VOLUME 1

COASTAL FISHES OF THE WESTERN INDIAN OCEAN

EDITED BY

Phillip C Heemstra • Elaine Heemstra • David A Ebert • Wouter Holleman • John E Randall

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COASTAL FISHES OF THE WESTERN INDIAN OCEAN

INTRODUCTION AND SUPPLEMENTARY MATERIAL

FOREWORD

Dr Peter Nick Psomadakis

Coastal Fishes of the Western Indian Ocean is the third of a series of extremely popular ichthyological books on southern African and Seychellois marine fish fauna produced by NRF-SAIAB. It fills a longstanding gap as existing reference publications, such as the *FAO Species Identification Sheets for Fishery Purposes, Western Indian Ocean (Fishing Area 51)* and NRF-SAIAB's *Smiths' Sea Fishes,* both released in the mid-1980s, are now largely out of date.

This authoritative publication follows the fine tradition of producing multi-authored, well-illustrated volumes on fisheries resources by FAO and on ichthyofauna by NRF-SAIAB. The format is similar to the one presented in *Smiths' Sea Fishes* but is improved in two fundamental aspects. Well-illustrated keys to all taxa, including orders for bony fishes are now included. An ordinal-level key to bony fishes was not available in *Smiths' Sea Fishes* and its inclusion is an important innovation that greatly assists the non-expert user in the complex task of keying out an unidentified specimen starting from the ordinal level, passing through the familial level and down to its specific identity. The second important improvement is the coverage of nearly all species included in this publication with colour photographs of species in fresh/live condition or with beautifully coloured illustrations. This will be of great use to the non-expert user who is unfamiliar with discoloured specimens held in museum collections and finds the black & white illustrations/line drawings more difficult to apply for the purpose of species identification. Also of note is the inclusion of photographs/colour illustrations of colour morphs of some species (e.g. *Rhinobatos punctifer*), as well as many instances of juvenile colour patterns which are especially helpful to correctly identify those species where juveniles strikingly differ from adult colouration.

While the Western Indian Ocean is home to about 20% of the world's marine fish fauna, current marine biodiversity research efforts are inadequate and/or unequal across the region. As a result, identities and distributions of several species are inaccurately understood and reported in the literature. Taxonomic uncertainty and unavailability of formal species names implies that species are frequently misidentified or not recognised in fishery statistics which could have implications for their sustainable management and conservation.

In a scenario of climate change and global impacts on fish populations, it is important that fishery resources are managed according to an ecosystem approach to fisheries (EAF) which incorporates the marine ecosystem and biodiversity concerns into fisheries management. The principles of EAF are all embedded within the Code of Conduct of Responsible Fisheries and its importance is highlighted in the Blue Transformation initiative of FAO.

Fisheries research surveys at sea offer a unique opportunity to provide further information on marine species and document marine biodiversity. Since 1975, surveys at sea have been an integral part of the Norway & FAO Nansen Programme, and marine fish taxonomists employed at NRF-SAIAB have participated in selected surveys in the region on board the R/V *Dr Fridtjof Nansen* to support the work with identification of species in the catches and develop capacities of local scientists and for sample collection. NRF-SAIAB also hosts some of the reference collections for the Programme. Throughout time, this collaboration has yielded important scientific outputs, including the discovery and formal description of numerous new fish species, especially from surveys conducted in Oman, Yemen, Mozambique, Tanzania, Kenya, Madagascar, Seychelles, Maldives and the Mascarene Plateau. These discoveries show the value of surveys at sea for increasing our understanding of marine biodiversity while providing coastal states with important knowledge for sustainable management of their resources.

According to a recent IUCN assessment, the Western Indian Ocean has the highest level of uncertainty in species conservation status (16.9% of species assessed as Data Deficient) compared to other tropical regions. This means that fundamental biological and ecological information to quantify trends in the population status of species occurring in the region is lacking—a condition that may hamper the progress towards international targets for biodiversity conservation, such as the United Nations Sustainable Development Goals (SDGs) and the Strategic Plan for the Convention on Biological Diversity (CBC).

Coastal Fishes of the Western Indian Ocean is the end product of over twenty years of collaboration between the editors Phillip C Heemstra (deceased), Elaine Heemstra, David A Ebert, Wouter Holleman, John E Randall (deceased) and more than 100 globally recognised experts (including scientific illustrators) on the various families of marine fishes occurring in the region. It will become the reference work for many years to come for both professional fish taxonomists and non-experts and is expected to improve the quality of identification and stimulate research on the biology and ecology of fish species in the region.

In congratulating the editors, authors and illustrators for this excellent production, I hope that the Institute will continue to lead research in marine fish biodiversity in the region, building on the legacy of the Smiths and all those who have devoted time and energy to the conception, production and realisation of this benchmark work.

Dr Peter Nick Psomadakis

EAF-Nansen Programme, Fisheries and Aquaculture Division, Food and Agriculture Organization of the United Nations (FAO) and Research Associate, Ichthyology – South African Institute for Aquatic Biodiversity (NRF-SAIAB)

NRF National Research Foundation | SAIAB South African Institute for Aquatic Biodiversity

FOREWORD

Dr Philemon Mjwara

Within South Africa's National System of Innovation, 'Aquatic Biodiversity' is a fragmented and unevenly attended discipline. As a National Research Facility of the National Research Foundation, which is an agency of the Department of Science and Innovation (DSI), the South African Institute for Aquatic Biodiversity (NRF-SAIAB) serves as a unifying force, covering the discipline from pure to applied science and infrastructure provision.

Twenty years since the Institute became a National Facility, the need for a national unifying force in the aquatic sciences is becoming increasingly relevant. South Africa's aquatic environment has key economic, social and environmental opportunities that are codified in the global Sustainable Development Goals, National Development Plan, Medium Term Strategic Framework, DSI White Paper and the DSI Decadal Plan.

Following the success of its previous international collaborative publication project, *Smiths' Sea Fishes* (first published in 1986), NRF-SAIAB – at that time known as the JLB Smith Institute of Ichthyology – embarked on a similar, but more ambitious, long-term project that provided the means to identify known shallow-water fishes from the tropical and warm-temperate waters of the entire Western Indian Ocean (WIO).

This project generated renewed interest worldwide in the diversity of fishes in the WIO, to the extent that new species of marine fishes from the WIO are still being described almost every month by scientists from Australia, Brazil, Britain, Japan and elsewhere. Over the years, several taxonomists from other countries have travelled to South Africa to come and work on the fish collections at NRF-SAIAB with taxonomists based at the Institute. This multi-volume work covers some 3 600 species of fishes in the largest area of ocean a book like this has ever covered – from Cape Point [18° E] in South Africa, to the Red Sea, Persian/Arabian Gulf and west coast of India, as far as Kanyakumari (formerly Cape Comorin), the southernmost point of India [~80° E] – as well as all the WIO islands north of 40° S and west of 80° E.

The resulting publication, far more substantial than JLB Smith could have imagined, is arranged in five volumes, and covers species that occur in waters generally shallower than 200 m. In addition, the publication includes the oceanography of the WIO, the origins of coral reefs, an account of the people who laid the foundations of our knowledge of the fishes of the WIO, the evolution of bony fishes, maps of the WIO, and more.

Globally South Africa is considered to be the 3rd most diverse country in the world. This current publication reflects the important contributions that the country is making to the world classification of species. The DSI congratulates the authors and the editors who have contributed to this seminal work that is globally highlighting South African expertise.

MP Mjwara

Dr Philemon Mjwara

Director-General: Department of Science and Innovation, South Africa

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ORIGINS

Michael N Bruton

After JLB Smith had described the first living coelacanth, caught off East London in December 1938, he predicted that it was a stray from tropical reefs up the east coast of Africa. As the internal organs of the first coelacanth had been discarded, he was determined to find and examine another specimen. After World War II, he mounted a series of fish-collecting expeditions into East Africa with his wife, Margaret, searching for coelacanths while also making extensive collections of other sea fishes. He had realised that, in order to fully understand the ichthyofauna of South Africa, he needed to know more about East African fishes, as many local species occurred or had close relatives further north.

Smith's research on the collections that he and Margaret Smith made in South and East Africa made it possible for him to write the authoritative book, *The Sea Fishes of Southern Africa*, illustrated by Margaret and a team of artists, and published in 1949. But Smith was not satisfied. In the early 1950s he began planning a more comprehensive book on the fishes of the Western Indian Ocean as a companion volume to the *Sea Fishes* book. In 1949 he told a Trustee of the Natal Museum that he was planning a major work on the fishes of the Western Indian Ocean that would be "… at least 4 times the size of my current volume and would probably occupy 6–10 years". Smith had briefly contemplated accepting the post of Director of the Natal Museum so that he could be closer to the Western Indian Ocean region in order to complete this book, but this appointment never materialised.

Smith had, however, not as yet abandoned his lofty ambition. In 1950 he received a grant of £1 800 for the WIO book project from the CSIR. In 1955 he applied for (and received) a further grant of £5 000 for the WIO project but used these funds, quite legitimately, for publication of the *Ichthyological Bulletin*, a periodical produced by Rhodes University's Department of Ichthyology.

In the introductory pages to the 1953 edition of the *Sea Fishes* book Smith wrote, "A vast collection of East African fishes and many hundreds of valuable photographs and colour sketches have been assembled. There is at present in preparation a Companion East African Volume, in the same scale as this, and as fully illustrated, so as to cover the fishes of the whole Western Indian Ocean". But this project also never came to fruition.

As it turned out, this was wishful thinking. By the end of 1956 Smith realised that he had underestimated the enormity of the project and expressed doubts that he would ever be able to complete it. On 1 December 1959 Stephan Meiring Naude, President of the CSIR, wrote to Smith, suggesting that he should reduce his work load and stating that his "… work is of such inestimable value to the country that you owe it to South Africa to take good care of yourself". Yet, on 12th June 1967, just six months before he died, Smith still wrote to Naude that he was hoping to "… live long enough to complete [the project] as it is likely to be the biggest work of all", and referred to it as the 'Sea Fishes of Mozambique'. This suggested that he had scaled down his vision for a WIO fishes book.

Instead, JLB and Margaret produced a series of carefully researched and well-illustrated scientific papers on the taxonomy and distribution of Western Indian Ocean fishes, family by family, which were published in the *Ichthyological Bulletin,* starting in 1956. By the time of JLB's death in January 1968, they had produced 32 reviews in the series, with a total of 682 pages, 100 pages more than the original *Sea Fishes* book. They had, therefore, achieved their goal from the scientific point of view, but the *Ichthyological Bulletin* publications were not designed for use by lay people. *Fishes of the Seychelles*, published by the Smiths in 1963, by contrast, was "designed to be of optimal value to anglers, skin divers, and other naturalists as well as scientists". This book covered 880 species, of which 95% are found in areas of the tropical Western Indian Ocean other than the Seychelles. The book was in great demand internationally and a second edition and reprints with addition of further species, especially of sharks, rays and clupeoids, were subsequently published.

Between the publication of the 1986 edition of *Smiths' Sea Fishes* (SSF) and the death of Margaret Smith in September 1987, informal discussions were held between then Director of the JLB Smith Institute of Ichthyology, Mike Bruton, past Director, Margaret Smith, and Phillip (Phil) Heemstra, Senior Curator of Marine Fishes at the Institute, on the feasibility of producing a WIO book, and the idea for the project was revived and its development encouraged, although it took some time to get off the ground. Paul Skelton, who became Director of the Institute in 1995, prodded it along, and by 2008 a small number of manuscripts had been submitted to Phil Heemstra. The project then gathered momentum, particularly when David Ebert agreed to coordinate the entire chondrichthyan fauna, and by 2014 most manuscripts had been submitted.

Paul Skelton handed both the Institute, now the South African Institute for Aquatic Biodiversity (NRF-SAIAB), and the book project on to Angus Paterson, who became Managing Director in 2015 and took the project to fruition.

The dream of producing a book on the fishes of the Western Indian Ocean has now finally been realised by the staff of NRF-SAIAB and many international collaborators. The first steps were taken in 1993 by Phil Heemstra, with the backing of John (Jack) Randall of the Bishop Museum in Hawaii. A major contribution to this huge task was Phil's revision of 16 fish families for *FAO Species Identification Sheets for the Western Indian Ocean*. In 2004, after a great deal of further field and laboratory work, Phil and his wife, Elaine, Senior Illustrator at the Institute, also published *Coastal Fishes of Southern Africa* (CFSA).

JLB Smith's original dream has now been fulfilled with the publication by NRF-SAIAB of this multi-volume treatise, *Coastal Fishes of the Western Indian Ocean*, edited by Phillip C Heemstra, with Elaine Heemstra, David A Ebert, Wouter Holleman and John E Randall. It is the culmination of the work of more than 100 authors, photographers and illustrators from 16 countries over a period of more than 20 years, with major contributions from Phillip Heemstra, David Ebert, David Smith, Bruce Collette, Stuart Poss, John Randall, Gerald Allen, Helen Larson, Dannie Hensley, Kunio Amaoka, Eric Anderson and Keiichi Matsuura.

The fine tradition of producing multi-authored, well-illustrated volumes on South and East African sea fishes, pioneered by JLB and Margaret Smith, has been successfully continued by Phillip Heemstra. This world-class, multi-volume book, *Coastal Fishes of the Western Indian Ocean*, is dedicated to the memory of JLB and Margaret Smith, and Phillip Heemstra.

ACKNOWLEDGEMENTS

The Editors

This project could not have been conceived – and realised – without the expertise, many hours of labour and endless patience from more than 100 contributors. In recognition, this first volume includes biographical sketches of these contributors. These contributors also provided many of the photographs used. Colleagues, friends and strangers (all fellow fish watchers) around the world were also approached for permission to use their photographs and, without exception, several hundred photographs were generously donated. Without them many species would not have been illustrated. Most prominent was the late John E Randall who contributed hundreds of images from his extensive library of species photographs.

It also takes the unflagging effort and encouragement of many people over many years to bring a project of this magnitude to fruition. It is almost inevitable that in recording the editors' collective thanks, names of people and institutions who have contributed in one way or another will somehow 'slip through the net', and we apologise at the outset for such omissions.

Our first thanks must go to the three Directors of the South African Institute for Aquatic Biodiversity ([NRF-SAIAB] formerly the JLB Smith Institute of Ichthyology): Michael Bruton, under whose watch *Coastal Fishes of the Western Indian Ocean* (CFWIO) was conceived in 1993; Paul Skelton, who was responsible for bringing the project into focus; and Angus Paterson, the current Managing Director, who supported and encouraged it through to completion.

The funding for such a venture is paramount and this book would not have been completed without the generous support of the South African Department of Science and Innovation and the National Research Foundation.

Dennis and Sally Polack provided the initial sponsorship for the project – without such seed funding the task would have been much more difficult. In addition, their friendship and enthusiastic support over many years has been invaluable. They also hosted several scientists during the course of CFWIO field work.

This work would not have been possible without the backup and support of all the staff at the NRF-SAIAB. In particular, we record our thanks to: Roger Bills, Linda Coetzee, Willem Coetzer, Kholiwe Dubula, Andrew Grant, Vuyani Hanisi, Penny Haworth, Hanoria Kalamashe, Bafo Konqobe, Mark Lisher, Sherwyn Mack, Bernard Mackenzie, Nkosinathi Mazungula, Maditaba Meltaf, Phumeza Mpambani, Vusi Mthombeni, Naniswa Nyoka, Jean Pote, Elvis Rungqu, Sally Schramm, Margie Shaw, Leslie Ter Morshuizen, Garth van Heerden and Joan Wright.

And then there are the people in the background without whom no work ever becomes published. Cindy Kulongowski did a fine job in copy editing the manuscripts which were then proofread by Robert McKenzie and Liz Gowans prior to layout. Stephen Walker of WalkerDigital was responsible for scanning all the plates of painted fishes. Roseanne Palmer contributed excellent drawings of photographs where needed. Susan Abraham helpfully recreated some of the illustrations for the introductory chapters, as well as finalising the inside-cover maps, in collaboration with Willem Coetzer. The bibliography was first compiled by Sheila Hicks from disparate sources. Aidan Wood contributed to completing the bibliography and also assisted with checking the page proofs. Particular thanks are due to Jenny Gon for her meticulous final proofreading of the page proofs.

Mike Schramm of NISC (Pty) Ltd was the independent eye who asked searching questions and whose publishing expertise guided the project through the later stages of the publication process. Liz Gowans tactfully guided the editorial and proofreading team; her efficient organisation, and coordination with the Ink Design design and layout team, greatly facilitated the process. Ink Design's creativity, layout proficiency, amenability to making changes, and endless patience during the lengthy production process is greatly appreciated. The end product is an accolade that cannot be bettered.

Sections of these volumes were reviewed by Gerald R Allen, M Eric Anderson, Geremy Cliff, Matthew T Craig, Brit Finucci, Phillip C Heemstra, Hisashi Imamura, Horst Kaiser, Rob W Leslie, John E McCosker, Hiroyuki Motomura, Richard L Pyle, Helen A Randall, Barry C Russell, David G Smith, Wayne C Starnes, Nico Straube, James van Hasselt, Simon Weigmann and Sabine P Wintner.

The invaluable reference resource provided by *Eschmeyer's Catalog of Fishes* underpinned this book. Where we were unsure, William Eschmeyer, Ronald Fricke and Richard van der Laan patiently and promptly answered the numerous questions our work generated.

Fish survey work which provided new species and fish distributions were undertaken with the help of many people who provided logistic support, hospitality, friendship and local

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NRF-SAIAB has over many decades benefitted from the input and help of fish enthusiasts, photographers, divers, aquarists, and anglers. There is a long history of citizen scientists photographing, collecting and sending interesting specimens that they had not seen before, often to find that the NRF-SAIAB ichthyologists did not recognise the species either. Or if they did, did not know of them occurring in that particular area. Their photographs (several of which appear in this book), specimens and detailed observations have led to the description of many new species and also documented species distributions. Their names and the many others who provided photographs are listed below.

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INTRODUCTION: ABOUT THIS BOOK

The primary purpose of this book is to provide a means of identifying the more than 3 200 species of coastal fishes known to occur in the Western Indian Ocean (WIO). Coastal fishes are those that inhabit waters generally less than ~200 m deep, the waters over continental and insular shelves, and upper continental slopes. The book also includes some oceanic species and species that live in deeper water, but are sometimes caught in trawls in less than 200 m, or that migrate into shallower waters at night to feed.

The Western Indian Ocean (WIO), as treated in these volumes, is the area between Cape Point, South Africa, and 77°34' E, at Kanyakumari (formerly Cape Cormorin), the southernmost point of India, and to 40° S, just south of St Paul Island. Although considered as separate water bodies, the Red Sea and Persian/Arabian Gulf have been included. Some contributors have also chosen to include species from Sri Lanka. The region thus encompasses the entire east and southern coasts of Africa, Madagascar and the various island clusters of the Comoros, the Seychelles, the Maldive and Lakshadweep islands, the Chagos Archipelago and the islands and sea mounts of the Mascarene Plateau, to as far as 40° S, and thus some fishes from St Paul and Amsterdam Islands have been included. This large expanse, stretching from tropical waters of the northwestern Indian Ocean to the warm temperate waters of False Bay, South Africa, includes a number of poorly known biogeographic areas.

A map of the entire Indian Ocean is placed on the inside front cover of each printed volume, with some areas in greater detail on the inside back cover. The book does not include distribution maps for species, but gives localities from which species are known, with emphasis on WIO localities; our understanding of distributions of many species is often incomplete.

Fishes are the most abundant and diverse group of vertebrates and have colonised every aquatic habitat on Earth: the oceans, lakes, rivers and caves, from polar seas at −2 °C to hot, freshwater springs at 44 °C, and from tropical reefs and mangrove forests to the deepest ocean depths. Fishes are also the most poorly known group of vertebrates. In the 2006 edition of Joseph Nelson's *Fishes of the World* the estimate of the number of species of extant fishes worldwide stood at about 23 000. This number is growing annually, and was thought to be about 33 460 species at the end of 2016 (www.fishwisepro.com). Between the years 2000 and 2015 an average of 150 new species of marine fishes were described each year – of which 10% of the total (156 species) were from the WIO. The WIO is home to about 15% of all the marine fish species in the world's oceans.

Another measure of the diversity of fishes of this area is its relatively high level of endemicity, particularly around southern Africa and in the Red Sea. About 13% of southern African marine fishes are endemic, most of these in only five families: Clinidae with about 44 endemic species, Gobiidae with 28, Sparidae with 28, Pentanchidae with 6, and Batrachoididae with 7 endemic species. In the Red Sea at least 170 of the more than 1100 species are endemic.

The WIO region is also home to a large human population, representing a wide range of ethnic and cultural backgrounds. The area includes the countries of South Africa, Mozambique, Tanzania, Kenya, Somalia, Eritrea, Sudan, Egypt, Israel, Jordan, Saudi Arabia, Yemen, Oman, United Arab Emirates, Qatar, Bahrain, Kuwait, Iraq, Iran, Pakistan, India and Sri Lanka, as well as the many island nations and territories. Many of the people living in coastal areas are dependent on fish catches and other marine resources for both sustenance and often a livelihood, as highly diversified artisanal fisheries make up the bulk of the fishing effort in the region.

And, as elsewhere in the world, many of the fish resources have been compromised by commercial interests (including those of other countries), often leaving fish stocks in a poor state. This book has a number of purposes, all of which coalesce around providing users with a better understanding of the area's fishes and their environment. Accordingly, it includes a number of background chapters covering subjects as diverse as the oceanography of the region, and the history and evolution of the bony fishes.

In recent years genetic analysis has proved to be a powerful tool for taxonomists. In many instances molecular results have caused taxonomists to rethink both the definitions of certain taxa and the interrelationships of taxa. In some instances, what were long considered cohesive (monophyletic) taxa were found to include groups of fishes that are in fact not closely related (paraphyletic), while in other instances taxa thought to be distinct were found not to be, meriting their merging with other exiting taxa. At times, long-accepted family groups have been divided into two or more distinct families, or separate families have been combined into a single one. Where possible such changes in our understanding of the relationships of fishes are reflected in these volumes. Where some contributors have taken a more conservative approach by awaiting more research and not adopting these changes, alternative taxonomies are noted (see also the introductory chapter on **Naming organisms and determining their relationships**).

For each species in the book, the literature pertinent to that species in the WIO is given: the original species description reference, synonyms for the region and other important taxonomic and biological references. For many commercially important species or fishes of interest to anglers there is additional information on life history, size and capture, and for some but not all species, their IUCN conservation status if Near Threatened, Vulnerable, Endangered or Critically Endangered (in the first instance, valid at the time of writing. See www.iucnredlist.org for current information. *Note:* we have not included the IUCN conservation status where species are of Least Concern or Data Deficient).

Most species are illustrated with photographs, drawings or paintings. Colour photographs and paintings are provided on plates for each volume. The coverage of each of the volumes of this book is outlined in the next chapter.

HOW TO USE THIS BOOK

The *Coastal Fishes of the Western Indian Ocean* has family and genus accounts, keys, species descriptions, illustrations, paintings and photographs of most of the known coastal fish species from the Western Indian Ocean (WIO).

The book has been divided into five volumes. The first part of Volume 1 contains all introductory material, including chapters of general interest, plus a list of abbreviations, a comprehensive glossary and a bibliography. The second part contains the cartilaginous fishes (hagfishes, sharks, rays and chimaeras). Volume 2 contains the bony fishes (teleosts) – eels, herrings, flyingfishes, seahorses, scorpionfishes, and others. Volumes 3 to 5 contain the many families of perciform (perch-like) fishes, as well as the flatfishes, spikefishes, triplespines, triggerfishes, filefishes, boxfishes, pufferfishes, porcupinefishes, molas and the coelacanth.

The book has been designed to help identify the shallow-water fishes (to ~200 m) found in the area: along continental and insular localities, in tidepools, estuaries and mangroves, along rocky coastlines and sandy beaches, on inshore and offshore reefs, banks and seamounts, as well as pelagic species of interest to commercial and sport fishermen. The various keys to orders, families, genera and species are for species that occur in the WIO and are not necessarily applicable in other areas.*

The maps printed on the inside covers (or separate PDF for digital version) show the areas covered in these volumes. Coordinates of place names used in the text can be accessed from a number of websites, such as www.geonames.org. The place names used in synonymies of species have been rendered in their currently accepted form, and not as they were originally used.

Each volume has an index to scientific names for the species described in the volume, as well as an index to English common names used for their families. Names that appear in synonymies are ***not*** included in the indexes, and can be found in *Eschmeyer's Catalog of Fishes* (see link at the end of this chapter). In addition, two full alphabetical lists of all family names (scientific and common) are provided with their corresponding volume number. These are included to assist the reader in identifying the correct volume for a particular family.

CLASSIFICATION

All living organisms are grouped in a hierarchical system – their classification – which is determined by how we understand the way in which the various groups of organisms are related to each other. The chapter on taxonomy explains how organisms are classified and given their names.

IDENTIFYING FISHES

To find more information about a particular fish species, you will need to identify the family to which the fish belongs. Scientific names of families end in -idae (e.g., Serranidae). If you know the family of the fish you want to identify, e.g., Serranidae (perchlets and seabasses), or Carcharhinidae (requiem sharks), use the index to go to the family account in the book.

If you do not know family, genus or species, decide if your fish is a cartilaginous fish – a shark, ray, hagfish or chimaera – or a bony fish. If it is a cartilaginous fish (a chondrichthyan), you will find the ***Key to Families of Chondrichthyans*** in Volume 1. If it is a bony fish, you will find the ***Key to Orders of Bony Fishes*** in Volume 2. If this key takes you to the Order Perciformes (the perch-like fishes), you will find the ***Key to Perciform Families*** in Volumes 3 to 5. The keys to families will help find the family account and the related keys to genera and species of that family. Some families have several different 'typical' shapes, and the outline drawings of the shapes also help place a fish in a family. Once you have identified a likely family, turn to the family account. Compare your fish with the drawing, painting or photograph. A plate reference will direct you to the relevant plate(s) if there are colour photographs or paintings for the species. Photographs and paintings have been grouped together in families to make identification easier. If the colour or shapes of the species illustration do not match, read the species description to check for variation within the species; check the account for the genus for details not

*Note: the drawings contained in the keys were mostly drawn for this book or sourced from *Smiths' Sea Fishes*, unless otherwise indicated.

duplicated in the species account. Distributions can confirm whether your fish is known from the area. However, bear in mind that the WIO distributions, as known at present, are often a result of sparse and uneven sampling. Many species not previously known from an area , or depths <200 m, have been brought to the attention of scientists by enthusiastic amateur ichthyologists.

The photographs of some species have been included without accompanying species diagnoses in the text. This is indicated by # after the caption and indicates that the species is likely to occur in the WIO but has not yet been confirmed, or is known from the area but a species account has not been included because of time constraints, or the species has not been described.

The families are placed in evolutionary (phylogenetic) order in the book. In other words, the oldest, supposedly most 'primitive', cartilaginous fishes (Class Chondrichthyes) are in Volume 1, with an account of their origins and evolution, followed by the more recently evolved or 'derived' bony fish families (Class Osteichthyes) in the other volumes. There is also an account of the origins and evolution of the bony fishes at the beginning of Volume 2.

The sequence in which the families are placed generally groups similar fishes together (e.g., all catsharks [Pentanchidae and Scyliorhinidae], gobies [Gobiidae], or jobfish and snappers [Lutjanidae]), which makes comparisons and identification easier. Within families, genera and species are arranged alphabetically by scientific name. A common English name has been given for most species; however, some species are known only from one or two specimens and have no common names; some well-known species may have several. The common names of many fishes can be accessed at www.fishbase.org and www.fishwisepro.com.

FAMILY ACCOUNTS

Each family account starts with a brief description of the family characteristics and biology. The worldwide geographic distribution of the family is given, as is the estimated number of genera and species in the family.

GENUS ACCOUNTS

Genus accounts give a short list of the characters of the species in that genus. *When certain characters, such as fin spine and ray counts are common to all species in the genus, they are usually not repeated in the species accounts.* The number of known species in the genus worldwide (at time of publication), as well as in the WIO, are given.

SPECIES ACCOUNTS

Each species account starts with a scientific and (usually) a common name. The scientific name comprises the genus and the species epithet, followed by the author(s) of that species and the year in which the name was published and the locality where the holotype was found. The oldest name is usually the valid name (or senior synonym) and is the one that is used. More recent names are considered junior synonyms (see ***synonymy*** below). The author is the person (or persons) who identified that fish as a new species *and* gave it its scientific name and description of the species. An author's name in parentheses indicates that the genus to which the species is currently allocated is different from the one in which it was originally placed. Some species have yet to be given a scientific name and have **sp.** (the abbreviation of species) after the genus name. Some families and genera are noted as 'monotypic', meaning there is only a single genus with a single species in the family, or only a single species in the genus. A few species names in the text and captions to illustrations are also given as '*Genus* cf. *species*', meaning the species is considered very similar to the name given, but the author is not absolutely sure.

Below the name (the heading) is the original name of the species, the author(s) and date of publication, and the type locality, i.e., where the fish was collected or caught. The type locality is usually given in parentheses; if the locality was not stated in the original description, but is known, it is written in square brackets. Next is a ***synonymy*** which lists the names used by various authors over time, including junior synonyms and misidentifications. A misidentification has the incorrectly used species name, and (in parentheses) *non* with the author of the misidentified species to show that the name given is valid but incorrectly applied to that species. A ? (question mark) means that the identification is not certain, and 'in part' means that only part of the reference applies to the species. *In most instances, only the names used in the Western Indian Ocean have been listed*. This has been done in the interests of brevity, as some species have very lengthy synonymies.

The first paragraph of the species account is the diagnosis of the species and includes fin ray and body scale counts, as well as other measurements and features that aid identification. Diagnostic data given for the family or genus are not usually repeated in species accounts. Measurements of body features are given as a ratio of a larger measurement, such as body length or depth, head length, fork length, standard length or total length, or as a percentage of a different length.

Colour descriptions are usually given where known, particularly when there is sexual dichromatism (different colour patterns for females and males), which is common for many species. Descriptions are accompanied by an illustration or photograph of the fish (or both, where available) and these may also document changes in colouration and body shape from juveniles to adults. Some species accounts are therefore accompanied by more than one image. If known, the length for each fish illustrated is given in the caption. For a number of species, however, there are few photographs, and the best image available has been used. The lengths are mostly given to the nearest centimetre or millimetre. Localities, where known, are in parentheses. To make comparisons easier, some drawings and photographs have been reversed so that the fish faces left, a convention used around the world when illustrating fishes. The colour notes include the known maximum size of the species.

The distribution of a species is given as the localities in WIO where a species is known to occur, while for *outside WIO, usually only approximate distribution ranges are noted.*

Finally, some additional remarks are often included that provide other relevant information about the species that may be of interest or importance, e.g., information about fisheries, feeding, habitat, reproduction, questions about identity, and IUCN conservation status where appropriate.

Many worthy sources of information on fishes, including taxonomic information, are available on the internet and we've listed a number of useful URLs below.

Eschmeyer's Catalog of Fishes: https://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp

FishBase: www.fishbase.org – *global information system on fishes*

FishWise Professional: www.fishwisepro.com – *relational database that can be interrogated*

International Union for Conservation of Nature: www.iucn.org

John E. Randall's Fish Photos: http://pbs.bishopmuseum.org/images/JER/images.asp

South African Institute for Aquatic Biodiversity: www.saiab.ac.za

NAMING ORGANISMS AND DETERMINING THEIR RELATIONSHIPS

Wouter Holleman and Gavin Gouws

The system of binomial nomenclature by which all plants and animals are given a genus name and a species name, was established by Carl Linnaeus in the first half of the 18th century. The names are based on Latin and Greek and, for animals, are governed by a set of rules laid down in the *International Code of Zoological Nomenclature*. The 10th edition of Linnaeus's *Systema Naturae*, published in 1758, is considered the starting point for all zoological nomenclature.

Organisms are given scientific names for several reasons. The first is for consistency so that everyone knows which species, genus or family is being referred to. The second is that the names are a reflection of the assumed relationship of organisms. The species in a particular genus are assumed to be more closely related to each other than to other less similar species, which are then placed in a different genus. In Linnaeus's words: *"Characterem non constituero Genus, sed Genus Characterem"*, which Darwin commented on as follows:

> Such expressions as that famous one of Linnaeus ... that *the characters do not make the genus, but that the genus gives the characters*, seem to imply that something more is included in our classifications, than mere resemblance. I believe that something more is included; and that propinquity of descent – the only known cause of the similarity of organic beings – is the bond, hidden as it is by various degrees of modification, which is partially revealed to us by our classifications. (Darwin 1859)

These relationships – the "propinquity of descent" – are implicit in Darwin's theory of evolution, as expounded in *On the Origin of Species by Means of Natural Selection*, first published in 1859. In the book he established the notion that all animals (and plants) vary and that species evolve by the process of natural selection so that, in effect, all species are descended from a single, common ancestor. In fact, the only illustration to appear in his book is a small hypothetical 'tree' that shows the relationships between three taxa.

Over the years, taxonomy and systematics have incorporated increasingly more information and techniques, thereby contributing to a better understanding of what species are.

For many years animals and plants have been grouped together based on their morphological similarity. Species that look most similar were assumed to be most closely related: note the similarity between the various species of butterfly fishes, the Chaetodontidae (Volume 3), with their deep, compressed bodies, bristle-like teeth and eye-catching colours, often in combinations of yellow, black, white and silver. This way of classifying is called *gradistic* taxonomy. Very often, when the similarities were derived from a common ancestor, the taxa that were created in this way were reflections of the actual relationship between organisms.

In 1963, Robert R Sokal and Peter HA Sneath developed a classification system which grouped organisms into taxonomic units by statistical methods, in which certain characters or character states were given numerical values. These 'numerical taxonomists' aimed to create a taxonomy using numeric algorithms like cluster analysis, rather than using subjective evaluation of similarity. They divided the field into *phenetics* in which classifications are formed based on the patterns of overall similarities, and *cladistics* in which classifications are based on the branching patterns of the estimated evolutionary history of the taxa.

Although this was intended to be objective, in practice, the choice and implicit or explicit weighting of characteristics was too often influenced by the data available and by the research interests of the investigator. What was objective were the explicit steps that were used to create dendrograms and cladograms using numerical methods, rather than any subjective synthesis of the data.

At about the same time, a German entomologist, Willi Hennig, developed a different approach, one based on the notion that species evolved suites of characters that enabled them to adapt to a particular environment. Such adaptations – or 'specialisations' – were named 'apomorphies' by Hennig, and if they were shared by a group of taxa they were termed 'synapomorphies'. A Hennigian system of classifying organisms thus was based not merely on the similarities between taxa, but on whether those similarities were both derived and shared in order to reflect the actual evolutionary relationships between taxa. In other words, the relationships were reflections of genealogies.

To discover the genealogical relationships between taxa involved comparing selected characters (bones, muscles and ligaments, colour patterns, behaviour patterns and so on) in one group of organisms or taxa, and then comparing the characters with the same suite of characters in a similar taxon called the ‘outgroup’. By this method one could then determine which characters were ‘specialisations’ shared by the organisms or taxa of the ‘in-group’, and which thus were ‘synapomorphies’. These were distinguished from characters spread more widely, and beyond the group under consideration, which are ‘plesiomorphic’ characters, or characters that were the result of parallel evolution, where two unrelated taxa evolved similar traits. Such characters are called ‘anologues’, and ‘homoplasies’ when occurring in two or more otherwise closely related groups. So, for example, all butterfly fishes (Chaetodontidae) possess many peculiar, bristle-like teeth on the jaws, not found in any other fishes. They do, however, have compressed bodies and yellow and black colour patterns similar to many rabbitfishes (Siganidae), but rabbitfishes have two spines in their pelvic fins, one on either side of five central rays, with the innermost spine connected to the body by a membrane, a character not found in any other group of fishes.

Another example, not from the world of fishes, will further illustrate this. All birds share a particular specialisation (synapomorphy), in that they have feathers and wings for flight. However, not all birds fly – think of rheas, emus and ostriches. These birds are called ratites, and have secondarily lost the ability to fly, which is in itself a derived or apomorphic characteristic. Birds also all lay shelled eggs, an adaptation for living on dry land (fishes and amphibians lay their eggs in water to prevent the embryos drying out). But, lizards, snakes, crocodiles and tortoises also lay eggs, as did many dinosaurs we know of. Since the shelled egg is an apomorphic character that it is shared by such a large groups of seemingly unrelated animals, it suggests that birds, lizards, tortoises, crocodiles and dinosaurs are all related. And so, because various anatomical and molecular data show clearly that they are in fact related, they are grouped together in a large taxon called the Archosauria.

This way of classifying organisms is now referred to as ‘cladistics’ or ‘phylogenetic systematics’, a clade being a number of genealogically related taxa. A clade with a single, common ancestor is considered the correct reflection of the evolutionary relationships between its constituent taxa, and is called ‘monophyletic’. Most taxonomists today apply cladistic methodology to their work. Taxonomists also began to look beyond mere morphological characters and include behaviour, physiology and various aspects of ecology in their suites of characters.

The 1960s saw the rise of the genetic sciences and the use of DNA analysis for a multitude of different purposes. Genetic information has always been an intrinsic part of marine fish systematics and taxonomy insofar as the characters used to define taxonomic units (whether species, genera, families or higher taxa) and the systematic arrangements of these are heritable and largely genetically determined. However, the development of techniques that allowed insights into the genetics of the organisms at the molecular level, either directly or by inference, has had a profound influence on ichthyology. The variety of techniques and markers for generating genetic data, and the range of applications of such information are myriad. This overview thus focuses only on the taxonomic and systematic applications, and those techniques that have been widely used in ichthyology.

Genetic data began to take hold in the 1960s, with the development of protein or allozyme electrophoresis. This involved placing a crude protein solution, extracted from particular tissues of the specimens of interest, in a gel matrix under an electric current. Protein molecules would migrate through the matrix, their mobility determined by the size, shape and charge of the molecules. Differences in the extent of movement of a specific protein, reflecting differences in the phenotype of that protein and amino acid variation among individuals, provided a rough indication of differences at the DNA level for the genes encoding these proteins. Individuals could then be genotyped and compared using the profiles of several proteins, and this data subjected to statistical analysis. However, the technique was crude; genetic diversity and divergence were often underestimated, and aspects of the genotyping were somewhat subjective. It also became increasingly difficult to apply to increasing taxonomic rank, as the homology of the specific proteins and alleles examined became difficulty to establish. Nonetheless, the technique was widely applied – molecular systematists commonly refer to the 1970s and 1980s as the “find ’em and grind ’em” era (in reference to the production of the protein extract). In ichthyology, this technique and the data generated were used extensively to examine diversity within and among species. It was a particularly powerful tool for testing species boundaries and for species delineation; any fixed differences (e.g., different sets of alleles) in the genotypes of these Mendelian-inherited markers among populations could be used to infer reproductive isolation among biological species. Hybridisation was also frequently studied, and the technique was invaluable for investigating population and fishery genetics.

While allozymes provided an indirect assessment of variation at the DNA-sequence level, restriction analyses allowed a closer look at the DNA molecule itself. In Restriction Fragment Length Polymorphisms (RFLPs), the DNA molecule is ‘cut up’ using endonuclease restriction enzymes. The resulting ‘digestion profiles’, sometimes referred to as ‘fingerprints’, are compared among samples. The presence of a particular fragment in one and its absence in another is as a result of differences in the DNA sequence at the restriction site, such that the enzyme was unable to cleave the DNA at that specific point in the DNA strand. This approach, used mostly to examine patterns of genetic variation and diversity within species, was short-lived and was superseded by DNA sequencing. However, the general principle is still applied in more modern and routinely used techniques, such as Amplified Fragment Length Polymorphisms (AFLPs).

The full power of genetic data was revealed following the invention of Sanger sequencing in 1977 and, particularly, Polymerase Chain Reactions (PCR) in 1985. Through these techniques it became possible to isolate, amplify, sequence, and directly visualise and analyse specific DNA sequences. This spawned a wealth of DNA-sequence-based studies, and the approach was firmly entrenched and widely used by the early to mid-1990s. Initially, these studies used mitochondrial DNA gene regions almost exclusively.

Mitochondrial DNA (mtDNA) is maternally inherited and is haploid; it gives only one perspective with respect to genetic structure, relationships and evolutionary history. However, the benefits of mtDNA are that the molecule is present in high numbers in the cells, and is technically simple to work with. Very quickly a range of primers and laboratory protocols were in place to amplify mtDNA fragments.

Technology developed, protocols were refined and competencies honed, and more studies began to incorporate more nuclear DNA markers, which are diploid markers and reflect the contributions of both parents in sexually reproducing species. They thus provide a more holistic picture of relationships. Moreover, computational advances and the incorporation of novel statistical approaches meant that larger datasets (with more markers and data, and/or wider taxonomic representation) could be analysed in less time and with more rigour and complexity.

Incorporating data from more and more gene regions meant that the final relationships revealed by the analyses of the various genes, each providing their own patterns of relationship of the gene itself (the gene tree), better approximated the true relationships and evolutionary history (the species tree) of the taxa under study. With this complexity, studies moved beyond just examining species boundaries and identifying new species, detecting hybridisation, and proposing and testing phylogenetic relationships and hypotheses (with obvious implications for taxonomy, systematic arrangements and character evolution), to investigating aspects of biogeography and dating evolutionary events and the divergence of taxa.

The taxonomic arrangements suggested by molecular or DNA data have not been without controversy. Some have been widely accepted, but others are still robustly debated among the morphological and molecular camps. Among the more controversial arrangements include the placement of the Scaridae (parrotfishes) within the Labridae (wrasses) rather than as an independent family; the inclusion of the fusiliers (Caesionidae) as a subfamily within the snappers (Lutjanidae); and the raising of the subfamily Epinephelinae (groupers, podges and soapfishes) from the larger group of serranoids (groupers, podges, soapfishes, sea basses, basslets and perchlets) as an independent family. The continuous state of flux of generic arrangements one sees in large groups, such as the Apogonidae, demonstrates the interaction between the molecular perspectives and the reappraisal of morphological characters. There is no doubt that many other taxa will experience similar rearrangements as DNA sequencing progresses.

A significant advancement, which has led to an exponential increase in the amount of DNA-sequence data available for marine fishes over the last decade, is DNA barcoding. Molecular systematists have long known that one can identify known species and detect new species using DNA-sequence data. However, an initiative was established for this particular application of DNA analysis, and was popularised by Paul Hebert and colleagues at the University of Guelph, Canada, under the banner of DNA barcoding. Their objective was to create a DNA-sequence (termed 'barcodes') reference library for all organisms on Earth. DNA barcodes included in the database (www.barcodinglife.org) would be derived from and underpinned by expertly identified, taxonomically validated specimens, lodged in reputable scientific/natural history collections, and accompanied by taxonomic information, repository and accession details, collection and geographic information, and an image. Standardised genetic markers were to be used. These would have sufficient information content to accurately and reliably discriminate species and be applicable across many different organismal groups. A fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene was chosen for most animals. For most marine fishes, this has proved to be effective, but additional markers have been considered for certain groups, such as the elasmobranchs, that show enigmatic mtDNA evolution. The reference database would enable reliable and unambiguous species identification for users without (or without access to) taxonomic expertise. Users would include ecologists, biologists, resource managers, biodiversity practitioners, conservationists, compliance and enforcement agencies, customs and excise officials, and the general public. Among the benefits, other than having rapid and accurate species identifications for unknown specimens, included assigning a species identity to different life-history stages or sexes, where one form might be unknown, to the forensic applications in being able to identify a species from a fragment or a piece of tissue. Barcoding was also suggested as a boon to solving the 'taxonomic impediment', the dwindling number of taxonomists and capacity in taxonomy in the face of immense undescribed and imperilled biodiversity. Here, barcoding could provide assistance to taxonomists, indicating new species requiring formal description or highlighting problematic groups.

DNA barcoding has not been without its detractors. Its validity as a scientific discipline (rather than a technical exercise), its assumptions, the depth of the analyses routinely used, its accuracy and performance, and its contribution towards solving the 'taxonomic impediment' have all been questioned. Nonetheless, for marine fishes, it has been a valuable tool in terms of compiling inventories, in forensic applications, and in linking eggs and larvae to adult forms. The last decade has also seen a plethora of new species described, combining DNA barcoding, morphological analyses and traditional taxonomy.

Recently, new technologies have brought us Next-Generation Sequencing (NGS). NGS 'parallelises' DNA sequencing, such that several million different sequences (upwards of 50 million on new platforms) can be generated in single reactions, rather than the single sequence produced by Sanger sequencing. Continuous improvements are increasing the numbers and lengths of the fragments that can be produced. The technology and the applications are still relatively expensive, but the high-throughput nature and the amount of data that is obtained result in a low 'cost per sequence'. As such, it is now feasible to generate full genomes, by piecing together these fragments, for the samples and species of interest and to analyse relationships using these. Alternatively, a 'shotgun' approach will randomly generate sequences from the genomes of many taxa, and researchers can select markers or fragments of DNA that are common to the species or samples studied, or that show appropriate levels of variation, to address the question at hand. Examples of the two approaches are the recent publication (in the journal *Nature*) of the coelacanth genome, and the large phylogenies involving several thousand species, being constructed using Ultra-Conserved Elements, to examine the relationships, evolutionary history and taxonomic arrangements within the percomorphs. The systematic discipline of phylogenetics has been expanded to accommodate the use and analysis of such genomic data, as phylogenomics. The full genomic information also gives one access to markers that are under selection, and a variety of markers such as Single Nucleotide Polymorphisms (SNPs) and microsatellites for population genetic studies. Similarly, these techniques can also be applied to produce data relevant to studies of gene expression and epigenetics. Analysis of such large datasets is always a constraint but computing (especially cluster or 'super' computing), bioinformatics and data analysis pipelines are continually being developed to serve this advancing field. The growth in NGS capability has been astounding, and one can only speculate what will be available to ichthyological geneticists in the future.

Carl Linnaeus was born on 23 May 1707, in Stenbrohult in southern Sweden. His father was a Lutheran pastor and an avid gardener, and from early on, Carl developed a deep love of plants and a fascination for their names. He studied medicine at the University of Uppsala, but actually spent most of his time studying plants. In 1731, while still a student with little money, he made an expedition to Lapland to collect plants, and in 1734 he made another expedition to central Sweden. The following year he went to Holland to study further at the universities of Hardewijk and Leiden and in the same year he published the first edition of a slim little book on the classification of living organisms, his *Systema Naturae*.

Linnaeus returned to Sweden in 1738 where he practiced medicine and lectured at the University of Uppsala, becoming a professor at the university in 1741. While in Stockholm, he restored the university's botanical garden, arranging the plants according to his system of classification.

Linnaeus arranged for some of his students to go on trade and exploration voyages all over the world. Daniel Solander, perhaps his most famous student, was naturalist on Captain James Cook's first voyage around the world. Another student, Anders Sparrman, was botanist on Cook's second voyage. These students brought back to Europe the first plant collections from Australia and the South Pacific. Others brought back specimens from Japan, North America, Southeast Asia, Africa and the Middle East. As more and more plant and animal specimens were brought to Linnaeus, he continued to add to and revise his *Systema Naturae*, until it comprised many volumes.

In 1758 he bought an estate called Hammarby, near Uppsala, and there built a museum for all his collections. Three years later he was made a nobleman and became Carl von Linné. When Linnaeus died in 1778, his son Carl, became professor in his place. But Carl died five years later and Linnaeus's mother and sisters sold Linnaeus's library, manuscripts and collections to Sir James Edward Smith, who founded the Linnean Society in London to look after them.

GLOSSARY

allele – a specific and unique form or variant of a particular gene or genetic marker; alleles typically refer to pairs of genes found on each of the two homologous chromosomes of a diploid organism.

allozyme – particular form of a given protein, coded by a particular allele of the gene responsible for encoding for that protein.

charge (of a molecule) – molecules possess a net electrical charge, determined by the structure of the molecule (amino acids in the case of proteins), the atomic make-up of the molecule itself and the arrangement and nature of subatomic particles, under certain physical conditions (e.g., pH, chemical composition of the medium).

cleave (DNA) – the breaking of the DNA molecule/strand into two (or more) fragments by breaking the phosphate bonds that link the individual nucleotides in the chain together. This can be done with the use of enzymes, chemically, physically or by radiation.

diploid – having both chromosomes of the paired homologous chromosome set and, thus, both copies of each gene present in the cell nucleus; resulting from sexual reproduction.

encoding (genes and proteins) – the function and process whereby a particular gene produces a protein or enzyme; a gene responsible for a certain character, product, process, behaviour or phenotypic trait is said to *encode* for that feature.

endonuclease restriction enzymes – bacterial enzymes that cleave (break) DNA molecules wherever a particular sequence of nucleotides (the restriction site) is recognised.

genotype – the genetic make-up (profile) of the individual organism; the specific combination of genetic variants (e.g., a DNA sequence or a combination of alleles) for a genetic marker being studied or underpinning a character (phenotype) being considered.

haploid – having only one chromosome (of the normally paired homologous chromosome set) and, thus, one copy of each gene present in the cell nucleus or cell organelle.

homology – sharing the same evolutionary origins.

Mendelian inheritance – the rules of genetic inheritance in diploid organisms, as deduced by Gregor Mendel's seminal 'genetic' hypotheses based on breeding, cross-breeding and observing the phenotypes of garden peas. This work suggested that phenotypes are controlled by two factors (alleles in a genetic context), one obtained from each parent; that these factors assort or act independently of factors for other phenotypes during cell division (meiosis) and fertilisation; that these factors can be dominant or recessive with respect to influencing the phenotype, and that the phenotypic outcomes can be predicted numerically/statistically, based on the phenotypes present in the population and by tracing a genealogy.

mitochondrial DNA – an extranuclear (i.e., occurring outside the cell nucleus), double-stranded, circular DNA molecule found in the mitochondria of animal cells; the molecule is maternally inherited and haploid.

percomorph – fishes belonging to the Percomorpha, a large clade of bony fishes, mostly perciform, characterised by having bony fin spines, a ductless swimbladder and ctenoid scales.

phenotype – physical features of the organism or aspects of the organism's biochemistry, physiology or behaviour that can be observed and are thought to reflect variation in the genotype or the interaction of the genotype and the environment.

population – a group of organisms belonging to the same species that co-occur in a distinct area.

protocols – a set of procedures or a methodology to be followed in the laboratory.

taxon (pl. taxa) – a group of organisms such as a species, genus or a family that share a common ancestor.

ASPECTS OF THE BIOLOGY OF FISHES

This brief introduction to some aspects of the biology of fishes serves as a background to the many species covered in these volumes, and has been included for two reasons. The first is that many of the topics covered, such as colour and aspects of reproduction and physiology, are important taxonomic tools used to identify different species. The second is to give some insight into the way fishes live in an environment very different to our own.

SHAPE, SIZE, SWIMMING AND SPEED

Fishes exhibit a tremendous variety of shapes: compressed (flattened from side to side, e.g., butterflyfish and moonies); elongate (e.g., snoek and cutlassfish); robust and streamlined (e.g. tunas); depressed (flattened from back-to-belly e.g., monkfishes and stingrays); spherical (e.g., porcupinefishes); or box-shaped (e.g., many boxfishes). The boxfish, *Tetrosomus reipublicae*, is triangular in cross-section. The ocean sunfish, *Mola mola*, resembles a truncate disc or the front end of a fish that has been cut in two, hence the name 'head-fish' by which it is sometimes known (Figure 1).

The largest fish in the world is the whale shark, which attains a length of at least 12 m, and perhaps as much as 19 m. Like the blue whale, which grows considerably larger, the whale shark also feeds on plankton. The smallest fishes in the world are *Paedocypris progenetica* (7.9 mm SL) from a peat swamp in Indonesia, *Schindleria brevipinguis* (8.4 mm SL) from the Great Barrier Reef and Coral Sea, the pygmy goby *Pandaka pygmaea* (9.0 mm SL) from the Philippines and *Trimmatom nanus* (8.5 mm SL), a tiny goby known from the Maldives and Chagos Archipelago in the Western Indian Ocean (WIO) (Figure 2).

Most fishes swim by moving the caudal peduncle and caudal fin. In the fastest fishes (tunas and other scombrids), the body flexes hardly at all, and the caudal fin provides all the thrust. In eels and some other elongate fishes, the whole body flexes in an undulating wave that passes from head to tail, and this backward-moving wave drives the eel forward. The majority of fishes fall in between these two extremes, with peduncles more flexible than tunas, but less flexible than eels.

Scombrids have several anatomical adaptations that contribute to their remarkable swimming abilities. The stiff, deeply lunate caudal fin is well adapted for rapid movements and minimal drag. A speeding tuna can drive its caudal fin at the incredible rate of 10 beats/second. The massive body muscles are connected to tendons that run along the narrow peduncle (which acts as a pulley) to attach at the base of the caudal-fin rays. Horizontal keels on the peduncle strengthen it and are thought to reduce turbulence from the rapid lateral movements as the tail beats back and forth. The body is very streamlined, with grooves and recesses for the first dorsal and pectoral fins when they are folded back, to reduce drag. This sustained high-speed swimming of scombrid fishes requires a high metabolic rate, which means a high oxygen consumption. The gills of scombrids have a much greater surface area than the gills of non-scombrid fishes, and are therefore much more efficient at extracting oxygen from the water.

Figure 1 *Mola mola*, the ocean sunfish (Indonesia). © M Fraser

Figure 2 One of the smallest fishes, the goby *Trimmatom nanus*, 8.5 mm SL (Palau). © R Winterbottom, ROM

Unlike the typical cold-blooded fishes, the tunas and lamnid sharks (mako, porbeagle and white sharks) are able to maintain their inner muscular temperature several degrees above ambient water temperature. In tunas, the blood leaving the body muscles passes through a special network of capillaries that function as a countercurrent heat exchanger that transfers the metabolic heat generated by the muscles to the cold blood running into the muscles and digestive system in order to assimilate food faster, and thus become ready for the next meal. The swimming muscles are thus able to operate at the higher temperatures necessary for the higher metabolic rate required for sustained high-speed swimming. Of all fishes, the bluefin tunas have the most efficient heat exchangers, and they are the scombrids that penetrate farthest into cold waters, often occurring along the coasts of Norway and Alaska, from 40° to 50° S. The Atlantic bluefin tuna (*Thunnus thynnus*) can maintain a core body temperature of about 25 °C in water temperatures as low as 2.8 °C. Another discovery is that the opah or moonfish (*Lampris guttatus*), an inhabitant of cold waters, is entirely endothermic, and circulates warmed blood throughout its entire body (Wegner *et al.* 2015).

There are other fast-swimming fishes besides the scombrids. Kingfishes (Carangidae), dolphinfishes (Coryphaenidae), marlins and sailfishes (Istiophoridae) and the lamnid sharks (Lamnidae) all have a stiff, lunate caudal fin and narrow peduncle. This shape of caudal fin is the most efficient for fast cruising. A broad truncate or rounded caudal fin, as in groupers (Epinephelidae) or kob (Sciaenidae), is better for the sudden fast acceleration required by a lurking predator.

Many fishes use their pectoral fins for propulsion. Wrasses, parrotfishes, damselfishes, and the oceanic opahs (*Lampris*) cruise by flapping their pectoral fins like wings. The pectoral fins of opahs are long and stiff, and the muscles that move them are enormous, so that they 'fly' through the water, much like penguins flapping their wings. Although wrasses and parrotfishes depend on their pectoral fins for cruising, they also use their caudal fin when they are in a hurry. Stingrays, manta rays and most other batoids use undulatory waves of their broad pectoral fins for propulsion and appear to fly effortlessly through the water. Electric rays, guitarfishes and sawfishes use their tail and caudal fin for swimming.

Ocean sunfishes (Molidae) have stiff paddle-like dorsal and anal fins which are their primary means of propulsion. In pufferfishes (Tetraodontidae), porcupinefishes (Diodontidae) and boxfishes (Ostraciidae), the short-based dorsal and anal fins as well as the pectoral fins are used for slow swimming. But, unlike the sunfishes which have no caudal fin, these fishes use the caudal fin when they want to swim faster. Fishes with long-based dorsal and anal fins, like triggerfishes and filefishes, use these fins for slow swimming by means of undulatory waves passed from the front to the rear of the fin.

Accurate measurements of the speed of the fastest fishes are difficult to make. The cruising speed of scombrids is in the order of 2–10 km/h, but their burst swimming speed, which they use when chasing prey or fleeing from predators, is much faster. A wahoo (*Acanthocybium*), reputedly the fastest swimming fish, has been timed at 77 km/h for short bursts of speed, and a yellowfin tuna achieved 74 km/h for a 5-second period (Walters & Fierstine 1964). The billfishes (marlin, sailfish, swordfish, etc.) are also very fast swimmers, and could rival the tunas at their top speeds.

FISH MIGRATION

Migrations are regular mass movements of animals from one place to another, usually for purposes of breeding or feeding. Many fishes undertake vertical migrations of several hundred metres every evening in order to feed on the abundant plankton in shallower, epipelagic waters. By feeding in surface waters at night, they are safe from birds and other predators that hunt visually. At dawn they return to depths of 100–1 000 m.

The elf or bluefish (*Pomatomus saltatrix*) migrates from KwaZulu-Natal to the southern Cape coast of South Africa during the late summer months to feed, and returns to warmer northern waters to breed from September to December. This species also occurs along the Atlantic coast of the USA and on the south coast of Australia where it is well known as a migratory fish.

Freshwater eels (*Anguilla* spp.) that live in the rivers of the south and east coasts of Africa and Madagascar must return to the open ocean to spawn. The transparent larvae (leptocephali) drift south in the Mozambique current from somewhere near Madagascar. When they enter freshwater, they turn into the wormlike little elvers that ascend the rivers, even wriggling up dam walls. Females go further up rivers than males, and the eels stay and grow in freshwater for about 14 years. When they are ready to return to the sea to breed, they stop eating, their eyes enlarge, and their dark skin becomes silvery. They migrate to off the east coast of Madagascar to spawn, but once they leave the rivers they are never seen again.

Marine fishes that live in freshwater and return to the sea to spawn are called catadromous. Freshwater eels are *obligate* catadromous species, in that they *have* to live their juvenile and subadult life in freshwater. On the other hand, the freshwater mullet (*Myxus capensis*) is a *facultative* catadromous species that spends its juvenile and subadult life either in estuaries or in their adjacent rivers, but returns to the sea to spawn. If an estuary does not provide access to freshwaters, it does not affect the life cycle of the mullet.

The annual migration of the pilchard (*Sardinops ocellatus*) to KwaZulu-Natal waters, known as the 'Sardine Run', is probably a feeding migration. These schools of pilchard appear to be following the abundant plankton which occur in the countercurrent flowing northward along the South African east coast in winter.

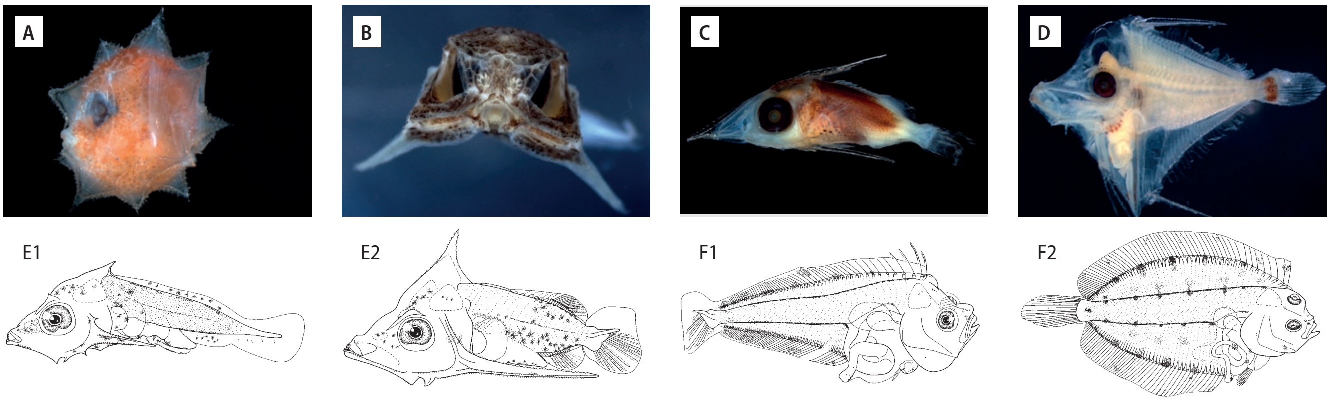

Figure 3 Larvae of various fish species. **A** *Mola mola*, **B** *Dactylopterus* sp., **C** a species of Holocentridae, **D** *Naso* sp., **E**. *Forcipiger* sp., at 3.3 and 5.2 mm, **F** *Poecilopsetta* sp., at 9.2 and 26.5 mm (two different spp.; note the migration of the eye). © **A–D:** GD Johnson; **E–F:** JM Leis & S Bullock

LARVAL FISH DISPERSAL

Most of the coastal fish species found in the WIO occur on or in association with reefs of some kind. The vast majority of these species have complex life histories that include pelagic larvae that spend a few days to a few weeks in the open ocean before settling into a 'reef existence'. When adult, these species are closely associated to a particular part of the reef – they are site-attached.

It was long assumed that larval fishes were passively dispersed by ocean currents, often over very large distances, which accounted for the way various populations were connected. Larvae were referred to as planktonic and were assumed to form part of the passively drifting biomass of the sea, and they could settle anywhere the ocean current took them. Reef fish populations were thus seen as 'open' as there was very little self-recruitment into local populations.

This traditional view of larval dispersal was supported by the fact that the larvae are small compared to the distances current could disperse them, and would generally not survive the distances. It was also thought that larvae lacked any kind of ability that could influence their dispersal. These assumptions were, however, based on the larval dispersal patterns for groups of fishes found in temperate waters, none of which are associated with tropical reefs.

In the 1990s these ideas were challenged and subsequent research showed that larvae of tropical reef fishes are not passively dispersed. This was not to say that the larvae of many reef fishes were not dispersed over very long distances, which is why species are found at oceanic islands separated by considerable stretches of deep ocean. There is clear evidence that long-distance dispersal does take place over 100s to 1000s of kilometres, but most fish larvae find a reef home much closer to their natal reef. This was first shown by studies on fish larvae collected by ship-towed nets that found the larvae of different reef fishes, originating on the same reef, had different distributions (see Leis 2015 and references therein).

Over time, laboratory and field research has shown that the tiny larvae are strong swimmers and are able to orient themselves in a featureless ocean. Further, as they develop morphologically, their swimming and orientation abilities develop and improve. These abilities also differ among species. Orientation abilities include a sense of sight which allow them to pick up celestial clues, the ability to hear reefs from several kilometres away, and a sense of smell that helps them find an appropriate place to settle (see Leis 2015 and references therein).

FOOD AND FEEDING

Fishes exploit a wide range of foods, from detritus and micro- and macro-plankton, to algae, a variety of invertebrates and vertebrates, including fishes, marine mammals, birds, turtles and sea snakes. Some fishes concentrate on invertebrate prey – tunicates, jellyfish, live coral, echinoderms, crustaceans, molluscs, worms and sponges – while others feed mainly on fishes or cephalopods. Most fishes, however, are essentially opportunists and will eat whatever is plentiful and easy to catch.

The teeth of a fish usually reveal much about its diet. Large canines are typical of predators that feed on fishes, mammals, birds or cephalopods; herbivores use incisors; and planktivores have small, villiform teeth or none at all. Molars indicate a diet of hard-shelled prey – crabs, gastropods or bivalves.

Herbivores such as surgeonfishes, angelfishes, some parrotfishes and some damselfishes feed on algae, seagrass or detritus. They are active by day and are usually seen near the bottom where they spend most of their time grazing. They often have small mouths with small incisors and long intestines to cope with the long digestive times demanded by such a diet. Planktivores are grouped into filter-feeders and plankton pickers. Bony fish filter-feeders such as pilchards, sardines and anchovies, have many, long gill rakers projecting between the gill arches. The mouth is moderate in size, and teeth minute or absent. The whale shark and manta rays are filter-feeders with a grid-like structure between the gill arches and, like bony fish filter-feeders, swim through concentrations of plankton with their mouths open. As the water current passes through the gills, minute planktonic animals (copepods, amphipods, mysids, arrow worms, larval fish, crustaceans, molluscs and echinoderms) are filtered out of the water and passed into the gullet. Pelagic bony fish filter-feeders are active in the open water during the day, making them vulnerable to predators. This accounts for their schooling behaviour, which makes it more difficult for predators to target individual fish.

Plankton pickers are either obligate pickers or facultative planktivores. Obligate pickers, such as fusiliers (Caesionidae), goldies (*Pseudanthias* spp.) and aggregating damselfish (*Chromis* spp.), occur in groups in midwater above the reef. They are active by day and have short snouts and large eyes with good binocular vision for targeting larger zooplankton, such as amphipods, mysids, fish larvae and salps that they pick out of the plankton. Like filter-feeding planktivores, they have many long gill rakers, a more or less protrusile upper jaw, and minute or no teeth. They also tend to live close to reefs which provide refuge from predators. Facultative planktivores include various omnivores, such as galjoen (*Dichistius* spp.), some damselfishes, chubs and batfishes (*Platax* spp.), which feed on a variety of plant and animal food, but will concentrate on plankton when it is abundant.

Many damselfishes, such as *Plectroglyphidodon* and *Stegastes* spp., are territorial herbivores that defend and feed on specific patches of benthic algae. These algae are covered with a layer of detritus, and a variety of small invertebrates as well as bacteria, fungi, diatoms and dinoflagellates that live on the algae. The damselfishes carefully weed out undesirable algae, which may be less nutritious or less conducive to the growth of the epilithic algal matrix.

Most fishes change their diet with growth. Juvenile groupers eat mainly crustaceans, but many adult groupers include a large portion of fish and cephalopods in their diet.

AGE AND GROWTH

The growth of fishes, like that of other poikilothermic animals, is dependent on the temperature of their environment. The availability of food is the other main factor that influences fish growth. Determining the age of fishes that live in temperate waters is relatively easy, because they grow faster in summer than in winter. This annual variation in growth is recorded in the form of growth marks (called annuli) in the otoliths (the ear bones), bones of the skeleton and scales of a fish, much like the growth rings of a tree. Fishes that live in tropical waters or in the deep sea, where water temperature is pretty constant all year round, do not have such marked growth rings and are often difficult to age (Figure 4).

The otoliths of fishes are often used to determine how old they are, because their annuli are more distinct than those of other bones or scales. In long-lived species, the accurate determination of age for a fish older than 10 or 20 years becomes complicated, because mature fishes grow more slowly than juveniles. After maturity the annuli become more crowded together and difficult to count. For older fishes it may be necessary to weigh or section the otolith to determine the growth increments. The ratio of radioactive isotopes of lead and radium in the sectioned otoliths of rockfish (a North Pacific scorpaenid fish) has shown that this cold-water species may attain an age of 80 years, despite growing to only 46 cm.

Larger fish species generally live longer than smaller ones, provided that the large species also grow slowly. The dolphinfish (*Coryphaena hippurus*), which attains a length of 2 m, is an exceptionally fast-growing species; it is mature at an age of one year (at 55 cm FL), and probably does not live more than four years. The enormous tunas and billfishes are also very fast growing and apparently do not live much past the age of 15. Tagging studies of sharks, together with otolith data and bomb radiocarbon dating, have given us ages for several species: white sharks more than 40 years; sandbar sharks 30 years and more; and spiny dogfish can live longer than 45 years. Some deep-sea bony fishes live very long — the orange roughy lives to ~150 years, maturing at 30+ years of age. It is likely that some deep-sea sharks are also long-lived. At the other end of the scale, several small gobies of the genus *Trimma* pack an entire life-cycle into only a few months: *Trimma nasa* lives for only about 87 days, spending some 35 days in the plankton (Winterbottom & Southcott 2008). Coelacanths are known to live to 100 years.

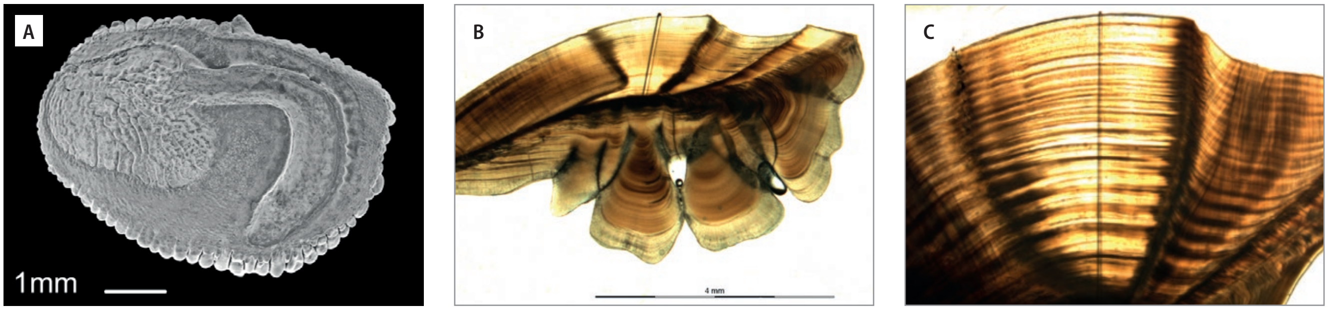

Figure 4 A Electron micrograph of otolith of *Argyrosomus japonicus*, **B** horizontal section of otolith, **C** section showing growth rings of 18-year-old fish [see also **Figure 9**]. © **A:** MJ Smale; **B, C:** A Childs, RU-DIFS

SENSES AND PHYSIOLOGY

Vision

For most fishes, as for almost all other animals, vision is important for finding food, avoiding predators, and identifying potential mates.

Fishes show a tremendous diversity in the development of their eyes. The major difference between a fish's eye and that of non-aquatic vertebrates is that the lens is spherical, whereas most vertebrates have a 'lens-shaped' lens, i.e., oval in cross-section. The human eye and the eyes of most other vertebrates are focused by the initial refraction of light rays by the cornea and by muscles that flatten an elastic lens. The cornea of the eye of most fishes is optically non-functional, as it has the same refractive index as water, except for fishes like mudskippers (*Periophthalmus* spp.) that use their eyes out of water. Focusing is done by moving the lens backwards and forwards in the eye. Fishes are generally long-sighted, especially in their lateral field of view, but their sharpest vision is in the forward field of view, because the back part of the retina has the greatest density of visual cells. As in many other vertebrates, the eyes of fishes have two types of sensory cells, 'rods' and 'cones'. Rods are most sensitive to low light, while cones give very sharp vision, and have the ability to distinguish colours.

In well-lit epipelagic and nearshore waters, fishes have a retina that is rich in cone cells. Fishes living at depths of 500–1 000 m, where light levels are low, usually have large eyes with mostly rods in the retina. In the deepest parts of the sea (below ~2 000 m), the absence of sunlight and rarity of bioluminescent fishes renders vision largely obsolete, and many fishes have vestigial eyes. Deep reef fishes such as the coelacanth and sharks have eyes with a layer at the back (the *tapetum lucidum*) that shines like a cat's eye at night and reflects light back through the retina.

The amazing array of colours and patterns of the many different fishes on a coral reef have evolved for many ecological reasons. Conspicuous colour patterns have two functions. The first is interspecific communication such as the possession and defence of territory and in recognising individuals of the opposite sex. This is particularly true for those species where males and females have strikingly different colour patterns, as in the sexually dimorphic parrotfishes and wrasses. The second is aposematic colouration, used to advertise that the fish is inedible, as with the soapfishes. Fishes are otherwise cryptically coloured or camouflaged to avoid predation (see section **Mimicry and protective resemblance in WIO fishes** in this chapter).

