Colln. 73: 27); also, Catulus Smith, 1837, junior synonym of Scyliorhinus Blainville, 1816 and junior homonym of Catulus Kniphof, 1759 in Insecta). Subfamily Galeinae Fowler, 1934, Proc. Acad. Nat. Sci. Philadelphia, 85: p. 234 (Family Scyliorhinidae). Type genus: Galeus Rafinesque, 1810. Family Halaeluridae White, 1936, Amer. Mus. Novit. (837), 4; White, 1936, Amer. Mus. Novit. (879), 18. Type genus: Halaelurus Gill, 1862. Family Atelomycteridae White, 1936, Amer. Mus. Novit. (837), 4; White, 1936, Amer. Mus. Novit. (879), 19. Type genus: Atelomycterus Garman, 1913. Subfamily Cephaloscylliinae Fowler, 1947, Notul. Nat. Acad. Nat. Sci. Philadelphia (187): 11 (Family Scyliorhinidae). Type genus: Cephaloscyllium Gill, 1862. Subfamily Schroederichthyinae Compagno, 1988, Sharks Order Carcharhiniformes: 107 (Family Scyliorhinidae). Type genus: Schroederichthys Springer, 1966.

FAO Names: En - Catsharks; Fr - Chiens, Holbiches; Sp - Alitanes, Pejegatos.
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, the first dorsal-fin base over or behind pelvic-fin bases, anal fin present, 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 caudal-fin 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 total length. Colour: many species with variegated colour patterns, some without them.

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 catshark 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. 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 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); Skaamoogs, Lazy sharks (South Africa).
Remarks: The Scyliorhinidae is the most diverse shark family with 17 genera and nearly 150 species. Of the 17 recognized genera within this family, 12 are considered to be deep-sea, of which 4 genera have representatives in the Southeastern Atlantic Ocean. The deep-sea genera are mostly the less colorful members of the family. The arrangement of this family follows revisions by Compagno (1988), Last, White and Pogonoski (2008) and the various chapters therein, Last and Stevens (2009), Ebert (2013) and Ebert, Fowler and Compagno (2013).

## List of Deep-sea Species Occurring in the Area:

Apristurus manis (Springer, 1979)
Apristurus melanoasper Iglésias, Nakaya, and Stehmann, 2004
Apristurus microps (Gilchrist, 1922)
Apristurus saldanha (Barnard, 1925)
Galeus polli Cadenat, 1959
Holohalaelurus regani (Gilchrist, 1922)
Scyliorhinus capensis (Smith in Müller and Henle, 1838)
Scyliorhinus cervigoni (Maurin and Bonnet, 1970)

## Key to Deep-sea Southeastern Atlantic Ocean Genera:

1a. Supraorbital crests present on cranium, above eyes (Fig. 149)

Scyliorhinus

1b. Supraorbital crests absent from cranium (Fig. 150)

2a. Head broadly flattened and spatulate, snout elongated and usually greater than mouth width (Fig. 151a). Labial furrows very long, uppers reaching upper symphysis (Fig. 151b)

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.

3a. Dorsal caudal-fin margin, and sometimes preventral margin, with a crest of enlarged denticles (Fig. 152) . .

Galeus

3b. No caudal crests of denticles (Fig. 153)
Holohalaelurus


Fig. 152 Galeus gracilis


Fig. 149 Scyliorhinus
Fig. 150 Galeus


Fig. 151 Apristurus

Fig. 153 Holohalaelurus regani

## 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 Deep-sea Southeastern Atlantic Ocean Species: 4.

Synonyms: Genus Apristurius Schulze, Kükenthal and Heider, 1926, Nomencl. animal. gen. subgen., Berlin, 1: 244. Apparent error for Apristurus Garman, 1913. Subgenus Parapristurus Fowler, 1934, Proc. Acad. Nat. Sci. Philadelphia, 85: 237 (Genus Pentanchus Smith and Radcliffe, 1912). Type species: Catulus spongiceps Gilbert, 1895, by original designation. Subgenus Compagnoia Springer, 1979, Nat. Ocean. Atmosp. Admin. Tech. Rept., Nat. Mar. Fish. Serv. Circ. (422): 102 (Genus Parmaturus Garman, 1906). Type species: Parmaturus (Compagnoia) manis Springer, 1979, by original designation. Subgenus Campagnoia Gubanov, Kondyurin, and Myagkov, 1986, Sharks World Ocean, Ident. Handbk., Moscow, Agropromizdat, 116 (Genus Parmaturus Garman, 1906). Apparently a consistent erroneous spelling of Compagnoia Springer, 1979.

Field Marks: Scyliorhinids with "the Apristurus look" with a 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 $2 / 5$ to $3 / 5$ of snout-vent length. Head greatly depressed, pointed and wedge-shaped in lateral view; head rather elongated, but usually slightly less than $1 / 4$ 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 sub-ocular 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 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 shark genera, having some 37 valid species, with several additional species of uncertain validity or still remaining to be described. Springer $(1966,1979)$ and Nakaya and Sato (1999) revised the genus while Nakaya (1975, 1988a, b, 1989, 1991) and others have revised and described new species, most recently from the Western South Pacific (Nakaya, Sato, and Iglésias, 2008; Kawauchi et al. 2008; Sasahara, Sato, and Nakaya, 2008; White, Last, and Pogonoski, 2008; Sato, Nakaya, and Yorozu, 2008; Iglésias, 2012; Sato, Steward and Nakaya, 2013). Despite these efforts, several species are still of uncertain validity, with over a third of the species known from the holotypes only, at least four species having the holotypes lost, and less than a third of the species known from a modest to good series of specimens. Judging from the frequency that new species are discovered, the wide geographic range of the genus, and the paucity of knowledge of slope faunas in many areas of the world, the number of new species is likely to increase. At least 4 species occur within the Southeastern Atlantic Ocean deep-sea, with at least one or two undescribed species. Specimens of Apristurus melanoasper from this area should be carefully examined as they may be of a different species.

## Key to Deep-sea Southeastern Atlantic Ocean Species:

1a. Body slender. Upper labial furrows longer than lowers (Fig. 154a). Supraorbital sensory canal discontinuous. Spiral valve turn counts 13 to 22 . Egg cases with long, coiled tendrils

a) UNDERSIDE OF HEAD

Upper labial furrows shorter than lowers

b) UNDERSIDE OF HEAD

Fig. 154 Apristurus spp.

2a. Interdorsal space very long, about equal to prespiracular head (Fig. 155) . . . . Apristurus saldanha

2b. Interdorsal space shorter, less than prespiracular head (Fig. 156) Apristurus melanoasper

3a. 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. 157) . . . . .

Apristurus microps
3b. Interdorsal space greater than first dorsal-fin base (Fig. 158). Pectoral-fin inner margins longer, half to about equal to pectoral-fin bases

Apristurus manis


Fig. 157 Apristurus microps


Fig. 158 Apristurus manis

## 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, $39^{\circ} 52^{\prime} \mathrm{N}$, $70^{\circ} 50^{\prime} \mathrm{W}$, SW 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. 159 Apristurus manis



DERMAL DENTICLE

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 times 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 the length of pectoral-fin bases. Interspace between pectoral and pelvic-fin 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, to 88 cm total length. Colour: grey or blackish, with light tips on pectoral and dorsal fins of young at least.

Distribution: In the Southeastern Atlantic Ocean recorded off Cape Town, South Africa. Also occurring in the Eastern and Western North Atlantic. Nominal records of "Apristurus profundorum" from off Mauritania (Golovan, 1976) are possibly of this species.

Habitat: A little known bottom catshark of the Atlantic continental slopes at depths from 600 to 1900 m , but most common at depths beyond 1500 m . Four specimens, possibly of this species, were taken on a bottom trawl at about 1700 m depth off Cape Town.

Biology: Unknown. Egg case of spongiceps-group type, small, vase-like, 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 deep-sea catshark likely feeds on small fishes, crustaceans, and cephalopods.

Size: Maximum total length 88 cm ; females mature at about 70 cm and reach 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.

Interest to Fisheries and Human Impact: Interest to fisheries none. Possibly caught occasionally as bycatch of deepwater trawl fisheries and discarded.


Fig. 160 Apristurus manis

Conservation status is Least Concern due to its very deepwater (usually over 1500 m deep) habitat.
Local Names: None.
Remarks: Several Apristurus species nominally referred to as $\boldsymbol{A}$. manis have been taken in very deepwater off Cape Town, South Africa (L.J.V. Compagno and D.A. Ebert, unpubl. data). These are the only known records of this species from the Southern Atlantic as all other records are from the North Atlantic.

Literature: Springer (1966, 1979); Compagno (1984b, 1988); Kiraly, Moore, and Jasinski (2003); Moore et al. (2003); Ebert (2004a); Flammang, Ebert, and Cailliet (2007); Ebert, Fowler and Compagno (2013); Ebert and Stehmann (2013).

## Apristurus saldanha (Barnard, 1925)

Scylliorhinus saldanha Barnard, 1925, Ann. S. African Mus. 21(1): 44. Holotype: South African Museum, 810 mm . adult male, discarded, off Saldanha Bay, 915 m.

Synonyms: None.
Other Combinations: None.
FAO Names: En - Saldanha catshark; Fr - Holbiche gatussau; Sp - Pejegato saldaña.


Fig. 161 Apristurus saldanha
Field Marks: A dark grey to grey-brown, somewhat slender bodied Apristurus with a long broad snout and nostrils, and relatively large eyes, mouth not projecting in front of eyes, labial furrows long, uppers longer than lowers, pectoral fins relatively large, dorsal fins similar in shape, first dorsal fin about equal to, or slightly smaller than second, origin over or slightly posterior to pelvic-fin midbases and anal fin elongated, subangular, and separated from lower caudal-fin origin by a notch.

Diagnostic Features: Snout moderately long, preoral snout about 7\% of total length. Gill slits probably small, less than eye length; gill septa without projecting medial lobes. Eyes about $2.6 \%$ of total length. Mouth possibly short and broadly arched, with dental bands not prominently expanded; and with lower ones falling well behind uppers; mouth and labial furrows possibly under eyes. Labial furrows possibly not expanded. Lateral trunk denticles probably flat. Interdorsal space considerably greater than first dorsal-fin base, about equal to prespiracular space. First dorsal fin slightly smaller in area than second. Origin of first dorsal fin about over pelvic-fin midbases. Insertion of second dorsal fin opposite to anal-fin insertion. Anal fin long, base about equal to prebranchial space in adults. Vertebral counts: monospondylous vertebral count 44 , diplospondylous vertebral count 33 . Spiral valve counts 13 to 16 . Adults large, to 89 cm total length. Colour: slate-grey.

Distribution: Namibia and South Africa (Western Cape Province). It also occurs in the Southwestern Indian Ocean off the Eastern Cape, South Africa.

Habitat: A catshark of the continental slopes of Namibia and South Africa at depths of 344 to 1009 m .
Biology: Oviparous, egg cases of an unknown scyliorhinid brought up from a trawl have tentatively been attributed to this
species and described (Ebert, Compagno and Cowley, 2006, figure 4c). However, no egg cases have been found in utero for this species. Diet includes small midwater bony fishes, primarily the myctophids Diaphus ostenfeldi and Symbolophorus barnardi, and cephalopods.

Size: Maximum total length 89 cm ; males mature between 69 and 74 cm , females mature at about 70 cm . Size at birth unknown.

Interest to Fisheries and Human Impact: Interest to fisheries none, taken as incidental bycatch of the deepwater hake (Merluccius paradoxus) bottom trawl fishery off South Africa and discarded.

The conservation status of this deepwater catshark is considered Least Concern.

Local Names: None.
Remarks: A little known endemic southern African Apristurus of the A. brunneus-group. Barnard's (1925) original description of this species was brief and not illustrated. Bass, D'Aubrey and Kistnasamy (1975a) described three small specimens (the largest 44 cm ) from off Saldanha, South Africa in the British Museum (Natural History), which they ascribed to this species, but Springer (1979) thought that the relatively narrow interdorsal spaces (considerably shorter than the prespiracular head) of these specimens did not fit $\boldsymbol{A}$. saldanha. However, a larger specimen ( 56 cm ) from the same locality taken by a


Fig. 162 Apristurus saldanha Soviet research vessel had a long interdorsal space about equal to the prespiracular head and may be this species (Golovan in Springer, 1979). As Barnard's original specimen was quite large, the possibility remains that the difference between it and the $\mathrm{BM}(\mathrm{NH})$ specimens are a matter of allometry in a single species.

Myagkov and Kondyurin (1978) erroneously reported that Apristurus saldanha was viviparous. However, the embryos depicted in their figure 1 are actually Galeus polli, a common species sympatric with A. saldanha that does exhibit a viviparous reproductive mode (see species account for G. polli below). Also, the adult female size stated by Myagkov and Kondyurin (1978) were much too small ( 37.5 to 39.5 cm ) for A. saldanha, but consistent for the size at maturity observed by Ebert, Compagno and Cowley (2006) for G. polli.

Literature: Barnard (1925); Bass, D’Aubrey and Kistnasamy (1975a); Myagkov and Kondyurin (1978); Springer (1979); Compagno (1984b, 1988); Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); Ebert, Cowley and Compagno (1996); Ebert (2004b); Ebert, Compagno and Cowley (2006); Ebert, Fowler and Compagno (2013).

## Galeus Rafinesque, 1810

Genus: Galeus Rafinesque, 1810, Caratt. gen. sp. anim. piant. Sicilia, Palermo, pt. 1: 13.
Type Species: Galeus melastomus Rafinesque, 1810, by subsequent designation of Fowler, 1908, Proc. Acad. Nat. Sci. Philadelphia, 60: 53.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 1.

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, 1810. 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. ?Subgenus Figaro Whitley, 1928 (Genus Pristiurus Bonaparte, 1834), Rec. Australian Mus., 16(4): 238. Type species: Pristiurus (Figaro) boardmani Whitley, 1928, by original designation.

Field Marks: Usually firm-bodied scyliorhinids with caudal crests of enlarged denticles, usually rather long and wedge-shaped snouts, short labial furrows, sub-ocular 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 sub-cylindrical 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-fin 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, sub-ocular 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 peduncle, and in some species on the preventral margin and lower edge of the caudal 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 pattern of dark saddles and blotches.

Local Names: Sawtail catsharks, Saw tail sharks, Rough cat sharks.
Remarks: The genus has 17 recognized species, with all except Galeus sauteri being considered deep-sea inhabitants. Only one species though is confirmed as occurring in the Southeastern Atlantic Ocean deep-sea.

## Galeus polli Cadenat, 1959

Galeus polli Cadenat, 1959d, Bull. Inst. Francaise Afrique Noire, ser. A, 22(1): 396, fig. 1-4, 7-17. Syntypes: Museum National d'Histoire Naturelle, Paris, MNHN-1959-44 and 1959-45, from off Senegal.

Synonyms: None.
Other Combinations: None.
FAO Names: En - African sawtail catshark; Fr - Chien râpe; Sp - Pintarroja africana.


Fig. 163 Galeus polli

Field Marks: A small, slender, long-nosed, Galeus with a narrow head, large eyes, and small labial furrows. The upper caudal-fin margin has a prominent crest of enlarged denticles. Colour is a bronzy-grey above, lighter below, often with darker saddles blotches, but may be plain.

Diagnostic Features: Snout long and pointed, preoral length about 7 to $9 \%$ of total length; prenarial snout virtually equal to eye length. Eyes lateral on head, subocular ridge virtually obsolete. 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 small, low, and angular. Interspace between pelvic and anal-fin bases much shorter than anal-fin base. Anal fin long, 14 to $17 \%$ of total length, much greater than interdorsal space; origin just behind first dorsal-fin insertion. Precaudal tail with base somewhat compressed. No subcaudal crest of enlarged denticles on preventral caudal margin. Vertebral counts: monospondylous precaudal vertebral counts 32 to 35 . Spiral valve counts 12 to 14 . Size small to moderate, adults up to about 43 cm total length. Colour: pattern of variegated dark saddle blotches on body and caudal fin, saddles well-defined and outlined with whitish, usually about 11 or less on back and tail; dorsal fins and caudal without black tips; mouth lining dark.

Distribution: It occurs in the Eastern Atlantic from southern Morocco to Namibia and South Africa (Northern Province).

Habitat: A deepwater bottom shark, on the upper continental slope at 200 to 720 m depth.

Biology: Reproductive mode unlike most other Galeus species is viviparous without a yolk-sac placenta. Litters range from 5 to 13 with a weak linear relationship between the total length of the mother and the number of embryos; larger females have more embryos. The sex ratio of embryos for a population of gravid females sampled off southern Namibia was 1:1. An erroneous report claiming that Apristurus saldanha exhibited viviparity was actually based on G. polli specimens that had been misidentified as A. saldanha. Galeus polli is the only confirmed Galeus species known to exhibit viviparity to date. The diet of this species consists mostly of teleosts, mostly myctophids, but also to a lesser extent crustaceans and cephalopods.

Size: Maximum total length about 43 cm ; males adult at about 30 cm ; females adult at 29 to 30 cm . Size at birth about 10 to 12 cm ; smallest free-swimming neonates were 15 to 19 cm .

Interest to Fisheries and Human Impact: Interest to fisheries limited, caught in bottom trawls and utilized fresh for human consumption and for fishmeal, or discarded as unwanted bycatch.

Conservation status is Least Concern.


Fig. 164 Galeus polli
$\square$ Known distribution

Local Names: None.
Literature: Poll (1951); Cadenat (1959d); Springer (1966, 1979); Springer and Wagner (1966); Cadenat and Blache (1981); Compagno (1984b, 1988); Compagno, Ebert, and Smale (1989); Compagno, Ebert and Cowley (1991); Compagno and Stevens (1993); Ebert, Cowley and Compagno (1996); Fowler (2004b); Ebert, Compagno and Cowley (2006); Ebert, Fowler and Compagno (2013).

## Holohalaelurus Fowler, 1934

Genus: Subgenus Holohalaelurus Fowler, 1934, Proc. Acad. Nat. Sci. Philadelphia, 85: 235 (Genus Halaelurus Gill, 1862).

Type Species: Scylliorhinus regani Gilchrist, 1922, by original designation, lost. Neotype: Holohalaelurus regani (Gilchrist, 1922) by designation SAM 32448, adult male 62.8 cm TL, RV Africana cruise 079, station A9830 082-3162, southeast of Hondeklip Bay, Northern Cape Province, South Africa, $30^{\circ} 57^{\prime} \mathrm{S}, 17^{\circ} 46^{\prime} \mathrm{E}, 234 \mathrm{~m}, 27$ January 1990.
Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 1.
Synonyms: None.

Field Marks: Extremely broad-headed short-snouted catsharks without labial furrows, with long mouths and long, low dorsal fins, slender tails, very bold, bright, spotted dorsal colour patterns, and scattered black dots on underside of head.

Diagnostic Features: Body not tadpole-shaped, fairly stout and 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-fin origin over $4 / 5$ of snout-vent length. Head greatly depressed and very broad, narrowly pointed and somewhat wedge-shaped in lateral view; head short, less than $1 / 5$ of total length in adults. Snout rather short, less than 3/5 of mouth width, thin, and very flattened, pointed in lateral view; snout somewhat expanded laterally, rounded-parabolic and slightly bell-shaped in dorsoventral view. Ampullar pores not greatly enlarged on snout. Nostrils fairly large, with incurrent and excurrent apertures only partly open to exterior; anterior nasal flaps broadly triangular, without barbels, well separate from each other but nearly or quite reaching level of mouth; internarial space about 1.0 to 1.3 times nostril width; no nasoral grooves. Eyes dorsolateral on head, very broad sub-ocular ridges present below eyes. Mouth semiangular, very long, with lower symphysis well behind upper so that upper teeth are exposed in ventral view. Labial furrows absent from both jaws. Tooth counts range from 40 to 72 upper jaw, 27 to 78 lower jaw. Branchial region not enlarged, distance from spiracles to fifth gill slits $2 / 5$ of head length; gill slits dorsolateral on head. Pectoral fins moderately large, their width subequal or somewhat less than mouth width. Inner margins of pelvic fins not fused over claspers in adult males. Claspers moderately long, slender, and distally pointed, extending about half of their lengths behind the pelvic-fin tips. Two dorsal fins present, with second slightly larger than first. Origin of first dorsal fin varying from about over the pelvic-fin midbases to slightly in front of their insertions. Origin of second dorsal fin about over the last third of the anal-fin base. Anal fin moderately large and definitely elongated, about as large as pelvic fins or larger, and larger than the dorsal fins; base length 1.5 to 2 times second dorsal-fin base; origin of anal fin well behind pelvic-fin bases, and insertion separated from lower caudal-fin origin by a broad space subequal to the anal-fin base. Caudal fin moderately elongated, between $1 / 4$ to $1 / 5$ of total length in adults. No crests of denticles on the caudal-fin margins. Supraorbital crests absent from cranium. Vertebral counts: total vertebral counts 85 to 132, monospondylous vertebral counts 23 to 33, diplospondylous vertebral counts 35 to 61 . Size small, adults up to about 51.5 cm total length. Colour: light with a conspicuous pattern of dark spots and blotches on dorsal surface and unique small black dots on underside of head.

Local Names: Izak catsharks.
Remarks: Compagno (1988) clarified the status of this genus relative to the closely related genus Halaelurus. This followed earlier works by Bigelow and Schroeder (1948), Smith (1949), Bass, D'Aubrey and Kistnasamy (1975a), Springer (1979), and Compagno (1984b) in recognizing distinct morphological and colour pattern differences between of this genus and Halaelurus. Human $(2006,2007)$ extensively revised this genus, which previously had two recognized species, Holohalaelurus punctatus and $\boldsymbol{H}$. regani, resurrecting a third species (H. melanostigma), and described two new species (H. favus and H. grennian) bringing the total number of valid species for this genus to five. A possible sixth species (H. polystigma) was found to be a junior synonym of $\boldsymbol{H}$. punctatus.

## Holohalaelurus regani (Gilchrist, 1922)

Scylliorhinus regani Gilchrist, 1922, Marine Biol. Survey S. Africa, (2): 45. Syntypes?: J.L.B. Smith Institute of Ichthyology, RUSI-952, two immature females, 215 and 269 mm total length, "Cape Seas" (RV Pickle sta. 234, $33^{\circ} 52^{\prime} 09^{\prime \prime} \mathrm{S}, 17^{\circ} 59^{\prime} 05^{\prime \prime} \mathrm{E}$, 173 m ; sta. $235,33^{\circ} 49^{\prime} 20^{\prime \prime} \mathrm{S}, 17^{\circ} 51^{\prime} 45^{\prime \prime} \mathrm{E}, 204 \mathrm{~m}$; $241,33^{\circ} 46^{\prime} 05^{\prime \prime} \mathrm{S}, 17^{\circ} 51^{\prime} 15^{\prime \prime} \mathrm{E}, 240 \mathrm{~m}$; sta. $243,34^{\circ} 03^{\prime} 50^{\prime \prime} \mathrm{S}, 18^{\circ} 01^{\prime} 50^{\prime \prime} \mathrm{E}$, 201 m; west of Cape Town, Western Cape, South Africa). Human (2006) investigated the status of the supposed syntypes (both females) and concluded that they did not match the specimen, a 50 cm total length male, referred to by Gilchrist. A neotype was therefore designated by Human (2006). Neotype: SAM 32448, adult male 62.8 cm TL , RV Africana cruise 079, station A9830 082-3162, southeast of Hondeklip Bay, Northern Cape Province, South Africa, $30^{\circ} 57^{\prime} \mathrm{S}, 17^{\circ} 46^{\prime} \mathrm{E}, 234$ m, 27 January 1990.

Synonyms: None.
Other Combinations: Halaelurus regani (Gilchrist, 1922).
FAO Names: En - Izak catshark; Fr - Holbiche isard; Sp - Pejegato reticulado.


Fig. 165 Holohalaelurus regani

Field Marks: A catshark with an extremely broad head, no labial furrows, nostrils separate from each other and mouth and without barbels or nasoral grooves, dorsolateral gill slits, second dorsal fin usually somewhat larger than first, first dorsal-fin origin about over rear end of pelvic-fin bases and second dorsal-fin base partly behind anal-fin base. Dorsal surface appearing dark brown with reticular pattern of light lines, underside of head with tiny dark dots, no conspicuous white spot over pectoral-fin insertion in adults.

Diagnostic Features: Anal-fin base over 3.5 times its height usually longer than interdorsal space (except in very young individuals). Second dorsal fin usually larger than first. Denticles on back and top of head not of uniform size, enlarged spiky denticles scattered among more numerous small denticles. Tooth counts 55 to 72 upper jaw, 27 to 78 lower jaw. Vertebral


## UNDERSIDE OF HEAD

 counts: total vertebral counts 106 to 132, monospondylous vertebral counts 28 to 33, diplospondylous vertebral counts 45 to 61 . Intestinal valve counts not available. Size moderate, to at least 69 cm total length. Colour: pattern variable but usually with large, irregular, sometimes light-centred, very closely-spaced brown spots on back giving back dark-brown cast with a reticular pattern of light lines; no white spot over pectoral-fin insertion in adults, although young have a line of white spots on sides; dorsal fins of adults generally spotted but without dark lines or double-Vs.Distribution: Known to occur off South Africa and southern Namibia. Lüderitz, Namibia appears to be the northern most range on the west coast, and Durban, South Africa on the east coast.

Habitat: A deepish water primarily cool temperate catshark, rarely extending northwards into the subtropical waters off Durban. The species has a broad depth range on the outer continental shelf and upper slope from 40 to 1075 m , but is most common between 100 to 200 m on the south coast and 200 to 300 m on the west coast of South Africa. Common off the Northern, Western, and Eastern Cape Provinces of South Africa, particularly on the offshore trawling grounds of the Agulhas Bank.