Seeing colours under water is, however, different to seeing colours above the water: water absorbs long-wavelength light on the red end of the spectrum (i.e., wavelengths of >600 nm), so that almost all red-orange light has been absorbed below 10 m. The red pigments on fishes at these depths appear dark grey. In recent years it has been discovered that more than 180, mostly small, species of fishes can generate red fluorescent light, often in species-specific patterns (Michiels *et al.* 2008; Gerlach *et al.* 2014; Meadows *et al*. 2014) (Figure 5).

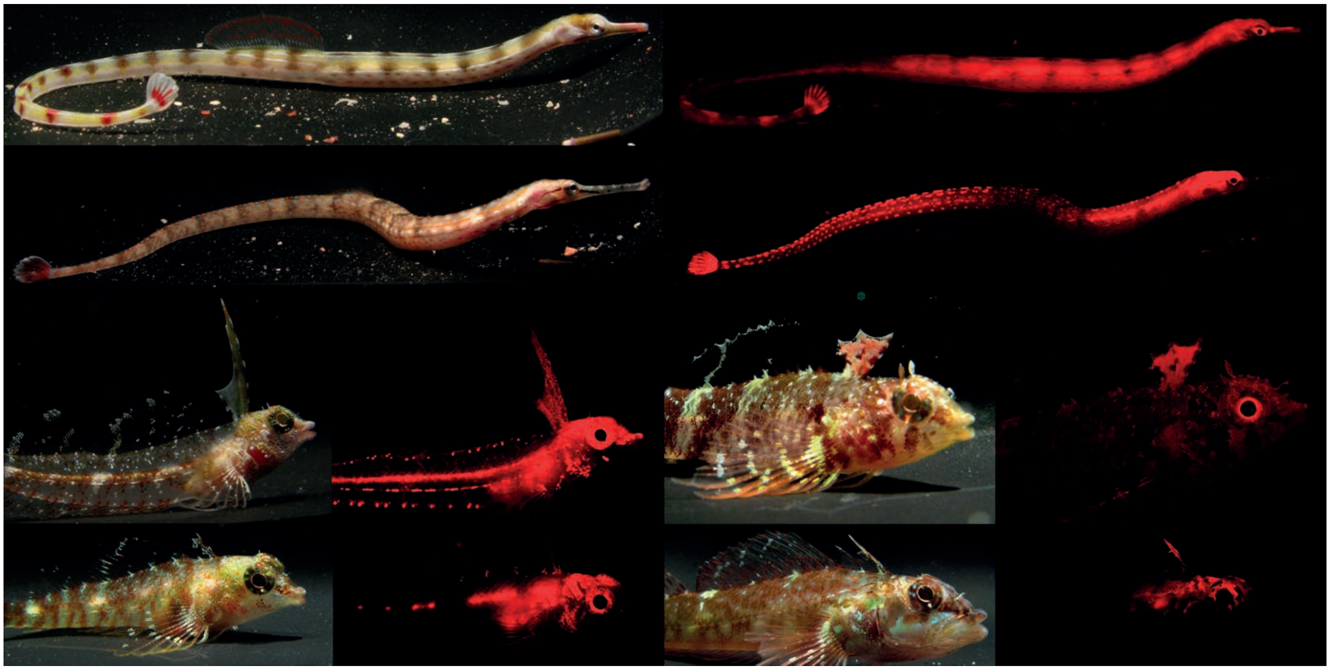

Figure 5 Red fluorescence in six species of reef fishes from the Red Sea: *Corythoichthys flavofasciatus*, *C. schultzi*, *Enneapterygius pusillus*, *E. destai*, *E. abeli* and *Helcogramma steinitzi*. © NK Michiels, University of Tübingen

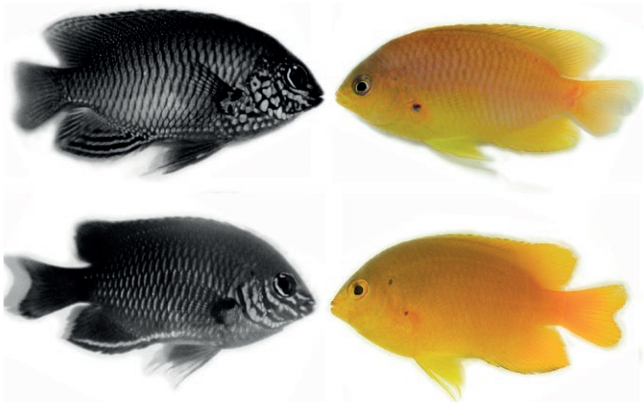

Figure 6 Colours and ultra-violet facial patterns of four individuals of two species of damselfish: *Pomacentrus amboinensis* (above), *P. moluccensis* (below). © UE Siebeck, UQ

Figure 7 *Periophthalmus takita* (Australia). © T Takita

Fluorescent patterns usually include the eye ring and parts of the head and chest. Emission of red fluorescence by fish, a colour absent from the background, may function as a means of communication or to attract conspecifics. Fluorescent light emission from the eyes in particular might assist in detection of cryptic prey (Meadows *et al*. 2014). Red fluorescence has been found to be associated with guanine crystals made by iridophores, well-known for producing iridescence in many bony fishes.

Reflective red pigmentation is widespread amongst reef fishes, and appears grey or black below around 10 m, allowing a fish to blend in with its background.

Another area where our knowledge of colour vision in fishes is poor, is their ability to detect ultraviolet light (UV). It is thought that UV signals must be bold, as they are scattered in air and water, and because, if present, there are few UV-sensitive cones in the eye. Recently researchers have discovered that two similar species of damselfishes use ultraviolet light *patterns* for face recognition (Siebeck *et al.* 2010) (Figure 6). This has led to the hypothesis that some fishes use UV as a secret channel for communication that is hidden from potential predators (see section **Colouration and bioluminescence**).

Fishes with eyes on the sides of their head typically have a wide field of view. Many species can also rotate their eyes independently, like a chameleon. Mudskippers (*Periophthalmus* spp.) (Figure 7) spend most of their time out of the water climbing about the roots of mangrove trees, and can see quite well in air. They can retract their protruding, periscope-like eyes and roll them around in the eye socket to keep them moist, erecting them again to scan the area for predators or possible prey.

Soles are flattened and lie on their sides on the bottom, so well-camouflaged that they are almost invisible. They do this by being able to match the colour of the upper (or eyed-side) of the body to the colour of the substrate. If a sole is blinded it loses the ability to blend with its surroundings (see section **Mimicry and protective resemblance in WIO fishes** in this chapter).

Hearing and lateral-line sense

The density of water is about 1 000 times greater than that of air, and water is thus much less compressible than air. This greater density and resistance to compression greatly affect the production and transmission of sound. In air, sound travels relatively slowly, as a periodic form of compression waves (Figure 8). In water, sound travels about five times faster, by particle displacement as well as by compression waves. The particle displacement form of sound energy is strongest close to the sound source, and is termed the near-field effect; compression waves extend farther from the sound source and are thus known as the far-field effect.

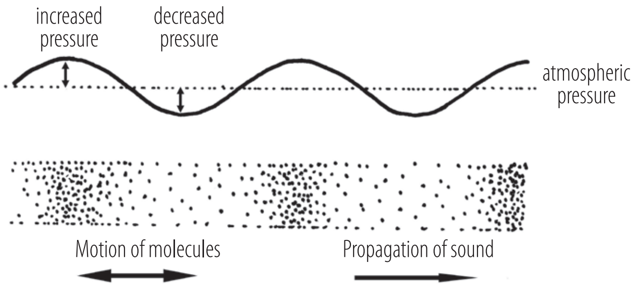

Figure 8 Sound waves travel in air as compression waves (above) and in water by particle displacement (below).

Fishes detect sounds with their lateral-line receptors and their ears. The sensory organs (called 'hair cells' or 'neuromasts') of the lateral line and the ears are very similar in structure. Lateral-line neuromasts are mechanoreceptors which are more-or-less directly exposed to the water surrounding the fish, and are especially sensitive to the near-field form of sound energy. Experiments have shown that lateral-line receptors are sensitive only to low-frequency sounds (10–200 Hz); the movements of fishes or other animals through the water primarily produce such low-frequency sound waves. Lateral-line neuromasts are usually found in small, perforated tubes running just under the skin of the head and/or along the side of the body (hence the 'lateral line').

The ability to detect the motion of other animals is useful to both predators and prey, especially at night or in deep sea where sunlight is non-existent. The greatly elongated lateral line of some midwater fishes, such as the frostfishes (Trichiuridae) and ribbonfishes (Trachipteridae), is very efficient at detecting any movements in their vicinity. Although the lateral line is absent from the body of most clupeid fishes (herrings, sardines and pilchards), the well-developed lateralis canals of the head are important for schooling behaviour by providing information on fish movements in their immediate vicinity.

The ears of fishes are convoluted, fluid-filled organs, called labyrinths, enclosed in bony chambers (otic capsules) on either side of the skull. The upper part of each labyrinth consists of three curved membranous tubes (semicircular canals) that join a central chamber called the utriculus. Two of the semicircular canals lie in vertical planes approximately at right angles to each other; the third canal is located in the horizontal plane. Movements of the head result in displacements of the fluid (endolymph) in the semicircular canals and utriculus, and the fluid displacements deform the sensory hair cells on the inner wall of the labyrinth. Stimulation of these hair cells then sends nervous impulses to the brain, to be read as information on the movement and orientation of the fish. A fish's perception of gravity appears to be primarily a function of the utriculus. The lower part of the labyrinth has two adjoining chambers, the sacculus and the lagena, each with a dense calcareous otolith, or 'ear bone'. The utriculus (which also contains an otolith) is usually joined to the sacculus (Figure 9).

Fishes are sensitive to sounds of a wide range of frequencies. The hair cells, located inside the otic capsules, are primarily sensitive to far-field sound energy. This pressure wave is either transmitted directly through the tissues of the skull to the ear, or, in the case of fishes with a connection between the swimbladder and the ears, the sound wave induces vibrations of the gas-filled swimbladder, and these vibrations are conveyed directly to the ears. Fishes with a connection between the swimbladder and the ears are especially sensitive to high-frequency sounds (up to 180 kHz). At the labyrinth, the sound wave vibrations are transmitted to the endolymph and otoliths,

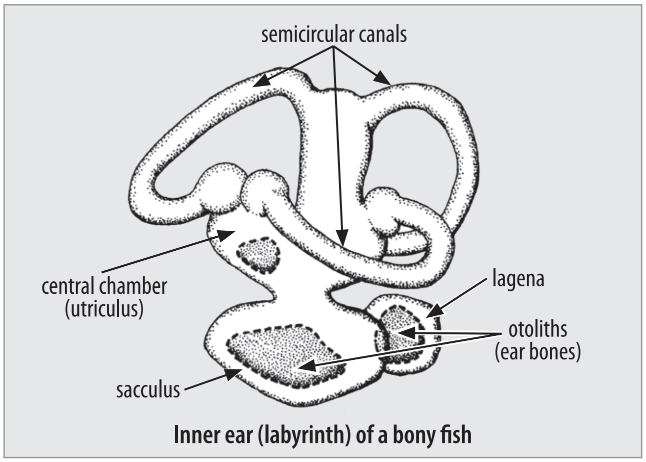

Figure 9 Labyrinth of a bony fish. Source: CFSA

and the vibrations of the otoliths stimulate the hair cells with which they are in contact.

Touch

Although fishes apparently lack the specialised touch receptors of birds and mammals, they are able to register touch sensations by means of a network of free nerve endings in the skin. The barbels of catfishes and goatfishes are equipped with taste buds as well as many free nerve endings, and they probably function as taste and touch receptors when the fish is foraging for prey. The enlarged free pectoral-fin rays of gurnards, fingerfins and threadfins probably serve the same functions.

Smell

A sense of smell is well developed in most fishes. The olfactory organs are round to oval plates of folded sensory epithelium located in nasal capsules on either side of the snout. Sharks (and most other elasmobranchs) have a keen sense of smell, as indicated by their well-developed olfactory organs and the large area of their brain that is concerned with olfaction. It is well known that sharks will approach a bait from downstream, following a scent trail to its source.

Taste

The taste receptors of fishes are not restricted to the mouth; they are also found on the lips, barbels and certain modified fin rays, and even scattered over the head and body (see above paragraph on the sense of touch). Sharks are greatly repelled by the taste of the Moses sole (*Pardachirus marmoratus*) which secretes a milky toxin from pores at the base of its dorsal- and anal-fin rays. The soapfishes, the Grammistinae, also secrete a toxin from glands in their skin. The name 'soapfishes' alludes to the thick slimy mucus that covers the skin in these fishes. If a predator tries to eat a soapfish, the bitter-tasting mucus will cause the predator to spit out the fish, which is usually not seriously injured. Predators soon learn to recognise and avoid soapfishes.

Electrical detection

Sharks, rays and some bony fishes, such as the marine catfishes of the genus *Plotosus*, have electroreceptors sensitive to the minute electric fields generated by all living animals. These receptors are called ampullary organs, or, in the case of elasmobranchs, ampullae of Lorenzini, after the man who first described them, and are located mainly on the front of the head in sharks. Each ampulla is a slender, flask-shaped organ with a long canal leading to a pore at the surface of the skin. Ampullary organs can detect minute electric fields caused by breathing prey buried in the substrate, and experiments have confirmed that benthic sharks and rays use this electrosensory ability to find their food.

We also know that fishes use their electroreceptors to detect the electric fields produced as the fish swims through the magnetic field of the Earth, and this sensory input might be used in navigation. A white shark, tagged at Gansbaai near Cape Town on 7 November 2003, was recorded 11 000 km away, off the northwest coast of Australia on 28 February the next year from a pop-up tag, and was then photographed off Cape Town, six months later, on 21 August 2004 (Bonfil *et al.* 2005).

Pain

Do fishes feel pain? This a much-debated question and the subject of considerable research. There are many tales of fishermen who have hooked a fish, let it go, only to hook it a short while later. This has led to the notion that a fish does not feel the pain of the hook in its mouth. Sharks seem to be indifferent to wounds, and thus presumably feel little or no pain.

This apparent inability to feel pain may have to do with the number and kind of receptors in the skin. One group of researchers (Sneddon *et al.* 2003) found nociceptors on the face and snout of a salmon. These are sensory receptors that respond to potentially damaging stimuli, such as heat or chemicals, by sending nerve signals to the spinal cord, which then triggers a reflex reaction. In a review article, Rose *et al.* (2014) record that the typical human cutaneous nerve cell contains 83% C-type trauma receptors (those that are sensitive to extreme pain), whereas sharks have none. The debate is not settled and it is likely that fishes sense 'pain' differently from other vertebrates. Another aspect of this debate is whether fishes are *sentient* or not: do they 'feel' in any way? In an extensive review paper, Key (2015) presents evidence that while fishes react to noxious stimuli, that drugs do modify their behaviour, and they do seem to react to physiological stress, fishes do not have the neural receptors or parts of the brain which birds and mammals have evolved that enable them to feel pain in the way that we understand it. Fishes may thus sense pain differently from other vertebrates, but the current state of knowledge does not explain how fishes sense pain.

PHYSIOLOGY

Respiration

The gills of fishes are equivalent to the lungs of other vertebrates. The bright red colour of the gills of a live fish indicates the abundant blood supply. Gas exchange take place at the thin walls of the gill filaments. Each gill filament has numerous lamellae, where the blood is separated from the water flowing through the gills by a very thin membrane. Oxygen diffuses from the water into the blood, and carbon dioxide from the blood into the water across this membrane. A further adaptation that facilitates oxygen uptake by the gills is a *countercurrent* system, where the flow of blood in the lamellae is opposite to the flow of water across the lamellae (Figure 10).

Fast-swimming fishes like scombrids have a high metabolic rate and much higher oxygen consumption, compared with more sluggish fishes like catsharks or anglerfishes. The gills of the more active fishes have become adapted for more efficient uptake of oxygen: the lamellar walls are thinner, with many more lamellae, providing a much greater surface area for diffusion of oxygen and carbon dioxide.

The water current for gill ventilation is provided either by a 'branchial pump' or by simple 'ram ventilation', where the fish simply swims with its mouth open, and the water flow through the mouth and gills is accomplished by the movement of the fish through the water. Ram ventilation is used by fast-swimming fishes (such as tunas), and by most plankton feeders (such as whale sharks), which swim about with the mouth

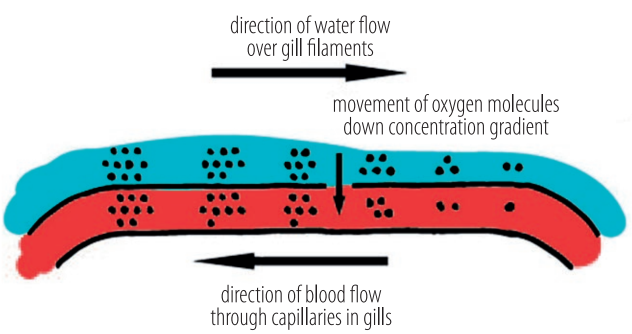

Figure 10 Diagram of a countercurrent system.

Figure 11 A whale shark, *Rhincodon typus.* © M Fraser

open to capture plankton. A branchial pump is used by less active fishes to force water through the gills. By alternately expanding and contracting the mouth and gill chambers, water is sucked into the mouth and pushed through the gills. There is also a flap of skin on the roof of the mouth that acts as a valve so that when the mouth is closed the water does not flow back out of it. This 'push-pull' way of breathing can be seen by watching fishes in an aquarium as they expand and contract their gill covers.

Some fishes have developed aerial respiration as a means for breathing out of the water, for a variety of reasons. Air breathing is best developed in freshwater lungfishes, which have lungs as well as gills. Freshwater eels (*Anguilla* spp., which spawn at sea; see Volume 2) normally take up about 10% of their oxygen through the skin, but if the eel is out of the water when it migrates from one water body to another, about 66% of their oxygen is taken in through the skin and the rest is extracted through the gills. A few marine fishes also use aerial respiration to supplement oxygen obtained from water. Mudskippers (*Periophthalmus* spp.), as mentioned previously, live out of the water for long periods during low tides. Here they have territories, with a burrow and often with low 'walls', which they will defend. When out of the water they acquire oxygen in two ways, in the same way as *Anguilla* spp. eels, through the skin, and by holding water in the gill chamber and quickly rocking the head from side to side to moisten the gills to absorb oxygen from the gill chamber (Jaafar & Murphy 2017).

Some species of mullet (Mugilidae) frequently jump out of the water. In warm stagnant water, which contains little dissolved oxygen, mullet jump more frequently than they do in well-oxygenated habitats. They apparently jump out of the water to take in air, which is then kept in bubbles in a chamber above the gills. These air bubbles provide an additional source of oxygen where oxygen is scarce.

Osmoregulation

This is the process by which the salt concentration of blood and other tissues is regulated within the limits necessary to sustain life. When one has two liquids on either side of a very thin membrane, water (or any other liquid) will flow from the side with lower concentration of dissolved substances to the side with higher concentrations, so as to equalise the concentration of these substance on either side of the membrane.

In marine bony fishes, the salt concentration of the blood and tissues is lower than that of sea water, and they thus lose water by diffusion through the gills and skin. To make up for this loss of water, bony fishes take in sea water and absorb the water (along with salts which they do not need) through the gut. The unwanted salt ions are then excreted via the gills, urine and faeces.

The salt content of cartilaginous fishes (Chondrichthyes) is only slightly higher than that of teleosts. However, because of the high concentration of urea in the blood, there is no tendency to lose water through the gills or skin. Cartilaginous fishes (and coelacanths, which also use urea to osmoregulate) are somehow able to tolerate concentrations of urea in their blood that would be fatal to most other animals. The influx of salt ions is countered by excretion of the ions via the gills, urine and a rectal gland. Rectal glands appear to be unique to coelacanths and chondrichthyans, and excrete most of the Na^+Cl^- (sodium and chlorine ions).

Euryhaline fishes, such as the bull shark (*Carcharhinus leucus*), are able to tolerate wide fluctuations in salinity. This shark is often found in rivers; juveniles are known from Malawi and the Kruger National Park in South Africa. Estuarine fish fauna comprises euryhaline species like moonies (*Monodactylus*), mullet (Mugilidae) and kob (*Argyrosomus*). In hagfishes, the salt concentration of the blood is similar to that of sea water, and hagfishes cannot tolerate even half-strength sea water.

Temperature

With a few notable exceptions, fishes are cold-blooded (poikilothermic or ectothermic) animals. This means that their body temperature is dependent on the temperature of the surrounding water. Except for certain oceanic fishes that often move through the thermocline, fishes cannot tolerate rapid changes of more than a few degrees. When an east wind blows along South Africa's southern coast, or when the northeast monsoon blows onto the coast of Somalia, it causes an upwelling of cold bottom water; this influx of cold water in the nearshore environment often kills fishes or makes them very lethargic.

Some large, fast-swimming fishes (tunas, marlins and lamnid sharks) are able to maintain their body temperatures above ambient water temperature and at a fairly constant level.

See section **Shape, size, swimming and speed** for more about these warm-bodied — or endothermic (homeothermic) — fishes.

Swimbladder, buoyancy and sound production

Most fishes have a gas-filled swimbladder in the upper part of the abdominal cavity. In some primitive fishes, such as lungfishes and the freshwater bowfins of North America, the swimbladder is connected to the oesophagus. A swimbladder's main function is to provide bouyancy.

In the spiny-rayed fishes the swimbladder has no connection with the gut, and any change in the amount of gas in the swimbladder is a slow process of secretion or resorption. If the fish is pulled rapidly to the surface from a depth of 20 m or more, the amount of gas in the swimbladder cannot be adjusted to the sudden decrease in external pressure (the pressure in the water changes by one atmosphere for every 10 m of depth). The result is a huge expansion of the gas and thus of the swimbladder, so that it may rupture or become pushed into the mouth. Anglers know that if they hook a large grouper in deep water and can bring it halfway up to the surface, the battle is won, as the expanding gas in the swimbladder makes it very difficult for the fish to swim back down to the bottom.

To get around the problem of rapid gas expansion with sudden changes in depth, some fishes have either replaced the gas-filled swimbladder with a partly or wholly fat-filled swimbladder, or they have lost their swimbladder completely. The swimbladder of the coelacanth (*Latimeria*) is completely filled with lipid (mainly low-density wax esters), and the body muscles are also rich in wax esters. The oilfish (*Ruvettus*) is notorious for the purgative properties of its flesh, the result of an abundance of wax esters in the body muscles. *Latimeria* and *Ruvettus* have thus evolved a similar solution to the problem of buoyancy: these two quite unrelated species occupy the same habitat at the Comoro Islands, and make extensive vertical migrations — and hence depth changes — in their search for the same prey.

Sharks (and other chondrichthyans) have no swimbladder, but also produce large amounts of lipid to provide buoyancy. This lipid is stored in the liver as oil (mainly squalene, a very low-density oil that incidentally also makes an excellent lubricant for fine machinery). The livers of some sharks are enormous, up to 25 per cent of their total weight.

The swimbladder is also used by some fishes to produce or amplify sounds. By contracting muscles attached to a gas-filled swimbladder, vibrations are produced that can be heard as growls, grunts, hoots and drumming noises. The muscles are either wholly attached to the swimbladder (intrinsic muscles) or attached by one end to the swimbladder and by the other to the skull, vertebral column or ribs (extrinsic muscles). These noises may be used in courtship and the defence of territory. Toadfishes (Batrachoididae) have a well-developed swimbladder with large intrinsic muscles. The cave bass (*Dinoperca petersi*) has a large, thick-walled swimbladder that is almost completely enveloped by three pairs of intrinsic muscles. Divers familiar with this species report that it is often seen at the entrance to its cave, making a loud drumming noise when approached.

REPRODUCTION AND DEVELOPMENT

Fishes reproduce in two main ways, by spawning eggs (oviparity), or by producing live young (viviparity). Most fishes are oviparous, and produce eggs that are fertilised, develop and hatch outside the body of the female. Unfertilised eggs are released into the water by a female at the same time as a male releases sperm to fertilise the eggs.

Oviparous species are the most fecund of all animals, some species releasing hundreds of thousands of eggs at a time. Tropical species generally spawn more than once a year and usually in small groups or in pairs. The small pelagic eggs float near the surface and take only a day or two to hatch. Soon after hatching, the rapidly growing larvae exhaust their small yolk supply and must begin feeding. In tropical waters larvae will spend about eight weeks drifting in the surface waters and feeding on plankton. In temperate seas, the larval stage may last four or five months (12 months or more for *Anguilla* spp. eels). Such long-lived pelagic larvae are often carried far from their place of origin and are thus a means of dispersal for shallow-water fishes (see section **Larval fish dispersal**).

Some oviparous species produce non-buoyant (demersal) eggs, which are larger than pelagic eggs and are generally attached to the substrate. Many species with demersal eggs, such as damselfishes (Pomacentridae) and triggerfishes (Balistidae) also guard their eggs until they hatch. A further adaptation for protecting the eggs is some form of incubation. A male seahorse has a pouch on his belly in which he keeps the eggs until they hatch; he then releases the baby seahorses from his pouch by bending his body and apparently pushing the juveniles out with contractions of his abdominal muscles. Once released, the little seahorses must fend for themselves. Sea catfishes (Ariidae) and many cardinalfishes (Apogonidae) practice oral incubation, in which the male keeps the eggs in his mouth until they hatch.

Larvae that hatch from demersal eggs are bigger than most larvae that hatch from pelagic eggs, and their larval stage is correspondingly briefer (sometimes even non-existent). In chondrichthyans (chimaeras, sharks and rays) the hatchlings are miniature copies of the adult, and the eggs that produce these well-developed juveniles are quite large — a whale shark egg-case measures 30 × 15 cm.

Although most oviparous fishes fertilise their eggs after they have been released from the body of the female, a few bony fishes and all chondrichthyans fertilise their eggs inside the female. Internal fertilisation is usually accomplished with special copulatory structures called intromittent organs, but some species, such as the coelacanth *(Latimeria)*, somehow manage internal fertilisation without an intromittent organ. In bony fishes, the intromittent organ can either be a fleshy 'penis' (as in Indo-Pacific Clinidae), or a modified anal fin, the andropodium of Hemirhampidae. A male chondrichthyan has paired intromittent organs (misnamed claspers) that are modified parts of the pelvic-fin skeleton.

Teleosts, such as Indo-Pacific Clinidae, and most elasmobranchs are viviparous and give birth to active, free-swimming young. Species that provide their embryos with no extra nourishment (other than their original yolk supply) are called ovoviviparous, amongst them the spiny dogfishes (*Squalus* spp.), the whitespotted smoothhound (*Mustelus palumbes*), and the coelacanth. The developing embryo of most viviparous elasmobranchs is provided with some nourishment from the mother in addition to its original yolk supply. Carcharhinoid sharks (e.g., *Carcharhinus* spp., *Mustelus mustelus*, and the hammerheads [Sphyraenidae]) have a yolk-sac-placental connection between the foetus and the oviduct of the mother. This placental source of nutrients develops during the later months of the gestation period, after the initial yolk supply has been exhausted. In some shark species the foetus is nourished by feeding on eggs and smaller siblings that may be found in the oviduct. These oophagous or adelphophagous (intrauterine cannibalistic) sharks (e.g., *Carcharias taurus*) give birth to only one or two large pups (one per uterus) at a time. In the oophagous foetal nourishment scheme, the ovary enlarges and functions as a kind of milk gland, sending little packets of yolk into each uterus to feed the developing foetus.

The occurrence of both sexes in the same individual, hermaphroditism, is normal and common in many bony fishes. Functional hermaphroditism may be either synchronous or sequential. The gonads of synchronous hermaphrodites produce ripe ova and sperm at the same time. Although synchronous hermaphrodites are capable of fertilising their own eggs, this does usually not occur, at least not in those species where spawning has been observed. The synchronous serranids that have been studied (*Serranus* and *Hypoplectrus* spp.) spawn in pairs and take turns fertilising each other's eggs. Successive hermaphrodites change sex, beginning the reproductive period of their lives either as females (protogynous) and after a few years or spawning periods they change to males, or they begin as males (protandrous) and then change to females. Although hermaphroditism is rare in freshwater fishes, it is common in marine fishes, especially in mesopelagic and coral-reef species. Many coral-reef fishes — such as Labridae, Scaridae, Serranidae, Anthiadidae, Sparidae, Lethrinidae, Polynemidae, and others — are successive hermaphrodites.

An interesting reproductive pattern has evolved in the sexually dichromatic fishes of the genus *Pseudanthias*. Species form small schools and occupy an area of a reef — a territory. Each school comprises a few (sometimes only one or two) large, distinctively coloured males, several smaller adult females and numerous juveniles coloured like the females. Each male spawns with several females in a harem-like fashion. If a male is removed from the group, the dominant (largest) female changes sex and colour pattern to take the place of the missing male. This sex and colour pattern change occurs within a few days, but if another male is introduced into the colony before the dominant female has completed her sex change, she returns to her female role and livery (Figure 12).

Figure 12 *Pseudanthias cooperi* (males with white streak under eye, females mauve, paler ventrally) and *P. squamipinnis* (males with yellowish sides and red pectoral fins, female orange) (South Africa).
© M Fraser

COLOURATION AND BIOLUMINESCENCE

Fishes living in the well-lit epipelagic region of the sea are countershaded (dark above and silvery below). Viewed from above, their dark greenish blue backs match the colour of the deep ocean. Seen from below, these fishes look like silvery streaks against a silvery mirror. Below 300–400 m, fishes are mostly uniform black; a few are bright red, but appear black in their natural environment because the red component of sunlight is filtered out in the first 10–20 m of water. In the neritic zone (the shallow area over a continental shelf) pelagic fishes, such as kingfishes, sardines and mackerels, are generally silvery and countershaded, but the more sedentary sublittoral fishes are often coloured in a variety of colours and patterns. The many beautiful coral-reef fishes are among the most colourful of all animals.

The silvery iridescent colours of fishes are due to special cells in the skin or scales. These cells, called iridophores, contain crystals of guanine arranged in layers which reflect several colours depending on the angle of the incoming light and position of the observer. The other (non-iridescent) colours of fishes are produced by chromatophores. These cells contain various pigments, and each chromatophore has only one kind of pigment. A chromatophore is typically irregular in shape, with numerous branching processes extending outwards from its centre. The pigment granules can be moved within the chromatophore: when the pigment is dispersed throughout the cell, the colour is intensified; when the granules are concentrated in the centre of the cell, the colour is diminished. The skin of fishes may contain several different chromatophores (red, yellow, black, etc.) and it is the alternating contraction and expansion of the pigment in the various chromatophores that produces the changes in colour pattern.

Rapid colour changes are under nervous control. For example, a dark galjoen (*Dichistius capensis*) swimming over dark rocks can change immediately to a pale colour when it swims over a light sandy area. The immediate contraction of the melanophores is responsible for this quick change. Fishes often have a night colour pattern that is quite different from their daytime colouration, and a fish under stress may display its night pattern during the day.

Long-term colour changes, such as the transition from juvenile to adult patterns, are affected by increases or decreases in the number of various chromatophores. This type of colour change is under hormonal control, as is that of sexually dimorphic fishes that change their colours when they change sex or become mature. Some fishes maintain their colour to match their habitat.

Disruptive colouration is exhibited by many coral-reef fishes. Bold black bars or stripes break up the general outline of the fish, and irregular patches of contrasting colour or tones distract the eye from the overall shape of the fish. When a boldly patterned fish is swimming over the complicated, multicoloured background of a coral reef, the fish is difficult to recognise and hard to follow.

Another type of disruptive colouration is the eye stripe, a black band or bar on the head that passes across the eye and makes it less obvious. Some butterflyfishes not only have a black eye stripe, but also have a false eye spot or conspicuous ocellus at the rear end of the dorsal fin. This false eye spot is supposed to deflect the attack of a predator to a less vulnerable part of the fish (see also section **Mimicry and protective resemblance in WIO fishes** in the following pages).

Different colour patterns probably also serve in species for sex recognition. Sexual dichromatism seems to be most highly developed in hermaphroditic species, such as parrotfishes, wrasses and some angelfishes. This conspicuous difference in males and females is obviously important in the reproductive behaviour of these species. Some fishes exhibit sexual dichromatism only when they are about to spawn. Species recognition is important not only for mating, but also for fishes that establish and defend a territory, and for those that want to 'advertise' their presence to others.

Bioluminescence, the ability to produce light, is better developed in fishes than in any other group of animals. At least 45 families of marine fishes have species with light-emitting organs (no freshwater fishes are light-producing). Most of the light-producing fishes are found at depths of 300–1 000 m, but there are some light-producing shallow-water species, such as the pineapple fishes (*Monocentris*), flashlight fishes (*Photoblepharon*) and cardinalfishes of the genus *Siphamia*.

Most luminous fishes produce substances that react chemically to produce light without heat. This reaction takes place in light organs (photophores) and is under nervous control. Some species rely on symbiotic luminous bacteria for their light. These bacterial light organs glow continuously, and the light can be turned off only by covering or occluding the light organ in some way. In the flashlight fish (*Anomalops*), the large bacterial light organ under the eye is 'turned off' by rotating it down into a black-pigmented pocket under the eye.

MIMICRY AND PROTECTIVE RESEMBLANCE IN WIO FISHES

Helen A Randall and John E Randall

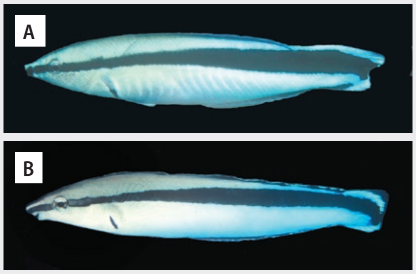

Figure 13 **A** The cleaner wrasse, *Labroides dimidiatus* (Oman); **B** the mimic blenny, *Aspidontus taeniatus* (Maldives).
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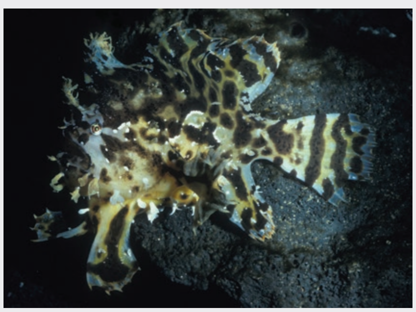

Figure 14 An aquarium photograph of the sargassumfish, *Histrio histrio* (Hawaii).
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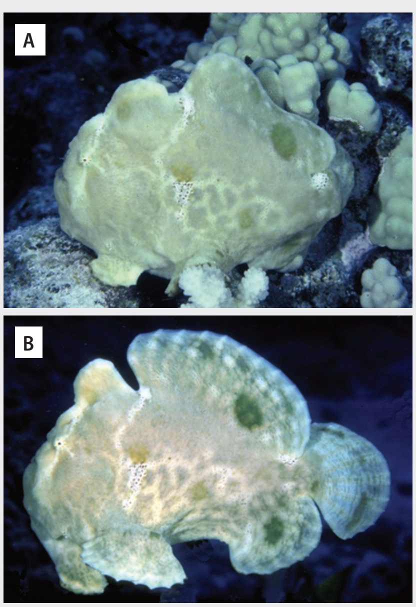

Figure 15 **A** *Antennarius commerson*, anglerfish, and *Porites lobata*, coral (Hawaii); **B** same fish as above, lifted off bottom (Hawaii). © JE Randall, Bishop Museum

The word mimicry is derived from the Greek term *mimetikos*, meaning imitative, and was first used in reference to people. Among animals other than *Homo sapiens*, the word has most often been used for insects. However, a surprising number of mimics have been discovered among marine fishes (Randall 2005). Classic examples include the resemblance of the black-and-white-barred snake eel *Myrichthys colubrinus* to the very venomous sea snake *Platurus colubrinus* (McCosker & Rosenblatt 1993), and the close resemblance of the false scorpionfish *Centrogenys vaigiensis* (from Indonesia) to the golden scorpionfish *Parascorpaena aurita*, with its full complement of venomous dorsal-fin spines (Whitley 1935).

There is a distinction between protective resemblance and mimicry. Poulton (1898) defined them as follows: protective resemblance is when an animal resembles some object which is of no interest to a predator, and is thus concealed; mimicry is when an animal resembles an object which is well known and avoided by predators, and in so doing becomes conspicuous.

Observations of the cleaner wrasse *Labroides dimidiatus* (Figure 13A) and the mimic blenny *Aspidontus taeniatus* (Figure 13B) led Randall & Randall (1960: 445) to revise Poulton's definition of mimicry to "... an animal resembles an object which is well known and is avoided, or not preyed upon by its enemy, and in so doing becomes conspicuous." Far from being avoided, the cleaner wrasse is sought by other fishes of the reef community to remove ectoparasites. It has a conspicuous pattern of bright blue with a broad horizontal black band from the snout to the caudal fin, and occupies a particular area (territory) of the reef, above which it swims in a distinctive, jerky up-and-down fashion. Fishes recognise the cleaner and come to its 'cleaning station' to be picked over for their parasites, and the cleaner is thus protected from becoming someone else's meal. But, the cleaner wrasse also serves as the model for the mimic blenny (also called the false cleaner) enabling the latter to get close enough to nip pieces from the fins of other fishes that mistake it for a cleaner wrasse. As long as the mimic is relatively rare (compared to the model), it is afforded some safety from predation and can successfully practise its game of deception.

Examples of protective resemblance in fishes are legion. Many fishes that rest on the bottom have the ability to blend with the background in colour, and some, such as scorpaenids (scorpionfishes), lophiids (monkfishes) and antennariids (frogfishes) have cirri or cutaneous flaps that augment their concealment. The venomous stonefish looks just like a lump of coral rock covered with algae, and is a real hazard to waders who might tread on it. The sargassumfish (*Histrio histrio*) (Figure 14) is among the first to come to mind. It is very difficult to detect when it is hiding in drifting masses of *Sargassum* weed. Another, *Antennarius commerson* (Figure 15), is well concealed by looking like a small colony of the coral *Porites lobata.* Flatfishes often match the pattern and colour of the substrate so well that they are almost impossible to see unless they move.

There are many fishes that resemble plants, reviewed by Breder (1946). Atz (1951) published a popular account and Randall & Randall (1961) added further examples, one being the deep-bodied yellow juveniles of *Platax orbicularis* (Figure 16) that is often seen flat on its side, on the surface of the water, drifting among yellow leaves of *Hibiscus tiliaceus.*

The fish was noticed only when it moved in a different direction from the leaves. A similar example was described for the juvenile of the tripletail (*Lobotes surinamensis*) by Schmid & Randall (1997) in the Red Sea. The juvenile of the peacock razorfish (*Iniistius pavo*) was mistaken as a blackened leaf moving to and fro with other plant debris from surge in shallow water over white sand. Its long filamentous dorsal-fin spine was held forward and looked like the stem of the leaf. Again, the fish was noticed only when it moved differently from the plant debris and, as it was approached, it quickly dived into the sand. Another remarkable juvenile wrasse, the rockmover (*Novaculichthys taeniourus*), looks like a small drifting mass of algae (Figure 17), and can be green, olive, maroon or brown.

Several fishes that inhabit seagrass beds or substrata with dense beds of algae are coloured like these plants. Prominent green examples include the alligator pipehorse *Syngnathoides biaculeatus* (Figure 18), the ghost pipefish *Solenostomus halimeda,* the wrasses *Novaculoides macrolepidotus, Pseudojuloides argyreogaster* and *Pteragogus pelycus*, the raggedtooth parrotfish *Calotomus spinidens*, the filefish *Acreichthys tomentosus*, and individuals of the klipfish, *Clinus superciliosus*, that live in kelp. Other individuals of this species will take on the colour of the substrate the juveniles settle on when they leave the plankton.

Seahorses are famous for being protectively coloured; our favourite is the tiny *Hippocampus bargibanti* that is difficult to spot until it moves on the sea fan *Muricella* sp. (Figure 19). It is not known from the Indian Ocean, but it is so easily overlooked when it might be present.

The most intriguing examples of mimicry in fishes are those where a harmless species mimics one with some repelling property such as a toxic species, or one with a venomous bite or fin spines. An example of the latter from the Red Sea is the fangblenny *Meiacanthus nigrolineatus*, which has a vicious venomous bite. It is strikingly mimicked by the blenny *Ecsenius gravieri* (Figure 20). A second mimicking blenny, *Plagiotremus nigrolineatus* enjoys the same benefit, despite its slender body (Springer & Smith-Vaniz 1972). Some polyclad flatworms are known to secrete toxins that makes them repellant to predators. A few species of soles have effectively mimicked these flatworms, as has the juvenile of *Platax pinnatus* (Randall & Emery 1971) (Figure 21). The young of the African pompano (*Alectis ciliaris*) (Figure 22) have very long, filamentous dorsal- and anal-fin rays that resemble the long thread-like tentacles of venomous jellyfishes, such as those of the virulent box jellyfishes of Indonesia and the Coral Sea.

Figure 16 Juvenile *Platax orbicularis* floating on side at surface where it resembles similar drifting yellow hibiscus leaves. © JE Randall, Bishop Museum

Figure 17 Juvenile *Novaculichthys taeniourus* drifting like a small mass of detached algae (Hawaii). © JE Randall, Bishop Museum

Figure 18 The pipehorse *Syngnathoides biaculeatus* in a seagrass bed (Philippines). © JE Randall, Bishop Museum

Figure 19 The tiny seahorse *Hippocampus bargibanti* on the seafan *Muricella* (Indonesia). © JE Randall, Bishop Museum

Figure 20 The blenny *Ecsenius gravieri* (left), a mimic of the sabretooth blenny *Meiacanthus nigrolineatus* to the right (Red Sea). © VG Springer, USNM

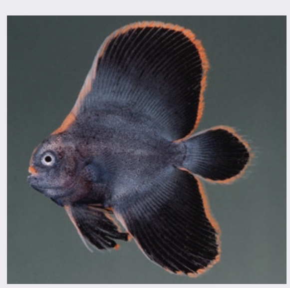

Figure 21 Juvenile of *Platax pinnatus*, a polyclad flatworm mimic (Palau). © JE Randall, Bishop Museum

Figure 22 A juvenile *Alectis ciliaris* with long dorsal and anal rays that resemble jellyfish, with long, thread-like, stinging tentacles (Hawaii). © JE Randall, Bishop Museum

Tobies (*Canthigaster* spp.) are well known to harbour crinitoxins that cause predaceous fishes to eject them when they attempt to feed on them. Species of the filefish genus *Paraluteres* have successfully mimicked these small puffers, thereby enjoying relative freedom from predation (Clark & Gohar 1953). The example here (Figure 23) is unusual in having both model *Canthigaster valentini* (lower) and its mimic *Paraluteres prionurus* (top) together, as if fooled by their own trickery. The mimicking filefish keeps its dorsal spine folded flat to augment this deception. The juvenile of the grouper *Plectropomus laevis* may also be a mimic of this puffer, though not as perfect.

The juveniles of some predatory fishes, such as the groupers *Anyperodon leucogrammicus* and *Epinephelus jayakari* and the snapper *Lutjanus bohar*, have evolved to mimic harmless fishes such as damselfishes or small species of wrasses, thereby being able to approach their prey more closely. Figure 24 shows the juvenile of *E. jayakari* from the Persian/Arabian Gulf that mimics the damselfish *Neopomacentrus sindensis*.

The biological basis for mimicry is usually clear. However, it took considerable time to determine why a surgeonfish of the genus *Acanthurus* should gain any benefit from mimicking a small angelfish of the genus *Centropyge*. Juveniles of *Acanthurus pyroferus* in the Pacific and eastern Indian Ocean and *A. tristis* in the Indian Ocean precisely mimic adults of the small angelfishes *Centropyge flavissimus* and *C. eibli* (Figure 25), respectively. When the surgeonfishes grow larger, they revert to the relatively drab colour of adults. It was first thought that the *Centropyge* models would be cleaners and enjoy freedom from predation. Hours were spent observing individuals of the little angelfishes, hoping to see them pick at the bodies of other fishes, but this was not ever seen. Then it was thought that they must have some toxic property to make them unpalatable. However, when served as bait, they were taken by predators as readily as control fish of the same size and shape. Finally, it was found that these little angelfishes never move far from shelter. They feed on algae and detritus in the immediate vicinity of their shelter. Surgeonfishes, by contrast, range widely in search of their preferred filamentous algae, and are therefore much more vulnerable to predation. If they resemble a small angelfish of the genus *Centropyge*, a potential predator moves on to easier prey.

Dafni & Diamant (1984) proposed the term 'school-oriented mimicry' when a normally solitary fish species mingles with a similar, aggregating species for the advantage of schooling. Their example is the juvenile of the fangblenny *Meiacanthus nigrolineatus* that in the Red Sea and Gulf of Aden joins a school of apogonid fishes of similar colour pattern. Randall & McCosker (1993) preferred the term 'social mimicry' for this. Their example from the Pacific, is a mixed plankton-feeding school of three anthiine fishes, a damselfish, and a blenny, all with a yellow and pink colour pattern. They also cited *Mulloidichthys mimicus* Randall & Guézé of the Marquesas and Line Islands that schools with the snapper *Lutjanus kasmira*. Uiblein (2011) described a new goatfish *Mulloidichthys ayliffe* from the Western Indian Ocean, and noted that it is similar to *M. mimicus*, and that it also schools with *Lutjanus kasmira*, as well as *M. vanicolensis* (Figure 26).

Figure 23 The model toby *Canthigaster valentini*, with its mimic, the filefish *Paraluteres prionurus,* above. © J Hall

Figure 24 **A** The Arabian demoiselle *Neopomacentrus sindensis*, and **B** its mimic, the juvenile Muscat grouper *Epinephelus jayakari* (both Persian/Arabian Gulf). © JE Randall, Bishop Museum

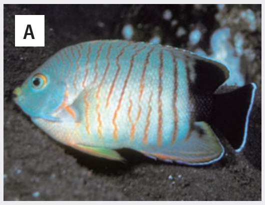

Figure 25 **A** The blacktail angelfish *Centropyge eibli* and **B** its mimic, surgeonfish *Acanthurus tristis* (both Indonesia). © JE Randall, Bishop Museum

Figure 26 *Mulloidichthys ayliffe* (centre) schooling with *M. vanicolensis* (lower right) and *Lutjanus kasmira* (in background) (South Africa). © DA Polack

THE OCEANOGRAPHY OF THE WESTERN INDIAN OCEAN

Johann RE Lutjeharms and Wayne S Goschen

For an appropriate understanding of the life histories and hence the geographic distributions of marine fishes, we need to know something about the basic oceanography (or oceanology) of a region. This includes the hydrographic and chemical characteristics of the main water masses, such as temperature, salinity and nutrient content, the major ocean currents, regions of upwelling, and prevailing primary productivity.

Observation, theory and numerical modelling are all used to describe ocean currents. These can provide a reasonable approximation of the largest water masses and their movements, though global or regional theories and models generally do not account for nonlinear and turbulent processes. *In situ* observations of ocean currents are relatively meagre in time and space, yet different water masses can be tracked according to their potential temperature and salinity (TS scatter plots) because these properties are retained from the place of formation. Remote sensing has become an important tool in determining surface currents, while subsurface floats, moorings and profiles can provide an account of the vertical water structure. Such knowledge is especially important for understanding the physical aspects of the Indian Ocean and its adjacent seas as this expanse covers a wide spectrum of ocean circulation patterns and conditions.

As described in the Introduction, the WIO region (Figure 1) is here defined as bounded by the southern coast of Africa, northward to the Arabian Sea, and eastwards to the longitude of Kanyakumari (formerly Cape Comorin) at the southern tip of India; southwards the region extends to the Subtropical Convergence Zone, the generic border between waters of tropical origin and the Southern Ocean.

By this definition, WIO encompasses a number of oceanic systems. The greater Agulhas Current system flows between the northern end of the Mozambique Channel and southern Cape coast of South Africa.

This system includes the various sources of the Agulhas Current proper as well as part of its outflow (Figure 2). To the north of this system, the powerful influence of the monsoonal winds drives the Somali Current and circulation in the Arabian Sea, which alters direction dramatically with transitions between seasons. The regional seas, the Red Sea and Persian/Arabian Gulf, comprise a separate grouping of ocean-like systems. In many aspects those systems are ‘artificial’ because water is continually exchanged between the peripheral water body and WIO, hence influencing each other. For instance, Red Sea Intermediate Water, with very high salinities, is formed in the Red Sea and Persian/Arabian Gulf from where it moves southward into WIO at depths to about 1 000 m, and still retains its identity upon reaching the southern end of the African continent and beyond.

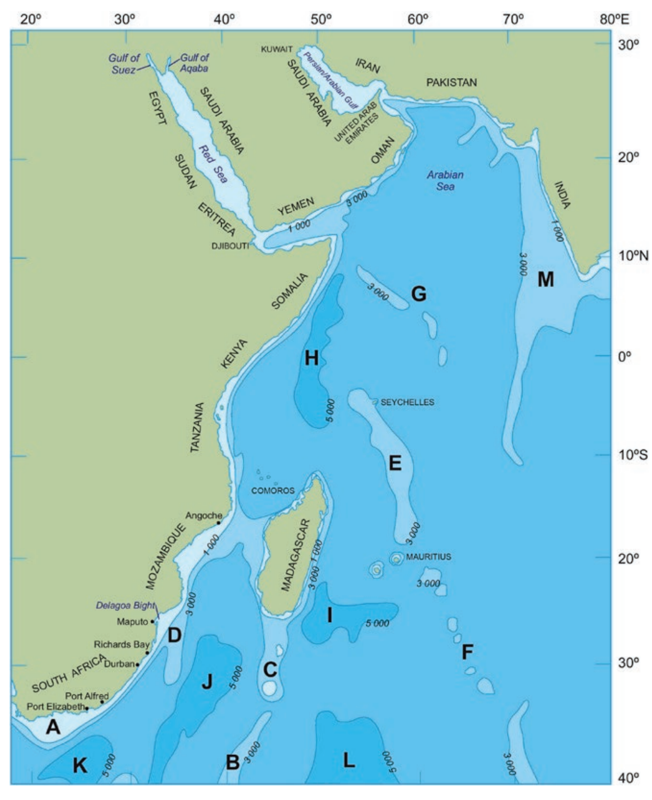

Figure 1 The geography of the Western Indian Ocean and its bottom configuration. Depths are given in metres at three levels. The names of some prominent ridges and plateaux are: **A** Agulhas Bank, **B** Southwest Indian Ridge, **C** Madagascar Ridge and Walters Shoals, **D** Mozambique Ridge, **E** Mascarene Plateau, **F** Southeast Indian Ridge, **G** Carlsberg Ridge, **H** Somali Basin, **I** Madagascar Basin, **J** Mozambique Basin, **K** Agulhas Basin, **L** Southwest Indian Basin, **M** Chagos-Laccadive Ridge.

THE GREATER AGULHAS CURRENT SYSTEM

South Equatorial Current

In the WIO, the South Equatorial Current occurs as a broad stream of mainly surface water, generally south of 10° S, which forms the westward component of the wind-driven Southwest Indian Ocean subgyre (Figure 2); this is the main source of the greater Agulhas Current system. The current is most strongly developed in the upper 300 m, and its surface waters exceed 28 °C at the end of the Southern Hemisphere summer (March) but are <26 °C in June to November. The current has a mixed-layer depth of ~40 m in March, and increases to 100 m by August. It has a shallow salinity minimum (i.e., an intrusion of low-salinity water) of Indian Tropical Surface Water, overlying higher-salinity South Indian Subtropical Surface Water (Figure 3). The speed of this current is relatively low, usually less than 0.3 m/s, and it extends to 8° S, but expands northward to 6° S in September.

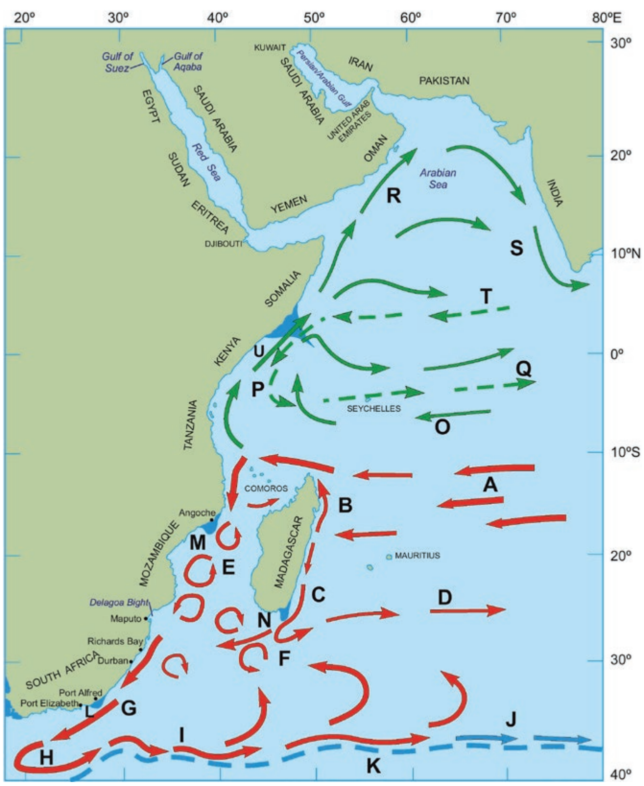

Figure 2 A stylised portrayal of the main surface currents of the Western Indian Ocean. Currents in the northern Indian Ocean are given as solid for the Southwest Monsoon period and as broken for the Northeast Monsoon. Blue regions indicate upwelling. The most prominent circulation features are: **A** South Equatorial Current, **B** northern branch of the East Madagascar Current, **C** southern branch of the East Madagascar Current, **D** South Indian Ocean Countercurrent, **E** Mozambique Channel eddies, **F** intermittent retroflection of the southern branch of the East Madagascar Current, **G** Agulhas Current, **H** Agulhas Current retroflection, **I** Agulhas Return Current, **J** South Indian Ocean Current, **K** Subtropical Convergence (blue broken line), **L** Port Alfred upwelling cell, **M** Angoche upwelling cell, **N** South Madagascar upwelling cell, **O** South Equatorial Current, **P** Somali Current during Southwest Monsoon, **Q** Southwest Monsoon Current, Equatorial Countercurrent during Northeast Monsoon, **R** East Arabian Current during Southwest Monsoon, **S** West Indian Current, **T** North Equatorial Current during Northeast Monsoon, **U** Somali upwelling during onset of Southwest Monsoon.

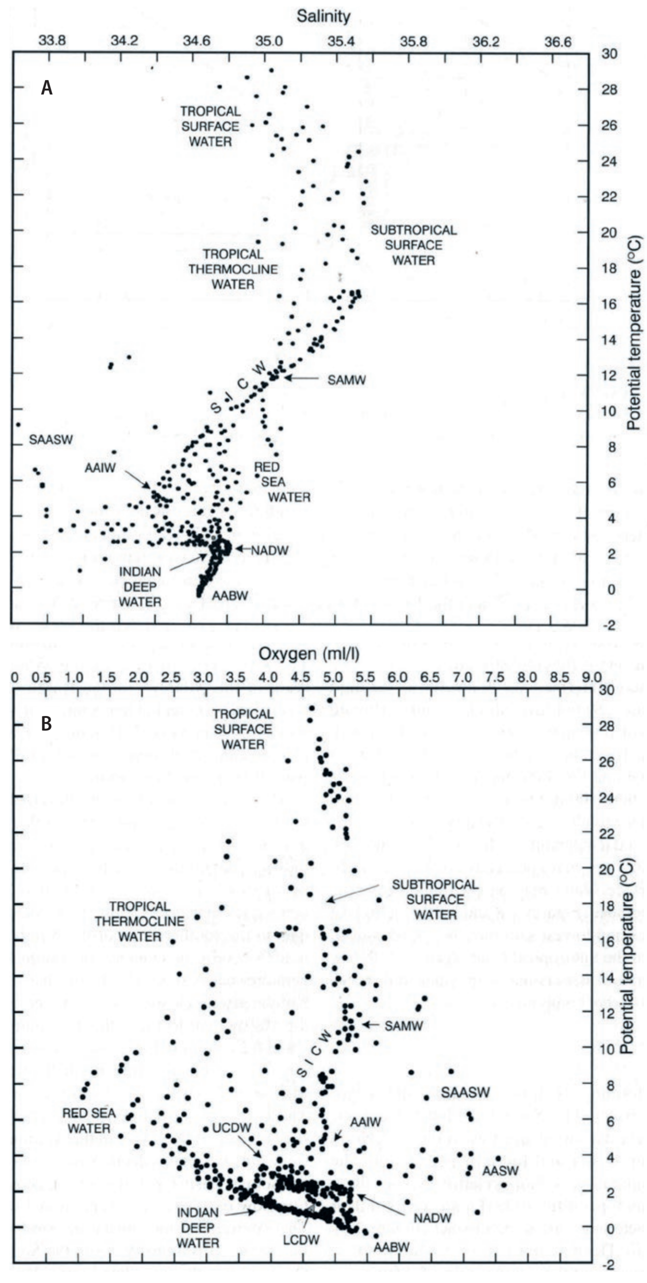

Figure 3 **A** Potential temperature–salinity and **B** potential temperature–dissolved oxygen relationships for the Western Indian Ocean. South Indian Central Water is identified by SICW, Sub-Antarctic Mode Water by SAMW, North Atlantic Deep Water by NADW, Antarctic Bottom Water by AABW, Antarctic Surface Water by AASW, Antarctic Intermediate Water by AAIW, Sub-Antarctic Surface Water by SAASW, Lower Circumpolar Deep Water by LCDW and Upper Circumpolar Deep Water by UCDW.

Source: Gordon *et al.* 1987

The South Equatorial Current flows from east to west; it receives a contribution of Pacific Ocean water at the Indonesian Throughflow and strengthens as it moves westward. South of the Seychelles, it is largely disrupted by the shallow Mascarene Plateau (Figure 1), which affects the flow even at 50 m depth. Water moves through two gaps in this plateau, so that the South Equatorial Current west of the plateau consists of two relatively intense jets: one at 13° S and the other at 18° S. The more intense northern jet passes the northern coast of Madagascar and the Comoros (Figure 2) and then divides at the coast of East Africa, with some water flowing southward into the Mozambique Channel and the remainder northward along the coast as the East African Coastal Current. These currents seem to be strongest during the Southwest Monsoon in May–September, with peak speeds in July.

South Indian Ocean Countercurrent

It is generally accepted that the surface flow of the southern Indian Ocean circulates in an anticlockwise direction, as typical of a subtropical gyre. The northern branch consists of the South Equatorial Current (described above). The main southern branch is the intense Agulhas Return Current, and east of about 70° E is the South Indian Ocean Current (Figure 2). Consequently, the border between the average eastward flow and westward flow lies at about 30° S, the latitude of the port city of Durban, South Africa. There is one notable and curious exception, however. From the southern end of Madagascar a narrow South Indian Ocean Countercurrent carries water at about 25° S across the greater width of the subtropical Indian Ocean, opposite the main general flow. Notwithstanding this current's limited width, it carries a substantial volume of water, about 10×10^3 m^3/s, and is evident to a depth of at least 800 m. The origin of the water in the South Indian Ocean Countercurrent is not yet known with certainty, but it is presumed to originate at the southern end of the southern branch of the East Madagascar Current (described below). Significantly, this countercurrent also presents a means for passive, non-swimming organisms from the tropics to be carried eastward across the southern Indian Ocean.

East Madagascar Current

Where the southern jet of the South Equatorial Current impinges on the east coast of Madagascar, at about 17° S, the current splits to form the northern and southern branches of the East Madagascar Current. Both branches closely follow the continental shelf edge and increase in speed and volume flux downstream. In their well-developed state, the waters reach a speed of 1.5 m/s and a volume flux of about 25×10^6 m^3/s. At this point they reach a width of about 80 km and depth of 600+ m and have no known distinctive seasonality. The northern branch of the East Madagascar Current joins the northern jet of the South Equatorial Current as it flows past the northern end of Madagascar. The southern branch terminates south of Madagascar in either a retroflection that feeds the above-mentioned South Indian Ocean Countercurrent, or else as a jet moving westward towards the coast of Africa.

The upper 50 m of the East Madagascar Current consist of Indian Tropical Surface Water, with temperatures of >23 °C and salinities of <35 (Figure 3). Offshore and below this water is South Indian Subtropical Surface Water, with salinities of >35.6 and a subsurface oxygen minimum of 4 ml/l at a depth of 200 m. The influence of this narrow and intense current on the adjacent coastal waters is unknown – but it can be assumed to be strong along the narrow continental shelf. A distinct upwelling cell forms on the wider continental shelf southeast of Madagascar, with a decrease of about 2 °C in temperature and an increase in chlorophyll *a* concentrations; maximum chlorophyll fluorescence is attained at depths of 40 –100 m. Some of this chlorophyll-rich continental shelf water may be taken up by clockwise eddies and shed in a westward direction.

East of the East Madagascar Current, in the open ocean, a strong seasonal phytoplankton bloom develops. It usually begins in January, is most intense during February–March, and may last until April. During its peak it extends over most of the Madagascar Basin, moving eastward (up to 70° E) as a wave of enhanced phytoplankton concentration. However, the bloom has failed in some years, which is assumed to be a result of seasonally increased wind strength that deepens the layer that is mixed, thus entraining nutrients into the photic zone. (The wind mixes the surface-layer waters to the same temperature; below this surficial mixed layer is the thermocline, defined by a sudden decrease in temperature with depth. Nutrients are trapped in the upper mixed layer, the photic zone, by the thermocline.)

Mozambique Channel circulation

Circulation in the Mozambique Channel was poorly understood until recently when it was discovered that the Mozambique Current consists largely of a series of clockwise and anticlockwise eddies, formed at (or just north of) the channel's narrows and which then drift southward. Water from the South Equatorial Current (Figure 2) leaks into the Mozambique Channel from the north, along Mozambique's coast. This course of water may be only ~150 m deep and 250 km wide, and likely flows at <0.5 m/s. It moves through the Comoros Basin south of the Comoro Islands (Figure 1), generally circulating anticlockwise. The eddies formed in the basin and at the Channel's narrows are about 300 km in diameter, extend all the way to the ocean floor, and move southward at ~5 km/day. Generally, one or more eddies are formed each year and collectively carry about 15×10^6 m^3/s of water southward through the Channel.

These eddies seem to have two noticeable effects on the local ecosystem. First, they may carry chlorophyll-rich water from the continental shelf to the centre of the Mozambique Channel; second, primary productivity seems to be concentrated at their margins, because frigate birds and other predators have been seen to feed there. It is likely that concentrations of tuna are found at these eddy edges, too. Furthermore, passing eddies may stimulate upwellings where the coastline forms bights, large bays, or capes (collectively termed offsets). For instance, intense upwelling has been observed off the town of Angoche (16°14' S, 39°55' E) where the highest concentrations of chlorophyll *a* in the Mozambique Channel have been recorded.

A deep countercurrent in the channel has been observed at intermediate depths, at ~1 000 m, and carries water towards the equator at a speed of ~0.5 m/s.

The continental shelf of Mozambique is wide, and in places this may be supported by runoff from major rivers. At the major shelf area at Sofala Bank, where the Zambezi River flows into the sea, the surface outflow signature can cover an area of 50–170 km^2. Salinities as low as 20 have been measured under flood conditions and as far as 50 km from the river mouth. Such relatively freshwater is usually restricted to the upper 10 m. Interestingly, in the case of Sofala Bank, this freshening of the marine waters of the continental shelf by river outflow may be compensated by an outflow of water with salinities as high as 37, originating from the salt marshes at the southern end of the bank. Low-lying coastal areas and estuaries, in Mozambique especially, contain extensive areas of salt marshes and mangrove swamps formed as a result of a tidal range of between 2 and 5 m. Over the wide, shallow areas of the Sofala Bank, strong tidal currents also cause the continuous movement of sand banks and create other sedimentary seabed features, such as sand ripples.

Delagoa Bight circulation

The Delagoa Bight, off the city of Maputo, Mozambique, forms the largest offset on the East African coastline. The circulation in the Bight is different to the circulation along the rest of Mozambique's continental shelf: often there is a clockwise eddy of surface waters flowing northward past Maputo and eastward along the northern border of the Bight (Figure 2). The sediment-laden waters of the rivers that drain into the Bight, in particular the Limpopo River on its northern side, then usually move along the coast with these currents. The cold water at the centre of the Delagoa Bight eddy is upwelled from a depth of ~900 m, and though this water may be rich in plant nutrients, such as nitrates, phosphates and silicates, currently there is no evidence that this addition of nutrients into the upper water layer leads to enhanced primary productivity.

What drives this eddy? It was long assumed that the passing and overshooting Mozambique Current induces the Delagoa Bight eddy as a trapped lee eddy. However, the discovery that the Mozambique Current is not a continuous boundary current discounts this hypothesis. The irregular passage of Mozambique Channel eddies, with their anticlockwise rotation, may possibly be sufficient to drive the Delagoa Bight eddy intermittently, but it is not known how prevalent this eddy is. It is possible that the eddy may sometimes escape from the confines of the Bight's area, dramatically modifying the circulation in the Bight until it gets spun around again. If and how often this happens, remains uncertain. At other places in the WIO where a boundary current, for example the Agulhas Current, passes from a narrow to a wide area of continental shelf, there is evidence of upwelling. If a constant Mozambique Current existed, one would similarly expect an upwelling cell at the northeastern bend of the Delagoa Bight. Such an upwelling arises only intermittently though; this suggests that water circulation in the Bight is driven by the occasional passage of Mozambique Channel eddies.

The water masses in the Delagoa Bight consist of South Indian Subtropical Surface Water, with salinities of 35.5–35.6 in the surface layers, with possible insertion of Indian Tropical Surface Water of lower salinities (<35.6) at times. Below these surface waters the South Indian Central Water extends to a depth of at least 1 000 m.

The northern Agulhas Current

It is not known exactly where the southwestward-flowing Agulhas Current becomes fully formed and starts to carry water past the African continental shelf. Sediment distributions suggest that the current takes form somewhere between Richards Bay in South Africa and Maputo in Mozambique (Figure 2). South of Richards Bay, the Agulhas Current increases in depth and volume, to a full volume flux of ~65×10^6 m^3/s, with surface speeds of more than 2 m/s, and a surface width of roughly 100 km. Here, the current follows the shelf edge closely (Figure 4) and is underpinned by a countercurrent occurring at depths of 800+ m and which hugs the continental slope and carries mostly cold Antarctic Intermediate Water northward towards the Equator. Similar undercurrents are found in the Mozambique Channel and also east of Madagascar, but models using water-volume data suggest that those undercurrents are not connected to the Agulhas Undercurrent.

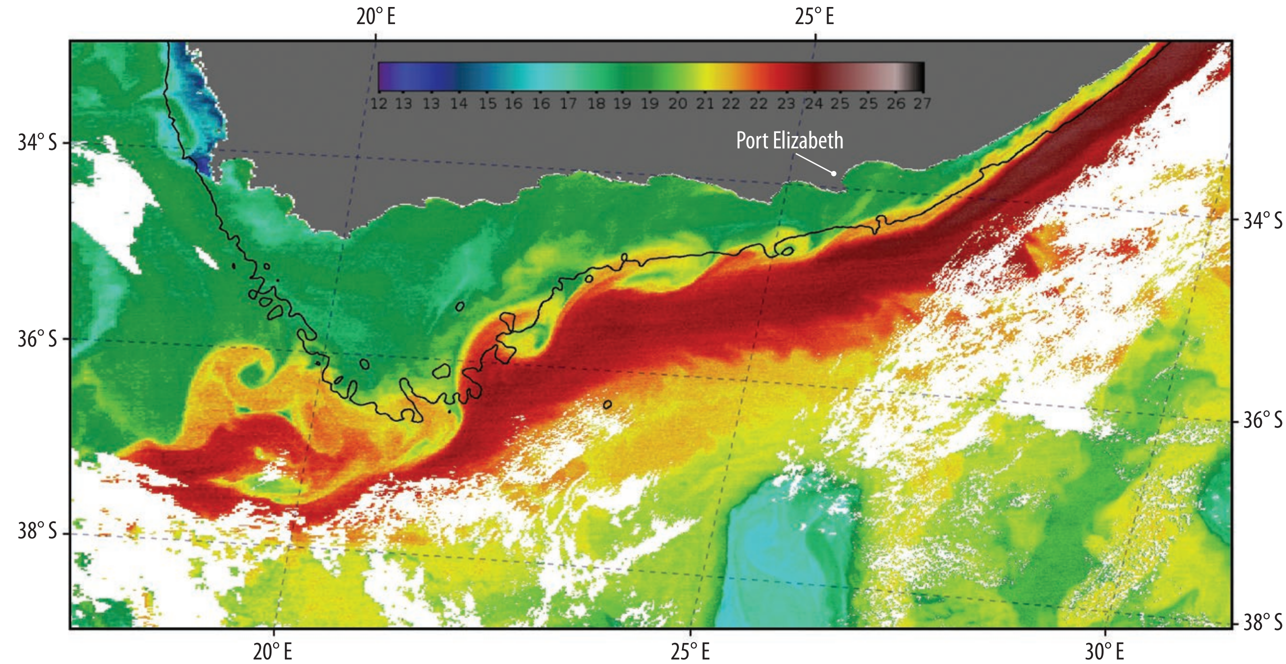

Figure 4 Satellite image in the thermal infrared of the surface layers of the Agulhas Current. The temperature scale (°C) is given on top; white areas represent clouds. The continental shelf edge at 200 m depth is indicated by a black line. Note how the northern Agulhas Current, up to Port Elizabeth, is nearly rectilinear whereas the southern Agulhas Current exhibits considerable sideways meandering and the formation of shear edge eddies and plumes of warm water. Regions shaded blue on the west coast indicate wind-driven, shelf-edge upwelling. Water of similar temperatures to the south represents cold Subtropical Surface Water poleward of the Subtropical Convergence. Source: Lutjeharms 2011

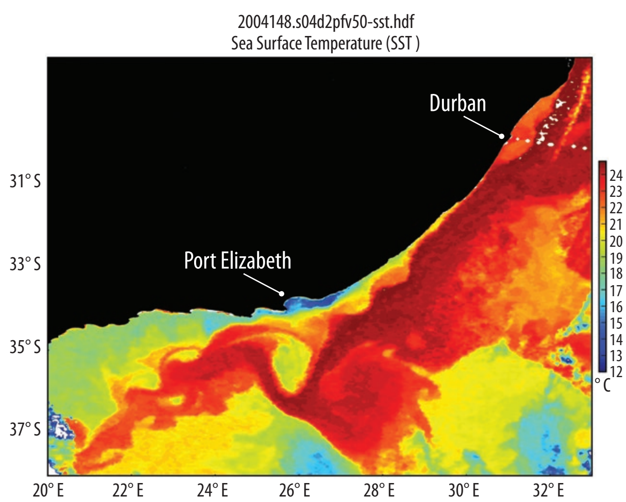

Figure 5 Satellite image in the thermal infrared of the surface temperatures of the Agulhas Current showing a Natal Pulse south of Port Elizabeth. The cyclonic eddy which nestled in the offshore portion of the meander is evident as are other shear cyclonic eddies, plumes and filaments on the inshore side of the Agulhas Current. Possible eddies in the KZN Bight and off Durban are evident. Water with higher temperature is represented by shades of red and cooler shelf water by shades of green. Coastal upwelled water around Port Elizabeth is shown as shades of purple and blue. Source: Lutjeharms 2006

The water masses of the northern Agulhas Current are largely Indian Tropical Surface Waters in the current's surface layers, with South Indian Subtropical Surface Water offshore. Subtropical Surface Water is also found within the current at a depth of 150–200 m. Plugs of Red Sea Water are found at intermediate depths on the inshore side of the current. The surface temperatures show a decline of ~2 °C moving southward along the length of the northern Agulhas Current and are ~28 °C in summer and ~23 °C in winter.