Biology: Oviparous, one egg per oviduct laid at a time. Off the Western Cape, adult females are reproductively active both in summer and winter. Egg-cases are about 3.5 cm long by 1.5 cm wide. Feeds heavily on teleosts, with lesser amounts of cephalopods and crustaceans.

Size: Maximum total length 69 cm . Males immature at 11 to 47 cm , adolescent at 27 to 54 cm , and adult at 41 to 69 cm ; females immature at 11 to 48 cm , adolescent at 31 to 50 cm and adult at 32 to 62 cm . Size at hatching uncertain, below 11 cm (size of smallest free-living individuals).

Interest to Fisheries and Human Impact: Interest to fisheries none, commonly taken by commercial bottom trawlers as a discarded bycatch of the hake (Merluccius spp.) fishery and broadly distributed over the entire hake


Fig. 166 Holohalaelurus regani
Known distribution fishing grounds. Despite the intensive bottom trawling that occurs throughout its range, the biomass of this shark has shown substantial increases of more than $40 \%$.

The conservation status of this species Least Concern.
Local Names: Izak, Izak catshark, Halalujah shark (South Africa).
Remarks: Bass, D'Aubrey and Kistnasamy (1975a) described two forms of this species, a "Cape" form, and a "Natal" form and suggested that these different forms may represent multiple species. Compagno (1984b, 1988) commented on these various forms, including Holohalaelurus melanostigma, which he suggested may be a separate species. Human (2006) revised the taxonomy of the genus and concluded that the "Natal" form did in fact represent a separate, new, species that he named $\boldsymbol{H}$. favus, while the "Cape" form represented true H. regani as originally described by Gilchrist. Therefore, previous information on the distribution and general biology of this catshark from north of Durban should be carefully reconsidered as it is likely not this species, but one of the other members of this genus. See Human (2006) for detailed descriptions, distribution, and taxonomic history of this genus.

Literature: Bass, D'Aubrey and Kistnasamy (1975a); Springer (1979); Compagno (1984b, 1988); Compagno, Ebert, and Smale (1989); Compagno, Ebert and Cowley (1991); Ebert, Cowley and Compagno (1996); Richardson et al. (2000); Human (2006, 2007, 2009); Ebert, Fowler and Compagno (2013).

## 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, 1862, Ann. Lyceum Nat. Hist. New York, 7(32): 407; equals Squalus canicula Linnaeus, 1758.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 2.

Synonyms: Subgenus Scyllium Cuvier, 1816 (Genus Squalus Linnaeus, 1758), Reg. Anim., ed. 1, 2: 124 . Type species: Squalus canicula Linnaeus, 1758, by subsequent designation of Jordan and Evermann, 1917, Stanford U. Pub., U. Ser., Gen. Fish. (1): 97. Whitley (1935, Australian Zool. 8[2]: 137) and [Eschmeyer (1998), Catalog of Fishes] note that Bory de St. Vincent (1828, Dict. Class. Hist. Nat. 14: 708) selected Squalus canicula Linnaeus, 1758 as type species of Scyllium Cuvier, (1816, Le Règne Animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Les reptiles, les poissons, les mollusques et les annélides. Edition 1: 124). Genus Scylium Eichwald, 1819, Selachus Aristotelus zoolog. geograph. specimen inaugur., Vilniae: 65 (not seen). Apparent error for Scyllium Cuvier, 1816. Genus Scyllia van Hasselt, 1823, Algemeene Konst-Letter-Bode, 1823, I, Deel, (21): 315 (error or emendation for Scyllium Cuvier, 1816). Subgenus Scylliorhinus Blainville, 1825 (Genus Squalus Linnaeus, 1758), in Vieillot et al., Faune Francaise, liv. 13-14: 68. Unjustified emendation of Scyliorhinus Blainville, 1816. Subgenus Catulus Willoughby in Smith, 1837 (Genus Scyllium Cuvier, 1816), Proc. Zool. Soc. London 5: 85; also Smith, 1838, Ann. Nat. Hist. Mag. Zool. Bot. Geol, 1: 73 (identical account). Smith (1837, 1838) listed three species in the subgenus Catulus: Squalus canicula Linnaeus, 1758, Scyllium marmoratum Bennett, 1830, and Catulus Edwardsii Smith (nomen nudum) without a type designation. Type species: Squalus canicula Linnaeus, 1758 by subsequent designation of Fowler, 1908, Proc. Acad. Nat. Sci. Philadelphia, 60: 53. According to Eschmeyer (1998, Cat. Fish.) erroneous type designations for Catulus Willoughby in Smith include: Scyllium capense Smith, 1838, which was placed in the subgenus Scyllium by Smith and furthermore is a nomen nudum, as given by Jordan (1919: 190); Scyllium stellaris Linnaeus, 1758 as given by Jordan and Evermann (1896: 23), which Smith cited as Catulus stellare and placed in the subgenus Scyllium. A junior homonym of Catulus Kniphof, 1759, in Insecta. Ultimately based on Catulus Valmont, 1769 (see below). Genus Catulus Garman, 1913, Mem. Harvard Mus. Comp. Zool., 36: 3, 71. Type species: Catulus saxatilis Valmont, 1769 by original designation, equals Squalus stellaris Linnaeus, 1758. A junior homonym of Catulus Kniphof, 1759 in Insecta. A revival of Catulus Valmont, 1768, Dict. Hist. Nat., 4: 51; Ibid., 1769, 10:. 114; Ibid, 1769, 12: 421. Valmont's names were rejected as being inconsistently binomial by the International Commission on Zoological Nomenclature (Opinion 89, 1925, Smithsonian Misc. Coll. 73(3): 27-33). "Pseudogenus" (= Subgenus) Alphascyllium Leigh-Sharpe, 1926 (Genus Scyllium Cuvier, 1816), J. Morph. 42: 322. Type species: "Scyllium canicula" by original designation, equals Squalus canicula Linnaeus, 1758. Leigh-Sharpe's "pseudogenera", based on clasper morphology, must be considered the nomenclatural equivalent of subgenera under Article 10e of the Third Edition of the International Code of Zoological Nomenclature (Ride, Sabrowsky, Bernardi, and Melville, eds, 1985, Intern. Trust. Zool. Nomen., London). "Pseudogenus" (= Subgenus) Betascyllium Leigh-Sharpe, 1926 (Genus Scyllium Cuvier, 1816), J. Morph. 42: 325. Type species: Scyllum catulus by original designation, equals Squalus catulus Linnaeus, 1758, a junior synonym of S. stellaris Linnaeus, 1758. Genus Scylliorhynchus Nobre, 1935, Fauna marin. Portugal. 1. Vertebrados (Mamiferos, Reptis e Peixes), Porto: 409. Probable error for Scyliorhinus Blainville, 1816. Genus Scylliorhynus Nobre, 1935, Fauna marin. Portugal. 1. Vertebrados (Mamiferos, Reptis e Peixes), Porto: 416. Probable error for Scyliorhinus Blainville, 1816.

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-fin 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 $\boldsymbol{S}$. canicula in which broad grooves are present. Eyes dorsolateral on head, broad sub-ocular 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 114 to 144, monospondylous vertebral counts 30 to 47 , precaudal vertebral counts 90 to 95 . Spiral valve turns 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 arrangement of this genus follows Springer (1966, 1979), Compagno (1984b, 1988), Shirai, Hagiwara and Nakaya (1992), and Ebert, Fowler and Compagno (2013). Of the 15 currently recognized species within this genus, nine are deep-sea inhabitants and two occur in the Southeastern Atlantic Ocean.

## Key to Deep-sea Southeastern Atlantic Ocean Species:

1a. Colour pattern with light spots, dark saddles, or both; no conspicuous small dark spots or lines on body (Fig. 167)

Scyliorhinus capensis


Fig. 167 Scyliorhinus capensis

1b. Colour pattern with conspicuous small dark spots or lines (Fig. 168)

Scyliorhinus cervigoni


Fig. 168 Scyliorhinus cervigoni

## Scyliorhinus cervigoni Maurin and Bonnet, 1970

Scyliorhinus cervigoni Maurin and Bonnet, 1970, Rev. Trav. Inst. Peches Marit. 34(2): 5, fig. 3. Holotype: Possibly in Museum National d'Histoire Naturelle, Paris, 380 mm TL female, Mauritania or Senegal, Eastern North Atlantic.

Synonyms: None.
Other Combinations: None.
FAO Names: En - West African catshark; Fr - Roussette thalassa; Sp - Alitán africano.


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Fig. 169 Scyliorhinus cervigoni

Field Marks: A fairly large, very stout catshark with relatively large, few, and scattered dark spots, dark saddles centred on dark spots on the midline of the back, and no white spots, small anterior nasal flaps that barely reach mouth, no nasoral grooves, labial furrows on lower jaw only, interdorsal space slightly less than anal-fin base, second dorsal fin much smaller than first.

Diagnostic Features: Body very stout, head broad and fairly flat, greatest width of head at least $2 / 3$ of head length. No nasoral grooves; anterior nasal flaps not expanded and just reaching mouth. Denticles fairly large and erect, skin relatively rough. First dorsal-fin origin slightly behind pelvic-fin insertions. Second dorsal-fin origin over last third of anal-fin base. Interdorsal space somewhat less than anal-fin base. Size large, maximum total length about 76 cm . Colour: pattern of scattered large and some small dark spots along body, 8 or 9 dusky saddle marks centred on dark spots on midback; no light spots.

Distribution: Probably wide-ranging off tropical West Africa, from Mauritania to Angola; places where it has been recorded include Mauritania, Senegal, possibly Gambia to Guinea, possibly Liberia, possibly Gabon to Republic of Congo, and Angola.

Habitat: A little-known tropical bottom catshark of the continental shelf and upper slope at depths of 45 to 500 m , on rocky and mud bottoms; observed temperatures where specimens were caught, 11 to $16^{\circ} \mathrm{C}$; salinity, 36 ppt; oxygen, 1.0 to 1.6 ppm .

Biology: Oviparous, egg-cases thought to be from this species were about 7 to 8 cm long by about 3 cm wide. Eats bony fish. Apparently replaces Scyliorhinus stellaris off tropical West Africa.

Size: Maximum total length about 76 cm ; adolescent male 64 cm , adult male 67 cm ; females to at least 76 cm .

Interest to Fisheries and Human Impact: Interest to fisheries uncertain, probably taken by offshore trawling fleets off West Africa, but because this species has been confused with Scyliorhinus stellaris in the past fisheries data for it has probably been reported under this latter species name.

The conservation status of this species is Data Deficient.
Local Names: None.


Fig. 170 Scyliorhinus cervigoni
Known distribution $\square$ Possible distribution 013).

Literature: Poll (1951); Maurin and Bonnet (1970); Springer (1979); Ebert, Fowler and Compagno (2013).

### 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 de Brito Capello, 1867, J. Sci. Math. Phys. Nat. Lisboa, ser. 2, (4): 321.
Number of Recognized Deep-sea Southeastern Atlantic Ocean Genera: 1.
Synonyms: Subfamily Golluminae Compagno, 1988, Sharks Order Carcharhiniformes: 192 (Family Proscylliidae). Type genus: Gollum Compagno, 1973.
FAO Names: En - False catsharks; Fr - Requins à longue dorsale; Sp - Musolones.
Field Marks: A distinctive group of small to large sharks with a narrowly rounded head and a more or less elongated bellshaped snout, a deep groove anterior to elongated, slit-like eyes, 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, a weak or absent ventral lobe on the caudal fin, colour 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, papillae distinctly present or absent 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 94 to 294, lower jaw 81 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. Vertebral counts: total vertebral counts 140 to 186 , monospondylous vertebral counts 44 to 52 , diplospondylous vertebral counts 107 to 115, precaudal vertebral counts 94 to 101. Valvular intestine with a spiral valve of 11 to 17 turns. Small to very large sharks with adults ranging from 65 to about 300 cm in total length. Colour: plain grey to brown or blackish.

Distribution: Wide ranging, but scattered for the large Pseudotriakis, but the smaller Gollum and Planonasus species have more restricted ranges around New Zealand and adjacent waters, the Philippines, and the Northwestern Indian Ocean, respectively.

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. The reproductive mode of the recently described Planonasus is unknown. 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.

The conservation status of these poorly known sharks ranges from Data Deficient to Least Concern.
Local Names: Gollumsharks, Keelbacked catsharks (English).
Remarks: Most writers recognize this family for the false catsharks, Pseudotriakis, but Compagno (1988) proposed that the New Zealand Gollum shark was the closest living relative of Pseudotriakis, and suggested an alternate scheme that included these two genera in a common taxon (Compagno, Dando and Fowler, 2005). The sharks of this genus exhibit a unique form of oophagy that unites them in this family.

A new genus of Pseudotriakidae was recently described by Weigmann, Stehmann and Thiel (2013) as Planonasus and was captured in the Northern Indian Ocean from the Arabian Sea (off Socotra Island), the Maldives, and off southwestern India on continental and insular slopes down to 1120 m (Compagno, Dando and Fowler, 2005). This new species of pygmy false catshark attains maturity between 49 and 56 cm for males (M. Stehmann, pers. comm.). The reproductive mode of the recently described Planonasus is unknown as of this writing. It arrangement in this family is based on morphological characters presented by Weigmann, Stehmann and Thiel (2013).

Literature: Compagno (1988); Compagno, Dando and Fowler (2005); Musick and Ellis (2005); Last and Gaudiano (2011); Ebert (2013); K.V. Akhilesh (pers. comm.).

## List of Deep-sea Species Occurring in the Area:

Pseudotriakis microdon de Brito Capello, 1868

## Pseudotriakis de Brito Capello, 1868

Genus: Pseudotriakis de Brito Capello, 1868, J. Sci. Math. Phys. Nat. Lisboa, (2), 1: 321.
Type species: Pseudotriakis microdon de Brito Capello, 1868, by monotypy.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 1.

Synonyms: Genus Pseudotriacis Günther, 1870, Cat. Fish. British Mus. 8: 395. Emended spelling of Pseudotriakis de Brito Capello, 1868, and therefore taking the same type species, P. microdon de Brito Capello, 1868.

Field Marks: See species account below.
Diagnostic Features: See species account below.
Remarks: See species account below.

## Pseudotriakis microdon de Brito Capello, 1868

Pseudotriakis microdon de Brito 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.


Fig. 171 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, a caudal fin without a strong ventral lobe or lateral undulations on its dorsal margin, colour 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, their length over two times the 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 dorsalfin 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 counts: total vertebral counts 180 to 186. Spiral valve turn count 17. Maximum total length 296 cm . Colour: uniform plain dark brown to blackish except for darker fins.

Distribution: In the Southeastern Atlantic, only known from two records on the Valdivia Bank off Namibia (E. Mostarda and P.J. Clerkin, pers. comm.). Elsewhere, sporadic but wide-ranging in most oceans with no records from the Eastern Pacific Ocean.

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: Oophagous, with litters of 2, but little else known. The gestation period for this species is unknown, but may last one year or more. Embryos at 8 to 32 cm length have large yolk sacs with abundant yolk, but the considerably larger size attained by term fetuses, the small litter size of this shark, and the immense number of eggs produced by adult females (estimated at 20,000 in one ovary for a 280 cm adult female) led Forster et al. (1970) to suggest that this shark may exhibit oophagy or uterine cannibalism as in lamnoid sharks. This hypothesis subsequently was proven correct making it the only non-lamnoid family of sharks to exhibit this reproductive mode.

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 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 296 cm ; adult males reported at about 260 cm ; adult females at about 265 cm . Size at birth variably between 70 and 85 cm ; smallest freeswimming specimen measured 96 cm .

Interest to Fisheries and Human Impact: Interest to 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.


Fig. 172 Pseudotriakis microdon
Known distribution

Local Names: False cat shark, Atlantic false cat shark, Keel-dorsal shark (English).

Remarks: Two species of Pseudotriakis have been recognized, the Atlantic P. microdon de Brito Capello, 1868 and the Pacific P. acrales Jordan and Snyder, 1904, but a detailed comparison by Yano and Musick (1992) confirmed this appears to be a single wide-ranging species. Examination of the holotype of P. acrages (Stanford University, SU 12903, 1765 mm immature male, from Suruga Gulf, Japan) and comparison of specimens of Pseudotriakis from the North Sea and from the Hawaiian Islands (Compagno, 1988) revealed no reliable characters to separate Atlantic and Pacific Pseudotriakis, although it was initially thought that the Atlantic species might have a longer snout. The morphological criteria that Jordan and Snyder (1904) and Bigelow and Schroeder (1948) proposed to separate these species do not hold based on the available data at this time. However, recent molecular studies (G.J.P. Naylor, pers. comm.) reveal significant genetic differences between the Atlantic and Pacific populations.

Literature: Capello (1868); Günther (1870); Bean (1883); Goode and Bean (1895); Jordan and Evermann (1896); Garman (1913); Bigelow and Schroeder (1948); Forster et al. (1970); Compagno (1984b, 1988); Yano (1992); Yano and Musick (1992); Kyne, Kazunari Yano and White (2004); Last and Stevens (2009); Ebert and Stehmann (2013); P.J. Clerkin (pers. comm.); E. Mostarda (pers. comm.); G.J.P. Naylor (pers. comm.).

## 3. Subclass NEOSELACHII - Cohort BATOIDEA

### 3.1 Order TORPEDINIFORMES - Electric rays

Order: Order Hypotremi, Suborder Sarcura, (group) suborder Torpedinoidea: Gill, 1893, Natn. Acad. Sci. (U. S.) Mem. 6, 6: 130 (group ranked as infraorder or superfamily, exclusively for torpedinoids).

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Families: 1.

Synonyms: Order Plagiostoma, Suborder Platosomia, "Group" Narcoidei: Garman, 1913 (in part), Mem. Mus. Comp. Zool. Harvard, 36: 257, 259 (group corresponding to infraorder or superfamily, and exclusively for the torpedinoids). Order Raiae, Suborder Pachyura: Gill, 1872 (in part), Smithsonian Misc. Colln. (247): 22, 23 (order for all batoids, suborder for all 'thick-tailed' batoids). Order Plagiostomi diplospondyli, Suborder Plagiostomi Tectospondyli, Group 2 Rajae Hasse, 1879 (in part), Nat. Syst. Elasmobr. (1): 48 (suborder for batoids, squatinids and pristiophorids, group equivalent to infraorder or superfamily and for rajoids and torpedinoids). Order Euselachii, Suborder Hypotremata, Division Narcobatoidei Regan, 1906a, Proc. Zool. Soc. London (1906): 723 (division ranking as infraorder or superfamily and exclusive to torpedinoids). Order Narcobatea, Suborder Narcaciontes, Superfamily Narcobatoidea: Whitley, 1940, Fishes Australia. Part I. Aust. Zool. Handbook: 69 (exclusive for torpedinoids). Order Batoidei, Suborder Sarcura: Jordan and Evermann, 1896 (in part), Bull. US Nat. Mus. 47(1): 59, 60 (common group for pristids, rhinobatoids, rajoids, and torpedinoids). Order Batoidei, Suborder Narcaciontes: Jordan, 1923, Stanford Univ. Publ., Univ. Ser., Biol. Sci., 3: 103 (exclusive for torpedinoids). Order Rajae, [group] Torpedinoidei Fowler, 1941, Bull. U.S. Natn. Mus. (100) 13: 290 (exclusive group equivalent to suborder or superfamily for torpedinoids). Order Rajae Smith, 1949, Sea fishes Southern Africa: 37, 62 (common group without subdivisions for all batoids). Order Selachii, Group 2, Division B, Subdivision 2, Suborder Rajiformes, Tribe 2, Group Torpedinoidei: Goodrich, 1909, In R. Lankester, ed., A treatise on Zoology (9), Vertebrata Craniata: 161 (tribe equivalent to infraorder, and group equivalent to superfamily and exclusive for torpedinoids). Order Narcobatea, Suborder Narcobatida, Superfamily Narcobatoidea: White, 1936 (in part), Amer. Mus. Novit. (837): 5; White, 1937 (in part), Bull. Amer. Mus. Nat. Hist. 74: 37, tab. 1 (taxa exclusive to torpedinoids). Order Hypotremata, Suborder Narcobatoidei: Engelhardt, 1913, Abh. math.-phys. Klasse K. Bayer. Akad. Wiss., Suppl., Beitr. Naturg. Ostasiens, 4: 101 (suborder exclusive to torpedinoids, order includes all living batoids). Order Torpediniformes: Berg, 1940, Trudy Zool. Inst. Akad. Nauk SSSR, 5(2): 139 (exclusive for torpedinoids); Berg and Svetovidov, 1955, Trudy Zool. Inst. Akad. Nauk SSSR, 20: 74; Arambourg and Bertin, 1958, In P.-P. Grasse, ed, Traité de Zoologie, 13: 2055 (exclusively for torpedinoids); Patterson, 1967, in W. B. Harland et al., Geol. Soc. London, Spec. Pub. 2: 673 (exclusively for torpedinoids); Lindberg, 1971, Fishes of the world (trans. 1974): 8, 263 (exclusively for torpedinoids); Rass and Lindberg, 1971, J. Ichthyol. (trans. Voprosy Ikhtiologii) 11(3): 305 (exclusively for torpedinoids); Compagno, 1973, J. Linn. Soc. (Zool.), 53, suppl. 1: 27 (exclusively for torpedinoids); Applegate, 1974, J. Mar. Biol. Ass. India, 14(2): 743 (exclusively for torpedinoids); Chu and Meng, 1979, Monogr. Fish. China, Sci. Tech. Press, Shanghai: 114, tab. 2 (exclusively for torpedinoids); Eschmeyer, 1990, Cat. gen. Recent fish.: 437 (exclusively for torpedinoids); McEachran, Dunn and Miyake, 1996, in Stiassny, Parenti and Johnson, Interrelationships fishes: 80 (exclusively for torpedinoids); Eschmeyer, 1998, Cat. Fish. (exclusively for torpedinoids). Order Torpediniformes, Suborder Torpedinoidea: Chu and Meng, 1979, Monogr. Fish. China, Sci. Tech. Press, Shanghai: 114, tab. 2 (suborder exclusively for torpedinoids, including Families Torpedinidae and Narkidae). Order Torpediniformes, Superfamily Torpedinoidea: Compagno, 1973, J. Linn. Soc. (Zool.), 53, suppl. 1: 27 (superfamily for hypnids and torpedinids). Order Torpediniformes, Superfamily Narcinoidea: Compagno, 1973, J. Linn. Soc. (Zool.), 53, suppl. 1: 27 (superfamily for narcinids and narkids). Order Plagiostomi, Suborder Rajiformes or Rayiformes: Lozano y Rey, 1928 (in part), Fauna lberica. Peces. Vol. 1: 281 (suborder for all batoids). Order Rajiformes: Nelson, 1976 (in part), Fishes of the world: 40 (order for all batoids; Nelson, ibid.: 41, suggests that torpedinoids could be recognized as a suborder Torpedinoidei following Compagno, 1973, but didn't utilize this taxon in his text or index). Order Rajiformes, Suborder Torpedinoidei: Nelson, 1984, Fishes of the world, ed. 2: 60 (suborder exclusively for torpedinoids, order for all batoids); Nishida, 1990, Mem. Fac. Fish. Hokkaido Univ. 37(1/2): 11 (suborder exclusively for torpedinoids, order for all batoids); Nelson, 1994, Fishes of the world, ed. 3: 58 (suborder exclusively for torpedinoids, order for all batoids). Order Squatinida, Suborder Rajoidei, Superfamily Torpedinoidea: Glikman, 1967 (in part), in Y. A. Orlov, ed., Fundamentals Paleontology, 11: 219 (superfamily for torpedinoids, suborder for all batoids, order also including squaloids, orectoloboids, cetorhinids, squatinoids, and pristiophoroids). Order Torpedinida, Suborder Torpedinina: Fowler, 1970, Q.J. Taiwan Mus. 23(1-2): 86 (exclusively for torpedinoids). Order Rajida, Suborder Torpedinina: Matsubara, 1955, Fish morphology hierarchy, (1): 1-789 (suborder exclusively for torpedinoids, order for all batoids). Order Batoidea: Romer, 1945, Vert. Paleont. (ed. 2): 577 (for all batoids). Order Batoidea, Suborder Torpedinoidea: Bigelow and Schroeder, 1953, Mem. Sears Fnd. Mar. Res. (1) 2: 14, 80 (suborder exclusively for torpedinoids, order for all batoids); Romer, 1966, Vert. Paleont. (ed. 3): 350 (suborder exclusively for torpedinoids, order for all batoids). Order Hypotremata, Suborder Narcobatoidea: Norman, 1966, draft syn. Recent fishes: 32 (suborder exclusively for torpedinoids, order includes all batoids). Order Rajiformes: Blot, 1969, in J. Piveteau, ed. Traité de Paleontologie. 2: 702-776 (group for all living batoids). Order Batoidea, Suborder Narcobatoidea: Schultz and Stern, 1948, Ways of Fishes: 226 (suborder for torpedinoids, order for all living batoids). Order Batoidea, Suborder Torpedinoidea: Carroll, 1988, Vertebrate paleont. evolut.: 599 (suborder exclusively for torpedinoids, order for all batoids). Order Torpediniformes: Cappetta, 1987, Handb. Paleoichthyol. 3B: 27, 160 (exclusively for torpedinoids). Order Torpediniformes, Superfamily Torpedinoidea: Cappetta, 1987, Handb. Paleoichthyol. 3B: 27, 160 (for torpedinids). Order Torpediniformes, Superfamily Narcinoidea: Cappetta, 1987, Handb. Paleoichthyol. 3B: 27, 162 (for narcinids). Ordo Plagiostomi, Subordo Rajini: Bleeker, 1859, Acta Soc. Sci. Indo-Neerl. 6: xiii (suborder for all batoids, order for
all elasmobranchs). Order Selachii, Suborder Tectospondyli: Woodward, 1889 (in part), Cat. fossil fish. BM(NH) (1): 30 (suborder for squaloids, squatinoids, pristiophoroids, batoids, psammodonts, petalodonts, and pristodonts, order for other living sharks, fossil neoselachians, hybodonts and cochliodonts). Order Torpediniformes, Suborder Torpedinoidei: McEachran, Dunn and Miyake, 1996, in Stiassny, Parenti and Johnson, Interrelationships of fishes: 80 (for hypnids and torpedinids). Order Torpediniformes, Suborder Narcinoidei: McEachran, Dunn and Miyake, 1996, in Stiassny, Parenti and Johnson, Interrelationships fishes: 80 (for narkids and narcinids). Order Rajiformes, Suborder Rajoidei, Superfamily Torpedinoidea: Shirai, 1996, in Stiassny, Parenti and Johnson, Interrelationships fishes: 34 (superfamily exclusively for torpedinoids, suborder also including rajoids and myliobatoids, order for all batoids).