The northern Agulhas Current flows along a generally narrow continental shelf (Figure 4). The current is intermittently absent (generally 1.6 instances per year, but >3 times per year is not uncommon) from the shelf edge. This is the result of the passage of large, solitary meanders of the current, the so-called Natal Pulses, that are thought to be triggered at the KwaZulu-Natal Bight (an unusually wide offset on an otherwise narrow shelf) by an offshore eddy encroaching on the coast (Figure 5). Natal Pulses move downstream at ~20 km/day, grow laterally as they move, and carry an embedded clockwise eddy. This eddy may reverse a portion of the currents on the shelf for a short period as it passes, and such reversals, as well as accompanying decreases in temperature, may have important effects on the distribution and movement of biota, but currently no data are available to confirm these suppositions.

KwaZulu-Natal Bight circulation

The KwaZulu-Natal (KZN) Bight between St Lucia and Durban forms an offset in the eastern coastline of South Africa (Figure 6), which in many aspects is similar to the Delagoa Bight to the north. The KZN Bight is much narrower and shallower, however, resulting in a very different circulation pattern, generally found to be clockwise, but which may contain a number of eddies at any given time, and it may be rapidly disrupted by strong winds. Nonetheless, the water masses and circulation of this bight are characterised by some interesting and important features.

The eastern side of the KZN Bight is bounded by the Agulhas Current proper. At Durban the shelf narrows sharply and the Agulhas Current overshoots it, only to join the shelf edge again further downstream. Thus, off Durban, a lee eddy with clockwise motion is generated. This eddy may be carried away with the formation of a Natal Pulse, but it otherwise seems a fairly persistent feature, bringing deeper waters closer to the surface at its centre. By contrast, at the northern edge of the bight a peculiar upwelling cell is located between Richards Bay and St Lucia.

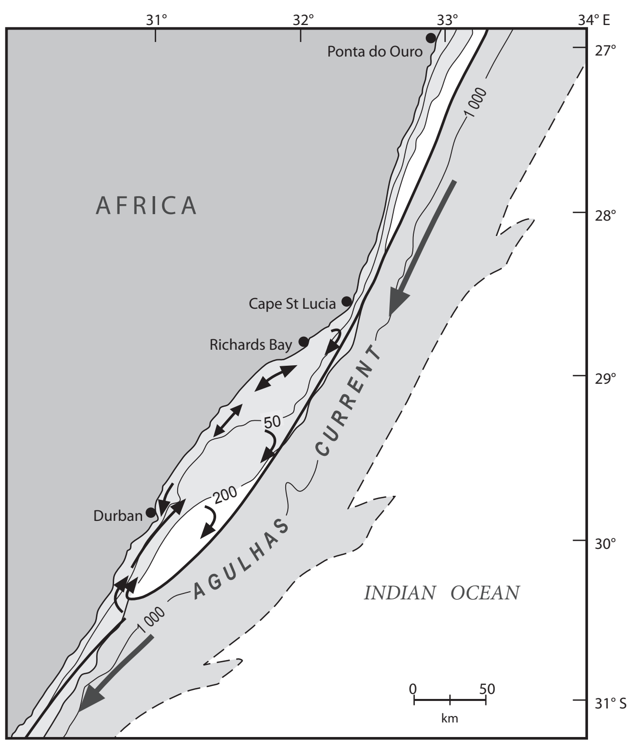

Figure 6 A conceptual illustration of the general cyclonic circulation patterns in the KZN Bight. The circulation of the bight consists of cyclonic eddies and is constrained in the coastline and the Agulhas Current, which is generally located near the 200 m isobath. Isobaths are in metres.
Source: Schumann 1987

This upwelling is both wind-driven and formed by the Agulhas Current as it moves from a narrow to a wider area of the continental shelf. The upwelled water originates from the South Indian Central Waters and is rich in nutrients.

This colder, nutrient-rich water moves along the seafloor at the KZN Bight, but can easily become mixed throughout the relatively shallow water column during a strong wind. The resulting increase in primary productivity at the St Lucia upwelling cell is well documented.

The phytoplankton generated in this cell is sometimes transported southwards in a strand of water along the shoreward edge of the Agulhas Current. Whether this upwelling cell has a noticeable influence on the benthic or pelagic ecosystems of the Natal Bight as a whole is still unknown.

The water masses of the KZN Natal Bight are mostly South Indian Subtropical Surface Water and Indian Tropical Surface Water, with an insertion of South Indian Central Water at the St Lucia upwelling cell. The slightly fresher (with lower salinity) Indian Tropical Surface Water is probably inserted onto the KZN Natal Bight sporadically as it may be found in varying amounts and degrees of purity in the Agulhas Current. The Thukela River is the only major river draining into this bight, but even during floods the dilution of water on the continental shelf by river water is only noticeable very close to the river mouth.

The southern Agulhas Current

Downstream of Port Elizabeth, in the Eastern Cape, the southern Agulhas Current can be distinguished from the northern Agulhas Current because it follows a quite different path. Whereas the northern portion is characterised by its nearly constant location at the shelf break, with the exception of the intermittent passage of a Natal Pulse, the southern portion meanders to either side of its 'mean' path along the shelf edge, with accompanying shear-edge eddies and plumes of warm surface water (Figure 7). These meanders grow as the current moves downstream. The warm-water threads are usually only ~50 m deep; their contribution to the water mass and heat budget on the adjacent shelf remains unknown, although the warmer water occasionally extends entirely to the coastline. The induced shear-edge eddies on the shoreward border of the southern Agulhas Current draw up deeper water in their centres, but this water has not been recorded on the Agulhas Bank, the wide shelf region south of Africa.

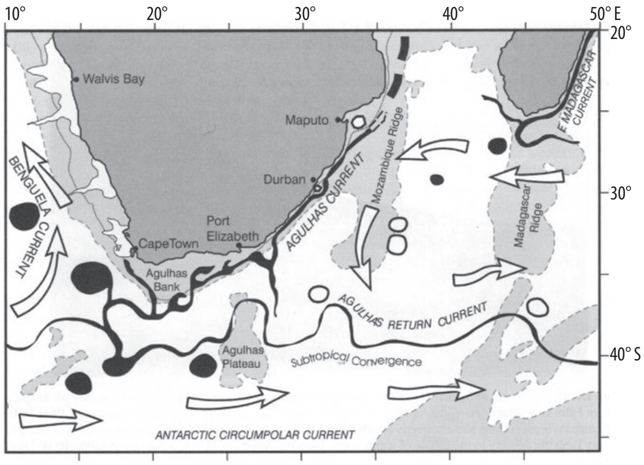

Figure 7 A conceptual portrayal of the Agulhas Current system. Areas shallower than 3 000 m are shaded. The edge of the continental shelf is marked by a dotted line. Intense currents are black and the general background circulation is indicated by open arrows. Cyclonic eddies are open; anti-cyclonic rings and eddies are black. Source: Lutjeharms 2006

The southern Agulhas Current sometimes moves southward at Port Elizabeth under the influence of a large Natal Pulse, and joins the Agulhas Return Current and thus does not continue along the shelf edge of the Agulhas Bank. Such a short circuit will usually last only a few weeks, but an unusual occurrence where the Agulhas Current has turned back on itself and flows eastward instead of westward for six months has been recorded.

The southern Agulhas Current extends to the seafloor and carries an estimated 70×10^6 m^3/s. In the upper 200 m, Indian Tropical Surface Water has a temperature of 16 °C or more; South Indian Subtropical Surface Water is usually found below this, with higher salinity; and deeper yet, South Indian Central Water has temperatures of 6–14 °C. At greater depths the southern Agulhas Current carries Antarctic Intermediate Water, a small amount of Red Sea Intermediate Water, and North Atlantic Deep Water. The warm surface waters of the current cool significantly as they move downstream. The temperature also changes with the seasons: during February (the Southern Hemisphere summer) it is ~23 °C, whereas in August (winter) it is only ~17 °C. As can be expected, the southern Agulhas Current has a strong influence on the circulation and water masses of the Agulhas Bank.

Agulhas Bank circulation

The Agulhas Bank (Figure 7) is the widest part of the continental shelf of South Africa, and it represents the centre of South African commercial fishing grounds. The Bank is unique as it lies between a westward-flowing boundary current on its east side, namely the Agulhas Current, and an eastward-flowing boundary current to the west, the Benguela Current of the South Atlantic Ocean gyre. These two currents largely influence the circulation, water masses and vertical stratification of the Agulhas Bank. These influences are reinforced by the bathymetry, with the shallow Alphard Banks shoal in the centre separating the circulation on the eastern and western sides of the Agulhas Bank.

On the eastern side of the Bank most of the bottom waters of the continental shelf follow the southwestward-moving Agulhas Current. There is occasional input onto the Bank of warm surface water via plumes from shear-edge eddies, as mentioned above. On the western side of the Bank the main water movement is northwestward. However, occasionally intense Agulhas Rings, which are large eddies rotating anticlockwise, may substantially increase the current speeds along the shelf edge. Just west of the southern tip of the Agulhas Bank, the Agulhas Current may also generate a clockwise lee eddy that forces water near the shelf edge towards the southeast. This eddy may escape westward or dissipate and lose its influence on the shelf circulation. Strands of warm surface water (~50 m deep) from the Agulhas Current also sporadically move along this western shelf edge. Coastal upwelling is common along the coastline of the Agulhas Bank under suitable wind conditions, particularly at coastal headlands.

The Agulhas Bank shows seasonal stratification of its waters. During summer the surface waters are warmed and a thermocline typical for the subtropics is formed. At the same time, however, the waters are cooled from below, considerably increasing the intensity of the thermocline. During winter this vertical stratification is destroyed by vigorous wind mixing to a depth of at least 75 m.

But, what cools the water from below? At the eastern corner of the Agulhas Bank, where the Agulhas Current diverges from the coastline, an upwelling cell forms off Port Alfred, Eastern Cape, drawing the colder South Indian Central Water into this cell. Although disputed, it is believed that the cell then moves onto the Agulhas Bank and forms an unusually cold bottom layer. The Agulhas Current itself may drive cold bottom waters far onto the continental shelf. It is possible that a resulting, exceptionally intense seasonal thermocline provides a more hospitable environment for spawning anchovy. The marine organisms occurring in the vicinity of the Port Alfred upwelling cell are also cold-water species, hence it has been suggested that this transitional area is a significant barrier to shelf biota along the southern and eastern shelf areas of South Africa.

Agulhas retroflection

After the Agulhas Current passes the southernmost tip of the Agulhas Bank, it abruptly turns to flow back into the southern Indian Ocean: this is known as the Agulhas retroflection

(Figure 2). This retroflection is not geographically stable but one of the most variable worldwide. The retroflection loop, with a diameter of ~400 km, moves into the southeastern Atlantic Ocean, occludes and forms an Agulhas Ring that then moves off into the South Atlantic Ocean. About 6–9 rings are formed each year, and most disintegrate close to where they are formed as a result of instability or interaction with other rings. Those that remain intact may move across the full width of the South Atlantic Ocean while slowly spinning down over a couple of years. The water masses of the rings are identical to those found in the Agulhas Current, but with heat loss, evaporation, and wind action the top layers may become colder, more saline, and substantially mixed by convection.

As part of the process of ring shedding, intrusions of cold, nutrient-rich, Sub-Antarctic Surface Water penetrate between a newly formed ring and the new retroflection. These intrusions have temperatures of <17 °C, salinities of <34.9, and are present in the region about 40% of the time. These water masses and their biological diversity make this a remarkably variable region. Biologically, the most important aspect of the southern termination of the Agulhas Current is that it affords access for Indo-Pacific species to be carried to the Atlantic Ocean by surviving in intact Agulhas Rings until these rings reach warmer latitudes more amenable to the survival of subtropical and even tropical species.

Agulhas Return Current

Most waters of the Agulhas Current, having passed through the Agulhas retroflection, eventually enter the Agulhas Return Current which flows eastward at about 40° S (Figures 2 and 7). Gradual cooling occurs as the waters move eastward and become mixed with ambient water masses, so that at ~70° E the last vestige of the Agulhas Current has dissipated.

The Agulhas Return Current flows roughly parallel to the Subtropical Convergence, and in the process large turbulent eddies are formed, with ever-changing meanders and eddy shedding. The first equatorward meander in the eastward flow of the current occurs as it passes the Agulhas Plateau (Figure 7). This meander is considered relatively stable in shape and location (although further research is needed), whereas meanders farther downstream are more variable.

The Agulhas Return Current is approximately 100 km wide, extends to depths of 4 000+ m, and carries about 44×10^6 m^3/s in the upper 1 000 m alone. At its origin (the Agulhas retroflection) the surface speeds are little different to those of the Agulhas Current. The surface speed at 25° E has been measured at 1.3 m/s, whereas at 60° E it is only 0.4 m/s. At intermediate depths of ~1 000 m the current speed is 0.4 m/s, at longitudes to approximately 40° E. One notable water characteristic of the Agulhas Current is a subsurface oxygen minimum, but this is rapidly mixed farther out in the Agulhas Return Current. An unusual and important feature of the Agulhas Return Current in combination with the Subtropical Convergence Zone is the enhanced primary productivity of this frontal system.

The Subtropical Convergence

The Subtropical Convergence Zone is the generic southern boundary of the Indian Ocean. This is where colder Sub-Antarctic Surface Water, with a high nutrient content (excepting silica) and an equatorward drift component subducts below the warmer and nutrient-poor Subtropical Surface Water. In the southwestern Indian Ocean, the southern border of the Agulhas Return Current sometimes meets with the front (Figure 7) but remains separate from it, thus a distinct Agulhas Front can be observed, particularly when the meridional temperature and salinity gradients of the Subtropical Convergence become steeper, rendering it one of the most intense fronts in all oceans. A temperature gradient of 5 °C has been observed over a distance of only 35 km.

The Subtropical Convergence lies in the vicinity of latitude ~40° S, in both the southeastern Atlantic and southwestern Indian Ocean; south of Africa, the zone may be pushed as much as 5° southward by the impact of the Agulhas Current. In general, the zone has a width of ~220 ± 140 km. This wide range is a result of a high degree of mesoscale turbulence resulting from north–south shifts of the front, as well as eddy shedding to either side (west and east). Furthermore, as a result of eddy formation and the presence of an Agulhas Front, many different fronts may exist at any one time, each with a different gradient and intensity. A special feature of this convergence, particularly west of 70° E, where the north–south gradients are strongest, is the presence of enhanced primary productivity.

The atmosphere above the Subtropical Convergence Zone is ordinarily a cloudy region. To obtain a relatively cloud-free view from space, satellite observations over a long period combine all the cloud-free expanses. This has led to the belief that the whole Subtropical Convergence Zone has enhanced (higher than usual) primary productivity. Research ships passing the front have occasionally recorded high concentrations of chlorophyll *a*, but at other times have found no evidence of such high levels. Studies using satellite technology and modelling have shown that primary productivity at the convergence occurs in the form of highly specific phytoplankton blooms of relatively short duration and limited geographic extent. The blooms are largely aided by eddy formation where high nutrient loads, originating south of the front, and a high degree of vertical stratification are combined to create favourable conditions. Furthermore, from a biological perspective, the Subtropical Convergence Zone is not just a border between sub-Antarctic and subtropical ecosystems, but forms a distinct ocean ecosystem of its own, with many endemic species of fauna. This is substantiated by assuming that most eddies that are shed at the front are eventually forced back and re-absorbed, thus continually reinforcing the front and not allowing much mixing or escape.

THE MONSOONAL SYSTEM

East African Coastal Current

The monsoonal system influencing the northern Indian Ocean involves of a complex set of ocean currents and water masses, all in some way affected by the seasonal monsoonal winds. Beginning in the south, the first current encountered is the East African Coastal Current, also known as the African Coastal Current or the Zanzibar Current. Fed by the South Equatorial Current (Figure 2), this is one of the few currents in the region that may be considered a permanent feature, even though it is affected by the seasonality of its source. During the Northeast Monsoon (December–March) the northward flow of the East African Coastal Current is opposed by the southward-flowing Somali Current. The boundary between these two currents begins near ~1° N at the beginning of the season, but shifts to ~4° S towards the end of the season. On meeting the opposing Somali Current, the waters of the East African Coastal Current then flow eastward into the Equatorial Countercurrent.

Where the two opposing currents meet, a large coastal upwelling system may form in the vicinity of 3° N, thus separating the currents along the coastline. As a result, two gyres are formed, a northern anticlockwise gyre carrying $\sim 27 \times 10^6$ m^3/s, and a southern clockwise gyre carrying $\sim 22 \times 10^6$ m^3/s, both in the upper 100 m of the water column. Phytoplankton from this upwelling area may be advected a long distance into the northern Indian Ocean by the Equatorial Countercurrent. The surface speeds of the East African Coastal Current may attain up to 2 m/s by the end of April, at which time the current flow volume reaches 15×10^6 m^3/s.

Somali Current

The inflow into the coastal currents of East Africa as well as their outflow into equatorial east–west currents varies with the monsoon season. The most important feature of the Somali Current is that it changes direction with season. During the Northeast Monsoon (December–March) the Somali Current flows southward along the Horn of Africa, yet south of 5° N the East African Coastal Current sets northward, as mentioned above. As the season advances the southward Somali Current strengthens and pushes increasingly farther south (up to ~ 4° S by the end of summer), its water deriving from the North Equatorial Current and flowing away from the coast in the Equatorial Countercurrent. The surface-water speeds of the Somali Current at the start of this monsoon season (in December) are 0.7–1.0 m/s, but by June the speed may already be as high as 3.5 m/s.

During the Southwest Monsoon (July–September) the Somali Current direction changes completely and flows northward, in contrast to all other currents along the African and Arabian coasts, thereby feeding directly into the East Arabian Current. South of 10° N the Somali Current is only ~150 m deep during this monsoon season, but its depth increases as the current moves northward into the Arabian Sea.

Arabian Sea circulation

The Arabian Sea fills the ocean basin to the west of the Indian subcontinent. Although called a sea, it has none of the characteristics of a regional sea such as the Red Sea or Persian/Arabian Gulf, but forms an inherent part of the broader circulation of the northern Indian Ocean. Water movement in the Arabian Sea is likewise dominated by the monsoonal winds and is therefore strongly seasonal.

During November–January the Northeast Monsoon causes a weak flow of less than 0.2 m/s in the Arabian Sea. Along the western continental shelf of India a current sets north-westward, approximately 400 km wide and 200 m deep, but increasing in depth as it progresses. The East Indian Winter Jet injects fresher water from the Bay of Bengal, past Kanyakumari (Cape Comorin) at the southern tip of India, and into the Arabian Sea. In the north, cold winds from over the land cause convective overturning. South of 15° N, at ~65° E, the current flows westward, and by the end of this monsoon season the flow is clockwise in the entire basin.

By April the Southwest Monsoon starts and the northward Somali Current is formed, moving water northward along the Horn of Africa towards the Arabian Sea. By May the continuation of this current, the East Arabian Current, is formed along the Arabian Peninsula, and carries water at ~0.7 m/s northward, while water movement in the greater part of the basin is clockwise (eastward). During the Southwest Monsoon strong coastal upwelling occurs along the continental shelf of the Arabian Peninsula, accompanied by a decline in water temperature of ~5 °C, as well as at the western shelf of India.

The circulation patterns in the adjacent seas are very different, as discussed below.

Red Sea circulation

The salinity of the Red Sea is higher than the world average of the oceans, as evaporation vastly exceeds precipitation; a salinity as high as 42 may be attained in the northern limits of the Gulf of Suez and Gulf of Aqaba. Its average depth is ~560 m, with a maximum depth of possibly 2 900 m, and a sill depth of ~110 m at the Strait of Bab-el-Mandeb, its entrance to the Gulf of Aden and WIO. The Red Sea's shape and its high salinity allow it to act as an inverse estuary. Inflow of ocean water occurs at the surface in winter and moves northward aided by seasonal winds. As this water moves northward, evaporation increases the salinities from averages of 36 to 40. In the northern reaches, the temperature of the surface water is 27–30 °C in summer, but decreases to 20 °C in winter when active convection takes place. In summer, deeper water begins to flow out over the sill and descends to a depth of 500–1 000 m in the northern Indian Ocean; here it has a temperature of 13–14 °C and salinity of >36.5. In summer the water is saturated with oxygen, but at such high temperatures the dissolved oxygen concentration is only about 4 ml/l (water with a salinity of 35 at 15 °C carries 8.5 ml/l oxygen). Waters with these particular characteristics are found in some form of dilution at intermediate depths throughout WIO, and water similar to Red Sea Water may correspondingly originate in the Persian/Arabian Gulf.

Persian/Arabian Gulf circulation

The Persian/Arabian Gulf is similar to the Red Sea in terms of area, and both are concentration basins. However, the Red Sea has a deep trough in the centre, whereas the Persian/Arabian Gulf basin forms an inherent part of the continental shelf and has a mean depth of only 25 m. Water in the interior of the Persian/Arabian Gulf also has very high salinity (~40), and the inflow of freshwater from the Euphrates and Tigris rivers makes little difference to this. The Gulf, however, has no pronounced sill holding back deep, dense waters. Just outside the mouth of the Gulf, at the Strait of Hormuz leading to the Gulf of Oman, the slightly diluted water retains a high salinity (~38) and an oxygen maximum. Although Persian/Arabian Gulf Water has a lower density than Red Sea Water and therefore does not descend as deeply, at large distances from these sources it becomes difficult to distinguish between waters of the Red Sea and the Persian/Arabian Gulf.

CONCLUSIONS

The WIO region shows high diversity in physical and chemical conditions and ocean ecosystems. From its border with colder sub-Antarctic waters, and northward into tropical waters near the equator, a great spectrum of temperature, salinity, nutrient content, mixed-layer depths and environments can be expected. A vast amount of this ocean region remains as yet unexplored and unmeasured, particularly the southwestern areas, and the hydrodynamics are imperfectly understood. Moreover, the peripheral seas of WIO, the Red Sea and Persian/Arabian Gulf possess some unique features and extreme environmental conditions. In certain portions of WIO, but specifically in much of the equatorial expanse, the currents may be quite stable, whereas in other portions, such as at the Agulhas retroflection south of Africa, some of the greatest current variability in the world's oceans can occur. While many of this region's ocean systems are currently under intense investigation, linking what is learnt through physical and chemical oceanography to the life histories and distributions of fauna, particularly fishes, will present a challenge to researchers for some time to come.

GLOSSARY

advect – to convey a fluid by horizontal mass movement.

convective overturning – reversals of water masses with well-defined temperature and salinity regimes/characteristics.

fluorescence – the property of absorbing light of short wavelength and emitting light of longer wavelength.

Indonesian Throughflow – an ocean current important for global climate, which moves warmer freshwater from the Pacific to the Indian Ocean, where most of the water flows from north of the Equator, past the south of the Philippines, between Borneo and Sulawesi and south between Bali and Lombok, Indonesia, into the eastern Indian Ocean.

meridional – along a meridian or in a north–south direction.

photic zone – the surface layer of the ocean that is reached by sunlight, and hence where photosynthesis can take place (roughly to 80+ m depth).

phytoplankton bloom – a large and sudden increase in microscopic algae caused by an increase in nutrient content in an area, common in the world's oceans, and often changing the local colour of the water.

salinity – the measure of dissolved salt content in water, usually expressed as a ratio in parts per thousand (ppt); average ocean salinity is ~35 ppt (or 3.5%, or 3.5 g of salt per litre of water).

silica – silicon dioxide, a mineral used by marine organisms such as diatoms to build the cell wall.

spinning down – losing energy, slowing down and dissipating.

thermocline – an abrupt transition between two layers of water with typically large temperature differences, with the colder water beneath the warmer.

volume flux – a measure of water flow, where a particular volume (m^3) flows across a unit area (m^2) in a unit of time.

THE ORIGINS AND GEOLOGY OF REEFS OF THE WESTERN INDIAN OCEAN

Charles RC Sheppard, Mebrahtu Ateweberhan, Nicholas AJ Graham and Bernhard Riegl

INTRODUCTION

The Western Indian Ocean (WIO) is a biologically coherent subdivision of the world's largest biogeographic province, the tropical Indo-Pacific. Its partial separation from the eastern portion of the Indian Ocean is largely a result of currents, great depths and substrate types, and not of land masses or to marked water temperature differences.

Reef types present in the WIO include all of Darwin's (1842) classic reef types: fringing reefs, barrier reefs and atolls. Added to these are numerous variations resulting from substantial vertical and horizontal movements of land related to plate tectonics, and to sea levels which have changed markedly over recent geological time. The area's two main embayments, the Persian/Arabian Gulf and the Red Sea, have very different reef conditions, which support fundamentally similar Indian Ocean marine biota, but with several characteristic and endemic species.

The distribution of substrate suitable for reef development is uneven (Figure 1), and is partly determined by depth and by a range of other factors which favour, or preclude, reef development (Sheppard 2000). One of the largest reef systems is the chain of reefs in the central Indian Ocean, most of which are classic atolls. Further to the west lie the granitic Seychelles and the volcanic Mascarene islands of Réunion, Mauritius and Rodrigues. Between and around these are numerous, extensive, submerged limestone platforms, sometimes called the Shoals of Capricorn, because they are located on the Tropic of Capricorn. These areas have thousands of square kilometres of reefal substrate lying within the photic zone, where water temperature is suitable for reef development. Further west of these shoals lie numerous groups of atolls, most of which are politically part of the Seychelles. Madagascar has very extensive fringing reefs, a very large barrier reef in the southwest, and numerous patch reefs and atoll-shaped structures dotted around it, mainly on its northwestern side. The shores of East Africa and its many islands have many variations of fringing and barrier reefs which extend southwards to South Africa.

Near the Horn of Africa, heavily sedimented shores preclude the development of extensive reefs, though reefs do occur in patches, and the Socotra archipelago is fringed by extensive coral reefs. In the Gulfs of Aden and Oman, cold water upwelling results in patchy reef development, though coral growth may be extensive in some areas.

Along the coasts of Pakistan and western India the marine substrate is mainly soft or heavily sedimented so that corals are few and reef development is poor or absent. These conditions persist as far as southern India and Sri Lanka where there are some extensive fringing reefs (Sheppard 2000). Elsewhere there are extensive submerged limestone platforms that are separated by large expanses of deep ocean or, around the rim of the ocean, by extended stretches of muddy shallow water not conducive to reef life. These areas are still largely unexplored.

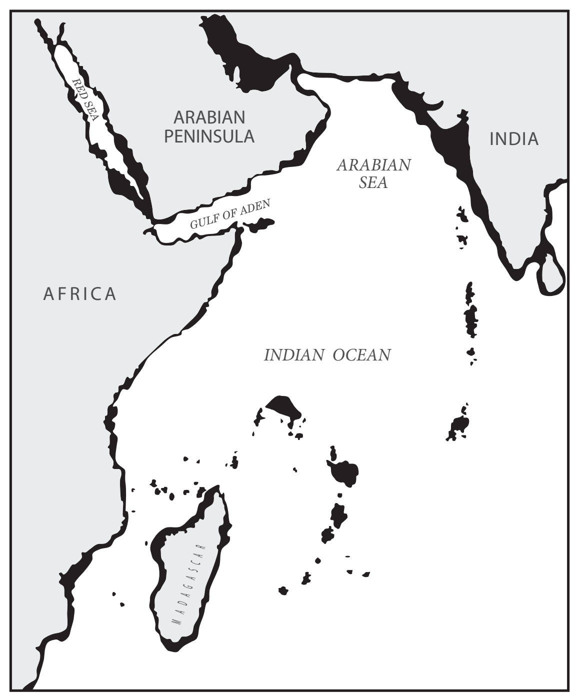

Figure 1 Map of the western and central Indian Ocean. Black-shaded areas represent ocean areas that are shallow enough to support coral reefs; in such areas reefs may be prolific and abundant as in mid-ocean sites, or they may be largely soft sediment with scattered reefs in some continental sites, such as western India. Redrawn from Sheppard 2000

Burgeoning human populations, poor management and overexploitation of marine resources has raised deep concern over the resilience of reefs and their ability to recover from impact. About 70% of the region's reef systems have been either destroyed, damaged, or impacted to some degree (Figure 2), and the existence and integrity of these huge geological features that are key to supporting much of the marine life are profoundly threatened.

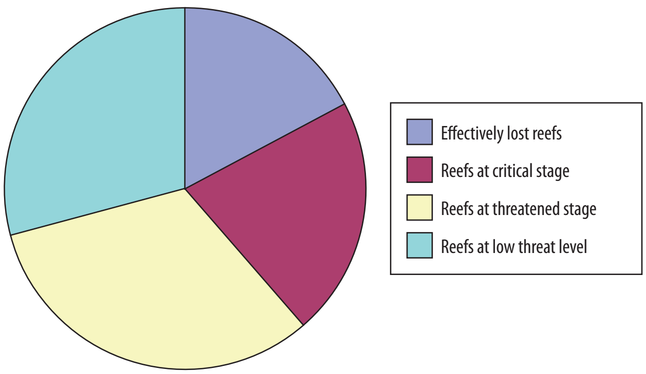

Figure 2 Pie chart of Indian Ocean coral reefs categorised into four main groups, from effectively lost to low threat and largely undamaged.
Source: data from Wilkinson 2008

POST-HOLOCENE SEA LEVELS

Present-day reef distribution depends on past distribution; modern reefs grow on old reefs where they can. During the last ice ages, sea level oscillated from a little higher than it is today to ~150 m below today's level, as a result of a series of warming and cooling episodes (Figure 3). Then, at the end of the last ice age, between 18 000 and 15 000 years ago, there was a marked rise in sea level which continued for ~10 000 years. As sea levels rose, reef growth probably continued in the shallowest 20–50 m. Where there were brief still-stands, horizontal reef accretion increased, but where sea level rise was continuous and rapid, reefs simply grew upwards — some near their maximum possible rate — until the sea level stabilised near its present level. This is, however, a very simplified description and clearly did not apply everywhere: much more reef substrate exists in ~5–50 m deep in the WIO than that which supports surface-reaching reefs today. This is illustrated by the well-mapped example from the Chagos Archipelago in the central Indian Ocean, where the area of reef substrate that remains submerged to several metres greatly exceeds the area which has reached the surface of the sea today (Figure 4) (Dumbraveanu & Sheppard 1999).

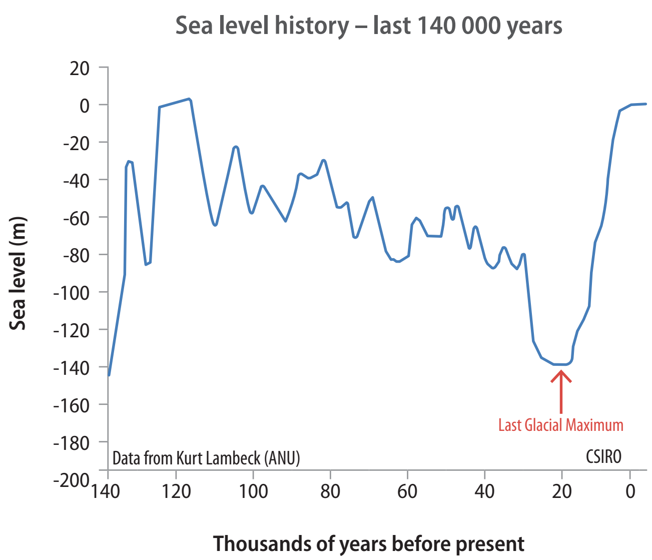

Figure 3 Sea level during the past 140 000 years, showing that major fluctuations have occurred during this period. Especially important today is the low sea level stand about 14 000–20 000 years before present, when sea level was depressed nearly 150 m relative to the present day.
Redrawn from Hopley 1982

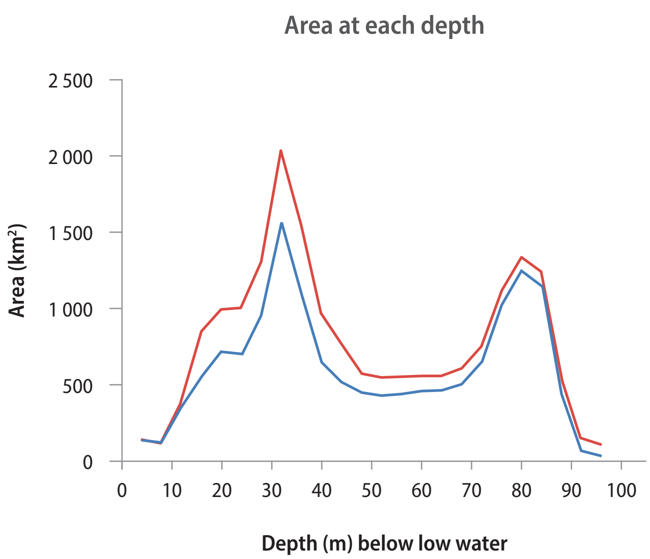

Figure 4 Area distribution from 0 to 100 m deep of a complex of coral atolls and banks in the Chagos Archipelago. Top line (red) represents the main atolls plus submerged banks and reefs; bottom line (blue) represents the five main atolls only. Source: Dumbraveanu & Sheppard 1999

THE NORTHWEST INDIAN OCEAN AND PERIPHERAL (ADJACENT) SEAS

Persian/Arabian Gulf, Gulf of Oman and Arabian Sea

The Persian/Arabian Gulf is a largely carbonate basin, where most substrate is <20 m deep (Figure 5). Only a narrow strip along its northern, Iranian, shore is deeper. The Arabian peninsula shoreline is geologically stable, while the Asian shoreline is unstable (Sheppard *et al.* 2000; Subba Rao & Al-Yamani 2000). During the Last Glacial Maximum (LGM), ~20 000 years ago, this Gulf was completely dry except for the channel which drained rivers such as the Tigris and Euphrates into the Indian Ocean. With the rise in sea level the Gulf flooded with water from the Indian Ocean, bringing with it an Indian Ocean biota. Today the marine climate is very hostile, being highly saline with enormous annual temperature ranges. These harsh conditions also create a kind of carbonate substrate which is rather uncommon in the Indian Ocean region: biogenic hard grounds of limestone dominated by microfauna and chemical depositions (Purkis 2011). While there is still reef growth, the diversity of limestone depositing species that can tolerate conditions in the Gulf is a quarter or less than that in the Indian Ocean (Figure 6), and these species become less diverse as salinity and temperature become more extreme.

Most of this vast limestone platform in the Gulf is thinly covered by carbonate sands, which form flat, featureless expanses with remarkably little relief, except for some raised mounds that resemble patch reefs. The summits of some of these are near low water level and, while several have rich coral growth, many have few corals because of the severe environmental conditions, and instead support large brown algae. These limestone platforms are formed in part by underlying salt domes forcing surface limestone upwards, a mechanism which also led to the creation of the archipelagos in the southern Red Sea.

Reef terraces are found at Bahrain and other small island groups such as the 10- to 15-m high islands of the Hawar Archipelago. Likewise, the small islands off Saudi Arabia probably also have uplifted limestone at their core, although these are now coral cays ringed by modern coralline algal and coral reefs that provide the most diverse hard substrate habitats known in the Gulf. The southernmost Gulf supports a complex mixture of limestone patches and sedimented areas colonised by seagrasses and algae, with extensive corals in patches. Large amounts of limestone sediments, dominated by foraminifera, form banks and shoals. The sediment becomes rapidly cemented to form extensive limestone crusts in both shallow subtidal and intertidal waters, the crusts sometimes dominated by algae or corals, or by both.

The Iranian side is poorly known. It has a steep slope, supports reefs in patches and, given the general anticlockwise circulation in the Gulf, may be the source of most of the propagules of corals and other marine life in the Arabian or southern side.

The entire Arabian Peninsula has rotated through ~7° anticlockwise since the opening of the Red Sea (Sheppard *et al.* 2000). Northeastern Arabia is being pushed into the Asian plate leading to fjord-like, mountainous structures in the Musandam Peninsula, a remarkable feature jutting into the Straits of Hormuz, the entrance of the Persian/Arabian Gulf. Today the peninsula is a 90-km spur of limestone mountains and cliffs of Cretaceous origin, long recognised as being an unusual geological structure, whose linear coastline is probably nearly 900 km (Figure 7). The substrate is mainly reefal, built by algae, and later by scleractinian corals, whose layers are folded and tilted. This area is biologically important because it provides substantial rocky substrate where, for hundreds of kilometres on either side, the shore is formed by soft substrate largely uncolonisable by reef biota. The area is spectacularly beautiful and, on land at least, inhospitable because the steep-sided hills shut off any breeze. The phrase 'going round the bend' is said to have originated here: officials posted to the telegraph relay station round a bend in a fjord in the 1860s used to be driven to distraction by boredom and heat. Missing the marvellous opportunities to study the reefs, they gave this area the reputation of being the most oppressive place in the world.

The Gulf of Oman is sedimentary and the sea water has near-normal oceanic salinity. The northern shore, Balochistan, remains almost completely unstudied. Its southern shoreline in Oman is a gently sloping sandy bay over 300 km long. The Daymaniyat Islands (Figure 8) provide almost the only significant coral-reef substrate, and the reefs are among the best examples of reef formation in the Sultanate, but they are isolated, relatively tiny expanses of reef in a very large sedimented area. The mainland shore is composed mainly of various sandstone and dolomite outcrops along with limestones and metamorphosed basalts, interspersed with beaches. There are some reefs, including extensive monospecific stands of *Pocillopora* (Figure 9). At 2–10 m above sea level there are early Pleistocene corals, some being 'stacked bioherms' rather than true fossil reefs, in which layered coral communities alternate with coarse wadi deposits and storm debris, and the coral layers are not fully consolidated reefs. Semi-fossilised drowned reefs have also been discovered along a 20-m depth contour on this section of the northern coast of coast.

The Arabian Sea shoreline of Oman is poorly known. From Ras Al Hadd (the easternmost part of Arabia) the shore has large, sweeping sandy bays backed by low-lying dunes, salt pans and, towards the south, cliffs. Masirah Island has some fairly

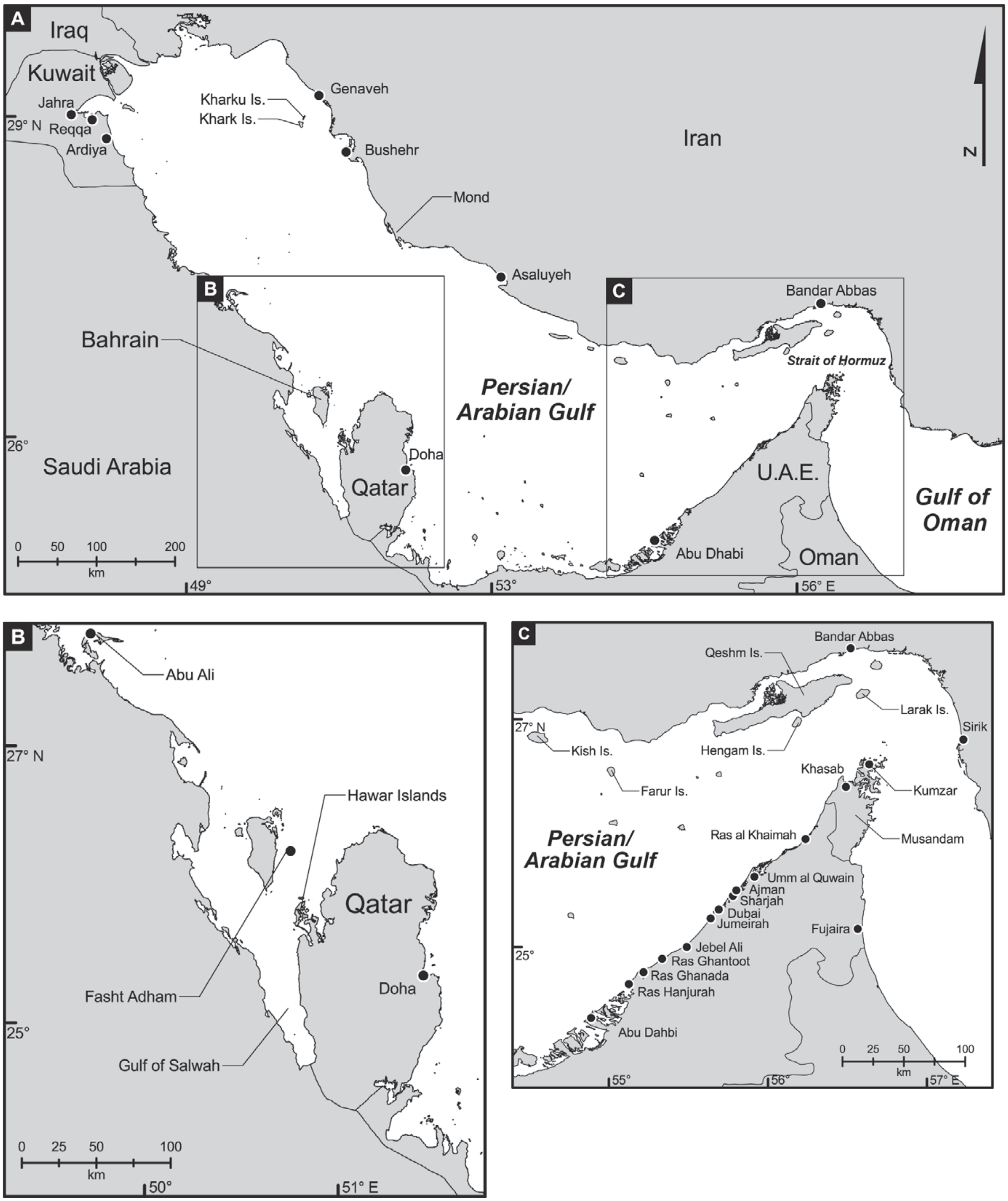

Figure 5 Map of the Persian/Arabian Gulf region. This shallow sea has high salinity and seasonally both high and low water temperatures.

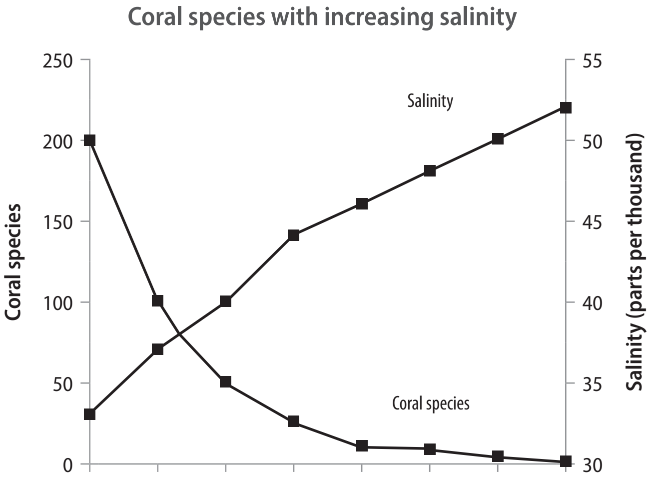

Figure 6 Number of coral species living in increasing salinity in the Persian/Arabian Gulf. Corals become less diverse as salinity increases.

Figure 7 The Musandam Peninsula forming the southern part of the entrance to the Straits of Hormuz. This is a heavily indented coastline with steep, deep slopes that are very suitable for coral growth and which is unlike the coastline that extends for many hundreds of kilometres east or west of it. © CRC Sheppard

Figure 8 The Daymaniyat Islands of Oman, being made of fossil reef and raised rock, provide hard substrate for coral growth which otherwise is very scarce in the Gulf of Oman. © CRC Sheppard

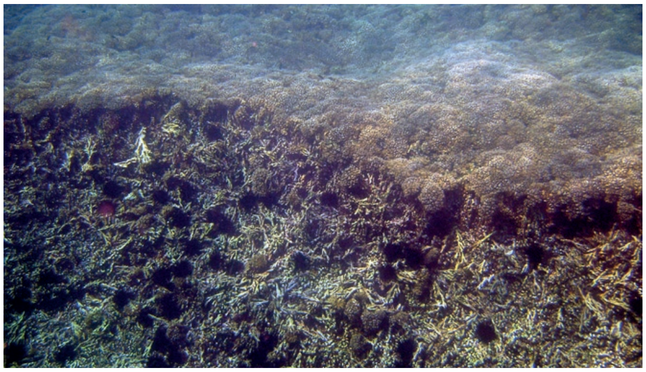

Figure 9 Underwater in the Daymaniyat Islands there exist reefs, or more properly bioherms, made of vast expanses of single species of corals. This example is of *Pocillopora*; further east there are similar stands of *Montipora*. © CRC Sheppard

Figure 10 Off Masirah Island in the Arabian Sea are large almost monospecific reefs of the leafy coral genus *Montipora*. © R Baldwin

Figure 11 Kelp and coral reefs. In upwelling areas such as southern Oman in the Arabian Sea, the benthic community is a mixed one of macroalgae characteristic of cold-water stands growth amongst corals. The kelp is *Ecklonia*, the tall alga is *Sargassopsis* (both genera of brown algae) and the coral is an *Acropora* species. © R Baldwin

well-known reefs with large expanses of *Montipora* (Figure 10). Midway down Oman the extensive dunes of the Wahiba Sands continue into the sea, precluding reef development.

Further south, rocky cliffs alternate with long stretches of littoral sand dunes and generally terminate near low water level. These areas are heavily scoured, so that the sublittoral of this high-energy coastline is predominantly a soft substrate environment below a few metres depth. Coastal rock is a complex mix of Tertiary shales, limestone and gypsum, with chert and marly bands interbedded with some igneous rock. Some remarkable locations occur where both seasonal and permanent stands of the Southern Hemisphere kelp *Ecklonia* and other related large brown algae form kelp forests amongst the coral communities, in a remarkable overlap between these two usually well-separated ecosystems (Figure 11). This is attributed to a seasonal, nutrient-rich, cold-water upwelling. This pattern continues along the Yemen coast, south to Aden, supporting patches of reefs, but mostly of corals veneering the underlying rock (Pichon *et al.* 2010).

The Socotra Archipelago lies on the Carlsberg Ridge. The southern rocky shores of the four main islands are steep and exposed to the full force of the summer monsoon, but the sheltered northern shores support significant coral communities between rocky outcrops dominated by macroalgae. The islands themselves lie on a broad and shallow, sedimented platform from which originates much of the sediment that controls the coral-reef communities. In some areas this accumulates into immense beaches (Figure 12).

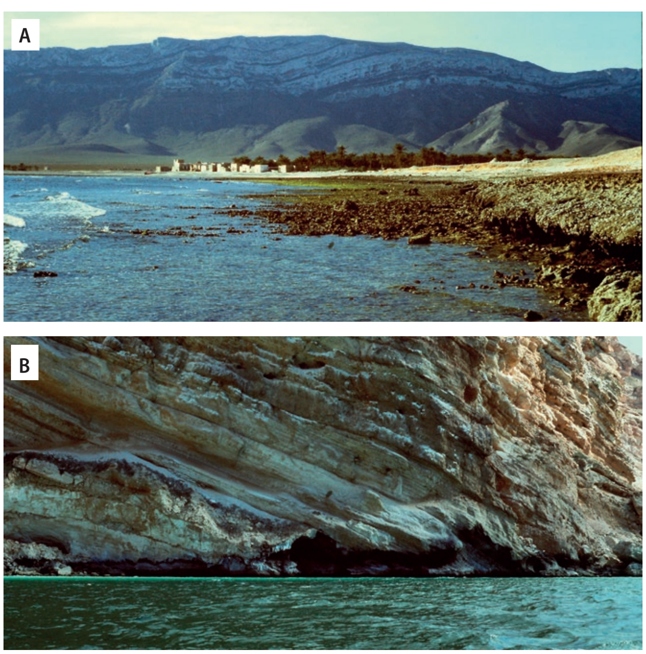

Figure 12 A Socotra Island in the Gulf of Aden is part of Yemen politically but is closer to the African coastline. This group of islands provides significant hard substrate suitable for corals in this sea.
B Socotra shoreline. © CRC Sheppard

Red Sea

The Red Sea and the Gulf of Aden, both rich in reefs (Figure 13) (Sheppard 2000), were formed by tectonic rifting of Arabia from Africa that started ~180 million years ago (mya) during the fragmentation of Gondwana. The separation formed the Afar Triple Junction (Figure 14) during late Oligocene–early Miocene, ~30 mya. This Junction forms the centre of a continuous rift between the Arabian, Nubian and Somalian plates. The Red Sea is considered to be a young ocean, its formation initiated by the magmatism that began ~31 mya. The trough started to form in the south-central part 25 mya (Bosworth *et al.* 2005), and was followed by a wave of volcanism throughout the entire Red Sea, from Afar and Yemen to northern Egypt. At ~20 mya the principal phase of shoulder uplift took place and water depth increased dramatically through the entire length of the sea. Rifting in the Gulf of Aden started earlier than in the Red Sea, as evident from the wider spreading. The rift connects directly to the worldwide system of oceanic plate boundaries via the Sheba Ridge in the Arabian Sea.

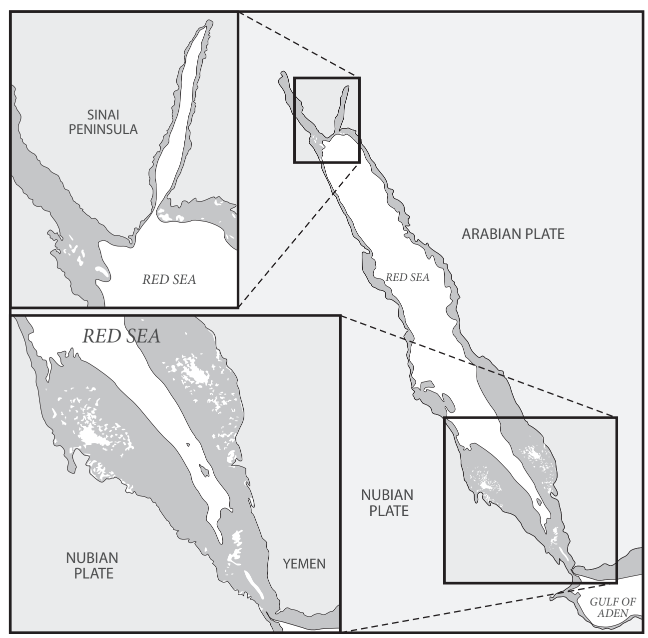

Figure 13 Sketch of the Red Sea and Gulf of Aden areas that are rich in coral reefs (darker-grey shaded areas). The Red Sea is particularly deep, being formed by tectonic rifting of Arabia from Africa. It is more diverse in corals and fishes than many parts of the Indian Ocean.

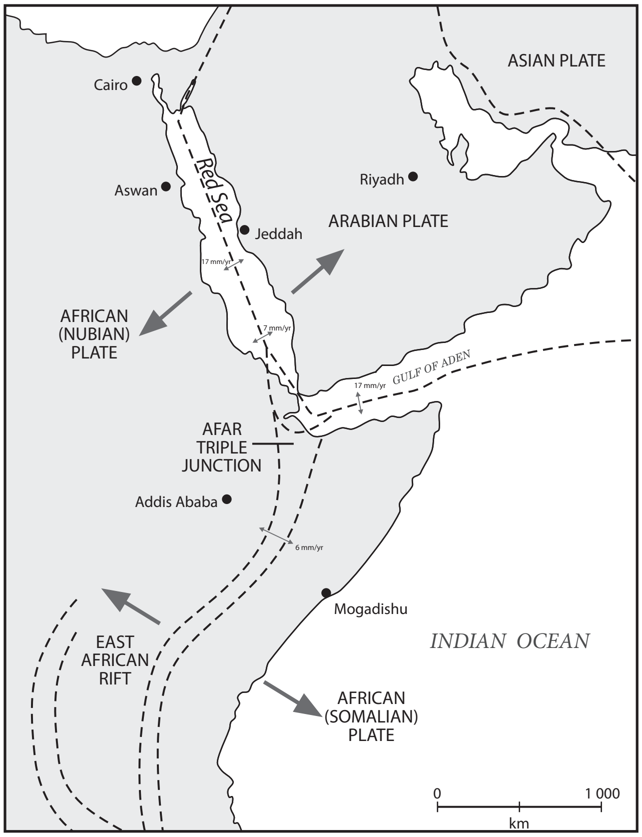

Figure 14 Map of the Afar Triple Junction.
https://commons.wikimedia.org/wiki/File:ATJ_map_%28color%29.jpg#filelinks

The Red Sea is connected to the Indian Ocean by the narrow and shallow Hanish Sill (at ~137 m depth) at the Bab-el-Mandab (the 'Gate of Lamentations', perhaps so named because of its stormy character). The Sea is also now connected in a minor way to the Mediterranean in the north by the Suez Canal. As a part of the great rift system which extends from eastern Africa, through the Gulf of Aqaba to the Dead Sea (Braithwaite 1987; Bosworth *et al*. 2005; Tiberi *et al*. 2005), the central depths of the Red Sea are both very hot and highly saline as a result of volcanic activity.

The region's climate is largely controlled by seasonal changes in atmospheric pressures (Edwards 1987), and weather variations are associated with the relatively large North–South gradient in atmospheric pressure. Much of the airflow to the Red Sea is from Northeast Trade Winds, and the mountain ranges along the sides of the sea ensure that the main wind systems blow predominantly along its length. The air near the sea surface is dry as a result of the desert and semi-desert surroundings. Associated with the variation in wind direction and water circulation, the Red Sea can be separated into two parts, north and south of 20° N. Palaeoclimatic evidence from fossil and recent coral cores show that the northern part is influenced by non-stationary circulation regimes associated with the ENSO teleconnections. Before 1970 patterns were associated with strong Pacific–North Atlantic teleconnection; those after 1970 are related to ENSO conditions and weaker Pan Pacific–North Atlantic Circulation regimes (Rimbu *et al.* 2003; Felis *et al.* 2004). The southern Red Sea seems to respond entirely to the Indian Ocean monsoon system (Klein *et al.* 1997).

Thermoclines established by the warm conditions prevent vertical mixing and cycling of nutrients from deeper water, so that the main source of nutrients is incoming Indian Ocean water. This exchange is stronger in winter when plankton-rich Gulf of Aden water flows into the Red Sea at the surface (Ponomareva 1968). Recent satellite observations, however, indicate higher chlorophyll *a* concentration in the south during summer months. The northern Red Sea, north of 18° N, is less affected by seasonal changes, and water movement is consistently southward throughout the year. It has lower nutrient levels, and surface chlorophyll *a* concentration is less than half that of the southern Red Sea.

The minimum water level in the early Holocene was close to the depth of the sill at the entrance. It is unlikely that the sill was exposed completely, so the Red Sea was probably not completely cut off (Siddal *et al.* 2003; Fennadez *et al.* 2006). However, the depth of the sill would have been very shallow so that water exchange with the Indian Ocean would have been extremely restricted. There is considerable evidence that the Red Sea became hypersaline during this period, and its principal biota may have been temperature- and salinity-resistant micro-organisms (Siddal *et al.* 2003; Fennadez *et al.* 2006). Under such conditions reef growth would have ceased, only to be resumed when sea levels rose and water flooded in over the sill, thus lowering salinities.

As a result, the biota forms distinct northern and southern biogeographic entities. While popular accounts continue to assume that this sea is fringed with rich coral reefs throughout, the southern third is, in fact, relatively poor in reefs, and its sedimentary character favours macroalgae, seagrasses and mangroves more than reefs. Reef structure in this part of the Red Sea resembles that in the Persian/Arabian Gulf more than it does that of the northern Red Sea (Sheppard *et al.* 1992). Reefs in the north commonly extend 60 m deep while many reefs in the south are limited to ~10 m, terminating on sandy bottoms (Loya 1972; Roberts *et al.* 1992; Sheppard *et al.* 1992). However, new investigations indicate equal or higher species richness of several groups, such as corals (JEN Veron *et al.* unpublished data), butterflyfishes, seaweeds and seagrass (Lipkin & Silva 2002; Ateweberhan & Van Reine 2005).

During the Pleistocene ice ages, reef growth in shallow water was spread over a vertical range of at least 100 m,

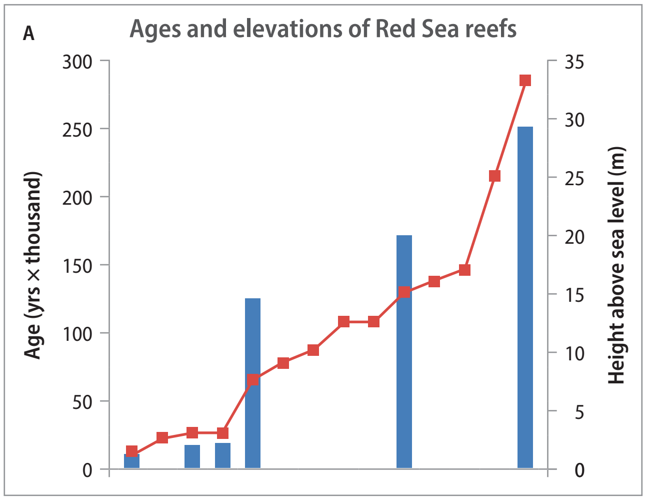

Figure 15 A Ages (bars) and elevations (line) of Red Sea reefs that align along both the African and Arabian shores. Present fringing reefs have surfaces at low sea level, while older, fossil reefs are found further inland on both shores at generally increasing elevations. **B** Photograph of the present reef flat which is submerged (left), while to the right is the youngest fossil reef elevated by 2–3 m.
A Redrawn from Medio *et al.* 2000 **B** © CRC Sheppard

resulting in the development of several substantial limestone ridges. Today these form modest-sized barrier reef systems offshore, and present-day coral reefs are therefore built on and veneer older reef systems that were formed during earlier interglacial periods. Many reefs also veneer alluvial fans formed from outwashed terrestrial material, and in some areas, cores have revealed alternating layers of alluvial fan and reef superimposed on one another. Because of the tectonic uplift of the shores, and the widening of the Red Sea by several millimetres per year, raised fossil reefs are found on the shores in a series of different steps in which height is related to age (Figure 15).

While classic, steeply sloping, fringing reefs are the best known, several other forms occur too, many given different names of greater or lesser popularity. Reef construction will, however, occur wherever substrate and environmental conditions allow, irrespective of how we classify them, and in the tectonically active Red Sea where variation in substrate is considerable, it leads to a corresponding variety of reef types (Figure 16).

- 'Contour reefs' develop on sites where mountains submerge into the sea. These are usually thin, typically only 3–4 m wide, but may extend outwards as much as 1 km in embayments and old wadi systems.
- Barrier reefs have developed on older offshore limestone platforms, now lying some distance from land along depth contours of 50–200 m along old Pleistocene shorelines.
- Patch reefs typically occur where temperature and salinity and, most importantly, high sedimentation constrain greater coral-reef development in the lee of barrier or fringing reefs. These rise from sandy substrate at 1–5 m depth.
- 'Ridge reefs' were first described as longitudinal ridges lying along the axis of the Red Sea, their base being the result of normal faulting and underlying salt deposits moving upwards along these faults (Guilcher 1988).
- Sanganeb, off Sudan, has been described as the only atoll in the Red Sea.

The most northerly reefs of the entire Indian Ocean region are in the sedimented Gulf of Suez. The patch reefs on its eastern shore reach 1–3 m in height above the soft substrate. The Gulf of Aqaba is like a small-scale Red Sea. It has a 200-m deep sill at its entrance and supports continuous fringing reefs that conform to their rock basement, and include some of the most recreationally used reefs anywhere in the world. These are mostly narrow reefs, sometimes only 10 m from the beach, but in one or two areas they broaden to almost 1 km.

The southern part of the Red Sea is generally poor in reefs along the mainland shores, as a result of increasing sedimentation, shallowing bathymetry and higher nutrient levels which favour algae. The continental shelf becomes broad and fringing reefs become intermittent, being replaced in many places by sand, mud and mangroves (Figure 17). Reefs occur where a gradual subsurface slope has allowed them to extend considerable distances seaward. Here, a different type of reef, constructed by calcareous red algae, and dominated by algae can be found. These reefs seem to be analogous to oceanic coral-reef crests. They rise from sandy substrates at 2–4 m deep, support few corals and are typically covered in *Sargassum*, whose fronds form thick mats on the water surface. These coralline reefs provide extensive hard substrate in otherwise sandy areas. Offshore, the Farasan and Dhalak archipelagos support rich reefs which extend into deeper water.

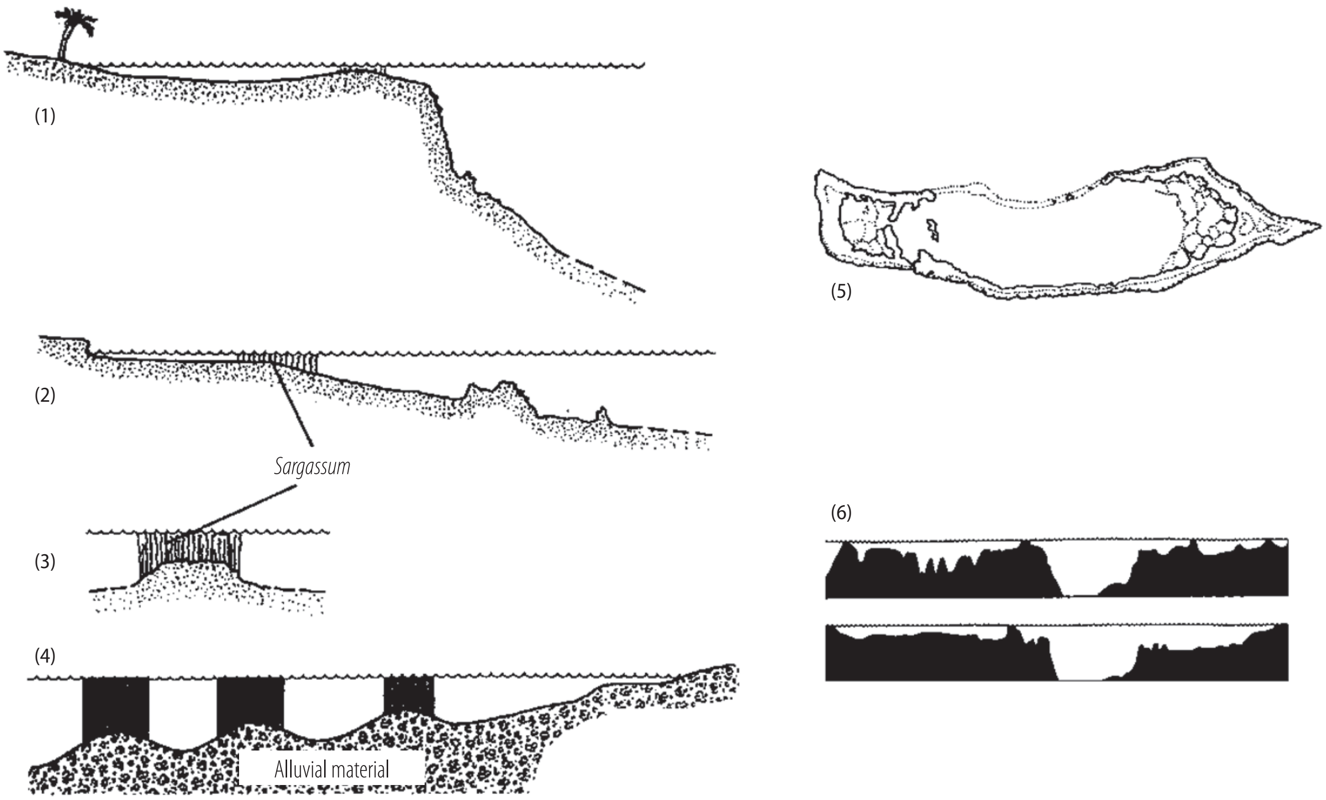

Figure 16 Variation in reef type is considerable within the Red Sea, from classic fringing reef (1) with reef flat and steep slope, through a range of patch reefs (2–4) to a few atoll-like structures (5). Sketch 6 shows two transects from shore to ~50 km to seaward that show numerous irregular pinnacles of coral growth and, in the right one-third of each trace, barrier reef structures. © CRC Sheppard

Figure 17 In the centre and south of the Red Sea, mangroves become increasingly common. These form extensive habitats of soft substrate unsuitable for coral growth although seaward of them where water is clear, coral reefs again flourish. © CRC Sheppard

Pakistan, India and Sri Lanka

The shores of western India and Pakistan are largely sedimented, with little coral-reef growth, although corals may be found in a few areas with hard substrate (Bakus *et al.* 2000). One exception is in the Gulf of Kutch in northwest India, where corals are abundant and where rudimentary reefs occur.

Coral diversity shows a marked gradient along this coast, with ~40 species of reef-forming corals in the north, to 200 or more in the south. Curiously, there are no modern branching corals in the north, though semi-fossilised *Acropora* has been found (Bakus *et al.* 2000). Fringing and patch reefs occur especially between India and Sri Lanka. In general, the reefs of this coastline have been heavily degraded by human exploitation, including extensive coral and reef mining for construction.

Around Sri Lanka, fringing and barrier reefs occur close to shore within the 30-m depth contour. However, little research has been done, and for many years civil conflict has made the northern area inaccessible. Some areas are declared protected (e.g., Hikkaduwa Reef), but heavy human exploitation has severely damaged most reefs.

Lakshadweep, Maldives and Chagos chain of atolls

The largest single chain of atolls in the Indian Ocean extends from the Lakshadweep (part of India and formerly the Laccadives), southwards to the Chagos Archipelago. This chain contains several hundred islands, and tens of thousands of square kilometres of coral reefs, formed by a deep hot spot under the Earth's crust. As India moved north with the break-up of Gondwanaland, this hot spot produced a chain of volcanoes over millions of years, and these eventually became seamounts and islands. Crustal movements later placed the hot spot under Mauritius, and today it lies under Réunion (Figure 18). Most reefs in this chain are classic atolls. The chain itself lies on the Ninety East Ridge. The island states on this ridge are commonly included in 'South Asia' in political terms, though ecologically they are part of the WIO.

Land area consists of mostly small islands on rims of coral atolls, invariably low-lying: most are less than 2 m above high tide. A typical atoll has a reef flat near present low water level and seaward reef slopes that are generally steep, plunging in steps or continuously to depths of hundreds of metres. Most atolls in the WIO have lagoons that are shallower than the depths to which sea level dropped just before the Holocene; most are between 10 and 20 m deep, and some as little as 2 m, while others reach as much as 60 m. Thus, even modest falls in sea level would expose the reef flats and much of a lagoon floor, greatly increasing the area of dry land. The sea level rise in the early Holocene thus greatly increased the area available for active reef growth.

Lakshadweep comprises 12 atolls with a total of 36 islands, with a surface area of just 32 km^2, and about eight submerged banks and reefs. The islands are heavily populated and the people are substantially subsidised by India (Bakus *et al.* 2000). The extraction of coral rock and rubble has destroyed many of the shallow reefs, leading to severe disturbances (Bakus *et al.* 2000).

The Maldives are a double chain of 26 atolls with more than 1 200 islands, extending another 1 000 km southwards (Risk & Sluka 2000). Some atolls are several tens of kilometres in diameter, and many have islands and circular reefs called 'faroes' within the lagoon, perhaps formed from earlier episodes of sub-aerial erosion of existing limestone reef that was periodically exposed above water level (Figure 19). There is a gradient of atolls from north to south: "in the north they are broad banks, discontinuously fringed by reefs, with small peripheral islands and many faroes. To the south, atoll lagoons are deeper, faroes are rare or absent, and the atoll rim becomes stronger and more cemented" (Risk & Sluka 2000).

As in the Lakshwadeep Islands, exploitation of marine resources, accompanied with heavy extraction of limestone rock, has caused severe ecological disturbances in several areas of the archipelago.

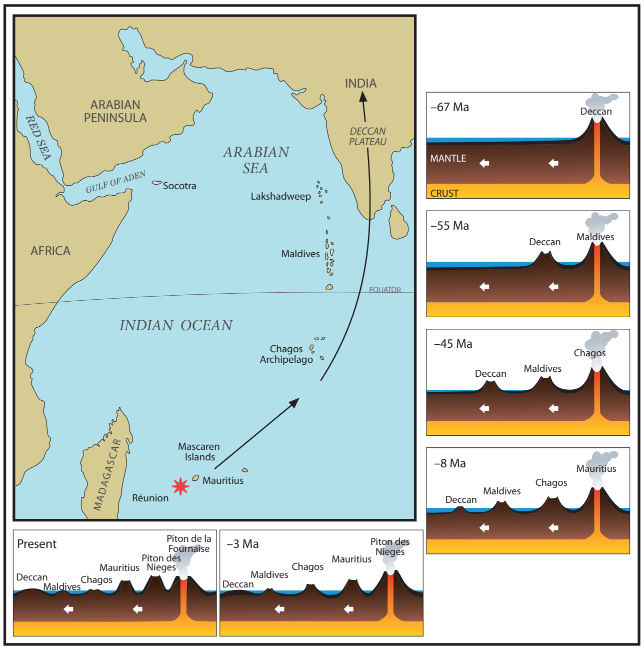

Figure 18 Sketch of movement of the Earth's crust over the deep Indian Ocean hotspot, from the Deccan Traps in India to the present and youngest islands of the Mascarene archipelago, that result from the hot spot.

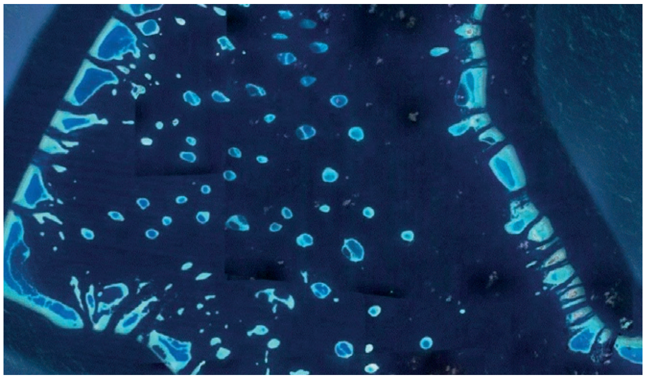

Figure 19 Maldives faroes. Vaavu atoll in the Maldives, Indian Ocean. The Maldives contain several atolls whose lagoons contain numerous annular reef structures called 'faroes'.

Google Earth, 2015. Data: SIO, NOAA, US Navy, NGA, GEBCO, Landsat Image, Image © 2015 Digital Globe

The Chagos Archipelago lies at the southern end of the Laccadive-Chagos ridge, in the geographical centre of the tropical Indian Ocean (Sheppard 2000). The archipelago consists of a limestone cap of a few hundred metres to a few kilometres thick which rests on volcanic rock (Francis & Shor 1966). The archipelago has five atolls with islands, and a greater number which are awash or completely submerged. Why some have islands, some are awash and others are drowned to 5 m or more is not known. The central feature is the Great Chagos Bank which is the world's largest atoll at 200 km by 100 km in area. The Bank is mostly submerged, but there are eight islands on its western and northern rims. Chagos contains the largest expanse of unimpacted reef in the WIO, as well as some of the most abundant with life. With the exception of part of Diego Garcia, the reefs have been undisturbed for at least 40 years.

The five atolls with islands and the great number of submerged atolls and reefs, all have profusely growing corals (Figure 20). Those reaching the surface, including Blenheim Atoll which is entirely awash at high tide, have the largest wave-resistant algal ridges and spurs in the Indian Ocean (Figure 21). Exposure in some areas is such that even lagoonal reefs support small spur and groove systems. Oceanic swell is substantial in Chagos, even in periods of relative calm. On some large deeper reefs, such as Speakers Bank and the Great Chagos Bank, corals and seagrasses are profuse, indicating high benthic productivity. The Great Chagos Bank, the largest system of all, has a complex pattern of reefs that have several ring-shaped structures within the main atoll rim, which attest to a complex past history of growth and erosion. Lagoonal faroes, such as those found at the Maldives, do not occur here.