FAO Name: En - Electric rays.
Field Marks: Body disc thick and flabby, oval to roundish, snout short, truncate or rounded, skin soft and loose, without armature of dermal denticles or their modifications, tail section thick, caudal fin well developed (except torpedinid genus Hypnos), as well as 0 to 2 dorsal fins.

Diagnostic Features: Disc oval, elliptical, rounded to circular, and with stout tail; snout not formed into a saw. Nostrils close together and close to the mouth, with anterior nasal flaps connected together to form a nasal curtain; nasoral grooves present; pectoral fins large. Teeth small and not fused into crushing plates; tooth counts 8 to 68 upper jaw, 7 to 75 lower jaw. Eyes small to obsolete, with several deepwater species that are blind. A stout to diminutive tail; trunk, head and pectoral fins forming a large disc; two, one or no dorsal fins present, usually large where present; the caudal fin usually large and well developed (tiny in Hypnos); skin completely naked; no stinging spine on caudal fin; pectoral electric organs present, but no caudal electric organs; powerful electric organs derived from branchial muscles visible as large bean-shaped contour at both sides of head; the rostrum variable, absent, greatly reduced, or moderately large and wide. These are very large, up to 200 cm long to rather tiny, adults less than 30 cm , batoids. Colour: dorsal surface coloration in these batoids can be rather brilliant, with bars or lines, blotches, eye-spots, ocelli, rosettes, and various sized spots, or may be rather drab dark to light black or grey without any mottling or other descriptive patterns.

Distribution: Circumglobal in the 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. Tetronarce californica, T. nobiliana). Most members of this order are found in tropical and subtropical waters, with a few species living in cool and warm temperate seas. They occur primarily inshore, on continental shelf waters, but a few species are considered deepwater inhabitants.

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 resulting in a fair survival rate. 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: Electric rays, Drilvisse (South Africa).
Remarks: Following Aschliman, Claeson and McEachran (2012) the order as restricted here has two families recognized globally, with each family having two subfamilies. The Narcinidae has the Narcininae (Numbfishes) and Narkinae (Sleeper rays), while the Torpedinidae has the subfamilies Torpedininae (Torpedo rays) and Hypninae (Coffin rays). Some classifications recognize as many as four families within this order (Compagno, 2005).

Literature: Compagno (1973, 1977, 2005); Carvalho (1999a, b); Compagno and Last (1999a, b, c); McEachran and Aschliman (2004); Nelson (2006); Compagno and Heemstra (2007); Aschliman, Claeson and McEachran (2012); Aschliman et al. (2012); Ebert and Stehmann (2013); Ebert (2014); Carvalho (In press); D.A. Ebert (unpubl. data); L.J.V. Compagno (pers. comm. and unpubl. data).

### 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 Duméril, 1806, Zoologie analytique, ou méthode naturelle de classification des animaux. Paris. Zool. anal.: 102, 343.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Genera: 1.

Synonyms: Family Narcaciontoidae Gill, 1862, Ann. Lyceum Nat. Hist. New York, 7(32): 386, also Subfamily Narcaciontinae Gill, 1862, ibid., 387. Type genus: Narcacion Gill, 1862, a revival of Narcacion Klein, 1776, 1777. Family Narcobatidae Gill, 1895, Proc. U.S. Nat. Mus. 18(1050): 163. Type genus: Subgenus Narcobatus Blainville, 1816 (Genus Raia Scopoli, 1777). Also as subfamily Narcobatinae Gill, 1895, ibid., 164. Subfamily Torpedinae Fowler, 1934, Proc. Acad. Nat. Sci. Philadelphia, 85: 240 (Family Torpedinidae). Erroneous spelling.

FAO Names: En - Electric rays; Fr - Torpilles, raies électriq.; Sp - Tremielgas, torpedos.
Field Marks: Mouth broadly arched, distensible, without labial cartilages and folds at corners of mouth, two subequal sized dorsal fins, with the first much larger than the second. Colour of dorsal surface uniformly plain, sometimes with small spots or variegated with blotches or marbling, sometimes with eyespots on pectoral fins; ventral surface of most species creamy to white.

Diagnostic Features: Small to moderately large (maximum total length to about 180 cm , but most species less than 100 cm in length), heavy-bodied batoids with short stout shark-like tails; body depressed and dorso-ventrally flattened, typically soft and flabby, and entirely naked above and below, without dermal denticles or thorns (except in one Eastern Central Atlantic species). Head, trunk and the broadly expanded pectoral fins forming a more or less circular disc. Anterior contour of disc conspicuously truncate or emarginate, snout extremely short. Two large powerful kidney-shaped electric organs at bases of pectoral fins, these visible through skin. Tail distinctly shorter than and marked off from body disc, with narrow dermal fold along either lower edge; tail abruptly narrower than trunk, no barbed sting (stinger or stinging spine) on dorsal surface of tail, and no electric organs in tail. 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. Mouth broadly arched and broad, without prominent knobs and depressions and with labial furrows absent; strong grooves at distal ends of mouth but not around its periphery. Oral teeth small, with flat bases and a prominent cusp, not laterally expanded and plate-like, similar in shape and in 20 to 75 rows in upper and lower jaws. Five small gill openings on underside of front half of pectoral-fin bases, not visible in lateral view; no gill sieves or rakers on internal gill slits. Pectoral fins large, 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. Pelvic fins low, broadly rounded and not divided into anterior and posterior lobes. Two relatively large dorsal fins, the first much larger than the second and close to it, rounded-angular in shape with apices, anterior, posterior and inner margins, and free rear tips more or less confluent, not falcate. First dorsal fin originates far behind anterior half of total length, origin over or just behind rear fourth of pelvic-fin bases and well anterior to midlength of tail. Caudal fin large, subtriangular, paddle-shaped, much larger than dorsal fins and about size of pelvic fins or larger, not shark-like, nearly symmetrical, with vertebral axis hardly raised above body axis; lower caudal-fin lobe absent. Spiral valve turn counts: 9 to 13 . Adults between 20 and 180 cm total length. Colour: variably plain or variegated above, from greyish or brownish to black; dark and light spots, blotches or marbling, variably present or absent, sometimes with eyelike spots (ocelli); usually lighter below, often uniformly white or with a dark margin to the pectoral and pelvic fins.

Distribution: Circumglobal, occurring from high latitude seas to the tropics and in most oceans, except for polar seas.
Habitat: Electric rays inhabit tropical to temperate shelf waters from inshore to about 100 m depth, but some have been reported from as deep as 1100 m . A few species are semi-pelagic, while others such as the Pacific electric ray (Tetronarce [=Torpedo] californica) have been observed swimming offshore at about 10 m below the surface in waters over 3000 m deep. A few species (e.g. T. nobiliana) are highly migratory, with the adults swimming pelagically. Electric rays usually lie quietly on the bottom during the day, often buried on soft bottoms in sand or mud and will appear sluggish when swimming, but 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 small to large fishes and invertebrates; their jaws and mouths are highly distensible to allow them to swallow very large prey. At least some species will deliberately shock potential fish victims with their powerful electric organs to stun them, and then use their flexible pectoral discs as manipulators to guide the prey into their mouths. The electric organs are also defensive, and can successfully protect these rays against predators such as sharks and octopuses.

Interest to Fisheries and Human Impact: Electric rays may locally be quite abundant in some areas, but 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. In some areas, such as southern California (U.S.A.) these rays are taken in small numbers for biological and medical research.

Fishermen are wary of these rays because of their discharge of strong electric shocks, so discard them quickly. Although
there are no confirmed fatalities from these rays, there are several suspicious, unexplained fatal scuba diving accidents that may have involved these rays; whereby divers possibly after being 'shocked' by these rays may have subsequently drowned.

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: Torpedo rays, Electric rays, Drilvisse (South Africa).
Remarks: The family consists of two subfamilies (Torpedininae and Hypninae), three genera, Hypnos, Tetronarce, and Torpedo, and about 25 nominal species. The genus Torpedo until recently consisted of two subgenera, Tetronarce and Torpedo, but Carvalho (In press) resurrected Tetronarce Gill, 1862 to full generic status. All three genera are primarily shelf dwelling species, but at least four Tetronarce species occur mainly on the upper slopes.

Literature: Compagno and Last (1999b); Carvalho, Stehmann and Manilo (2002b); Ebert (2003); Haas and Ebert (2006); Welter-Schultes and Feuerstein (2008); Ebert and Stehmann (2013); Ebert (2014); Carvalho (In press); L.J.V. Compagno (pers. comm.).

## List of Deep-sea Species Occurring in the Area:

O-4 Tetronarce cowleyi Ebert, Haas, and de Carvalho, 2015

## Tetronarce Gill, 1862

Genus: Tetronarce Gill, 1862, Ann. Lyceum Nat. Hist. New York, 7: 387.
Type species: Torpedo occidentalis Storer, 1843, by monotypy, a junior synonym of Torpedo nobiliana Bonaparte, 1835. According to Gill, 1895, Proc. U.S. Nat. Mus. 18(1050): 163, the spelling Tetronarce was a printer's error.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 1.

Synonyms: Genus Gymnotorpedo Fritsch, 1886, Arch. Anat. Phys. Leipsig: 365. Genus Tetronarcine Tanaka, 1908, Journ. Coll. Sci. Tokyo, 23: 2. Type species: Tetronarcine tokionis Tanaka, 1908, by monotypy according to Fowler, 1941. Genus Notastrape Whitley, 1932, Rec. Australian Mus., 18(6): 327.

Field Marks: Similar to family account above, except that members of the genus Tetronarce are generally uniformly coloured a dark to light black, grey, or dark purplish above (some species with small dark spots, and white below), and have smooth-edged spiracles without knobs or papillae.

Diagnostic Features: Disc subcircular, soft and flabby, and naked above and below, without dermal denticles or thorns; anterior disc margin conspicuously truncate or emarginate, snout extremely short; rostral cartilage absent or reduced. Tail short, stout, distinctly marked off from disc, with narrow dermal fold along either lower edge abruptly tapering posteriorly from disc; electric organs absent in tail. Eyes relatively small, but fully developed. Spiracles small, moderately oblique, with smooth posterior margins, and no papillae; inner anterior margin with 8 to 14 pseudobranchial folds. Nostrils relatively large, oblique, 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. Mouth broadly arched and broad, without prominent knobs and depressions and with labial furrows absent; strong grooves at distal ends of mouth but not around its periphery. Teeth small, with flat bases and a prominent cusp, not laterally expanded and plate-like, similar in shape. Tooth counts 18 to 66 upper jaw, 19 to 61 lower jaw. Gill openings small, first and fifth slightly smaller than third and fourth openings. Electric organs kidney-shaped, length about one-half disc length, these visible through skin. Pelvic fins low, broadly rounded, not divided into anterior and posterior lobes. Dorsal fins relatively large, first much larger than second and close to it; rounded-angular in shape with apices, anterior, posterior and inner margins, and free rear tips more or less confluent, not falcate. Caudal fin large, subtriangular paddle-shaped, much larger than dorsal fins, similar in size to pelvic fins or slightly larger; lower caudal-fin lobe absent. Vertebral counts: total vertebral counts 95 to 106, monospondylous vertebral counts 25 to 36, precaudal vertebral counts 68 to 77 , caudal fin vertebral counts 20 to 24 . Spiral valve turn counts: 9 to 14 . Adults up to 180 cm total length. Colour: dorsal surface variably plain, from purplish to grayish or brownish to black, some species with darker inconspicuous spots; usually lighter below, often uniformly white or with a dark margin along the pectoral and pelvic fins.

Local Names: Torpedo rays.
Remarks: This genus until recently has been considered a subgenus of Torpedo, but Carvalho (In press) recently resurrected Tetronarce to full generic status. Members of the genus Tetronarce can be distinguished from the genus Torpedo by their uniformly drab, often dark black, purplish-black to brown dorsal coloration, and smooth margined spiracles
that lack knobs or papillae. Torpedo species by contrast are usually ornately coloured on their dorsal surface, and have knobs or papillae around their spiracle margins.

The genus Tetronarce has about 11 nominal species, but many are poorly described. Most species occur along continental shelves, but at least four species are considered deep-sea inhabitants of upper continental and insular slopes.

The conservation status of most members of this group is poorly known and as such is assessed as Data Deficient.

## Tetronarce cowleyi Ebert, Haas, and de Carvalho, 2015

Tetronarce cowleyi Ebert, Haas, and de Carvalho, 2015, Zootaxa, 3936(2): 237, figs. 2-6, tab. 1. Holotype: SAIAB 25190, 626 mm TL, mature male, F.R.S. Africana survey cruise 033, station A2768, haul 062, SE Atlantic, off the west coast of South Africa, 33³9.0'S, $19^{\circ} 58.5^{\prime} \mathrm{E}, 262 \mathrm{~m}, 20$ January 1985.

Synonyms: Torpedo nobilianus: Barnard, 1925, p. 89. Narcobatus nobilianus: Norman, 1935, p. 37; Barnard, 1947, p. 30, pl. 4, fig. 10. Torpedo hebetans: Thompson, 1914, p. 159; Von Bonde and Swart, 1923, p. 15.

Other Combinations: None.
FAO Name: En - Cowley's torpedo ray.


Fig. 173 Tetronarce cowleyi
Field marks: Front margin curved, with overall disc shape ovate, tail section stout and massive, with two large, separated dorsal fins, of which the first one about twice as large as the second one, a large, paddle-like caudal fin and margins of spiracles smooth, without tentacles. In life upper side mostly shiny black or dark grey, ventral surface white to creamy-white.

Diagnostic Features: Disc fleshy, circular, anterior margin broadly rounded; disc widest at about one-third its length, thickest at anterior margin; disc does not overlap origin of pelvic fins. Eyes small, orbital diameter about 2.1 to 2.7 times spiracle length, close to spiracles, space between them about equal to interspiracular width. Spiracles with smooth margins, without tentacles or papillae (diagnostic feature of genus Tetronarce), inner margins with pseudobranchial folds numbering from 9 to 13 , numbers differing between spiracles within individuals. Teeth set in quincunx, similar in upper and lower jaws. Tooth counts 26 to 32 upper jaw, 26 to 28 lower jaw. Tail stout and massive, with long pelvic fins attached to sides of its origin; dorsal fins distinct and large, the first one about one-third larger than second one; caudal fin large, paddle-like, with upper and lower lobes of about equal size. Dorsal and ventral skin surfaces totally smooth, without dermal denticles or thorns. Vertebral counts: total vertebral counts 103 to 106, trunk vertebral counts 32 to 33, caudal (post-trunk) vertebral counts 71 to 73 . Spiral valve turn counts: 14 to 16 . Adults up to 120 cm total length. Colour: in life dorsal surface is a uniform shiny black or dark grey, mostly plain and without distinct darker dots or whitish spots; ventral surface white to
creamy-white; juveniles darker on disc and pelvic margins, but fading in adults. After death and preservation dorsal surface fades to a brownish grey.

Distribution: Algoa Bay, Eastern Cape, South Africa to Walvis Bay, Namibia; records from Namibia are very rare.

Habitat: A deep-sea species occurring off South Africa and Namibia along the outer continental shelf and upper slopes from 110 to nearly 500 m depth, but most common below 200 m .

Biology: Yolk-sac viviparous, but nothing known about its litter size or reproductive cycle in Southern Africa. Neonates have been collected during pelagic plankton tows on the edges of the outer continental shelf southwest of Cape Town (Compagno, Ebert and Cowley, 1991). It is suspected that this species may move well off the bottom while foraging for food and other large prey; evidence for this comes from large pelagic fish species found in their diet. The diet of this electric ray consists mainly of large bottom and pelagic bony fishes and small sharks. Smaller juveniles feed mostly on smaller benthic fish and invertebrates.

Size: Maximum total length about 120 cm for females; size at maturity about 100.5 cm for females and 58.2 cm for males. Size at birth uncertain, but the smallest recorded free-swimming neonate measured 18.6 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 use to handle these rays with respect trying to avoid their powerful electric shocks.

The conservation status of this common, but recently described electric ray has not been assessed.
Local Names: Atlantic electric ray, Atlantiese drilvis (South Africa).
Remarks: Globally there are several nominal species referred to as Tetronarce cf. nobiliana, but these regional forms may in fact each represent a different Tetronarce species. The southern African T. cowleyi until recently was referred to as T. nobiliana in most literature accounts.

Literature: Stehmann and Bürkel, Torpedinidae, in: Whitehead et al. (1984); Compagno, Ebert, and Smale (1989); Compagno, Ebert and Cowley (1991); Iglésias (2011); Ebert and Stehmann (2013); Ebert, Haas, and de Carvalho (2015); Carvalho (In press); D.A. Ebert (unpubl. data).

### 3.2 Order RAJIFORMES - Skates

Order: Rajae: Müller and Henle, 1841, Syst. Besch. Plagiost. [Part] 2, (3): 103 (group equivalent to order for batoids).

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Families: 2.

Synonyms: Batoidei, Batoidea, Batoidimorpha (partim)

Field Marks: Skates have a completely dorsoventrally flattened body and greatly extended pectoral fins forming a disc, a slender tail sharply distinct from the disc, small dorsal fins, a caudal fin rudimentary or absent and body and tail never completely covered by overlapping, very densely set placoid scales.

Diagnostic Features: 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 thread-like, usually not much longer than disc; two dorsal fins small, or absent; caudal fin rudimentary or absent; pelvic fins with two lobes 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 ranges from pygmy to more than 200 cm total length. Colour: dorsal surface varying from whitish to pale, to darker colours, from reddish, brown, grey, purplish to black, with either plain surface or with blotches, reticulations, spots, ocelli, and lighter to darker variations; ventral surface mostly lighter, but some species darker coloured or with blotches.

Distribution: Circumglobal in the Atlantic, Indian and Pacific Oceans, including Arctic and Antarctic waters (except for Rhinobatidae).

Habitat: The skates are mostly marine inhabitants, except for one uniquely endemic species found in estuarine waters, and are found in all oceans from tropical to polar latitudes and from shallow inshore waters down to the deep sea abyssal plains (to a depth over 4000 m ). The majority of species are demersal on subtropical to polar shelves and upper slopes, where they can be locally rather abundant; a few large species mainly in deepwater are also benthopelagic and may migrate over long distances.

Biology: All skate species are oviparous, with some species producing relatively large 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, until they hatch from capsules. The life span of these batoids may range from about 10 years to nearly 40 years or possibly 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 Asian and European countries of fishing for skates 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. In the Southeastern Atlantic Ocean deep-sea skates are mostly taken as bycatch, but very little information is available on catch rates.

The conservation status of many skates, especially the deep-sea species, is Data Deficient.

## Local Names: Rôe (South Africa).

Remarks: The order Rajiformes is still largely unresolved with morphological and molecular data being strongly at odds regarding the relationship of the skates to other extant batoids (Aschliman, Claeson and McEachran, 2012; Aschliman et al., 2012). Nelson (2006) combined five families of very different morphological appearance, Rhinidae, Rhynchobatidae, Rhinobatidae, Rajidae, and Arhynchobatidae 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 five families, more than 30 genera, and over 350 species. The descriptive account above is based solely on the skate families Arhynchobatidae and Rajidae, to the exclusion of the other three families. The families Rhinidae, Rhynchobatidae, and Rhinobatidae mostly occur in warm temperate to tropical nearshore waters, while the families Arhynchobatidae and Rajidae contain many deep-sea species. Only the two latter skate families will be discussed further.

For detailed information on southern African skates (Namibia and South Africa) see Compagno, Ebert and Cowley (1991), Ebert, Cowley and Compagno (1991), Compagno and Ebert (2007), and Ebert, Compagno and Cowley (2008).

Literature: McEachran and Konstantinou (1996); McEachran and Aschliman (2004); Compagno (2005); Nelson (2006); Aschliman, Claeson and McEachran (2012); Aschliman et al. (2012).

## Key to Deep-sea Southeastern Atlantic Ocean Families:

1a. Snout soft, flabby, due to delicate flexible rostral cartilage (Fig. 175) .
family Arhynchobatidae

1b. Snout rigid, stiff, not flexible due to solid, stiff rostral cartilage (Fig. 176) . . . . family Rajidae


DETAIL OF SNOUT SKELETON
After Stehmann and Bürkel
in Whitehead et al. (1984)
Fig. 175 Arhynchobatidae


DETAIL OF SNOUT SKELETON After Stehmann and Bürkel
in Whitehead et al. (1984)
Fig. 176 Rajidae

### 3.2.1 Family ARHYNCHOBATIDAE

Family: Subfamily Arhynchobatinae Fowler, 1934, Proc. Acad. Nat. Sci. Phil., 85: 240.
Type Genus: Arhynchobatis Waite, 1909

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Genera: 1.

Synonyms: Family Pseudorajidae Bigelow and Schroeder, 1954a, Breviora Mus. Comp. Zool. Harvard, (24): 2. Type genus: Pseudoraja Bigelow and Schroeder, 1954a. Tribe Pavorajini McEachran, 1984, Copeia, 1984(1): 55. Type genus: Pavoraja Whitley, 1939. Subfamily Arhynchobatidinae Steyskal, 1980, Proc. Biol. Soc. Washington, 93(1): 170, suggested emendation of Arhynchobatinae Fowler, 1934 according to the case of a basonym (batis) ending in -is for correct orthography.

FAO Name: En - Softnose skates.
Field Marks: Rostral cartilage flexible, delicate and extending to snout tip, or being incomplete not reaching rostral node in snout tip, or rostral cartilage basally segmented or separated from neurocranium, or limited to distal section of snout, anterior pectoral-fin radials and their basal elements extended forward to close to, or being in touch with snout tip. Snout characteristics can be checked by touch, or against strong light.

Diagnostic Features: Disc large, broad, and flat rhomboidal to heart-shaped, with a tail narrow and slender, slightly shorter to nearly twice as long as pectoral disc; dorsal disc either smooth or covered with small dermal denticles; more or less enlarged, sharp hooked denticles or thorns usually present on dorsal surface, on the midline of the tail and often on the midline of the disc, on the snout, orbits, and shoulders. Trunk depressed and flattened, not shark-like. Precaudal tail cylindrical or moderately depressed but not whip-like, with lateral ridges or folds on sides; tail abruptly narrower than trunk, no barbed sting (stinger or stinging spine) on dorsal surface of tail behind dorsal fins, electric organs present in tail. Head broad and depressed; snout short to long and bluntly to acutely angular or rounded-angular, supported by a more or less reduced, soft, slender rostral cartilage. Five small gill openings on underside of front half of pectoral-fin bases, not visible in lateral view. Eyes dorsolateral on head and just anterior to spiracles. Mouth transverse and straight to moderately arched, without prominent knobs and depressions. Nostrils just anterior to mouth and separated from it by less than half their own widths, connected by broad nasoral grooves with mouth; anterior nasal flaps elongated, posteriorly expanded and reaching mouth, but separate medially and not forming a nasal curtain. Teeth small, rounded-oval in shape, with or without cusps on their crowns, and not laterally expanded and plate-like, similar in shape and in over 20 rows in either jaw. Pectoral fins large, originating in front of mouth and reaching snout tip or not, attached to sides of head and forming a large pectoral disc with free rear tips ending posterior to pelvic-fin origins; disc not subdivided by a notch at eyes. No electric organs at bases of pectoral fins. Pelvic fins high, rounded-angular or angular, and distinctly bilobed (except in Pseudoraja) through deep incision in joint outer margin. Claspers of mature males slender to relatively stout, and elongated, nearly extending to first dorsal fin in some species, and with the glans short and only slightly widened; external clasper glans components relatively few and very similar for most species. Alar thorns of mature males sharp, hooked, permanently erect, not retractable into dermal pockets. Usually two small, subequal and close to widely separated dorsal fins present, these of similar rounded or rounded-angular shapes with margins more or less confluent, not falcate; only one dorsal fin or none in some species. First dorsal fin when present originates far behind anterior half of total length, base far behind rear tips of pelvic fins and junction between trunk and tail, and well behind midlength of tail. Caudal fin small to rudimentary, and vertebral axis parallel to body axis; lower caudal-fin lobe absent. Maximum total length between 30 and 175 cm , with most species less than 100 cm . Colour: dorsal surface varying from whitish to dark brown, purplish, or black, either unmarked or with light or dark spots, blotches, or basal ocelli on pectoral
fins; usually white below but often dark or blotched along midbody in dark-bellied species, or faint grey edging of disc and pelvic fins in light-bellied species.

Distribution: Worldwide in all oceans, including Antarctic waters, from continental shelves down the continental slopes to the deep-sea abyssal plains. Absent in tropical shelf waters.

Habitat: Demersal from close inshore in cold temperate and boreal latitudes down to the continental slopes and from far offshore islands and on submarine elevations to deep-sea plains to more than 4000 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 deep-sea members of this family are very long lived and do not mature until over 20 years in age. Diet includes various bottom living invertebrates and fishes; larger species tend to consume more bony fishes.

Interest to Fisheries and Human Impact: Most members of this family are deep-sea species and are generally taken as bycatch rather than as targeted species. However, where these skates are caught there generally is very little speciesspecific information available on catch rates.
The conservation status of these skates in the Southeastern Atlantic Ocean is mostly Data Deficient to Least Concern.
Local names: None.
Remarks: The family Arhynchobatidae is considered a subfamily (Arhynchobatinae) by some authors (McEachran and Aschliman, 2004; Nelson, 2006; Aschliman, Claeson and McEachran, 2012; Aschliman et al., 2012), but given full family status by others (Compagno, 1999, 2005; Last and Compagno, 1999; Ebert and Compagno, 2007). Aschliman et al. (2012) and Naylor et al. (2012a, b) analysed the phylogenetic relationships within the Rajoidei and concluded that the Arhynchobatidae is a monophyletic group, and should be retained as a full family (Ebert and Stehmann, 2013). The above account is modified after Last and Compagno (1999), Ebert and Stehmann (2013), Ebert (2014) and Aschliman and Ebert (In press).

The family has 12 or 13 genera and about 102 species, of which one genus (Bathyraja) and a single species occur in the Southeastern Atlantic Ocean deep-sea.

Literature: Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); Stehmann (1995); McEachran, Dunn and Miyake (1996); McEachran and Dunn (1998); Compagno (1999, 2005); Last and Compagno (1999); Compagno and Ebert (2007); Ebert and Compagno (2007); Aschliman, Claeson and McEachran (2012); Aschliman et al. (2012); Ebert and Stehmann (2013); Ebert (2014); Aschliman and Ebert (In press).

## List of Species Occurring in the Area:

Bathyraja smithii (Müller and Henle, 1841)

## Bathyraja Ishiyama, 1958

Genus: Bathyraja Ishiyama, 1958: 325 (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 Deep-sea Southeastern Atlantic Ocean Species: 1.

Synonyms: "Pseudogenus" (= subgenus) Zetaraia Leigh-Sharpe, 1924 (Genus Raja Linnaeus, 1758), J. Morph. 39: 568, 575. Type species: Raja brachyura Günther, 1880, by original designation, = Raja brachyurops Fowler, 1910. "Pseudogenus" (= subgenus) Thetaraia Leigh-Sharpe, 1924 (Genus Raja Linnaeus, 1758), J. Morph. 39: 568, 577. Type species: Raja eatoni Günther, 1876, by original designation. Subgenus Arctoraja Ishiyama, 1958 (Genus Breviraja Bigelow and Schroeder, 1948), J. Shimonoseki Coll. Fish. 7(2-3): 337. Type species: Raja smirnovi Soldatov and Pavlenko, 1915, by original designation. Subgenus Actoraja Stehmann, 1990 (Genus Breviraja Bigelow and Schroeder, 1948), in J.-C. Quero et al., eds., 1990, CLOFETA. Check-list fish. E. trop. Atlantic, 1: 29. Apparent error for Arctoraja Ishiyama, 1958.

FAO Names: En - Bathyraja rays; Fr - Raies Bathyraja; Sp - Rayas Bathyraja.
Field Marks: Large soft-nosed skates, with soft flexible, slender, uncalcified, rostral cartilage, sub-rhomboidal disc, with a broadly triangular, short to long pointed snout, pectoral tips angular or broadly rounded, tail length mostly shorter than disc
width, disc dorsal surface depending on species without thorns or may have nuchal, midback, or scapular thorns present. Colour above uniform or with blotches or spots on some species; ventral surface mostly uniform except for disc edges may be darker in some species.

Diagnostic Features: Disc rhombic-shaped, rather broad, width usually greater than disc length, with lateral corners angular or broadly rounded at tips. Snout flabby, flexible, and soft. Mouth small to relatively wide, and slightly arched; teeth with single large cusp, arranged in quincunx. Tooth row counts upper and lower jaws 22 to 36 . Anterior pelvic-fin lobes of moderate length, not extending to posterior margin of posterior lobe. Tail relatively short, its length equal to or less than disc width. Dorsal fins usually two, subequal, similar in shape. Skin smooth or roughly textured by dermal denticles on dorsal and ventral surfaces. Thorns on dorsal surface, if present, usually on nuchal, scapular, and midback areas; predorsal tail thorns mostly in single midline row; inter-dorsal thorns present or absent; ventral surface usually without thorns. Vertebral counts: trunk vertebral counts 31 to 39 , predorsal vertebral counts 68 to 122 . Spiral valve counts 8 to 15 . Maximum total length is about 175 cm . Colour: dorsal surface varying from whitish to dark brown, purplish, or black; dorsal surface either unmarked or with blotches or spots on pectoral fins; ventral surface usually white but may have dark blotches between gills or on abdomen, or grey edging of disc and pelvic fins.

Remarks: Globally about 50 nominal valid species have been described and named, but with several additional mostly deepwater species remaining to be described; this genus is one of the most diverse of elasmobranchs. In the Southeastern Atlantic Ocean deep-sea one species (Bathyraja smithii) is known to occur (Compagno and Ebert, 2007), but with increased deep-sea exploration it would not be surprising if additional species within the genus were discovered.

## Bathyraja smithii (Müller and Henle, 1841)

Raja smithii Müller and Henle, 1841, Systematische Beschreibung der Plagiostomen. Veit und Comp., Berlin, 150, pl. 49. Syntypes: (2) BMNH 1953.8.10.1 (skin), South Africa; MNHN 0000-1594 (1), Bosphorus, likely not this species. Type catalogue: Bertin, 1939: 84, Séret and McEachran, 1986: 17, with MNHN specimen as paratype.

Synonyms: Raja smithii Müller and Henle, 1841: 150, pl. 49, fig. 1 (South Africa); Gray, 1851: 112; Bleeker, 1860: 58; Duméril, 1865: 553; Günther, 1870: 467: Gilchrist, 1902: 168; Thompson, 1914: 159. Raia smithii Garman, 1913: 366; von Bonde and Swart, 1923: 5. Raia smithi Barnard, 1925: 66, fig. 4, pl. 4. Raja smithi Norman, 1935: 41; Fowler, 1941: 364. Breviraja smithii: Hulley, 1970: 213; 1972a: 2.

Other Combinations: None.
FAO Names: En - African softnose skate; Fr Raie de Smith; Sp - Raya de Smith.

Field Marks: A large soft-bodied skate, with a broadly triangular, bluntly pointed snout, pectoral tips angular, tail shorter than disc length, disc dorsal surface without thorns, but tail with a single row of large thorns, young with single row of midback thorns, but these are lost with growth. Colour a uniform light grey, without any prominent pattern; ventral surface whitish-grey.

Diagnostic Features: Disc rhombic-shaped, rather broad, width about 1.2 to 1.4 times disc length, with lateral corners broadly rounded at tips; snout length about $12 \%$ of total length, moderately produced, obtuse; snout angle in front of spiracles about $90^{\circ}$ to $100^{\circ}$. Total pectoral radial counts not available. Nasal curtain not fringed. Mouth broad and slightly arched; teeth with a single large cusp, arranged in quincunx; sexual dimorphism present, anterior most teeth
 of adult males more erect, robust, than found in adult females and juveniles. Tooth row counts 24 to 28 upper jaw, not available for lower jaw. Anterior pelvic-fin lobes not extending to posterior pelvic-fin lobe tips; anterior lobe length about 66 to $75 \%$ of posterior pelvic-fin lobe length. Tail relatively short, its length about 1.3 to 1.6 times in distance from tip of snout to posterior margin of cloaca. Dorsal fins medium-sized, similar in shape with rounded apices and size. Skin mostly smooth, with fine, widely spaced, spicules on upper disc surface; ventral surface mostly smooth. Thorn pattern on dorsal surface (adult): rostrum, orbital, nuchal, scapular, and midback thorns absent. Predorsal tail thorns in single midline row and number 14 to 19; 0 to 1 inter-dorsal thorns; juveniles with 3 small orbital thorns, 2 nuchal thorns, and

3 to 4 scapular thorns, followed by a row of about 30 midback thorns from nuchal region to first dorsal-fin origin, and 1 interdorsal thorn; all dorsal surface thorns except predorsal tail thorns and presumably interdorsal thorn disappear with growth. Ventral surface usually without thorns at all stages. Vertebral counts: predorsal vertebral counts 68 to 71. Spiral valve counts not available. Maximum total length is about 120 cm . Colour: uniform light to medium grey above, sometimes with small white spots; underside white to cream with darker edges around disc and blotches between gills and around vent.

Distribution: Widely distributed off the west coast of Africa from off Mauritania, Senegal, Gulf of Guinea, Gabon, Angola, south to Namibia and the west coast of South Africa, with its range extending to the Eastern Cape, South Africa. This is the only bathyrajid skate known from this area.

Habitat: Benthic in deepwater along upper continental slopes between 295 and 1040 m depth, but mostly below 600 m ; neonates usually below 700 m .

Biology: Oviparous, with very large egg cases and very long horns. Nothing is known about the reproductive cycle of this species. The diet consists of invertebrates including crustaceans and cephalopods, but larger individuals prefer bony fishes including hake; this skate species appears to be a very formidable predator in its habitat.

Size: Maximum total length about 120 cm . Males mature between 95 to 100 cm , and females mature at about 87.5 cm . Size at hatching is about 12 cm total length based on smallest free-swimming neonate.

Interest to Fisheries and Human Impact: This deepwater skate is taken mostly in small numbers as bycatch by bottom trawlers targeting hake (Merluccius spp.) around Southern Africa.

Conservation status is Data Deficient.
Local Names: Rog (Afrikaans).


Fig. 178 Bathyraja smithii
$\square$ Known distribution

Remarks: Although not uncommon at depth, the life history of this deep-sea skate is relatively unknown. It is the only member of this genus known to occur off the southern African coast.

Literature: Hulley (1970, 1972a, 1986); Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); Ebert, Cowley and Compagno (1991); Stehmann (1995); Compagno and Ebert (2007); Ebert, Compagno and Cowley (2008); Smale, Holtzhausen and McCormack (2009); Ebert (2014); Aschliman and Ebert (In press).

### 3.2.3 Family RAJIDAE

Family: Genus or Family Raia Blainville, 1816, Bull. Sci. Soc. Philomat. Paris, (8).
Type Genus: Raja Linnaeus, 1758
Number of Recognized Deep-sea Southeastern Atlantic Ocean Genera: 7.
Synonyms: None.
FAO Names: En - Rays and skates; Fr - Rajidés; Sp - Rayidos.
Field Marks: Rostral cartilages 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: Disc shape from nearly circular to subrhombic or subquadrate, with snout from very short and bluntly angled to very long and pointed. Pectoral fins large, originating in front of mouth and reaching snout tip or not, attached to sides of head and forming a large pectoral disc with free rear tips ending posterior to pelvic-fin origins; disc not subdivided by a notch at eyes. Eyes dorsolateral on head and just anterior to spiracles. Mouth transverse and straight to strongly arched, without prominent knobs and depressions. Nostrils just anterior to mouth and separated from it by less than half their own widths, connected by broad nasoral grooves with mouth; anterior nasal flaps elongated, posteriorly expanded and reaching
mouth, but separate medially and not forming a nasal curtain. Oral teeth small, rounded-oval in shape and with or without cusps on their crowns, not laterally expanded and plate-like, similar in shape and in 30 to 70 rows in either jaw. Pelvic fins high, rounded-angular or angular, and subdivided into anterior narrow lobes, and posterior broad lobes with a connecting web. Mature male claspers from very long, nearly reaching 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; sharp, hooked male alar thorns not permanently erect, but retractable into dermal pockets. Tail solid, sharply marked off from disc, somewhat shorter than, to about as long as, or slightly longer than disc and gradually tapering to tip, with two small, subequal, close to widely separated dorsal fins at rear and rudimentary upper caudal fin. Upper and lower disc may be completely covered by rough dermal denticles, or partly or entirely smooth. Thorns on upper disc usually present, at least in juveniles, and arranged typically in pattern of orbital, nuchal, scapular and mid-dorsal thorns along trunk and tail in at least one median row, but mostly also parallel rows of thorns and often lateral thorns along tail do occur. Interdorsal thorns present or absent. Adults range between 20 and 250 cm total length. Colour: dorsal surface varying from whitish to dark brown or black, usually white below but often dark or blotched; dorsal surface either unmarked or with light or dark spots, blotches, or basal ocelli on pectoral fins; ventral surface white with dark edging and blotching, or dark with white markings, or totally dark.

Distribution: Worldwide in all oceans from inshore on continental shelves to upper slopes and to deep-sea plains, also at distant offshore islands and on submarine elevations; absent from shallow tropical shelf waters, but present in Arctic and Antarctic waters.

Habitat: Demersal from enclosed bays and estuaries, to coastal waters in boreal and cold temperate to subtropical latitudes down the continental slopes and far offshore islands and on submarine elevations to deep-sea plains to more than 4000 m depth. Larger deepwater species may be benthopelagic.

Biology: Oviparous, with embryonic development taking from a few months to possibly years depending on temperatures of environment. Egg capsules mostly rectangular, with two pairs of long horns at both ends. Skates feed on a variety of bottom living invertebrates and fishes.

Interest to Fisheries and Human Impact: Skates have been the subjects of target and non-target fisheries worldwide, mostly in temperate seas.

The conservation status of skates is variable as many are listed as Data Deficient, while others have largely been extirpated on a local scale. A problem in many regions where skates are caught is that species specific identification has been lacking.

Local names: Rôe (South Africa).
Remarks: All rays and skates at one time 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 with about 26 genera and nearly 200 species recognized. The above family account is modified after Last and Compagno (1999), Ebert and Stehmann (2013), and Ebert (2014).

Literature: Stehmann and Bürkel, in: Whitehead et al. (1984); McEachran and Dunn (1998); Ebert and Stehmann (2013); Ebert (2014); Aschliman and Ebert (In press).

## List of Species Occurring in the Area:

I. Amblyraja robertsi (Hulley, 1970)

Amblyraja taaf (Meissner, 1987)
Cruriraja durbanensis (von Bonde and Swart, 1923)
A. Cruriraja hulleyi Aschliman, Ebert, and Compagno, 2010

Dipturus doutrei (Cadenat, 1960)
2. Dipturus pullopunctatus (Smith, 1964)

Dipturus springeri (Wallace, 1967)
Dipturus stenorhynchus (Wallace, 1967)
Leucoraja compagnoi (Stehmann, 1995)
Leucoraja wallacei (Hulley, 1970)
Malacoraja spinacidermis (Barnard, 1923)
2. Neoraja stehmanni (Hulley, 1972)

Rajella barnardi (Norman, 1935)
Rajella caudaspinosa (von Bonde and Swart, 1923)
Rajella dissimilis (Hulley, 1970)
L Rajella leoparda (von Bonde and Swart, 1923)
Rajella ravidula (Hulley, 1970)

## Key to Deep-sea Southeastern Atlantic Ocean Genera:

1a. Anterior pelvic-fin lobes not limb-like, separated by a notch from posterior lobes along outer fin margin (Fig. 179)

1b. Anterior pelvic-fin lobes elongated, limb-like, separated externally from posterior fin-like lobes (Fig. 180).

Cruriraja

2a. Snout distinctly elongated, pointed; anterior disc margins deeply concave; internarial width usually less than $70 \%$ of distance from nostril to snout tip (Fig. 181)

Dipturus

2b. Snout moderately long to relatively short; anterior disc margins somewhat convex, slightly concave or undulated; internarial width usually more than $70 \%$ of distance from nostril to snout tip

3a. Dorsal disc surface and tail finely covered with dense dermal denticles giving it a velvet-like texture; ventral surface of tail partially to completely covered with dermal denticles. Median row of tail thorns decreasing rearwards in size and disappearing completely on posterior third of tail among dense dermal denticles.

3b. Dorsal disc surface and tail partially to completely covered with less dense, but very coarse dermal denticles, giving it a rough texture; ventral surface of tail usually smooth. Median row of tail thorns may somewhat reduce in size rearwards, but is distinctly continuous to origin of first dorsal fin


Fig. 179 Dipturus


Fig. 181 Dipturus pullopunctatus


Fig. 182 Malacoraja spinacidermis


Fig. 183 Neoraja stehmanni

5a. Tail short, stout, length about equal to or shorter than precaudal length; 2 to 3 scapular thorns on each shoulder; median row of enlarged thorns extending from nuchal area to first dorsal fin may be incomplete or interrupted, but always present (Fig. 184).

Amblyraja

5b. Tail length about equal to or usually longer than precaudal length 6


Fig. 184 Amblyraja robertsi

6a. Multiple rows of median thorns along midback of disc and tail, with mid-row smaller than those in lateral row(s); absent in large juvenile and adult specimens (Fig. 185).

Leucoraja

6b. One to several rows of similar sized thorns along midback of disc and tail in juvenile and adult specimens (Fig. 186).

Rajella


Fig. 185 Leucoraja wallacei

## 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 Deep-sea Southeastern Atlantic Ocean Species: 2.

Synonyms: Raja (Amblyraja), subgenus (Stehmann, 1970).
Field Marks: Thick bodied skates with outer disc corners angular, a relatively short, stout tail usually less than the disc length, reduced thorns on snout, but conspicuous on orbital rims, nuchal, shoulder region, and midback and tail. Colour above greyish brown to dark brown or reddish, strikingly mottled with light blotches and spots in some species in life; creamy to white below.

Diagnostic Features: Disc shape subquadrate to subrhombic, outer corners angular. Tail rather massive along anterior one-half and shorter than precaudal length. 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: dorsal surface 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; ventral surface white, but in deepwater species only in young becoming 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 species is not clarified. Two species are recognized as occurring in the Southeastern Atlantic Ocean. However, both species are known only from a very few specimens and any additional specimens should be retained for examination. The genus account follows Ebert and Stehmann (2013) and Ebert (2014).

## Key to Deep-sea Southeastern Atlantic Ocean Species:

1a. Disc dorsal surface without stellate-based thorns on anterior margins, rostral cartilage and posterior angles; ventral surface uniform grey with white triangular patches between nostrils, and around pectoral girdle (Fig. 187)
. . . . . . . . . . . . . . . . . Amblyraja robertsi
1b. Disc dorsal surface with stellate-based thorns on anterior margins, rostral cartilage and posterior angles; ventral surface white with some scattered darker blotches (Fig. 188) .

Amblyraja taaf


Fig. 187 Amblyraja robertsi


Fig. 188 Amblyraja taaf

## Amblyraja robertsi (Hulley, 1970)

Raja robertsi Hulley, 1970, Annals of the South African Museum, 55(4): 190, pl. 8 (figs. a-b), figs. 12a-b. Holotype: ZMH 25250, 773 mm TL, immautre male, trawled west of Cape Town by RV Walther Herwig, station WH 196/67, 33 $51^{\prime} \mathrm{S}, 17^{\circ} 14^{\prime} \mathrm{E}, 1350 \mathrm{~m}$ deep.

Synonyms: Raja (Amblyraja) robertsi, Hulley: 1972a: 77.
FAO Name: En - Bigmouth skate.
Field Marks: Disc subrhombic, with angular outer corners, tail short, less than disc length, snout short, bluntly angled, and with a stiff rostrum, snout with one small thorn, one preand one post-orbital thorn, two scapular thorns on each shoulder, midback with a single row of 14 to 25 enlarged thorns. Colour greyish above with scattered dark blotches, ventrally uniform grey to black.

Diagnostic Features: Disc subrhombic, with anterior margins concave just behind snout tip, becoming more deeply concave posterior to level of spiracles; disc outer angles relatively pointed, posterior margins nearly straight; disc 1.3 times as broad as long; snout angle in front of spiracles about $96^{\circ}$. Tooth rows in upper jaw 42, teeth in quincunx pattern, with large, rounded base, and sharp cusp. Tail length, short, solid, less than disc length. Snout short, not produced, obtuse, preorbital length 2.4
 times interorbital length. Thorn pattern on dorsal surface: rostrum with small stellate-based thorn, 1 preorbital, 1 postorbital thorn; 1 supraspiracular thorn; 2 scapular thorns on each shoulder; 2 median nuchal thorns; 14 to 25 middorsal thorns extending from nuchal region to almost first dorsal-fin origin; lateral thorn rows on disc and tail absent; entire dorsal surface of disc and tail covered with close set spinules; ventral surface smooth. Vertebral counts (holotype): total vertebral count 87, trunk vertebral count 32, predorsal vertebral count 55 . Spiral valve counts not available. Maximum total length is at least 91.5 cm . Colour: dorsal surface greyish with a few scattered darker blotches on disc and tail; pelvic fins slightly darker; ventral surface uniformly grey to black, slightly darker at posterior disc margins and on tips of anterior pelvic-fin lobes and on tail.

Distribution: Only known from off Cape Town, South Africa.
Habitat: A rare, deep-sea skate known from only a very few specimens collected from west of Cape Town from 1141 to 1350 m depth.

Biology: Oviparous, with egg capsules measuring 130 mm in length, excluding the horns; surfaces are striated and rough
to the touch. Four egg cases trawled up off Cape Town each had near-term embryos of this species.

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 known total length is 91.5 cm ; males mature at about 91.5 cm in length, immature at 77.3 cm ; females not reported for this species. The size at birth is about 16 to 18 cm total length.

Interest to Fisheries and Human Impact: A rare skate species taken on occasion as bycatch in deepwater bottom trawls, and mostly discarded.

The conservation status of this skate is Least Concern.
Local Names: Robert's skate.
Remarks: This rare deep-sea skate is known from only two specimens, both males, and from four egg cases collected with near-term embryos. All were collected in a similar area off Cape Town. This large distinctive skate may be a regional endemic, but it should be closely compared to other similar Amblyraja species found in the Southern Ocean.

Literature: Hulley (1970, 1972a); Hulley in Smith and
Heemstra (1986); Compagno, Ebert and Smale (1989);


Fig. 190 Amblyraja robertsi
$\square$ Known distribution
Compagno, Ebert and Cowley (1991); Compagno and Ebert (2007); Ebert, Compagno and Cowley (2008); Smale (2009a).

## Cruriraja Bigelow and Schroeder, 1948

Genus: Cruriraja Bigelow and Schroeder, 1948, Journal of Marine Research, 7: 549.
Type Species: Cruriraja atlantis Bigelow and Schroeder, 1948. Type by original designation.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 2.

Synonyms: None.
Field Marks: Small legskates lacking a terminal filament on the snout, with deeply incised pelvic fins, tail stout at base, two dorsal fins, lateral tail folds, and weakly developed caudal fin with a very weakly developed or absent hypocaudal lobe. Disc ventral surface and tail smooth. Colour uniformly brownish to tan or yellowish above, whitish to yellow below.

Diagnostic Features: Disc quadrangular, width 1.3 times disc length; snout pointed, lacking distal process or filament; disc anterior margins to spiracles weakly convex with short concavity near snout tip, weakly concave from spiracles to rounded apices of pectoral fins (more concave in adult males), becoming more convex on posterior margins; snout angle about $80^{\circ}$ to $100^{\circ}$. Eye diameter about equal to or slightly greater than inter-orbital distance. Spiracle small, diameter less than eye length. Nostril sub-circular to oval, anterior flap forming a posterolaterally directed tube, mostly obscured by nasal curtain; posterior lobes well developed meeting medially to form nasal curtain; distal ends sub-rectangular with fringe on posterior margin. Mouth slightly arched, teeth arranged in quincunx. Tooth row counts 37 to 50 upper jaw, 38 to 48 lower jaw. Pelvic fins large, deeply incised separating anterior from posterior lobes. Tail broad anteriorly, tapering posteriorly to first dorsal fin; width at pelvic-fin insertions about two times width at first dorsal-fin origin; tail moderately long, length greater than disc length; lateral tail folds long and well developed. Two dorsal fins, medium-sized, similar in size and shape with rounded apices. Skin with fine denticles on upper surface; ventral surface mostly smooth. Thorn pattern on dorsal surface (adult): 0 to 5 rostral thorns; 7 to 12 regularly spaced orbital thorns arranged in semi-circular pattern from pre-orbit to anterior margin of spiracle; 1 to 2 post-orbital thorns; 1 to 3 nuchal thorns; scapular thorns in close-set irregular patches, and numbering from 2 to 9 ; midback thorns arranged in 1 to 9 linear rows followed by tail thorns usually in 3 to 5 linear rows; 39 to 47 predorsal thorns; 2 to 6 inter-dorsal thorns; adult males with malar thorns ranging from 1 to 8 (at greatest distance) rows of short strongly recurved thorns and alar thorns ranging from 1 to 5 longitudinal rows each with 16 to 20 transverse rows; ventral surface without thorns. Vertebral counts: predorsal vertebral counts 66 to 70 . Spiral valve counts: 6 to 7 for one species. Maximum total length is about 60 cm . Colour: dorsal surface uniformly pale brown to tan, reddish, or yellowish; conspicuous dark brown blotches and spots in juveniles; ventral creamy to white or yellowish.

Remarks: The genus comprises eight described species globally, two of which occur in the Southeastern Atlantic Ocean. Generic account and Key to species (below) modified after Aschliman, Ebert and Compagno (2010).

Key to Deep-sea Southeastern Atlantic Ocean Species:
1a. Thorns absent on snout tip, and along rostral ridge and interdorsal space (Fig. 191) .