The 1998 El Niño event warmed Chagos and other coral islands in the WIO so severely that coral-reef mortality was substantial. An investigation into the speed of recovery from this event, and of its chemical contamination, reef condition, abundance of corals and fish, made Chagos the least contaminated reef site in the Indian Ocean. In 2010, the United Kingdom declared the archipelago a no-take marine protected area out to the 200-nautical-mile limit, but recently that declaration was found to violate international law, and Mauritius claims legal rights over the archipelago.

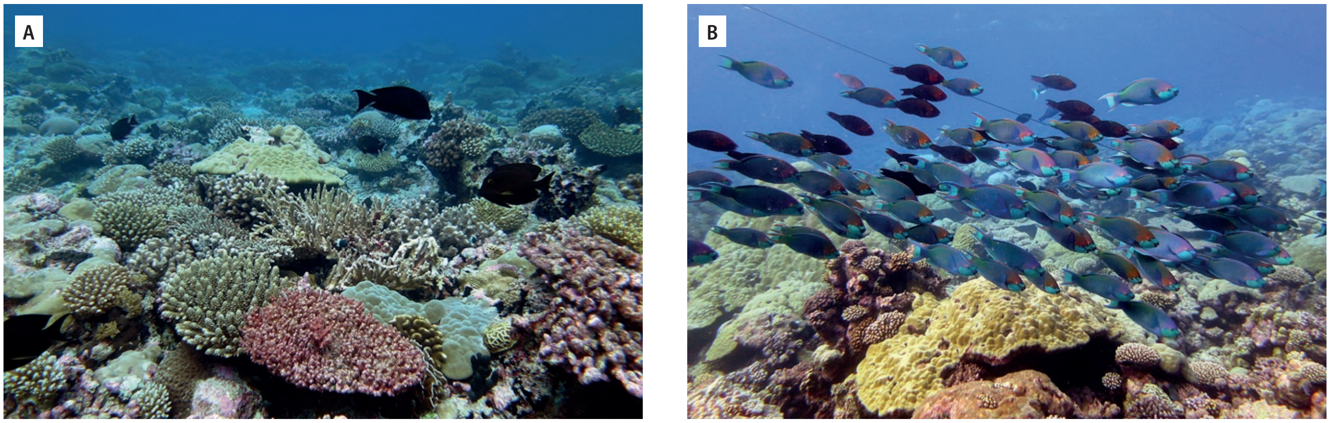

Figure 20 Rich and diverse coral cover on reefs of the Chagos Archipelago, central Indian Ocean. **A** Ocean-facing slope, **B** lagoon slope. © CRC Sheppard

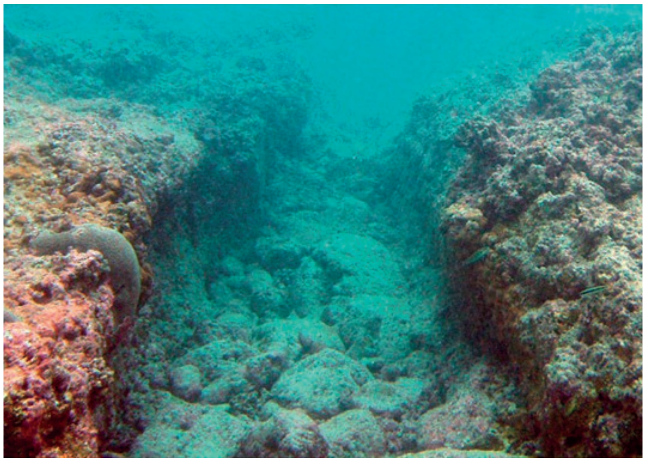

Figure 21 Spur and groove structures that are found on the edge of many high-energy reefs in the Indian Ocean. These structures are essential to the survival of such reefs. They are made by a calcareous red algae which is particularly hard and resistant to erosion and which can survive high temperatures when exposed at low tides. Image on the left is an underwater scene showing both the calcareous red algae and a general absence of corals in this high-energy location. © CRC Sheppard

Seychelles

The Seychelles consists of 41 tall granitic islands and 74 coralline islands with a total land area of 455 km^2. Despite this small area, the country has an Exclusive Economic Zone of almost 1.4 million km^2, and extensive coral reefs (Jennings *et al*. 2000). The archipelago can be broadly split into the 'inner' granitic islands to the north and the 'outer' coralline islands and atolls to the south and west. The inner islands contain most land, the largest islands being Mahé, Praslin and La Digue, where 97% of the people live. These are high granitic islands on the Seychelles Bank which broke away from the ancient supercontinent of Gondwanaland ~135 million years ago. This Bank, ~43 000 km^2 in area, is of Precambrian origin, dating to ~650 million years. Mean water depths over the Bank are between 44 and 65 m, and the islands rise to 914 m above sea level (Figure 22). The Amirantes Bank of ~6 300 km^2, lies to the south and is built on a base of basalt with 13 km of granite above, and is capped by a carbonate sediment layer of ~500 m thick. Low-lying coral islands of sand, such as Bird Island, have formed several metres above sea level on both these banks. Further to the southwest lie higher limestone islands forming the atolls of Aldabra, Assumption, Astove, Cosmoledo and St Pierre. Like other atolls, these are formed on the basalts of old volcanoes that emerge from depths of over 2 000 m, and now rise to 8 m above sea level.

The reefs of Seychelles fall into three categories: fringing and platform reefs and atolls. The fringing reefs are most well-developed around the granitic islands of Mahé and Praslin, covering 20 and 27 km^2 respectively, whereas such reefs occupy only 10 km^2 in the outer islands. These reefs typically only extend down to 10 m, and sometimes to 20 m. The most extensive and continuous reefs off Mahé are found on the more exposed eastern side of the island, whereas those to the north and western sides are more patchy and broken up, with most coverage in sheltered bays. The fringing reefs off Praslin are large and can extend up to 3 km offshore. Granitic outcrops in the sea also commonly have corals growing on them. The 1998 coral-bleaching event heavily impacted the reefs of the inner Seychelles, killing off nearly 90% of the corals (Goreau *et al.* 2000). Recovery is very slow and, with many of the dead reefs eroding, the diversity of reef fishes has declined (Graham *et al.* 2006).

Figure 22 The central high islands of the Seychelles are unusual in being granitic, and are fringed with coral reefs. These are near Baie Ternay, Mahe. © CRC Sheppard

Platform reefs cover ~200 km^2 and can be found in the Amirantes and Farquhar groups. These reefs either form shallow lagoons and reef areas with very little emergent land, such as the African Banks, Île Plate and Providence, or raised platform reefs, reaching 8 m above sea level, such as Assumption and St Pierre islands.

The atolls in the Seychelles may be low-lying or raised. Low-lying atolls include Farquhar, St Joseph, St Francois and Alphonse with a total reef area of some 20 km^2. Raised atolls include Aldabra, Cosmoledo and Astove, with ~200 km^2 reef area.

The Mascarenes

The Mascarene basin is over 4 000 m deep, and is bordered on the east by the Mascarene Plateau, which contains the banks of Saya de Malha (28 350 km^2), Nazareth (7 625 km^2), St Brandon Shoals (1 208 km^2), Soudon and Rodrigues (1 688 km^2). The largest islands are Mauritius (8 my old), Réunion (2.1 my old) and Rodrigues (1.3–1.6 my old) (Naim *et al.* 2000). They are all volcanic in origin and were formed by the same hot spot that produced the Lakshadweep, Maldives and Chagos archipelagos.

Mauritius has a 200-km long coastline surrounded by 243 km^2 of lagoons, fringing reefs and barrier coral reefs. Réunion only has 10–12 km of fringing reef, located on the southwest. Reef initiation at Réunion is likely to have kept pace with rising sea levels from 8 000 yrs BP. Rodrigues is situated on a shelf of 950 km^2, and is enclosed by a large fringing reef and lagoon complex totalling ~200 km^2. This complex is up to 13 km wide to the south. St Brandon Shoals consists of 55 low-lying sand cays and islands, with a total reef area of 190 km^2.

The extensive Shoals of Capricorn banks situated between the Mascarenes and Seychelles consist of carbonate sediment overlaying a thick band of granite on a basalt base. Very little is known about the ecology of the banks, but reports indicate large sandy areas interspersed with coral outcrops and areas dominated by algae (Turner *et al.* 2000).

The Comoros

These are located at the northern end of the Mozambique Channel, between Madagascar and mainland Africa and consist of four main islands: Grande Comore, Moheli, Anjouan and Mayotte. They are all isolated volcanic seamounts increasing in age toward the east. Grande Comore is an active volcano with limited fringing reef growth. Moheli and Anjouan both have extensive fringing reef growth, and Mayotte, the oldest island, has patch reefs, fringing reefs, a barrier reef that extends for 197 km, and a rare double-barrier reef system (Quod *et al.* 2000).

Africa and Madagascar

Africa and Madagascar both have huge continental shelves where the slopes are much more gradual compared to atoll slopes, especially along the coast of Africa. Rising and falling sea levels, together with the resulting extensive movement of the coastline have influenced both the nature of the reefs and their extent. In several areas tectonic rise and fall of the shore has added to these effects, modifying the patterns greatly. Many patch reefs located midway on shelves probably lie on substrate that lay in water much shallower than today, their growth matching rising sea levels. Chains of present-day patch reefs are situated on top of old reefs which used to line palaeo-shores, with some excellent examples in Somalia.

PRESENT-DAY GEOMORPHIC FEATURES

The coast from South Africa to Central Mozambique is mostly composed of unconsolidated Quaternary to Recent sandy sediments, interspersed with heavier-textured alluvium at river mouths. The considerable deposition and transport of sediments has caused significant seaward growth of the shoreline in central Mozambique. North of small areas of Tertiary basalt at ~16° S, heavily-faulted Cretaceous to Tertiary sediments line the coast of northern Mozambique (Tinley 1971; Rodriguez *et al.* 2000).

The area from northern Mozambique to ~8° N in northern Somalia consists of the top of a Pliocene–Pleistocene sequence of sedimentary deposits, the result of aeolian and biogenic processes. A combination of these processes, sea-level fluctuations, Holocene climate changes and tectonic movements produced the modern coastlines characterised by intertidal reef platforms, beach cliffs and rocky platforms. There are deeper platforms at depths below 8 m and 35 m.

These coastal areas also have extensive limestone coral cliffs and numerous coralline islets formed during the Pleistocene that became exposed by a subsequent drop in sea level. Some exceptions are Mafia Island in central Tanzania, which originated during tectonic uplift of the continental shelf, and Pemba Island located in northern Tanzania, which broke away from the mainland ~10 mya along the Pemba Rift (Kent *et al.* 1971; Gallup *et al.* 1994; Ngusaru 1997). Pemba is separated from the continental shelf by a 400-m deep channel. Palaeoecological investigation of the rocky cliffs and platforms suggests similar ecological conditions as the present, with transition from early colonising forms to *Acropora* dominance at intermediate stages, and to the dominance by massive forms, e.g. *Porites* and faviids, at the final stage. A comparison of gastropods between Pleistocene and modern reefs shows 1–21% loss in the number of species (Crame 1980, 1981, 1986).

Coastal habitats of East Africa and Madagascar

The continental shelf along most of East Africa is narrow, averaging 8–10 km wide, except around some of the archipelagos. Coral reefs, seagrass meadows, algal beds and mangrove forests are found along the entire coastline. Deepwater channels, river outlets and bays break the dominantly fringing coral reefs in places. High sedimentation and low salinities restrict coral-reef development near river mouths to a few offshore islands. Luxuriant stands of estuarine mangroves occur at the mouths of the major rivers: the Limpopo, Zambezi, Tana, Juba and Shebeli rivers, and the Rufiji Delta. The Rufiji Delta supports the largest mangrove forest area in East Africa at ~100 km^2 (Darwall & Guard 2000). Many of the shallow waters and bays along archipelagos and islands support luxuriant growth of coral reefs, seagrass beds and mangroves.

The reefs of South Africa represent the southernmost distribution of coral reefs in the WIO (Reigl *et al.* 1995). The southward-flowing Agulhas Current creates warm subtropical climatic conditions that are suitable for reef development. The reefs are, however, not well-developed, lack well-defined zonation and have a modest coral diversity of 143 species in 43 genera. Environmental conditions do not appear to limit coral growth and low abundance seems to be the main reason for the low accretion. Overall, soft corals dominate the reefs, though stony coral cover can reach as high as 63% in some places (Schleyer 2000).

Mozambican reefs are among the least studied, but include some of the highest coral diversity in the region – Pemba Island reefs, for example, have 208 species in 51 genera. Here the coast is divided into three regions. North of the Rovuma River

(17°20' N), extending for ~770 km, are the most extensive, well-developed reefs in the country. The barrier reef surrounding Primeiras and Segundas Islands that form the Quirimbas Archipelago is well known for its diverse coral-reef life. The central coast is an area of many rivers and reef development and is limited by low salinity, high turbidity and sedimentation. The area, however, supports well-established mangrove stands. The area south of Bazaruto Island (26°50' S), the third region, is characterised by a patchy distribution of reefs.

The reefs of Tanzania are amongst the best developed and, except near river mouths, are widely distributed. Coral diversity is high, with 200–280 species in 50–60 genera (Johnstone *et al.* 1998; Obura 2003; Obura & Machano 2004; Obura *et al.* 2000, 2006). The Tanzanian coastal area is broadly divided into northern and southern regions. The area south of Dar es Salaam consists of complex coastal ecosystems of estuarine, mangrove, coral-reef and marine-channel habitats (Darwell & Guard 2000). The waters of Mafia Island, the Songo Songo Archipelago and Mtwara-Msimbati are well known for their well-developed reefs with coral cover (in the early 2000s) of 50–60%. The northern section includes the island of Pemba and Zanzibar and the mainland coasts of Tanga, Dar es Salaam and Bagamoyo. A fringing reef along the mainland coast is broken by bays and estuaries, with many patch reefs adjacent to the continental shelf. The reefs of Tanga are among the best along the Tanzanian mainland coastline (Horrill *et al.* 2000). There is also a well-developed fringing reef along the seaward sides of islands near Dar es Salaam that make up the Dar es Salaam Marine Reserve System. These are separated from the mainland by a 3-km lagoon, where coral cover reaches ~70% on back reef edges at 2–4 m depth, and where the dominant species are adapted to high turbidity. Reef development around Zanzibar is variable. There is some patchy fringing reef on the northern and eastern coasts, but Mnemba Island, north of Unguja, has a well-developed reef (Horrill *et al.* 2000)

Kenya has well-developed reefs along its southern coast, whereas reef development is less extensive in the north mainly because of freshwater influx. Most older studies on Kenyan reefs have concentrated on the Malindi-Watamu National Marine Park, but recent investigation has included sites further south, near Mombasa and Kisite Island, near the border with Tanzania (McClanahan & Shafir 1990; McClanahan 1994, 1997). Reefs in the north still remain the least studied (Obura & Church 2004). Coral species diversity in the south is estimated at 200 species in 55 genera (Obura *et al.* 2000). Generally, the reefs are characterised by dominance of poritiid, acroporid and faviid species arranged broadly into four depth zones (Obura *et al.* 2000). There seems a clear separation of the coral community of Kisite Island which resembles more northern Tanzanian reefs compared to other Kenyan reefs (McClanahan *et al.* 2007).

Although Somalia has the longest national coastline in Africa with an estimated shelf area of 32 500 km^2, cold water upwelling and freshwater influx restricts reef development along most of the coast (Carbone & Accordi 2000; Carbone *et al.* 2003). Well-developed fringing reefs are found in the Bajuni Archipelago, north of the border with Kenya. Fleshy macroalgae dominates most hard substrate, while *Thalassodendron* seagrass beds dominate the shallow soft substrate. Benthic communities of typical mobile sandy substrates are limited to beach ridges and shoals. Coral carpets of dense assemblages of massive and encrusting corals are found along with crustose corallines, soft corals, sponges and *Halimeda* in some areas where mobile sandy cover and *Thalassodendron* meadows are missing. Most mangrove forests of Somalia are in the south, although some isolated stands are found in the northern coast. In a few places wide salt flats occur along some channels.

Madagascar has probably the most variable reefs in the region because of its diverse oceanographic provinces. The main coral-reef areas are located in the northeast (417 km), north and northwest (578 km) and southwest (458 km in extent) (Gabrié *et al.* 2000). The northern and northwestern part of the country have the highest coral species diversity in the WIO, with 318 species in 62 genera (Pichon 1978; McClanahan & Obura 1998; Veron & Turak 2005). However, information on environmental conditions, reef development and ecology is still very limited (Gabrié *et al.* 2000; McClanahan *et al.* 2009). Reefs in the southwest are probably the most developed, with fringing reefs, barrier reefs and reefs with sand cays. The Grand Recif of Toliara is the best known; the mid-west is poorly known, although with high sedimentation from river discharge, reef development is probably very limited (Gabrié *et al.* 2000). There are isolated reefs at the Barren Islands in the south and Pracel Shoal in the north, where there is also a submerged barrier reef further offshore. Reef development is better further north where the submerged ancient reef extends 10–60 km towards the open sea and supports 100% coral cover dominated by *Pachyseris speciosa* on the outer slopes (Gabrié *et al.* 2000). Except near estuaries and bays, fringing reefs surround the islands and line the mainland coasts of the northwest. Fore-reef areas are dominated by *Acropora*, back-reef areas by massive *Porites,* and lagoons by seagrass beds. The northeastern reefs of Masoala are less well-known, but modern coral growth dominated by *Acropora* borders the exposed ancient reefs.

PRESENT-DAY ENVIRONMENTAL CONSTRAINTS TO REEF GROWTH

Reef growth and size depends to only a very minor degree on the number of species of the main reef-building organisms, corals and coralline algae. Low-diversity areas can produce substantial reefs, just as high-diversity coral areas may produce small, weakly developed reefs because of various factors involved in limestone deposition. Thus, except at extreme boundaries of the WIO reef province, such as South Africa, there is probably very little correlation between coral diversity and reef development.

Environmental constraints include temperature (both high summer and cold winter temperatures), salinity, sedimentation and nutrients. Preferred temperature ranges of most corals have been understood at least since Darwin, and for most – but not all – species the lowest survivable temperatures are from 15–18 °C, to a high of ~30 °C. Several species tolerate greater extremes. Table 1 shows the species in one or two locations in extreme areas around Arabia, and the temperature ranges they survive. Increasing salinity likewise results in declining numbers of coral species (see Figure 6). Similarly, freshwater from rivers impedes coral growth so that reefs do not occur near estuaries, a major constraint along parts of the African shoreline. This is also true of the northern Arabian Sea.

The Arabian Sea has exceptionally high oceanic productivity, especially adjacent to the coast of Oman, where seasonal upwelling between May and September brings nutrient-rich, cool water to the surface, impeding reef development. Here, although the diversity of corals exceeds 100 species, sometimes occurring in thick stands which have the superficial appearance of a reef, most are not truly accreting corals. Instead, the corals are attached directly to sublittoral and non-limestone rock. In such marginal reef areas, macroalgae develop which, visually at least, are as dominant as the corals.

Reef development is generally associated with waters of poor productivity, and in the Indian Ocean productivity ranges widely. Expressions like ‘stressful environment’ or ‘increasing stress’ are meaningless, since stress for any one group of organisms may be inconsequential or even desirable for another. For reef-building organisms increasing stress refers to an environmental gradient along which, at some point, corals can no longer live. Severe stress kills off reef-building organisms and hinders reef development. Table 2 shows physical characteristics of reef and other hard substrate areas where corals live but where reefs do not develop and where fleshy macroalgae dominate much of the shallow substrate along with corals.

Along an environmental gradient, the demise of reef growth may take place at quite different points according to prevailing combinations of temperature, salinity, nutrients and other factors such as exposure to severe waves and sedimentation. While we now understand that reefs do not simply develop because of coral growth, we still do not really understand the main mechanisms of reef growth which require explanations that incorporate microbial and micro-chemical processes.

Table 1 Coral species that survive temperature extremes of the range indicated (data from Sheppard 2000; Sheppard & Loughland 2002).

Temperature fluctuation (°C)	8–15	15–20	20–28	30
Acropora horrida				
Stylophora pistillata				
Porites nodifera				*Sargassum* only
Cyphastrea microphthalma				
Siderastrea savignyana				
Porites compressa				
Platygyra daedalea				
Porites lutea				
Psammocora contigua				
Pavona varians				
Coscinaraea monile				
Leptastrea purpurea				
Favia pallida				
Favia speciosa				
Favia favus				
Favites pentagona				
Turbinaria crater				

Table 2 Physical characteristics of reef and other hard substrate areas where corals live in conditions where reefs do not develop and where fleshy macroalgae dominate some or all of the shallow substrate. This excludes coralline algal ridges and reef crests made mainly from encrusting red algae (from Sheppard 2000).

REEF/ALGAL CHARACTERISTICS	RAISED SALINITY	HIGH SUMMER TEMPERATURE	LOW SUMMER TEMPERATURE	LOW WINTER TEMPERATURE	RAISED SEDIMENTATION	RAISED NUTRIENTS	AREAS
Red algal patch reefs covered with *Sargassum*, very low coral cover	No	Yes	No	No	Yes	Yes	Southern Red Sea
High to moderate coral cover, *Sargassum* dominated reef crest but coral domination on reef slope	Slight, 36 to 40 ppt	Yes	No	No	No	Yes	Central, southern Red Sea
Limestone domes, mainly devoid of corals, in 1–5 m deep	Yes, > 40 ppt	Yes	No	Yes	Yes	No	Central and eastern Arabian Gulf
Reef flats at 0–1 m below low-water springs, high-energy areas, abundant algae on reef flats, but high coral diversity deeper	No	No	No	No	Yes, some areas	Yes, some areas	e.g., Western Sri Lanka
Upwelling areas, mainly dominated by *Fucales* but including *Ecklonia*	No	No	Yes	No	No	Yes	Oman to Somalia, *Ecklonia* in southern Oman, possibly also Yemen
Simplest 'corals-on-corals' mode of reef development	No	No	No	No	Yes	Yes, some areas	Embayments, these are notably formed by *Porites*

INDIAN OCEAN REEFS IN THE FUTURE – THE ANTHROPOCENE

Given that the limestone foundations of reefs are hundreds of metres thick, and have persisted for millions of years, it is tempting to imagine that coral reefs are timeless and immutable. But their history has been punctuated by long episodes when they did not grow at all, and this may be happening again today. Reefs are constructed for the most part by living organisms which have undergone enormous stress in the past. Noticeable declines in coral reefs were first noticed more than a century ago (Gardiner 1936). By the 1960s it was commonly asserted that traditional (mostly subsistence) fishing was centuries old, implying they made little or no impact on an ecosystem, but subsistence fishing was soon realised to be no less destructive of marine habitats than subsistence farming was of land (Ray 1969). In many countries many reefs have been reduced to rubble as a result of destructive fishing, amongst other factors (Salm 1983).

Reefs are extremely productive environments (Table 3) and essential to human well-being. The poor condition of at least two-thirds of the reefs of the Indian Ocean (see Figure 2) is probably surprising to those who encounter them only as holiday destinations which, naturally, are located at the best places. It is difficult to see how an environment conducive to reef growth can continue when runoff of pesticides and soils from poor agricultural practices continues to increase, and where overfishing persists. More than 30 years ago it was already known that many tons of topsoil per hectare per year was being washed into the WIO as a result of poor agricultural practices, and that the total exceeded 500 million m^3 per year. This has obliterated many coastal reefs, effectively converting them into soft substrate habitats. Finn (1983) summarised this: "this is not a pretty picture. It will be extremely difficult for the region's governments to confront such large scale and diffuse problems."

Since then the picture has become even uglier. It is estimated that human population will increase by another three billion between now and the middle of this century. About half of these people will be in countries bordering or in the Indian Ocean. Pressures on reef resources will increase regardless of any improvements in reef management. Climate change, which will cause further coral bleaching and ocean acidification, is expected to interact with other human-induced disturbances. The WIO, particularly the central–northern half, suffered one of the highest global coral-reef mortalities during the strong 1998 ENSO event.

Although regional average sea surface temperature (SST) is increasing by a little more than 0.1 °C per decade, the frequency and intensity of extreme temperature events are expected to increase further, resulting in recurring bleaching events and extinction of coral-reef organisms. Such fundamental shifts may cause negative feedback loops, weaken the critical role of scleractinian corals as reef ecosystem engineers and their major ecosystem functions and services, including biodiversity, fisheries and tourism.

The consequences to coral reefs are dire, to the extent that living coral reefs will quite possibly become the first major earth habitat to become functionally extinct. Coral reefs create a large proportion of the hard, sublittoral substrate in tropical seas and, with increase in ocean acidification, coral bleaching and diseases, this substrate itself is turning rapidly from being biogenetic structures to erosional ones, further threatening biodiversity, and ecosystem goods and services that are critical to the many, largely poor, communities. Indeed, since the first draft of this chapter, further ocean heatwaves have severely reduced the coral cover on reefs in this region.

Table 3 Values for productivity of Indian Ocean systems, from numerous sources (Sheppard 2000). Some of the generalised data are from outside the Indian Ocean, for which much less data exist than for the Pacific and Caribbean. Values are g C/m²/d.

SYSTEM	PRODUCTIVITY (g C/m²/d)		P/R RATIO*
	COMMON OR AVERAGE VALUES (g C/m²/d)	EXTREME RECORDS (g C/m²/d)	
Reefs			
Whole reef systems	3.2–4.0	2.3–6.0	Usually ~1
Outer slopes	2.0–7.1		0.7–1.1
'High activity areas'	9.0–14.0	8.0–23.0	0.6–1.7
Reef flats, lagoons	3.0–7.0	2.9–19	0.7–2.5
Corals with zooxanthellae	2.63		
Sandy reef areas	0.9–1.5	0.6–2.7	0.6–1.1
Mangroves			
Global averages	6.0–15.0		1.2
'Dwarf' in Red Sea	<6.0		
Seagrasses			
Global averages	6.0–15.0		1.2
Thalassia, Syringodium, Lakshadweep	5.8		
Northwest Indian Ocean	3.0		
Algae			
Turfs and pavement	2.0–7.0	1.0–14.0	0.5–13.7
Coralline algae	0.8–1.0	7.0	1.3–1.4
Sargassum belts	60	(dry organic wt)	
Tropical kelp (Oman)	4.0	(dry organic wt)	
Halimeda beds	0.2–6.0		
'Mixed algae' Lakshadweep	1.9		
Cyanophytes	0.62–1.39		
Endolithic algae (*Ostrobium*)	0.4–0.6		
Benthic diatoms (sand, 5 m)	0.41		

* P/R Ratio is ratio of production to respiration

SYSTEM	PRODUCTIVITY ($g\ C/m^2/d$)		P/R RATIO*
	COMMON OR AVERAGE VALUES ($g\ C/m^2/d$)	EXTREME RECORDS ($g\ C/m^2/d$)	
Bacterial			
Pelagic	0.007–0.11		
In sediments	1.2		
On coral rubble	0.01–0.1		
Planktonic			
Open ocean	0.04–0.06	0.003–0.4	0.3–1.4
Arabian upwelling, Southwest Monsoon	1.16		
Arabian upwelling, Northeast Monsoon	0.23		
Arabian Sea, central	0.12–0.76		
East Africa, Southwest Monsoon	0.83		
East Africa, Northeast Monsoon	0.42		
Bay of Bengal	0.21		
Atoll lagoons	0.10–0.42		
Near shore or reefs	0.2–0.9	0.1–1.0	
North Red Sea	0.21–0.50		
Central Red Sea	0.39		
Southern Red Sea	1.60		

* P/R Ratio is ratio of production to respiration

ACKNOWLEDGEMENT

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GLOSSARY

aeolian – relating to the action of wind; wind-blown.

biogenic – produced by living organisms.

ENSO – El Niño–Southern Oscillation; a recurring climate pattern involving changes in the temperature of waters in the central and eastern tropical Pacific Ocean.

ENSO teleconnections – the link between what happens in the Pacific Ocean during an El Niño event and what happens in the Indian Ocean.

hypersaline – with salinities higher than that of sea water, i.e., more than 35 parts per thousand (ppt).

monospecific – composed of a single species.

palaeoclimatic evidence – what geological information can tell us about climates thousands to millions of years ago.

photic zone – the depth of water in which photosynthesis takes place.

propagule – a vegetative/living structure that becomes detached from a parent to give rise to a new organism; an agent of reproduction, e.g., a sucker on a plant or the eggs fishes or corals shed into the water.

scleractinian corals – stony or hard corals that form coral reefs today.

thermocline – the boundary between two layers of water with large differences in temperature, the colder water beneath the warmer.

Links with other chapters in this volume:
The oceanography of the Western Indian Ocean
Socotra and islands in the eastern Gulf of Aden: their fishes and fisheries

SOCOTRA ARCHIPELAGO: FISHES AND FISHERIES IN THE EASTERN GULF OF ADEN

Uwe Zajonz

INTRODUCTION

The Socotra Archipelago, part of Yemen, lies in the northwestern Indian Ocean, at the Horn of Africa. It is globally recognised for its outstanding biodiversity and endemism, the reason why the entire island group was designated a UNESCO World Heritage Site in 2008 (Scholte *et al*. 2011; Van Damme & Banfield 2011). While Socotra's recognition as the 'Galapagos of the Indian Ocean' often alludes primarily to the diversity of its terrestrial ecosystems, the marine ecosystems are also highly diverse and unique in several ways (Cheung & DeVantier 2006).

HISTORY

The time of the first colonisation of Socotra by earlier settlers is not known, but dates at least from the first millennium BCE, according to earliest archaeological evidence. The origins of the first human population also remain unclear, but are likely to have been tribespeople from South Arabia, and possible occasional arrivals from Africa.

Recent discoveries of writings in several languages tell of the diverse origins of the people who used the islands as a trading base between the 3rd century BCE and the 6th century CE. There is a tradition that the islands and their inhabitants were occupied by Greeks sent by Alexander the Great around 330 BCE, and subsequently visited by Thomas the Apostle (in 52 CE), Marco Polo (c. 1293 CE) and the Chinese fleet of Admiral Zheng He (1420 CE). Around 50 CE Socotra likely belonged to the Hadramaut state of Eleazos. The Arab geographer Abu Mohammad al-Hasan al-Hamdan recorded in the 10th century CE that most of the inhabitants were Christians. Between 900 and 1300 CE the islands were notorious as a base for pirates. From about 1200 CE, and for several centuries, Socotra gained strategic importance for maritime trade and transport. After a brief conquest of Socotra Island by the Portuguese in 1507 as a strategic base to control sea traffic from the Red Sea en route to the Indian Ocean, it was abandoned four years later, and the archipelago came again under the control of the Mahra Sultanate of Qishn and Socotra, established early in the 16th century, and included what is now eastern Yemen and the island of Socotra. It thus became finally Islamised (Islam may have gradually taken roots already from 700 CE onwards). In spite of strong Omani and European interest to take control of Socotra, the Mahri sultans maintained more or less continuous power over Socotra until the mid-18th century. From around 1600, however, the islands were on the maps of especially British and Dutch trading fleets for replenishment of water and stocking of local produce such as aloe. In the first half of the 18th century the building of the Suez Canal prompted European powers, Britain, France and Austria, to compete for the control of the Gulf of Aden, including Socotra. In 1886 the islands finally became part of the British Protectorate that included Aden and the Mahri Sultanate (while locally the Sultanate retained power), and remained so until the British withdrew from Aden in 1967. Soon after, the islands became part of the socialist People's Democratic Republic of Yemen (PDRY, commonly South Yemen). Socialist policies resulted in an initial wave of development in Socotra during this period that included the building of roads, schools and clinics. It also came under the influence of the Soviet Union as a result of the PDRY's political association with the latter which impacted on, e.g., its military and scientific activities. In 1990 Yemen was unified and in 1999 the islands were administratively assigned part of the Governorate of Hadramaut with its capital Al Mukallā. In 2013 Socotra was declared a governorate of its own as part of the political reforms in Yemen. This current status grants Socotra relative independence and protection from the political instability prevailing at the Yemeni mainland (composed from Cheung & DeVantier 2006 and https://en.wikipedia.org/wiki/Socotra – 25.07.2016).

RESEARCH

In the late 19th century Socotra had been the subject of a series of scientific expeditions, led by Balfour in 1880, by Riebeck and Schweinfurth in 1881, by Forbes and Ogilbie-Grant in 1897–1898, and by Paulay and Simony in 1898. Very little research took place in the first half of the 20th century, but in the 1970s interest in the former South Yemen was renewed. Scientific efforts gained momentum from 1996 onwards, with the so-called 'Socotra Biodiversity Project'

(SBP) of the United Nations Development Programme (UNDP) (Cheung & DeVantier 2006). The 43 reports that were generated by an international team of more than 30 scientists contributed substantially to greater understanding of its marine ecosystems and biota (Krupp *et al*. 2002). These included key works on coastal and nearshore marine habitats (Klaus & Turner 2004), coral reefs and their communities (e.g., DeVantier *et al*. 2004), and macroalgae communities (e.g., Schils & Coppejans 2003). Research on the fish communities and fisheries was documented in a large number of reports, yet only a few of the results have been published to date (e.g., Kemp 1998, 2000; Gill & Zajonz 2003; Gill & Zajonz 2011; Lavergne *et al*. 2016).

After the termination of the SBP in 2002 the author continued to investigate the fish communities of the island group. From 2007 to 2015 funding for a follow-on research programme became available through the Senckenberg Biodiversity and Climate Research Centre (BiK-F). Some of the results of this work have already been published (e.g., Lavergne *et al.* 2013, 2014, 2016; Zajonz *et al*. 2016, 2019), and various publications are currently in preparation. Results of a survey in 2014 by a team of King Abdulasiz University, Jeddah, contributed to a number of recent publications (e.g., DiBattista *et al*. 2015). Since 2011 fieldwork around the Socotra Archipelago has frequently been hampered by the political situation on mainland Yemen.

THE ISLANDS AND THEIR OCEANOGRAPHY

The Socotra Archipelago lies in the northwestern corner of the Indian Ocean at 53°00'–54°35' E and 12°05'–12°43 'N, at the junction between the Gulf of Aden and the Arabian Sea (Figure 1). It includes the main island of Socotra, together with three smaller islands, Samha, Darsa, Abd al-Kuri and twoislets, Sabuniya and Kal Farun. The westernmost island Abd al-Kuri is separated from mainland Africa by the Socotra Passage, a narrow strip of water only 95 km wide, and the eastern tip of Socotra Island is 330 km from the nearest point of mainland Arabia, at Ras Fartak, Yemen. The main island of Socotra is 134 km long and has a total area of about 3 600 km^2 — after Madagascar it is the second largest island in the Western Indian Ocean.

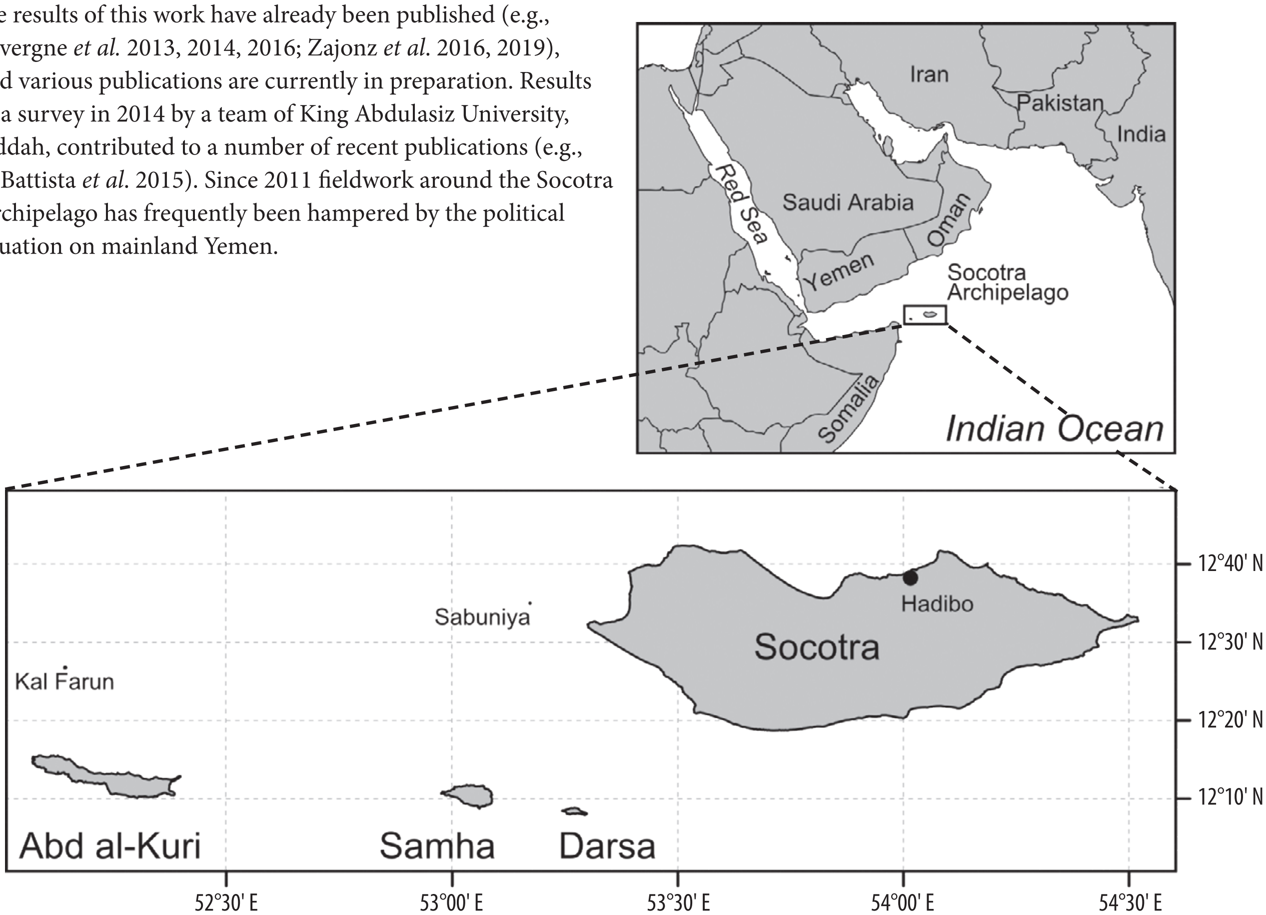

Figure 1 Map showing position of Socotra off the Horn of Africa.

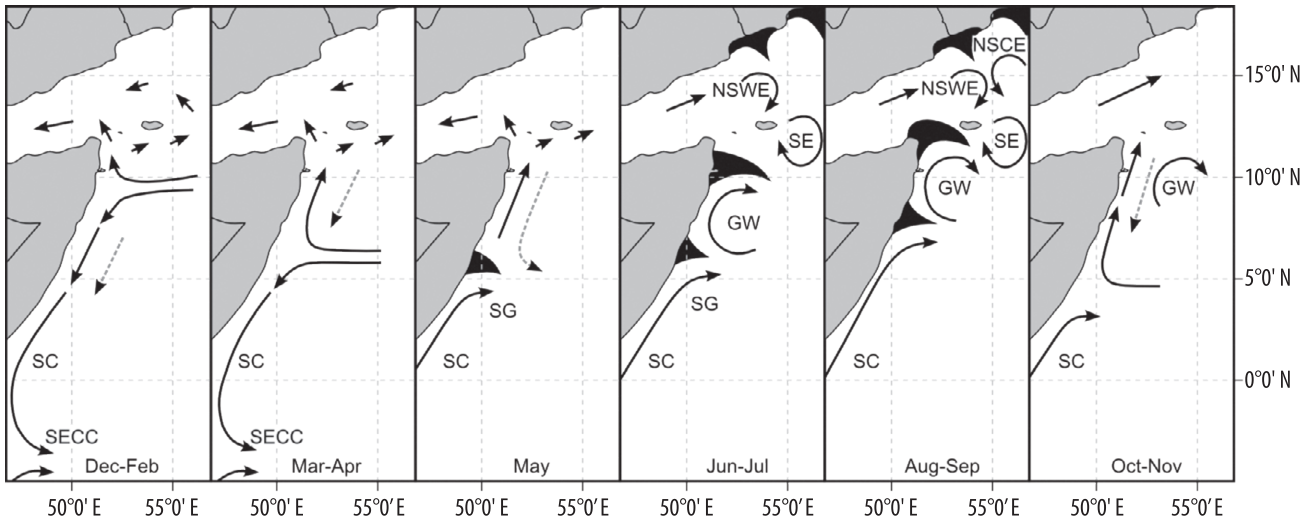

Figure 2 Schematic diagram of the seasonal variation of the major ocean currents and circulatory features in the northern Indian Ocean and Gulf of Aden region. Solid black arrows indicate surface currents (0–100 m), dashed grey arrows indicate subsurface currents (100–400 m depth) when they flow opposite to surface currents. Black shaded areas show the areas of seasonal cold-water upwelling. Abbreviations: South Equatorial Countercurrent (SECC), Somali Current (SC), Southern Gyre (SG), Great Whirl (GW), Socotra Eddy (SE), North Socotra Warm Eddy (NSWE), and North Socotra Cold Eddy (NSCE). Modified from Klaus & Turner 2004, compiled and adapted from several sources

The islands are subject to the alternating monsoon seasons in the northern Indian Ocean: the weak and wet winter, or northeast monsoon (November to February), and the forceful and dry summer, or southwest monsoon (May to September). This seasonally reversing monsoon system creates particular oceanographic conditions around these islands. The most important is the cool-water, nutrient-rich upwelling during the summer monsoon season which temporarily establishes more temperate ('pseudo-temperate') sea conditions in an otherwise tropical environment. With the onset of the southwest (summer) monsoon the surface flow of the Somalia Current is dramatically reversed along the African mainland coast, from southward to northward. The reversed Somali Current, in combination with the southwest monsoon winds, results in the formation of two distinct upwelling systems at the coast of Somalia and at the southeastern Arabian coast of Yemen and Oman (Figure 2) (e.g., Wyrtki 1973; Schott *et al.* 1990; Fischer *et al.* 1996).

The high primary productivity resulting from these monsoonal dynamics provide the basis for exceptionally high productivity levels of fishes and other organisms (see below). The fish biomass is exploited by a large and productive fishery (IFAD 2010; Zajonz *et al*. 2016): "The north-eastern part of the Gulf of Aden and the area south of Socotra are among the most productive marine areas in the world, with productivity levels comparable to those off the coasts of Peru and West Africa" (Hariri *et al*. 2002).

The monsoon-driven oceanographic dynamics and the coastal upwelling also influence the spatial and (especially) the temporal distribution and composition of the benthic and associated fish communities (e.g., Zajonz & Khalaf 2002; Klaus & Turner 2004; Zajonz *et al.* 2016). Moreover, the situation of the islands and the dynamics of changing monsoons places the island group literally at the crossroads (DeVantier *et al*. 2004) between the regional ocean currents, which has implications for the dispersal and genetic connectivity of marine organisms, and therefore for patterns of marine diversity and biogeography in the wider northern and western Indian Ocean (Kemp 1998; Zajonz & Khalaf 2002; DeVantier *et al.* 2004; Schils 2006; DiBattista *et al.* 2015; Zajonz *et al*. 2019; Zajonz *et al*. in press).

HABITATS AND BIODIVERSITY

The shallow, nearshore benthic habitats around the Socotra Archipelago support highly heterogeneous and spatially variable benthic communities. These range from sandy habitats with seagrass beds and other soft sediment habitats, to rocky habitats with turf and macroalgae and sponges, mixed macroalgal and hard and soft coral communities, and highly diverse hard coral dominated communities (Klaus & Turner 2004). Coral-reef growth is constrained as a result of the marginal 'pseudo-temperate' conditions and the generally gently sloping or flat coastal topography. Where reefs are found they are typically situated in the lee of headlands, or within embayments that are sheltered from the monsoon winds. Coral-dominated communities usually grow directly on a rock substrate and coral cover and diversity is high, with some

253 scleractinian species (58 genera, 16 families) recorded to date (DeVantier *et al*. 2004; Klaus & Turner 2004).

Diverse macroalgae-dominated assemblages cover a substantial part of the inshore areas, particularly on the south coast of Socotra Island, which is most exposed to the southwest monsoon and upwelling. Here algal communities have the highest number of species and a relatively homogeneous community structure, which shows a lower affinity with the (sub-)tropical Indian Ocean flora, and is marked by disjunctly distributed species. Along the northern coast more species commonly known from the tropical Indian Ocean occur (Schils 2002; Schils & Coppejans 2003).

The main island of Socotra has about 30 estuaries and one lagoon. Most of the estuaries are separated from the sea by berms of gravel or sand and are only temporarily connected to the sea after flash floods or by storm surges (Klaus & Turner 2004; Lavergne *et al*. 2016). As a result, and in combination with the local topography, they vary greatly in morphology, freshwater and seawater inputs and ecological conditions; the monsoonal changes contributing to the marked seasonal changes in water flow, salinity and temperature regimes and, hence, very variable and heterogeneous estuarine environments. There are no such ecosystems on the other islands.

FISH DIVERSITY

The Socotra Archipelago lies at the centre of a region with relatively poorly known coastal and marine fish faunas, with limited information published on the taxonomy and ecology of the coastal fishes of the islands. Fishes were sampled for the first time on Socotra Island during the German expedition of Riebeck and Schweinfurth in 1881–1882, resulting in an account of eight species being published by Taschenberg (1883). His records are, however, not entirely reliable. Steindachner published more extensively, on material collected by the Austrian Expedition to Socotra and South Arabia in 1898–1899. He listed 56 species of marine and brackish water fishes and described *Gerres socotranus* and *Hirundichthys socotranus* as new to science (Steindachner 1902; Lavergne *et al*. 2016). A number of expeditions visited the island group after that, but did not contribute substantially to our knowledge of its fishes. Kemp (1998, 2000) was the first to assess the inshore fish communities and reported 215 species based on visual records. He also made the first regional zoogeographical analysis based on distribution data of four families. The SBP inventories and quantitative fish community surveys made in 1999–2002, found the fish communities to be rich in species, with some unique regional reef fish assemblages (Zajonz *et al*. 2000; Zajonz & Khalaf 2002; Zajonz & Saeed 2002). Investigation of inshore and estuarine fish assemblages continued, with the first description of a new species of fish (*Halidesmus socotraensis*) from the islands for more than a century (Gill & Zajonz 2003). This was followed by a study of pseudochromine and pseudoplesiopine dottyback fishes, which included the descriptions of *Pseudochromis chrysospilus* and *P. socotraensis* (Gill & Zajonz 2011).

Inshore and coral-associated assemblages

A preliminary account of the coastal fishes reported 682 confirmed and 51 unconfirmed species, totalling 733 species in 108 families. Using incidence-based richness models of Colwell *et al.* (2012), between 830 and 890 species (Figure 3) are predicted to occur (Zajonz *et al*. 2016; Zajonz *et al.* 2019). Of the 86 families encountered in the field, the Labridae are the most speciose, with about 10% of the species, followed by the Gobiidae, Pomacentridae and Serranidae. When compared to the species richness recorded in adjacent regions, the species diversity of Pseudochromidae (13 spp.), Chaetodontidae (29 spp.) and Acanthuridae (29 spp.) were found to be particularly high. In comparing the species richness of eight key families (Acanthuridae, Balistidae, Chaetodontidae, Labridae, Pomacentridae, Pomacanthidae, Pseudochromidae and Epinephelidae, with 411 species in total) used to analyse the relatedness of 10 putative Arabian ecoregions, the richness at Socotra was the highest (Figure 4) (modified from Spalding *et al.* 2007; see section on biogeography). This diversity is especially striking when comparing species-area relationships with neighbouring ecoregions (Figure 5). Certain 'reef' associated families and functional groups are as diverse, or more so, than these groups in the entire Red Sea, even though the islands' coastline is but one-eighth in length that of the Red Sea, and supports considerably fewer biogenic reefs (Zajonz *et al*. 2019; Zajonz *et al.* in press). The islands thus appear to be endowed with the highest diversity of marine fishes of any reasonably comparable biogeographic unit in the wider Arabian region (Zajonz *et al*. 2019). Certain small, cryptic, and nocturnal groups are still under-assessed and further work is expected to reveal the presence of more species, particularly of Blenniidae, Gobiidae, Tripterygiidae, Labridae, Platycephalidae, Mugilidae, Ophichthidae, Scorpaenidae, Syngnathidae and various families of flatfishes.

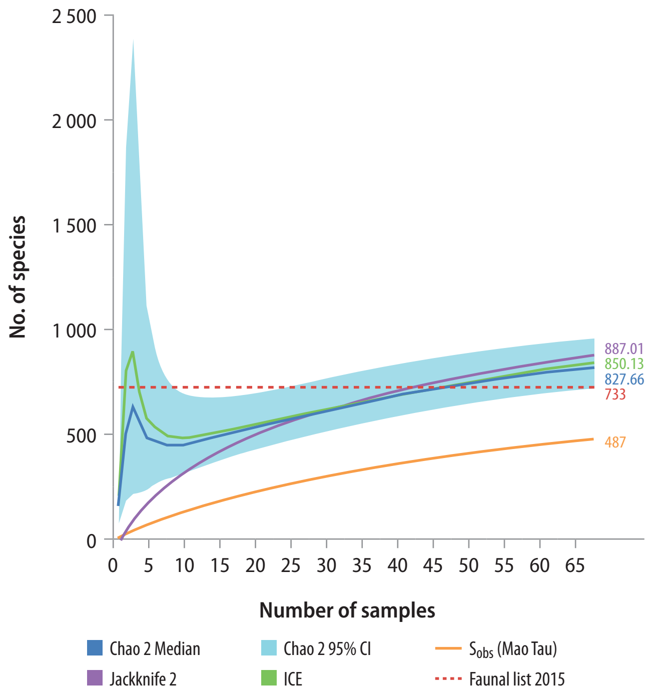

Figure 3 Fish species-richness modelling for Socotra Archipelago using incidence-based richness estimators (Chao 2, ICE, Jackknife 2), based on 68 fish inventory sites (FIS) and 487 species (six of 74 FIS were excluded from the richness modelling in order to avoid spatial bias). Source: Zajonz *et al.* 2016

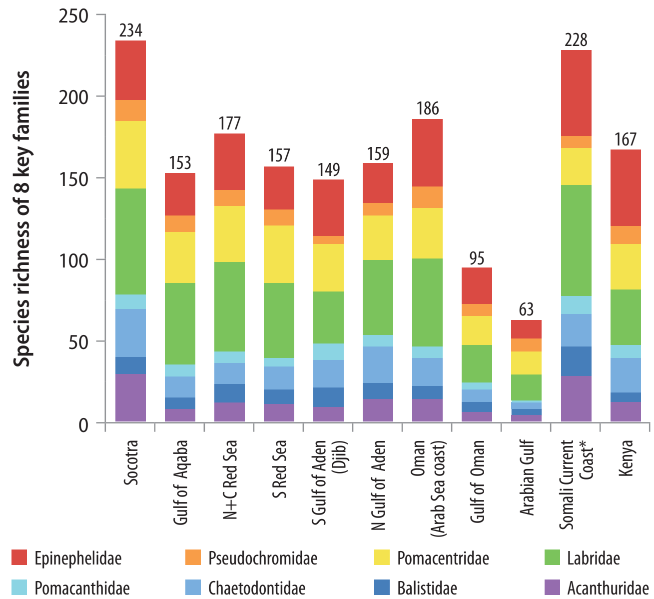

Figure 4 Comparison of actual species richness of eight key families in 10 putative ecoregions (ecoregions modified from Spalding *et al.* 2007, see Zajonz *et al.* 2019) comprising the wider Arabian region and Kenya as an external reference (compare Zajonz *et al.* in press for ecoregional delimitations and a regional species distribution list for these families). *comprises approximately the 'Central Somali Coast' and 'Northern Monsoon Coast' ecoregions of Spalding *et al.* (2007). Source: Zajonz *et al.* 2016 modified, Zajonz *et al.* in press

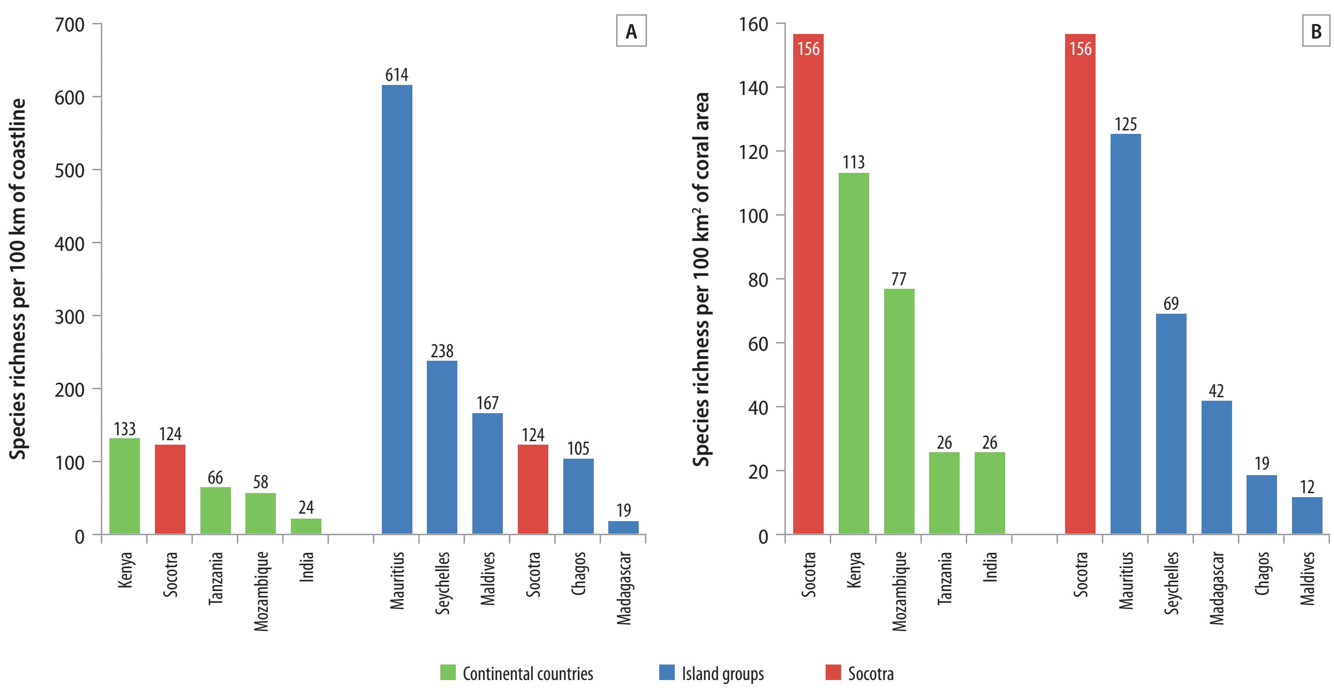

Figure 5 Comparison of fish species-area relationships (SAR) between Socotra Archipelago and neighbouring geographical units, using **A** the number of species per 100 km of coastal length, and **B** the number of species per 100 km^2 of coral area. Source: comparative data from FishBase (Froese & Pauly 2017), www.fishbase.org, sourced 2012; and ReefBase, www.reefbase.org, sourced 2015, verified and adjusted (Zajonz *et al.* 2016)

Estuarine and lagoonal assemblages

Lavergne *et al*. (2016) analysed estuarine and lagoon fish diversity and fish assemblage structure at 13 sites at Socotra Island, and compared them to three sites on the coast of Yemen. Their study included collections and surveys made between 1999 (SBP) and 2009. A total of 65 species in 32 families were recorded from Socotra, with but 20 species in 17 families from mainland Yemen. Twenty-one species were new records for Socotra. If Steindachner's historical records are included, the number of fish species of the estuaries and lagoons is 76, and richness models suggest that the actual estuarine fish species richness might be even higher than this.

Mugilidae and Gobiidae are the most speciose estuarine families, followed by Lutjanidae, Gerreidae and Sparidae. Five species dominate occurrence and abundance frequencies: *Terapon jarbua*, *Hyporhamphus sindensis*, *Aphanius dispar*, *Ambassis dussumieri* and *Chelon macrolepis*.

BIOGEOGRAPHY

The Socotra Archipelago has long been considered to be located at the intersection of several distinct biogeographic entities, by Rosen (1971), Klausewitz (1972), Briggs (1974), Hayden *et al.* (1984), and others. Based on the zoogeography of the corals, the archipelago was thought to be at the junction of the Arabian and the Western Indian Ocean subprovinces, within an Indian Ocean marine province, or, in terms of fishes, just north of that boundary (e.g., Klausewitz 1978; Ormond & Edwards 1987; Sheppard & Salm 1988; Klausewitz 1989; Sheppard & Sheppard 1991; Sheppard *et al.* 1992). Klausewitz (1989) suggested the archipelago was located close to the boundaries between the Eritrean and South Arabian section, and between the South Arabian and "Persian" section of the Arabian subprovince, and close to a centre of speciation and endemism identified on the Arabian Sea coast of Oman (see Randall 1995; Randall & Hoover 1995). These studies were, however, based on very limited data for the archipelago.

The marine biogeographic affinities of the archipelago were summarised by Kemp (1998), DeVantier *et al.* (2004), and others. DeVantier *et al.* (2004) applied the term 'zoogeographic cross-roads' to characterise the particular biogeographic attributes of the archipelago. The location of hypothetical biogeographical boundaries and the evidence for putative barriers that give rise to faunal and floral breaks in the seas around the archipelago, have been and are still a matter of considerable scientific debate (see, for example, Sheppard & Salm 1988; DiBattista *et al.* 2015; Priest *et al.* 2015; Hodge & Bellwood 2016).

Kemp (1998) was the first to study the zoogeography of the coral-reef fishes of the archipelago, and substantially advanced our understanding of the marine biogeography of the north-western Indian Ocean (Kemp 2000; Kemp & Benzoni 2000). He identified a distinct South Arabian region, combining parts of southern Oman and eastern Yemen, and recognised strong affinities of this region to the Socotra Archipelago, together with an East African influence. These studies indicate that the Gulf of Aden (including the Socotra Archipelago) is probably not a homogeneous biogeographic entity; an important result that – surprisingly – was largely ignored in most subsequent publications that referred to Kemp's work (e.g., Spalding *et al.* 2007; Briggs & Bowen 2012; Kulbicki *et al.* 2013; DiBattista *et al.* 2015). The data Kemp (1998) primarily dealt with covered the regional distribution of five families of reef-associated fishes, with a focus on the Chaetodontidae, and has now been superseded by newer inventories of Zajonz *et al.* (2016) and Zajonz *et al.* (2019) (Figure 6).

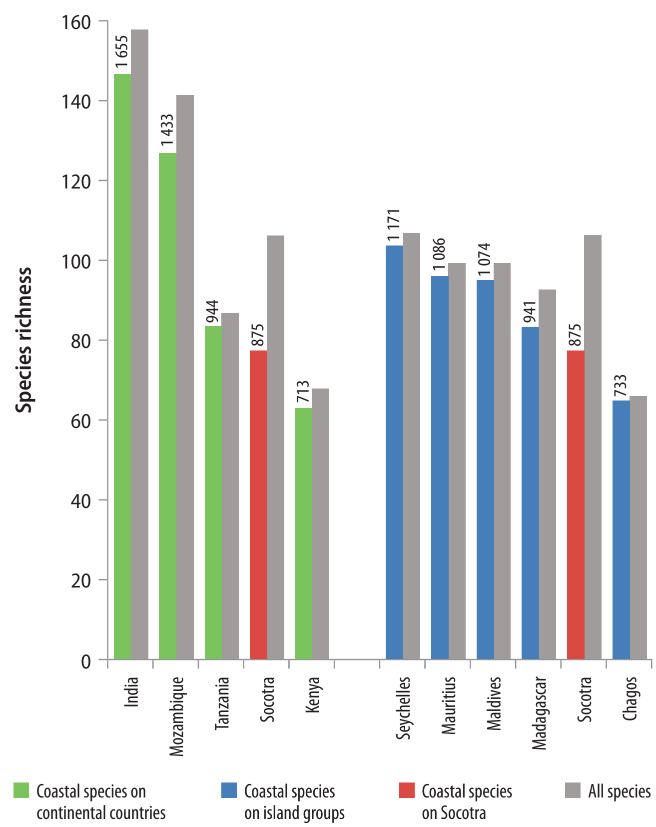

Figure 6 Comparison of coastal and marine ('All species') fish species richness between Socotra Archipelago and neighbouring geographical units ('Coastal' species number follows the total archipelagic richness extrapolated from the species richness models; 'All species' includes an estimate of expected deep-dwelling species based on unpublished regional data of Zajonz & Bogorodsky). Source: comparative data from Froese & Pauly 2014, www.fishbase.org, sourced 2012, verified and adjusted

Recently, a string of primarily phylogeographic and phylogenetic studies have contributed information relevant to the ichthyogeography of both the Socotra Archipelago and the Gulf of Aden, and have been reviewed by Zajonz *et al.* (2019) and Zajonz *et al*. (in press). Of these studies, the work of DiBattista *et al.* (2015) is especially noteworthy because it recognises the archipelago as a prominent hotspot for marine fish hybridisation. None of these recent studies, however, aimed at reviewing the distributional or ecological ichthyogeography or marine biogeography of the Socotra Archipelago, the wider Gulf of Aden and the adjacent seas. To date, the results of contemporary global metastudies as well as of taxon-specific regional studies do not yet correspond to one another in a satisfactory way, and are altogether based on outdated fish species lists for the Socotra Archipelago and southern Arabia; since then number of recorded species has more than tripled (Zajonz *et al.* 2016; Zajonz *et al.* 2019). Based on updated inventories Zajonz *et al*. (in press) analysed the distributional ichthyogeography of the archipelago, challenging current ecoregional concepts.

Species distribution ranges and converging distribution limits

Based on records of 658 species with reliably known distribution ranges the fish assemblages of the archipelago are dominated by species from the Indo-Pacific (almost half) and the northwestern Indian Ocean (Zajonz *et al.* 2019). A relatively high number of species have both pan-Indian Ocean and wider, Indo-Pacific, distribution ranges.

Among 234 species of 8 key families (see Figure 4), the proportion of species with distribution range limits converging on Socotra is >50% (Zajonz *et al*. in press). Such a high rate of convergence inevitably leads to the sympatric co-existence of sister species or very closely related species, and also offers an explanation for the comparatively high rate of hybridisation, and a relatively low number of only five endemic species (Zajonz *et al.* 2019). The island group can then also be characterised as a 'faunal melting pot'. Given that the number of species at their northern distribution boundary is more than twice as high as those at their southern boundary, and that species with a northern Indian Ocean distribution pattern are substantially underrepresented (compared to 'Arabia' as a whole, *sensu* Manilo & Bogorodsky 2003), strongly suggests that the archipelago's role in promoting species dispersal in a northward direction is more pronounced than it is in a southward direction (Zajonz *et al*. in press).

Kemp (2000) was the first to recognise the eastern Gulf of Aden coastline as an important region for the hybridisation of reef fishes, based *inter alia* on the occurrence of *Pomacanthus maculosus* × *semicirculatus* at the Hadramaut and Shabwa coast of the Yemeni mainland. The occurrence of this hybrid on Socotra Archipelago was first reported by Zajonz & Khalaf (2002). Recently, DiBattista *et al*. (2015) identified seven fish hybrids from Socotra Island – combinations of 14 species – which led them to recognise the archipelago as a global hotspot for fish hybridisation. Based on this and additional observations from both Socotra Archipelago and the eastern Arabian mainland coast, it seems reasonable to assume an 'eastern Gulf of Aden hybrid zone' which encompasses the eastern Arabian hybrid zone proposed by Kemp (2000), and the Socotra hybridisation hotspot proposed by DiBattista *et al*. (2015) (Zajonz *et al*. in press).

FISH BIOMASS PRODUCTIVITY

The impressive biological diversity of fishes and many other marine taxa, and the unique community and biogeographic features, are matched by the high fish biomass productivity around the island group, which sustains a substantial local fishery sector (see below). Fishing is thus the second-most important source of income and food for the islanders after its pastoralist economy (Cheung & DeVantier 2006).

The generally high fish biomass productivity in the eastern Gulf of Aden and the wider Arabian Sea was determined by a series of fisheries research cruises during the 'Indian Ocean Programme' (IOP) of the FAO and UNDP, conducted by the research vessel *Dr Fridtjof Nansen* between 1975 and 1984. Saetersdal *et al.* (1999) reported a standing stock of demersal and pelagic (small pelagics and mesopelagics) resources for the area Somalia–NE Arabian Sea in the order of 110 t/nmi^2, which corresponds to standing biomass in excess of 3 million tons for the area Somalia–southern Arabia based on 1975–1977 data (matching earlier data of Cushing 1971). Surveys in 1983–1984 confirmed standing biomass of small pelagics and mesopelagics of 0.93 million tons for Somalia and Yemen alone (Saetersdal *et al.* 1999). While these figures highlight that the Socotra Archipelago is situated in one of the most productive seas and upwelling areas globally, very few data on inshore and reefal fish biomass exist from this region.

Inshore biomass estimates based on visual underwater length-frequency counts were started in 2007 by the author as a proxy for the coastal secondary and tertiary productivity of the Socotra Archipelago, adding to the permanent transect-based ecological monitoring program operated since 2000 (Zajonz & Saeed 2002). Standing crop in 2007 (pre-monsoon) averaged 2.08 t/ha across eight sites (six at Socotra Island, one at Darsa Island and one at Samha Island) and 3.04 t/ha at five deeper sites (> 6 m). These biomass values are impressive, especially considering that fishing activities had already harvested the coastal productivity for the six months following the summer monsoon. Pre-monsoonal maxima of 5.13 t/ha (SD ± 5.64) were recorded around Socotra and 5.95 t/ha (SD ± 9.34) around Darsa in 2007. In 2011 the post-monsoon maxima recorded at individual sites were 5.03 t/ha (SD ± 1.67) and 6.77 t/ha (SD ± 3.06). These maxima rank among the highest in the Indian Ocean (e.g., Garpe & Öhman 2003; McClanahan *et al.*

2007; Burt *et al.* 2011; McClanahan 2011; McClanahan *et al.* 2011) and are only surpassed by biomass estimates recorded from the Chagos Archipelago (>7 t/h), which is one of the most strictly enforced fishery closures globally (Sheppard *et al.* 2012).

Comparisons between pre- and post-monsoon biomass of 113 fish species in 2011 indicate a substantial replenishment of biomass following the summer monsoon. Biomass increases of 1012% (SD ± 722%) were recorded from 12 relatively undisturbed sites on the northeast coast of Socotra, representing an increase from an average of 0.183 t/ha (SD ± 0.275) in May to 2.035 t/ha (SD ± 2.052) in November 2011. Increases in biomass were non-linearly related to an increase of more than fourfold in the in number of fishes and of 40% in the number of species. The increase in biomass is also related to higher average weight per individual (+270%) in the post-monsoon period (Zajonz *et al.* 2016 and unpubl. data).

These findings correspond with the marked seasonal effects of the summer monsoon. The replenishment appears to be mainly and closely related to enhanced primary productivity rates during and following the monsoon seasons, notably the more pronounced summer monsoon, as inferred from sea surface temperatures and of chlorophyll *a* concentrations (Figure 7).

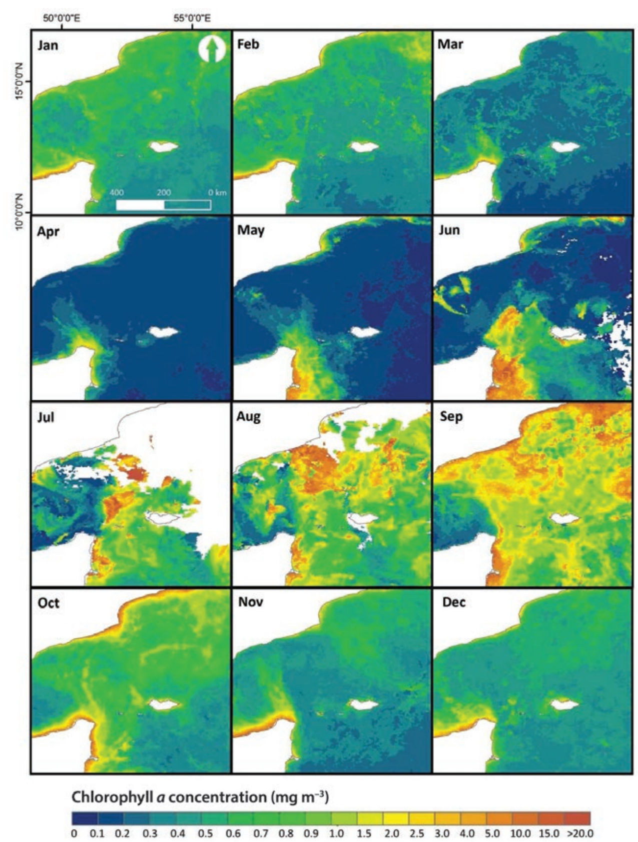

Figure 7 Mean monthly Chl *a* concentration 2000–2011 around the Socotra Archipelago. Source: OceanColourWeb (sourced 2013)

FISHERIES

The Socotra Archipelago supports productive fisheries that supply both domestic and commercial markets. Research into these fisheries has however been limited. Most of the information available about these fisheries up to 2002, come from two documents: the *Fisheries Management Plan* prepared during the SBP (Nichols 2001; Esseen & Al-Saqaf 2002; Hariri 2002), the only one of its kind in Yemen, and the *Fisheries Feasibility Study*, prepared as part of the Socotra Archipelago Master Plan study (Reid *et al.* 2002).

Most of the fishing activities around the islands are essentially artisanal, beach-landing fisheries. These operate within 10 km of the coast, over the shelf, to 200 m depth, and cover an area of 14 417 km^2 (Nichols 2001). The islands are also targeted by industrial-scale fishers, notably longliners, mid-water and a few demersal trawlers, and gillnetters, especially during the summer monsoon, despite the 12 nmi conservation buffer zone and a 5 nmi non-trawling zone. This poaching is deplored by local fishers.

Artisanal fisheries cease during the summer monsoon season in almost all areas. The average fishing season is then only 8 to 9 months out of the year, during which a fisherman will spend 160 to 180 days – 220 at most – fishing (Hariri & Yusif 1999; Nichols 2001; Reid *et al.* 2002), depending on various factors. Fishers operate from some 86 coastal villages and settlements across the islands, ten of which are on Samha and Abd al-Kuri. For many years there was a single cooperative, the Socotra Fishermen Cooperative, established in 1970. In 1993 it had 1 500 members, but it ceased to operate in 1994. There are now 25 cooperatives after the concept was promoted by the SBP and other fisheries development projects (Yusuf & Kassem 2000; Riet *et al.* 2000; Nichols 2001).

Socotran fishermen predominantly use two types of Yemen-crafted boat. The first is an open, fibre-glass reinforced plastic skiff, known locally as *bushenda*, *qareeb, qa'difa, plastic* or *houri*. These are 7.7–9.5 m long and equipped with one or two 15–40 hp outboard engines and have a crew of 2–4 fishers. These are the most abundant and are used for day-range activities. The second is larger and is known as a *sanbuq* or *sambuq*. They are up to 15 m in length, made of wood or fibreglass, have insulated holds with ice to store the catch, and are equipped with 40–75 hp outboard engines. They take 5 to 7, and occasionally as many as 12, crew. *Sambuqs* are used primarily for gillnetting, longlining, and catch-buying journeys lasting several days (Figure 8).

Figure 8 Main types of fishing crafts in Socotra's artisanal fishery: **A** fibre-glass reinforced skiff with outboard engine (*houri, qa'difa, bushenda*); **B** wooden (as here) or fibre-glass boat with inboard diesel engine (*abriy*, *sambuq*). © U Zajonz

The fisheries primarily target shallow demersal and 'reef' fishes inshore, and large pelagic species and sharks offshore. There is also a rock lobster and sea-cucumber fishery, and a more limited deep demersal fishery, which have only developed over the last decade. Some of the larger estuaries are also opportunistically or seasonally fished during spawning and foraging migrations of valued species (e.g., Nichols 2001; Mohsen 2002; Zajonz pers. obs).