Cruriraja durbanensis

1a. Thorns present on snout tip, and along rostral ridge and interdorsal space (Fig. 192)

## Cruriraja hulleyi



Fig. 191 Cruriraja durbanensis


Fig. 192 Cruriraja hulleyi

## Cruriraja hulleyi Aschliman, Ebert, and Compagno, 2010

Cruriraja hulleyi Aschliman, Ebert, and Compagno, 2010, Copeia, 2010 (3): 364, figs. 1, 2a-b, 3a-b, tab. 1. Holotype: SAM $37618,514 \mathrm{~mm}$ total length, mature male, R/V Africana cruise 122, south coast hake biomass survey, station A16438 122083 3640, South Africa, $34^{\circ} 29.6^{\prime} \mathrm{S}, 25^{\circ} 28.3^{\prime} \mathrm{E}, 308$ m, 1 July 1994.

Synonyms: Raia parcomaculata von Bonde and Swart, 1923: 9, PI. 21, fig. 2. Raia miraletus Barnard, 1925: 68; types of Cruriraja parcomaculata Fowler, 1941: 375; KwaZulu-Natal, South Africa, also including Raia parcomaculata von Bonde and Swart, 1923, in synonymy. Raja caudaspinosa Norman, 1935: 43, west of Cape Town, South Africa. Raja parcomaculata Norman, 1935: 46, KwaZulu-Natal, South Africa, doubtful species. Cruriraja parcomaculata, Bigelow and Schroeder, 1948: 550, KwaZulu-Natal, South Africa; Bigelow and Schroeder, 1953: 315, KwaZulu-Natal, South Africa; Bigelow and Schroeder, 1962: 199, KwaZulu-Natal, South Africa; Smith, 1964: 288, pls. 26-27, Algoa Bay, SouthAfrica; Hulley, 1970: 157, PI. 1a, figs. a, b, off Durban, KwaZulu-Natal, South Africa; Hulley, 1972a: 86-96, figs. 58-59; Hulley, 1986: 117, fig. 25.3, Lüderitz, Namibia, to Durban, South Africa; Compagno, Ebert and Smale, 1989: 84, ill., Lüderitz, Namibia, to Durban, South Africa; Raia smithi, Smith, 1949: 66, fig. 68, South Africa, thought to be the young of Bathyraja smithii; Cruriraja 'parcomaculata', sensu Smith, 1964. Compagno and Ebert, 2007: 141-143, fig. 8b; Lüderitz, Namibia, to Algoa Bay and possibly to East London, SouthAfrica; Ebertand Compagno, 2007: 122; Ebert, Compagno and Cowley, 2008:84-86, figs. 2a, 3a.

## Other Combinations: None.

FAO Names: En - Roughnose legskate; Fr Raia á nez hérissé; $\mathbf{S p}$ - Raya nariz áspera.

Field Marks: A rough-nosed legged skate with an acute snout covered with large conspicuous light coloured thorns that are also around the eyes, on shoulders, and in multiple rows from the nape to the first dorsal fin. Colour dorsally is a light brown often with scattered darker and lighter spots, very conspicuous on young, but obscure in adults; ventral surface white.

Diagnostic Features: Disc quadrangular, width slightly greater than disc length; snout tip pointed, lacking distal process or filament; disc anterior margins to spiracles weakly convex with short concavity near snout tip, weakly concave from spiracles to rounded apices of pectoral fins (more concave in adult males), becoming more convex on posterior margins; snout angle about $80^{\circ}$ to $90^{\circ}$. Eye diameter about equal to inter-orbital space. Spiracle small, diameter about 0.5 to 0.8 times eye length; opening sub-rhomboidal in


Fig. 193 Cruriraja hulleyi
shape. Nostril sub-circular to oval; nasal anterior flap forming an open posterolaterally directed tube, mostly obscured by nasal curtain; posterior lobes well developed meeting medially to form nasal curtain; distal ends sub-rectangular with fringe on posterior margin. Mouth weakly arched; teeth arranged in quincunx, sexually dimorphic, with a single acute cusp in adult males, blunt and flat in juveniles and females. Tooth row counts 37 to 47 upper jaw, 38 to 39 lower jaw. Pelvic fins large, anterior lobes well developed with deep incised separation from posterior lobes. Tail broad anteriorly, tapering posteriorly to first dorsal fin; width at pelvic-fin insertions about two times width at first dorsal-fin origin; tail moderately long, length about $61 \%$ of total length; lateral tail folds long and well developed. Dorsal fins medium-sized, similar in shape with rounded apices, first dorsal fin slightly higher and with slightly longer base length that second dorsal fin. Skin smooth except for thorns on dorsal surface; ventral disc surface smooth and lacking thorns. Thorn pattern on dorsal surface (adult): 4 to 5 small rostral thorns; 9 regularly spaced orbital thorns arranged in semi-circular pattern from preorbit to anterior margin of spiracle; 2 post-orbital thorns; 1 to 3 nuchal thorns; scapular thorns in close-set, irregular patches, and numbering from 3 to 9 ; mid-back thorns arranged in 1 to 5 linear rows followed by tail thorns usually in 5 linear rows; 39 to 47 predorsal thorns; 6 inter-dorsal thorns; adult males with malar thorns ranging from 1 to 5 (at greatest distance) rows of short strongly recurved thorns and alar thorns ranging from 1 to 5 longitudinal rows each with 16 columns. Vertebral counts: predorsal vertebral counts 66 to 69 . Spiral valve counts 6 to 7 . Maximum total length is about 59 cm . Colour: dorsal surface yellowish to sandy brown, lighter near fin margins and lateral to rostral cartilage; conspicuous dark brown blotches and spots in juveniles; ventral surface creamy to white.

Distribution: The roughnose legskate occurs in the Southeastern Atlantic and Southwestern Indian Oceans from Lüderitz, Namibia to Algoa Bay, and possibly East London, South Africa.

Habitat: A moderately common species of the outer continental shelf and upper slope from 39 to 545 m , but most common between 200 and 500 m .

Biology: Oviparous with no defined reproductive seasonality, and females with egg cases in utero year-round. Egg cases small, vase-like, measuring less than 50 mm long excluding horns; surface coarsely striated and with narrow lateral keels; posterior horns about $45 \%$ longer than anterior horns, tapering to thin tips curving inwards and with fine attachment fibers; anterior horns hook-shaped, with acute tips.

Diet mainly consists of mysids, and other crustaceans including euphausids and amphipods, cephalopods and small teleosts relatively unimportant.

Size: Maximum total length 59.4 cm (female); females mature between 46 and 50 cm ; male maximum length 58 cm , size at maturity between 45 and 50 cm . Females and males mature at a slightly smaller size on the south coast compared to the west coast of South Africa. Size at birth uncertain, smallest free-swimming individual was 9.6 cm total length.

Interest to Fisheries and Human Impact: A common bycatch of trawl fisheries, but discarded due to its small size.


Fig. 194 Cruriraja hulleyi
Known distribution

The conservation status of this species was assessed as Least Concern, but as Cruriraja parcomaculata. As discussed below, $\boldsymbol{C}$. parcomaculata is now known to be a senior synonym of $\boldsymbol{C}$. triangularis and what was formerly referred to C. parcomaculata from the west and south coasts of Southern Africa is now known to be C. hulleyi.

Local Names: Hulley's skate.
Remarks: Aschliman, Ebert and Compagno (2010) clarified the taxonomic status of this species, which had been incorrectly referred to as Cruriraja parcomaculata, a Southwestern Indian Ocean species originally described by von Bonde and Swart (1923). Smith (1964) in describing Cruriraja triangularis stated that the type material of C. parcomaculata was lost, but in fact the type material for $\boldsymbol{C}$. parcomaculata had not been lost and had been deposited into the fish collection at the British Museum Natural History (BMNH 1935.7.14.1). In comparing the type material of $\boldsymbol{C}$. parcomaculata with the two common Cruriraja species it is clear that Smith (1964) had misidentified the species described by von Bonde and Swart (1923), and in effect renamed C. parcomaculata as C. triangularis. In the same publication Smith (1964) redescribed what he believed was C. parcomaculata (now = hulleyi), but which was in fact an undescribed species. Most subsequent authors since Smiths' description had perpetuated this mistake until Compagno and Ebert (2007) recognized this error and the need to formally redescribe Smiths' C. parcomaculata.

This is one of three legged skates of the genus Cruriraja that occurs in the waters off Southern Africa. Of the other two species, Cruriraja parcomaculata is commonly taken in bottom trawls off the east coast of South Africa and the other
species $\boldsymbol{C}$. durbanensis is known only from two specimens taken in deepwater off the west coast of South Africa.
Literature: von Bonde and Swart (1923); Smith (1964); Hulley (1970, 1972a); Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); Ebert, Cowley and Compagno (1991); Compagno and Ebert (2007); Ebert and Compagno (2007); Ebert, Compagno and Cowley (2008); Aschliman, Ebert and Compagno (2010); Ebert (2014); Aschliman and Ebert (In press).

## Dipturus Rafinesque, 1810

Genus: Dipturus Rafinesque, 1810, Caratt. Gen. Spec. Sicil.: 16.
Type Species: Raja batis Linnaeus, 1758 by original designation.
Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 4.
Synonyms: Raja (Dipturus) as subgenus (Stehmann, 1970).
Field Marks: Most striking external morphological characteristics are the usually long and pointed snout (internarial width less than $70 \%$ of prenarial snout length), along with markedly concave anterior disc margins. Except for small juveniles, thorns on disc are usually 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. Colour uniformly grey, brown to dark brown to blackish; ventral surface with an irregular pattern of numerous mucus and sensory pores 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.

Diagnostic Features: Disc rhombic-shaped, moderate to very broad, with outer corners of disc sharply rounded to angular. Snout long to very long, generally exceeding $60 \%$ of head length, acutely angled, and moderate to greatly produced beyond anterior margin of disc. Eyes relatively small, diameter less than interorbital distance. Pelvic fins bilobed and continuous, with anterior lobe moderate to very long and approaching length of posterior lobe. Tail relatively short to moderately long and moderately narrow to narrow at base and slightly tapering to slightly broadening distally. Upper disc mostly free of denticles and with few moderately small to small thorns. Thorn pattern on dorsal surface: orbital thorns present or absent, if present 1 pre-orbital thorn to about 9 thorns on orbital margin; thorns either present or absent on remainder of disc, if present 1 to several thorns may occur on each shoulder girdle, on nuchal region and in single row from nuchal region to base of tail; usually males with 1 thorn row, females with 3 to 5 rows along midline of tail to origin of first dorsal fin. Vertebral counts: pre-dorsal caudal vertebral counts 42 to 72 ; trunk vertebral counts 30 to 35 . Maximum total length may reach over 200 cm . Colour: dorsal surface usually grey, dark brown to almost black and plain or maybe vaguely patterned; ventral surface greyish white to greyish brown with ampullary pores and sometimes ampullary canals darkly pigmented.

Remarks: About 47 species, four of which occur in the Southeastern Atlantic Ocean deep-sea.
The following Key to Species is modified after Aschliman and Ebert (2014) and Ebert (In press).

Key to Deep-sea Southeastern Atlantic Ocean Species:
1a. Disc ventral surface broadly covered with denticles (Fig. 195). . . . . Dipturus springeri

1b. Disc ventral surface not broadly covered with denticles, although denticles may occur on snout and along anterior margin . 2

2a. Tail relatively short, distance from snout tip to posterior margin of cloaca equal to or greater than sum of distance from posterior margin of cloaca to tip of tail plus distance from tip of snout to anterior margin of upper jaw (Fig. 196).

Dipturus doutrei


Fig. 196 Dipturus doutrei

3a. Snout very long, greatly produced, distance from snout tip to anterior margin of orbit about 5.5 times interorbital distance; preoral snout length about 3 times internarial distance (Fig. 197).

Dipturus stenorhynchus

3b. Snout moderately long to long, moderately produced to produced, distance between snout tip and anterior margin of orbit about 3.0 to 4.5 times interorbital distance; preoral snout length about 2.5 or fewer times internarial distance (Fig. 198)


Fig. 197 Dipturus stenorhynchus


Fig. 198 Dipturus pullopunctatus

## Dipturus pullopunctatus (Smith, 1964)

Raia pullopunctata Smith, 1964, Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening, Kjøbenhavn, 126: 285, pl. 25. Holotype: SAIAB [formerly RUSI] 37, 205 mm total length, juvenile male, Algoa Bay, Eastern Cape Province, South Africa, $31^{\circ} 7^{\prime} \mathrm{E}, 29^{\circ} 59^{\prime} \mathrm{S}, 183 \mathrm{~m}$.

Synonyms: Raia batis (non Linneaus) Thompson, 1914: 156; von Bonde and Swart, 1923: 3; Barnard, 1925: 70. Raia strabuliforis von Bonde and Swart, 1923: 12. Raja batis Norman, 1935: 39. Raja campbelli Wallace, 1967: 24, fig. 12. Raja pullopunctata Hulley, 1966: 505, figs. 4-5; Hulley, 1970: 166, pl. 2a-b, figs 6a-c; Hulley, 1972a: 86, figs. 58-59; Hulley, 1986: 123, fig. 25.15, pl. 6; Compagno, Ebert and Smale, 1989: 92, ill.; Compagno and Ebert, 2007: 139.

## Other Combinations: None.

FAO Name: En - Slime skate.
Field Marks: A longnose skate with an elongated, acutely triangular snout, a stout tail, about equal to body length, and not conspicuously swollen along mid-section; disc with rounded corners and smooth underside except for small denticles on edges and tip of snout; thorns on nape and midback to first dorsal fin. Colour is a medium brown above, with large conspicuous brown blotches on upper base of each pectoral fin and with numerous smaller dark spots; grey ventrally.

Diagnostic Features: Disc rhombicshaped, broad, 1.2 to 1.4 times as wide as long, and with lateral corners angled with slightly rounded tips; snout moderately produced, length 15 to $17 \%$ of total length, acutely triangular but not attenuating from the anterior margin of disc; snout angle in


Fig. 199 Dipturus pullopunctatus front of spiracles about $92^{\circ}$ to $108^{\circ}$. Mouth broad, slightly arched; nasal curtain not fringed; teeth sexually dimorphic, with a single large cusp on adult males, more or less flattened in females; arranged in quincunx. Tooth row counts 53 to 58 upper jaw, Anterior pelvic-fin lobes of moderate length, not extending to posterior margin of posterior lobe. Tail moderately long, about equidistant from tip of snout to posterior margin of cloaca, and narrow at base, slightly attenuated distally. Dorsal fins separated. Skin mostly smooth. Thorn pattern on dorsal surface differs between adults and juveniles: juvenile arrangement with 2 preorbital thorns; 1 postorbital thorn; 1 median nuchal thorn; 8 to 12 mid-dorsal thorns from above vent to first dorsal-fin origin; 1 interdorsal thorn; dorsal surface otherwise smooth above; adult arrangement with 5
to 8 orbital thorns; 1 to 2 median nuchal thorns, usually very large; 26 to 27 mid-dorsal thorns from above vent to first dorsal-fin origin; 3 to 4 interdorsal thorns; a single, irregular row of lateral caudal thorns ( 15 to 20 ) on each side of tail, from about posterior edge of pelvic fins to interspace between dorsal fins; dorsal surface otherwise smooth above; ventral surface with spinules on snout tip, anterior margins of disc, and internasal region. Total pectoral radial counts not available. Vertebral counts: predorsal vertebral counts 50 to 58 . Spiral valve counts not available. Maximum total length is at least 124.5 cm . Colour: dorsal surface light brown to biscuit, especially in juveniles, but maybe lost in adults, usually with a very large dark blotch at each pectoral-fin base; occasionally darker, with numerous darker spots and blotches; ventral surface greyish, with dark pigmented mucus pores appearing as black spots and streaks.

Distribution: Southern Africa, occurring from Lüderitz and possibly Walvis Bay, Namibia to at least Algoa Bay, South Africa. Records of it from off Durban, South Africa need to be confirmed as they may be based on Dipturus campbelli.

Habitat: A common skate, mostly in South African waters, of the outer continental shelves and upper slopes from 15 to 457 m depth, but appears to be most common between 200 and 300 m .

Biology: Oviparous, with large-sized egg cases measuring over 130 mm , excluding horns, with a striated surface covered with dense fibers, and with broad lateral keels, making up about $19 \%$ of the maximum width. There does not appear to be a defined breeding season as females with egg cases in utero have been observed year-round. The age at maturity has been estimated at about nine years, with an estimated longevity of 18 years. The diet of this skate mostly includes small bony fishes and to a less extent crustaceans; large individuals, over 70 cm total length consume large and more mobile fish species such as hake, Merluccius species.

Size: Maximum total length 124.5 cm (female); size at maturity differs between the west and south coasts of South Africa; west coast males mature at 96.6 cm total length and on the south coast at about 87.9 cm total length. Females on the west coast mature at about 100 to 112 cm total length, while on the south they mature at about 81.2 cm total length. Size at birth uncertain, possibly less than 19 cm total length; smallest known free-swimming individuals measured 23 and 28 cm total length.


Fig. 200 Dipturus pullopunctatus

Interest to Fisheries and Human Impact: This species is taken as bycatch in bottom trawl fisheries, but there is no information on trends in catches of this species where it is known to occur.

The conservation status of this endemic skate is Least Concern due extensive areas of its range being untrawlable.
Local Names: None.
Remarks: Dipturus pullopunctatus and D. campbelli were referred to collectively by earlier researchers as the European Raja batis (Thompson, 1914; von Bonde and Swart, 1923) until Smith (1964) distinguished D. pullopunctatus from R. batis. Hulley (1966) confirmed Smith's distinction, but noted that two large "black bellied" skates occurred in South African waters, one being D. pullopunctatus and the other being $\boldsymbol{D}$. campbelli that was later described by Wallace (1967). These two species were synonymize by Hulley (1970) who did not find any substantial differences between the two species. The present author (D.A. Ebert) and L.J.V. Compagno (unpubl. data) later revisted the issue and concluded that these two species were indeed separable and resurrected D. campbelli (Compagno, Ebert and Smale, 1989). Also, examination of the reproductive biology of these two species further supports their separation (Ebert, Compagno and Cowley, 2008).

Literature: Smith (1964); Wallace (1967); Hulley (1970, 1972a); Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); Ebert, Cowley and Compagno (1991); Smale (2004a); Compagno and Ebert (2007); Ebert, Compagno and Cowley (2008); Aschliman and Ebert (In press); D.A. Ebert (unpubl. data).

## 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 Deep-sea Southeastern Atlantic Ocean Species: 2.

Synonyms: Raja (Leucoraja) as subgenus (Stehmann, 1970).
Field Marks: Disc subcircular, tail length about equal to or somewhat longer than body length, median row of thorns on back and trunk and along tail becoming gradually reduced with growth and completely disappearing in large adults, concurrently one or more parallel rows of thorns increasing in size, orbital thorns set as continuous half-rings, with additional thorns over nape and shoulder region forming a triangle. Colour on dorsal surface ranges from a light to dark background and with a plain to colorful pattern of spots, rings, ocelli or reticulations.

Diagnostic Features: Disc heart-shaped, moderate to relatively broad, usually greater than $52 \%$ of total length, with outer corners narrowly to broadly rounded. Snout moderately short and broad, with tip slightly produced beyond anterior margin of disc as a small oblique process. Orbits moderately sized, diameter slightly less to slightly greater than interorbital distance. Pelvic fins bilobed and continuous, with anterior lobe usually much shorter than posterior lobe, rarely about as long as posterior lobe. Tail relatively short, generally less than $60 \%$ of total length, and relatively broad at base and attenuated distally. Dorsal fins rather large and confluent or separated by a distance less than half of first dorsal-fin base. Dorsal surface sparsely to densely covered with coarse denticles, generally more dense in juveniles than in adults. Moderate sized thorns on tip of snout, along orbital rim, medial to spiracles, forming triangular patch on nuchal and scapular regions, and along mid belt of disc and tail in several fairly regular rows, with mid row along mid length of disc and tail reduced or absent in large juveniles and adults. Vertebral counts: predorsal caudal vertebral counts 64 to 81. Adult maximum total length about 40 to 150 cm . Colour: dorsal surface tan to dark grey or brown, and either plain or patterned with spots, bars or ocelli; ventral surface light and either plainly coloured or with dark blotches.

Remarks: The genus comprises 13 species, with a few more known but not yet described species. Two species are known to occur in the Southeastern Atlantic Ocean. The genus arrangement follows Aschliman and Ebert (In press).

## Key to Deep-sea Southeastern Atlantic Ocean Species:

1a. Anterior pelvic-fin lobe about as long as posterior lobe; dorsal fins confluent at base; tooth rows about 38 (Fig. 201) .

## Leucoraja compagnoi

1b. Anterior pelvic-fin lobe considerably shorter than posterior lobe; dorsal fins separated by small interspace; tooth rows 43 to 69 (Fig. 202) . . . Leucoraja wallacei


Fig. 201 Leucoraja compagnoi


Fig. 202 Leucoraja wallacei

## Leucoraja wallacei (Hulley, 1970)

Raja wallacei Hulley, 1970, Ann. S. African Mus., 55(4): 210, pl. 12, figs. 19. Holotype: ORI B. 126, 842 mm total length, adult male, off Cape Town, $34^{\circ} 10^{\prime} \mathrm{S}, 17^{\circ} 45^{\prime} \mathrm{E}, 292 \mathrm{~m}$.

Synonyms: Raja barnardi (non Norman) Wallace, 1967: 39, figs. 20-21. Raja (Leucoraja) wallacei Hulley, 1972a: 77.
Other Combinations: None.

FAO Name: En - Yellowspotted skate.
Field Marks: A distinctive medium-sized skate with a relatively short, blunt, broad snout, moderately broad disc, with 2 to 4 very rough rows of thorns from mid-back to first dorsal fin, disc apices broadly rounded and tail longer than the disc length. Colour is a yellowish-brown with very distinctive bright yellow spots, often in rosettes and whorls, sometimes forming eye-like markings on pectoral-fin bases; ventral surface mostly white.

Diagnostic Features: Disc moderately broad, 56 to $62.5 \%$ of total length, 1.2 to 1.3 times as wide as long, with outer corners broadly rounded. Snout relatively short in length, slightly produced, obtuse, with rounded terminal process; snout length 9.6 to $11 \%$ of total length, 2.3 to 3.1 times interorbital distance; angle of snout anterior to spiracles $110^{\circ}$. Nasal curtain fringed. Mouth slightly arched. Tooth row counts in upper jaw 59 to 67; teeth sexually dimorphic, with male cusps
 sharper than those of females. Anterior pelvicfin lobes relatively short, considerably shorter than posterior lobes. Tail relatively short, 53 to $55 \%$ of total length, and moderately broad at base and attenuated distally. First dorsal fin larger than second, separated by a small space. Between 7 to 10 small thorns on orbital rim, 2 to 3 supraspiracular thorns, triangular patch of thorns over nuchal and scapular region, mid-dorsal thorns either absent or about 34 from nuchal region to first dorsal-fin origin, flanked by an additional row on each side, becoming two flanking rows at pelvic fins to first dorsal-fin origin; no interdorsal thorns. Mid row of thorns on disc and tail either small, partially absent or totally absent in large juveniles and adults. Dorsal surface with spinules on snout tip, anterior margin of disc and tail; below, spinules on snout tip and anterior margin of disc. Vertebral counts: predorsal caudal vertebrae 64 to 74 . Spiral valve counts not available. Moderate-sized skate, maximum size 96.3 cm total length. Colour: yellowish-brown above with scattered, bright yellow spots sometimes in rosettes or whorls; mottled eyespot at the base of each pectoral fin; lower surface pale, with a single, dark blotch on tip of anterior lobe of pelvic fins.

Distribution: The yellowspotted skate occurs in the Southeastern Atlantic and Southwestern Indian Oceans, from southern Namibia to southern Mozambique.

Habitat: A little known skate with a patchy distribution off the west and south coasts of South Africa. It occurs from the outer continental shelf to upper slopes from 73 to 517 m deep, with most records from between 150 and 300 m . The distribution of this species is bimodal off the west and southeast coasts of South Africa, with the highest concentrations between the Orange River and Cape Columbine, and between Cape Point and Cape Agulhas to Algoa Bay.

Biology: Oviparous, with medium-sized egg cases measuring about 80 to 83 mm , excluding horns, with a surface of very fine striations, smooth, no fibres or lateral keels, and a posterior horn length nearly twice that of the anterior horns. There does not appear to be a defined breeding season as females with egg cases in utero have been observed year-round. The age at maturity has been estimated at about seven years, with an estimated longevity of 15 years. The diet of this skate mostly includes prawns and small bony fishes including dragonets and ophichthid eels.

Size: Maximum total length is 87.0 cm (males) and 96.3 cm (females); size at maturity is between 64 and 77 cm for males and 64 to 73 cm for females. Size at birth is uncertain, but based on the smallest free-swimming individuals it is less than 16 cm .


Fig. 204 Leucoraja wallacei
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Interest to Fisheries and Human Impact: Of no commercial fishing interest, this moderate-sized skate species is a common bycatch species, but is usually discarded.

The conservation status of this skate is Least Concern.
Local Names: Yellowspotted skate, Blancmange skate, Witpoeding-rog.
Remarks: The above genus and species accounts are modified after Ebert and Stehmann (2013), Aschliman and Ebert (In press), and Ebert (2014).

Literature: Hulley (1970, 1972a); Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); Ebert, Cowley and Compagno (1991); Compagno and Ebert (2007); Ebert and Compagno (2007); Ebert, Compagno and Cowley (2008); Smale (2009b); Ebert (2014); Aschliman and Ebert (In press).

## Malacoraja Stehmann, 1970

Genus: Malacoraja Stehmann, 1970, Arch. FischWiss. 21(2): 151-152.
Type Species: Raja mollis Bigelow and Schroeder, 1950 by original designation equals Malacoraja spinacidermis.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 1.

Synonyms: Raja (Malacoraja) Stehmann, 1970 as subgenus.
Field Marks: See Diagnostic Features below.
Diagnostic Features: Disc heart-shaped, with snout moderately long and pointed; anterior disc margins straight and in mature males weakly undulated. Tail length equal to, or slightly less than body total length. Upper disc surface densely covered with velvet-like dermal denticles, similar but coarser on tail; ventral surface at least edged with, or completely covered with dermal denticles. Usually with a median row of 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. Colour of dorsal surface usually plain whitish, medium greyish-brown or dark grey to brown; ventral surface plain whitish often with dark brown blotches, becoming completely dark brown with growth.

Remarks: This genus comprises four species, all of which occur in the Atlantic Ocean, but only one species occurs in the Southeastern Atlantic Ocean.

## 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; $\mathbf{S p}$ - Raya piel áspera.

Field Marks: A moderate-sized deepwater skate, with a heart-shaped disc, 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 surface densely covered with fine dermal denticles, velvetlike to touch, but underside smooth except for usually totally prickly tail. Colour of dorsal surface from light

greyish-brown in smaller individuals to darker grey in adults, with semi-translucent areas flanking rostrum; ventral surface 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 matching the colour of underside of tail, but creamy-white patches remain medially.

Diagnostic Features: Disc evenly inverse heart-shaped, 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 posterior 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 become 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. Vertebral counts: total vertebral counts 88 to 93 , trunk vertebral count 28 , predorsal vertebral counts 60 to 65 . Spiral valve counts not available. Maximum total length is about 71 cm . 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: Southern Namibia to Cape Point South Africa. North Atlantic: Western North Africa, Rockall Trough, Iceland-Faroe-Ridge, off south Iceland, around southern Greenland and across the Davis Strait to off the Grand Banks, Scotian slope and Georges Bank.

Habitat: Benthic in deepwater between 475 and 1570 m, usually deeper than 1000 m depth, and adults may live deeper than 1500 m and down to the abyssal plains.

Biology: Oviparous, egg cases small, partially described from South African specimens. The diet of this skate includes crustaceans, mainly shrimps, and small benthic fishes.

Size: A moderately small skate, with a maximum total length of about 71 cm . Size at maturity is about 59 cm for females, and 58 cm for males. Size at birth uncertain, but the smallest free-swimming specimen was 12.7 cm in length.

Interest to Fisheries and Human Impact: A rare deepwater skate only sporadically taken by deep-sea fisheries as bycatch and discarded or preserved for scientific reference.

The conservation status is Least Concern.
Local Names: Roughskin skate; Ruwevel-rog (Afrikaans).


Fig. 206 Malacoraja spinacidermis
$\square$ Known distribution
Remarks: Raja mollis Bigelow and Schroeder, 1950
(= M. spinacidermis) is the type species of the genus Malacoraja Stehmann, 1970. The species was described from off Cape Town, South Africa, but is also known to occur in the North Atlantic where it was synonymized with Malacoraja mollis. North Atlantic and southern African specimens should be closely examined to confirm if they are the same species. The above genus and species accounts are modified after Ebert and Stehmann (2013) and Ebert (2014).

Literature: Bigelow and Schroeder (1953); Hulley (1970, 1972a); Hulley and Stehmann (1977); Stehmann and Bürkel, in: Whitehead et al. (1984); Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); Ebert, Cowley and Compagno (1991); Stehmann (1995); Compagno and Ebert (2007); Ebert and Compagno (2007); Smale and Kulka (2007); Ebert, Compagno and Cowley (2008); Ebert and Stehmann (2013).

## 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 Deep-sea Southeastern Atlantic Ocean Species: 1.

Synonyms: Breviraja (partim), Neoraja (Neoraja) subgenus.
Field Marks: Dwarf-sized skates with heart-shaped disc, short bluntly angled snout, tail usually 55 to $60 \%$ of total length, upper disc and tail with dense coverage of fine dermal denticles, underside of tail at least edged with, or totally covered with dermal denticles and typically a median thorn row 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. Colour is a brown to greyish brown above; light with wide margin of brown to greyish brown below.

Diagnostic Features: Disc heart-shaped and relatively narrow, usually 50 to $60 \%$ of total length, with broadly rounded outer corners; anterior margin of disc strongly concave to straight; anterior most extension of pectoral fin abutting or nearly abutting tip of snout, not separated from snout by semi-translucent area. Snout moderately short and broadly rounded or angular, usually 8 to $10 \%$ of total length, with tip slightly produced beyond anterior margin as a small triangular process. Eyes relatively large, diameter equal to or greater than inter-orbital distance. Pelvic fins bilobed and continuous, with anterior lobe relatively long but failing to reach posterior margin of posterior lobe. Tail moderately long, usually 55 to $60 \%$ of total length, moderately slender at base and tapering distally. Dorsal surface densely covered with fine denticles. Thorn pattern: small thorns on orbital margin, on nuchal and scapular region but not forming triangular patch, along back of disc and on at least basal half of tail in one to three irregular rows. Vertebral counts: predorsal caudal vertebral counts 65 to 74 . Very small skates growing to a maximum total length of about 38 cm . Colour: a light ochre to medium greyish-brown above, 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, all of which occur in the Atlantic Ocean, with one species range extending just into the Eastern Cape Province, South Africa.

## Neoraja stehmanni (Hulley, 1972)

Breviraja stehmanni Hulley, 1972b, Ann. S. African Mus., 60(9): 254, figs. 1-5. Holotype: SAM 26636, 354 mm total length, adult male, $33^{\circ} 53.7-57.3^{\prime} \mathrm{S}, 17^{\circ} 23.9-22.2^{\prime} \mathrm{E}, 640 \mathrm{~m}$.
Synonyms: None.
Other Combinations: None.
FAO Name: En - African pygmy skate.
Field Marks: A dwarf skate with a bluntly pointed snout and very large, close-set eyes, a tail length greater than disc length in adults, an angular disc with rounded corners, small to moderate sized orbital thorns, scapular thorns, and an interrupted row of back and tail thorns. Colour is a brownish grey above, paler ventrally, with 6 to 7 darker bands on tail.

Diagnostic Features: Disc heart-shaped, length about 54 to $58 \%$ of total length, with broadly rounded outer margins, and anterior edges more undulated in adult males than females; snout moderately short, obtuse, 8.9 to $11.5 \%$ of total length, 2.9 to 3.8 times inter-orbital space; snout angle about $115^{\circ}$ to $130^{\circ}$. Anterior pelvic-fin lobes relatively long, nearly reaching posterior margin of posterior lobes. Tail relatively long, 58 to 60\% of total length, moderately slender at base and attenuated distally. Eyes close-set, orbit diameter slightly greater than inter-orbital space. Spiracles


Fig. 207 Neoraja stehmanni
small. Nasal curtain fringed. Mouth weakly arched; teeth arranged in quincunx, sexually dimorphic, with a single long acute cusp in adult males, blunt and flat in juveniles and females. Tooth row counts 38 to 44 upper jaw, counts not available for lower jaw. Dorsal fins continuous, similar in shape and size. Disc covered with denticles above, naked below. Thorn pattern on dorsal surface (adult): 2 to 10 small to moderate sized orbital thorns arranged in semi-circular pattern from preorbit to anterior margin of spiracle; 1 to 4 nuchal thorns; 1 scapular thorn on each shoulder; mid-back and tail thorns arranged in single row of 11 to 39 thorns usually interrupted between the pectoral and pelvic girdles and extending to mid-length or two-thirds tail length; adult males with alar and malar thorns; ventral surface smooth, without thorns. Vertebral counts: predorsal vertebral counts 65 to 74 . Spiral valve counts not available. Maximum total length is about 38 cm . Colour: greyish to greyish-brown above; disc with irregular darker blotches and scattered paler spots; tail with 6 to 7 irregular, dark crossbars, either continuous across dorsal surface or interrupted, the two most posterior crossbars nearly black and passing through first and second dorsal fins. Lower surface of disc pale but tip of snout with black spot; thin darker areas along anterior margin of pectorals, wider along posterior margins and margins of pelvic fins; dusky, irregular areas sometimes between nostrils, around mouth, between gills and on belly.

Distribution: Only recorded off South Africa, from southwest of the Orange River mouth, Western Cape Province, to Algoa Bay, Eastern Cape Province.

Habitat: A little known skate with a patchy distribution on the west and south coasts of South Africa. It occurs from the outer continental shelf to upper slopes from 102 to 1025 m deep, with most records from below 600 m . The distribution of this species is unusually localized compared to other offshore southern African skates, but it may be that they have very specialized habitat requirements. Several records of this species have come from around offshore seamounts and may suggest an association with this habitat.

Biology: Oviparous, with very small, smooth surfaced egg cases with broad lateral keels, but lack attachment fibers. Nothing is known about its reproductive cycle or age. The diet of this skate is poorly known, but includes small benthic shrimps.

Size: Maximum total length is 37.6 cm (males) and 36.8 cm (females); size at maturity is about 31 cm for males and 29.5 cm for females. Size at birth is uncertain, but based on smallest free-swimming individuals it is less than 15 cm total length.

Interest to Fisheries and Human Impact: Of no commercial fishing interest, this rather small skate species is not likely taken in large numbers given its size and patchy distribution. Probably incidentally caught by hake bottom trawlers.


Fig. 208 Neoraja stehmanni
$\square$ Known distribution

The conservation status of this skate is Data Deficient.
Local Names: South African pygmy skate.
Remarks: The above genus and species accounts are modified after Ebert and Stehmann (2013), Aschliman and Ebert (In press), and Ebert (2014).

Literature: Hulley (1972a, b); Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); Ebert, Cowley and Compagno (1991); Smale (2004b); Compagno and Ebert (2007); Ebert and Compagno (2007); Ebert, Compagno and Cowley (2008); Ebert and Stehmann (2013); Ebert (2014); Aschliman and Ebert (In press).

## Rajella Stehmann, 1970

Genus: Rajella Stehmann, 1970, Arch. FischWiss. 21(2): 151.
Type Species: Raja fyllae Lütken, 1887 by original designation.
Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 5.
Synonyms: Raja (Rajella), as subgenus (Stehmann, 1970).

Field Marks: Disc usually subrhombic, with outer corners rounded to angular, snout short and bluntly angled, or moderately elongated and pointed, median thorn rows on back of trunk and along tail range from one to several rows in parallel; 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. Colour is mostly uniformly dark or light.

Diagnostic Features: Disc heart-shaped to rhombic-shaped and narrow to moderately narrow, generally 49 to $61 \%$ of total length, with outer corners obtusely angled to broadly rounded. Snout moderately long to moderately short, acutely angled to broadly rounded and slightly to moderately produced beyond anterior margin of disc. Eyes of moderate size, diameter slightly greater to slightly less than inter-orbital distance. Pelvic fins bilobed, continuous, with anterior lobes short to moderately long but considerably shorter than posterior lobes. Tail moderately long to long, 51 to $60 \%$ of total length, and moderately broad at base and attenuated distally. Dorsal surface largely covered with denticles and relatively densely covered with moderate to large sized thorns; usually a complete row of thorns on orbital rim, triangular patch of thorns on nuchal shoulder region, and one to several rows of thorns extending from shoulder region to origin of first dorsal fin, with thorns of mid-row equal in size or larger than those of lateral rows, and one to several thorns between dorsal fins. Vertebral counts: predorsal caudal vertebral counts 55 to 73 . Maximum total length to about 90 cm . Colour: dorsal surface uniformly light grey, brown to brownish black; ventral surface whitish to nearly black.

Remarks: The genus currently has 17 or 18 nominal species described with several additional species awaiting formal description. Five species occur in the Southeastern Atlantic Ocean.

Key to Deep-sea Southeastern Atlantic Ocean Species:

1a. Two rows of thorns along mid-dorsal region of back and tail; median row absent; no thorns above rostral cartilage (Fig. 209)

Rajella ravidula

1b. Three or more rows of thorns along mid-dorsal region of back and tail; median row either continuous or interrupted 2

2a. Tail length from cloaca to tip much longer than disc length from snout tip to cloaca (Fig. 210) . . . Rajella caudaspinosa

2b. Tail length from cloaca to tip about equal, or slightly shorter than disc length from snout tip to cloaca. 3

3a. Median row of thorns along back reduced in size or interrupted (Fig. 211)

Rajella dissimilis

3b. Median row of thorns along back and tail continuous.


Fig. 209 Rajella ravidula

Fig. 211 Rajella dissimilis


3 or more rows of thorns along mid-dorsal region of back and tail


Fig. 210 Rajella caudaspinosa

Dorsal surface medium grey to brownish often with blackish spots


Fig. 212 Rajella leoparda


Fig. 213 Rajella barnardi

## Rajella leoparda (von Bonde and Swart, 1923)

Raia leopardus von Bonde and Swart, 1923, Fish. Mar. Biol. Surv. Union S. Africa 3 (Spec. Rept. 5): 7, pl. 20, fig. 2. Syntypes: several specimens at NHM, but only one specimen mentioned in description, 181 mm total length, 99 mm disc length, female, from RV Pickle Sta. 336, $32^{\circ} 03^{\prime} 00^{\prime \prime}$ S, $16^{\circ} 12^{\prime} 00^{\prime \prime} \mathrm{E}$, west of Lambert's Bay, Western Cape, 512 m .

Synonyms: Raia quadrimaculata ?von Bonde and Swart, 1923: 5 (Natal); Barnard, 1925: 70, pl. 4, fig. 5 (West Coast, Cape Peninsula, Saldanha Bay, 183 to 458 m); ?von Bonde, 1934: 16 (west coast of South Africa). Raia lintea Barnard, 1925: 72 (west coast off Cape Peninsula). Raia naevus Barnard, 1925: 72 (in part?, off Cape Peninsula and Saldanha Bay). Raja leopardus Norman, 1935: 37 (west of Cape Town, South Africa); Compagno, Ebert and Smale, 1989: 98, ill. ?Raja barnardi Norman, 1935: 37, fig. 14 (west of Cape Town, South Africa). Raja (Rajella) leopardus: Hulley, 1972*, 1986*; Stehmann, 1990: 46, 1995: 87; Compagno, Ebert and Cowley, 1991: 105. Rajella leopardus: McEachran and Dunn, 1998: 286; Compagno, 1999: 492; 2005; Compagno and Ebert, 2007: 135; Last and Stehmann, 2008: 135.

Other Combinations: None.
FAO Name: En - Leopard skate.
Field Marks: A large grey skate with a moderately long snout, and small, close-set eyes; tail about as long as disc length; small, inconspicuous light coloured thorns on upper disc including snout, and mid-dorsal line of thorns not reduced. Colour a medium grey to brownish above, with black scattered spots, ventral surface whitish or mottled with dusky patches.

Diagnostic Features: Disc angular with rounded outer corners, 1.1 to 1.3 times as wide as long; snout moderately long, length 2.8 to 4.4 times interorbital distance, obtusely pointed with triangular terminal process; angle anterior to spiracles $100^{\circ}$ to $110^{\circ}$. Tail about 1.1 to 1.5 in length from middle of vent to first dorsal-fin origin, thick at base. Eyes moderate in size and close-set. Mouth relatively large, with blunt teeth. Tooth count upper jaw 52 to 70 , lower jaw not available. Thorn pattern on dorsal surface (juvenile):


Fig. 214 Rajella leoparda snout and anterior margins of disc and sides of tail with spinules; 4 to 5 orbital thorns arranged in semi-circular pattern; 0 to 1 inter-orbital and supra-spiracular thorns; 1 inter-spiracular thorn; 3 to 5 median nuchal thorns; 1 to 2 scapular thorns; 25 to 30 mid-dorsal thorns from nuchal region to first dorsal-fin origin; 3 to 6 lateral tail thorns on each side of pelvic fins; dorsal fins confluent at base; (adult): snout and anterior margins of disc and sides of tail with small spines; orbital thorns arranged in semi-circular pattern with 5 to 13 inter-orbital and supra-spiracular thorns; 1 to 2 inter-spiracular thorns; 4 to 9 median nuchal thorns, forming triangular patch of 1 to 2 rows; 2 to 3 scapular thorns; 19 to 29 mid-dorsal thorns in single median row from nuchal region to first dorsal-fin origin; lateral tail thorns with 2 to 3 parallel rows flanking 1 median row along tail to first dorsal-fin origin. Vertebral counts: predorsal caudal vertebral counts 55 to 58 . Spiral valve counts not available. Maximum total length is about 93 cm . Colour: medium grey to brown above, with numerous dark spots more common in juveniles; pale below or mottled with dusky blotches and patches.

Distribution: The leopard skate occurs from Walvis Bay, Namibia to Cape Agulhas, South Africa with a few scattered records to Algoa Bay and one record from KwaZulu-Natal. Most records are from central Namibia to Cape Point, South Africa. Also present in the Eastern Central Atlantic off Mauritania, Senegal, and Guinea.

Habitat: A skate of the outer shelf and slope found at depths of 200 to 1023 m , with a few records from the outer shelf at 73 m , but with majority of records from 200 to 600 m . On the west coast of South Africa adults are most common below 700 m , while adolescent and juveniles are more common between 400 and 600 m . Rajella leoparda along with $\boldsymbol{R}$. barnardi are the two most common deep-sea skates off the west coast of Southern Africa.

Biology: Oviparous, but little else known about its reproductive cycle. Egg cases have been described as being small, about 55 mm long excluding horns, with a smooth surface, and broad feathery lateral keels extending the length of the entire egg case from horn to tip; the latter has a fibrous tendril attachment. Females with egg cases in utero have been found during the summer months.

The diet includes decapod crustaceans and teleosts including dragonets, rattails, hake, and lanternfish; also takes sea pens, cuttlefish and polychaete worms.

Size: Maximum total length is about 93 cm ; males mature at about 61 to 73 cm , and females mature at about 61 to 70 cm . Size birth is about 15 cm or less.

Interest to Fisheries and Human Impact: None, except taken occasionally as bycatch in commercial bottom trawl fisheries.

The conservation status of this skate is Least Concern due to its wide geographic distribution and lack of intensive fisheries that occur throughout its range.

Local Names: None.
Remarks: Records of this species from off KwaZuluNatal should be confirmed as they may be misidentified with Rajella barnardi.

Literature: von Bonde and Swart (1923); Hulley (1970, 1972a); Compagno, Ebert and Smale, (1989); Compagno, Ebert and Cowley (1991); Ebert, Cowley and Compagno (1991); Smale (2004c); Compagno and Ebert (2007); Ebert, Compagno and Cowley (2008); Aschliman and Ebert (In press); D.A. Ebert (unpubl. data).


Fig. 215 Rajella leoparda

### 3.3 Order MYLIOBATIFORMES - Stingrays

Order: Order Plagiostoma, Suborder Platosomia, "Groups" Dasybatoidei, Myloidei, Mobuloidei: Garman, 1913 (in part), Mem. Mus. Comp. Zool. Harvard, 36: 258, 259 (groups corresponding to infraorder or superfamily, and containing the families Dasybatidae [plus Urolophidae and Gymnuridae] and Potamotrygonidae, Myliobatidae and Rhinopteridae, and Mobulidae. Essentially separate groups for the stingrays and butterfly rays, eagle and cownosed rays, and devil rays, respectively).

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Families: 1.