The large pelagic fishery targets primarily kingfish (*Scomberomorus commerson*), yellowfin tuna (*Thunnus albacares*), rainbow runner (*Elegatis bipinnulata*), dorado (*Coryphaena hippurus*), kawakawa (*Euthynnus affinis*) and longtail tuna (*Thunnus tonggol*), with sailfishes, marlin and other tunas being caught incidentally. These boats primarily use surface-set gillnets, pelagic longlines and trolling lines.

The shark fishery targets 12–15 species of requiem, hammerhead and mako sharks, using longlines and gillnets, but also baited single hook-and-line. The catches are predominantly silvertip shark (*Carcharhinus albimarginatus*), spottail shark (*C. sorrah*) and scalloped hammerhead (*Sphyrna lewini*), as well as the shortfin mako (*Isurus oxyrinchus*). In catches landed along the southern coast of Socotra Island, species such as the blacktip reef shark (*Carcharhinus melanopterus*), Human's whaler shark (*Carcharinus humani*) and tiger shark (*Galeocerdo cuvier*) are also abundant (Saeed 2000; Nichols 2001).

The shallow demersal and reef fishery targets about 120 different species, primarily in shallow coastal habitats, particularly species of high-value families, such as groupers (Epinephelidae), trevallies or jacks (Carangidae), snappers (Lutjanidae), sweetlips (Haemulidae) and emperors (Lethrinidae). Species of many other families are taken opportunistically and, if not sold, are used for domestic consumption. The dominant gear is a baited vertical hook-and line. Traps are used occasionally at discrete sites, with beach seines and cast-nets being resorted to by older and poorer fishers for subsistence fishing.

Fisheries catch and effort

As with other multi-gear, multi-species artisanal fisheries, there are numerous isolated landing sites, and a large number of stakeholders with different vested interests. Catches are marketed directly on the beach or to buyer vessels, most of which come from the mainland. Unlike the rest of Yemen, fish are sold by the piece and not by weight, and there are no direct records of these transactions. Instead, the value (price) is supposed to be reported to the fisheries office which uses price–weight coefficients by species to recalculate the weight – obviously not very accurate a recording procedure. The dispersed nature of the landing sites, the method by which catches are sold, combined with a local fisheries administration with limited capacity, make monitoring fisheries around Socotra a serious challenge.

Efforts to establish a fishery monitoring programme on Socotra started in 1998, during the SBP. The data collected were partly of limited usefulness (Nichols 2001) on the one hand, and partly put to limited use only on the other hand. Further, the data analysis was restricted to 6 of 17 fishing areas, simply because of the enormity of the task. The data were never used to calculate catch-and-effort trends, or make stock assessments, and then ceased to be used after the project ended in 2005.

The basic data for the estimates presented in this account (Zajonz *et al.* 2016) were partly compiled from the reports of fisheries consulting teams that visited the islands between 1998 and 2002, on projects funded by the UNDP-GEF and the EU. The data were then verified and updated using various other unpublished sources, reports and personal observations. Data on catch and effort before 1998 and after 2001 are primarily derived from records from the fishing cooperatives and accounts from fisheries authorities, are consequently very unreliable (Nichols 2001; Reid *et al*. 2002; Zajonz pers. obs.), and required careful verification, as explained below. Data on fishing effort from before 1993 are not available and those data that do exist only refer to the numbers of vessels and fishermen, and estimates of fishing days per unit and per year, and has been reported by Esseen & Khanbash (1999), Hariri & Yusif (1999), Yusuf & Kassem (2000), Zajonz *et al.* (2010), Scholte *et al.* (2011), and others. Catch-and-effort data between 2005 and 2014 were collected *de novo* from the fisheries stakeholders.

The effort data from these sources were reviewed altogether and used to produce two time-series curves (Figure 9) illustrating the lower and upper range of the total numbers of boats and fishers over the past 21 years. These data show that between 1996 and 2014 the number of boats increased by 41% to approximately 1 100, and the number of fishers rose by 32%, to about 3 800. Overall effort seems to have reached a maximum in 2006 before levelling out. One of the reasons for the increase in number of fishers on Socotra is a result of population growth. Another is the increasing number of Bedouins from the island interior that have joined the fishery during the last decade, to supplement family incomes derived from traditional pastoral livelihoods.

There is some uncertainty with these data because recent statistics refer only to fishers registered (organised) with the cooperatives, whereas earlier figures also included 'unorganised' fishers i.e., among the approximately 5 000 fishers given in Hariri & Yusif (1999) and IFAD (2010). There may thus be an additional few hundred fishers, part-time fishers, deck-hands and helpers that are not accounted for as they have not joined one of the cooperatives, and the total numbers are probably closer to 1 300 boats and 4 500 fishers, with unconfirmed reports of 2 000 boats and up to 6 000 fishers.

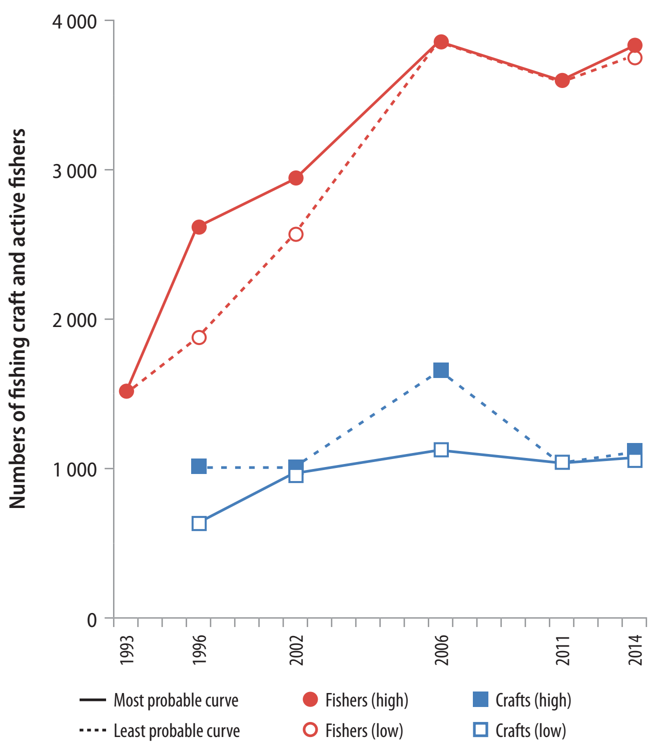

Figure 9 Basic consolidated effort trends for Socotra Archipelago from 1993–2014, based on the numbers of fishing craft and active fishers, showing for both the upper and lower range margin of plausible data. Years that are completely data deficient are not listed on the X-axis.
Source: Zajonz *et al.* 2016

The substantial increase of overall fishing effort around Socotra during the last 20 to 30 years corresponds with similar trends observed for the Gulf of Aden mainland (Zajonz & Akester 2005) and Yemen as a whole (e.g., Tesfamichael *et al.* 2012). Zajonz *et al.* (2010) reported that the number of boats in Yemen had more than tripled between 1997 and 2006, from 7 150 to 22 600, and was likely to have reached 29 000 by 2010. Likewise, the number of fishermen had doubled between 1997 (37 600) and 2006 (63 200), and further increased to 83 200 by 2010 (Zajonz *et al.* 2010).

Total catch

The data available for the main fisheries and the total fisheries production for the Socotra island group are, like the effort data, also limited and unreliable, and for several years such data are not available (Zajonz *et al.* 2016). There are principally two sources for data, each with different biases and levels of accuracy. The first source is actual 'catch records' (and associated revenue data) registered by the fishing cooperatives, and partly compiled and summarised by resource group (e.g., 'sharks', 'demersals', 'large pelagics', etc.), by the local branch of the Ministry of Fish Wealth of Yemen. The second source is 'catch estimates' produced by trained fishery scientists or technicians, and is based on field samples of catch and effort and fleet counts. They are usually higher than actual records, as explained below. No catch records were available for years the estimates were produced for, and thus cross-validation is not possible.

In the 1990s the catch records seem to have been checked for accuracy, and corrected by fishery scientists of the then Marine Science and Resources Research Centre in Aden (MSRRC) of the Ministry of Fish Wealth (MFW), and appear relatively plausible (see Saeed 2000 or Mohsen 2002). From 2000 onward no catch data that have been quality-guided and consolidated by local fisheries experts from the cooperatives or MFW, are available. When the SBP database system was in operation there were no data from the cooperatives (c. 1998–2004). Data for 2005–2007 are in a range that could be considered plausible, whereas data from 2008 onwards appear to be pretty inaccurate, and several years' records are missing.

The available data were then used to reconstruct long-term catch trends over a period of 25–30 years (Figure 10). As with the effort trends, two time-series curves are illustrated, showing the lower and upper margins of the plausible range of fisheries production. The same data were also used to extrapolate mid-term catch trends for the period 1990 to 2014 (Figure 11), based on the relative proportion the main resource groups had on average in 2005–2007: sharks (49%), large pelagics (27%), reefal-demersals (23%), and other (1%). During this 25-year period, data for reefal-demersals are available for 12 years, while data for the other groups are fewer and more scattered.

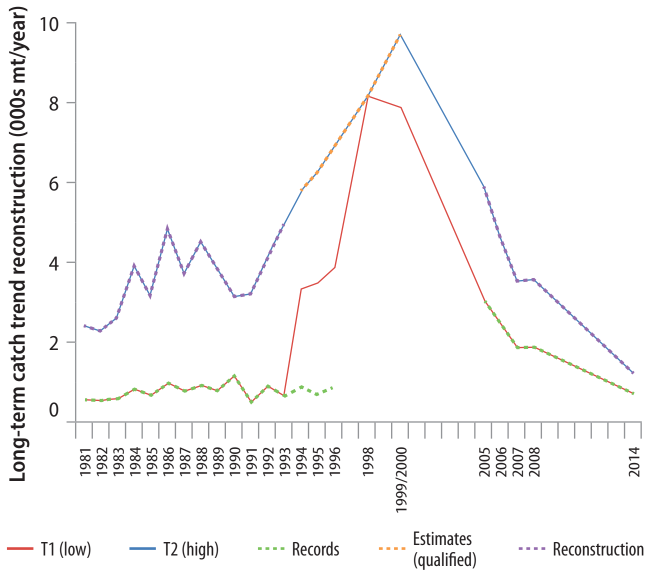

Figure 10 Consolidated long-term trend of total finfish catch for Socotra Archipelago from 1981–2014, based on available records, qualified estimates and partial reconstruction, showing the upper (T2) and lower (T1) range margin of plausible data. From 1981–1993 and 2005–2014 T2 is based on reconstructed catch data. Trend curves (T1, T2) are given as continuous lines bridging data-deficient years. The figures of 1999/2000 refer to fishing season and not to calendar year but were used in the absence of alternative data. Years that are completely data deficient are not listed on the X-axis. Source: Zajonz *et al.* 2016

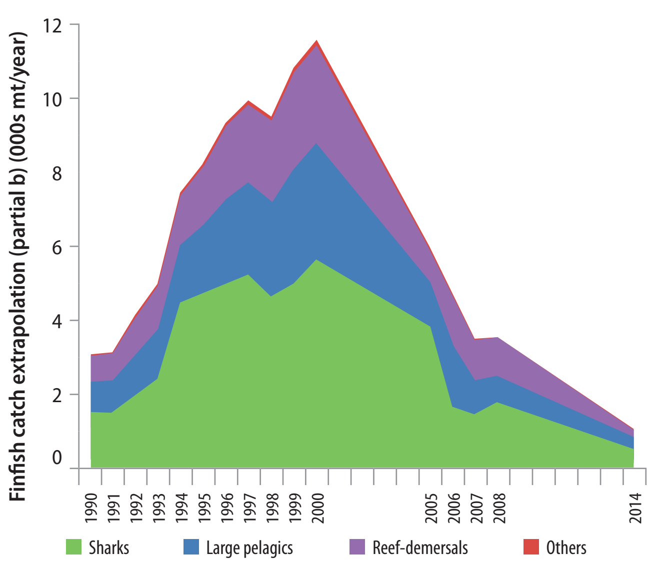

Figure 11 Mid-term trend extrapolation of total finfish catch for Socotra Archipelago from 1990–2014, based on available records and reconstruction of missing data according to the average proportional shares of the main resource groups in 2005–2007. Data from 2005–2014 represent actual catch data adjusted to account for assumed under-reporting. Years that are completely data deficient are not listed on the X-axis. Source: Zajonz *et al.* 2016

The reefal-demersal data were used to estimate the missing potential catch data of the other groups (retaining extant values) using average group shares for 2005–2007, the only years for which data are concurrently available.

Records available for 1981–1996 from the then Socotra Fishing Cooperative indicate a total annual catch of 391 metric tons (mt) in 1981, 1036 mt in 1990 and 705 mt in 1996 (Nichols 2001). According to unpublished estimates of the SBP (in collaboration with international development agencies), annual production rose dramatically to 7 284 mt in 1998, based on a fleet of 843 craft, a 160-day working season and an average catch of 54 kg per boat per day (also in Reid *et al.* 2002).

For the same fleet and season Hariri & Yusif (1999) provide an estimate of 8 270 mt, based on a breakdown of production by boat type. Based on recorded length-frequencies (which are converted into weights) for the catch of a subsample of the actual total boat trips, the SBP team (unpubl.), using length-weight coefficients, extrapolated a total annual catch of 1 516 mt for 6 of 17 fishing areas for the 1998/1999 season. According to Nichols (2001), artisanal catch estimates for the main groups for the 1999/2000 season ranged between 6 030 and 6 139 mt in total. Substituting the implausibly low shark-catch figure used by Nichols (2001) with the median of 5 000 mt for the estimated range of the shark catch given by Huntington & Al-Sakaf (2000) [unavailable, see Reid *et al.* 2002], the catch production of Socotra's fisher fleet was probably some 9 885 mt in 1999/2000. The alternative values from the reefal-demersal-based extrapolations are between 13–25% higher, at 11 560 mt in 1999/2000. These figures mark the peak catch production for the 35 years for which data are available. These statistics represent a sharp rise in production from the early 1990s, followed by a steep decline, with current production figures reported by the cooperatives similar to those reported from the early 1980s.

An assessment of the buyers' records of a single large fishing cooperative on the Hadramaut coast was made to validate these findings, and gives a total of 3 612 mt of fish traded in from Socotra from 2007 to 2011. These data also show a severe decline in catch available to buyers, from 2 384 mt in 2007, to a mere 244 mt in 2009, and to only 68.8 mt in 2011, corroborating the negative trend observed from the Socotra records.

Figure 12 shows the annual total finfish production per boat and fisher as basic proxies of catch-per-unit-effort (CPUE), and the trend from 1993 to 2014. The CPUEs peaked in 1999–2000 ranging between 8.1 and 11.4 mt per boat and 3.1 and 3.9 mt per fisher, depending on the ranges of boats, the number of fishers and total catch, with a potential maximum of 14.6 mt per boat in 1999. It has slumped dramatically since then, even though there is no doubt that the actual catch production is still substantially higher than the available official records would suggest. This negative trend most likely reflects a period of unsustainable yields for the past decade, and has severely impacted the exploited fish populations over the long term.

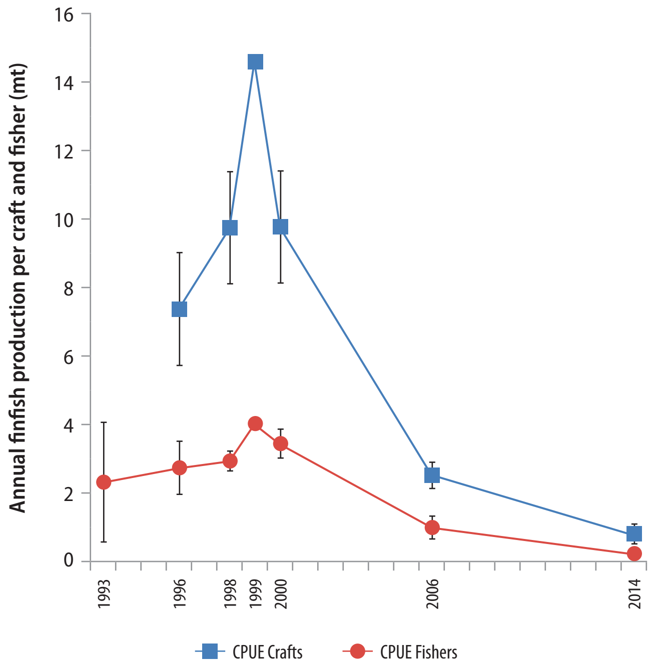

Figure 12 Mid-term trend of basic catch-per-unit-effort (CPUE) for Socotra Archipelago from 1993–2014, based on the means of the plausible value-ranges for the number of crafts and fishers. Years that are completely data deficient are not listed on the X-axis. Source: Zajonz *et al.* 2016

There are four main reasons why actual exploitation levels in the waters around Socotra are substantially higher than those reflected in the available catch records. First, the fishermen pay a 3% levy to their cooperative, based on catch value registered by them, which creates a disincentive to provide the correct values. Second, a similar disincentive applies to the buyers, who are (theoretically) obliged to pay a 5–7% levy on the total purchase value, which is shared between the cooperatives, the MFW, and the governorate. Thus, the catch reports from Socotra (which include local consumption and marketing, and exports to the mainland) should actually be higher than the trading records from the islands to the mainland. The fact that one out of 11 trading records (the mainland cooperatives recorded not only their own catch, but also purchases from elsewhere) exceeded the direct records on Socotra itself, illustrates how flawed and severely underreported the Socotra data are (see Zajonz & Akester 2005). The misreporting of catch in order to evade fees and taxes, led IFAD (2010) to re-estimate the total catch production of Yemen to be in the order of 250 000 mt instead of the 109 000 mt officially reported by the MFW to FAO in 2009. This would translate into the actual catch on Socotra ranging from 22 600 to 26 500 mt for 1999/2000. Third, a substantial proportion of the catch has thus far gone completely unrecorded in Socotra's record books. This includes the catches of Yemeni fishers landed at sites on the mainland, predominantly at Hadramaut, Al-Mahara and Shabwa, and occasionally elsewhere such as at Oman. These catch numbers have thus far never been added to the catch statistics for the island group. Hariri & Yusif (1999) noted that the shark production from Socotra, which is landed at Hadramaut and Al-Mahara, is about as high as the production registered on Socotra itself (although the actual figures provided by them are too low). Fourth, comparing the average annual production per boat in Al-Mahara with that on Socotra, strongly suggests that the Socotra CPUE resulting from present data is much too low to be credible. In 2003, a total of 7 197 fishers operating 2 479 crafts (crew of 3) landed a total catch of 75 818 mt in Al-Mahara (Zajonz & Akester 2005), equivalent to 30.6 mt annual production per boat and 10.5 mt per fisher, compared to 8.1–11.4 mt per boat and 3.1–3.9 mt per fisher at Socotra in 2000 (crew of 3). Most of the Socotran fishermen would evidently migrate to fish at the mainland if the productivity of their 'home turf' were really that much lower. In reality, however, more mainland fishers are attracted to Socotra than the other way around. This illustrates how severely flawed the catch records from Socotra have become, essentially rendering them useless to inform sustainable fisheries management.

Socotran fisher communities have in the past been recognised for managing their stocks wisely, according to traditional management methods (Morris 2002; Reid *et al.* 2002; Cheung & DeVantier 2006). These included banning fishing for small pelagics and the use of fish traps, imposing temporal or spatial closures and temporal bans on nets, or, more recently, promoting traps in the lobster fishery instead of nets. Strong peer pressure and community-imposed penalties on infringements were reported as resulting in high levels of compliance with the customary management system. It used to be common sense that the local fishery is more or less sustainable with only a few target species such as sharks and rock lobsters being overexploited (Hariri & Schotah 1999; Nichols 2001; Cheung & DeVantier 2006). The customary management norms of the fishermen of Socotra have long been unique in Yemen and probably the entire Arab region. Indeed, many of the existing traditions that have helped the Socotrans manage their fisheries to date are what organisations elsewhere are only now trying to reinstate by establishing Locally Managed Marine Areas (LMMAs) (Rocliffe *et al.* 2014). At the same time, the relative isolation of the islands, their limited fish processing facilities, long transportation routes and ill-developed marketing paths created a 'natural' control mechanism that prevented an unsustainable growth of the fishing sector. Historical catches (1981–1996) for all main groups (sharks, kingfish, reef fish and rock lobster) were considered as being at "light exploitation levels", and stocks in the 1999/2000 season generally "in a healthy condition" (Nichols 2001; Hariri *et al.* 2002, on reefal-demersals). These were most probably already unjustified statements at the time.

It is highly questionable whether the small-scale fishery on Socotra is sustainable nowadays. The increase of the local fleet size over 20 years, an increase in local ice-making, cold storage and primary processing facilities, and an ever-increasing share of production exported to buyers on the mainland, makes Socotra's fishery today a more commercial enterprise and undermines its traditional, artisanal roots and best customary practices. Other underlying causes include rapid population growth, increasing coastal development and expansion of tourism, which exert increasing pressure and higher demand on living marine resources, particularly at key tourist sites. More recently, Socotra's fishing industry has partly come under the control of Arabian Gulf states which adds a lot to the existing fishing pressure. Overfishing now presents a major challenge to the Socotran fisheries sector, not least because the strongly negative trend in fish production, as inaccurate as catch statistics might be, is corroborated by fishers and others in the fisheries sector who unanimously report that catches and CPUE are declining.

CONCLUSIONS

The Socotra Archipelago has a unique marine environment with tropical and 'pseudo-temperate' features that are generated by particular regional oceanographic conditions driven by the Indian monsoon. Although the diversity and ecology of its fish communities have been studied for about 20 years, the information available has only recently been pulled together. Even less was known about the local fisheries, which had long been sustainably managed through traditional, community-based practices. Furthermore, no information on fish productivity (in terms of biomass) on which these fisheries were based was available. At a time when Yemen is torn by a severe political and humanitarian crisis its living marine resources are likely to experience increasing pressures, as are those of the archipelago.

The coastal fish diversity of Socotra Archipelago is the highest of any 'ecoregional unit' (e.g., Spalding *et al*. 2007) in the northwestern Indian Ocean, and ranks high compared to similar areas in the wider WIO, especially when considering species richness in relation to length of coastline, shelf area and reef area. It is especially striking that many typical reef fish species – such as 29 species of chaetodontids – occur here, and that the island group supports unique reefal and coastal fish communities, in spite of the limited extent of coral reefs. The Socotra Archipelago is therefore critically important to the region's marine and fish conservation management.

The marine biogeographic affinities of the archipelago are characterised as being at a crossroads. The location of hypothetical biogeographical boundaries and barriers in the seas around the archipelago are still a matter of scientific debate. The most eminent biogeographic studies do not yet correspond to one another, and used to be based on outdated fish inventories for Socotra. The archipelago is perhaps less a source than a sink for regional fish diversity. It represents a globally important hybridisation hotspot for marine fishes, forming likely part of an eastern Gulf of Aden hybrid zone and it is a faunal melting pot and key stepping stone for regional marine biogeographic patterns.

The coastal fish biomass productivity of the inshore waters of Socotra Archipelago is high, and certain sites rank among the most productive in the Indian Ocean. Biomass productivity and the underlying communities are seasonally highly dynamic, driven by the seasonal upwellings created by the northeast monsoon.

Recent data point to a sharp decline of standing crop and fisheries productivity over at least the past ten to fifteen years, pointing to serious socio-ecological and livelihood problems in the future. Whether the once traditionally managed small-scale fishery on Socotra is sustainable is extremely doubtful. The following statement of Reid *et al*., in the fisheries section of the Socotra Master Plan study (2002), is sobering: "... the current liberal management regime, lack of regulation and the ready availability of finance [lending for investment in the fisheries sector] is likely to lead to an unsustainable and poorly structured industry that will not properly serve the Socotran people". Likewise, Hariri *et al*. (2002) predict that "Socotra's fisheries will come under threat if the islands' societal structure changes markedly or outside interests begin to exploit resources on an unsustainable basis". Overfishing is now prevalent around Socotra Archipelago posing a major problem. The markedly increased fishing efforts, combined with the severe, real, decrease of the fisheries production, raises serious concerns about the future sustainability of Socotra Archipelago's fisheries and not least, the food security for the islands' coastal communities. The deterioration of the traditional, community-based fishing regulations needs to be halted, and the poor enforcement of the regulation effecting existing marine protected areas (MPAs) must be overcome. Effective management of MPAs including 'no-take-zones' will allow recovery of populations, increase fish biomass and will, in the long term, benefit adjacent use-areas through the supply of adult fish and larvae for recruitment (spill-over). Active fisheries management through gear and catch restrictions and export limitations will further limit overfishing and habitat destruction, and thus improve the sustainability of the local fisheries. First and foremost, however, it is pivotal to organise and fund fishery research based on biological and fisheries data in tandem, in order to understand the resource base. Effective evidence-based fisheries management has to take priority over perpetual investment into the production, processing and marketing sector, or else these severely negative trends will not be reversed.

ACKNOWLEDGEMENTS

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Finally, I would like to thank the people of Socotra, notably the fishers and coastal communities and the Environment Protection Authority Yemen and Socotra, who kindly provided access to their knowledge and to the areas under their care.

Figure 13 Scenes from Socotra's artisanal fishery: **A–B** pelagic fishery, **C–E** shark fishery, **F–G** reefal-demersal fishery, **H** lobster fishery, traps.
© **A:** JJ Brown; **B, C, F, G:** SV Bogorodsky; **D:** A Bollen; **E, H:** U Zajonz

FISHERIES OF THE WESTERN INDIAN OCEAN

Rudy van der Elst

INTRODUCTION

The thousands of fishes described in these volumes reflect the marvellous diversity of Western Indian Ocean (WIO) marine life. The species are nestled in an equally diverse array of ecosystems and habitats that make up the region's natural environment. Not surprisingly, this great biodiversity provides the basis for a range of fisheries and fishers who depend on this resource for food, employment and other ecosystem benefits, including medicinal, scientific and cultural. From humble but often innovative subsistence fishers to sophisticated industrial operations, the WIO region sustains the livelihoods of millions of people and their dependants. Notwithstanding the great value placed on the fishery resources, sustainable harvests can only be assured if they operate within the regenerative capacity of species and their ecosystems. In turn, this calls for the wise and restrained use of resources as well as collaboration between stakeholders. Such regional initiatives do exist and many undertakings are in place to manage the use of WIO resources.

About half the world's population lives in countries that border on the Indian Ocean, and, in most cases, seafood represents an important source of food security, employment and a national resource that contributes to the gross domestic product of the countries. It is estimated that some 30 million people in the 10 countries of the WIO coastal zone depend directly on harvesting marine fishes and contribute to elements of socioeconomic stability in these coastal regions. While large industrial fisheries, such as those targeting tuna and shrimp, supply the world's markets, most developing countries in the region have a large contingent of artisanal fishers that contribute to local food security and the economy.

THE NATURE OF WIO FISHERIES

There is an amazing variety of fisheries taking advantage of almost every ecosystem and habitat. The most elementary are subsistence fisheries, which include large numbers of fishers engaged in a daily chore of providing food security to their families. Many simply harvest food gathered from the intertidal zone, whereas others might use traps, canoes, handlines and small seine nets to secure their catch. In some cases the fishers supply local markets, mostly using modest, low-technology fishing gear. Such artisanal fishers are common throughout the WIO region and fulfil an important role in the local socioeconomics of different areas. Artisanal and subsistence fisheries are mostly located in the shallower coastal zone. Some fisheries are classed as semi-industrial, making use of larger motorised vessels and various forms of technical innovation, such as GPS devices, radios, icing facilities, and even diving. Still larger vessels, capable of fishing in oceanic waters, are termed industrial fisheries and use fishing gear such as trawls, purse seines and longlines. Many industrial vessels operating in the WIO region are foreign owned and operate under bilateral fisheries agreements, whereby the catch may be taken directly to the vessels' flag country. In some cases the catch is trans-shipped at sea or directly supplied to canneries in the region, such as the large fish processing factory in the Seychelles. Fisheries can also be grouped by the type of gear used, as reflected in the WIOFish Database (http://www.wiofish.org) in which 211 different fisheries are described (Table 1).

Table 1 Different fisheries' gear types used per country. Source: WIOFish

GEAR	SEYCHELLES	MAURITIUS	KENYA	TANZANIA	MOZAMBIQUE	SOUTH AFRICA	TOTAL
Diving	2	0	6	4	4	5	21
Harpoon	1	0	0	0	0	1	2
Hook & line	15	10	3	5	7	14	54
Industrial nets	1	1	3	3	4	3	15
Large nets	0	1	2	0	1	0	4
Mixed gears	0	2	0	0	0	0	2
Other	0	0	0	2	0	1	3
Shore gathering	6	2	7	11	3	18	47
Small nets	6	3	8	8	6	10	41
Traps	5	1	4	2	5	3	20
Unknown	2	0	0	0	0	0	2
TOTAL	38	20	33	35	30	55	211

FISHERY TRENDS IN WIO

Global trends in fisheries landings are documented by the Food and Agriculture Organization of the United Nations (FAO). The FAO divides the world's marine waters into 19 major fishing areas, and each nation or territory that harvests marine resources in any of the areas voluntarily submits statistics to the FAO. This global repository of fisheries statistics can be accessed through FishStat (http://www.fao.org/fishery/statistics/global-production/en) and includes national and regional information on total capture production from 1950 to near-current. The Western Indian Ocean, designated as Area 51, is the fifth largest of these fishing areas; it is some 29.3 million square kilometres in extent, or about 8.1% of the global ocean area, stretching from latitude 45°00' S roughly to the southern Cape coast of South Africa (30°00' E longitude) to Somalia and the Arabian Sea, Red Sea and Persian/Arabian Gulf, and eastwards to the southern tip of India (Figure 1). The WIO region is complex with respect to geopolitical boundaries and Exclusive Economic Zones (EEZs), which extend 200 nautical miles (370 km) out from the coast, and in some cases territorial claims are disputed. Not insignificantly, ownership of a tiny atoll can infer the rights to exploit a much larger surrounding EEZ. For example, France is granted extensive fishing rights in WIO by virtue of its sovereignty of numerous small islands and atolls in the region. Also, of consequence is that national and EEZ waters account for approximately one-fifth of Area 51, hence leaving a huge expanse of WIO as international waters. This has received attention in the development of certain international agreements, such as the Southern Indian Ocean Fisheries Agreement (SIOFA), which aims to document catches and regulate landings in remote ocean expanses, such as fisheries for tunas, orange roughy, Patagonian toothfish, sharks, and other oceanic and deepwater species.

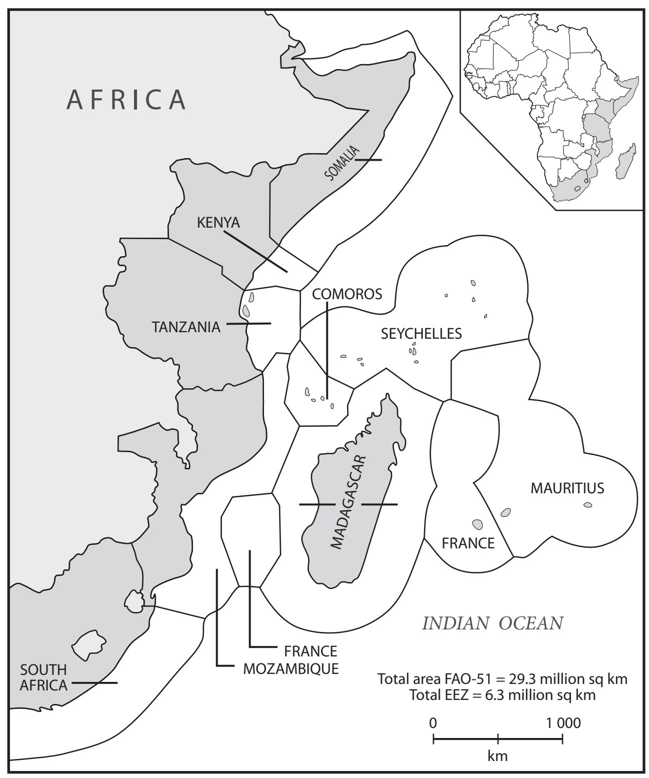


Figure 1 African section of the WIO study area (FAO-51), showing national Exclusive Economic Zones (EEZs). Source: FAO

The records collated each year by the FAO focus primarily on formal, more industrialised fisheries, and provide useful insight into broad trends and the status of particular species stocks. Although the FAO continues to report a decline in the global fisheries catch, Area 51 is one of the few fisheries regions of the world that contradicts this trend. Landings in Area 51 peaked at 4.5 million metric tons (mt) in 2012, which

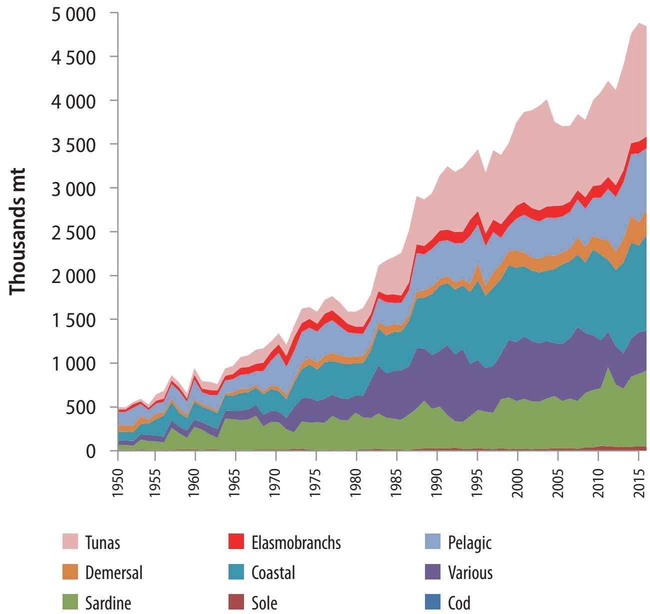


Figure 2 Growth in relative tonnage of fish types harvested annually in the WIO, 1950–2019. Source: FAO

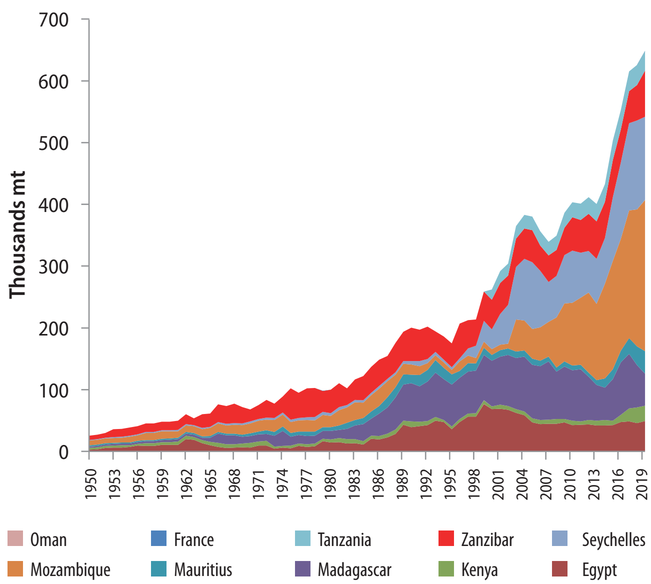


Figure 3 Growth in annual tonnage of catch taken in the WIO by African nations which reported at least 30 000 mt. Period 1950–2019. Source: FAO

represented about 5.7% of the global industrialised fish catch, considerably more than the 1.6 million mt harvested in the nutrient-rich southeastern Atlantic (FAO 2014).

Figure 2 shows the broad composition of WIO fish landings over time. The total fish catch in WIO has increased substantially over the decades, largely attributable to greater fishing effort and a growing tuna harvest that exceeds 1 million mt per annum. Indeed, the tuna canning factory in the Seychelles is the second largest in the world and annually processes around 300 000 mt of tuna. The catch of several other species has also increased, notably that of the Indian oil sardine, which accounts for 300 000 mt per annum.

While the increasing total catch may superficially seem reassuring, in reality it masks several areas of concern. One of these relates to the number of species being harvested, which has risen from at least 85 in 1970 to more than 150 today. This increase is partly due to better reporting and enhanced technology, such as the use of fish aggregating devices, but also reflects a wider demand for 'new' species in the context of declining economic viability of stocks of traditional species. Such trends could be an indication of serial overfishing, whereby one species replaces a depleted species, so as to retain fishing capacity in the region. The Southwest Indian Ocean Fisheries Commission reported that <25% of the region's fisheries were exploited at unsustainable levels in 2010, moderately better than the global average of 30%. While this may seem positive, it leaves no room for complacency, especially as it does not take into consideration the effects of ecosystem overfishing.

As catches in several of the world's fishing zones decline, so the fishing fleets shift their focus to new regions. The number of countries that have reported catches from WIO has reached 60, up from approximately 46 in 2005. About half of these are nations that do not border WIO but operate in the region as part of fisheries agreements with local nations. In some cases foreign vessels operate outside the declared EEZs, mostly in pursuit of tuna, sharks and other oceanic species. Clearly, this highlights the global demand for fish. Based on FAO data it appears that about 20% of the total catch in WIO is taken by such foreign operators. Some insight into the respective and growing harvest taken by countries operating in WIO can be gauged from Figure 3.

While the FAO reporting system is an innovative and useful tool to evaluate the overall conservation status of marine resources, it is imperfect. There are clear indications that not all catch records are fully reported by every country, especially the under-reporting from artisanal fisheries. Some estimates have suggested that the total catch may well be double that which is reported to FAO.

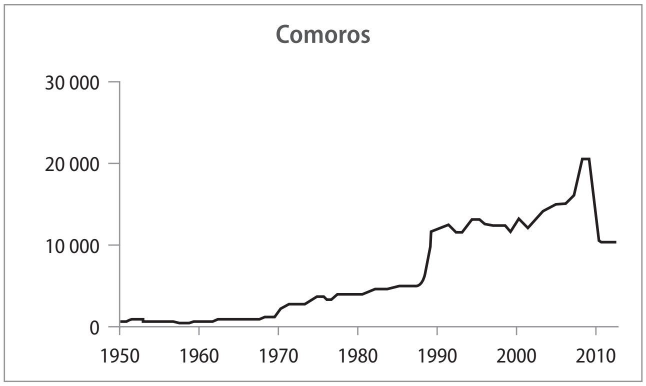
Based on country surveys and research projects, some estimates of the artisanal fisheries in several WIO countries have been made; a preliminary overview is given in Table 2. These fisheries are restricted mostly to inshore areas and carried out over a range of coastal habitats, such as sandy beaches, estuaries, coral reefs, lagoons, wetlands, bays, mangrove forests and seagrass beds, but rarely in oceanic waters. The participants are local coastal communities who fish on a small scale using simple equipment (often boats without engines), fishing for their own use or to supply local markets and in rare cases surplus for export. Typically, individual daily catches per fisher are a few kilograms. Significantly, however, this low-yield but widespread fishery accounts for more than 80% of the total marine catch in Tanzania, Kenya, the Comoros and Madagascar. Regardless of the exact figure of total fish landings from WIO, based on the *declared landings* there is growing concern that the region may be approaching its maximum harvest potential.

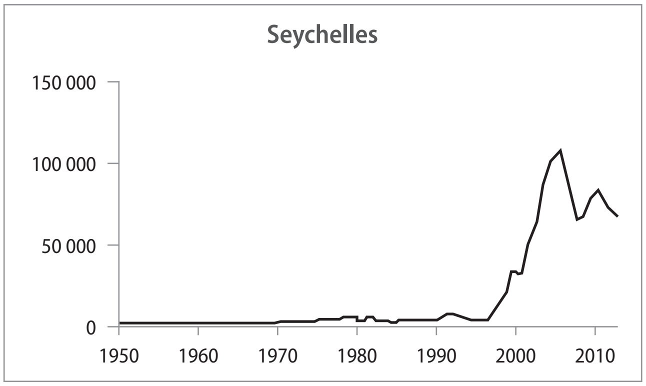
Table 2 An overview of selected artisanal fisheries for several WIO countries (modified from UNEP/Nairobi Convention, 2009).

COUNTRY	NO. ARTISANAL FISHERS	ARTISANAL CATCH (mt/yr)	PRINCIPAL FISH FAMILIES
Maldives	14 000	~100 000	Carangidae, Lutjanidae, Scombridae, Lethrinidae, Epinephelidae, Coryphaenidae, Istiophoridae
Comoros	8 000–8 500	5 500–7 507 – 13 500 ('97)	Scombridae, Gempylidae, Carangidae
Seychelles	1 700–1 800	4 000–5 000	Carangidae, Sphyraenidae, Scombridae, Siganidae, Epinephelidae, Scaridae
Madagascar	10 651	12 382–70 000	Mugilidae, Epinephelidae, Carangidae, Gerreidae, Hemiramphidae, Elopidae
Mauritius	2 365	950	Lethrinidae, Mugilidae, Siganidae, Acanthuridae, Scaridae
Réunion	521	866	Scombridae, Carangidae
Somalia	4 200	6 000	Lobsters, sharks
Kenya	10 000	8 000 –16 000	Lethrinidae, Siganidae, Scaridae, Lutjanidae, Epinephelidae, Scombridae, Carangidae, shrimp
Tanzania (incl. Zanzibar)	58 000	70 000	Lethrinidae, Epinephelidae, Siganidae, Mullidae, Lutjanidae, Carangidae, Scombridae, Clupeidae
Mozambique	70 000	100 000 –120 000	Siganidae, Lethrinidae, Sparidae, Labridae, shrimp
South Africa (KZN only)	5 183	2 153	Mugilidae, Carangidae, Sparidae, Scombridae, Leiognathidae, Gerreidae

SELECTED COUNTRY PROFILES

The salient features of the fishery sector in several countries of the WIO region and trends in annual landings are presented in Figure 4.





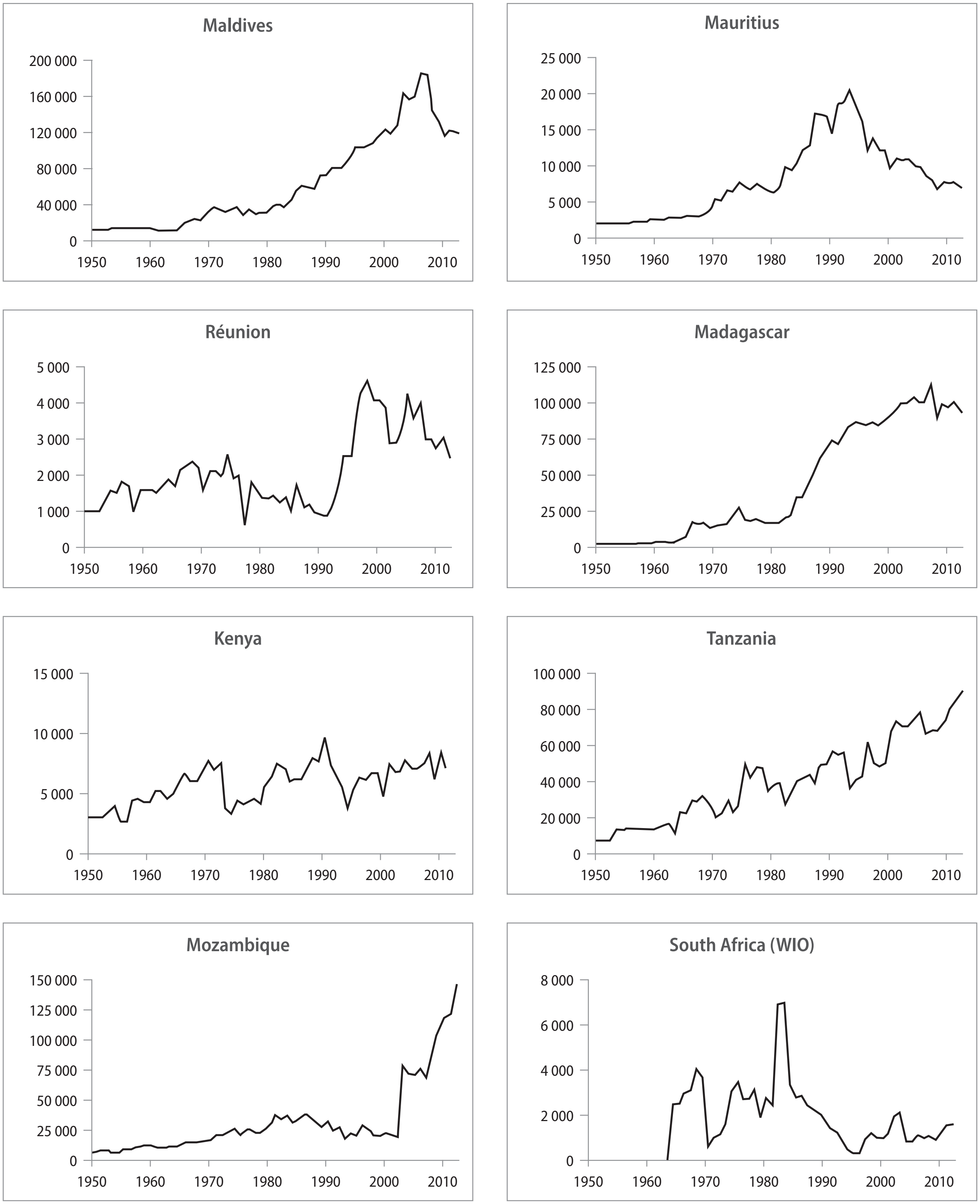


Figure 4 Annual catches (mt) declared to FAO by WIO countries.

Comoros

This archipelago of four small volcanic islands consists of French-controlled Mayotte and the three islands that constitute the sovereign nation of the Union of the Comoros. These islands only have a small continental-shelf area for artisanal fishing, despite the population's considerable dependence on fish for food security and employment. The islands have no industrial fisheries of their own, although a total catch of 12 000 mt is reported annually. Instead the nation has fisheries agreements with the European Union (EU) authorising 60–70 purse seine or longline vessels to catch about 5 000 mt of tuna, marlin and related species annually. Despite its oceanic setting, artisanal and subsistence fishing is prominent among its half-million people, with about 5 000 fishers operating from dugout canoes (pirogues) or engine-powered *vedette* boats, using handlines, gillnets and traps. Prominent artisanal landings include species of the families Lutjanidae, Lethrinidae, Epinephelidae and Carangidae. At times these fishers also venture offshore to catch oilfish and the occasional coelacanth. Recently, permits have been issued to some countries that authorise the targeting of sharks with gillnets, raising concern in some circles. Nevertheless, most of the fisheries in the Comoros are considered to be fully exploited.

Seychelles

An archipelago of 115 islands (with only a few inhabited) just south of the Equator, the Seychelles provides many fishing opportunities, which include industrial, artisanal and recreational. Domestic and foreign industrial fleets land up to 400 000 mt of tuna and billfish every year, creating employment and providing the country with critical foreign exchange. Artisanal fisheries are equally important, with about 1 000 fishers on 400 vessels, providing food security, employment and cultural identity. Smaller boats (especially pirogues) operate in inshore areas, with handlines, traps and seine nets, whereas larger fully decked inboard-engine vessels ('schooners') operate on offshore banks and ledges of the Mahé Plateau. The total catch from the artisanal sector has remained relatively constant since 2000, with landings between 4 000 and 5 000 mt per year. Besides lobster, crab, octopus and sea cucumber, the most popular fishes are diverse species of the families Lutjanidae (particularly *Lutjanus sebae* and species of *Pristipomoides* and *Aprion*), Siganidae, Carangidae and Epinephelidae. In most cases the nation's marine resources are considered to be moderately to fully exploited. However, the fisheries for Siganidae (rabbitfishes) and especially the much-valued *L. sebae* are of concern and known to be fully exploited.

Figure 5 A French purse-seiner in the Seychelles. © B Everett, ORI/SAAMBR

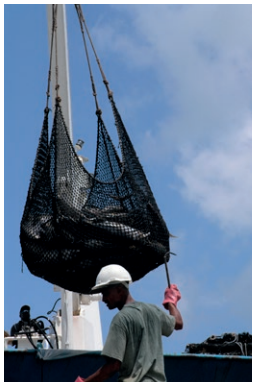


Figure 6 Offloading tuna to the cannery in the Seychelles. © B Everett, ORI/SAAMBR

Figure 7 A Seychellois cucumber fisher. © B Everett, ORI/SAAMBR

Figure 8 A typical Seychellois catch. © B Everett, ORI/SAAMBR

Figure 9 A Seychellois fisher. © B Everett, ORI/SAAMBR

Mauritius

This small island nation includes the islands of Mauritius and Rodrigues, several outer islands (including Agaléga, and those of St Brandon Shoals), the Chagos Archipelago and extensive areas of the Mascarene Plateau. The Republic of Mauritius, with a huge EEZ covering some 1.9 million km^2, is the custodian of considerable fishery resources, specifically for tuna, deepwater shrimps, and so-called 'distant bank fisheries' that comprise captures of Lutjanidae, Lethrinidae and Sparidae, including a new fishery for *Polysteganus baissaci* (Frenchman seabream). However, the total reported landings are modest, at approximately 6 000 mt per annum, about one-third of the peak in the mid-1990s. This is in part attributable to tight management controls and limits to access imposed by the Mauritian authorities, although there remains concern about the status of the reef fisheries.

Fisheries in Mauritius provide direct and indirect employment to approximately 10 000 people, with nearly 3 000 fishers, mostly engaged in the artisanal fishery. Besides octopus (mostly from Rodrigues), a wide range of shallow-water reef fishes are traditionally taken in the lagoons and fringing reefs using pirogues equipped with handlines, basket traps, large nets, gillnets, harpoons and hand spears. As the lagoon fisheries have been badly depleted, authorities are providing incentives for fishers to either exit the fishery or shift to less vulnerable offshore fisheries employing fish aggregating devices. Recreational fisheries play a significant role in the tourist economy, with about 350 mt of marlin and other gamefish caught annually.

Réunion

Although politically an overseas department of France, Réunion has its own fishing industry that generates valuable fishery products, primarily tuna and billfishes, for export. This small volcanic island has little continental shelf and a coastline of just over 200 km. Hence, industrial fisheries predominate. These comprise mainly tuna fisheries as well as a semi-industrial billfish operation that produces high-quality smoked products. The total declared industrial catch has decreased to less than 3 000 mt after peaking at 4 600 mt in 2005, largely attributable to a lower tuna catch. An artisanal fishery engages some 500 fishers operating from small outboard-powered boats using handlines, driftlines and trolling. Collectively, these fishers take 300–800 mt of linefish around the main island annually, mainly species of Scombridae but also Carangidae (e.g., *Selar crumenophtalmus*), Clupeidae (e.g., *Sardinella*), Mullidae, Epinephelidae and Lutjanidae. Catches have declined in recent years, suggesting that the exploitation levels may have exceeded sustainability. On outer islands and reefs within the large EEZ of Réunion, larger mother ships with attendant dories harvest reef fishes using handlines to catch mainly Lethrinidae, especially *Lethrinus mahsena* and *L. variegatus*. Réunion also serves as a base for French vessels that undertake trawling for Antarctic fishes around the Kerguelen Is. and lobsters from Saint-Paul and Amsterdam Is.

Madagascar

With a coastline of 5 600 km and a shelf area of 177 000 km^2, this large island supports a great diversity of fisheries, ranging from traditional to industrial operations. The total declared industrial catch increased enormously, from 20 000 mt in 1980 and peaking at almost 120 000 mt in 2004, but has since slowed to about 80 000 mt per year. Notable is the offshore tuna fishery, which is accessed by roughly 100 vessels, mostly from the EU. Shrimps are an important but declining resource, with domestic trawlers landing about 8 000 mt per year. Artisanal fisheries involve at least 60 000 fishers, mostly using dugout canoes cleverly rigged with sails and traditional gear such as gillnets, traps and beach seines. Although poorly documented, their landings are believed to be in the region of 75 000 mt annually, and this may rival the industrial catch. These traditional fishers contribute significantly to the nation's food security. Besides catches of fish as food, the harvesting of sea cucumbers, octopus, crabs and aquarium fish for export is popular in some locations.

Figure 10 Pirogues drawn up on the beach (Madagascar).
© R van der Elst, ORI/SAAMBR

Maldives

This tropical archipelago of 26 atolls comprising more than 1 100 small coral islands depends heavily on its fish resources as the main source of protein supply, for employment and export revenue, and as a basis for its tourist industry. The declared industrial catch peaked near 186 000 mt in 2005, but has since declined by one-third, possibly a signal of climate-change impact on the tuna catch. Almost 1 000 domestic fishing boats are operational, the majority being mechanised pole-and-line vessels, but an additional large component of the catch is taken by traditional handlines, often making use of live bait. Skipjack tuna (*Katsuwonus pelamis*) predominates in catches, but other tunas and a variety of oceanic (*Coryphaena hippurus*, *Elagatis bipinnulata* and *Scomberomorus* spp.) and coastal fishes (Carangidae, Lutjanidae, Lethrinidae and Epinephelidae) comprise about one-third of the total catch. Although many of the islands are remote, improved access has led to increased reef-fish exploitation, and negative catch trends of Epinephelidae (groupers) are of concern. Illegal fishing is also believed to have contributed to declining trends.

Somalia

The Horn of Africa is an area of huge seasonal upwelling, providing a basis for high concentrations of fishes, including valuable small pelagic species and larger tunas. However, the nomadic lifestyle of the Somali people and political turmoil have thwarted fisheries in the country. For a number of years foreign vessels harvested large quantities of tuna (often illegally), and numerous, now defunct, fish factories were established with foreign aid in anticipation of harvesting small pelagic species. Recently, the fisheries have been dominated by 3 000–4 000 locally based artisanal operators that supply limited local markets with a diversity of linefish. Shark fins are also a popular commodity, with extensive gillnets set parallel along many sections of the coast. Also prominent is an inshore lobster fishery along the northeastern Puntland coast, which uses a variety of gear types to harvest up to 300 mt annually for export. Remarkably, a number of the species of shellfish and finfish harvested in Somalia are similar to species taken in KwaZulu-Natal, South Africa, suggesting an antitropical distribution. Included among these are *Pomatomus saltatrix*, *Pomadasys olivaceum*, *Dinoperca petersi*, *Argyrosomus japonicus*, the lobster *Panulirus homarus* and, periodically, Cape fur seals.

Kenya

While Kenya's 640-km tropical coastline and its 142 000 km^2 EEZ are rich in fish, only 5% of the national catch comes from the sea; the remainder (especially the highly valued Nile perch, *Lates niloticus*) is taken from Kenya's Rift Valley lakes. Declared industrial marine landings have been stable at just below 7 000 mt for several years. This includes shrimp trawling in Ungwana Bay, where trawler damage to seagrass meadows, a large bycatch, high sea turtle mortality, and conflict with artisanal fishers over access has led to closure of this fishery for several years.

The artisanal sector is much larger, with some 10 000 fishers who land up to 16 000 mt per year. Dhows, outrigger canoes and planked boats are used to fish with gillnets, handlines and tangle-nets. Popular fishing zones include Lamu, Malindi, the Tana River Delta, and the south coast around Majoreni, Gazi and Vanga. Here, fishers target Scombridae, Sphyraenidae, Siganidae, Mugilidae, Carangidae, Lutjanidae and Lethrinidae. After years of growth, the artisanal fishery is now considered fully exploited, with intense fishing and even overfishing reported from coral reefs and seagrass beds in several locations. Reef degradation has further adversely affected the productivity and diversity. However, several sites in Kenya are famed for sport fishing and attract tourist anglers from around the world; although the total landings are not known, this fishery represents an important socioeconomic benefit.

Figure 11 Fisher and dhows (Kenya). © B Everett, ORI/SAAMBR

Figure 12 Going fishing (Kenya). © B Everett, ORI/SAAMBR

Mozambique

Mozambique is a fishing nation, drawing on the rich resources of Lake Malawi (known as Lago Niassa in Mozambique) as well as its extensive coastline and wide continental shelf. The fishing industry has been one of the country's largest generators of foreign revenue, with shrimp contributing up to 50% of the export value in the late 1990s. Annual declared industrial landings increased to more than 70 000 mt in 2006, following decades of reported landings of approximately 30 000 mt (this dramatic increase is possibly attributable to the recent inclusion of data from artisanal landings, however).

While industrial fishing at various levels contributes significantly to the economy, it is the artisanal fisheries that provide a livelihood for more than 70 000 fishers and their families, thereby supplying food to a large part of the population. Some 700 landing sites and 15 000 artisanal vessels are in operation, mostly wooden, non-motorised canoes and similar craft. Handlines, cast-nets, beach seines, gillnets, trolling lines, traps and cages are popular gear. Total landings vary but exceed 100 000 mt annually, encompassing a wide range of species, from coral-reef fishes, estuarine species, and inshore pelagics such as Carangidae and Scombridae. Sharks and rays are an increasingly popular resource for both food security and fins for export. Apart from fishes and shrimps, other important exploited marine resources near urban centres include invertebrates such as crabs, clams and sea urchins.

Figure 13 Mozambique artisanal fisher. © B Everett, ORI/SAAMBR

Figure 14 Fishing boat launch in Bazaruto (Mozambique).
© R van der Elst, ORI/SAAMBR

Figure 15 Ngalawas drawn up on the beach, Pemba Island (Tanzania).
© R van der Elst, ORI/SAAMBR

Figure 16 Community fishing dhow, Zanzibar (Tanzania).
© R van der Elst, ORI/SAAMBR

Figure 17 Trawlers off Dar es Salaam (Tanzania). © B Everett, ORI/SAAMBR

Recreational fishing (mainly by South African tourists) has increased significantly over the years, but this has occurred with low levels of compliance, many reports of excess catches, and conflicts with local operators. Research indicates that the majority of fisheries in Mozambique are moderately to fully exploited, so that conservation measures are being progressively implemented.

Tanzania

Although access to the Rift Valley lakes provides Tanzania with high catches of freshwater fishes, marine fish landings are persistently high as well, at approximately 70 000 mt per year, inclusive of some 20 000 mt taken by Zanzibar fishers. Virtually the entire marine catch is taken by artisanal fishers, who now number more than 58 000, and many are associated with coral-reef ecosystems. Catches are landed from dhows and outrigger canoes (ngalawas), using gillnets, beach seines, handlines, fixed traps and basket traps. Technically, beach seines are illegal yet popular, while the use of poison, dynamite, spear guns and other destructive gear persists. A wide variety of species are landed, ranging from reef fishes to small and large pelagics. Sharks, rays, lobsters, octopus and squid are also freely taken. Industrial fisheries often take the form of joint ventures between Tanzanian and foreign companies. Recently, deepwater tuna fishing has been established in Zanzibar, based on a projected potential of 8 000–24 000 mt per year from 70 licensed vessels. Compliance is generally poor, with sea cucumbers and several species of fish overexploited, including sharks for the fin trade. While clearly important in Tanzania, artisanal fishing has contributed to considerable degradation of the marine environment and reduced overall catches.

Figure 18 Zanzibar artisanal fish market (Tanzania). © R van der Elst, ORI/SAAMBR

Figure 19 Prawn trawler catch, KwaZulu-Natal, South Africa. © J Robey, ORI/SAAMBR

South Africa

Although South Africa is a significant fishing nation, with annual landings that can attain 1 million mt, only about 1 000 mt is taken in WIO Area 51. These include shrimps, deepwater lobster, swordfish, and a range of bony fishes taken by small-scale operators. Although the purse-seine fisheries for small pelagic species (anchovy, pilchard, round herring and juvenile horse mackerel) are traditionally located on South Africa's west coast (in the southeastern Atlantic), recent landings have moved further east, closer to Area 51. A range of small, engine-powered boats are used to access sea conditions that can be challenging. Mainly hook-and-line gear is used, but beach seines are used at times, especially during the winter sardine run of *Sardinops sagax.* Recreational fishing is also especially important along the coastline.

While the South African fisheries are generally well-managed, the status of many endemic species has fallen below acceptable threshold levels. This includes especially the Sparidae and some of the Scianidae. The trend in WIO catches taken in KwaZulu-Natal, for example, has steadily declined since the peaks attained in the early 1980s.

SPECIFIC CHALLENGES FOR WIO FISHERIES

Many of the fisheries in WIO share similar problems. The growing need for food security and employment in generally low-income locations are primary drivers that escalate fishing pressure to or beyond levels of sustainability. Globalisation is also a factor, with the industrial fisheries of many nations reaping an ever-growing harvest in the region. Ultimately, it is a will to implement and enforce scientifically based management policies that is required for the region to meet its development challenges while protecting its biodiversity. There are several specific issues:

- ***Fishing capacity.*** There are few limits on fishing volume in the region and many of the fisheries are in essence open access. Clearly, this impacts on the entire fish resource and lowers the productivity of individual fishers. Fishing is often an 'employment of last resort,' but overexploitation is a collective threat to all stakeholders. Consequently, a major challenge is to ensure that fishing effort is maintained within levels of sustainability, even while access to fisheries resources becomes equitably allocated.
- ***Fisheries data.*** Notwithstanding the value of FAO statistics, most fisheries are poorly documented and data are incomplete. In more than half of the WIO fisheries the existing level of monitoring and reporting is considered to be inadequate for management, while approximately only 4% of the fisheries have been scientifically fully assessed.
- ***Destructive fishing practices.*** In many cases the fishing gear used is destructive to the environment. For example, trawling gear often degrades the biodiversity of traditional fishing grounds, including the ecosystems on which fishes depend for nurseries and reproduction. Most disconcerting is that fishing with dynamite is still practised, albeit illegally, in several areas. The use of inappropriately small mesh-sizes,

gillnets, beach seines and fish poisons also raises concern. Trampling in shallow, intertidal areas while collecting octopus, shellfish, sea cucumbers and seaweeds also causes physical damage to sensitive habitats and fishing grounds.

- ***Habitat destruction.*** Of ever-growing concern is the physical alteration of marine habitats. Climate change, coral bleaching, mangrove-forest clearance and seagrass-meadow destruction all pose threats to essential habitats that are being transformed or destroyed with consequent impact on the ichthyofauna.
- ***Inadequate enforcement.*** While all countries of the WIO region have domestic fishing regulations, ensuring compliance is a huge and costly task, especially as most fishing activities are carried out in remote areas. A lack of funds and technical support frequently hampers the effective management of marine fisheries. Only 21% of the 211 fisheries surveyed in WIO are considered to have an adequate management plan.

MANAGEMENT APPROACHES

Fisheries management is always challenging. Dealing with people in a mainly open-access resource, large numbers of dispersed operators, and, in WIO, a very large number of species, with many not adequately studied, continually complicates fisheries management. Each of the WIO nations has its own domestic policy and regulations to manage the harvesting of fishes in its waters. However, these domestic fisheries regulations alone may be inadequate as many species are common to more than one country and straddle national borders. Many other species migrate freely across different areas of WIO, so that a collective approach for management is required.

Such an approach can be achieved, in part, through the programmes of the FAO. As signatories to the United Nations Convention on the Law of the Sea (UNCLOS), the WIO nations participate in regional fisheries management through the FAO's activities. Besides the key annual submission of catch information, the FAO provides support in a number of ways. For example, in order to ensure a fair distribution of shared species among nations, several conventions, agreements and structures have been established. Thus, there are FAO-supported regional fisheries management organisations (RFMOs). For WIO, there are the Southwest Indian Ocean Fisheries Commission (SWIOFC) and the Indian Ocean Tuna Commission (IOTC). Both these bodies assess annual trends and make recommendations to their member countries about levels of exploitation.

Several international agreements and protocols have been adopted by most countries in the region. Specifically, the *Southern Indian Ocean Fisheries Agreement* (SIOFA) for stocks outside of any EEZ, the 1995 United Nations *Agreement for the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks*, and the 1995 *Code of Conduct for Responsible Fisheries* are all designed to guide best fisheries management practices. In recognition of the important link between the environment and fisheries, the FAO promotes an ecosystem approach to fisheries management (EAFM) framework, which is designed to consider fisheries impacts on the environment as well as the social implications. For countries in the Southern African Development Community (SADC) region there is the SADC Protocol on Fisheries, an instrument that spells out a common approach of member countries to ensure a sustainable approach to fishing in their collective waters. A further notable instrument is the Nairobi Convention (UNEP/Nairobi Convention Secretariat 2009), which is a UNEP-hosted structure that promulgates protocols relating to land-based sources of pollution, and protection of coastal biodiversity and its resources. While the level of compliance of these important instruments by WIO countries is variable, they do play an increasing role in guiding management approaches that will ensure greater levels of sustainability and better equip authorities to deal with diverse management problems, including climate change.

CONCLUSIONS

There can be some consolation that WIO fisheries may be generally in a better state than the fisheries of other regions, despite the several negative trends that have emerged. However, there is no room for complacency as the need for implementation of wise approaches to fisheries management is more pressing than ever. Currently, several large regional programmes are contributing to transboundary collaboration, which bodes well for the future.

Note: There are many inconsistencies in the modestly available statistics, which also change over time. Much of the information presented here is based on the sources given below. It is suggested that these websites are visited periodically to obtain updated information:
http://www.fao.org: for global fisheries statistics.
http://www.unep.org/
http://www.wiofish.org: for updated information on different WIO fisheries.

THE OCEANOGRAPHY AND FISHERIES ALONG THE WEST COAST OF INDIA AND AT LAKSHADWEEP

Elayaperumal Vivekanandan

INTRODUCTION

Fisheries along the west coast of India are unique in the Indian Ocean with respect to the diversity of resources, catch volume, magnitude of fishing activities, economic returns and livelihood opportunities provided. Marine fisheries along the eastern Arabian Sea are among the largest in the Indian Ocean, providing vast food security and large contributions to export earnings and the gross domestic product of India. Long time-series of fisheries statistics on catches and fishing effort with high spatial and temporal resolution are available and provide insight into the development issues facing the sector.

The west coast of India extends 3 335 km and is characterised by a wide shelf in the north (about 250 km wide off Mumbai), which narrows to some 60 km wide off Kochi in the south (Figure 1). However, while nearly 80% of the continental shelf area lies along the northwestern coast, more than half of the fisheries catch comes from the southwestern coast.

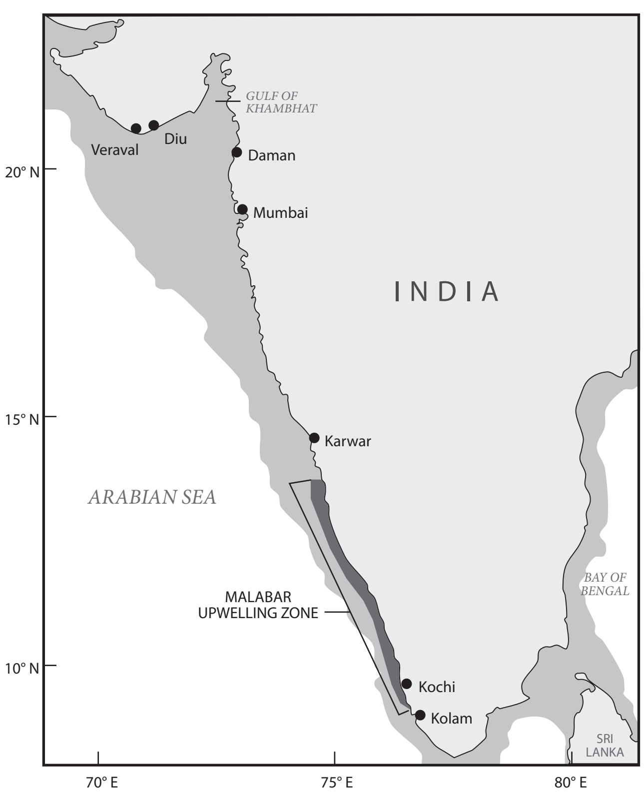


Figure 1 Map of India showing extent of the continental shelf.

Table 1 Fishing areas in the EEZ along the west coast of India.

STATE/UNION TERRITORY	COAST LENGTH (km)	CONTINENTAL SHELF AREA (000 km^2)
Kerala	590	40
Karnataka	300	25
Goa	104	10
Maharashtra	720	112
Gujarat	1 600	164
Daman & Diu	21	0.1
TOTAL	3 335	351.1

From an oceanographic and fisheries perspective, the west coast of India can be divided into two geographical areas, north and south of 15° N. The region is generally highly productive; the main features contributing to this productivity are an upwelling during the summer monsoon, and a cooling of the northern Arabian Sea during winter. These two processes bring large amounts of nutrients into the upper water layers, which enhance primary productivity and thus fundamentally contribute to the fisheries. Marine fish landings along this coast have increased in the last six decades and continue to rise (as also along the east coast of India and in the Bay of Bengal). However, the threats to sustainability with the increase in fisheries production masks several issues of concern. Fishing and other anthropogenic impacts on finite resources need to be regulated to sustain coastal resources.

METEOROLOGICAL AND OCEANOGRAPHIC FEATURES

The Arabian Sea is influenced by the southwest and northeast monsoons. Nearly 80% of the rainfall in the region occurs during the southwest monsoon, which lasts from June to September. The northeast monsoon lasts from October to January. Seasonality in the Arabian Sea can be clearly divided into four seasons, albeit with some variability from one year to the next. This is also reflected in seasonal variations in productivity that differ between regions. During the spring inter-monsoon period (March–May), a transition from winter to summer, the entire Arabian Sea generally has very low primary productivity (14–21 mmol C m^{-2} d^{-1}) and low levels of chlorophyll (~45 mmol C m^{-2}). A more or less similar scenario prevails during September–October, the transition from summer to the winter monsoon. During these periods the waters have an increased sea surface temperature (SST) of ~28 °C, shallow mixed-layer depths of ~20–30 m, and strong stratification. Many nutrients, especially nitrate, the main limiting factor in primary production, are then undetectable in the surface waters. With the onset of the summer monsoon in June, the situation changes considerably. The current, which flows northward along the coast during the northeast monsoon, reverses and flows southward, whereas the wind blows from the west and west-northwest. During the southwest monsoon, a strong southward drift, especially along the southwestern coast, is prominent in the upper water layers; and there is a northward countercurrent along the lower boundary of the thermocline, but it is comparatively weaker and discontinuous.

Southwestern coast

The prime oceanographic feature on the southwestern coast is an upwelling during the southwest monsoon. During July–August the surface mixed-layer becomes more or less obliterated, with the temperature decreasing to 26.5 °C and the oxygen-deficient layer reaching upwards, even to the surface. This indicates a coastal upwelling, which extends from Kanyakumari to Karwar (~8–14° N), though the intensity is much less south of Quilon (~9° N). It has also been noticed that this upwelling starts at the southern tip of the west coast in late May/early June and then extends northwards with the progress of the southwest monsoon season. These conditions prevail until late August/early September, when the upwelling subsides. No major upwelling occurs north of Goa, at ~16° N.

While the strong wind along the shore induces upwelling in the south, the cross-shore component of the wind in the north modifies the density structure of the water surface in the northern part to reduce the intensity of the upwelling (Muraleedharan & Kumar 2014). The upwelling increases the nutrient content, thereby increasing the productivity of the region, and at its peak the bloom is on par with some of the most fertile waters in the world's oceans. The productive value of upwelling is reflected in the total zooplankton biomass, which in turn is associated with high-volume fisheries along this coast during the southwest monsoon (Banse 1959, and others).

The southwest monsoon is also the period when mud-banks are formed at places along the southwestern coast of India, especially along the Kerala Coast. The mud-bank extent is inconsistent, varying from 5 to 10 km in length and normally 2 to 5 km outwards from the shore. The source of mud for these banks is the sea bottom and the huge, adjoining Vembanad Lake (the longest in India), which empties into the sea at ~10° N. The mud-banks are not formed every year, but when they do, they remain for 2–3 months during June to August. The mud, which contains a high phosphorus content, is largely composed of very fine particles, with a relatively high organic carbon content. Plant pigments and carbohydrates are present in low concentrations, consequently rendering the mud of low caloric and poor nutrient value. The advantage of mud-bank formation from a fisheries perspective is that organisms, especially the shrimp *Parapenaeopsis stylifera*, aggregate and become trapped in the calm, shallow muddy waters, resulting in plentiful catches of this high-value species.