Synonyms: Order Myliobatiformes, Suborder Hexatrygonoidei Heemstra and Smith, 1980, Ichth. Bull. J.L.B. Smith Inst. Ichthyol. (43): 13. Suborder of myliobatoids for the Hexatrygonidae. Order Hexatrematobatiformes Chu et al., 1981, Oceanol. Limnol. Sinica, 12(2): 111. Order of batoids for the family Hexatrematobatidae (= Hexatrygonidae). Suborder Hexatrematobatoidea Chu et al., 1981, Oceanol. Limnol. Sinica, 12(2): 111. Suborder of batoids within the Order Hexatrematobatiformes for the family Hexatrematobatidae (= Hexatrygonidae). Order Raiae, Suborder Masticura: Gill, 1872 (in part), Smithsonian Misc. Colln. (247): 22, 23 (order for all batoids, suborder for all myliobatoids). Order Hypotremi, Suborder Masticura, (group) Dasybatoidea: Gill, 1893, Natn. Acad. Sci. (U. S.) Mem. 6, 6: 130 (suborder for all myliobatoids, group ranked as infraorder or superfamily for stingrays, river rays, and butterfly rays). Order Hypotremi, Suborder Masticura, (group) Aetobatoidea: Gill, 1893, Natn. Acad. Sci. (U.S.) Mem. 6, 6: 130 (suborder for myliobatoids exclusively, group ranked as infraorder or superfamily for myliobatids, mobulids, and rhinopterids). Order Plagiostomi diplospondyli, Suborder Plagiostomi Tectospondyli, Group 2 Trygones Hasse, 1879, Nat. Syst. Elasmobr. (1): 47 (suborder for batoids, squatinids and pristiophorids, group equivalent to infraorder or superfamily for myliobatoids). Order Batoidea, Suborder Masticura, Superfamily Dasyatoidea: Whitley, 1940 (in part), Fishes Australia. Part I. Aust. Zool. Handbook: 69 (suborder exclusively for myliobatoids, superfamily for stingrays and eagle rays). Order Batoidea, Suborder Masticura, Superfamily Mobuloidea: Whitley, 1940 (in part), Fishes Australia. Part I. Aust. Zool. Handbook: 69 (suborder exclusively for myliobatoids, superfamily for devil rays). Order Batoidei, Suborder Masticura: Jordan and Evermann, 1896, Bull. U.S. Nat. Mus. 47(1): 59, 79 (exclusively for myliobatoids); Jordan, 1923 (in part), Stanford Univ. Publ., Univ. Ser., Biol. Sci., 3: 104 (for myliobatoids, with ptychodonts). Order Rajae, [group] Myliobatoidei Fowler, 1941, Bull. U. S. Natn. Mus. (100) 13: 290 (exclusive group equivalent to suborder or superfamily for myliobatoids). Order Rajae Smith, 1949, Sea fishes Southern Africa: 37, 62 (common group without subdivisions for all batoids). Order Euselachii, Suborder Hypotremata, Division Batoidei Regan, 1906a, Proc. Zool. Soc. London (1906): 724 (division ranking as infraorder or superfamily and inclusive of all batoids other than torpedinoids). Order Selachii, Group 2, Division B, Subdivision 2, Suborder Rajiformes, Tribe 2, Group Centrobatoidei: Goodrich, 1909, In R. Lankester, ed., A treatise on Zoology (9), Vertebrata Craniata: 161 (tribe equivalent to infraorder, and group equivalent to superfamily and exclusively for myliobatoids). Order Batea, Suborder Batida, Superfamily Dasybatoidea: White, 1936 (in part), Amer. Mus. Novit. (837): 5; White, 1937 (in part), Bull. Amer. Mus. Nat. Hist. 74: 38, tab. 1 (superfamily for myliobatoids, suborder also for rhinobatids, rhinids, platyrhinids, pristids, and rajoids, order for all rays apart from torpedinoids). Order Hypotremata, Suborder Batoidei: Engelhardt, 1913, Abh. math.-phys. Klasse K. Bayer. Akad. Wiss., Suppl., Beitr. Naturg. Ostasiens, 4: 101 (suborder for all living batoids except torpedinoids, order includes all living batoids). Order Euselachii, Suborder Trygoniformes: Bertin, 1939, Bull. Inst. Oceanogr. Monaco (775): 11 (suborder exclusive to myliobatoids, order for all living elasmobranchs). Order Rajiformes: Berg, 1940 (in part), Trudy Zool. Inst. Akad. Nauk SSSR, 5(2): 139 (includes all batoids except torpedinoids). Order Plagiostomi, Suborder Rajiformes or Rayiformes: Lozano y Rey, 1928 (in part), Fauna Iberica. Peces. Vol. 1: 281 (suborder for all batoids). Order Rajiformes: Lindberg, 1971 (in part), Fishes of the world (trans. 1974): 8, 260 (including all batoids other than torpedinoids); Nelson, 1976 (in part), Fishes of the world: 40 (order for all batoids; Nelson, ibid.: 41, suggests that myliobatoids could be recognized as a suborder Myliobatoidei with two superfamilies Dasyatoidae for stingrays and Myliobatoidae for eagle, cownose, and devil rays following Compagno, 1973, but doesn't utilize these taxa in his text or index). Order Rajiformes, Suborder Myliobatoidei: Nelson, 1984, Fishes of the world, ed. 2: 63 (suborder exclusively for myliobatoids, order for all batoids). Order Rajiformes, Suborder Trygonoidei: Berg and Svetovidov, 1955, Trudy Zool. Inst. Akad. Nauk SSSR, 20: 73 (suborder exclusive for myliobatoids, order for all batoids except torpedinoids). Order Myliobatiformes: Rass and Lindberg, 1971, J. Ichthyol. (trans. Voprosy Ikhtiologii) 11(3): 304 (exclusively for myliobatoids); Compagno, 1973, J. Linn. Soc. (Zool.), 53, suppl. 1: 27 (order exclusively for myliobatoids); Applegate, 1974, J. Mar. Biol. Ass. India, 14(2): 743 (exclusively for myliobatoids); Chu and Meng, 1979, Monogr. Fish. China, Sci. Tech. Press, Shanghai: 114, tab. 2 (exclusively for myliobatoids); Cappetta, 1987, Handb. Paleoichthyol. 3B: 27, 162 (exclusively for myliobatoids); Eschmeyer, 1990, Cat. gen. Recent fish.: 438 (exclusively for myliobatoids); McEachran, Dunn and Miyake, 1996, in Stiassny et al., Interrelationships fishes: 80 (for myliobatoids, zanobatids and platyrhinids). Order Myliobatiformes, Suborder Myliobatoidei: McEachran, Dunn and Miyake, 1996, in Stiassny et al., Interrelationships of fishes: 81 (suborder for all myliobatoids, order also for zanobatids and platyrhinids). Order Myliobatiformes, Suborder Myliobatoidei, Superfamily Hexatrygonoidea: McEachran, Dunn and Miyake, 1996, in Stiassny et al., Interrelationships of fishes: 81 (superfamily exclusively for hexatrygonids). Order Myliobatiformes, Suborder Myliobatoidei, Superfamily Dasyatoidea: McEachran, Dunn and Miyake, 1996, in Stiassny et al., Interrelationships fishes: 81 (superfamily for myliobatoids other than hexatrygonids). Order Myliobatiformes, Superfamily Dasyatoidea: Compagno, 1973, J. Linn. Soc. (Zool.), 53, suppl. 1: 27 (for stingrays and butterfly rays). Order Myliobatiformes, Superfamily Myliobatoidea: Compagno, 1973, J. Linn. Soc. (Zool.), 53, suppl. 1: 27 (for eagle and cownose rays). Order Myliobatiformes, Superfamily Mobuloidea: Compagno, 1973, J. Linn. Soc. (Zool.), 53, suppl. 1: 27 (for devil rays). Order Myliobatiformes, Suborder Dasyatoidea: Chu and Meng, 1979, Monogr. Fish. China, Sci. Tech. Press, Shanghai: 114, tab. 2 (suborder for urolophids, dasyatids, and gymnurids). Order Myliobatiformes, Suborder Myliobatoidea: Chu and Meng, 1979, Monogr. Fish. China, Sci. Tech. Press, Shanghai: 114, tab. 2 (suborder for myliobatids, aetobatids, and rhinopterids). Order Myliobatiformes, Suborder Mobuloidea: Chu and Meng, 1979, Monogr. Fish. China, Sci. Tech. Press, Shanghai: 114, tab. 2
(suborder for mobulids). Order Rajiformes, Suborder Rajoidei: Patterson, 1967 (in part), in W.B. Harland et al., Geol. Soc. London, Spec. Pub. 2: 672 (suborder for rajoids and myliobatoids, order includes all batoids other than torpedinoids). Order Squatinida, Suborder Rajoidei, Superfamily Myliobatoidea: Glikman, 1967 (in part), in Y.A. Orlov, ed., Fundamentals Paleontology, 11: 220 (superfamily for myliobatoids, suborder for all batoids, order also including squaloids, orectoloboids, cetorhinids, squatinoids, and pristiophoroids). Order Rajida, Suborder Rajina, Superfamily Dasyaticae: Fowler, 1969b, Q. J. Taiwan Mus. 22(3-4): 179 (superfamily for myliobatoids other than mobulids, order and suborder for batoids other than torpedinoids). Order Rajida, Suborder Rajina, Superfamily Mobulicae: Fowler, 1970, Q. J. Taiwan Mus. 23(1-2): 80 (superfamily exclusively for mobulids, order and suborder for batoids other than torpedinoids). Order Rajida, Suborder Rajina: Matsubara, 1955, Fish morphology hierarchy, (1): 1-789 (suborder for rhinobatids, rhinids, platyrhinids, rajoids, and myliobatoids, order for all batoids). Order Batoidea: Romer, 1945, Vert. Paleont. (ed. 2): 577 (for all batoids). Order Batoidea, Suborder Myliobatoidea: Bigelow and Schroeder, 1953, Mem. Sears Fnd. Mar. Res. (1) 2: 15, 331 (suborder exclusively for myliobatoids, order for all batoids); Romer, 1966, Vert. Paleont. (ed. 3): 351 (suborder exclusively for myliobatoids, order for all batoids). Order Hypotremata, Suborder Batoidea: Norman, 1966, draft syn. Recent fishes: 35 (suborder for batoids other than torpedinoids, order includes all batoids). Order Rajiformes: Blot, 1969, in J. Piveteau, ed. Traité de Paleontologie. 2: 702-776 (group for all living batoids). Order Batoidea, Suborder Rajiformes: Schultz and Stern, 1948, Ways of Fishes: 225 (suborder for all batoids other than torpedinoids, order for all living batoids). Order Rajiformes, Suborder Dasyatoidei: Arambourg and Bertin, 1958, In P.-P. Grasse, ed, Traité de Zoologie, 13: 2051 (suborder for myliobatoids and ptychodonts, order for all batoids other than torpedinoids). Order Batoidea, Suborder Myliobatoidea: Carroll, 1988, Vertebrate paleont. evolut.: 600 (suborder exclusively for myliobatoids, order for all batoids). Order Myliobatiformes, Superfamily Dasyatoidea: Cappetta, 1987, Handb. Paleoichthyol. 3B: 162 (for stingrays). Order Myliobatiformes, Superfamily Myliobatoidea: Cappetta, 1987, Handb. Paleoichthyol. 3B: 170 (for eagle and cownosed rays). Order Myliobatiformes, Superfamily Mobuloidea: Cappetta, 1987, Handb. Paleoichthyol. 3B: 175 (for mobulids). Ordo Plagiostomi, Subordo Rajini: Bleeker, 1859, Acta Soc. Sci. IndoNeerl. 6: xiii (suborder for all batoids, order for all elasmobranchs). Order Selachii, Suborder Tectospondyli: Woodward, 1889 (in part), Cat. fossil fish. $B M(N H)$ (1): 30 (suborder for squaloids, squatinoids, pristiophoroids, batoids, psammodonts, petalodonts, and pristodonts, order for other living sharks, fossil neoselachians, hybodonts and cochliodonts). Order Rajiformes, Suborder Myliobatidoidei: Nishida, 1990, Mem. Fac. Fish. Hokkaido U. 37(1/2): 1, 97 (suborder exclusively for myliobatoids, order for all batoids). Order Rajiformes, Suborder Myliobatidoidei, Infraorder Plesiobatides, Superfamily Plesiobatoidea: Nishida, 1990, Mem. Fac. Fish. Hokkaido U. 37(1/2): 97 (infraorder and superfamily for Family Plesiobatididae, suborder for all myliobatoids, order for all batoids). Order Rajiformes, Suborder Myliobatidoidei, Infraorder Hexatrygones, Superfamily Hexatrygonoidea: Nishida, 1990, Mem. Fac. Fish. Hokkaido U. 37(1/2): 97 (infraorder and superfamily for Family Hexatrygonidae, suborder for all myliobatoids, order for all batoids). Order Rajiformes, Suborder Myliobatidoidei, Infraorder Myliobatidides: Nishida, 1990, Mem. Fac. Fish. Hokkaido U. 37(1/2): 98 (infraorder for myliobatids other than plesiobatidids and hexatrygonids, suborder for all myliobatoids, order for all batoids). Order Rajiformes, Suborder Myliobatidoidei, Infraorder Myliobatidides, Superfamily Dasyatidoidea: Nishida, 1990, Mem. Fac. Fish. Hokkaido U. 37(1/2): 98 (superfamily for dasyatids and urolophids). Order Rajiformes, Suborder Myliobatidoidei, Infraorder Myliobatidides, Superfamily Myliobatidoidea: Nishida, 1990, Mem. Fac. Fish. Hokkaido U. 37(1/2): 98 (superfamily for gymnurids and myliobatids sensu lato). Order Rajiformes, Suborder Rajoidei, Superfamily Myliobatidoidea: Shirai, 1996, in Stiassny et al., Interrelationships fishes: 34 (superfamily exclusively for myliobatoids, suborder also for myliobatoids and rajoids, order for all batoids).

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-shaped, no more than 1.3 times as wide as long, with long whip-like tail (Dasyatidae), pectoral fins completely fused with sides of head, eyes and spiracles on top of head; or disc 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 as wide as 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, 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, followed by one or more long serrated spines. 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 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 are also semi-pelagic and at least one species 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: Stingarees, Giant stingarees, Sixgill stingrays, Pan rays, Stingrays, Butterfly rays, Eagle rays, Cownose rays, Devil rays, Mantas.

Remarks: The order has 10 families, with several subfamilies, most of which are shallow water benthic or semi-pelagic species. The monotypic family Hexatrygonidae, represented by Hexatrygon bickelli is the only deep-sea species of this order known to occur in the present region. This is based on a couple of records of this species from the Eastern Cape Province, South Africa.

### 3.3.1 Family HEXATRYGONIDAE

Family: Family Hexatrygonidae Heemstra and Smith, 1980, Ichth. Bull. J.L.B. Smith Inst. Ichthyol. (43): 1. Type genus: Hexatrygon Heemstra and Smith, 1980.

Type Genus: Hexatrygon Heemstra and Smith, 1980.
Number of Recognized Deep-sea Southeastern Atlantic Ocean Genera: 1.
Synonyms: Family Hexatrematobatidae Chu and Meng, in Chu et al., 1981, Oceanol. Limnol. Sinica, 12(2): 111. Type genus: Hexatrematobatis Chu and Meng, 1981.

Field Marks: A large soft-bodied stingray unique in that it is the only batoid species with six-paired gill openings.
Diagnostic Features: Disc shape nearly circular posterior to snout, with rounded pectoral apices; body depressed, flattened, soft, very flabby with a greatly elongated, thick, fleshy pointed snout; snout shape changes ontogenetically with growth. Nostrils very wide, located just anterior to mouth, separated from it by a distance much less than their own width, not connected by broad nasoral grooves with mouth; anterior nasal flaps very short and medially expanded and fused into a very broad, very short nasal curtain that ends just anterior to mouth. Mouth transverse, nearly straight, moderately broad, without prominent knobs, depressions or labial folds; no oral papillae on floor of mouth. Oral teeth small, rounded-oval in shape and with low ridges on their crowns, not laterally expanded and plate-like, similar in shape. Tooth row counts 44 to 102 in upper and lower jaws (more rows present in adults than in young). Only known batoid with six paired gill openings. Eyes small and dorsolateral on head, well anterior to spiracles. Disc smooth, without denticles or thorns. Pelvic fins low, rounded, and not divided into anterior and posterior lobes. Tail short, moderately stout, not whiplike, well developed, without a dorsal fin, length about 0.5 to 0.7 times disc length. Precaudal tail moderately depressed or cylindrical, without lateral folds on sides, tail abruptly narrower than trunk, with 1 or 2 prominent barbed stinging spines on dorsal surface of tail well behind pelvic fins; no electric organs in tail. Caudal fin moderately large, not shark-like, nearly symmetrical and very elongated (about half length of tail) and leafshaped, with vertebral axis not raised above body axis; lower caudal-fin lobe absent. Vertebral counts: total vertebral count 101, vertebral count from first synarcual to cloaca 51 , vertebral count from cloaca to stinging spine 50 . Spiral valve count 14 for one individual. Maximum total length to at least 168 cm . Colour: in life, purplish-brown on dorsal surface becoming dark brown after preservation; ventral surface white with dusky margin on disc and pelvic fins; underside of tail dark.

Distribution: See species account below.
Habitat: See species account below.
Biology: See species account below.
Interest to Fisheries and Human Impact: See species account below.
Local Names: None.
Remarks: The family account above is after Compagno and Last (1999d).
Literature: Heemstra and Smith (1980); Compagno and Last (1999d); Last and Stevens (2009); Ebert (2014).

## List of Species Occurring in the Area:

Hexatrygon bickelli Heemstra and Smith, 1980

## Hexatrygon Heemstra and Smith, 1980

Genus: Hexatrygon Heemstra and Smith, 1980, Ichth. Bull. J.L.B. Smith Inst. Ichthyol. (43): 1.
Type species: Hexatrygon bickelli Heemstra and Smith, 1980, by original designation (also monotypic).
Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 1.
Synonyms: Genus Hexatrematobatis Chu and Meng, in Chu et al., 1981, Oceanol. Limnol. Sinica, 12(2): 111. Type species: Hexatrematobatis longirostrum Chu and Meng, 1981 by original designation. Genus Hexatrematibatis Chu and Meng, in Chu et al., 1981, ibid.: 116. Error for Hexatrematobatis.

Field Marks: See species account below.
Diagnostic Features: See family account above.
Local Names: None.

## Hexatrygon bickelli Heemstra and Smith, 1980

Hexatrygon bickelli Heemstra and Smith, 1980, Ichth. Bull. J.L.B. Smith Inst. Ichthyol. (43): 6, figs. 1-13, 15. Holotype: J.L.B. Smith Institute of Ichthyology, SAIAB [formerly RUSI] 997, 103 cm total length, 50 cm disc width, immature or nearadolescent female, washed up on beach at Port Elizabeth, South Africa, ca. $33^{\circ} 59.5^{\prime} \mathrm{S}, 25^{\circ} 40.7^{\prime} \mathrm{E}$.

Synonyms: Hexatrematobatis longirostrum Chu and Meng, in Chu et al., 1981, Oceanol. Limnol. Sinica, 12(2): 111, fig. 4. Holotype: South China Sea Fisheries Research Institute, SCSFRI-00072, 63.3 cm total length immature male, South China Sea, in block $112-114^{\circ} \mathrm{E}, 18.5-21^{\circ} \mathrm{N}, 350$ to 1000 m . Hexatrygon yangi Shen and Liu, 1984, Act. Oceanogr. Taiwanica, (15): 201. Holotype: National Taiwan University Museum, NTUM-06100, 1040 mm TL, 545 mm disc width subadult male, TungKong fish market, SW coast of Taiwan (Province of China), $22^{\circ} 28^{\prime} \mathrm{N}, 120^{\circ} 26^{\prime} \mathrm{E}$ (Tung-Kong [Tongkang] fish market), trawled off the coast at about 500 m depth. Hexatrygon taiwanensis Shen, 1986a, J. Taiwan Mus. 39(1): 175, fig. 1-5. Holotype: National Taiwan University Museum, NTUM-0655, 582 mm TL, 353 mm DW juvenile female, Tung-Kong fish market, SW coast of Taiwan (Province of China), $22^{\circ} 28^{\prime} \mathrm{N}, 120^{\circ} 26^{\prime} \mathrm{E}$ (Tung-Kong [Tongkang] fish market), trawled at depth of 370 m . Hexatrygon brevirostra Shen, 1986b, J. Taiwan Mus. 39(2): 106, fig. 1-3. Holotype: National Taiwan University Museum, NTUM-06597, 621 mm TL, 365 mm DW juvenile (?) female, Tong-Kung fish market, SW coast of Taiwan (Province of China), $22^{\circ} 28^{\prime} \mathrm{N}, 120^{\circ} 26^{\prime} \mathrm{E}$ (Tung-Kong [Tongkang] fish market), trawled at depth of 362 m .

FAO Name: En - Sixgill stingray.
Field Marks: Distinctive among batoids with six pairs of gill slits, large rounded-rhomboidal disc without denticles, body flabby, with an elongated, thick snout, oral papillae absent, nasal curtain very broad not extending to mouth, spiracles set far behind eyes, a short tail with a long, low caudal fin, no dorsal fins, and 1 or 2 prominent stinging spines. Colour is a dark violet blue or pinkish above, white below except for darker edges along disc.

Diagnostic Features: See family account above.
Distribution: The sixgill stingray has a wide but patchy distribution. In the Southeastern Atlantic and Indian Ocean it occurs off South Africa (?Western and Eastern Cape).

Habitat: This unique ray occurs on soft bottoms, mostly on the upper continental and insular slopes at depths of 300 to 1120 m , but with occasional (including a live pregnant female with term


Fig. 216 Hexatrygon bickelli
foetuses) stranding on sandy beaches. Additionally, there is a possible angler's catch off the southwest coast of South Africa at depths of 20 to 30 m or less, and one was photographed feeding at moderate depths by a Japanese scuba diver (H. Ishihara, pers. comm.).

Biology: Viviparous, without yolk-sac placenta, three to five embryos per litter, but little is known about their reproductive cycle.

Feeding habits unknown, although the very flexible snout tip and strongly protractible mouth in combination are used to probe about the bottom in search of food. This was observed by underwater video footage of an individual feeding on the bottom. One specimen examined had a wound from a 'cookie-cutter' shark.

Size: Maximum total length to at least 168 cm (adult female); females and males mature at 105 to 113 cm in length. Size at birth is about 48 to 50 cm total length.

Interest to Fisheries and Human Impact: Interest to fisheries minor, infrequently caught in bottom trawls as bycatch and mostly discarded, although in Taiwan (Province of China) it is retained and marketed.

The conservation status is Least Concern.
Local Names: None.


Fig. 217 Hexatrygon bickelli
(g. 217 Hexatygon bickeli
$\square$ Known distribution

Remarks: Several species of sixgill stingrays have been named from the Western Pacific based mostly on snout length and shape, but these nominal species were based on allometric variation with growth (the snout is much longer in adults than young) and after preservation the snout is very soft, turgid, and watery, and may shrink greatly if allowed to dry out, if stored in a freezer for too long, or if treated with strong fixative and preservative.

Literature: Heemstra and Smith (1980); Compagno, Ebert and Smale (1989); Compagno and Last (1999d); Last and Stevens (2009); McCormack et al. (2009); Babu, Ramachandran and Varghese (2011); Ebert (2014); Ebert and Aschliman (In press); L.J.V. Compagno (pers comm. and unpubl. data.).

## 4. Subclass HOLOCEPHALI

### 4.1 Order CHIMAERIFORMES - Chimaeras

Order: Chimaeriformes: Patterson, 1965, Philos. Trans. R. Soc. London B Biol. Sci. 249: 101-219.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Families: 2.

Synonyms: See Bigelow and Schroeder, 1953 Order Chimaerae page 516. See Garman 1901, 1906, 1911
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 conically rounded, 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, ovoid-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 lower than first, elongated, with margin either relatively straight or undulating distally, and terminating anterior to upper caudal-fin lobe. 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 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, dorsal lobe margin with or without tubercles; lower lobe without tubercles; 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. Size small $(60 \mathrm{~cm})$ 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 Western Indo-Pacific has the highest diversity of these fishes followed by the North Atlantic 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; most members of both these families are primarily deep-sea. The shallow water 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 of 500 m to more than 2500 m . A few species, mainly those in the family Callorhinchidae, occur in relatively shallow, coastal waters. Chimaeroids 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, segregate 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 present arrangement of the Chimaeriformes families and genera follows recent revisions by Didier (1995, 2004) and Didier, Kemper and Ebert (2012). The shallow water occurring Callorhinchidae are not discussed further.

Literature: Garman (1901, 1908, 1911); Bigelow and Schroeder (1953, 1954b); Compagno, Stehmann and Ebert (1990); Didier (1995, 2002, 2004); Nelson (2006); Last and Stevens (2009); Ebert and Winton (2010); Didier, Kemper and Ebert (2012); Ebert (2014); Ebert and Stehmann (2013).

Key to Deep-sea Southeastern Atlantic Ocean Families:
1a. Snout short and blunt (Fig. 218) .
family Chimaeridae

1b. Snout elongated and tapering (Fig. 219).
family Rhinochimaeridae


Fig. 218 Chimaeridae


Fig. 219 Rhinochimaeridae

### 4.1.1 Family CHIMAERIDAE

Family: Chimaeridae Bonaparte, 1831, Giornale Arcadico di Scienze, 49: 1-77.
Type genus: Chimaera Linnaeus, 1758.
Number of Recognized Deep-sea Southeastern Atlantic Ocean Genera: 2.
Synonyms: None.
FAO Name: En - Shortnose chimaeras.
Field Marks: Small to large bodied chimaeras, with massive heads, but tapering posteriorly to a filamentous whip-like tail, snout fleshy, short, conical, and pointed at tip, first dorsal fin triangular, preceded by a 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 very 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 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 robust with patches of dense hypermineralized tissue that appear 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, and terminating with a whip-like 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 distribution 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 area they do not appear to occur in is the Antarctic region.

Habitat: Members of the Chimaeridae generally inhabit the deep-sea, usually at depths greater than 200 m , with some species known to occur 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, but for some of the deeper living species the gestation time may be much longer.

Attempts to age chimaeras have met with mixed results, with the age not being validated for any 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. Most shortnose chimaeras occur too deep and are not caught in sufficient
numbers to warrant a targeted fishery, but are often retained as bycatch. The North Atlantic Chimaera monstrosa is one shortnose chimaera species for which landings are reported.

The conservation status of most members of this family are Data Deficient or Least Concern, but some species are considered Near Threatened due to current or potential fisheries that may impact their populations.

Local Names: Ratfishes, Rabbitfishes, Ghostsharks, Silver sharks.
Remarks: 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.

The current arrangement of this family follows Didier, Kemper and Ebert (2012) and Ebert (2013; unpubl. data) in recognizing two genera and 38 species. Four species, including the recently described Chimaera notafricana, are known to occur in the Southeastern Atlantic Ocean, but the three Hydrolagus species are only tentatively identified here pending taxonomic resolution by the author (D.A. Ebert, unpubl. data) who is currently investigating the issue.

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); Ebert and Winton (2010); Didier, Kemper and Ebert (2012); Ebert and Stehmann (2013); Ebert (2014); Kemper and Ebert (In press); D.A. Ebert (unpubl. data).

## List of Species Occurring in the Area:

## $\xrightarrow[\longrightarrow]{\longrightarrow}$ Chimaera notafricana Kemper, Ebert, Compagno and Didier, 2010 <br> Hydrolagus cf. africanus (Gilchrist, 1922) <br> Hydrolagus cf. mirabilis (Collett, 1904) <br> Hydrolagus cf. trolli Didier and Séret, 2002

## Key to Deep-sea Southeastern Atlantic Ocean Genera:

1a. Anal fin present (Fig. 220). . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Chimaera
1b. Anal fin absent (Fig. 221) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Hydrolagus


Fig. 220 Chimaera

## 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 Deep-sea Southeastern Atlantic Ocean Species: 1.
Synonyms: Genus Chimera Rafinesque, 1815, An. Nat:: 92; emended spelling for Chimaera Linnaeus, 1758, by ref. to Linnaeus. Genus Chimaira Duméril, 1856, Mem. Acad. Sci. France, 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 chimaeras 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 at least 16 species globally, with possibly up to four undescribed species from the Southwestern Indian Ocean. Only a single species (Chimaera notafricana) is confirmed from the Southeastern Atlantic Ocean. Previous records of $\boldsymbol{C}$. monstrosa were based on misidentification of $\boldsymbol{C}$. notafricana.

## Chimaera notafricana Kemper, Ebert, Compagno and Didier, 2010

Chimaera notafricana Kemper, Ebert, Compagno and Didier, 2010, Zootaxa, 2532: 55-63, figs. 1-2, tabs. 1-2. Holotype: SAM 34517, adult male, 837 mm total length, 509 mm body length. Type locality: Cape Agulhas, Southern Africa ( $34^{\circ} 49^{\prime} \mathrm{S}$, $20^{\circ} 00^{\prime} \mathrm{E}$ ), by the M/V Boulonnais, station 36.09.72, 18 September 1996.

Synonyms: Chimaera monstrosa Duméril, 1865: 688; Gilchrist, 1902: 162; Thompson, 1914: 166; Gilchrist, 1922: 5; Barnard, 1925: 94; Fowler, 1936: 143; Fowler, 1941: 489; Barnard, 1947: 30, probably not PI. 5, fig. 3 = C. monstrosa from European sea; Smith, 1949: 76; Stehmann and Bürkel, 1984: 213; Compagno, 1986: 144, not fig. 32.1, which is European C. monstrosa; van der Elst and Vermeulen, 1986: 4. Chimaera vaillanti: Dean, 1906: 7 (MNHN 2557), nomem nudum. Chimaera sp.: Compagno, Ebert and Smale, 1989: 120, ill.; Compagno, Ebert and Cowley, 1991: 70; Compagno, 1999: 120.

Other Combinations: None.
FAO Name: En - Cape chimaera.


Fig. 222 Chimaera notafricana

Field Marks: A uniform blackish brown coloration with dark bluish streaking and longitudinal light and dark stripes along body flanks, pelvic claspers short, not extending past distal tip of pelvic fins, divided for distal one-third of length, distal edge of pelvic fins slightly rounded, dorsal-fin spine when depressed extending past origin of second dorsal fin and large triangular pectoral fin reaching to pelvic-fin origin when depressed.

Diagnostic Features: Body elongate, slender, tapering from head to whip-like tail filament; caudal filament length about 44 to $57 \%$ total body length. Snout short, conical, and bluntly pointed. Eyes moderately large, 26 to $33 \%$ of head length. Lateral line canals on head appear as open grooves, canals on snout characterized by wide dilations. Preopercular and oral lateral line canals share a common branch off the infraorbital canal. Skin deciduous, smooth. Pectoral fins large and triangular in shape, reaching to origin of second dorsal fin and just to origin of pelvic fin when laid back. Pelvic fins slightly rounded at apices, about one-half size of pectoral fins. Adult males with frontal tenaculum, slender, curving along dorsal surface to a rounded bulbous tip, and adorned with small denticles on the dorsal surface; length about one-half eye length. Pelvic claspers short, slender, rod-like, smooth, and with small dilated tip; fleshy tips bulbous and covered with shagreen of denticles; prepelvic tenacula with four spines along medial edge. First dorsal fin high, triangular, preceded by a keeled spine, strongly serrate along the posterior edge of the distal tip; spine tip when depressed reaches beyond second dorsal-fin origin. Second dorsal fin long and continuous to upper caudal fin, relatively straight along its length, slightly higher along posterior one-third of fin length, but margin not undulating. Anal fin small, low, and with pointed tip extending at least to second dorsal-fin insertion. Caudal-fin dorsal lobe slightly anterior to ventral lobe, about equal in height, but height nearly equal to or slightly less than second dorsal-fin height. Maximum total length 93 cm . Colour: uniform blackish brown, with dark bluish streaks laterally on body trunk, precaudal with longitudinal light and dark stripes, but no lighter spots or silvery sheen; pectoral, pelvic, and dorsal fins moderate to dark brown, with a bluish hue near the fin edges; pectoral fins lighter along posterior edges; dorsal-fin spine light brown, becoming darker in grooves; caudal-fin lobes moderately brown, darker near fin base, lighter near fin apices.