Northwestern coast

Notwithstanding that convectional upwelling does not occur along this coast, the waters of the northwestern coast also have a fairly high abundance of phytoplankton and zooplankton during the southwest monsoon, probably as a result of land/river run-off. An additional feature of this segment of the coast is the winter cooling effects of the northern Arabian Sea (north of ~15° N). From November to February, the cold, dry continental air blowing over the northern Arabian Sea cools the sea surface to ~24 °C, and the denser surface waters sink, leading to deep mixed-layers below 100 m. The weak winds do not generate convective mixing in summer yet do inject nutrients into the surface layers, thus leading to the higher productivity.

In summary, the seasonally higher productivity in the eastern Arabian Sea is mainly through upwelling during summer, to ~15° N along the southern coast, and cooling north of ~15° N during winter. In both cases the photic zone obtains some nutrients from the deeper layers, which results in higher productivity.

FISHERIES PROFILE

The favourable meteorological and oceanographic conditions along the west coast of India have resulted in highly productive, high-volume fisheries, making India by far the largest fish producer in the WIO, contributing over 46% of total production. However, the number of fish-landing centres along the west coast has not been constant over recent decades, as new ones have been opened and others became defunct; even so, they remain at around 640. With an increasing population, the number of active fishermen involved in actual fishing on the west coast has increased threefold over five decades, from 118 000 in 1961/62 to 350 000 in 2011. Meanwhile, the catch per active fisherman has persisted at around 5 metric tons (mt) per year (Table 2).

Table 2 Fisheries profile of the west coast of India during different time periods (CMFRI 2006, 2012).

YEAR	LANDING CENTRES	ACTIVE FISHER POPULATION (000s)	FISH CATCH (mt/fisher)	NUMBER OF CRAFT		
				MECHANISED	MOTORISED	NON-MOTORISED
1961–62	NA	118	5.1	5 456	0	40 147
1973–77	639	171	5.1	6 030	0	41 570
1980	727	218	4.6	14 304	0	67 774
1998	NA	NA	NA	32 926	22 800	24 656
2005	582	326	4.7	37 626	30 200	28 644
2010	594	350	5.5	41 801	30 150	13 961

NA – not available.

Table 3 Number of mechanised boats in the fishery along the west coast of India (CMFRI 2006, 2012).

CRAFT TYPE	SOUTHWEST COAST		NORTHWEST COAST	
	2005	2010	2005	2010
Trawler	7 327	7 359	12 536	17 732
Gillnetter	1 729	672	5 083	7 486
Dolnetter	0	0	6 905	6 607
Liner	38	29	257	10
Ring-seiner	480	495	0	0
Purse-seiner	755	778	160	435
Others	635	169	1 721	29
TOTAL	10 964	9 502	26 662	32 299

Three types of craft are operated in the fishery. The larger boats with inboard engines (mechanised boats) are 13–20 m in length, with engines of 100–400 hp (Figure 2). The number of these boats in operation increased from 5 456 in 1961/62 to 41 801 in 2010; the increase, especially of trawlers, was ~40% along the northwestern coast between 2005 and 2010 (Table 3). Fishing efficiency also increased substantially; with the increase in the size and engine power of boats, extended fishing trips to distant fishing grounds (lasting five days or more) became possible. These boats employ a variety of gear, of which trawls are the most prominent. A second type of craft is smaller, with outboard engines of 10–40 hp (Figure 3). Outboard engines were introduced in the mid-1980s and became popular among small-scale fishermen, particularly as the government provided subsidies for the engines to empower these fishermen. In 2010, more than 30 000 boats operated along the northwestern coast (Table 3). Consequently, the number of a third type and non-motorised craft, which depend on the wind, decreased substantially.

Figure 2 Typical boat with inboard engine. © E Vivekanandan

Figure 3 Boat with outboard engine. © E Vivekanandan

Figure 4 Ring-seine operation, Karwar, Karnataka, India. © E Vivekanandan

A wide variety of target-specific and non-specific fishing gear is used along the entire coast, and these can be broadly classified as trawls, gillnets, lines, seines and bag nets. Improvements are regularly made to the gear to achieve better efficiency. High-opening trawlnets, monofilament gillnets of a wide range of mesh sizes, longlines, purse seines, ring seines and dolnets are intensively operated (Figure 4).

FISH LANDINGS

The Central Marine Fisheries Research Institute (CMFRI) in Kochi has collected data on fish landings and fishing effort from all landing centres in India since 1956, using stratified multistage random sampling. The CMFRI database shows that the annual average landings have increased from 584 235 mt

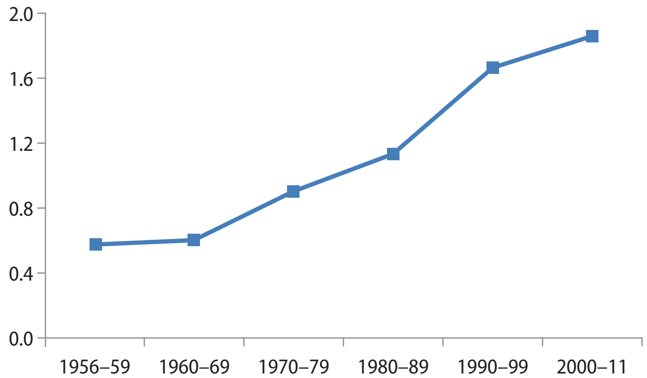


Figure 5 Annual average landings (million mt) along the west coast of India during 1956–2011. Source: CMFRI

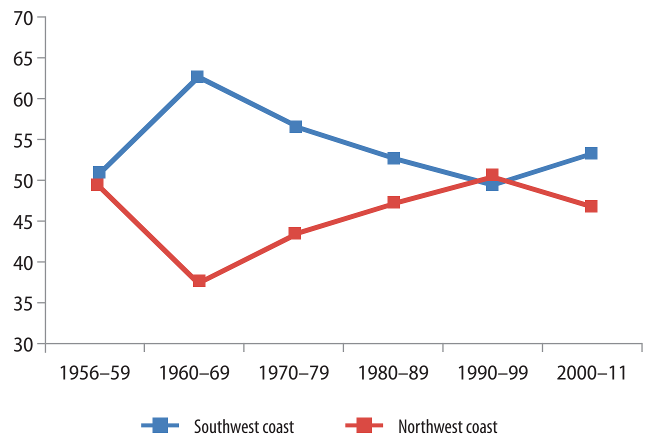


Figure 6 Contribution to west-coast landings (%). Source: CMFRI

Figure 7 Sharks landed at Azheekal beach, Cherthala, Kerala (India). © E Vivekanandan

during the period 1956–1959 to 1 862 375 mt during 2000–2011 (Figure 5), a threefold increase in 56 years. The contribution of the two major subregions has fluctuated over the years, but the overall contribution of each over the period was almost equal, with the southwestern coast contributing 53% of the total (Figure 6).

The two regions are rich in biodiversity. The CMFRI records show that at least 800 species, including elasmobranchs, teleosts, crustaceans, cephalopods, gastropods and bivalves, occur in the catches, with some 200 species contributing to a minor or major fishery in one subregion or the other. A single trawl haul, on average, lands ~40 species. In addition, several non-targeted groups, including jellyfish, echinoderms and other invertebrates, sea snakes, and protected animals such as turtles and dolphins, are also incidentally caught. CMFRI publishes the annual landing statistics by aggregating landings into 80 major species/groups. Analysis of data for the years 2004–2011 shows that the Indian oil sardine, *Sardinella longiceps*, tops the list and contributes 19% to the west-coast landings (Table 4). This is followed by another small pelagic species, the Indian mackerel, *Rastrelliger kanagurta*, at 7.4%. Penaeid and non-penaeid shrimps together contribute 13.3%.

Table 4 Annual average landings of top 10 species/groups on the west coast of India during 2004–2011.

SPECIES/GROUP	LANDINGS	
	mt	%
Oil sardine	354 548	19.0
Indian mackerel	137 213	7.4
Penaeid shrimps	125 454	6.7
Non-penaeid shrimps	122 618	6.6
Ribbonfish	116 179	6.2
Threadfin breams	107 470	5.8
Sciaenids	93 641	5.0
Bombay duck	71 596	3.8
Cuttlefish	51 317	2.8
Squids	49 546	2.7
TOTAL	1 229 582	66.0

Figure 8 Oil sardine haul, Tamil Nadu coast (India). © E Vivekanandan

Though the two subregions contribute equivalent quantities to fish landings, the composition of the landings differs substantially between them. Whereas small pelagic fishes, such as the oil sardine (34.5%), Indian mackerel (12%), whitebait (3.5%) and scads (3.1%), contributed 58.1% to the landings on the southwestern coast, small pelagics amounted to only 21% of northwestern-coast landings (Figure 9). The northwest subregion lands predominantly bottom-dwelling species, consisting of small demersal fishes (threadfin breams, small sciaenids, lizardfishes and soles) and larger fish species (catfish, pomfrets, large sciaenids, groupers and snappers), which together contributed 31.3% to the total landings. Crustaceans, such as non-penaeid shrimps (13.8%), penaeid shrimps (8%), crabs, lobsters and stomatopods, together contributed 24.7% to northwestern-coast landings.

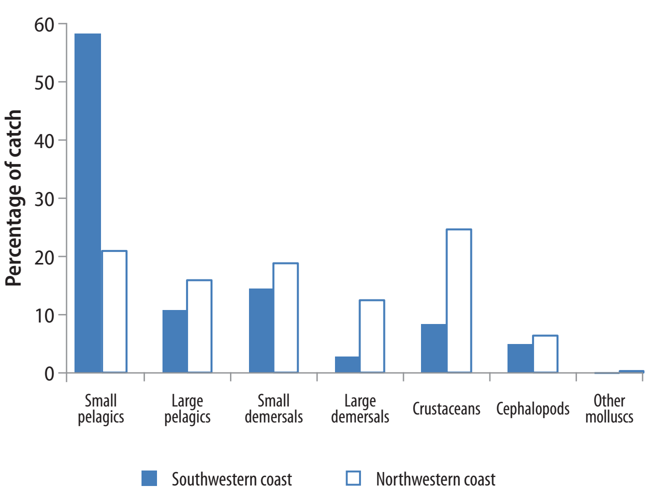


Figure 9 Contribution (%) of fish groups to southwestern- and northwestern-coast catches. Source: CMFRI

The list of the five most-caught species differs between the southwestern and northwestern coasts (Table 5). The contribution of the top five species for the southwestern coast accounted for 62% of the total catch, whereas that of the northwestern coast totalled only 46%, revealing the dominance of only a few species/groups along the southwestern coast compared with along the northwestern coast. It is evident that each species/group has a strong habitat preference, determined mainly by the oceanographic features of each region (Vivekanandan & Krishnakumar 2010). The ecosystem of the southwestern coast is influenced by seasonal upwelling and high productivity, and thus is the domain of small pelagics with generally short lifespans and rapid generational turnover. By contrast, the northwestern-coast ecosystem is driven by the sinking of higher-density, nutrient-rich masses of water during the winter months, which promotes an abundance of demersal species.

The major small pelagic contributors to northwestern landings are Bombay duck (*Harpadon nehereus*, 8.2%), gold-spotted grenadier anchovy (*Coilia dussumieri*, 2.4%) and Indian mackerel (*Rastrelliger kanagurta*, 2.1%). *Harpadon nehereus* forms the largest single-species fishery along the northwestern coast, and is dominant in the Bombay duck–*Coilia*–non-penaeid shrimp (mainly *Acetes indicus*) complex. This complex constitutes a unique predator–prey relationship.

Bombay duck inhabits waters to the 70 m isobath, and is inconspicuous or totally absent along the southwestern coast. However, the species forms a minor fishery at the same latitudes in the Bay of Bengal. Devaraj (1987) considered the high-tidal range, characteristic of the northwestern coast between 18° N and 23° N (as at the corresponding latitudes along the northeastern coast in the Bay of Bengal) as the major factor influencing the distribution of Bombay duck. The northwestern coast, especially the Gulf of Khambhat (22° N, 72° E) experiences a tidal range of ~10 m; the tidal range along the northeastern coast is also high, at ~6 m.

Table 5 Top five species (%) in respective region's catch during 2004–2011.

RANK	SW COAST		NW COAST	
	SPECIES/GROUP	Catch %	SPECIES/GROUP	Catch %
1	Oil sardine	34.5	Non-penaeid shrimps	13.8
2	Indian mackerel	12.0	Sciaenids	9.4
3	Threadfin breams	6.5	Ribbonfish	9.2
4	Penaeid shrimps	5.3	Bombay duck	8.2
5	Whitebaits	3.7	Penaeid shrimps	5.4
TOTAL		62.0		46.0

Neither strictly pelagic nor demersal, Bombay duck effectively uses the high tidal range to conserve energy while foraging on non-penaeid shrimps and *Coilia*, which are abundant in the habitat. The species is harvested with a specialised dolnet, which is a fixed bag net that operates to a depth of 40 m, depending upon the turn of the tides since a strong tidal current is essential for operation of the net. The mouth of the net is always held in the direction of the tide so that the net functions as a filter to retain the fish, while the strong tidal current prevents the fish from escaping from the net.

To gain an understanding of trends in landings, catches of major species/groups were compared between 2004–2007 and 2008–2011. For this analysis, groups that showed <25% difference in landings for the two periods were considered as 'no change'. Of 57 species/groups that were investigated, 36 did not show any change (Table 6), 17 showed an increase in landings, and 4 (namely, hilsa shad *Tenualosa ilisha*, gold-spotted grenadier anchovy *Coilia dussumieri*, adalah *Psettodes erumei*, and several species of gastropods) showed a decrease in landings over the total period.

Table 6 Status of fish groups in the landings along the west coast of India; the values are percent difference in the landings during 2008–2011 from that of 2004–2007; difference between –25% and +25% is considered as 'no change'.

SPECIES/GROUP	NO CHANGE	INCREASE	DECREASE
Sharks	–3		
Skates	–10		
Rays	–12		
Eels	–22		
Wolf herring	13		
Oil sardine	4		
Other sardines	10		
Other shads	–16		
Thryssa	0		
Bombay duck	–11		
Halfbeaks	12		
Groupers	11		
Emperors	20		
Threadfins	–21		
Sciaenids	23		
Ribbonfish	–9		
Horse mackerel	9		
Scads	–2		
Leather-jackets	9		
Other carangids	24		
Silverbellies	–18		
Black pomfret	3		
Silver pomfret	14		
Chinese pomfret	4		
Seerfish	–10		
Kawakawa	–10		
Mullets	–24		
Unicorn cod	–16		
Soles	6		
Penaeid prawns	0		
Non-penaeid prawns	24		
Lobsters	–2		
Stomatopods	5		
Bivalves	14		
Cuttlefish	20		
Octopus	20		
Catfish		69	
Whitebaits		115	
Other clupeids		57	
Lizardfish		65	
Flyingfish		77	
Snappers		76	
Threadfin breams		28	
Other perches		28	
Goatfish		56	
Whitefish		109	
Indian mackerel		56	
Skipjack tuna		286	
Longtail tuna		37	
Billfish		180	
Barracudas		26	
Crabs		34	
Squids		65	
Hilsa shad			–77
Coilia			–25
Indian halibut			–27
Gastropods			–50

LAKSHADWEEP

Lakshadweep is a group of scattered islands in the Laccadive Sea, between 08°00' N and 12°30' N and 71°00' E and 74°00' E, about 200–400 km off the southwestern coast of India. The archipelago consists of 11 inhabited and several uninhabited islands, islets and submerged reefs. The surface area of the islands is just 32 km^2, but being oceanic their continental-shelf area is about 4 336 km^2, and the lagoons have an area of 4 200 km^2, offering rich biotic diversity and potential. Furthermore, the area of the territorial waters (or exclusive economic zone, EEZ) around the islands covers an area of some 400 000 km^2, offering immense fisheries potential.

CMFRI reported 601 fish species in Lakshadweep waters in 2011. Of this total, more than 300 species belonging to 35 families are recognised as ornamental fishes. The major fisheries resources of the islands also include oceanic species such as tunas, billfish, pelagic sharks, marlins, sailfish, and other various groups such as barracuda, seerfish, snappers, breams, carangids, rays and octopus. Twenty-one species are utilised as bait (e.g., species of *Spratelloides*, *Apogon* and *Chromis*), and ornamental fishes are exclusive to the islands.

The live bait fishery is important for the capture of tunas in a traditional pole-and-line fishery in the islands. This major fishery accounts for more than 97% of the tuna landings, of which skipjack tuna (*Katsuwonus pelamis*) makes up 86%, yellowfin tuna (*Thunnus albacares*) 12%, frigate tuna (*Auxis thazard thazard*) 1%, and kawakawa (*Euthynnus affinis*) 1%. For the past 15 years, about 300 pole-and-line boats have operated in the islands, in addition to an estimated 1 401 non-motorised, 1 249 motorised and 10 mechanised boats. The pole-and-line boats are 7.5–10.5 m in overall length and make one-day fishing trips.

Figure 10 Pole-and-line fishing (Lakshadweep Archipelago).
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The annual potential yield of tunas is estimated at 50 000 mt, and potential yield of all other fish collectively at an additional 50 000 mt, as compared with the current yield of 15 000 mt, which amounts to only 15% of the potential yield. The current yield of tuna (about 10 000 mt) is small compared with that from the Maldives, at 148 000 mt, and from Sri Lanka, at 27 000 mt (CMFRI 2011).

CLIMATE CHANGE

Global warming and the consequent changes in climatic patterns will have strong impacts on fisheries with far-reaching consequences to the food and livelihood security of a sizeable portion of the global population. Any changes in sea temperatures, acidity, salinity and dissolved oxygen concentration would significantly influence the metabolism, growth rate, productivity and reproduction of aquatic organisms, as well as their susceptibility to diseases and toxins. Some species and ecosystems may gain, but others will lose. This in turn will impact ecosystem structures and functions.

Data on sea surface temperature (SST) collected from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) for the years 1961–2009 for the southwestern coast show that the number of decadal SST anomalous months increased from only 19 during 1960–1969 to 53 during 2000–2009. Anomalies in the multivariate ENSO index for variables observed over the tropical Pacific also increased over these periods. The SRES A2 scenario prediction generated by the Intergovernmental Panel on Climate Change (IPCC) shows that the annual average SST along the southwestern coast may increase from 28.5 °C in 2000 to 31.5 °C by 2099.

The annual mean SST trend shows that the northwestern coast has also warmed, from 26.04 °C in 1985 to 26.1 °C in 2005, at the rate of 0.03 °C per decade. The SRES A2 scenario also indicates that the annual average SST along the northwestern coast may increase from 26.05 °C in 2000 to 29.5 °C in 2099. By the turn of this century, the annual average SST on the northwestern coast (between 15° and 24° N) will be higher than the current SST in the southern latitudes of 8°–14° N.

An interesting climate-driven change in the distributional boundary of the Indian oil sardine (*Sardinella longiceps*) has been observed in the last 20 years (Vivekanandan 2011). This sardine is a small pelagic fish of tropical coastlines and forms the basis of a massive fishery — perhaps the largest exploited stock in the Indian Ocean. It is a cheap source of protein and forms a staple, sustaining and nutritious food for millions of coastal inhabitants. The species has a rapid population-doubling period of 15–24 months; it is known to have a restricted distribution between latitudes 8° and 14° N and longitudes 75° and 77° E (the Malabar upwelling zone), where

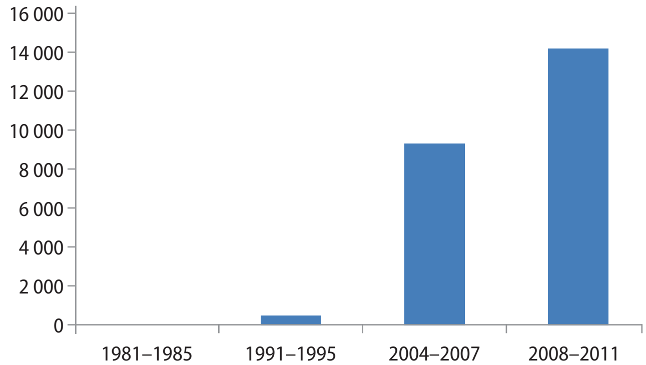

Figure 11 Oil sardine landings (mt) along the northwestern coast, 1981–2011. Source: CMFRI

the annual average SST is 27–29 °C; and, its distribution and abundance are governed by the vagaries of oceanic climate conditions. Until 1985, almost the entire catch of oil sardine was taken from the Malabar upwelling zone; north of 14° N the catch was either very low or there was no known catch at all (Figure 11). In the last two decades, however, the catches from latitudes 14°–23° N consistently increased, reaching an annual average of 14 152 mt during 2008–2011. The surface waters of the Indian seas have warmed by 0.03 °C per decade, and a warmer wedge (27–28.5 °C) of surface waters has expanded north of 14° N, enabling the oil sardine to extend its range further north.

It was also found that the catches of oil sardine from within its original home range (the Malabar upwelling zone) have not decreased, indicating a distributional extension and not a distributional shift. The annual average catch has increased over time and reached 354 548 mt during 2004–2011 in the upwelling zone off the southwestern coast. Time-series data on different climatic and oceanographic parameters gathered from different sources show that, corresponding to the annual SST, the annual average scalar wind speed increased from 3.58 m/s to 6.05 m/s during 1967–2007 along the southwestern coast (Manjusha *et al.* 2010). The zonal wind speed during the southwest monsoon season (June–September) increased from 3.34 m/s in 1967 to 5.52 m/s in 2007, with the speed exceeding 5 m/s in several years during 1992–2007. The monsoonal coastal upwelling index (CUI) nearly doubled, from 485 m^3/s to 713 m^3/s, during 1997–2007. This substantial increase in CUI elevated the chlorophyll *a* concentration, from 4.54 mg/m^3 in 1997 to 13.85 mg/m^3 in 2007, during the monsoon season. The increasing CUI and chlorophyll *a* concentration sustained an increasing catch of oil sardine, especially during the post-monsoon season (Vivekanandan 2011). The peak spawning activity of oil sardine is during the southwest monsoon. If wind speed and direction are ideal, the larvae are dispersed to favourable destinations where they find enough food and fewer predators. Egg development and growth of transforming larvae are rapid, and the fish normally reach about 10 cm in length in 3 months. Individuals, which spawn during the southwest monsoon, are thus recruited to the fishery during the post-monsoon period.

This trend in oil sardine catches indicates that, in this instance, the current change in climate can be beneficial to production of small, pelagic, herbivorous fish (Vivekanandan 2011). However, the relationship between climatic and oceanographic variables, and fish distribution, abundance and biological characteristics has to be monitored continuously. If the SST increases in the southern latitudes beyond the physiological optimum of a fish species, and if other oceanographic variables likewise change unfavourably, it is possible that populations may not be able to adapt but instead will shift towards northern latitudes.

As the southern latitudes are warmer, the northwestern-coast fisheries may benefit from positive impacts for several years. Movement of fish from southern latitudes, as in the case of the oil sardine in the last two decades, would be an additional resource on the northwestern coast. Preliminary analysis using the Ecopath mass-balance trophodynamic model shows that incursion of oil sardine to the northwestern coastline would not immediately affect the abundance of other fish stocks in the area (CMFRI 2009). The ecosystem model also shows that the abundance of several other stocks would likewise increase. However, stress may be placed on the dominant species — Bombay duck *Harpadon nehereus* and goldspotted grenadier anchovy *Coilia dussumieri*. The distribution of these two species is restricted to northern latitudes of the Indian coast. As the northernmost boundary of the Indian coastal region is landlocked, these species cannot move further north. Because the region experiences a large tidal variation, up to 10 m in the Gulf of Khambhat (22° N), it is not clear how a rise in sea level will impact on tide levels, which may in turn affect the tide-dependent dolnet fisheries for Bombay duck. Moreover, the whale shark *Rhincodon typus*, which is a protected species, migrates from southern latitudes and aggregates off Saurashtra (in Gujarat) during December to March each year. Studies conducted elsewhere indicate that the migratory patterns of such large marine animals will be altered as a result of warming and acidification of the oceans.

In the long term, changes in ecosystem structures and functions and predator–prey relationships are likely. There is a need to assess the potential positive or negative impacts of additional species coming into the region on fisheries. Development of predictive models for fish abundance for different greenhouse-gas-emission scenarios is essential, because new fisheries will emerge depending on the adaptive capacity of species to different levels of these emission. Hence, it is important to consider additional post-harvest infrastructure requirements for species new to a locality, changes in craft–gear combinations, and increases in the entrepreneurship of fishermen. It is also imperative to monitor invasions of new fish parasites and diseases from southern latitudes to understand changes in host–parasite specificity.

FISHERIES MANAGEMENT

The increase in marine fish production along the west coast of India (and along the east coast as well) is contrary to the trend in several other regions of the world, where catches are either decreasing or are stagnant. However, the increase in catches along the Indian coasts masks the following dynamics:

1. The increase in catches is a result of increasing fishing efficiency and extension of fishing grounds. When all fishing grounds have become fully exploited, the stocks will decline and elevated catches cannot be sustained.
2. The current catches (annual average 1.86 million mt for 2008–2011) along the west coast are approaching the estimated potential yield of approximately 2.4 million mt (Ministry of Agriculture 2001), and hence any further increase in fishing effort and fish catches should be viewed with caution.
3. Evidence is accumulating that stocks of catfish, whitefish and sharks are declining, but such changes are not reflected in recorded catches.
4. Decline in the composition and quality of fish stocks has been observed, as is evident from the exploitation of juvenile fishes and a reduction in the average size of the fish caught.

In India, fisheries within 12 nautical miles off the coast are managed by the state governments, and offshore and oceanic fisheries beyond 12 nautical miles are managed by central government. In the past 50 years, marine fisheries operations in the region have developed from a subsistence activity, practised almost exclusively by traditional fishermen, to the status of a capital-intensive industry. In the early years, the emphasis of fisheries management was on increasing production by training fishermen in advanced fishing methods, and encouraging introduction of efficient fishing craft and gear by providing loans and subsidies. Support from research and development institutions, coupled with investments by private entrepreneurs in an export trade, supplemented government efforts to expand the growth of the fishery sector.

In recent years, the government has attempted to regulate the proliferation of fishing activities through various measures, such as limits on the number of boats, seasonal bans on fishing, mesh-size regulations, bans on destructive gear, declarations of Marine Protected Areas and protection of endangered or vulnerable species. As a result, India's marine fisheries are moving from an open-access system towards one of regulated access. However, implementation of such measures is challenging since the large population of coastal fishers is actually dependent on fishing, thus any proposal for regulatory measures tends to be resisted by the fishermen.

In addition to the overexploitation of resources, other key issues affecting fish stocks are habitat degradation, pollution and climate change. Critical habitats such as mangroves, coral reefs, and seagrass beds occur in the region, and these are affected by coast development and urbanisation. Some trade in products from these habitats also exists. The discharge of sewage, an increasing load of litter, and organic and inorganic pollutants further degrade coastal ecosystems. Fisheries sustainability must be addressed in an integrated way by considering the issues of all anthropogenic interferences — especially increasing fishing intensity, damage to the physical-chemical and biological integrity of the ecosystems, and climate change. As India's fisheries are impacted by the developmental needs of several other prime sectors, such as agriculture, industries and power generation, it is not possible to find solutions to the issues of the fisheries sector alone. For instance, problems such as water contamination, the enforcement of standards for water discharge, maintaining the quality of river runoff, and reducing greenhouse gas emissions, need to be addressed by non-fisheries sectors. Considering the development needs of other important sectors, the challenges for the fisheries sector have increased as never before, and these demand adopting an ecosystem approach to fisheries management with the involvement of all stakeholders.

GLOSSARY

decadal sea surface temperature (SST) anomalous months – monthly sea surface temperatures are compared to average sea-surface temperatures for 1971–2000, and plotted on a map. Where they are higher or lower than the average they are referred to as anomalous months.

isobath – a line on a map that joins all points of the same water depth in the sea.

thermocline – the layer where the temperature of the sea (and of lakes, where it is called the metalimnion) changes suddenly, with a layer of warm water lying over a deeper layer of colder water.

THE COLLECTORS: ICHTHYOLOGICAL EXPLORATION OF THE WESTERN INDIAN OCEAN

Wouter Holleman and Barry C Russell, with Theodore W Pietsch

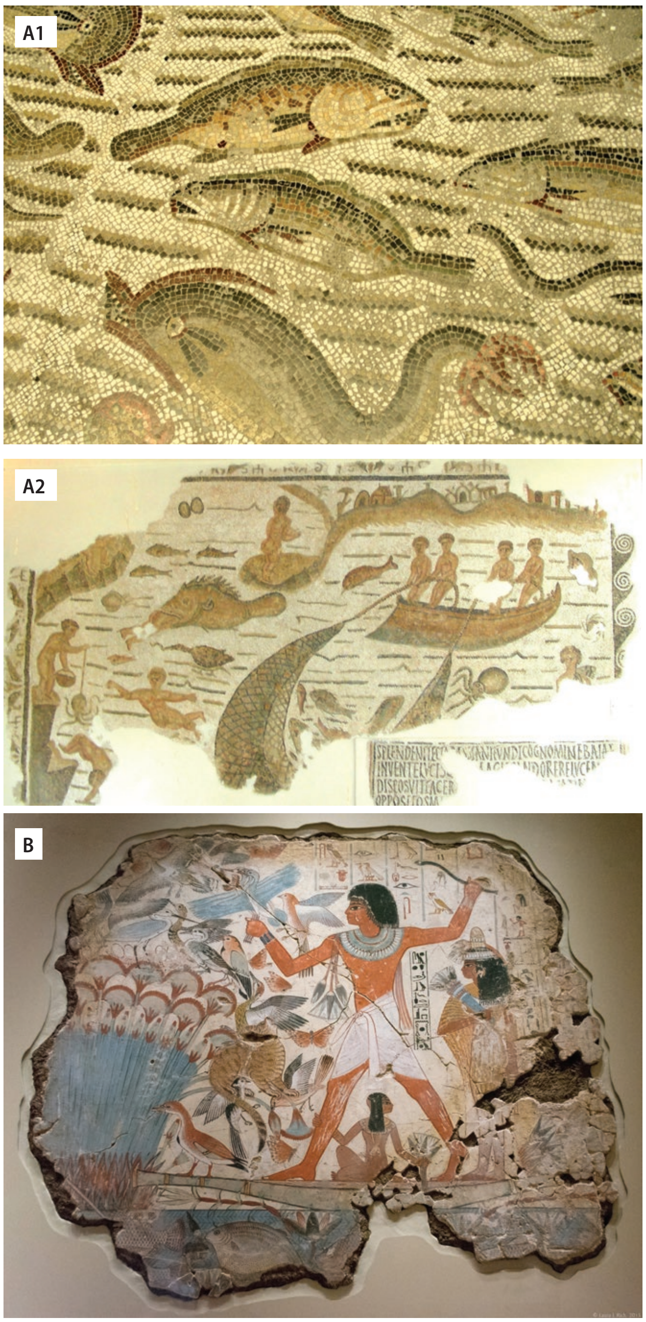

Figure 1 **A** Mosaics of fishes, Bardo Museum, Tunis. © W Holleman, NRF-SAIAB
B Mural from Nebamun's tomb-chapel, c. 1350 BCE. © L Rich

The Mediterranean Sea and the rivers that flow into it were the source of fishes for the Egyptians, Phoenicians, Greeks, Romans and others who sailed, explored and fished it for food. Some of the fishes they caught are immortalised in mosaics, such as those in the Bardo Museum in Tunis and pictured on the walls of the tomb of Nebamun (c. 1350 BCE), near Thebes in Egypt. They gave names to the fishes they caught, some of which are still in common use today, such as *kōbios* and *thynnos* (the Greek words for goby and tuna). Later, Roman and Arab traders – and probably Egyptians before them – ventured down the Red Sea and the Persian/Arabian Gulf, and into the Indian Ocean to trade with India. Centuries later, Portuguese and Dutch explorers carved out sea routes around the Cape of Good Hope to the spice islands of the East Indies. All seas were naturally a source of food for people who lived along their shores, as shown by the many middens archaeologists have discovered along the coast.

The origins of our current knowledge of fishes were first recorded by ***Georges Cuvier*** in his *Historical Portrait of the Progress of Ichthyology, from Its Origins to Our Own Time*, first published in 1828. While the earliest collections and descriptions of Western Indian Ocean (WIO) fishes were made in the 1600s, it was only in the 19th century that scientific interest was focused on fishes, as epitomised in Cuvier and Valenciennes's *Histoire naturelle des poissons* published between 1828 and 1849. Later in this chapter we reveal more about these two remarkable scientists and their contributions to ichthyology.

The early WIO ichthyologists and collectors can be broadly grouped into three kinds: those who collected, named and described the fishes they found; those who collected fishes for others; and those who received, described and named specimens sent to them. In this chapter we trace these pioneers from the 17th century to the early 21st century. From these early foundations, their work has gradually and continuously built up the foundations on which current WIO ichthyological research is based. It is out of these threads that the story is woven, and, as you read and use this book you will come across some of their names, and so recognise their contribution to our knowledge of these fishes.

BEGINNINGS

The first person that we know of who collected and illustrated fishes from the WIO was ***Isaac Johannes Lamotius***. He was born in Beverwijk, in Holland, in about 1646, joined the Dutch East India Company (VOC), and arrived in Mauritius as Governor in 1677. In 1682, Joan Huydecoper II, an administrator of the VOC and an amateur botanist, urged colonial administrators to undertake botanical research and make drawings of local plants. Lamotius, who was interested in natural history, became an expert on the fauna and flora of Mauritius, and over the next 15 years he collected plants and animals, describing and making drawings of them until his departure in 1692. They include about 250 drawings of fishes, now housed in Paris.

Philibert Commerson was the first of the explorer-collectors to visit islands in the Indian Ocean. He was born in Châtillon-les-Dombes, Ain, in France, in 1727, studied medicine, and was passionate about natural history. In 1766 he joined one of Louis Antoine de Bougainville's expeditions, visiting Brazil, the Falkland Islands, Tierra del Fuego and Tahiti. Along the way he collected plants, fishes and mammals. After visiting New Guinea and Java, Bougainville sailed to Mauritius, where Commerson stayed on. While on Mauritius, Commerson made a collecting trip to Madagascar. In all, he collected and made extensive notes on more than 160 species of fishes, and made fine drawings of many of them. Commerson did not live to publish any of his work. He died on Mauritius in 1773 and soon after his death, his papers and collections were sent to the Ministry of the Navy in France, which handed them over to Georges Buffon. Buffon used fragments of this material on birds, but ignored the rest. Later the material was deposited in the Jardin des Plantes (which became the Muséum national d'Histoire naturelle) in Paris. The fishes Commerson collected were unaccounted for until discovered by André Duméril, still in their original cases, in Buffon's attic some 20 years later. Pietsch writes:

> Commerson's talent as an ichthyologist might have been lost if it were not for the fact that his manuscripts and drawings were later incorporated by ***Bernard Germain Etienne de Lacépède*** (1756–1825) in the latter's *Histoire Naturelle des Poissons*, originally published in five volumes between 1798 and 1803. Despite the fact that many authors have cited Lacépède as the original describer of these species (and have erroneously attributed the names to him), he provided no Latin binomials, referring to the species only in the French vernacular (Anon. 1910, 1925). Commerson had named all his fishes by lengthy Latin polynomials, but most of his species were described in great detail, and many were represented by illustrations that leave no doubt about their identity. (Pietsch & Grobecker 1987: 9)

The first of the men who never travelled or collected their own specimens, but worked solely on fishes lodged in collections and those sent to them, is ***Marcus Elieser Bloch***, who is considered one of the most important ichthyologists of the 18th century. He was born at Ansbach, in what is now Germany, in 1723. His parents were very poor and he grew up barely literate – at the age of 19 he could not even read German. He did, however, know some Hebrew which enabled him to obtain a teacher's position in the house of a Jewish surgeon in Hamburg. There he became fluent in German and mastered some Latin. He also studied anatomy, which led to an interest in science. Bloch then went to Berlin, where he studied all branches of natural science and medicine. After taking the degree of MD. at Frankfurt-an-der-Oder in 1747, he settled in Berlin, where he became established as a physician.

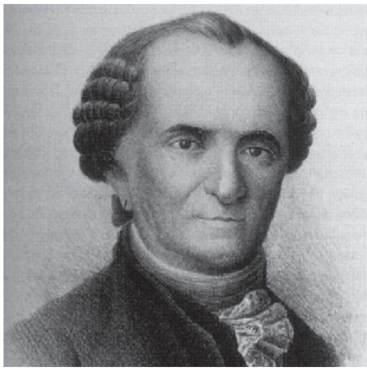

Figure 2 Philibert Commerson.
Source: Wikimedia Commons

Figure 3 Bernard de Lacépède.
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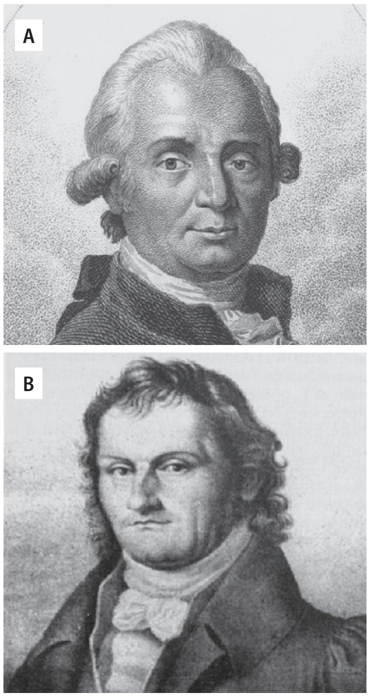
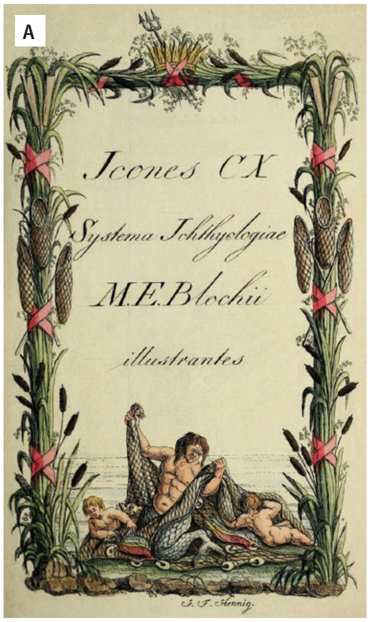


Figure 4 **A** Marcus Bloch; **B** Johann Schneider.
Source: Wikimedia Commons



Between 1782 and 1795 Bloch produced twelve volumes on the general natural history of fishes. The last eight volumes dealt with fishes from other parts of the world and were titled *Naturgeschichte der ausländischen Fische*. Many of the fishes described in this work were supplied by Missionary John, a Danish missionary working at Tranquebar (today Tharangambadi), on the coast of Tamil Nadu in southern India; other fishes he bought from merchants or vendors. In 1801 Bloch's work was corrected and expanded by ***Johann Gottlob Schneider*** and published as *Systema ichthyologiae iconibus CX illustratum*, by Bloch & Schneider. Bloch described 290 fish species, as well as a further 425 species with Schneider. Bloch's collection of about 1 500 specimens is today preserved at the Museum of Natural History of the Humboldt University in Berlin.

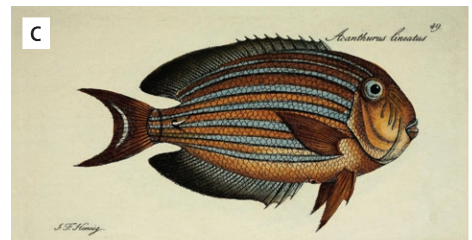


Figure 5 **A** Title page of *Systema Ichthyologiae iconibus CX illustratum* by Bloch & Schneider 1801; **B** *Scomberomorus guttatus*; **C** *Acanthurus lineatus*.
Source: Wikimedia Commons

Figure 6 Jean (Georges) Cuvier.
Source: Wikimedia Commons

Figure 7 Achille Valenciennes.
© NRF-SAIAB (by R Palmer)

THE 19TH CENTURY, THE AGE OF DISCOVERY

The most remarkable partnership in ichthyology was that of ***Georges Cuvier*** and ***Achille Valenciennes***. Their work laid the foundations of the modern study of fishes and is encompassed in the 22 volumes of *Histoire naturelle des poissons*, published between 1828 and 1849. The volumes provided descriptions of 4 055 species of fishes, 2 311 of which were new to science. This monumental work could not have been carried out without the participation of many donors and collectors, several of whom we acknowledge in the following pages.

Jean Léopold Nicolas Frédéric (known as Georges) Cuvier was born in 1769 at Montbélliard, France. It soon became evident that young Georges was exceptionally intelligent, and was interested in the natural sciences. His family did not have the means to educate him adequately, but his talent was spotted by the sister-in-law of the Duke of Württemburg (who lived in the castle at Montbélliard). She gave him a stipend so that he could complete his schooling. Georges learned to speak German and the then universal language of academia, Latin. In 1788 he became a tutor in Normandy, where he met the famous botanist Abbé Alexander Henri Tessier, who, impressed by the young man's knowledge of natural history, recommended Georges to his colleagues at the newly established Muséum national d'Histoire naturelle in Paris.

Cuvier arrived in Paris in 1795, and in December of that year taught his first class in anatomy at the museum. In 1798 he published a summary of the classes he gave at the École central du Panthéon, and in the preface he wrote: "Linnaeus, M Bloch and Citizen Lacepède have been my principal guides for reptiles and fishes, …" (Bauchot *et al.*, in Pietsch & Anderson 1997, 29). With his rapidly growing and extensive knowledge he conceived of *Le Règne Animal distribue d'apres son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée* (The animal kingdom arranged according to its organisation, to be used as a basis for the natural history of animals and as an introduction to comparative anatomy). The first edition appeared at the end of 1816.

While gathering information for *Le Règne Animal*, Cuvier met a young zoologist, Achille Valenciennes, 25 years his junior. Valenciennes was born in Paris in 1794. His father was one of the first naturalist aides at the museum, but died leaving his widow and five children. Achille, the eldest at 18, was left to support the family. He became employed by the museum at the behest of the renowned zoologist Lacepède, a friend of an uncle, and was taken into the service of Lamarck, an early proponent of evolution, to work on invertebrate collections. It was in Lamarck's laboratory that he met Cuvier, and began to work with him on vertebrates.

Lamarck gradually became blind, and died in 1825. Valenciennes continued to work in the laboratory of his successor, André Marie Constant Duméril, until 1832, when Cuvier persuaded Lacepède to allow him to work in Cuvier's laboratory. It appears he had already been unofficially assisting Cuvier for about 17 years at that stage – in the 1827 prospectus announcing the publication *Histoire naturelle des poissons*, Cuvier wrote "Monsieur Valenciennes has not ceased to help me during the past twelve years in all my preparatory work" (Bauchot *et al.*, in Pietsch & Anderson 1997, 31).

The first volume of *Histoire naturelle des poissons* was published in 1828, and on the title page was printed "by Monsieur le Baron Cuvier… and by Monsieur Valenciennes," in same-sized font, an apparent acknowledgement that Cuvier's collaborator had become his equal in ichthyology. Together the two published five volumes of the *Histoire naturelle*, and when Cuvier died in 1832, Valenciennes continued the work, eventually publishing the 22 volumes on which the modern science of ichthyology has been built.

The first person to make extensive scientific collections in the Red Sea was ***Peter (Pehr) Simon Forsskål***, who was born in Helsinki, Finland, in 1732. By the time he was 18 he had acquired a degree in theology from the University of Uppsala in Sweden, where he was one of Linnaeus's students (1756–1759) and qualified as a botanist. He was a bright young man and, amongst other subjects, studied oriental languages. With Linnaeus's approval Forsskål joined an expedition to Arabia in 1760. After a year in Egypt, where he studied Arabic dialects, the expedition travelled to South Yemen in 1762, where they were supposed to stay for 2–3 years. It seems all the expedition members picked up various diseases and, within a year, all the participants except ***Carsten Niebuhr***, had died, Forsskål in 1763. Of the extensive collections of plants and animals, his fish collections coming mainly from Saudi Arabia and Yemen, little survived: most of the information we have is found in Niebuhr's copies and translations.

After Niebuhr's return to Denmark in 1767 he immediately started to publish the work of his colleagues, especially that of Forsskål – the fish specimens were described and published in 1775. Niebuhr's work was inconsistent and full of errors, but many of the fish species described are still considered valid today.

Exploration really gathered momentum in the middle of the 19th century. Two naturalists who collected but did not describe many fishes, were ***Wilhelm Friedrich Hemprich*** and ***Christian Gottfried Ehrenberg***.

Wilhelm Hemprich was born in Glatz, Prussian Silesia, in 1795. His father was a doctor and he also studied medicine (at Breslau and Berlin). His first interest, however, was zoology, and he was appointed as a lecturer in natural science and physiology at the university in Berlin. He also became a collaborator at the Zoological Museum. Hemprich met Ehrenberg at university in Berlin and they became friends. Ehrenberg was born in Delitzsch in Germany in 1796 and first studied theology, followed by studies in medicine and the natural sciences in Berlin, where he met and became a friend of the explorer Alexander von Humboldt.

Sharing an interest in natural history, Hemprich and Ehrenberg were invited to participate in an expedition to Egypt in 1820. In 1821 they separated from the main expedition and spent the next two years collecting thousands of plant and animal specimens from Egypt, the Nile Valley, Libyan Desert and northern Red Sea. With renewed funding, the two set out in 1823 to investigate marine life in the Gulf of Suez, and along the Arabian coast, as far as Mohila. They collected many fishes, made drawings of unknown species and notes on anatomy. They also collected molluscs, crustaceans and various coelenterates.

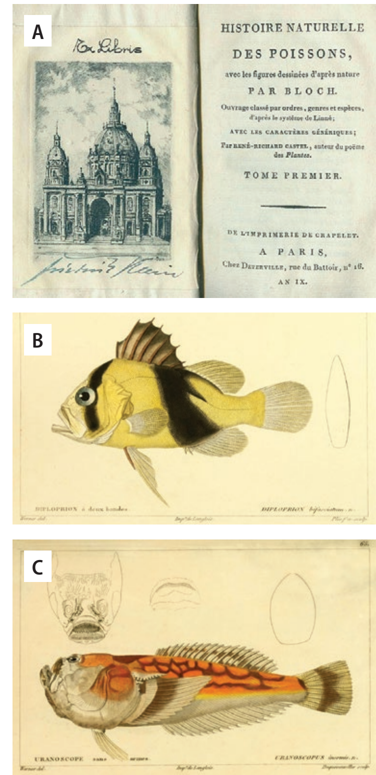


Figure 8 **A** Cover of Volume 1 of *Histoire naturelle des poissons* by Cuvier & Valenciennes 1828; **B** *Diploprion bifasciatum*; **C** *Uranoscopus lebeck*.
Source: www.biodiversitylibrary.org

Figure 9 Peter Forsskål. M Wallerstedt

Figure 10 Christian Ehrenberg.

Figure 11 **A** Eduard Rüppell, as a young man of about 30 years old; **B** in 1869, at the age of 75.

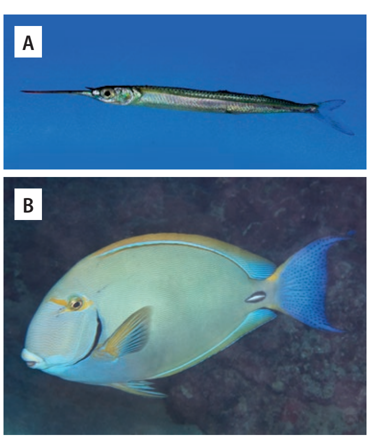


Figure 12 Fishes named after Jean-Jacques Dussumier: **A** *Hyporhampus dussumieri*. PC Heemstra © NRF-SAIAB **B** *Acanthurus dussumieri*. © SV Bogorodsky

In 1824 the two men started their last expedition, to the southern Red Sea, travelling to the islands, mapping them, and collecting specimens along the way. After reaching the African coast, Hemprich undertook a trip to the Gedem Mountains whilst Ehrenberg remained in the camp due to illness. Hemprich's journey was catastrophic as he and most of his assistants died of fever in Massawa in 1825. Ehrenberg recovered from his illness and eventually returned to Germany at the end of that year.

When Valenciennes visited Berlin in 1827, Ehrenberg showed him his notes and drawings of fishes. In 1829 Ehrenberg travelled with Humboldt to the Ural and Altai mountains, and on his return donated specimens from the Red Sea, Nile River and Caspian Sea to the Paris museum.

Wilhelm Peter Eduard Simon Rüppell, the son of a prosperous banker, was born at Frankfurt-am-Main in 1794, and was destined to become a merchant. However, a visit to the Sinai Peninsula in 1817 awakened an interest in natural history. After attending lectures in botany and zoology at the universities of Pavia and Genoa, he taught himself systematics. He set off on his first expedition in 1821, travelled through the Sinai and reached the Gulf of Aqaba in 1822. In 1826 Rüppell began his work on Red Sea fauna, collecting large numbers of crustacea from the Gulf of Suez. This was followed by travels to the Dahlak Islands and Massawa coast, making diverse collections of fishes, crustaceans and other invertebrates that he sent back to the Senckenberg Museum. He also travelled up the Nile to Nubia in 1823 and collected specimens around Ambikul, now in northern Sudan. Between 1828 and 1840, he published the results of his travels, eventually describing 23 new genera and 221 new species of fishes (Klausewitz 2002).

Bordeaux ship-owner, merchant and natural history enthusiast ***Jean-Jacques Dussumier*** (1792–1883) made at least 11 commercial voyages between 1816 and 1840 in his own vessels, the *Buffon* and the *Georges Cuvier*. He sailed the Indian Ocean and made large collections of fishes, plants and other animals from the Seychelles, Réunion, Mauritius, India, and Sri Lanka to the South China Sea. On his return from a voyage, he gave the specimens to the Muséum national d'Histoire naturelle in Paris, together with descriptive notes and drawings he made of fresh specimens. Cuvier wrote in an 1824 report (as quoted by Lassius 1973: 390), "One awaits his returns and one notes them down in the fashion of the custom-house or the Stock Exchange." On many occasions Cuvier praised "this merchant, clever and enlightened in all branches of natural history, who has already given the most positive and incontestable proof of his unselfish motives in the matter of scientific research" (Cuvier, Archives Nationales, Paris, AJ 578, no. 26–33, as quoted by Laissus 1973: 399).

Often the fishes comprised the most interesting collections, particularly fishes from Indonesia and the Ganges from the third voyage (1821–1823), and fishes from the Seychelles gathered on the fourth voyage (1825–1826), "most being entirely new and others having been seen only by Commerson" (Cuvier, in *Rapport fait à l'Académie royale des sciences* [1830], as quoted by Laissus [1973: 391]). On the fifth voyage (1826–1827), Dussumier brought back from the coast of Malabar and from the Seychelles, according to Cuvier, "one of the finest and most abundant collections of fishes ever seen" (Cuvier, in *Rapport fait à l'Académie royale des sciences* [1830], in Lassius [1973: 392]), totalling 550 specimens representing 200 species. The collection included some freshwater species, many from the State of Mysore.

The most productive and extensive of his voyages was the sixth, starting late 1827 and lasting 33 months, 27 of which were spent at sea, with ports of call in the Seychelles, India (Mumbai, Puducherry, Mahé, the Ganges delta), Bengal, Réunion, Mauritius and St Helena. He returned with a total of 1 500 fishes representing 481 species. Cuvier described Dussumier's samples as follows:

> It is especially the fishes in Monsieur Dussumier's gift that amaze naturalists and inspire in them the keenest gratitude… Not a ray, not a prickle is broken; their scales, even their colors, are usually preserved, and whenever the fluid has altered them, one finds in Monsieur Dussumier's descriptive notes whatever is necessary for completing the

description… And fortunately too, all these fishes, thanks to incisions made in their abdominal skins, have their viscera preserved in the best condition, so that they may be used in any anatomical research that one may desire. (Cuvier, in a report to the Royal Academy of Sciences: *Rapport fait à l'Académie royale des sciences* [1830], as quoted by Laissus [1973: 398])

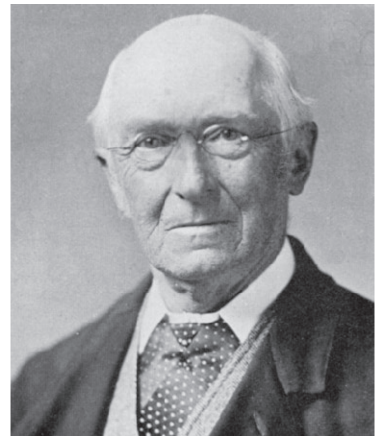


Figure 13 Albert Günther.
Source: Wikimedia Commons

Dussumier was named Correspondent of the Museum in 1827, made a Knight of the Legion of Honour in 1831, and an Officer in 1841. In 1865 he gave the museum the systematic catalogues of collections brought back from his voyages, as well as an album of watercolour drawings of the cyprinids of China, which he had made at Canton in 1820. He died in 1883 and 31 species of fishes today carry Dussumier's name.

Two further names linked with WIO fishes, are those of Albert Günther and Lambert Playfair. ***Albert Charles Lewis Gotthilf Günther*** was born in 1830 in Esslingen in Swabia. He graduated in medicine in 1852 and in the same year published a handbook on zoology for medical students. In 1855 he visited England, where he met John Edward Gray, Keeper of Zoology at the British Museum (Natural History), and palaeontologist Richard Owen at the Museum. In 1857 he was offered a position at the museum, his first job being to classify some 2 000 snakes. When Gray died in 1875, Günther was appointed Keeper of Zoology, a position he held for a further 20 years. His major work was the compilation of eight volumes of the *Catalogue of Fishes* (1859–1870). He also established the *Record of Zoological Literature* in 1864, and served as its editor for six years.

Robert Lambert Playfair was born in St Andrews, Scotland, in 1828. He became a military cadet and in 1846 joined the Madras Army and became an artillery officer. In 1854 Playfair was appointed Political Agent at Aden, and in 1862 he became Political Agent and then Consul of Zanzibar, a position he held until 1867. In that time he made extensive collections of fishes from Zanzibar, the Seychelles and Madagascar, which he sent to Albert Günther at the British Museum in London, and published his findings in the *Proceedings of the Zoological Society of London*. In 1866, in collaboration with Albert Günther, he published *Fishes of Zanzibar*, the first comprehensive account of the fishes of the east coast of Africa (see Myers, in Playfair & Günther 1971 reprint). Playfair described 36 species of fishes, of which 15 are still valid.

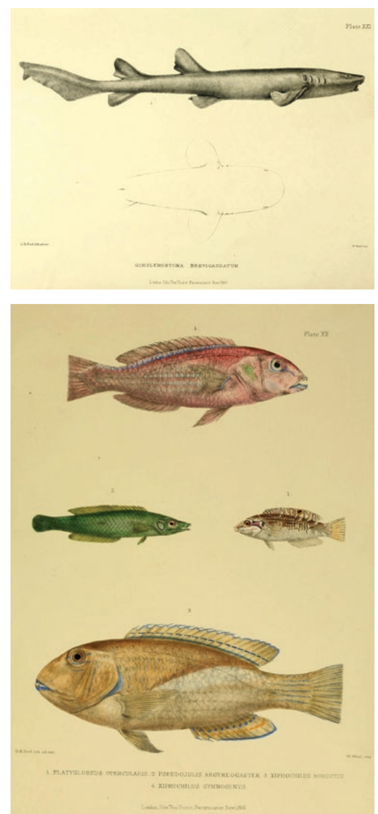


Figure 14 Plates from Playfair & Günther's *Fishes of Zanzibar*.
Source: Playfair & Günther 1866 Public domain

François Paul Louis Pollen was born in 1842 in Rotterdam and, at the age of only 20, financed his own expedition to Madagascar. In 1862 he moved to Leiden to study medicine but was encouraged by Hermann Schlegel to study zoology. After some training and scientific preparation, Pollen departed with his friend, ***Douwe Casparus van Dam***, reaching Réunion in 1864. After much successful collecting in northwest Madagascar, Mayotte and Réunion, they returned via Mauritius in July 1866. Sponsored by Pollen, Van Dam again collected on Madagascar from 1868–1872 (or 1873). Later, Pollen engaged Joseph Peter Audebert to continue the explorations, which he did until 1882. Pollen's large collection of fishes (as well as birds, mammals and insects) were given to the Rijksmuseum in Amsterdam. The fishes collected by Pollen and Van Dam were the subject of several papers by Bleeker (see below) (Boeseman, in Pietsch & Anderson 1997: 81–100).

Traveller, collector and describer ***Franz Steindachner*** was born in Vienna in 1834. He began to study fossil fishes at the recommendation of a friend. His growing interest in natural history led to his appointment, at the age of only 26, as director of the fish collection at the Natural History Museum in Vienna. His reputation as an ichthyologist grew, and in 1868 Louis Agassiz invited him to accept an appointment at the Museum of Comparative Zoology at Harvard in the United States. He returned to Vienna in 1874 and, in 1887, was appointed director of the natural history department. From 1895 to 1896, Steindachner was in charge of the First Red Sea Expedition of His Majesty's Academy of Sciences. On the return journey, he travelled through Palestine, Syria, Anatolia, and northern Greece. In 1897, he took part in the Second

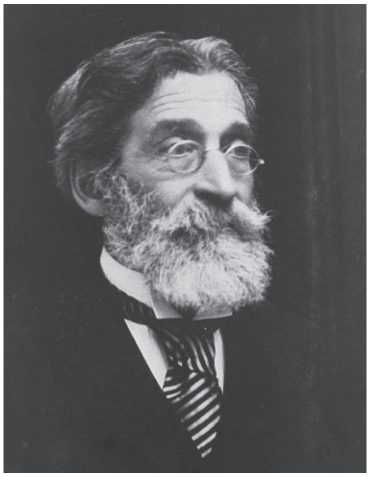


Figure 15 Franz Steindachner.
Source: Carl Leavitt Hubbs Papers. SMC 5. Special Collections and Archives, UC San Diego Library

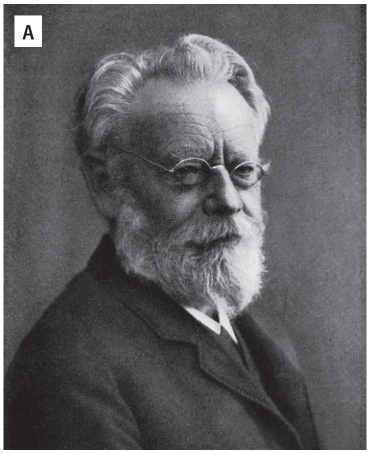


Figure 16 A Carl Klunzinger. Source: Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg, LXXI, 1915
B *Thalassoma rueppelli*, originally *T. klunzingeri*. © R Field

Red Sea Expedition but had to return early following year to take over the administration of the entire Kaiserlich-Königliches Naturhistorische Hof-Museum in Vienna. He also undertook trips to the Canary Is., Senegal and Latin America, described 1 034 species and published >200 papers on fishes.

Carl Benjamin Klunzinger, born in Güglingen, Germany, in 1834, also started his professional life as a physician. He later attended lectures in geology and zoology in Vienna and Prague. In 1862 Klunzinger travelled to Cairo and spent the next 18 months learning Arabic. He worked as a physician at Kosseir (now Al-Qusayr) on the Red Sea. Over the next five years, Klunzinger built up an enormous collection of Red Sea fishes and other marine animals, which were sent back to the Staatliches Museum für Naturkunde in Stuttgart. In 1869 he returned to Stuttgart and spent the next few years working on the collection. He published the two volumes of *Synopsis der Fische des Rothen Meeres* in 1870 and 1871. Two years later, he was back in Kosseir, collected more material, and returned to Stuttgart in 1875. In 1884 he published *Die Fisches des Rothen Meeres*, which was followed by books on the coral animals and the Cyclometopa crabs of the Red Sea before his death in Stuttgart in 1914.

The last of the 19th century explorers who contributed significantly to our knowledge of fishes of the northern WIO was Surgeon-Major ***Atmaram Sadashiv Grandin Jayakar*** (1844–1911). We know little of his early life, and presume he was born in India. He arrived in Oman in 1879 as successor to Surgeon-Major Mr Apothecary Gaspar de Rozario. Rozario had been appointed British Political Agent in Oman in 1861, responsible for medical services and recording the health of the population, as well as documenting the fauna and flora, socio-cultural practices and informing headquarters (in India) of political and military matters. During his 21-year tenure in Oman, Jayakar made extensive collections of marine fishes in the area, which he sent to the British Museum.

George Albert Boulenger was born in Brussels, Belgium, and joined the staff of the British Museum in 1880, was charged with the task of attending to Jayakar's donations. In 1887, he wrote of the first consignment:

> The Natural History Museum has received a large and most valuable collection of Fishes, obtained at Muscat and presented by Mr. Jayakar, which I have been directed by Dr. Günther to examine. This collection, containing specimens of 172 species, many of which were unrepresented in the National Collection and 14 of which are apparently new to science, fills a gap in our knowledge of the distribution of the fishes of the Indian Ocean. Scarcely anything is known of the fauna of the Persian/Arabian Gulf and the neighbouring coasts, a district intermediate between two others, the fishes of which have been tolerably well investigated, viz. the North-eastern coast of Africa and the West coast of India. It therefore seems to me that, in addition to the description of the new species, the publication of a full list of the fishes obtained will be useful. With the exception of three (the names of which are preceded by an asterisk) all the species enumerated are marine. (Boulenger 1887: 653)

Two years later, further consignments arrived, and Boulenger wrote:

> At the close of last year, the Natural History Museum received a second collection of Fishes from its generous correspondent at Muscat, Surgeon-Major A. S. G. Jayakar; this was shortly followed by a third, received a few days ago. Other examples of a number of the rare or new species enumerated in my preceding list having been sent again, I have, in some cases, been able to supplement my former descriptions; but all of the species enumerated hereafter, and to which numbers are attached, are new to the fauna of Muscat. Eight of the known species are altogether new to the Indian Ocean… Five species are considered to be new. The Sharks and Rays, which were hardly represented at

all in the first collection, have now reached us in numbers, and, from the size and beauty of most of the skins, will, to say nothing of the great zoo-geographical interest that attached to many of them, form a welcome addition to the Fish-Gallery of the Museum, where Mr. Jayakar's previous donations of large Sea-Perches, Scombroids, Sphyraenas, and Sword-fishes have already had conspicuous place. Thanks to the exertions of Mr. Jayakar, the number of Fishes recorded from Muscat now known amounts to 256. (Boulenger 1889: 236)

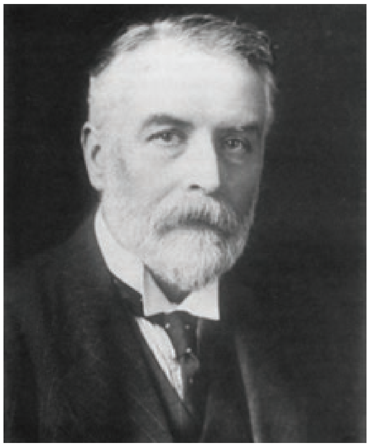


Figure 17 George Boulenger. © BMNH

Figure 18 Pieter Bleeker.
© Rijksmuseum, Amsterdam

By the time of his retirement in 1820, Boulenger had described 1 137 species of fishes, many of them from the WIO.

There are other men whose interests lay elsewhere but who, during the 18th, 19th and early 20th centuries, contributed to our knowledge of WIO fishes by collecting specimens and sending them back to Europe: ***Pierre Poivre*** (1719–1786) who was General Commissioner of Mauritius and Réunion from 1767 to 1772, sent fish specimens from Mauritius; French naturalist ***Jean-Baptiste Bory de Saint-Vincent*** (1778–1846), also spent time on Mauritius and Réunion during his travels; and ***Julien François Desjardin*** (1799–1840), born on Mauritius, was a founding member of the Society of Natural History of Mauritius. The latter's specimens and notes were used by ***Jean-Louis Hardouin Michelin de Choisy*** for his *Essai d'une fauna de l'Ile de Maurice*, published in 1849. ***Jean Baptiste Leschenault*** (1773–1826) sent many fish specimens from India (Puducherry), Sri Lanka, Mauritius and Réunion to the Paris museum. Additionally, ***Harald Blegvad*** (1886–1951) was a fisheries biologist who spent two winters in the Persian/ Arabian Gulf in 1836 and 1938, where he greatly expanded our knowledge of the fish fauna with the publication in 1944 (with the assistance of Berndt Løppenth) of *Fishes of the Iranian Gulf*.

The British Empire controlled much of Africa's eastern coastline, from Egypt to Tanganyika (Tanzania) in the 19th and early 20th centuries, – and all of India. Captain ***FrederickWilliam Townsend***, commander of the Indian cable ship *Patrick Stewart*, which worked in the Persian/ Arabian Gulf and Gulf of Oman from 1893 to1914, collected molluscs and deep-sea fishes, many of which he sent back the British Museum, and other museums in the United Kingdom.

In September 1933, an Anglo-Egyptian expedition was launched to investigate the fauna and oceanography of the northwestern Indian Ocean, an area that was relatively unknown. The expedition was financed from a bequest of Sir John Murray, one of the scientists on the *Challenger* expedition of 1872 to 1876, and was conducted using the Egyptian research trawler HEMS *Mabahiss*. The fishes (and other organisms) collected were lodged at the British Museum under the care of ***John Roxborough Norman***.

John Norman, born in London in 1898, started his working life as a bank clerk. In 1921 he joined the staff of the British Museum where he worked for Charles Tate Regan. Norman published extensively on fishes and their classification – amongst his works are *A History of Fishes* (1931) and *A Draft Synopsis of the Orders, Families and Genera of Recent Fishes* (1957). He published accounts of nearly 250 species of fishes from the *Challenger* expedition (including deep-sea fishes), of which 29 were new to science (Norman 1939).

One other name stands out, that of ***Pieter Bleeker***, who was stationed in the Dutch East Indies from 1842–1860. He was employed as a medical doctor with the Dutch East India Army, which is when he did most of his ichthyological work. He built up a network of contacts who sent him fishes from outlying government outposts on the many islands. In all, he collected some 12 000 specimens (which were eventually sent to the Natural History Museum in Leiden), and described more than 500 new genera and 1 932 new species. Of Bleeker it can be said that he described close to an entire fauna, something we cannot say of anyone else. While only some of the fishes were collected from the WIO (see under Castelnau below), many of the species in these volumes were named by Bleeker, and one of his many papers dealt specifically with fishes from the Cape (Bleeker 1860).

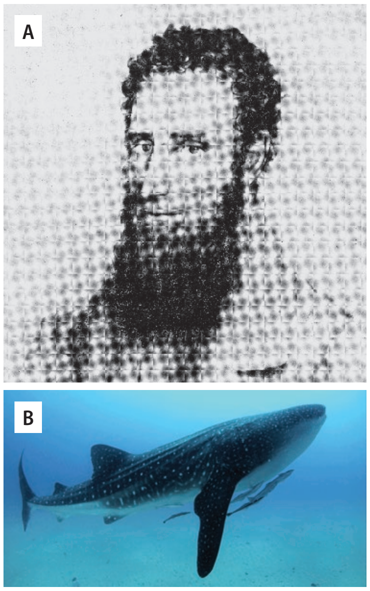


Figure 19 **A** Andrew Smith.
© Iziko South African Museum
B *Rhincodon typus*, the whale shark described by Smith in 1828. © M Fraser

Figure 20 **A** François Nompar de Caumont Laporte, Comte de Castelnau.
Source: Joanne 1847
B Two clinids, drawn by Castelnau.
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EXPLORATION OF THE SEAS AROUND SOUTHERN AFRICA

We next turn our attention to the south, where exploration of fishes developed in a very different way. Prior to the turn of the 19th century, few fishes had been collected from southern African waters. It was only with the establishment of the first museums in the Cape Colony, which was under British control from 1795–1803, and then from 1807 onwards, that collections were initiated.

Early in 1825, Governor Lord Charles Somerset travelled to Grahamstown to visit the military garrison. There he met a young medical officer, ***Andrew Smith***, who showed him a small collection of reptile, bird and mammal skins he had made, and who raised the question of establishing a museum for the Colony. Just a few months later, Somerset transferred Smith to Cape Town and made him the first Superintendent of the South African Museum, which was founded in 1825. Smith thus became the first museum scientist in South Africa and his collections the first research collections at a South African institution/museum. The museum's first annual report (1830) described the fishes that had been collected to date: "... about 90, including several of great rarity and interest, particularly in the family of the sharks, of which the species are above 20." These were all specimens which had been donated to the museum. Over the next few years Smith also described 26 marine fish species from South African waters.

Smith was born in Kirkton, Scotland, in 1797. He studied medicine in Edinburgh and later joined the army as a hospital assistant before completing his medical degree in 1819. It was during this period that he became interested in natural history – as part of his military training – at McGrigor's museum at Fort Pitt, Chatham. He arrived in Cape Town in 1821 and was posted to Grahamstown a few weeks later. When Smith returned to England in 1837, he took his private collections with him. They had been on loan to the South African Museum for 12 years, and their removal depleted the museum's fish collection considerably.

The next person to collect fishes from around South Africa was Castelnau. ***François Louis Nompar de Caumont Laporte, Comte de Castelnau***, was a widely travelled naturalist and diplomat. Born in London in 1802 (Evenhuis 2012), he later studied natural science in Paris under Georges Cuvier, Geoffroy Saint-Hilaire, and other notable French zoologists. From 1837 to 1841 he travelled in the United States and Canada, and from 1843 to 1847, he led an expedition to South America, crossing from the Mato Grosso to Peru and returning via the Amazon River. After the 1848 French Revolution, he took up a diplomatic career, and from 1848 to 1855 was French Consul at Salvador, Bahia, Brazil. In 1855, he returned to France and later travelled by steamer to the Cape of Good Hope, where he was French Consul from 1856 to1858. Following this posting, he took up the position of French Consul to Siam (Thailand) from 1858 to 1862. In 1863, Castelnau was appointed Consul-General for France, in Melbourne, Australia, where he remained after his retirement in 1877, until his death in 1880. He published several important papers on the Australian fish fauna during the 1870s.

Castelnau was a prolific ichthyologist. En route to the Cape Colony, he visited Île Bourbon (Réunion) where he collected and sketched a number of fishes. In South Africa, assisted by his son Ludovic, who visited Port Natal (now the city of Durban), and preparator Frédéric Daviaud, who visited Lake Ngami (Botswana), he collected fishes from Table Bay, Simons Bay (Kalk Bay) and Algoa Bay. Some of these specimens were sent to the famous Dutch ichthyologist, Pieter Bleeker, who in 1860 published a paper on the fishes of the Cape of Good Hope, describing several new species (Bleeker 1860). Castelnau himself published a monograph, *Mémoire sur les poissons de l'Afrique Australe* (Castelnau 1861) which included 71 new species. In 1865, Professor Jean-Theodore Lacordaire purchased most of Castelnau's specimens as well as a number of his sketchbooks, including unpublished watercolour paintings of many South African fishes, for the Zoological Museum, University of Liege, Belgium (Loneux 2006). Today this collection of Castelnau's specimens and paintings remains one of the earliest and most important records of South Africa's natural history heritage.

Several other museums were soon established in South Africa, in Grahamstown in 1855, in Port Elizabeth a year later, and in Durban in 1887. The fish specimens that found their way into collections at these museums and into the literature were all donated. That all changed in 1895. A growing concern that poor fishing practices would harm the fishing industry engendered an interest in the biology of fishes. The need to review the fishery industry led to the appointment of ***John Dow Fisher Gilchrist*** (1866–1926), a British marine biologist, to take charge of a survey of South African fishes and fish stocks.