Distribution: The Cape chimaera is known only from off Lüderitz, Namibia, to the Cape of Good Hope and eastwards to Algoa Bay, Eastern Cape Province, South Africa.

Habitat: Upper continental slope from 680 to at least 1016 m.

Biology: Virtually unknown.
Size: Maximum total length 93 cm for an adult female, and about 84 cm for an adult male. Size at birth is unknown.

Interest to Fisheries and Human Impact: Occasionally caught by hake trawlers, but not utilized.

The conservation status of this species is Least Concern.
Local Names: None.
Remarks: This species was previously referred to as Chimaera monstrosa, a common European chimaera species, but close examination of the southern African form with the European C. monstrosa revealed that it is a distinctly different species.

Literature: Compagno, Ebert and Smale (1989); Compagno, Ebert and Cowley (1991); Kemper et al. (2010); Kemper and Ebert (2011); Ebert (2014).


Fig. 223 Chimaera notafricana
Known distribution

## 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, U.S.A., by monotypy.
Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 3.
Synonyms: Subgenus Bathyalopex Collett, 1904. Forh. VidenskSelsk. Krist., (9): 5. Type: Chimaera (Bathyalopex) mirabilis Collett, 1904 (by monotypy) as a subgenus to Chimaera. Faroe Channel and Faroe Bank, 720 to 1200 m.
FAO Names: En - Ratfishes; Fr - Chimères; Sp - Quimeras.
Field Marks: Blunt-snouted chimaeras 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: As for family, but species placed into the genus Hydrolagus lack an anal fin.
Local Names: None.
Remarks: Worldwide there are 23 species recognized within this genus, of which three occur in the deep-sea Southeastern Atlantic Ocean. The three species known to occur within this region are tentatively identified as Hydrolagus cf. africanus, Hydrolagus cf. mirabilis and Hydrolagus cf. trolli, but they are currently under investigation by the author (D.A. Ebert) to confirm their identification. The key below to the Hydrolagus is provisional. These three species will not be discussed further here.

Key to Deep-sea Southeastern Atlantic Ocean Species (modified after Didier, Kemper and Ebert, 2012):
1a. Large-bodied fish, adults sometimes massive; body colour dark black, purplish, blue, or grey (Fig. 224) .

Hydrolagus cf. trolli


Fig. 224 Hydrolagus cf. trolli

1b. Small-bodied, slender fish, some adults almost dwarf-like; body colour pale, brown, tan, or silvery-grey.

2a. Second dorsal fin straight or only slightly indented in centre; adult males with lateral patch of denticles on pre-pelvic tenaculae (Fig. 225).

Hydrolagus cf. africanus

2b. Second dorsal fin deeply indented in centre; adult males without lateral patch of denticles on pre-pelvic tenaculae (Fig. 226). . . . . . Hydrolagus cf. mirabilis


Fig. 225 Hydrolagus cf. africanus


Fig. 226 Hydrolagus cf. mirabilis

### 4.1.2 Family RHINOCHIMAERIDAE

Family: Rhinochimaeridae Garman, 1901, Proc. New England Zool. Club, 2: 75-77.
Type genus: Rhinochimaera Garman, 1901.

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Genera: 3.

Synonyms: None.
FAO Name: En - Longnose chimaeras.
Field Marks: Medium to large-sized chimaeras with large head, elongated bodies tapering posteriorly to filamentous tail, very long snout, distinctively spear-shaped, and flexible, first dorsal fin preceded by prominent fin spine, and anal fin, depending on the genus, 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, broad, 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 robust with patches of dense hypermineralized tissue that appears as ridges and bumps on the surface; some lacking robust ridges, with tooth plates that appear smooth. 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 tubercles along margin; lower lobe without tubercles; 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 tenaculum 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: Rhinochimaerids have a circumglobal distribution with most members being wide-ranging although many species have a patchy or scattered distribution; the other chimaeroid families tend to exhibit a higher degree of endemism.

Habitat: Very little known about the habitat preference of longnose chimaeras. They tend to occur over muddy or soft bottoms, although this may be an artifact of sampling methods, and usually occur 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, Langneus-chimaeras (South Africa).
Remarks: The above family account is modified, and updated, after Didier (1995, 2002, 2004), Didier, Kemper and Ebert (2012), and Kemper and Ebert (In press) and recognizes three genera and at least eight described species; all three genera and four species occur in the Southeastern Atlantic Ocean.

Literature: Garman (1901); Bigelow and Schroeder (1953, 1954b); Krefft in Hureau and Monod (1973c); Stehmann and Bürkel in Whitehead et al. (1984); Didier (2002, 2004); Nelson (2006); Last and Stevens (2009); Ebert and Winton (2010); Didier, Kemper and Ebert (2012); Ebert and Stehmann (2013); Ebert (2014); Kemper and Ebert (In press); D.A. Didier and D.A. Ebert (unpubl. data).

## List of Species Occurring in the Area:

Harriotta raleighana Goode and Bean, 1895
Neoharriotta pinnata (Schnakenbeck, 1931)
Rhinochimaera africana Compagno, Stehmann and Ebert, 1990
Rhinochimaera atlantica Holt and Byrne, 1909

Key to Deep-sea Southeastern Atlantic Ocean Genera:
1a. Anal fin present (Fig. 227). . . . Neoharriotta

1b. Anal fin absent. . . . . . . . . . . . . . . . . . . 2


Fig. 227 Neoharriotta
2a. Lateral head profile convex; mouth located slightly in front of or just below eyes; tooth plates with raised hypermineralized tritors on the surface; margin of upper caudal-fin lobe without tubercles (Fig. 228)

Harriotta

2b. Lateral head profile straight; mouth located well in front of eyes; tooth plates smooth, lacking raised hypermineralized tritors on the surface; margin of upper caudal-fin lobe with tubercles (Fig. 229)

Rhinochimaera


Fig. 228 Harriotta


Fig. 229 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 Deep-sea Southeastern Atlantic Ocean Species: 1.

Synonyms: None.
FAO Name: En - Narrownose chimaeras.
Field Marks: Elongated snout, fleshy at base, and tapering to a fine point at the tip, distal tip of snout curved upwards, more so in adult males 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: Body large, elongate, tapering posteriorly to a whip-like filamentous tail; head relatively large, snout very long, fleshy, wide at base, tapering anteriorly to a pointed tip; snout may or may not curve upwards (depending on species) and with or without knobby protuberances at distal end. Eyes oval, small to moderately large. Nostrils moderate, slightly longer than wide. Mouth relatively small, located below eyes. Tooth plates thick, hypermineralized with transverse ridges and rounded tritors (except in small juveniles), anterior edge of tooth plates form sharp nipping blades. Canals on head relatively widely spaced; nasal canal on ventral surface of either not expanded or expanded, and may or may not join rostral canal; lateral line canals on trunk straight, not wavy. Pectoral fins broad, large, with tips extending, or not, to pelvic-fin origin (depending on species). Pelvic fins broadly rounded. First dorsal fin small, short-based, its height not much greater than second dorsal fin; fin spine relatively short, height less than or slightly greater than fin height; spine may be recurved or straight. Interdorsal space small when first dorsal fin laid back, fin spine either reaching origin of second dorsal fin or not. Second dorsal fin relatively even or slightly convex in height, base short. Anal fin absent. Caudal-fin upper and lower lobes similar, or slightly different, in length and height; upper dorsal-fin margin without tubercles. Tail short and filamentous. Colour: uniform light to dark brown above, may be darker below and along fin edges; fin spine light to whitish.

Local Names: None.
Remarks: This genus has two wide-ranging, but patchily distributed species. These are very poorly known chimaeras and if encountered should be retained for detailed examination. One species, Harriotta raleighana, is known to occur in the area, but the other species (Harriotta haeckeli Karrer, 1972) has not been confirmed from this region. However, given its spotty distribution and very deep-sea habitat $\boldsymbol{H}$. haeckeli may eventually be found to occur within this area.

## Harriotta raleighana Goode and Bean, 1895

Harriotta raleighana Goode and Bean, 1895, Proceedings of the United States National Museum, 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, ( $39^{\circ} 37^{\top} \mathrm{N}, 71^{\circ} 18^{\prime} \mathrm{W}$ ), 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 (2012) a lectotype was established in Jordan and Evermann (1900) from the caption to plate 19, p. 3234, "Fishes of North and Middle America".

Synonyms: None.

## Other Combinations: Harriotta chaetirhamphus.

FAO Name: En - Narrownose chimaera.


Field Marks: A relatively 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 tubercles 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; snout tip curves upwards. Eyes moderately large, ovoid. Head 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 fin 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. Prepelvic tenaculum with six stout spines along medial edge. Pelvic claspers in mature males rod-like with a small fleshy denticulate tip. First dorsal fin relatively small, with a small spine about equal in length to height of first dorsal fin, keeled and weakly serrate along distal one-half. Interdorsal space small, first dorsal and fin spine reach origin of second dorsal fin when laid back. Second dorsal fin gently slopes anteriorly and posteriorly but relatively even in height. Caudal fin with short filament. Maximum total length about 120 cm . Colour: uniform dark brown; fin edges much darker, pelvic fins blackish.

Distribution: In the Southeastern Atlantic Ocean it occurs off the Western Cape Province, South Africa and Namibia. Elsewhere circumglobal, but patchily distributed, most commonly found in the North Atlantic and around New Zealand.

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 spp.). There appears to be an ontogenetic shift between 300 and 1000 m depth with large individuals occurring deeper than smaller individuals.

Biology: Oviparous, but little else known of its 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 Harriotta 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.


Fig. 231 Harriotta raleighana
Known distribution

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: Bigspine spookfish, Pacific longnose chimaera, Long-nosed chimaera, Longnosed chimaera (English).
Remarks: This wide-ranging longnose chimaera is occasionally mistaken with Harriotta haeckeli, another wide-ranging member of this genus characterized by a relatively small eye and dorsal-fin spine significantly shorter than height of first dorsal fin.

Literature: Goode and Bean (1895); Bigelow and Schroeder (1953, 1954b); Stehmann and Bürkel in Whitehead et al. (1984); Compagno, Ebert and Smale (1989); Compagno, Stehmann and Ebert (1990); Compagno, Ebert and Cowley (1991); Moore et al. (2003); Møller et al. (2004, 2010); Dagit (2006a); González et al. (2007); James et al. (2009); Last and Stevens (2009); Dunn et al. (2010); Ebert and Winton (2010); Didier, Kemper and Ebert (2012); Ebert and Stehmann (2013); Ebert (2014); Kemper and Ebert (In press); D.A. Ebert (unpubl. data).

## Neoharriotta Bigelow and Schroeder, 1950

Genus: Neoharriotta Bigelow and Schroeder, 1950, Bulletin of the Museum Comparative Zoology, 103(7): 406.
Type species: Harriotta pinnata Schnakenbeck, 1931, by original designation (also monotypic).

## Number of Recognized Deep-sea Southeastern Atlantic Ocean Species: 1.

Synonyms: None.
FAO Name: En - Sicklefin chimaeras.
Field Marks: No knobs or tubercles on snout tip or on upper caudal-fin margin, and a distinct anal fin present, separated by a deep notch from the ventral caudal-fin lobe.

Diagnostic Features: Body elongate, tapering to a caudal fin with whip-like filamentous tail. Head relatively large. Snout fleshy, slender, very long, wide at base, tapering to a pointed tip; snout not curve upwards and without tubercles at distal end. Eyes oval, relatively large. Nostrils moderate, slightly longer than wide. Mouth relatively small. Tooth plates thick, with transverse ridges and hypermineralized tritors. Canals on head narrow to widely separated; lateral line canals on trunk straight, not wavy. Pectoral fins short and broad. Pelvic fins broadly rounded. First dorsal fin small, short-based; fin spine serrated, height about equal to or slightly greater than fin height; spine mostly straight, or slightly recurved. Second dorsal fin height relatively even or convex. Anal fin present, separated from lower caudal-fin lobe by a deep notch. Caudal fin upper and lower lobes uneven in height, lower lobe mostly greater in height than upper lobe; upper dorsal-fin margin without tubercles. Tail filamentous, whip-like. Colour: uniform light to dark brown or greyish, or mottled grey-brown for some species, with darker head, snout, and paired fins, becoming lighter ventrally.
Local Names: None.
Remarks: This genus has three very poorly known and patchily distributed species.

## Neoharriotta pinnata (Schnakenbeck, 1931)

Harriotta pinnata Schnakenbeck, 1931, Mitt. Aus. Dem Zool. Mus. Hamburg, 44: 40, figs. 6-9. Syntypes: (3) ZMH 10470 (only 1 now). Type locality: Walvis Bay, Namibia, in deepwater.

Synonyms: Harriotta pinnata Smith, 1949: 78 (in part, included in synonymy); Rodriguez-Roda, 1961: 89, figs 1-2 (off Cabo Blanco, Spanish Sahara-Mauritania, 330 m ).

Other Combinations: None.
FAO Names: En - Sicklefin chimaera; Fr - Chimère faucillée; Sp - Narigón aletas de haz.


Fig. 232 Neoharriotta pinnata
Field Marks: A narrow elongated, slightly flattened, blunt-edged snout, oral and preopercular lateral line canals not branching, widely separated, first dorsal-fin spine height greater than fin apex, second dorsal fin uniform in height, pectoral fins short and broad, pelvic fins rounded, anal fin distinct and curved, caudal fin with short terminal filament, frontal tenaculum prominent in adult males. Colour is a uniform dark chocolate brown without any distinctive blotches, spots or stripes.

Diagnostic Features: See Field Marks above.
Distribution: The sicklefin chimaera is known to occur in the Eastern Atlantic Ocean off the west coast of Africa from Spanish Sahara to Walvis Bay, Namibia. Also recorded in the Indian Ocean (Arabian Sea and off southwestern India).

Habitat: In the Southeastern Atlantic Ocean, this long-nosed chimaera is only known from a few specimens. The species is most commonly found off the southwestern coast of India. It occurs from 200 to 550 m , but nothing else known.

Biology: Oviparous, but nothing else known. Diet includes small invertebrates and fishes.
Size: Maximum total length 127 cm ( 58 cm body length); males and females mature at 50 to 60 cm body length. Size at birth uncertain, but smallest free-swimming individuals ranged from 7 to 10 cm body length ( 13 to 23 cm total length).

Interest to Fisheries and Human Impact: Uncommon and of no fishery importance throughout most of its range, except off southwestern India where this species is commonly taken in a deepwater fishery that includes other uncommon deep-sea elasmobranchs such as Echinorhinus brucus.

The conservation status of this chimaera is Data Deficient, but should be monitored in those areas where deep-sea fisheries are developing.
Local Names: None.
Literature: Compagno, Ebert and Smale (1989); Manilo and Movchan (1989); Krefft (1990); Compagno, Ebert and Cowley (1991); Didier and Stehmann (1996); Dagit (2006b); Didier, Kemper and Ebert (2012); Ebert and Stehmann (2013); Ebert (2014); Kemper and Ebert (In press); Didier (unpubl. data); D.A. Ebert (unpubl. data).


Fig. 233 Neoharriotta pinnata

## 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 Deep-sea Southeastern Atlantic Ocean Species: 2.

Synonyms: None.
FAO Names: En - Knife-nosed chimaeras; Fr - Chimères-couteau; Sp - Quimeras-navaja.
Field Marks: Snout elongated, fleshy, tapering 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 height of upper lobe, margin of upper caudal-fin lobe with row of tubercles, and no anal fin present.

Diagnostic Features: Body bulky, elongated, tapering posterior to pectoral fins, ending in a filamentous tail. Snout very elongate, straight, broad at base, fleshy from base to mid-length, distal tip of snout not fleshy, tip bluntly pointed, not upturn. Adult males with short frontal tenaculum, flat, not deeply curved, and with a distal fleshy bulb with numerous small denticles. Eyes relatively small. Mouth in front of eyes. Tooth plates thin, smooth, blade-like cutting edges, not formed as crushing plates, lacking hypermineralized tritors on surface. Pectoral fins elongate, oval to narrow, rounded apex and along distal edge near base. Pelvic fins broad or elongated, rounded at apex. Pre-pelvic tenaculum spatulate with denticles along the medial edge. Pelvic claspers simple, rod-like structures with a small, fleshy bulbous tip in which there are small pointed denticles. First dorsal fin short-based, low and relatively small, preceded by a serrated spine that extends beyond first dorsal fin height; spine tip does not reach second dorsal fin when depressed. Second dorsal fin low and elongate, separated from first dorsal and caudal fins by distinct gap; dorsal margin convex. Anal fin absent. Caudal-fin dorsal margin narrow or sickle-shaped, with series of 19 to 68 tubercles along upper margin in adults; lower caudal fin lobe similar in height to second dorsal fin, its origin anterior to upper caudal-fin origin. Tail short to very elongated ending in whip-like filament, which is often broken. Colour: uniform dark to pale brown, greyish-brown or white, with no distinctive markings on body or fins.

Local Names: None.
Remarks: Following Didier, Kemper and Ebert (2012) three wide-ranging species are recognized within this genus. Rhinochimaera atlantica is primarily found in the Atlantic Ocean, while R. pacifica is found in the Pacific Ocean. The wide-ranging $\boldsymbol{R}$. africana overlaps both these species and in fact the holotype was collected off the west coast of South Africa, off Doring Bay.

## Key to Deep-sea Southeastern Atlantic Ocean Species:

1a. Body colour an even dark brown; snout broad and paddle-shaped; eye is small; junction of supraorbital and infraorbital canals on ventral side of snout closer to the tip of the snout than to the nasal canal (Fig. 234)

Rhinochimaera africana


Fig. 234 Rhinochimaera africana

1b. Body colour a pale brownish grey with dark fins; snout narrow and conical shaped; junction of supraorbital and infraorbital canals on ventral side of snout nearly equidistant between the tip of the snout and the nasal canal (Fig. 235)

Rhinochimaera atlantica


Fig. 235 Rhinochimaera atlantica

## Rhinochimaera africana Compagno, Stehmann and Ebert, 1990

Rhinochimaera africana Compagno, Stehmann and Ebert, 1990, South African Journal Marine Science, 9: 206, figs. 2-5. Holotype: SAIAB [formerly RUSI] 27744, immature female, 1119 mm total length, 901 mm precaudal length. Type locality: west of Doring Bay, Western Cape, South Africa ( $31^{\circ} 59.8^{\prime} \mathrm{S}, 15^{\circ} 56.2^{\prime} \mathrm{E}$ ), by RV Africana, station A4361 046 E12, 850 m, 17 July 1986.

Synonyms: Rhinochimaera atlantica Penrith, 1969: 66 (in part); Shcherbachev, 1978: 8 (in part); Compagno, 1986: 46 (in part). Rhinochimaera pacifica Shcherbachev, 1982: 28 (in part). Rhinochimaera sp. Compagno, Ebert and Smale, 1989: 122, ill.

Other Combinations: None.
FAO Name: En - Paddlenose chimaera.


Fig. 236 Rhinochimaera africana
Field Marks: A Rhinochimaera with an extremely long, broad, paddle-shaped, bluntly pointed snout, a low, relatively small first dorsal fin and short spine, and a short caudal fin with a minute filament. Colour is a uniform blackish-brown.

Diagnostic Features: Snout elongate, broad, fleshy, paddle-shaped and bluntly pointed at tip; snout slightly depressed at base, more so distally, tip not upturn; preorbital snout about 1.1 to 1.7 times in body length. Eyes small, diameter about 4 times in distance between eye and dorsal-fin spine; mouth located forward of eye. Supraorbital and infraorbital canals junction is closer to the tip of the snout than to the nasal canal. Tooth plates thin, smooth, with sharp blade-like cutting edges, not formed as crushing plates. Pectoral fins moderately long and narrow, rounded apex and along distal edge near base; apices when laid back do not reach pelvic-fin insertions. Pelvic fins broad, paddle-shaped, and short, with convex anterior margin, rounded apex, and moderately convex posterior margin. First dorsal fin low and small, preceded by a serrated spine; spine tip does not reach second dorsal fin when depressed; first dorsal-fin apex below tip of dorsal-fin spine; spine free from anterior margin of dorsal fin for about the distal $1 / 3$ of length; relatively long interdorsal space. Second dorsal fin low, moderately long, distal margin convex. Caudal fin relatively short and broad, sickle-shaped, not greatly elongated; dorsal caudal-fin margin broadly convex; ventral caudal-fin origin anterior to dorsal lobe origin; ventral lobe margin deeper than upper lobe; dorsal lobe with 27 to 46 tubercles from along upper edge in adults; caudal fin ends in a very short vestigial filament. Colour: uniform dark brown to black, with no distinctive markings on body or fins.

Distribution: The paddlenose chimaera is known to occur in the Southeastern Atlantic Ocean off Namibia and South Africa. Also known from the Western and Eastern Indian Ocean, Western Pacific and Southeastern Pacific.

Habitat: A little known longnose chimaera that occurs from about 500 to at least 1500 m . It appears to occur mostly on soft-bottom habitats on deep-sea slopes and around seamounts.

Biology: Oviparous, but nothing else known of its reproductive biology or feeding habits. Unlike the other two Rhinochimaera species R. africana does not appear to aggregate in large numbers, since it is usually caught singly or in small numbers.

Size: Maximum total length about 112 cm (body length about 65 cm ). Adult males at 40 to 50 cm body length; females are adult at about 50 cm body length. Size at birth is unknown.

Interest to Fisheries and Human Impact: Of no commercial value, this species is taken occasionally as bycatch in bottom trawl fisheries.

The conservation status is Data Deficient due to its widespread biogeography, deepwater habitat, and lack of directed commercial fisheries.

Local Names: None.
Remarks: Rhinochimaera africana was first recognized as being distinct from other Rhinochimaera species when it was caught in a trawl along with several R. atlantica off Doring Bay, South Africa. Prior to its recognition as being distinct, it was long misidentified with the other two more common Rhinochimaera species, R. atlantica and R. pacifica, and therefore the geographic distribution of this species may eventually prove to be more wide-ranging than currently known. The above descriptive account is based on Compagno,


Fig. 237 Rhinochimaera africana
$\square$ Known distribution Stehmann and Ebert (1990) and Kemper and Ebert (In press).

Literature: Compagno, Ebert and Smale (1989); Compagno, Stehmann and Ebert (1990); Compagno, Ebert and Cowley (1991); Dagit (2006c); Didier, Kemper and Ebert (2012); Ebert (2014); Kemper and Ebert (In press); D.A. Ebert (unpubl. data).

## 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 southwestern 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 nez mou; $\mathbf{S p}$ - Narigón sierra.


DETAIL OF DORSAL CAUDAL-FIN TUBERCLES
Fig. 238 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, moderate sized eyes, 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 not fleshy; snout length 50 to $87 \%$ 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 branches separate 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, 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 from 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: The straightnose rabbitfish is known to occur throughout the Atlantic Ocean with records in the Southeastern Atlantic Ocean off the Western Cape, South Africa to Namibia. It is most common in the Atlantic Ocean, but also occurs off the east coast of South Africa in the Western Indian Ocean.

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 total length about 140 cm (precaudal length about 90 cm ). Males adult at 107 cm total length (81.3 precaudal length, 47.3 cm body length), adolescent at 105.5 cm ( 80.3 cm precaudal length, 47.7 cm body length), maximum total length at least $112.7 \mathrm{~cm}(82.3 \mathrm{~cm}$ precaudal length, 46.6 cm body). Females adult at 127.4 cm ( 99.0 cm precaudal length, 59.0 cm body length), adolescent at 99.4 $\mathrm{cm}(75.0 \mathrm{~cm}$ precaudal length), maximum length at least 140 cm . Size at birth about 15 cm total length.
Interest to Fisheries and Human Impact: Of no commercial value, this species is taken occasionally as bycatch in bottom trawl fisheries.

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.


Fig. 239 Rhinochimaera atlantica

Local Names: Atlantic longnose chimaera, Spearnose chimaera, Straightnose rabbitfish, Broadnose chimaera, Knifenose chimaera (English).

Remarks: The differences between this species and Rhinochimaera pacifica is based exclusively on the number of caudal tubercles; a character that overlaps these two species. It will likely take molecular studies to resolve this issue. Another wide-ranging Rhinochimaera, R. africana, overlaps the distribution of both R. atlantica and R. pacifica, and is often misidentified with these two latter species.

Literature: Holt and Byrne (1909, 1910); Bigelow and Schroeder (1953, 1954b); Stehmann and Bürkel in Whitehead et al. (1984); Compagno, Ebert and Smale (1989); Compagno, Stehmann and Ebert (1990); Compagno, Ebert and Cowley (1991); Didier (2002); Moore et al. (2003); Møller et al. (2004, 2010); Dagit and Compagno (2006); Didier, Kemper and Ebert (2012); Ebert and Stehmann (2013); Ebert (2014); Kemper and Ebert (In press); 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.
Roman : Suborders, subfamilies, tribes, and FAO and local names
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This volume is a comprehensive, fully illustrated Catalogue of the Sharks, Batoid Fishes, and Chimaeras of the southeastern Atlantic Ocean, encompassing FAO Fishing Area 47. The present volume includes 10 orders, 23 families, 45 genera, and 78 species of cartilaginous fishes occurring in the southeastern Atlantic. It provides accounts for all orders, families, and genera and all keys to taxa are fully illustrated. A species representative account of each genus is also provided and includes: valid modern names and original citation of the species; synonyms; the English, French, and Spanish FAO names for the species: a lateral view 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, an extensive glossary, and a dedicated bibliography.


[^0]:    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)*