Gilchrist was educated in Scotland, graduating from Edinburgh with a BSc and MSc. He pursued his studies on the feeding habits of fishes of Munich and Zurich Jena University, where he was awarded a PhD, and returned to Edinburgh in 1892 as assistant lecturer in zoology. In 1895, Gilchrist was appointed marine biologist in the Department of Agriculture of the Cape of Good Hope.

At Gilchrist's urging, the Government acquired a steam trawler in 1897, "to make a thorough investigation into what fishes are really in the sea and where they occur (Anonymous 1897). In the years that followed, the *Pieter Faure* trawled first in Cape waters, and then later off East London. Most of the trawling and dredging was from 40–200 m, and large quantities of marine organisms were collected. To identify the material, Gilchrist enlisted the help of Georges Boulenger of the British Museum, who was thus one of the first of those who named, but did not collect fishes from southern Africa.

Following the success of the *Pieter Faure's* survey in Cape waters, the Cape Government agreed to a similar survey off the Natal coast, and in 1901, the ship spent several months collecting material between Durban and Cape Vidal. A year later, Gilchrist produced the first, though preliminary, checklist of the marine and freshwater fishes of South Africa which included 55 families, 164 genera and 336 species. Then followed several years of personality clashes and arguments about who owned the collections made by the *Pieter Faure* and where they should be deposited. During this period few fishes were collected.

The next person to play a significant role in our understanding of WIO fishes (and crustacea) was ***Keppel Harcourt Barnard*** (1887–1964), an unusually gifted and versatile scholar. He was born in Lambeth in the United Kingdom, attended school in England, and then spent some time in Germany to polish his German, before entering Christ's College at Cambridge to read the Natural Sciences Tripos of Botany, Geology and Zoology. He added Anthropology, Ethnology and Geography to these, and then read law, becoming a barrister in 1911. In the same year he came to South Africa, joined the staff of the South African Museum, and was appointed Director in 1921.

In 1912, Barnard went on his first collecting trip, spending four months in Natal (now KwaZulu-Natal) and Mozambique. He also worked on the *Pieter Faure* collections, which had by then been lodged at the South African Museum. By the end of 1914, he reported that 670 species of marine fishes had been identified. The annual report for that year also listed HW Bell-Marley as a donor for the first time. Another notable collector during this period was JB Romer Robinson.

Harold Walter Bell-Marley was born in the United Kingdom in about 1872, and after the Second Anglo-Boer War he settled in Durban, where he was employed by a shipping company. In 1918 he was appointed Principal Fisheries Officer of the Natal Fisheries Board, a post he occupied for 19 years. Bell-Marley was an ardent naturalist with a rare talent for collecting. Primarily interested in insects, he also made extensive collections of plants and animals from all over South Africa, He was also the first to collect molluscs from the stomachs of deep-sea fishes. Like Robinson, he donated the specimens to overseas and South African museums and gave hundreds of his fish specimens to the Natal Museum.

JB Romer Robinson was the son of the Natal Prime Minister, Sir John Robinson, and also had a great interest in natural history, particularly fishes. He loved angling and was, for a long time, President of the Natal Coast Angling Association. Robinson understood the importance of research, collecting and donating many fish specimens to museums in South Africa

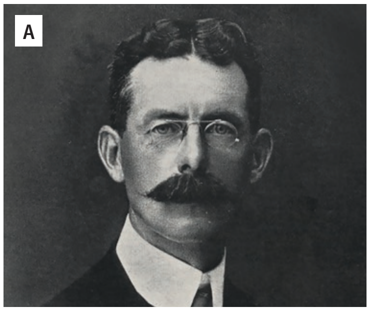


Figure 21 **A** John Gilchrist. Source: Ritchie 1918; courtesy of UCT
B *Paralichthodes algoensis* described by Gilchrist. Source: CFSA

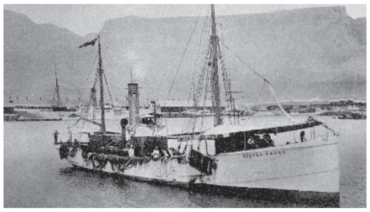


Figure 22 SS *Pieter Faure.* © NRF-SAIAB

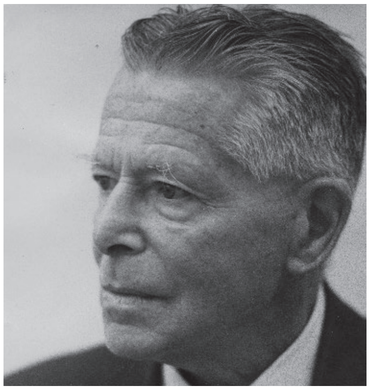


Figure 23 Keppel Barnard. © Iziko South African Museum

Figure 24 Harold Bell-Marley. © NRF-SAIAB

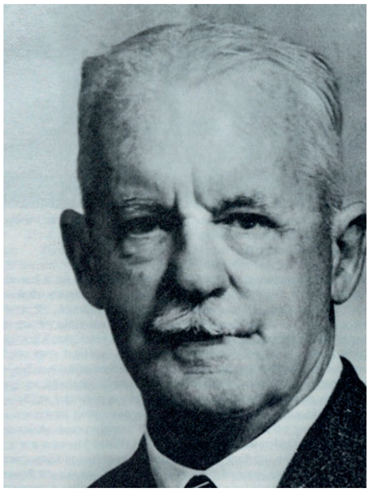


Figure 25 JB Romer Robinson.
Source: *Natal Mercury*

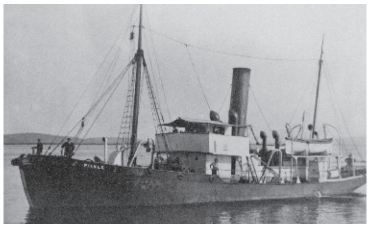


Figure 26 SS *Pickle*. © NRF-SAIAB

Figure 27 Cecil von Bonde.
© NRF-SAIAB (by R Palmer)

Figure 28 JLB and Margaret Smith sorting through a local fish catch, East African coast, c. 1952.
Source: NRF-SAIAB archives

(particularly the Natal Museum in Pietermaritzburg) and overseas, all at his own expense. He also photographed many of the fishes he collected, but in 1911, his relationship with the Natal Museum apparently ended, and none of his fish photographs have ever been found.

When Barnard was working on the flatfishes collected by the *Pieter Faure*, he formulated an idea, and in 1919 he wrote, "… the soles collected by the SS *Pieter Faure* have been sorted, classified and incorporated. I have completed a short, descriptive account of the S.A. representatives of this family, which it is hoped will eventually form part of a more comprehensive work embracing the whole of S.A. marine fishes" (South African Museum, 1920). Barnard's *Monograph of the Marine Fishes of South Africa* was published by the South African Museum in two parts, in 1925 and 1927.

In addition to Bell-Marley, another name that repeatedly appeared on the list of donors of fishes to the South African Museum collection during the 1920s and early 1930s – that of ***JLB Smith***, of whom more will be written later in this chapter. In 1936, Barnard made an arrangement with the Cape Town-based commercial trawling company, Irvin & Johnson, that trawler skippers keep any unusual fishes for the museum. Accessions rocketed to thousands per year. Further impetus to ichthyological exploration was the replacement of the old *Pieter Faure* with a larger vessel, a 30-m whaler, the SS *Pickle*, modified for trawling, which worked Cape and Natal waters in 1921 and then again in 1925, travelling as far north on the west coast as Walvis Bay, and on the east coast to Lourenço Marques (now Maputo). The large amount of material collected from as deep as 540 m (and on occasion nets were lowered to 1 800 m) resulted in the description of many new species.

Probably due to personality issues between Gilchrist and Péringuey, Director of the South African Museum, the museum did not receive these collections. It also seems that neither ***Cecil von Bonde*** (Director of the Marine Biological Survey from 1928–1952), nor Barnard approached each other about the future of the *Pickle* collections. Correspondence between ***James Leonard Brierley Smith*** and Von Bonde suggests that the collections were stored in a building at Cape Town harbour. On a visit to Cape Town in 1931, JLB Smith was given permission by Von Bonde to take any specimens he wanted as a donation to the Albany Museum. Eventually, after about two years, the relationship between these two men also broke down and no records of donations during this period were kept. Later the relationship resumed and, in 1947, Von Bonde suggested donating the collection to Rhodes University, and wrote accordingly to the Registrar, who accepted his offer. Smith then arranged for a Mr Kock to estimate the size of the collection prior to making arrangements for its removal to Grahamstown. As a result of Kock's report, Smith wrote to Von Bonde: "I am rather puzzled by the report sent by Kock. He was surely not shown the collection I worked on in 1933 which contained many thousands of specimens, including numerous types. Perhaps you can give me more information as Kock estimates there not to be more than five hundred fish in all." To this Von Bonde replied: "Mr Kock was shown the same collection ... but owing to our having to use the containers ... it was necessary to get rid of many duplicates ... only about 500 are left now" (Gon & Skelton, in Pietsch & Anderson 1997: 147).

JLB Smith was born in Graaff Reinet, South Africa, in 1897. He obtained an MSc in Chemistry at Victoria College (Stellenbosch University), and served on the staff of the college for several years before going to Cambridge in 1919. In 1922 he was appointed as a lecturer in organic chemistry at Rhodes University, Grahamstown. He was also a keen angler and this interest in fishes grew over the years as Smith trained himself as an ichthyologist.

In 1938 Smith married ***Mary Margaret McDonald***, thus initiating one of the most remarkable partnerships in biology, producing work that influenced ichthyology worldwide. Soon after their wedding they headed north to Mozambique on their first expedition, collecting at Inhaca Island, and as far north as Beira.

In December that same year, the first coelacanth was caught by a trawler near East London, and Smith spent the next six months describing *Latimeria chalumnae*, as it became named. It was, without doubt, the fish discovery of the century, and catapulted the Smiths to world fame.

Further expeditions followed, including another to Mozambique in 1946, and later that year, Smith joined an Irvin & Johnson trawler to collect deepwater fishes. These collections added 1 000 specimens to the collections, 17 of which were of undescribed species. In time, Smith became the pre-eminent collector and describer in the southern part of the WIO (and southeastern Atlantic).

The year 1946 also saw the establishment of a Department of Ichthyology at Rhodes University, with JLB Smith as Research Professor in Ichthyology, funded by the Council for Scientific and Industrial Research. With this security, the Smiths travelled to Bazaruto in 1948, and returned to Inhaca a year later. In 1949 *Sea Fishes of Southern Africa* was published, covering 1 249 species of marine fishes. In the same year Smith noted that he was planning a major treatise on the fishes of the WIO, a book that would be "at least twice the size of my current volume and would probably occupy six to ten years". In preparation for this work, the couple ventured further north, collecting fishes from Beira to Pinda reef in 1950, and Mozambique Island, Pinda, Ibo and the Kerimba (Quirimba) Islands a year later. In 1952 they travelled to Zanzibar, Pemba (Tanzania) and Kenya; and in 1953, went back to northern Mozambique, then to the Seychelles, Aldabra and Amirante Islands in 1954. They brought back large numbers of specimens, photographs and colour notes, and for the next ten years, JLB worked through the material family by family, which Margaret Mary (as she became known) illustrated. The result was a series of 32 major papers on the fishes of the WIO and Red Sea, and a book on the fishes of the Seychelles in 1963. By the end of his career – and life, in 1968 – Smith had described 397 new species, of which 71 are still valid today.

Figure 29 JLB and Margaret Smith with *Fishes of the Seychelles*.
Source: NRF-SAIAB archives

Figure 30 Francis Day.
Courtesy Australian Museum

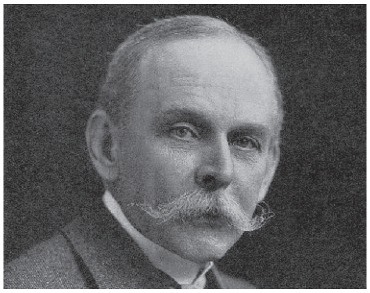


Figure 31 Alfred Alcock. CC BY 4.0

Figure 32 AGK Menon.
Courtesy of R Menon & U Menon

INDIA

The first substantive work carried out on the fishes of Indian seas was by ***Francis Day***, an army surgeon and naturalist based in Madras. He was born in Maresfield, England, in 1829, was schooled at Shrewsbury (the same school Charles Darwin attended). In 1852 he joined the British East India Company as an assistant surgeon in the Madras Army. In 1858 Day moved to Hyderabad and then to Cochin (Kochi) where he became interested in fishes. In 1865 he published *The Fishes of Malabar*, a catalogue of the freshwater fishes of the region. After a spell in England, Day was appointed Inspector-General of Fisheries for India in 1871. Over the years he made extensive collections of fishes and birds. His major work, two volumes on the *Fishes of India* was published in 1878 and 1879, and includes descriptions of more than 300 species. While writing these volumes in England, he offered his fish collections to the British Museum, but Albert Günther, a fierce critic of Day, refused to purchase them. Day eventually sold an extensive collection to the Australian Museum. He deposited his drawings of fishes with the Zoological Society of London. Day was made a Fellow of both the Linnean Society and Zoological Society and also received awards from by France, India and Italy for his work.

Alfred William Alcock, born in Bombay (Mumbai) in 1859, a physician and naturalist, spent four years with the Royal Indian Marine Survey Ship *Investigator*, surveying and describing the deep-sea fishes of the Arabian Sea.

The work of Day and Alcock paved the way for several generations of Indian ichthyologists. One of the most widely-acclaimed was ***Ambat Gopalan Kutty Menon*** (1921–2002), mentored by the ichthyologist and biogeographer ***Sunder Lal Hora***, who was unusual in that he worked on both marine and freshwater fishes. His publications range from a monograph on the soles of the genus *Cynoglossus*, to a *Checklist of the Freshwater Fishes of India*. Another ichthyologist trained by SL Hora was ***KS Misra***, who published extensively on elasmobranchs between 1947 and 1969, and was also the editor of *Fauna of India*, published in 1976.

THE POST-WAR PERIOD

From the 1940s, the momentum to explore the fauna of the Red Sea and Indian Ocean grew rapidly. In October 1957, the yacht *Xarifa* set sail for the Red Sea and Indian Ocean. The expedition leader was Hans Hass, who pioneered scuba gear and diving, and took the first photographs of fishes under water. On board was a young ***Wolfgang Klausewitz*** from the Senckenberg Museum, charged with collecting fishes, at the Farso and Farasan islands in the Red Sea and then at the Maldives.

The establishment of ichthyology in Israel led to growing exploration of Red Sea fauna, with two large expeditions to the Dahlak Archipelago (southern Red Sea), in 1962, under the leadership of ***Heinz Steinitz***, and again in 1965. It was also in those early days that the extent and significance of the migration of species from the Red Sea into the Mediterranean through the Suez Canal began to be understood. The canal, developed by the diplomat and entrepreneur Ferdinand de Lesseps, was opened in 1869, and such species are now known as Lessepsian migrants.

Figure 33 Wolfgang Klausewitz.
© F Krupp

John E Randall collected fishes in the Gulf of Aqaba in 1972, and two years later again in the Gulf of Aqaba, and in the Red Sea. Further Red Sea, Sri Lanka and Maldives collections followed in 1975, and a long voyage in 1977 took him from the Red Sea to the Seychelles and South Africa. In 1977, as a consultant to the United Nations Food and Agriculture Organization, he made extensive collections in the Persian/Arabian Gulf and Gulf of Oman. He made further extensive collections in the WIO in 1979 and 1980, in the Persian/Arabian Gulf in 1984 and 1985, and in Oman in 1993. Randall has described 826 fish species and has added more to our knowledge of WIO fishes than any other 20th-century ichthyologist. Randall was accompanied on several WIO trips by his former student and Australian ichthyologist ***Gerald R Allen***, who eventually published new species descriptions of more than 30 WIO coral reef fishes, mainly in the family Pomacentridae.

Figure 34 Phillip Heemstra, John Randall and Gerald Allen in Grahamstown in 1979.

In March 1976 ***Victor G Springer*** and colleagues travelled by schooner from the Seychelles to St Brandon Shoals and the Agaléga Islands and made numerous collections of fishes, which were lodged in the National Museum of Natural History in Washington, DC.

The JLB Smith Institute for Ichthyology (JLBSI), now South African Institute for Aquatic Biodiversity (SAIAB), was established shortly after JLB Smith's death in 1968 and built on the foundations laid down by the Smiths. ***Thomas H Fraser***, with an interest in coral-reef fishes, was appointed to the new institute in 1970, and soon went on exploratory expeditions to KwaZulu-Natal, Inhaca Island and Mauritius. Three years later ***Richard Winterbottom*** succeeded Fraser and led two collecting trips to northern KwaZulu-Natal. Soon after Winterbottom's return to Canada (in 1977) he participated in the 1978–1979 Joint Services Chagos Research Expedition and made extensive collections of fishes. This was followed in 1988 by another extensive expedition with the JLB Smith Institute to the Comoro Islands. Additional collecting expeditions to Indian Ocean localities followed: the joint Smithsonian Institution / JLB Smith Institute expedition with ***Phillip C Heemstra*** to Mauritius and Rodrigues in 1995.

While based at JLBSI/SAIAB, Heemstra also made collecting trips to Kenya in 1980, the Comoros in 1991 and 1993, Mozambique in 1992, 1994, 1995, 1997 and 2007, Yemen in 1998, Rodrigues in 2001, Seychelles in 2005, and Madagascar in 1995, 1999 and 2010. He also made at least 20 collecting trips along the east coast of South Africa with Rhodes University students.

The R/V *Dr Fridtjof Nansen*, manned and operated by staff of the Institute of Marine Research in Norway, has made several surveys of areas in the Indian Ocean. These trips were made in collaboration with various institutions and programmes, including the Agulhas and Somali Current Large Marine Ecosystems project (ASCLME), the Centre National de Recherches Océanographiques (CNRO), the Mozambique Fisheries Institute, the universities of Cape Town and Western Cape, the Oceanographic Research Institute (ORI), South Africa, and SAIAB. The first destination (in 2007) was Mozambique, followed in 2008 by a survey around Madagascar, Seychelles and Mauritius. In 2009, the focus was on the Comoros, northern Mozambique, and the southern seamounts. Fishes collected on these and subsequent trips are deposited at SAIAB.

Collections and general interest in Indian Ocean fishes have steadily grown. Consequently there is greater understanding of the faunal diversity, as well as a proliferation of new species descriptions. This high level of interest is reflected on a global scale with 4 064 new fishes having been described between 2003 and 2012, including 140 marine species from the WIO (Fishwisepro database). Certainly many more new discoveries can be expected from this diverse region.

CONTRIBUTORS

Note: biographical information correct at time of writing.

GERALD R ALLEN

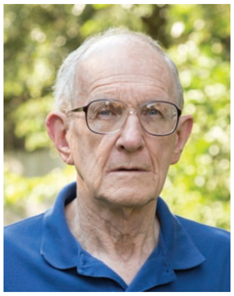
Gerald (Gerry) R Allen is an international authority on the classification of coral reef fishes. Born and raised in the USA, he received a PhD in Marine Zoology from the University of Hawaii in 1971. He served as senior curator of fishes at the Western Australian Museum in Perth from 1974 to 1997 and has subsequently worked as a private consultant, primarily involved with coral reef fish surveys in Southeast Asia for Conservation International. Gerry has logged well over 12 000 hours of scuba diving in all tropical seas, especially the vast Indo-Pacific region. Underwater photography is a consuming passion and hundreds of his photos have appeared in a variety of international publications. He is the author of more than 400 scientific articles and 35 books, is a past president of the Australian Society for Fish Biology, an honorary foreign member of the American Society of Ichthyology and Herpetology, and recipient of the K. Radway Allen Award for outstanding contributions to Australian ichthyological science.

KUNIO AMAOKA

Kunio Amaoka is an emeritus professor of Hokkaido University, honorary member of the Ichthyological Society of Japan and honorary foreign member of the American Society of Ichthyology and Herpetology. Before he retired in 2000, he was a professor of Hokkaido University for about 40 years, where he spent most of his career mentoring graduate students and teaching ichthyology to undergraduates. He led and participated in many projects on research of flatfishes, deep-sea fishes, fish diversity, and conservation of freshwater and marine fishes. Kunio has also led a number of expeditions to undeveloped islands, such as the Kurile Islands. He has published more than 120 papers and 20 books (as editor and author) on taxonomy and systematics of flatfishes and deep-sea marine fish, as well as numerous faunal works, and work on early life history stages.

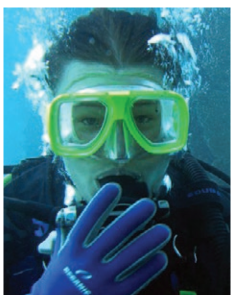
M ERIC ANDERSON

M Eric Anderson began his studies on deep-sea fishes in the early 1970s in the USA. He obtained an MA on the mesopelagic fishes of the Monterey Submarine Canyon at the Moss Landing Marine Laboratories on Monterey Bay, California. A PhD on the systematics of the Zoarcidae from the Virginia Institute of Marine Science followed. Eric specialises in the cold-water, high-latitude suborder Zoarcoidei, but also studies many other deep-sea groups, especially lanternfishes, dragonfishes, batfishes, deep-sea anglerfishes, grenadiers and cuskeels. He has published 90 scientific papers, usually as sole author, chiefly on deep-sea fish systematics and ecology, but also on their development and zoogeography, and on his fossil fish discoveries in South Africa. Eric has been a co-investigator aboard 28 deep-sea biological voyages in the North Pacific, North and South Atlantic and Western Indian oceans, and has dived twice in deep-sea research submersibles (California and the Arctic). His museum work includes study or collection in 25 countries and he has named as new to science 73 species, 12 genera and one subfamily of fish.



WILLIAM D ANDERSON Jr

William D Anderson Jr received his PhD degree at the University of South Carolina in 1960 and spent the summer of that year on the coast of the Gulf of Mexico at the University of Texas, Institute of Marine Science (Port Aransas). During the academic year 1960–1961 he taught biology at Susquehanna University, Selingsgrove, Pennsylvania, and from July 1961 to August 1965 he was a fishery biologist at the United States Fish & Wildlife Service's biological laboratory in Brunswick, Georgia. Following that, he held an interim appointment for one year in the Department of Biological Sciences, University of Florida (Gainesville), followed by three years as an associate professor of biology at the University of Chattanooga in Tennessee, moving in 1969 to Charleston, South Carolina, to teach and do research in the College of Charleston's Department of Biology and its Grice Marine Biological Laboratory (located on James Island near Charleston Harbor). Anderson retired in June 1996, becoming an emeritus professor and continuing to study systematic ichthyology, publishing on the families Callanthiidae, Lutjanidae, Serranidae (subfamily Anthiinae), and Symphysanodontidae.



RACHEL J ARNOLD

Rachel J Arnold is a marine sciences faculty member at Northwest Indian College in Bellingham, Washington State. She received her PhD from the University of Washington where her research focused on the evolution of the anglerfishes (Order Lophiiformes). Her research resulted in the addition of six newly described species, new information about distinct life histories and reproduction, and a novel hypothesis of the evolutionary relationships of anglerfishes based on molecular data. She is currently studying the population genetics of forage fishes important to the Coast Salish peoples. As a graduate student, she enjoyed being involved in and supervising undergraduate research and education, and therefore encourages undergraduates to become involved in her research as much as possible.

NEIL C ASCHLIMAN

Neil C Aschliman completed his PhD at Florida State University under the supervision of Gavin Naylor. For his dissertation he generated a taxon- and data-rich molecular phylogeny of skates, rays, and allies (batoid fishes), against which he reinterpreted their body plan evolution and fossil record. He had previously researched the morphological systematics of batoids with John McEachran and of needlefishes with Bruce Collette, as well as zebrafish development and elasmobranch endocrinology. He has completed fellowships at the University of Tokyo's Ocean Research Institute and the Smithsonian's National Museum of Natural History, and has visited collections on four continents. His other interests include elasmobranch conservation and descriptions of new species. He is currently an assistant professor in the Biology Department at St Ambrose University in Davenport, Iowa.

MEBRAHTU ATEWEBERHAN

Mebrahtu Ateweberhan is co-author of the introductory chapter "The origins and geology of reefs of the Western Indian Ocean" in this book. He is a visiting Research Fellow at the University of Warwick, United Kingdom. Ateweberhan is a coral reef ecologist and environmental consultant involved in environmental impact assessments, marine environmental surveys. His interests include climate change, adaptations to climate change, and its impacts.

DAVID R BELLWOOD

David R Bellwood is a professor of marine biology based in the Australian Research Council Centre of Excellence for Coral Reef Studies, and College of Science and Engineering, at James Cook University (JCU), Townsville, Australia. Although he studies reef fish ecology, palaeontology, systematics, taxonomy, biomechanics and behavioural ecology, he is best known for his functional studies of reef fishes. David started keeping reef fish in aquaria in the early 1970s in the UK, before studying biology at the University of Bath, training in fisheries (at Lowestoft, UK) and in taxonomy and systematics at the British Museum (Natural History) as it was then (now the Natural History Museum, London). His taxonomic work started with crustacea before he moved on to fossil then extant fishes. His key mentors were Geoff Boxshall and Howard Choat. With over 270 publications, David is one of the most published workers in coral reef studies (with an h-index of 69, and over 20 000 citations). His research achievements were recognised by JCU in 2004 when he was awarded a Personal Professorial (Research) Chair in Marine Biology, and in 2015 he was awarded the title, Distinguished Professor of Marine Biology. In the same year he was recognised by the Australian Society for Fish Biology for his "outstanding contribution to fish or fisheries science" with the K. Radway Allen Award. He is an editor of *Journal of Biogeography and Ecology Letters*, continues to teach three courses at James Cook University on fishes and biogeography, has supervised over 35 Honours and 30 PhDs; and continues to lead an active research group looking at the evolution and ecology of reef fishes.

EUGENIA B BÖHLKE

Eugenia (Genie) B Böhlke was born in Washington State in 1928. While studying for her MS degree at Stanford University, she met and married James (Jim) E Böhlke, a student of the noted ichthyologist George S Myers. After completing graduate school, Jim took a position at the Academy of Natural Sciences of Philadelphia, where he and Genie spent the rest of their careers. Genie joined Jim in his ichthyological work, and the two of them formed a productive scientific team. She became particularly interested in moray eels (Muraenidae). After Jim's death in 1982, Genie continued her ichthyological studies, and eventually became the world's leading authority on morays. Her accomplishments include editing the volume on eels for the *Fishes of the Western North Atlantic* series. She formally retired in 1994, but continued her studies until shortly before her death in 2001.

JOHN C BRIGGS

John (Jack) C Briggs graduated from Oregon State University in 1943. From 1943 to 1946, he served as a pilot in the US Army Air Corps. Support from the "G.I. Bill" made it possible to enter Stanford University where he was employed as a teaching assistant in the Biology Department and earned an MA degree in 1947, then a PhD in 1952. His early studies were devoted to fish life history and systematics which led to an interest in the evolutionary implications of biogeographic patterns. Work on contemporary patterns of distribution and biodiversity resulted in the study of palaeobiology and the historical development of such patterns. After two years of post-doctoral work at Stanford, he held faculty positions at the University of Florida, University of British Columbia, University of Texas, and University of South Florida (USF). In 1990 he retired from USF and became an emeritus professor. For the following ten years he did research at the Natural History Museum, University of Georgia, then returned to the west coast, where he once again became affiliated with Oregon State University. Jack has produced 164 publications, including six books or monographs. In 2005, he received the Alfred Russell Wallace Award from the International Biogeography Society for his lifetime contributions to biogeography. Jack died in May 2018.

KENT E CARPENTER

Kent E Carpenter is a professor in biological sciences at Old Dominion University in Norfolk, Virginia where he has been in residence since 1996. He also manages the Marine Biodiversity Unit of the Global Species Programme of the International Union for Conservation of Nature. He completed undergraduate studies in biology at the Florida Institute of Technology and his graduate studies in zoology at the University of Hawaii. He was a US Peace Corps Volunteer and post-doctoral research associate in the Philippines, a marine scientist at the Kuwait Institute for Scientific Research, and a senior fisheries research officer of the Food and Agriculture Organization of the United Nations in Rome, Italy. His primary research interests are marine conservation biology, systematics and evolution of bony fishes, ecology of coral reefs, and marine biogeography and phylogeography of the Indo-Pacific.

JOHN H CARUSO

John H Caruso's research has focused on the systematics and distribution of chaunacid and lophiid anglerfishes. He received his PhD from Tulane University in 1977, and has worked at several academic institutions, including Lafayette College in Easton Pennsylvania, the Louisiana Universities Marine Consortium (LUMCON) in Chauvin, Louisiana, the University of New Orleans and Tulane University in New Orleans, Louisiana. Teaching was always his primary responsibility at these institutions, and this continues to occupy most of his time. He has also served as Curator of Fishes and Reptiles at Audubon Zoological Garden in New Orleans, and Interim Curator of Fishes for the Tulane Museum of Natural History. Currently, John is Emeritus Senior Professor of Practice at Tulane University, New Orleans, Louisiana, USA.

PROSANTA CHAKRABARTY

Prosanta Chakrabarty obtained his BSc from McGill University and PhD from the University of Michigan in 2006. He has been Curator of Fishes at the Louisiana Museum of Natural History since August 2008, and is an associate professor in the Department of Biological Sciences at Louisiana State University (LSU). He is a systematist and an ichthyologist studying the evolution and biogeography of both freshwater and marine fishes. His work includes studies of Neotropical (Central and South America, Caribbean) and Indo-Pacific fishes. Collecting efforts by his laboratory at LSU include local and international collecting trips to Japan, Australia, Taiwan, Honduras, Guatemala, Kuwait, amongst others. He has described over a dozen new fish species, including several anglerfish and cavefish taxa new to science.

FRANÇOIS CHAPLEAU

François Chapleau did undergraduate studies in biology and completed a MSc (on darters) at Université de Montréal (Montréal, Canada), and his PhD at Queen's University, Kingston, Canada. François is currently a professor in the Department of Biology of the University of Ottawa, Canada. Teaching in French and in English, he has won multiple teaching awards and was invited to teach a biology course in China. Throughout his long academic career (including his PhD and post-doctorates at the Australian Museum, Sydney, Australia and Canadian Museum of Nature, Ottawa, Canada), he has studied the systematics, taxonomy and ecology of freshwater and marine fishes. His taxonomic and systematics research, carried out in collaboration with students and colleagues, includes species revisions, phylogenetic analyses and morphological studies of several groups of flatfishes (Order Pleuronectiformes).

DANIEL M COHEN

Daniel M Cohen received his BA degree from Stanford University in 1952 and a PhD under George S Myers in 1958 on the deep-sea family Opisthoproctidae. In 1959 Dan was hired as a systematist at the US Bureau of Commercial Fisheries at the Smithsonian Institution, Washington, DC, a position he held until transferring to the Alaska Fisheries Science Center in Seattle, Washington, from 1981 to1982. During his time at the Smithsonian, Dan developed research programmes on ophidiiform fishes, often in conjunction with Danish colleague, Jørgen G Nielsen, and gadiforms, culminating in the organisation of the 1986 Workshop on Gadiform Systematics at the Los Angeles County Museum of Natural History (LACM). In 1982 Dan accepted a position at the LACM which he held until retirement in 1995. He was a sea-going ichthyologist, and participated in several international collecting expeditions in the Pacific, Atlantic and Indian oceans, and authored more than 120 research papers on systematics and the biology of deep-sea fishes. He received several professional honours and awards. Dan died in September 2016.

BRUCE B COLLETTE

Bruce B Collette received his PhD from Cornell University for a taxonomic study of a small group of freshwater fishes called darters that live along the coastal plain from Maine to Florida. In 1960, he accepted a position as an ichthyologist at the National Systematics Laboratory in what is now the National Marine Fisheries Service of the National Oceanographic and Atmospheric Agency, housed in the National Museum of Natural History of the Smithsonian Institution in Washington, DC. Bruce's research focuses on the anatomy, systematics, evolution, and biogeography of tunas and their relatives, plus other fishes such as halfbeaks, needlefishes, and toadfishes. Results of his research have been published in over 270 papers in many scientific journals. He is also the author of two regional fish books, *The Fishes of Bermuda* and *Bigelow and Schroeder's Fishes of the Gulf of Maine*, and an ichthyology textbook, *The Diversity of Fishes: Biology, Evolution, and Ecology*, now in its second (2009) edition and the most widely-used college-level ichthyology text in the world. He is Chair of the IUCN Species Survival Tuna and Billfish Specialist Group. Bruce is a past president of the American Society of Ichthyologists and Herpetologists, and has earned many honours such as the first Robert H. Gibbs, Jr. Memorial Award for an outstanding body of published work in systematic ichthyology, the Joseph S. Nelson Lifetime Achievement Award in Ichthyology, and a gold medal from the US Department of Commerce for his leadership in using IUCN Red List standards to assess extinction risk of tunas, mackerels, and billfishes.

MRINAL K DAS

Mrinal K Das received his BSc (Honours) and MSc in Zoology from the University of Calcutta, Kolkata, India. He then received a Government of India Fellowship and joined the Zoological Survey of India as a research fellow under the supervision of Dr KC Jayaram and worked on the systematics of the cyprinid genus *Labeo*. To continue his passion for fish systematics, Mrinal joined the laboratory of Dr Joe Nelson at the University of Alberta (U of A), Edmonton, Canada, and received his MSc and PhD in Zoology from that university. After graduating, he worked as a member of the teaching faculty at Augustana University, Camrose, Alberta, Bishop's University, Lennoxville, Quebec, and the U of A. He received a U of A Graduate Student Teaching Award in 1992 and a Teaching Excellence Award from the Alberta Chapter of the Delta Chi in 1999. In 2001, Mrinal joined Grant MacEwan University (then College) as an instructor of Biological Sciences. His research interests are the systematics and phylogeny of the fishes of the Suborder Trachinoidei and hybridisation in *Phoxinus eos* and *P. neogaeus*.

MARCELO R DE CARVALHO

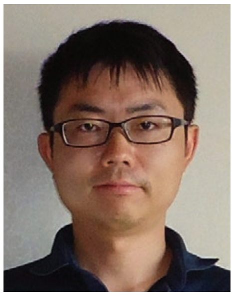
Marcelo R de Carvalho obtained his PhD in 1999 from the American Museum of Natural History/City University of New York joint programme in Evolutionary Biology, studying under Gareth Nelson and John Maisey. His greatest interests are in the systematic morphology and comparative anatomy of chondrichthyan fishes, both fossil and living. He has published widely on the systematics and morphology of sharks and rays, including the description of many new species of living electric rays and Neotropical freshwater stingrays, as well as new genera and species of fossil thornback rays, electric rays, and marine stingrays. As a professor in the Department of Zoology of the University of São Paulo, he taught vertebrate zoology, comparative anatomy, ichthyology, and systematics, and led a large laboratory with post-doctoral, graduate and undergraduate students, that focused on different aspects of chondrichthyan evolution. Major studies undertaken included taxonomic revisions of potamotrygonid stingrays and of many marine genera from the southwestern Atlantic Ocean and worldwide, as well as investigations in the comparative anatomy and development of sharks and rays.

MARTINE DESOUTTER-MENIGER

Martine Desoutter-Meniger has worked at the Museum national d'Histoire naturelle in Paris for more than forty years, much of that time in the Collections of Fishes. She has worked as an alpha-systematist on the Order Pleuronectiformes, better known as flatfishes, and especially on the species belonging to the family Soleidae. She has produced many papers on the systematics of the Soleidae in collaboration with Dr François Chapleau of the University of Ottawa, Ontario, Canada. Identifying the numerous fishes collected by different oceanographic expeditions is one of her main activities. She uses morphological and osteological features to describe species and also collaborates with a team working on the phylogeny of acanthomorph fishes, using both morphological and molecular features.

FABIO DI DARIO

Fabio Di Dario received his PhD in Zoology from the University of São Paulo (USP), Brazil, in 2005 after conducting studies in the Museum of Zoology (MZUSP) and the National Museum of Natural History, Smithsonian Institution. His research focuses on morphology, systematics (taxonomy and phylogeny) and conservation of fishes, especially clupeomorphs and basal teleosts. His passion for African fishes and the history of ichthyology in the continent began as a child when he first learned about the coelacanth discovery in South Africa. His experiences in African countries include Benin, Ethiopia and Burundi, where he attended the Third, Fourth and Fifth Meetings of the Pan African Fishes and Fisheries Association (PAFFA) respectively, in addition to academic visits to Mozambique and Tanzania, and a four-month residence at SAIAB between 2015 and 2016. Fabio is Professor of Zoology at the Federal University of Rio de Janeiro, in the city of Macaé, Rio de Janeiro, Brazil. He is also a member of the Brazilian Society of Ichthyology (SBI) and the Deep-Sea Fishes Research Group (GEOProf).



RYU DOIUCHI

Ryu Doiuchi obtained a PhD in Agriculture in 2005 at Kyoto University, Japan, where he worked on the phylogeny of the Stromateoidei using both morphological and genetic techniques. While at Kyoto University he also investigated the taxonomy of Indo-Pacific species of the Sphyraenidae, including a description, with his supervisor Dr Tetsuji Nakabo, of a new species from Japan, *Sphyraena iburiensis*, which had been caught in abundance by local commercial fishermen but had been confused with similar species. Ryu is a researcher in the Marine Resources Department of Fisheries Experimental Station at Wakayama, Japan, and is working on the resource management of several fish species, such as *Trichiurus japonicus* (Trichiuridae), *Parapristipoma trilineatum* (Haemulidae), *Pagrus major* (Sparidae), and *Paralichthys olivaceus* (Paralichthyidae), all commercially important fishes in Japan. He has authored more than ten academic papers, reports and other publications on fish taxonomy and marine ecology, an article focusing on age and growth, reproductive biology, and other ecological traits of *P. trilineatum*. He is particularly interested in understanding the rich and diverse fish fauna in Wakayama, the coast swept by the Kuroshio Current.

TERRY J DONALDSON

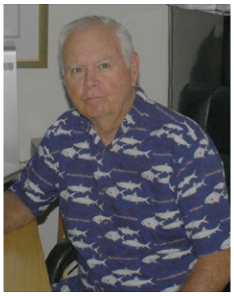
Terry J Donaldson is Professor of Ichthyology and Director of the University of Guam Marine Laboratory. He was educated at Michigan State University (BS Fisheries, 1977), the University of Guam Marine Laboratory (MS Biology, 1981) and the Louisiana State University Museum of Natural Science (PhD Systematics and Evolutionary Biology – Ichthyology, 1988). His graduate education was supplemented by work undertaken at the Marine Biological Laboratory, Woods Hole, the Laboratory of Ethology at Illinois State University, and the University of Arizona. He was a Japan Society for the Promotion of Science Fellow at Kyushu University (Japan, 1993–1994) and a US National Science Foundation, Japan Society for the Promotion of Science Research Fellow, also at Kyushu University (1997–1998). He is the author or co-author of several papers and book chapters in fish taxonomy, biogeography and biodiversity, behavioural ecology (especially mating systems and habitat utilisation), and conservation biology (extinction risk analyses). Terry has worked variously in government, in a conservation non-governmental organisation, and in academia. Most of his work has been undertaken in the Indo-Pacific region.

JAMES K DOOLEY

James (Jim) K Dooley obtained a BS in Biology from the University of Miami (Miami, Florida), an MS in Zoology from the University of South Florida (Tampa), and a PhD in Zoology from the University of North Carolina (Chapel Hill). After receiving his bachelor's degree, he worked for two years at the University of Miami Rosenstiel School of Marine and Atmospheric Sciences; on projects for the United States Navy's (ASW) Bioacoustic Programme in the Bahamas; for juvenile shrimp and sports fisheries in the Everglades National Park; and at the National Oceanic & Atmospheric Administration (NOAA), Tropical Atlantic Biological Laboratory in the fish museum collections. For his MS thesis at the University South Florida, he worked on the pelagic sargassum community in the Florida Current, and in his early years at Adelphi University he was Principal Investigator for NOAA/ICAT Atlantic Bluefin Tuna sports fishing project, for New York State. Other early projects included research at Friday Harbor Laboratory, University of Washington, on homing behaviour of sculpins; and Principal Investigator for Earthwatch on a study of shore fishes of the Canary Islands, Spain. He is Professor of Biology at Adelphi University, Garden City, New York, and also served as Biology Department Chair for nine years and as head of the Science Division for Adelphi University. Jim has been a fisheries consultant for United Nations FAO and consultant for IUCN; board member of New York State Marine Sciences Consortium; and private consultant for numerous New York, Connecticut, Pennsylvania and Massachusetts environmental companies for freshwater environmental impact projects. He has published more than 50 papers, numerous book chapters, and is co-author of two books on biology laboratory procedures. His ongoing research is on the tilefish families Branchiostegidae and Malacanthidae, including 43 species worldwide, based on morphology and molecular characters, and describing 12 new species.

DAVID A EBERT

David A Ebert earned his BA degree from Humboldt State University in northern California, a Masters from Moss Landing Marine Laboratories in central California, and his PhD at Rhodes University, Grahamstown, South Africa. He is Programme Director for the Pacific Shark Research Center, a research faculty member at Moss Landing Marine Laboratories, and an honorary research associate for the South African Institute for Aquatic Biodiversity and the California Academy of Sciences Department of Ichthyology. He serves as an advisor and consultant for the Food and Agriculture Organization of the United Nations on shark-related issues, and is the IUCN Shark Specialist Group Vice Chair for taxonomy, regional co-Chair of the IUCN Northeast Pacific Regional Shark Specialist Group, and a member of the American Elasmobranch Society, American Society of Ichthyologists and Herpetologists, and Oceania Chondrichthyan Society. Dave's research on sharks and their relatives (the rays, skates and ghost sharks) focuses on the biology, ecology and systematics of this enigmatic fish group. He has conducted research on six continents and in over 25 countries. He has authored 25 books, including the *Sharks of the World,* has published over 400 scientific papers and book chapters, and contributed over 120 IUCN Shark Specialist Group Red List species assessments. His research has been featured on Discovery Channel's *Shark Week* and on the acclaimed BBC series *Shark*. He has supervised more than 40 graduate students, and enjoys mentoring and helping develop aspiring marine biologists. His current research efforts are focused on finding, documenting, and raising awareness of the world's 'lost sharks', those little-known or unknown shark species that have largely been lost from the public and scientific awareness.

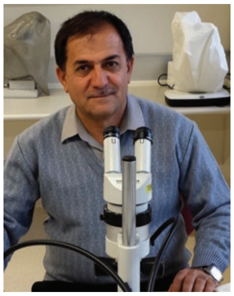


THOMAS H FRASER

Thomas H Fraser received a PhD in 1970 from the University of Miami, Florida, for an osteological study of the family Apogonidae that initially set the modern classification for 19 genera and 14 subgenera. He spent three years at Rhodes University, South Africa, as a senior lecturer at the JLB Smith Institute of Ichthyology studying marine fishes. He has collected Indian Ocean fish in South Africa, Mozambique, Mauritius, and twice on St Brandon Shoals (Cargados Carajos Bank). Another year was spent at the Smithsonian Institution as a post-doctoral fellow studying apogonids with Ernest A Lachner at the Division of Fishes. A private-sector position at Charlotte Harbor, Florida, allowed Tom to set in motion the descriptive research on water quality, primary production and fish communities in Florida's second largest estuary affected by freshwater inflow. He was appointed successively by two Governors of Florida to the Florida Marine Fisheries Commission, the rule-making body for living marine resources, and provided its recommendations for guiding state policies on marine natural resources to the governor and legislature. He served for eight years, two years as Vice-Chairman and four years as Chairman. Tom has published or co-authored at least 59 papers, many about the systematics and taxonomy of the Apogonidae, describing new subfamilies, tribes, genera (fossil and recent), and many new species. A research fellowship at the Australian Museum, Sydney, set in motion a renewed study of cardinalfish. He continues to be involved with the description of new species and genera of cardinalfishes as an adjunct scientist at Mote Marine Laboratory, Sarasota, Florida, and as a research associate at Florida State Museum, University of Florida, Gainesville, Florida. In the emerging field of molecular phylogeny he has joined Japanese colleagues in research concerning relationships within the Apogonidae as expressed by colour patterns, morphology and DNA. Tom has assessed apogonids in the Caribbean and Gulf of Mexico as part of the IUCN programmes.

RONALD FRICKE

Ronald Fricke studied in Braunschweig, London, Hamburg and Freiburg, before being appointed Senior Curator of Fishes at the Staatliches Museum für Naturkunde Stuttgart, Germany. Apart from the collection of and research on freshwater fishes of central Europe that this position requires, his wider research interest focuses mainly on the taxonomy, zoogeography and evolution of marine fishes of the Indo-Pacific, eastern Atlantic and Mediterranean Sea. After initial revisionary studies on callionymid, draconettid and tripterygiid fishes, he expanded his taxonomic range to syngnathids, gobiesocids, blenniids, gobiids and other fish families, but specialised on small and sometimes cryptic fish species. In the WIO he focuses on the Red Sea, the Persian/Arabian Gulf and southern Arabia, and the Mascarenes and Esparses Islands. Outside the region, he works on the fish fauna of New Caledonia, New Guinea, the South China Sea, the Mediterranean, Canary Islands, Cape Verde Islands, Ascension and St Helena islands. He has collected fishes in 63 countries and participated in several research expeditions. In addition, he has been working in conservation of marine and freshwater habitats and species as an independent expert for the European Union for the NATURA 2000 protected area network, and has published several Red Lists of fishes in Europe and overseas. He also acted as national representative in the OSPAR, HELCOM and ICES organisations. Fricke has published the descriptions of eight new genera and 149 new species of fishes. He has authored 471 scientific papers, including nine books as a single author, five books with multiple authors, and 174 refereed papers in journals. He is a co-editor of *Eschmeyer's Catalog of Fishes* online database.



JAVAD GHASEMZADEH

Javad Ghasemzadeh is an associate professor in the Department of Fisheries and Aquaculture, Faculty of Marine Sciences at Chabahar Maritime University, Iran. He completed his undergraduate studies in Fisheries and Natural Resources Management at Tehran University, and worked for a few years in the Iranian Fisheries Organization before moving to Australia to pursue his postgraduate studies in 1990. He did his MSc in Marine Ecology at the University of New South Wales, and his interest in ichthyology motivated him to work on the taxonomy and phylogeny of Indo-Pacific mullets (family Mugilidae), with special reference to the mullets of Australia, for his PhD at Macquarie University. For this project he collected mullets from all around Australia and many parts of the Indo-Pacific, and examined the extant type specimens of mugilids in Australia and most of the European museums. During his studies he collaborated closely with the Ichthyology Department of the Australian Museum, and after graduation, he examined all the mullet holdings of this museum through a visiting fellowship in 1998. Apart from teaching and guiding postgraduate students, he is actively involved in research and scientific collaboration with interested ichthyologists in resolving the very ambiguous and confusing systematics and phylogeny of mullets.

ANTHONY C GILL

Anthony (Tony) C Gill is Natural History Curator in the Macleay Museum, University of Sydney, Australia. He previously held positions in the Natural History Museum, London, and in the School of Life Sciences and International Institute for Species Exploration, Arizona State University. Tony received his PhD from the University of New England, Australia, in 1991, based on research conducted at the Australian Museum, Sydney. He was later a Smithsonian post-doctoral fellow in the National Museum of Natural History, Washington, DC, and Lerner-Grey Research Fellow in the American Museum of Natural History. His research is primarily on the taxonomy and historical biogeography of Indo-Pacific shorefishes, and on the systematics and anatomy of acanthomorph fishes. Among other topics, he has published on the classification and taxonomy of the Indo-Pacific dottyback family Pseudochromidae, and on the classification of the perciform suborders Gobioidei and Percoidei.

ULISSES L GOMES

Ulisses L Gomes was awarded his PhD by the Museu Nacional, Rio de Janeiro, Brazil in 2002. Since 1981 he has been a professor in the Zoology Department of the Universidade do Estado do Rio de Janeiro, Brazil. Dr Gomes has been conducting research and publishing papers on the anatomy and taxonomy of elasmobranchs, describing new species of Rajidae and Dasyatidae since the early 1980s. He is member of the Sociedade Brasileira de Ictiologia and the American Society of Ichthyologists and Herpetologists. Recently, he published as lead author an identification guide for sharks and rays known to occur in Rio de Janeiro state, Brazil.

MARTIN F GOMON

Martin F Gomon is a long-standing senior curator of Ichthyology at Museum Victoria, the state museum of Victoria in Melbourne, Australia, and is a senior member of Australia's ichthyological community where he is regarded as a taxonomic authority on fishes in that country. Educated in the USA, he received degrees at Florida State University (BSc) and University of Miami (MSc, PhD), during which time he spent five years at the National Museum of Natural History, Smithsonian Institution, as a museum technician in the Fish Division and a finishing graduate student. Martin's research began with a focus on interrelationships within the Labridae, which provided an early advocacy for a wider view of the family incorporating the Scaridae and Odacidae, based on phylogenetic principles. Arriving in Australia, he turned his attention to other groups and has published taxonomic descriptions of species of a wide assortment of families from the Scyliorhinidae to the Soleidae, as well as labrids, with current work incorporating genetic and morphological methodologies investigating the Aulopidae, Chlorophthalmidae and Paraulopidae. Many of his studies arose from efforts to elucidate the taxonomy of temperate Australian species in preparation for what have become the most comprehensive field guides to southern Australian fishes published, *Fishes of Australia's South Coast* (Gomon, Glover & Kuiter 1994) and its successor *Fishes of Australia's Southern Coast* (Gomon, Bray & Kuiter 2008). A founding member of *OzFishNet*, an Australasia-based consortium of fish taxonomists organised to promote and disseminate information about Australia's fish diversity, he continues to work collaboratively and attract funding for projects, such as the consortium's *Fishes of Australia* website launched in 2012 (www.fishesofaustralia.net.au).

OFER GON

Ofer Gon completed his MSc in oceanography and marine biology at the Hebrew University, Jerusalem, under the supervision of A Ben-Tuvia in 1979. His first research experience was at the Bernice Pauahi Bishop Museum, Honolulu, working on fishes of the tropical and subtropical Pacific Ocean under JE Randall. Professionally, this was a very important period as he acquired first-hand knowledge of many families, genera and species of fishes and published his first taxonomic papers on new species and records of fishes from Hawaii. In 1982 he was hired by Margaret Smith of the then JLB Smith Institute (now the South African Institute for Aquatic Biodiversity) in Grahamstown, South Africa, to assist with the preparation of *Smiths' Sea Fishes*. This was followed by a contract to produce *Fishes of the Southern Ocean* and a permanent research position at the Institute. In the course of his long career Ofer studied the taxonomy of mostly marine tropical and Antarctic fishes, but was also involved in some estuarine and freshwater fish studies while supervising students. He retired in 2014 and is now Curator Emeritus at SAIAB.

WAYNE S GOSCHEN

Wayne S Goschen obtained his BSc (Hons) degree in physics from the University of Natal (now UKZN). He then chose to switch to physical oceanography where his talent for applied mathematics and physics could be put to practical use. This led to a study of ocean dynamics associated with prominent capes and bays off the south coast of South Africa and to a PhD in Oceanography from the University of Port Elizabeth (now NMMU) in 1991. Wayne's research included a study of features of the Agulhas Current in the southeastern region of the Western Indian Ocean and its influence on the adjacent coastal ocean. He then spent 15 years in the IT industry developing software, databases and websites (culminating in an MSc in IT from UCT) before returning to oceanography in 2008 with the South African Environmental Observation Network (NRF-SAEON). His interests are in the physical oceanography of nearshore, coastal and shelf waters, mostly along the east coast of South Africa and around Algoa Bay, but also including the Agulhas Current. His advances in research have been in the field of wind-driven circulation and coastal upwelling, Agulhas Current influences on shelf and coastal waters, coastal trapped waves and dynamics of large log-spiral bays.

GAVIN GOUWS

Gavin Gouws is a former senior scientist at the National Research Foundation – South African Institute for Aquatic Biodiversity (NRF-SAIAB) in Grahamstown, South Africa. He initially intended training as a broad zoologist but was bitten by the genetics bug during his postgraduate studies. He became excited by this developing field and the possibilities it opened up to address a range of questions around systematics and evolution, irrespective of the organism and the system. He subsequently chose to pursue studies on freshwater isopods, crabs and crayfish in South Africa and Australia, and was eventually employed by NRF-SAIAB as a fish taxonomist. Using genetics as an entry point, his research programmes have involved large-scale studies of reef fish biogeography, phylogeography and diversity across the Western Indian Ocean, more-focused studies on the systematics and taxonomy of specific groups (e.g., goatfishes, snappers, emperors and cardinalfishes), and population genetic studies of species of commercial and subsistence fisheries importance. His more recent or esoteric research interests include genomics, epigenetics, metagenomics, and the study of sexual selection and the evolutionary biology within certain fish families.

NICHOLAS AJ GRAHAM

Nicholas AJ Graham is a chief investigator and Principal Research Fellow in the ARC Centre of Excellence for Coral Reef Studies, James Cook University, Australia. He is funded through an Australian Research Council Fellowship. Prior to being based in Australia, Nick completed his PhD in the School of Marine Science and Technology, Newcastle University, UK. His research tackles large-scale ecological and social-ecological coastal issues under the overarching themes of climate change, human use and resilience. He has worked extensively on the ecological ramifications of fishing and closed area management. He has assessed the long-term impacts of climate impacts on coral reef fish assemblages, fisheries and ecosystem stability. He has studied the patterns and processes by which degraded coral reefs recover, and how this can be incorporated into, or influenced by, management action. Increasingly Nick works with social scientists and economists to assess methods of linking social-ecological systems for natural resource assessment and management. Much of his work is in the Western Indian Ocean, particularly Seychelles, Chagos, Maldives, Mauritius, Kenya and Tanzania.

DAVID W GREENFIELD

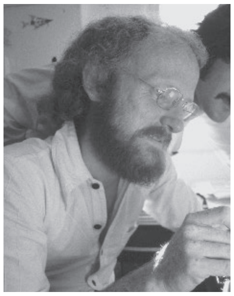
David W Greenfield is a research associate in the Department of Ichthyology at the California Academy of Sciences in San Francisco and an emeritus professor at the University of Hawaii, where he taught ichthyology. He is also a research associate at the Bernice Pauahi Bishop Museum in Honolulu, and a past president of the American Society of Ichthyologists and Herpetologists. David has published over 150 scientific papers on fishes and a book, *Fishes of the Continental Waters of Belize*, and has described over 100 species new to science, mainly from the families Batrachoididae, Holocentridae and Gobiidae. He has conducted extensive field work on both freshwater and marine fishes in North, Central and South America, as well as in Hawaii and Fiji. His latest research is on the systematics of Indo-Pacific coral-reef fishes, particularly the gobiid genus *Eviota*.

ELAINE HEEMSTRA

Elaine Heemstra was introduced to fishes and fish illustration at the JLB Smith Institute (now SAIAB) where she has spent most of her career, and also where she met and married her ichthyologist husband, Phil Heemstra. Later she succumbed to the attraction of fishes and became fascinated by their beauty, form and variety. Phil introduced her to scuba diving and they dived together whenever possible. They also collaborated on numerous scientific papers as well as a book on the coastal fishes of southern Africa. In preparation for this WIO book, Elaine and Phil undertook several fish survey expeditions to learn more about the fishes of the region. Wherever they collected fishes they met fellow enthusiasts keen to share their local knowledge and photographs. This book is a record of an ongoing quest to learn more about WIO fishes and is also a celebration of the camaraderie Elaine and Phil encountered *en route*.

PHILLIP C HEEMSTRA

Phillip (Phil) C Heemstra, an American ichthyologist, completed his MSc and PhD in marine biology at the University of Miami in the late 1960s and early 1970s. After some early work on taxonomy of sharks of the Gulf of Mexico and Caribbean, and various bony fishes in Miami, Phil accepted a position at the Academy of Natural Sciences in Philadelphia. After a year in Philadelphia, he took up a three-year position in the Australian CSIRO Fisheries Division at Cronulla. After the contract finished in 1978, Phil accepted an offer from Margaret Smith of the JLB Smith Institute of Ichthyology (now South African Institute for Aquatic Biodiversity) in Grahamstown, South Africa, to help her write a revision of her husband's book, the *Sea Fishes of Southern Africa*. This was a research post and Phil became Senior Curator of Fishes. Phil did much work in the WIO, collecting the fishes that laid the foundation for this book. He participated in R/V *Dr Fridtjof Nansen* research cruises off Kenya and Mozambique, and organised or participated in fish surveys of Mauritius, Rodrigues, Madagascar, Comoros, Seychelles and South Africa. He was honorary foreign member of the American Society of Ichthyologists and Herpetologists. Phil died in 2019 after a long illness.

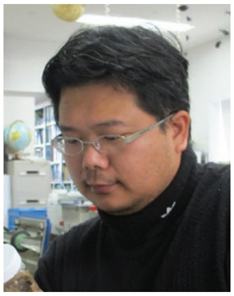


DANNIE A HENSLEY

Dannie A Hensley was a faculty member at the University of Puerto Rico, Mayagüez, for 28 years where he served as an assistant professor from 1980 to1984, an associate professor from 1984 to 1991, and was promoted to a full professor in 1991. His education in ichthyology started at the California State University, Fullerton, in 1970, where his advisor was David W Greenfield. From 1974 to 1978, Dannie was an ichthyologist with the Marine Research Laboratory of the Florida Department of Natural Resources in St Petersburg. For much of that time, he studied toward his PhD at the University of South Florida under John (Jack) C Briggs' guidance. It was during this time that he wrote his first paper on flatfishes, describing the larval development of *Engyophrys senta* (Bothidae). In it he discussed the systematic importance of intermuscular bones in flatfishes, and became the first author to use phylogenetic terminology when discussing relationships of flatfishes. Perhaps Dannie's most significant contribution to the classification of flatfishes was a chapter he wrote with Elbert Ahlstrom for Ahlstrom's 1984 volume on the development of flatfishes, and his synthesis is still widely cited. Dannie died in 2008. His final contributions to fish systematics were the accounts he wrote for this book, which were revised and edited by Kunio Amaoka.

ERIC J HILTON

Eric J Hilton received his bachelor's degree in Wildlife Ecology and Management in 1996 and his PhD in Organismic and Evolutionary Biology in 2002, both from the University of Massachusetts, Amherst. Before coming to the Virginia Institute of Marine Science (VIMS) in 2007, he conducted post-doctoral research in the Geology Department at the Field Museum of Natural History, Chicago, and the Division of Fishes of the US National Museum of Natural History (Smithsonian Institution) in Washington, DC. He is a broadly trained vertebrate zoologist, with a primary research interest in the anatomy, evolution and diversification of the ray-finned fishes. He uses a multidisciplinary approach to study evolution, drawing on the data and techniques of palaeontology, comparative anatomy, developmental biology, biogeography, and histology. Other ongoing research projects include the ecology of larval fishes, the biology and management of Atlantic sturgeon, and monitoring the population of anadromous shad and herring in Virginian waters. As a faculty curator, he oversees the growth and use of the VIMS Nunnally Ichthyological Collection, in addition to teaching ichthyology and training graduate students and post-doctoral researchers.



HSUAN-CHING HO

Hsuan-Ching (Hans) Ho is an associate research fellow of the National Museum of Marine Biology and Aquarium and an associate professor of the National Dong Hua University in Taiwan. He started to work on fish taxonomy as a graduate student in Academia Sinica in 2002 and obtained his PhD degree in 2010 with his thesis on the phylogenetic relationship and revision of Indo-Pacific genera of the batfish family Ogcocephalidae. He is interested in various fish groups, especially the anglerfishes, sand perches, lizardfishes and many other deep-sea fishes. He has published more than 80 scientific papers and described 45 new fish species. He has also spent a lot of time on the history of the work on Taiwanese fishes, and he hopes to review all Taiwanese fishes in the future.

WOUTER HOLLEMAN

Wouter Holleman became involved in taxonomy as a postgraduate student at the request of Rick Winterbottom, then a lecturer at the JLB Smith Institute (now the South African Institute for Aquatic Biodiversity [SAIAB]), who needed some tripterygiids identified. In 1979 he moved to the Albany Museum and became involved in museum management for more than 20 years, whilst maintaining his interest in Tripterygiidae. After early retirement from the museum he moved back to SAIAB as a research associate. In the following ten years his research was interrupted by periods spent teaching English in Taiwan. It was during this time that he was asked to take on this WIO book project as an editor, and in between, he became involved in the taxonomy of South African clinids and some other groups of fishes. He is also on the team of fish editors for *Zootaxa*.

BRETT A HUMAN

Brett A Human completed his PhD in 2003 in South Africa under the supervision of Dr Leonard Compagno at the University of Cape Town and South African Museum. For his thesis, he revised three African catshark genera, performed shape variation analyses on those genera, and published one of the first molecular phylogenetic studies on chondrichthyans. While in South Africa, Brett participated in the dissection of the first megamouth shark recorded from WIO. From 2006–2008 Brett was employed at the Marine Science and Fisheries Centre in the Sultanate of Oman. During this period he spent 112 days at sea where he collected over 2 000 specimens of marine fishes and established a fish collection there. Before his death in 2011, Brett lived in Perth, Australia, his country of origin, where he was continuing his work on elasmobranch taxonomy through the Western Australian Museum. Brett authored 11 chapters on various shark families for this book.

J BARRY HUTCHINS

J Barry Hutchins was Curator of Fishes at the Western Australian Museum, Perth, until his retirement in 2007. His research was centred on the taxonomy and phylogeny of the Monacanthidae (filefishes) and Gobiesocidae (clingfishes), but also included studies of the biodiversity of the Western Australian reef fish fauna. After his retirement he maintained his connection with the museum as a research associate. Barry continues to work on the recruitment of tropical reef fishes at Rottnest Island, which is located off the Western Australian coast near Perth. This long-term investigation, started in 1976, has shown remarkable fluctuations in annual tropical recruitment that follow the El Niño/La Niña pattern of ocean circulation in the Australian region.

HITOSHI IDA

Hitoshi Ida is an emeritus professor of the School of Marine Biosciences, Kitasato University, Kanagawa, Japan. His research interests are ecology of the fishes of the family Salmonidae and he was the first to report the density dependence of *Oncorhynchus keta* in the northern Pacific in the early 1980s. He also cautioned against the practice of stock enhancement of the species, by the release of fry into the environment. He reviewed fishes of the family Ammodytidae and described two genera, viz. *Protammodytes* from continental shelves of both the tropical Pacific and Atlantic, and *Lepidammodytes* from Hawaiian waters. In this review he also described new species of *Protamodytes* and *Bleekeria* from the southern Indian Ocean with John Randall, with a focus on specialisations in the families of Perciformes, which accompany their sand-diving behaviour, such as elongation of the body, loss of scales, protrusion of lower jaw, degeneration of pelvic fins and specialisation of the olfactory organs. He retired from Kitasato University in 2007, but continued to focus on his interest in the fish diversity of Palauan waters. He contributed a description of the most primitive form of an anguilliform *Protanguilla palau* from an underwater cave in Palau. The taxon probably represents a new suborder of the order Anguilliformes.

WALTER IVANTSOFF

Walter Ivantsoff was born in Shanghai, China, in 1938, to Russian parents whose own parents had left Russia at the time of the Russian Revolution in 1917. Walter attended several schools whilst in China, the most important of which was a school run by English and French Jesuit monks. In 1949, the United Nations Refugee Organization (IRO) was instrumental in moving Russian refugees out of China to a temporary location in the Philippines (a small island, Tubabao, off Samar Island) where he enjoyed living in a tent for 11 months with no school to go to. At the end of that year his family was accepted by Australia and he began his education which culminated in a PhD from Macquarie University, Sydney, where he remained as teacher and researcher for the rest of his working life. Walter published 60 research papers, mostly with his postgraduate students and colleagues, restricting his interests to families Atherinidae, Notocheiridae, Atherinonidae, and Pseudomugilidae, with some publications on melanotaeniids and telmatherinids. Walter died on 13 March 2019.

YUKIO IWATSUKI

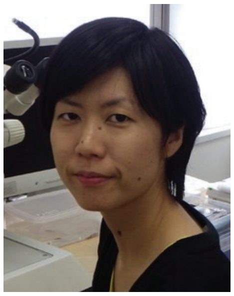
Yukio (Yuk) Iwatsuki is a professor in the Department of Marine Biology & Environmental Sciences, Faculty of Agriculture, University of Miyazaki, Japan. His research interests are the taxonomy, speciation, biogeography and rich resources of coastal fishes (snapper, silverbiddy, seabream, grunt, and others). He served as an editor of the Ichthyological Society of Japan, and as a member of the IUCN Snapper, Seabream and Grunt Specialist Group.

KELSEY C JAMES

Kelsey C James is pursuing a PhD at the University of Rhode Island with Dr Lisa Natanson and Dr David Bengtson. Her research focus is on the age and growth of skates and rays. This complements her MSc in Marine Science from Moss Landing Marine Laboratories under Dr Gregor Cailliet and Dr David Ebert where she worked on the life history of the starry skate. She also described a new species of chimaera, *Hydrolagus melanophasma*, from the eastern North Pacific, and compiled and managed a global database on fisheries bycatch of marine megafauna (chondrichthyans, marine mammals, seabirds and sea turtles) at San Diego State University. She developed her passion for and skills in animal husbandry and scientific collecting during her BS at University of California, Santa Barbara.

PATRICIA J KAILOLA

Patricia J Kailola is an Australian who has spent most of her working life in the Pacific region, with shorter periods in Australia and Southeast Asia. Her interest is in tropical fish systematics (emphasis on ariid catfishes), zoogeography, fisheries management and tropical aquatic biodiversity (particularly invasive fish species). Patricia co-authored *Continental shelf fishes of northern and north-western Australia: An illustrated guide* (1985, with K Sainsbury and G Leyland) and *Trawled fishes of southern Indonesia and north-western Australia* (1984, with Thomas Gloerfelt-Tarp). In Papua New Guinea, she maintained and added to the national fish collection for many years and later collated a substantial library of 'grey' fisheries literature (2003, *Aquatic resources bibliography of Papua New Guinea*). Patricia lives most of the time in the Republic of the Fiji Islands where she works with a human-rights orientated national non-governmental organisation and fulfils her obligations as an Honorary Fellow at the Institute of Applied Sciences, University of the South Pacific.



ERI KATAYAMA

Eri Katayama received her BSc, MSc and PhD in Biology at the Kochi University in Japan from 2000 to 2011. She continued her studies for a further year in the Laboratory of Marine Biology under Dr Hiromitsu Endo and worked on a taxonomic review of the family Trichonotidae at the Laboratory of Marine Biology. She started to dive around Shikoku Island in southern Japan in 2004 and collected many shore fishes. She has participated in compiling several field-guide books and checklists of islands of southern Japan. In 2012 she moved to Tsukuba to work as a research assistant in the Department of Zoology, National Museum of Nature and Science, where she worked on building a database of SEM images. In 2017 she started to work at the Research Institute of Marine Invertebrates, where she is working to coordinate these supporting projects for Japanese researchers of the marine invertebrates. Her current research is a taxonomic study of the genus *Limnichthys* using morphology and molecular analysis. She is particularly interested in the systematics, biogeography and diversity of shore fishes, such as sanddivers, clingfishes and gobies.

TOSHIO KAWAI

Toshio Kawai obtained a PhD degree from the Graduate School of Fisheries Sciences, Hokkaido University, Hakodate, Japan, in 2006. He joined several deep-sea research cruises in Japanese, Indonesian and Peruvian waters during his school days. He worked in Bali, Indonesia, as a senior researcher at a private research laboratory sponsored by Kyowa Concrete Industry Co., Ltd, in July 2006 until March 2007, during which time he researched the marine environment around Bali by remotely operated vehicle (ROV). He returned to Japan in April 2007, and worked in the Fish Division of the National Museum of Nature and Science, Tokyo, as a research assistant for two years. Thereafter he became an assistant professor at the Hokkaido University Museum, and advises on the ichthyology course in the School of Fisheries Sciences and the Graduate School of Fisheries Sciences, Hokkaido University. In addition, Toshio is the collection manager for fishes in the Fisheries Science Center, which is a branch of the Hokkaido University Museum with more than 200 000 fish specimens that have been deposited in the branch. He also runs an annual parataxonomist training course in ichthyology. Toshio's research interests focus on the systematics, taxonomy and morphology of Peristediidae. He is dedicated to documenting marine fish fauna in northern Japan, including Hokkaido, which is the northernmost main island in Japan, where several species new to the area are discovered every year. He is also interested in marine fish fauna around Southeast Asia, especially the deep-sea fishes. He has authored more than 50 academic papers, reports and books.

JENNY M KEMPER

Jenny M Kemper received her BS in Biology from Florida State University in 2007 and her MS in Marine Biology with the Pacific Shark Research Center at Moss Landing Marine Laboratories in 2012. Her MS thesis research was on the feeding ecology of skates in Prince William Sound, Alaska. While working on her MS thesis, Jenny described two new species of chimaeroid fishes, one from South Africa, and the other from the Bahamas, which stimulated her interest in taxonomy and systematics. In 2012, she began her PhD at the Medical University of South Carolina in the Marine Biomedicine and Environmental Sciences Programme. Her dissertation research is on the phylogenetics of extant chimaeroid fishes (Chimaeriformes), an important yet understudied group of chondrichthyan fishes. Her goal is to use molecular data to estimate the evolutionary relationships of chimaeras, with comprehensive species sampling and the use of both nuclear and mitochondrial markers. She has further described another species of chimaera from New Zealand in 2015. She has co-authored several book chapters on chimaeras. Her main research interests are phylogenetics and systematics of chimaeroid fishes, cytogenetics, and understanding sex determination mechanisms and chromosome evolution in vertebrates.

SEISHI KIMURA

Seishi Kimura received his BSc and MSc degrees in fisheries science from Mie University, Japan, and was then employed as an assistant professor at the Fisheries Research Laboratory, Mie University (FRLM), located in Shma, Mie Prefecture, in 1978. He studied fisheries ecology of some commercial fishes, especially the haemulid *Parapristipoma trilineatum*, and obtained a PhD degree from Kyoto University in 1987. Seishi is now a professor and director of FRLM, and his research interests are the taxonomy, phylogeny and zoogeography of Indo-Pacific fishes, especially Atherinidae, Carangidae and Leiognathidae. He is also interested in coastal fish fauna in Southeast Asia. He served as Editor-in-Chief (2004–2007) and President (2012–2013) of the Ichthyological Society of Japan. He has published more than 150 scientific papers and edited three field guides of fishes: *Fishes of Bitung, Northern Tip of Sulawesi, Indonesia*; *Fishes of Liobong Island, West Coast of Southern Thailand*; and *Fishes of Andaman Sea — West Coast of Southern Thailand*. His latest work is on *Fishes of Ha Long Bay, Northern Vietnam*.

LESLIE W KNAPP

Leslie W Knapp obtained his BS from Cornell University in 1952, an MA in Fisheries Biology in 1957, and a PhD in Vertebrate Zoology in 1964 from Cornell. From 1963 to1992 he was Supervisor for Vertebrates at the Smithsonian Oceanographic Sorting Center and was its director from 1982 to 1988. In 1992 he joined the staff of the National Museum of Natural History, Smithsonian, as a marine biologist, and became a research associate in 1998. Les played an active role in the American Society of Ichthyologists and Herpetologists (Publications Secretary, 1968–1973; Board of Governors, 1973–1978); the Biological Society of Washington (Proceedings Vertebrate Editor, 1976–1978; Treasurer 1981–1986; President, 1990–1991); and the American Association of Zoological Nomenclature (President, 1996–1997). His field experience included collecting freshwater fishes in eastern US and marine fishes in the Red Sea, various Western Indian Ocean locales, coasts of Colombia, Peru and Chile and in the Philippines. Les published extensively on fishes of the families Percidae, Bembridae and Platycephalidae before he passed away in 2017.

JAMES DS KNUCKEY

James DS Knuckey earned his BS in Marine Biology at San José State University, California and is working on his MSc at the Pacific Shark Research Center at the Moss Landing Marine Laboratories under the supervision of Dr David Ebert. During his undergraduate studies James, in collaboration with Dr Ebert, described a new species of lanternshark (*Etmopterus*) from the western North Pacific. His MSc thesis research project is on the phylogenetics of eastern North Pacific skates (Arhynchobatidae: *Bathyraja*), incorporating both traditional morphological and meristic methods, and newer innovative molecular techniques. James has also studied fish assemblages in San Francisco Bay, and researched the gill morphology of mosquitofish (*Gambusia affinis*). His main research interests are taxonomy, phylogenetics, parasitology of fish, and deep-sea assemblages.

HELEN K LARSON

Helen K Larson is Emeritus Curator of Fishes, Museum and Art Gallery of the Northern Territory, Darwin. She is also a research associate, Museum of Tropical Queensland, Townsville, and Adjunct Associate Professor, School of Marine and Tropical Biology, James Cook University, Townsville. Her research interests are the taxonomy, systematics, ecology and behaviour of Indo-Pacific mangrove and coral reef fishes, especially gobioid fishes (gobies, gudgeons, mudskippers). Much of her work is on the taxonomy of estuarine and coral reef gobiid fishes, preferably by way of generic revisions. The goby subfamily Gobionellinae is of particular interest to her. She has been actively publishing since 1975. Helen retired from the Museum and Art Gallery of the Northern Territory in late 2009 and moved to north Queensland where she works on gobies in association with the Museum of Tropical Queensland. Her expertise as a taxonomist/systematist is regularly sought from around the world, whether as a reviewer of manuscripts or identifier of unknown fish species, and she has the honour of being the recipient of 13 eponyms to date. She is on the editorial boards of several journals and is an honorary foreign member of the American Society of Ichthyologists and Herpetologists.

PETER R LAST

Peter R Last is the former director of the Australian National Fish Collection, Hobart, Australia, and now a retired honorary research fellow. Over the past 40 years he has specialised in the taxonomy and biogeography of Indo-Pacific fishes, with particular emphasis on shark and ray faunas across the region. He has more than 300 publications, including technical works, books and book chapters, aimed at both scientists and the general public.

JEFFREY M LEIS

Jeffrey M Leis is a senior (retired) fellow in Ichthyology at the Australian Museum in Sydney, and an adjunct professor at the University of Tasmania. He has studied fish larvae in the warmer waters of the Indo-Pacific since the late 1970s. Jeff did his BSc in Zoology at the University of Arizona and began to study the porcupine fishes (Diodontidae) whilst a graduate student. He subsequently received his PhD in Biological Oceanography at the University of Hawaii. After 18 months in southern California, studying the impact of nuclear power stations on fish larvae, he moved to Australia. Jeff's research on fish larvae has provided a taxonomic base for their study in the Indo-Pacific. He has used them to reveal the relationships of fishes, and has shown their behaviour can strongly influence dispersal in the ocean. In 2014, he retired from the museum and took up an adjunct professorship with the University of Tasmania's Institute for Marine and Antarctic Studies, where he continues his ichthyological studies.

JOHANN RE LUTJEHARMS

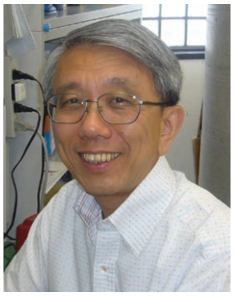
Johann RE Lutjeharms had an intense interest in the biogeography and life history of fishes and their relationship to the physical/ chemical marine environment. This outlook had its origin in the multi-disciplinary PhD education he received at the University of Washington after gaining his MSc degree at the University of Cape Town in 1971. His oceanographic interest extended geographically from the Southern Ocean near the continent of Antarctica to the tropical seas of the Indian and Atlantic oceans. His research activities in these regions resulted in approximately 500 publications, including the internationally acclaimed book, *The Agulhas Current*. He collaborated closely with colleagues from many countries, including the Netherlands, Germany, France, Italy, Russia, Brazil, Israel, Mozambique and Kenya. For his academic work he received numerous awards, amongst others, the Humboldt-Forschungspreis from Germany, the Fridtjof Nansen Medal of the European Geosciences Union, the Havengaprys for physical sciences of the Suid-Afrikaanse Akademie vir Wetenskap en Kuns and the John F. W. Herschel Medal of the Royal Society of South Africa. He received honorary doctorates from Rhodes University, the University of Pretoria and the University of Johannesburg and was a recipient of the Order of Mapungubwe, the highest civil honour the South African State bestows. Johann passed away in 2011.

B MABEL MANJAJI-MATSUMUTO

B Mabel Manjaji-Matsumoto is a senior lecturer and head of the Endangered Marine Species Research Unit, Borneo Marine Research Institute, Universiti Malaysia Sabah. She holds a PhD in Zoology (University of Tasmania), and BSc (Hons) in Marine Science (Universiti Kebangsaan Malaysia), and has 20 years of work experience in the field of elasmobranch (sharks and rays) biodiversity. Her range of research interests includes ichthyology (fish studies), marine conservation, and sustainable fisheries.

ANDREA D MARSHALL

Andrea D Marshall has been working in Mozambique since 2003. Educated in the United States and Australia, Andrea was the first person in the world to complete a PhD on manta rays. After completing her thesis, Andrea stayed on to spearhead the conservation efforts of manta rays in Mozambique. Her research examines aspects of the biology, reproductive ecology, habitat use, migrations and social behaviour of both species of *Manta*.



KEIICHI MATSUURA

Keiichi Matsuura is Curator Emeritus of Department of Zoology at the National Museum of Nature and Science, a major natural history museum in Japan, where he has studied fishes since 1979. His research specialty is tetraodontiform fishes, particularly their taxonomy and phylogeny. His field work has taken him to many parts of Japan and its adjacent areas, and also to tropical regions in the Indo-Pacific. He served as the president of the Ichthyological Society of Japan and as a vice-chair of Global Biodiversity Information Facility (GBIF). He has published many papers and books on fishes, including field guides for tropical marine fishes in Southeast Asia.

JOHN E MCCOSKER

John E McCosker is Senior Scientist and the first Chair of Aquatic Research at the California Academy of Sciences. From 1973 to 1994, he was Director of the Steinhart Aquarium in San Francisco. He received his PhD in Marine Biology from the Scripps Institution of Oceanography. His research activities around the world include field and laboratory studies ranging from microscopic bioluminescent bacteria to macroscopic man-eating elasmobranchs. He has also studied the taxonomy of snake eels and moray eels, the marine life of the Galápagos, and the biology of salmonid fishes. In addition he has researched dispersed and renewable energy sources as alternatives to national vulnerability and war, and contributed to the public understanding of sustainable seafoods. He is the author of more than 260 popular and scientific articles and books. His research on white shark behaviour and the deep-sea life of the Galápagos have been featured in numerous television documentaries.

MICHAEL MAIA MINCARONE

Michael (Mike) Maia Mincarone is Professor of Zoology at Universidade Federal do Rio de Janeiro, and curator of the NUPEM Fish Collection. He obtained his Bachelor degree in Oceanography from the Universidade do Vale do Itajaí (Itajaí, SC) and his PhD in Zoology from the Pontifícia Universidade Católica do Rio Grande do Sul (Porto Alegre, RS). Part of his PhD was conducted at the National Museum of Natural History, Smithsonian Institution (Washington, DC), and California Academy of Sciences (San Francisco, CA). At the beginning of his career Mike focused on the systematics of hagfishes (Myxiniformes), but his current research includes the systematics and conservation of many other deep-sea fishes.

RANDALL D MOOI

Randall D Mooi received his PhD in Zoology from the University of Toronto (Ontario, Canada) in 1991, working on the systematics and biogeography of percoids, particularly the Plesiopidae and putative relatives. Following a post-doctoral fellowship in the Division of Fishes of the Smithsonian Institution investigating systematics of deep-sea fishes (Chiasmodontidae, Champsodontidae), he was Curator of Fishes and Section Head of Vertebrate Zoology at the Milwaukee Public Museum in Wisconsin (USA) for 12 years. While there he was involved in several collaborative expeditions to Indo-Pacific coral reefs, surveying fishes in Thailand, French Polynesia, the Philippines, Solomon Is., Vanuatu and Australia. In 2004 he became Curator of Zoology at the Manitoba Museum (Winnipeg, Manitoba). This necessitated a broadening of research interests and field work to include freshwater fishes, birds, snakes and amphibians. He is an adjunct professor in the Department of Biological Sciences at the University of Manitoba and also serves on the Steering and Technical Committees of the Manitoba Breeding Bird Atlas. He continues to examine systematics of percomorph taxa, particularly gobioids, and ponders systematic methods.

KATE A MOOTS

Kate A Moots completed a BSc in Zoology at the University of Alberta, followed by an MSc at the University of British Columbia in Vancouver. She completed her MPhil and PhD at the University of Kansas, working with Dr Edward O Wiley and Dr Frank B Cross, on the phylogenetic relationships of ~80 species of North American freshwater darters (Percidae). Both during and after completion of her PhD, Kate worked as Collections Manager for the University of Kansas Division of Ichthyology, where she was responsible for ~500 000 specimens. In 2000, Kate married Jeffrey Moots and moved to Saipan, where she worked as a fisheries biologist, an environmental consultant, and taught Developmental Mathematics and Marine Biology at Northern Marianas College. In 2004, she was awarded an NRF post-doctoral fellowship at the South African Institute for Aquatic Biodiversity, where she worked on the families Solenostomidae and Syngnathidae, and participated in field research in the Seychelles. This work served as the nucleus for her work on the chapters in this book and helped to develop her current research programme. Kate is now an associate professor at the University of Guam, where she teaches a variety of undergraduate biology lectures and labs, including Human Anatomy and Physiology, Comparative Vertebrate Anatomy, and Principles of Biology. During the summer, she travels, works on research, and scuba dives as much as possible.

HIROYUKI MOTOMURA

Hiroyuki Motomura completed his PhD in 2001 at Miyazaki University, Japan. For his thesis, Dr Motomura revised the family Polynemidae (threadfins) and published part of the thesis as an issue of FAO Species Catalogue series (*Threadfins of the World*). He worked at the National Museum of Nature and Science, Tokyo, in 2002, and at the Australian Museum, Sydney, and CSIRO Marine & Atmospheric Research, Hobart, between 2003 and 2005. Hiroyuki has been employed at the Kagoshima University Museum, Japan, since October 2005, and has established a fish collection of 100 000 specimens collected mainly from southern Japan. He has published more than 350 papers and 40 books, and is currently working on a revision of the family Scorpaenidae in the Indo-Pacific. He has been a Professor of Ichthyology since 2010 and currently is the director of the Kagoshima University Museum.

THOMAS A MUNROE

Thomas (Tom) A Munroe received his BS and MS degrees in Marine Biology from Southeastern Massachusetts University located in North Dartmouth, Massachusetts. He began his career at the Systematics Laboratory in 1987 after finishing a PhD degree at the Virginia Institute of Marine Science, College of William and Mary, and a post-doctoral fellowship in the Division of Fishes, Museum of Natural History, Smithsonian Institution where he is now employed as an ichthyologist at the National Systematics Laboratory (NOAA's National Marine Fisheries Service). Tom specialises in the systematics and taxonomy of the Pleuronectiformes, the flatfishes, with a special interest in the families Cynoglossidae (tonguefishes) and Soleidae (soles). He has conducted research on these and other flatfishes at sites located in different regions of the world. Past work has included systematic revisions of tonguefishes from both the eastern and western Atlantic Ocean and he has also described several species of tonguefishes from the eastern Pacific and Indo-Pacific oceans. Tom has contributed species assessments for tonguefishes and other flatfishes for several FAO regional species identification guides. His present research interests focus on continued efforts to discover and describe the biodiversity of flatfish species in the cynoglossid genera *Symphurus*, *Cynoglossus*, and *Paraplagusia*, as well as the soleid genus *Soleichthys*. Other research involves systematic studies of flatfishes from New Zealand, Australia, the eastern Pacific and Indo-Pacific regions, and the Americas.

TETSUJI NAKABO

Tetsuji Nakabo is co-author of the account of the Sphyraenidae. He is a Japanese ichthyologist who was based at the Kyoto University Museum, and a professor at Kyoto University, Kyoto, Japan, until his retirement in 2015. Nakabo has published on fish systematics and taxonomy.

JOSEPH S NELSON

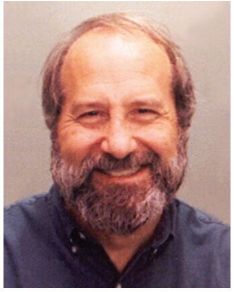
Joseph S Nelson obtained his PhD in 1965 from the University of British Columbia under Dr CC Lindsey and then spent three years at Indiana University. A long career at the University of Alberta followed from 1968, where he taught courses and supervised many graduate students before his retirement in 2002. Joe passed away in 2011. He wrote research papers on a wide variety of topics, such as hybridisation, gasterosteids, *Antipodocottus*, psychrolutids, creediids, percophids, and trichonotids. He is probably best known as author of *Fishes of the World* (4th edition, 2006) and co-author of the *Fishes of Alberta* (2nd edition, 1992). He served as Chair of the American Fisheries Society/American Society of Ichthyologists and Herpetologists, Committee on Names of Fishes (1991–2010), resulting in the 2004 book *Common and scientific names of fishes from the United States, Canada, and Mexico*, 6th edition, American Fisheries Society, Special Publication 29. He received many awards such as: the Robert H. Gibbs, Jr. Memorial Award, 2002; the Robert K. Johnson Award for Excellence in Service, 2010, American Society of Ichthyologists and Herpetologists; the J. Dewey Soper Award, 2003, Alberta Society of Professional Biologists; the Artedi Lecturer Diploma, 2008, Royal Swedish Academy of Sciences; and the Fry Medal, 2010, Canadian Society of Zoologists.

JØRGEN G NIELSEN

Jørgen G Nielsen, Curator Emeritus of Fishes at the Zoological Museum, Natural History Museum of Denmark, worked at the museum as a curator from 1959 until he retired in 2002. In his first years, he continued his MSc interest in flatfishes, but soon changed to the study of deep-sea fishes, especially those belonging to the very diverse order, the Ophidiiformes. During his retirement he has continued revising ophidiiform genera, often in collaboration with his successor, Peter Rask Møller. He has participated in several deep-sea cruises and published about 160 scientific papers.

LYNNE R PARENTI

Lynne R Parenti has been a curator of fishes and research scientist at the Smithsonian's National Museum of Natural History since 1990. She received a BS in 1975 from the State University of New York at Stony Brook and was awarded a PhD in 1980 from the joint graduate training programme in systematic biology between the American Museum of Natural History and the City University of New York. Her research focuses on the comparative anatomy, phylogenetic systematics and biogeography of freshwater and marine fishes, in particular atherinomorphs and gobioids; higher-level phylogenetic relationships of osteichthyans; historical biogeography; and the use of new or under-studied morphological characters in systematic ichthyology, such as those of reproductive morphology. Lynne is a co-editor of *Interrelationships of Fishes* and *Ecology of the Marine Fishes of Cuba*, which received an annual award from the Academia de Ciencias, Cuba, in 2002, for an outstanding scientific publication. She is also co-author of *Cladistic Biogeography* and *Comparative Biogeography,* which received the Smithsonian Secretary's Award for an outstanding research publication in 2010. Among her other honours, Lynne was elected President of the American Society of Ichthyologists and Herpetologists (ASIH), the first female ichthyologist to hold that office, and received the Robert H. Gibbs, Jr. Memorial Award for Excellence in Systematic Ichthyology for an outstanding body of published work in systematic ichthyology from ASIH in 2013. She is an elected Fellow of the American Association for the Advancement of Science and was an Artedi Lecturer, 2005, at the Royal Swedish Academy of Sciences. As an adjunct professor at the George Washington University, she directs the research of and advises graduate students in systematic ichthyology. Fieldwork has taken her around the globe to areas including New Guinea, Sulawesi, Borneo, the Malay Peninsula, Tasmania, China, Taiwan, Singapore, Surinam, Cuba and Hawaii.



THEODORE W PIETSCH

Theodore (Ted) W Pietsch is Professor Emeritus at the School of Aquatic and Fishery Sciences, and Curator Emeritus of Fishes at the Burke Museum of Natural History and Culture, University of Washington, Seattle, where he has spent most of his career as a professor mentoring graduate students and teaching ichthyology to undergraduates. He is a fellow of the California Academy of Sciences, the Gilbert Ichthyological Society, the Linnean Society of London, the American Association for the Advancement of Science, the University of Washington Teaching Academy, an honorary member of the Ichthyological Society of Japan and of the Russian Hydrobiological Society, a member of the Washington State Academy of Sciences, and Correspondant du Museum, Museum national d'Histoire Naturelle, Paris. He is interested primarily in marine ichthyology, focusing on the relationships, evolutionary history, functional morphology, behaviour, and reproductive biology of teleosts, particularly deep-sea taxa. As former curator of the fish collection of the Burke Museum of Natural History and Culture, he is also interested in natural history collections and collection building, and in biotic survey and inventory, the latter best exemplified by a decade-long series of expeditions to collect plants and animals on the islands of the Kuril Archipelago in the Russian Far East. He has published extensively on the history of science, especially the history of ichthyology.

STUART G POSS

Stuart G Poss received a BA in Zoology at UCLA (*cum laude*), a MS in Marine Biology at San Francisco State University, and a PhD in Evolutionary Biology at the University of Michigan. He was a post-doctoral fellow at the Academy of Natural Sciences, Philadelphia, worked as Collections Manager at the California Academy of Sciences, and was Senior Ichthyologist and Curator at the Gulf Coast Research Laboratory before retirement. He is currently a research associate at the California Academy of Sciences. He is interested in the biology of scorpaenoid fishes, particularly their taxonomy and systematics, with special emphasis on the study of morphometrics and variation in body morphology and its implications for other facets of their zoology. His work makes use of multivariate analyses to identify and characterise species and to study relative rates at which various morphological features change in both ontogeny and phylogeny. In addition, he is interested in the application of single-plane structured light range-sensing to morphometric studies and its potential for automated identification and feature extraction. He has also published on lancelets and the biology of endangered and non-indigenous species in the Gulf of Mexico.

HELEN A RANDALL

Helen A Randall obtained her BA in Biology at Boston University (*cum laude*) in 1949, followed by an MA in 1950. She was a teaching assistant in zoology at the University of Hawaii from 1950 to 1953, and married Jack Randall in 1952. In 1955, with a fellowship from Yale University and the Bishop Museum, Jack, Helen, their two-and-a-half-year-old daughter, Loreen, plus one crew member sailed their ketch to Tahiti to study the food habits of groupers and snappers being considered for introduction to Hawaiian waters. They spent an idyllic year doing their research in Moorea. Then followed almost ten years in the Caribbean, before returning to Hawaii, where, over the years, Helen was involved in a variety of projects. Since 1975, she has been a research assistant at the Bishop Museum in Honolulu, working with Jack on the systematics of Indo-Pacific fishes and as a reviewer of scientific manuscripts. She has also been Managing Editor for *Indo-Pacific Fishes* since 1982. Helen has published 11 papers.

JOHN E RANDALL

John (Jack) E Randall began his ichthyological studies at UCLA in 1948 and obtained a BA in Zoology with honours. This was followed by employment as a teaching assistant and other work to pay off his debts before sailing his ketch, the *Nani*, to Hawaii in 1950 where he took up a post as a graduate assistant in zoology. His long career has included innumerable field trips, with thousands of hours underwater and five years as Professor of Zoology at the University of Puerto Rico (1961–1965). He is widely regarded as the undisputed master of Indo-Pacific fishes, and has more than 550 papers to his name. He wrote several regional taxonomic guide books, authored more than 500 new species of fishes, and had 39 species named after him. He was the first to explain the origin of ciguatera poisoning, and discovered that the broad band of bare sand around reefs, now known as the Randall Zone, was the result of overgrazing by herbivorous fishes. He developed the technique of taking photographs of fishes posed in specially designed photo tanks. In his nineties, Jack still continued to write and describe species. He died in April 2020 at the age of 95.

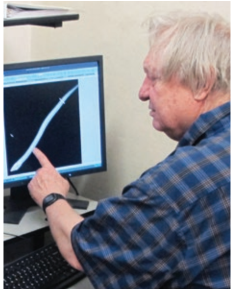
WILLIAM J RICHARDS

William (Bill) J Richards received his BA degree from Wesleyan University in 1958, his MS from Syracuse University and SUNY College of Forestry in 1960, and his PhD from Cornell University in 1963. He has been employed by NOAA Fisheries (and predecessor agencies) in Washington, DC and Miami throughout his career. Bill has received numerous awards from the United States Department of Commerce, including its Silver Medal in 1985, Bronze Medal in 2007, and NOAA's Distinguished Career Award in 2003. The American Fisheries Society honoured him with the O.E. Sette Award in 2002 and the Elbert H. Ahlstrom Lifetime Achievement Award in 2009. In 1992 he was chosen as a Scholar-in-Residence, Bellagio, Italy by the Rockefeller Foundation. He is a fellow of the American Institute of Fishery Research Biologists and a life member of the American Society of Ichthyologists and Herpetologists. He is also a member of Sigma Xi. He has presented aspects of his research at many scientific conferences in the US, and in Scotland, Japan, Guam, Italy, Spain, Canada, Mexico, Poland, France, Australia, South Africa, and Norway, thus earning wide international peer recognition. He served as editor of the *Fishery Bulletin* for three years, the *Bulletin of Marine Science,* and *Studies in Tropical Oceanography* for 23 years, as well as serving on the editorial boards of *Copeia*, *Fishery Bulletin*, and *Fishes of the Western North Atlantic*. In academia he served as a professor on the adjunct faculty of the University of Miami, has taught courses on the early life history of fish, and directed student research as chairman for seven PhD students and five MS students, plus served on committees of seven PhD and eleven MS students. His research interests have been broad, with over 300 published articles and three books on various aspects of ichthyology and marine ecology, including the ecology of early life history stages of fish, shrimp, and lobsters; the distribution and abundance of scombroid larvae; the relation of climate and environment to fisheries; and systematic studies of the trigloid fishes. He has participated in many research expeditions in the eastern Atlantic, Caribbean Sea, and Gulf of Mexico.

BERNHARD RIEGL

Bernhard Riegl is a professor of marine science and the head of the Department of Marine and Environmental Sciences at Nova Southeastern University in Fort Lauderdale, Florida. He is also a director of the National Coral Reef Institute at his university. His PhD is from the University of Cape Town. Since then, he has worked on coral reefs, first in the Western Indian Ocean and Red Sea, and later, all around the world. Other lines of research are in carbonate sedimentology and acoustic mapping of marine and lagoonal systems. Work has progressed from empirical to increasingly quantitative/theoretical, with a heavy modelling component. He has been actively engaged in the conservation of coral reefs, having served with or advised the marine conservation services in several African, Middle Eastern and South American countries. He is also actively involved in conservation initiatives in his home-base, Florida.

TYSON R ROBERTS



Tyson R Roberts is a research associate at the Smithsonian Tropical Research Institute, Panama, and advisor to the Institute of Molecular Biosciences, Mahidol University, Nakorn Pathom, Thailand. He studied at Stanford University where his greatest influences were ichthyologists George S Myers and Robert R Harry (name later changed to Robert Rofen). From there he travelled to Mexico, and to the Central Pacific on the Tethys Expedition of Scripps Institute of Oceanography in the summer of 1960. His undergraduate and graduate years at Stanford were interrupted by three years in tropical Africa: two years teaching at Achimota School in Ghana, during which time he collected fishes throughout the country, and he spent a year collecting fishes in the Congo including the rapids of the Lower Congo and the rain forest of the Cuvette Centrale. His preference for fieldwork led him to spend many years in the tropics with a particular focus on freshwater fish fauna. He has travelled to the Congo Basin and Lake Tanganyika, Cameroon, Thailand, Myanmar, India, Laos, Cambodia, Indonesia, Papua New Guinea, and most countries in South America.

BARRY C RUSSELL

Barry C Russell is Curator Emeritus of Fishes at the Museum and Art Gallery of the Northern Territory, and is a research fellow at Charles Darwin University, Darwin, Australia. He also co-chairs the IUCN Snapper, Seabream and Grunt Specialist Group. He has more than 45 years' research experience on the systematics, ecology and behaviour of tropical demersal fishes of the Indo-Pacific, has published more than 150 papers on the taxonomy and ecology of fishes, and has contributed 270 IUCN Red List assessments of fishes. His current research interests include the taxonomy and phylogenetics of lizardfishes (Synodontidae) and threadfin breams (Nemipteridae). He is also interested in the history of ichthyology, and is presently researching the ichthyological contributions of Lt James Barker Emery (HMS *Beagle*), and the French explorer, diplomat and naturalist, FL de Castelnau.

HUGO RS SANTOS

Hugo RS Santos is a biologist and curator of the Ichthyological Collections of the Zoology Department of the Universidade do Estado do Rio de Janeiro. He earned his PhD from the Museu Nacional in Rio de Janeiro, Brazil, in 2006. Hugo has been researching stingrays since 2004, and his PhD thesis includes taxonomic revision and morphology of western Atlantic dasyatid stingrays. He has described two new species of stingrays, and has published other papers, mainly on stingray taxonomy. He has also co-authored a popular identification guide to sharks and rays from Rio de Janeiro state, Brazil.

KUNIO SASAKI

Kunio Sasaki received his PhD degree in 1989 from Hokkaido University in fishery sciences (systematic ichthyology). In the same year, he joined the Department of Biology, Kochi University, as an assistant professor in marine biology. Since April 2006 he has been a professor at the same university, responsible for classes in marine biology, vertebrate zoology, and systematic ichthyology. His areas of research interest are taxonomy (mostly of croakers or drums) and the anatomy of fishes, the latter including bones, muscles and nerves. Recent publications are mainly focused on neuroanatomical aspects of various fish groups such as cyprinids, gobies, and puffers (co-authored with his MS and PhD students), in an attempt to use the structure of the nervous system as a source of phylogenetic characters. He has served as an editor of *Ichthyological Research* (published by the Ichthyological Society of Japan) since 1996.

BERNARD SÉRET

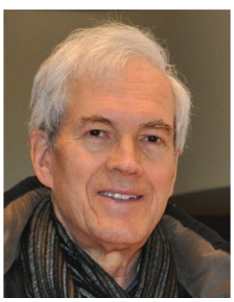
Bernard Séret is an ichthyologist specialising in the study of the chondrichthyan fishes (sharks, rays and chimaeras). He worked at the Institut de recherche pour le développement (IRD) for almost 40 years, and has been hosted by the Muséum national d'Histoire naturelle, Paris, for about 20 years. Retired since 2014, he continues his scientific work and consultancies. His research work concerns the biodiversity, fisheries and conservation of the chondrichthyan fishes. He has undertaken several scientific missions and participated in many exploratory cruises in the Atlantic, Southern Ocean and South Pacific. He is author/co-author of about 180 papers, with more than 120 on Chondrichthyes, including the description of several new species of sharks, rays and chimaeras; chapters on batoids in the FAO catalogue for ECA; and contributions to the *Rays of the World* book (Last *et al*. 2016). His interest in shark fisheries includes analysis of fishery data of French shark fisheries in European waters (he was the French representative at the ICES-WGEF); analysis of shark by-catches of French tuna fisheries (in collaboration with IRD fishery biologists); involvement in the programme MADE (measures to mitigate adverse impacts of fisheries targeting large pelagic fishes in the open ocean); and training fishery observers and officers to identify sharks and rays. His interest in shark conservation includes assessments made for both French and European bodies, and international organisations. He provided scientific advice on proposals for listing shark and ray species (CITES, IUCN Red List, OSPAR, etc.) and has been involved in the elaboration of several plans of action for the management and conservation of shark populations. He continues to be involved in the analysis of shark attack cases and provides advice on this matter. Bernard Séret is the former scientific head of the European Elasmobranch Association (EEA), and a member of the IUCN-SSG.

ILIA B SHAKHOVSKOY

Ilia B Shakhovskoy studied at Moscow State Institute of Food Industry from 1993 to 1998, majoring in Aquatic Bioresources and Aquaculture. He completed his postgraduate studies at the PP Shirshov Institute of Oceanology of Russian Academy of Sciences (IORAS) in 2001, under the supervision of Professor NV Parin. From 2001 to 2007 he was an engineer at the Laboratory of Ocean Ichthyofauna (IORAS). In 2011 he became a junior scientist, and in 2011 was appointed a scientific associate at IORAS. Ilia's primary interest is in systematics, distribution, biology, ecology and biogeography of flying fishes, and he worked on these fishes for 20 years before receiving his PhD in 2016. He has also worked on keeping and breeding hydrobionts in a closed system and on the marine biology of the White Sea. He has published 12 peer-reviewed papers.

CHARLES RC SHEPPARD

Charles RC Sheppard is Professor Emeritus at the University of Warwick, UK. His research has been focused on marine habitats in the tropics, especially coral reefs and the effects of humans upon them. He has been longstanding editor of the journal *Marine Pollution Bulletin*, and has written numerous papers and articles, including about 12 books on marine science during this time. He is on advisory panels for EU, Arabian and UK grant bodies (marine science); served on the advisory panel for the establishment of the first University of the Republic of Seychelles; became a review member of the Intergovernmental Panel for Climate Change from 2004; and has lately been the advisor on environmental matters to the Commissioner of UK Overseas Territories. In 2014 he was awarded the OBE for his services as advisor.



DAVID G SMITH

David G Smith received his undergraduate education at Cornell University where he was introduced to fishes by the noted ichthyologist, Edward C Raney. He subsequently attended the University of Miami, Florida, completing his MS and PhD degrees under the direction of C Richard Robins. He worked at the University of Texas Medical Branch at Galveston, and later, at the Museum of Comparative Zoology at Harvard University, before arriving at the Smithsonian Institution in 1989. David has specialised in the study of eels (Anguilliformes) and is considered one of the foremost authorities on the group. He officially retired in 2012, but continues his research. He is also interested in the history of ichthyology and has written several papers on this subject.

W LEO SMITH

W Leo Smith works at the Kansas University Biodiversity Institute and Natural History Museum where he is an associate professor and associate curator. His research focus is the comparative evolutionary biology of fishes and he contributed the section on the classification of serranoid fishes.

SHIRLEEN SMITH

Shirleen Smith is a museum specialist in the Division of Fishes, National Museum of Natural History, Smithsonian Institution, in Washington, DC. She has been with the museum since 1996.

WILLIAM F SMITH-VANIZ

William F Smith-Vaniz received his master's degree in Fisheries Biology from Auburn University and his PhD in Marine Sciences from the University of Miami. While in graduate school, he spent three months in Sri Lanka collecting specimens and data for a Smithsonian project on jacks and trevallies, which stimulated his interest in this family of approximately 150 species and led to his recognition as a global expert on the group. He has published descriptions of more than 80 new species in about a dozen families. He began his ichthyological career as a technician in the Smithsonian Fish Division before returning to graduate school; was a curator at the Academy of Natural Science of Philadelphia for 19 years; and then worked as a research scientist for the then-named Biological Resources Division of the US Geological Survey in Gainesville, Florida, before retiring in late 2006. He is a research associate of the Smithsonian Institution and the University of Florida, and also serves as consultant to the International Union for Conservation of Nature, participating in foreign workshops, and helping with IUCN Red List species assessments. He has authored two books, one on freshwater fishes of Alabama, the other on fishes of Bermuda, and over 100 scientific papers and book chapters. He was the recipient of the Robert H. Gibbs, Jr. Memorial Award presented by the American Society of Ichthyologists and Herpetologists (2011) for "an outstanding body of published work in systematic ichthyology."

MATEUS C SOARES

Mateus C Soares completed his PhD at the Universidade de São Paulo in 2011, under the supervision of Marcelo de Carvalho. His thesis focused on the myology and phylogeny of Chondrichthyes, describing, comparing and raising new morphological characters to test the hypothesis of shark monophyly (i.e., without the rays). He published articles on mandibular and hyoid musculature of sharks and was co-author of an anatomical guide to musculature of sharks, rays and chimaeras. He is chiefly interested in the comparative anatomy and evolution of fishes, especially Chondrichthyes. Currently he is working as an environmental consultant and professor.

JOHN S SPARKS

John S Sparks, Curator-in-Charge and Professor, Department of Ichthyology, American Museum of Natural History, travels the world in search of bioluminescent and biofluorescent marine organisms. His research focuses on the systematics and biogeography of recent fishes, with a particular interest in the evolution and diversification of luminescent signalling systems and fluorescence in marine fishes. For these studies, John is heavily involved in the design and implementation of state-of-the-art underwater cameras and lighting systems. He has led numerous expeditions to Madagascar, where his work focuses on the diversity and biogeography of the island's endangered freshwater fishes, including cavefishes, and specialised hearing in cichlids. His recent fieldwork includes biotic surveys and inventories of freshwater, nearshore marine, and deep-sea fishes in Madagascar, the Indo-Pacific region, throughout Southeast Asia, South America, the western Atlantic, eastern Pacific, and the Caribbean. He is a professor in the Richard Gilder Graduate School at the Museum, an adjunct professor at CUNY and Columbia University, and a principal investigator with the museum's Sackler Institute for Comparative Genomics. He joined the museum in 2002 and served as lead curator of the museum's travelling exhibition *Creatures of Light: Nature's Bioluminescence*, and as co-lead curator of the new travelling exhibition *Life at the Limits: Stories of Amazing Species*. He also curated the temporary exhibit *The Exosuit* and produced two short films on marine biofluorescence, *Reefs Illuminated* and *Capturing the Ocean's Glow*. He received his PhD in Ecology and Evolutionary Biology from the University of Michigan in 2001.

VICTOR G SPRINGER

Victor G Springer obtained a BA from Emory University in 1948; an MS (Marine Biology), University of Miami, Florida in 1954 (major professor, Luis R Rivas); and a PhD (Zoology) in 1957 with Clark Hubbs at the University of Texas. He served in the US Army Medical Corp from October 1950 to September 1952 (the second year in Korea). His professional career includes work as a freshwater fisheries biologist (1950) and then as marine ichthyologist for the State of Florida from 1957 to 1961 (primarily life-history, ecological studies of fishes). From 1961 to 1962 he was contracted by the Division of Fishes, US National Museum of Natural History (USNM), to do systematic studies on sharks, before being employed as Associate Curator, Curator and Senior Scientist in Systematics, Anatomy, and Biogeography of Fishes (1962–2005). From 2005 he has been Curator Emeritus at the USNM. He has participated in fish-collecting expeditions to Florida, Texas, northern Mexico, Bahamas, Dominica, US North Atlantic, Bermuda, Great Barrier Reef, Taiwan, Korea, Philippines, Indonesia, Israel, Eritrea, St Brandon Shoals, Agalega, Pohnpei, Fiji and Rotuma.

KENNETH A TIGHE

Kenneth A Tighe graduated from Union College, Schenectady, New York, in 1970 after which he attended graduate school in the Department of Zoology, University of Rhode Island, completing his studies in 1975. Since 1982, he has worked at the National Museum of Natural History, Smithsonian Institution, where he has conducted research on the eel families Chlopsidae, Serrivomeridae and Synaphobranchidae.

FRANZ UIBLEIN

Franz Uiblein is a principal scientist in fish taxonomy and marine biology at the Institute of Marine Research, Norway (IMR). He is also a research associate at the South African Institute of Biodiversity (SAIAB) and the Vietnam National Museum of Nature (VNMN). In addition he has served as Editor-in-Chief of the international journal *Marine Biology Research*. His main research interests are ecology, diversity and evolution of marine fishes, but he has also worked on freshwater fishes, ostracods and salamanders. Franz began his work on goatfish and deep-sea fish taxonomy in 1992 as a deputy head of the marine fish collection at the Senckenberg Museum, Frankfurt, Germany. Three years later he co-organised a deep-sea conference in Vienna, Austria, and subsequently participated in research cruises off the Canary Islands and to the Great Meteor Seamount (eastern Central Atlantic). His *in situ* studies of deep-sea fishes began in 2000 when he analysed video footage from submersible dives in the NE Atlantic, followed by dives with the *Johnson Sea Link* submersible in deep canyons of the Gulf of Maine (NW Atlantic). After writing a review article in 2007 emphasising the importance of goatfishes (family Mullidae) for coastal monitoring and management, he began working on taxonomic revisions of the two goatfish genera *Upeneus* and *Mulloidichthys*.

RUDY VAN DER ELST

Rudy van der Elst, a research associate at the Oceanographic Research Institute (ORI), Durban, was born in Utrecht, Holland, but completed schooling and studies in South Africa. He graduated from the University of South Africa (BSc) and the University of Natal with an MSc. Since 1969 he has been employed at the South African Association for Marine Biological Research (SAAMBR), serving as Head of Research at ORI (1992–2011) where he was responsible for research management, including the planning, funding and execution of marine research programmes. Rudy has been engaged in diverse marine resource-use and conservation studies, especially those relating to management problems in small-scale, recreational and artisanal fisheries. These have included some unpopular conservation plans, including the protection of the shad (*Pomatomus saltatrix*), reduced beach netting and the conservation of sharks. He has been involved in the development of long-term fisheries monitoring and assessment projects, including the National Marine Linefish catch and effort system and the nationwide ORI tagging project that both interact with the fishing public. He also played a role in the original development of marine protected areas in KwaZulu-Natal, including the application for World Heritage status of the iSimangaliso Wetland Park. He has played a role in new fisheries and coastal zone policies of South Africa as well as in diverse projects in the West Indian Ocean for a variety of international agencies, including the World Bank, UNDP, Norad, IUC, WWF and WIOMSA. Rudy has supervised postgraduate students, published a considerable number of scientific papers, and several popular books on the fishes of southern Africa.

RICHARD P VARI

Richard P Vari began his research career working on the Terapontidae, a widespread family in marine, estuarine and freshwaters of the Indo-Pacific region. His subsequent research involved western North Atlantic seahorses (Hippocampidae) and phylogenetic, revisionary and biogeographic studies of various families in the Characiformes of South America and Africa, Gymnotiformes in South America, and Siluriformes in South America, Africa and South Asia. Richard passed away in 2016.

BENJAMIN C VICTOR

Benjamin C Victor is a research associate at the Guy Harvey Research Institute at Nova Southeastern University in Florida, USA, and founded the Ocean Science Foundation based in southern California, USA. Born and raised in Johannesburg, South Africa, Ben received a BA from Cornell University in New York, USA, and then moved to graduate school at the University of California, Santa Barbara (UCSB), where he received his PhD studying the population dynamics of bluehead wrasses in the Caribbean. He was part of the small group of pioneer researchers in the 1980s establishing larval recruitment as one of the most important factors controlling the populations of some coral reef fishes. As part of his studies, he was among the first researchers to use daily otolith increments to age reef fishes, and subsequently spent many years identifying larval reef fishes and exploring various aspects of the age and size of settling reef fish larvae. In addition, Ben surveyed fishes in the Galapagos Islands (where he discovered a new razorfish species, *Xyrichtys victori*), Baja California, Panama and Palau. After his graduate studies, Ben attended medical school at the University of California, Irvine (UCI), did an internship at Stanford University, and finished his residency in pathology (and an MBA) at UCI. He presently directs several medical laboratories in addition to continuing research on reef fishes. More recently, Ben has specialised in applying DNA-barcoding techniques to reef fish taxonomy, describing a number of new Caribbean gobies and blennioids. He has collaborated with taxonomists in resolving taxonomy and describing new species in the Indo-Pacific, mainly labrids, and more recently, the pempherids. He founded and edits the *Journal of the Ocean Science Foundation* as a vehicle for rapid, free, open-access publication of reef fish taxonomy.

ELAYAPERUMAL VIVEKANANDAN

Elayaperumal Vivekanandan (Vivek) acquired an MSc degree (Marine Biology, Annamalai University) in 1972 and his PhD degree (Fish Energetics, Madurai University) in 1976. He joined the Indian Agricultural Research Service as a scientist in the Central Marine Fisheries Research Institute (CMFRI) in 1976. Since then, he has served CMFRI as Senior Scientist and Principal Scientist, and in a variety of other capacities, including Head, Demersal Fisheries Division and Scientist-in-Charge, Madras Research Centre of CMFRI. He retired on superannuation as Principal Scientist and Scientist-in-Charge, Madras Research Centre of CMFRI in April, 2012, and rejoined the same centre as Emeritus Scientist and Consultant. Vivek's core areas of research are fish stock assessment, the valuation of coastal and marine biodiversity and ecosystems, coastal fisheries management, marine mammal conservation, and climate change. His contributions include fisheries management advisories, regional collaboration on marine fisheries in South and Southeast Asia with organisations such as FAO, Bay of Bengal Large Marine Ecosystem, Bay of Bengal Programme – Intergovernmental Organisation, and GiZ, Germany. On invitation, he served as Fisheries Team Leader in the UN Project "Oceanographic Survey in Support of Damage Assessment" at King Fahd University of Petroleum & Minerals, Dhahran, Saudi Arabia, for one year in 2003. FAO and BOBLME have recognised him as a Regional Trainer on Ecosystem Approach to Fisheries Management, and Science Communication. He has conducted a number of training programmes and trained about 200 young researchers on scientific paper writing and paper presentation in Phuket, Male, Colombo, Penang and Kochi. He was Chief Editor of the *Journal of Marine Biological Association of India* between 2008 and 2011. He has supervised PhD research programmes and five students acquired doctoral degrees from Madras University under his guidance. He has authored 157 publications, including 67 research papers in peer-reviewed journals, 15 books/chapters, and a number of national and international technical reports.

JEFFREY T WILLIAMS

Jeffrey (Jeff) T Williams is an ichthyologist and until recently was Collections Manager of Fishes at the National Museum of Natural History (NMNH), Smithsonian Institution, where he managed the largest fish collection in the world, conducting research on the systematics, taxonomy and biogeography of marine fishes, and on the interrelationship between the tectonic history of the Indo-Pacific and the geographic distribution of fishes. He received his BS from the Florida State University, MS from the University of South Alabama and PhD from the University of Florida. He has collected and studied marine fishes around the world and is an authority on the cryptic marine fishes, particularly in the Indian and Pacific oceans. He has led and participated in fish-collecting expeditions to the Gulf of Mexico, western Atlantic Ocean, Caribbean Sea, Hawaiian Islands, Ryukyu Islands, Philippine Islands, Seychelles, Fiji Islands, Tonga Islands, New Caledonia, Loyalty Islands, Australia, Vanuatu, Solomon Islands, Wallis & Futuna, French Polynesia (Mururoa, Moorea, Rapa, Gambier Archipelago, Marquesas) and Palau. He was with the NMNH from 1983–2020. He continues to focus his research on discovering and describing tropical marine fishes from remote and poorly surveyed areas around the world.

RICHARD WINTERBOTTOM

Richard (Rick) Winterbottom graduated with a BSc (Hons) from the University of Cape Town in 1967, and obtained a PhD from Queen's University, Ontario, in 1971. Post-doctorates at the Smithsonian Institution and the National Museum of Canada were followed by a three-year stint as Senior Lecturer at the JLB Smith Institute of Ichthyology at Rhodes University (now the South African Institute for Aquatic Biodiversity). He was appointed Assistant Curator of Fishes at the Royal Ontario Museum (ROM), Toronto, in 1978, as Associate Curator in 1979, and as Senior Curator in 1984. He was cross-appointed as Assistant Professor at the University of Toronto in 1980, Associate Professor in 1986, and Full Professor in 1990. He retired from the ROM in 2010, and was appointed Curator Emeritus. Rick's main research interests have involved the higher relationships of teleosts, which he investigated through studies of osteology and myology, and his 1974 paper on tetraodontiform comparative myology was one of the first to use Hennigian phylogenetic methodology for a group of fishes. His 1974 synonymy of teleost muscles is still frequently cited today. He has also been a proponent of historical biogeography, especially for the complex area known as the Coral Triangle. He has actively collected marine and mangrove fishes throughout the Indo-Pacific, and has been on or instigated about 20 major synoptic field trips. Thirteen species of fishes (mainly gobies) have been named in his honour. Current research interests devolve mostly on the systematics and biogeography of the Indo-Pacific goby genus *Trimma*, of which he has described or co-described 72 of the 106 currently recognised valid species.

MEGAN V WINTON

Megan V Winton grew up near the coast of Florida, USA, where she developed an early love for the ocean and a particular fascination with sharks. She has spent the past ten years researching elasmobranch populations on both coasts of the United States. Since 2019, Megan has been a research scientist at the Atlantic White Shark Conservancy, where she is working to improve scientific understanding of a new white shark aggregation site off Cape Cod, Massachusetts, USA. She is currently a PhD candidate at the University of Massachusetts Dartmouth's School for Marine Science and Technology and previously received her MSc in Marine Science from Moss Landing Marine Laboratories and her BSc in Biology from Emory University. Her research focuses on various aspects of fisheries biology and ecology, as well as the development of quantitative frameworks for interpreting and integrating tagging data into population assessments. Through her work on white sharks, Megan has become increasingly interested in the human dimensions of wildlife management and decision making.

DAVID J WOODLAND

David J Woodland completed his BSc Honours degree at the University of Queensland, studying the fishery potential of the Heron Island inner reef flat, operating a 100-metre arrowhead trap. With Dick Slack-Smith, who was running poison stations on the outer reef, they collected over 400 species and published, in effect, the first checklist of Great Barrier Reef fishes in 1963. Following three years with Victoria Fisheries working with trout, David moved to the University of New England (UNE) where he completed his PhD with a study on the energy budget of a population of freshwater crayfish. After being appointed as a tenured lecturer in population ecology at UNE, sabbatical leaves afforded him an opportunity to work overseas. Encouraged by Jack Randall, he began a revision of the Siganidae, the rabbitfishes, collecting in locations as varied as the Seychelles, Andaman Islands, Tonga and Palau. FAO asked him to add the Gerreidae and Leiognathidae to his contributions to their species identification publications, which led to revisionary studies of these families as well. In addition to publications in the zoogeography of the Indo-Pacific region, his other research interests have ranged from insect physiology to evolution of alarm signals. As an Adjunct Research Fellow at UNE, he continues his studies on the Siganidae.

LEANDRO YOKOTA

Leandro Yokota is post-doctoral student at the Universidade de São Paulo, Brazil, where he is leading a worldwide taxonomic review of the family Gymnuridae (Myliobatiformes, Chondrichthyes). He earned his bachelor degree in biological sciences from Universidade Estadual Paulista in 2002. His master's degree in animal biology was obtained in 2005 at Universidade Federal de Pernambuco, and he completed his doctorate in zoology in 2010 at Universidade Estadual Paulista. His primary research interests focus on the biology and taxonomy of sharks and rays, but he is also interested in the ecology, conservation and fishery biology of the group. Leandro Yokota is a member of the Sociedade Brasileira para o Estudo dos Elasmobrânquios (SBEEL).

UWE ZAJONZ

Uwe Zajonz, an aquatic zoologist by qualification, is an ichthyologist, ecologist and conservationist specialising in tropical marine ecosystems, notably of the Indian Ocean and the Arabian region. As an ichthyologist he started his career at the Senckenberg Research Institute and Museum of Nature, Frankfurt am Main, Germany, studying deep-dwelling fishes of the Red Sea and Gulf of Aden. He worked up a number of important deep-sea fish collections, describing several new species, and planned to earn his PhD from these studies. However, his participation in a number of research expeditions excited his interest in reef fishes, particularly in the Socotra Archipelago. The scope of his studies has expanded to include fish faunistics, community ecology, biogeography, trophic ecology and fisheries. His work also covers little-studied adjacent coastal regions of the northern Indian Ocean. Uwe's varied career includes experience in marine resource use and coastal zone management, conservation at the interface to sustainable development, marine climate change research, and project management. Uwe has returned to the Senckenberg Research Institute to manage a large conservation project on Socotra for the United Nations Environment Programme. He has since also obtained his long overdue PhD in Biology/Zoology.

ABBREVIATIONS AND ACRONYMS

aff. – abbreviation of the Latin *affinis*, meaning having a relationship with, but not identical to.

BD/A – body depth at anus.

BD/GO – body depth at gill opening.

BL – body length.

cf. – abbreviation of the Latin *confer*, *conferatur* (meaning to compare [with]).

CFSA – *Coastal Fishes of Southern Africa*.

DW – disc width.

FL – fork length.

FSO – *Fishes of the Southern Ocean*.

GR – gill rakers.

HL – head length.

IO– infraorbital (bone).

IP – initial phase.

IUCN – International Union for the Conservation of Nature.

LL – lateral line.

LSS – lateral scale series.

MVF – the number or mean number of predorsal, preanal and total vertebrae.

MVF H – mean number of vertebrae when the first vertebra arises on the head (H).

MYA – million years ago.

NWIO – northwestern Indian Ocean.

PA LL – preanal lateral line.

PCD – pharyngocutaneous duct.

POM – preoperculomandibular.

SFSA – *The Sea Fishes of Southern Africa*.

SL – standard length.

SO – supraorbital (bone).

sp. (pl. spp.) – a single species; used when the genus is known, but not the species name.

SSF – *Smiths' Sea Fishes*.

ST – supratemporal (bone).

SWIO – southwestern Indian Ocean.

TL – total length.

TP – terminal phase.

TRB – transverse rows of scales backwards (see figure, Family Gobiidae, Volume 5).

TRS (also TSR) – transverse rows of scales (or transverse scale rows).

VF – vertebral formula.

WIO – Western Indian Ocean.

GLOSSARY

For terms that are not included here, refer to the *Dictionary of Ichthyology* at http://www.briancoad.com/dictionary/complete%20dictionary.htm

A

abdominal – on or pertaining to the belly or abdomen.

acanthodian – a class of early jawed vertebrates that resembled sharks in overall appearance, characterised by fin spines on their dorsal and paired fins (sometimes in between these), divided into three or four orders, and presently considered not to be monophyletic; acanthodians were entirely Palaeozoic ranging from the early Silurian to the Permian.

acanthomorph / Acanthomorpha – the formal name for the ray-finned fishes.

acinar glands – glands formed by a cluster of cells, looking a bit like a raspberry; found in Synanceiidae (stonefishes).

acoustico-lateralis system – the sensory system that includes the ears and lateral line.

acronurus – the specialised larva of a surgeonfish (Family Acanthuridae).

acuminate – tapering to a point.

acuspidate – without cusps.

acute – sharply pointed.

adductor mandibulae – main muscle that closes the jaw.

adelphophagy – the consumption of one embryo by another within the uterus.

adenohypophysis – the anterior of the pituitary gland.

adhesive filaments – filaments that attach the eggs to the substrate.

adipose (tissue) – fatty.

adipose eyelid – more or less transparent tissue that partially covers the eye.

adipose fin – a small, fleshy fin behind the rayed dorsal fin, without bony elements.

adnate – joined from having grown together.

adpressed – flat against the body.

advect – to convey a fluid by horizontal mass movement.

aeolian – relating to the action of wind; wind-blown.

afferent circulation – taking blood to an organ.

air bladder – see *swimbladder*.

alar spines or thorns – very sharp spines near the lateral margins of the pectoral fins of male skates that serve to 'anchor' the male to the body of a female during copulation.

allele – a specific and unique form or variant of a particular gene or genetic marker; alleles typically refer to pairs of genes found on each of the two homologous chromosomes of a diploid organism.

allometric – differential changes with growth, e.g., eyes become larger relative to head length.

allopatric (distribution) – populations or species occupying mutually exclusive geographic areas.

allozyme – particular form of a given protein, coded by a particular allele at the gene responsible for encoding for that protein.

alveolar process of premaxilla – the thickened ridge on the premaxilla that contains the tooth sockets.

alveolar ramus – the tooth-bearing area of the lower jaw.

amphipods – a group of bilaterally compressed crustaceans.

amphitemperate – referring to a species that occurs in temperate water in both hemispheres, but is absent from the tropics.

ampullae of Lorenzini – jelly-filled tubes that open on a shark's skin and act as electroreceptors.

anadromous – fishes born in freshwater but spending most of their lives in the sea.

anal fin – the median, unpaired fin located on the ventral surface in front of the caudal fin.

anal papilla – see *genital papilla*.

anastomosing – joined together.

anchialine habitat – flooded inland marine caves with no direct connection to the sea.

anterior – on or towards the front (head) end of the fish.

anteromesial – toward the front and along the middle axis of the body.

anteroventral – relating to the underside of the front of the head; situated in front and below or toward the ventral side.

antitropical (distribution) – the distribution pattern where a group is found north and south of, but not in, the tropics (also anti-equatorial).

antrorse – pointing or curving anteriorly, specifically spines or fin elements.

anus – the exterior opening to the intestine; vent.

apex predator (apex of pelagic food web) – the predators that no other species tend to kill for food.

aphakic space – a space in the eye of fishes which is said to either enlarge the binocular field of vision or enhance the relative illumination of a portion of the retina of the fish.

apomorph / apomorphy / apomorphic – an evolutionarily derived or 'specialised' character or feature of an organism.

aposematic – denoting colouration or markings serving to warn or repel predators.

arcuate – curved like a bow.

articular process – the projection of a vertebra that articulates with the adjacent vertebra; also called a zygapophysis.

articulating – attached by means of a moveable joint.
artisanal fishery – a traditional fishery involving skilled but non-industrialised fishers; typically a small-scale decentralised operation.
ascending process – a vertical extension of the anterior of the premaxilla.
ascidians – tunicate animals, including sea-squirts and red bait.
attenuate – thin and stretched out.
autapomorphic characters – characters that are unique to a clade, and not shared with any other clade, such as the teeth fused into a beak and fused to the jaws.
autogenous – independently generated; without external influence.
autotomy or self-amputation – the ability of certain animals to deliberately cast off part of the body, most commonly known in lizards that 'lose' part of their tail when threatened.
auxiliary scales – small scales superimposed on the surface of larger scales.
axil – the inner or posterior part of the base of a fin.
axillary process (or scale) – enlarged, usually elongated scale or group of scales at the base of the pectoral or pelvic fins of some fishes.

B

bacterial luminescence – the generation of light by the action of an enzyme on the light-producing molecule luciferin.
barbel – fleshy, tentacle-like process near the mouth of some fishes.
barotrauma – gas expansion in the swimbladder leading to haemorrhaging and death.
basal – at or towards the base.
basibranchial – median ventral cartilage or bony element in a branchial arch, behind the tongue.
basidorsals – two wedge-shaped, arched cartilages that form a continuous neural arch with the interdorsals to protect the spinal cord.
basipterygial process – processes on either side of the throat.
basipterygium – pelvic bone or cartilage to which the pelvic fin is attached.
bathyal – the benthic habitat from 200 m to ~1 000 m.
bathypelagic – the deep part of the oceanic zone, from 1 000 m to 4 000 m.
batoid – a flat elasmobranch fish, e.g., skate or ray, with the pectoral fins fused to the sides of the head and the gill openings on the ventral surface.
batoids – refers to the monophyletic group that contains all of the orders of rays.
bauplan – a body plan; a generalised set of morphological features shared by a group of organisms, especially at higher levels of classification, such as a phylum.
benthic – living on or close to the bottom.
benthopelagic – occurring near or just above the bottom of the sea; the depth zone about 100 m off the bottom at all depths below the edge of the continental shelf.
bicuspid – a tooth with two cusps or points.
bifurcate – split or divided into two parts; forked at tip.
bilobate – having two lobes.
biogenic – produced by living organisms.
bioluminescence – the production and emission of light by a living organism; the ability to produce light.
bioluminescent oesophageal diverticula – outgrowths of the oesophagus that contain bioluminescent bacteria.
biserial – arranged in two rows or series.
body length – the distance from the posterior opercular margin to caudal-fin base.
bommie – a large mound of corals some distance from the shore.
bony contact organs – in *Oryzias*, dermal bony outgrowths that project from a fin ray, surrounded by epidermis through which the bony outgrowths may protrude.
brachyuran crabs – typical crabs with the abdomen folded in under the thorax/carapace.
brack / brackish – with a salt concentration or salinity between fresh and sea water, i.e., 0.5–30 parts per thousand.
branched ray – a soft or segmented fin ray that is split into two or more parts distally.
branchial – pertaining to the gills.
branchiostegal membrane – the tissue supported by the branchiostegals and forming the lower wall of the gill cavity.
branchiostegals – bony 'rays' supporting the branchiostegal membrane on the underside of the head.
buccal – pertaining to the mouth cavity.
buccopharyngeal pads – pads at the back of the mouth and beginning of the gut.
bucklers – bony plates located at the base of certain fins or on the belly.
bulla (pl. bullae) – a rounded structure.
bycatch – the other fish and organisms trapped by commercial fishing nets during fishing for a particular species.

C

caducous – easily shed (deciduous), usually scales.
calanoid copepods – small crustacea belonging to Order Calanoida, and found in the plankton.
canine – conical pointed tooth, usually larger than other teeth in the mouth.
caniniform – having the shape of a canine tooth.
cardiform teeth – numerous, pointed teeth arranged in distinct rows.
carinate – with a keel or edge.
carnivorous – feeding on animals.
cartilage – skeletal tissue, usually soft and flexible, and in bony fishes it is mostly replaced by bone during the early growth stages.
catadromous – a term for fishes that are spawned in the sea and enter freshwaters as juveniles to grow to maturity, then return to the sea to spawn and die (opposite: anadromous).
catadromy – a life history strategy characterised by migration between marine habitats (used for reproduction) and freshwater habitats (used for growth).
cauda of sagittal sulcus – the posterior of the sulcus.
caudal concavity – difference between the longest (outer) and shortest (middle) rays of a lunate caudal fin.
caudal fin – the fin at the rear of the fish; tail fin.
caudal peduncle – the part of the body from the rear end of the anal fin base to the base of the caudal fin.
centrum (pl. centra) – one of the bones of the backbone.
cephalic – pertaining to the head.
cephalic tenacula – appendage(s) on the head in male chimaeroids, both fossil and living, used to help grasp the female during copulation (at least in living species; function in fossils possibly the same).

cephalopod – a group of molluscs, including squid and octopus, which have a tubular siphon under the head and a group of muscular suckered arms around the mouth.
ceratobranchial – longest bones or cartilages of the branchial arches, situated immediately below the angle of the arch, between the epibranchials and the hypobranchials.
ceratohyal – bone, or cartilage, in ventral part of hyoid arch.
ceratotrichia – slender soft or stiff filaments of an elastic protein that resembles keratin.
chaetognath – torpedo-shaped, translucent, planktonic marine invertebrate organisms; arrow-worms.
character-based approach – an approach to defining a taxonomic group that includes all taxa that possess (at least ancestrally) a specified character or feature.
character reversal – the evolution of a character or feature of an organism to return to an ancestral condition.
charge (of a molecule) – molecules possess a net electrical charge, determined by the structure of the molecule (amino acids in the case of proteins), the atomic make-up of the molecule itself and the arrangement and nature of subatomic particles, under certain physical conditions (e.g., pH, chemical composition of the medium).
cheek – area between the eye and the edge of the preopercle bone.
chondrichthyans – cartilaginous fishes (chimaeras, sharks, rays, etc.).
chorion – the layer of tissue surrounding an oocyte, egg, or embryo.
chromatophore – pigment cell in the skin responsible for skin colour.
ciguatera poisoning (ciguatoxic) – a type of food poisoning affecting the nervous system in humans caused by eating certain large reef fishes contaminated with ciguatoxin, a toxin produced by the dinoflagellate *Gambierdiscus toxicus*.
circuli – a concentric ridge on a scale of a fish.
circumnarial – around the nostrils.
circumoesophageal – around the oesophagus.
circumpeduncular – around the caudal peduncle.
circumtropical – distributed throughout the tropics.
cirri (sing. cirrus) – small, slender, filamentous appendages.
cladistics – a method for hypothesising relationships among organisms (phylogeny) by defining hierarchical groups defined by shared, derived features or characteristics (vs. defining groups based on overall similarity).
claspers – intromittent (copulatory) organs attached to the pelvic fins of male chondrichthyans.
cleave (DNA) – the breaking of the DNA molecule/strand into two (or more) fragments by breaking the phosphate bonds that link the individual nucleotides in the chain together. This can be done with the use of enzymes, chemically or by radiation.
cleithral process – a process on the major bone of the pectoral girdle.
cleithrum (pl. cleithra) – the major bone of the pectoral girdle, extending upward from the pectoral-fin base and forming the rear margin of the gill cavity.
cloaca – the cavity at the end of the digestive tract into which the genital tract also opens.
cnidarians – jellyfishes and relatives, of the phylum Cnidaria, characterised by the possession of special stinging cells called cnidocytes.
coalesced – fused or grown together.
coelenterate – radially symmetrical invertebrate animals including the corals, sea anemones and jelly fishes.
commensal – the relationship between two animals where one benefits and the other does not, nor is harmed.
common name – the informal vernacular name for a fish (or other organism), which may vary from place to place.
compressed – flattened from side to side.
confluent – joined together.
congeneric – of the same genus.
conspecific – of the same species.
continental shelf – the sea bottom from the shore out to a depth of 200 m.
continental slope – the sea bottom from 200 m to 2 000 m.
convective overturning – reversals of water masses with well-defined temperature and salinity regimes/characteristics.
convex – curved outward.
copepods – tiny planktonic crustaceans of major importance in marine food chains; some species are parasitic.
Coral Sea – the sea basin surrounded by northeastern Australia, New Guinea, the Solomon Islands and New Caledonia.
corselet – a densely scaled area in certain tuna-like fishes usually behind the pectoral fins.
cotylephore – a flap of skin that develops on the inner side of the pectoral fins of females, and in which the eggs are wrapped to provide them with nourishment.
cranial fontanelle – basically a 'hole in the skull'.
craniates – animals with a 'backbone' and a bony or cartilaginous skull.
cranium – the part of the skull containing the brain.
crenate (cutting edge) – a scalloped edge (see *crenulate*).
crenulate(d) – having a margin shaped into small, rounded scallops.
crepuscular – active at dawn and dusk.
crown chondrichthyans – present-day sharks, rays, skates and holocephalans and their immediate fossil relatives.
crown-group – a group comprising all extant members (and their extinct relatives) of a monophyletic group of organisms.
crumenal – see *epibranchial*.
cryptic – fishes with colour that conceals or camouflages them.
ctenacanths – a group of mostly Palaeozoic sharks characterised by specific dentitions and fin spines, usually phylogenetically placed on the chondrichthyan stem below the elasmobranch/holocephalan divide.
ctenoid scale – a scale with minute teeth or spines (ctenii) on the rear margin, which gives the fish a rough feel when stroked towards the head.
ctenophores – comb jellies, of the phylum Ctenophora, that live in all oceans.
cuirass (cuirassed) – body armour, with breastplate and backplate fastened together.
cultrate – sharp-edged.
cuneal – wedge-shaped.
cuneate (teeth) – wedge-shaped teeth.
cusp – where two curves meet; top of.
cutaneous – pertaining to the skin, dermal.
cutaneous papillae (dermal papillae) – small papillae on the skin.
cycloid scale – thin, flexible scale with a smooth surface.

Cymodacea – a genus of seagrass.
cyprinodontiforms – an order of small, mostly freshwater fishes.

D

decadal sea surface temperature (SST) anomalous months – monthly sea surface temperatures are compared to average sea surface temperatures for 1971–2000, and plotted on a map. Where they are higher or lower than the average they are referred to as anomalous months.
deciduous – easily shed or rubbed off.
demersal – living on or just above the bottom of the sea or a lake.
demersal habitat – on or near the sea floor.
dendritic – tree-like in shape or markings.
dentary – the anterior and largest of the bones making up the lower jaw that carry teeth.
dentate – bearing teeth or tooth-like projections.
denticle – the tooth-like scale of elasmobranchs; a tooth-like projection.
denticulate – tooth-like.
dentition – the characteristic arrangement and shape of the teeth.
depressed – flattened from top to bottom (dorsoventrally).
dermal – pertaining to the skin.
dermal plicae – folds in the skin.
diandric – protogynous species where some females change into (terminal) males.
diastema – the gap between two teeth.
diatom – unicellular alga with silica walls.
dichromatic – having two colour forms in the same species.
dignathic – teeth differing in shape in the upper and lower jaws.
dimorphic – having two forms.
dioecious – sexes are separate.
diphycercal – a type of caudal fin with a subtriangular shape in which both dorsal and ventral lobes are symmetrical and vertebrae continue towards the extremity of the fin.
diploid – having both chromosomes of the paired homologous chromosome set and, thus, both copies of each gene present in the cell nucleus; resulting from sexual reproduction.
diplospondylous – having two vertebrae in each body segment, as in the tail region of certain fishes.
disc – the combined head, trunk and pectoral fins of rays and skates.
distal – furthest away from the point of attachment.
distal-type teeth – borne on distal extreme of long and closely packed fibrous strands, derived from jaw bones and supported by lip tissue.
diurnal – pertaining to the daytime; active during the day.
dorsal – on or towards the back or upper part of a fish.
dorsal-fin insertion – the rear end of the fin, at the last ray; the anterior end of the fin is the origin.
dorsomedian fontanelle (see also *fontanelle*) – a gap between bones in the middle at the top of the skull, closed by a membrane.
dorsorostrally – upwards position of rostrum.
dorsoventral – stretching from the dorsal to the ventral surface.
double emarginate – with a double-notched margin.
drumming muscles – the muscles that are attached to the swimbladder and produce drumming sounds when contracted.
durophagous – eating of hard-shelled (exoskeleton-bearing) organisms as a major part of the diet.

E

ectoparasites – parasites on outside of body.
edentate – without teeth.
efferent circulation – taking blood from an organ.
elasmobranchs – the group of fishes which includes the sharks, rays and skates.
elements – the spines or rays of a fin.
emarginate – with a slightly concave margin.
enameloid – an enamel-like tissue forming the outer layer of shark teeth and dermal denticles. Although the origin of enameloid is debated, it is probably more similar to dentine than true enamel.
encoding (genes and proteins) – the function and process whereby a particular gene produces a protein or enzyme; a gene responsible for a certain character, product, process, behaviour or phenotypic trait is said to *encode* for that feature.
endemic – native or restricted to a particular area.
endochondral ossification – a type of ossification (formation of bony tissue) in which osteoblasts replace hyaline cartilage with bone.
endonuclease restriction enzymes – bacterial enzymes which cleave (break) DNA molecules wherever a particular sequence of nucleotides (the restriction site) is recognised.
endopterygoids – paired dermal bones in the roof of the mouth of fishes.
ENSO – El Niño–Southern Oscillation; a recurring climate pattern involving changes in the temperature of waters in the central and eastern tropical Pacific Ocean.
ENSO teleconnections – the link between what happens in the Pacific Ocean during an El Niño event and what happens in the Indian Ocean.
entire – with a smooth or even margin.
Eocene – the period of geological time from 56–33.9 million years ago.
epaxial muscles – muscles that lie dorsal to a horizontal plane through the body of vertebrates (except humans).
epibenthic – living on the sediments on the bottom of the sea.
epibranchial – bone or cartilage forming the upper part of the gill arch, immediately above the angle of the arch.
epibranchial organ – a paired dorsal diverticulum at the back of the pharynx in some osteoglossiform, cypriniform, gonorhynchiform and clupeiform fishes.
epioccipital ridges – a ridge on a bone that lies above the eye.
epiotic – paired bones at the outer posterior margin of the skull.
epipelagic – the upper part of the oceanic zone from the surface to about 200 m.
epithelium – the thin tissue forming the outer layer of a body's surface and lining the alimentary canal and other hollow structures.
epural – an elongate detached bone above the urostyle and behind the last neural spine supporting caudal-fin rays.
equatorial submergence – used for fishes and other marine creatures that move into deeper, cooler water when nearing the equator.
erectile – can be raised or erected.
erisma (ventral arm of) – a thin bone with two 'arms' that lies in the middle between the skull and anteriormost dorsal interneural spines and below the rostral cartilage.

esca – the terminal lure or 'bait' on the angling apparatus (illicium) of anglerfishes (Lophiiformes).
ethmoid – the bone that separates the nasal cavity from the brain cavity.
ethmo-maxillary ligament – a ligament joining the ethmoid bone and maxilla that aids jaw protrusion in some fishes.
euphausiids – shrimp-like, planktonic crustaceans, which include krill.
euryhaline – able to live in waters with a wide range of salinity.
evaginations – pouched-shaped structures.
eversible – can be turned inside out.
excurrent – liquid flowing outwards.
exoskeleton – hard outer parts that form an external skeleton to support and protect the body.
exserted – elongate; protruding.
extrinsic (musculature) – muscles 'outside' that act on a structure.

F

facultatively monogamous – a mating system in which a male is not fully committed to one female, but chooses to stay with that female because there are no other mating opportunities available.
falcate – sickle-shaped.
family – a category of organisms (taxon) which includes those genera that all share a common ancestor (see *genus*).
filamentous – thread-like.
filter feeding – to strain small food particles from the water by means of gill rakers.
fimbriate – with a fringed margin.
finlet – a small fin of one or two branched rays.
fish aggregating device (FAD) – man-made device used to attract pelagic fish species and used for fishing.
fluorescence – the property of absorbing light of short wavelength and emitting light of longer wavelength.
fontanelle – a gap between bones in the skull, closed by a membrane, where ossification of cartilage or connective tissue did not occur.
foramen – an opening through bone or tissue.
foraminifera – single-celled organisms with shells of various minerals, the shells with many tiny holes; may be planktonic or benthic.
fork length – the length from the tip of the upper jaw or snout to the end of the shortest ray of the caudal fin of a forked caudal fin.
fossa – a groove or pit.
frenum – a connecting or restraining membrane.
frontoparietal fenestra – a space between the frontal and parietal bones of the cranium through which a major nerve and blood vessel passes.
frontoparietal striae – the slight ridges or grooves on the bones above and behind the eyes.
fulcral scale – spine-like scales on the dorsal margin of the caudal fin.
fusiform – tapering toward each end; spindle-shaped.

G

Galaxea clavus* & *Galaxea fascicularis – species of coral.
galeomorphs – a diverse group of sharks that includes the orders Heterodontiformes (bullhead sharks), Orectolobiformes (carpet sharks), Lamniformes (mackerel sharks) and Carcharhiniformes (ground sharks).
ganoid scale – a thick, bony scale covered by a layer of a hard tissue (ganoine); typically rhomboid or diamond shape; adjacent scales articulate by a peg-and-socket articulation.
gas bladder – see *swimbladder*.
genital papilla – a short, fleshy tube behind the anus from which the sperm or eggs are released; the sex of a fish can often be determined by the shape of its papilla.
genotype – the genetic make-up (profile) of the individual organism; the specific combination of genetic variants (e.g., a DNA sequence or a combination of alleles) for a genetic marker being studied or underpinning a character (phenotype) being considered.
genus – a category of organisms (taxon) which includes species more closely related to each other than to other, similar species, i.e., share a common ancestor.
geographically disjunct – two populations that occur far apart.
ghost-lineage – a branch of a phylogenetic tree that is inferred to have existed, but does not have a fossil record.
gibbous – convex or protruding.
gill arch – the bony or cartilaginous arches to which the gill filaments are attached.
gill chamber – the space on each side of the head containing the gills.
gill cover – the bones of the head that cover the gill chamber, comprising the preopercle, opercle, subopercle and interopercle; the operculum.
gill filaments – the soft, red, fleshy part of the gills, through which oxygen is taken into the blood from the water passing through the gills.
gill membrane – see *branchiostegal membrane*.
gill opening – the opening from the gill chamber to the outside; in elasmobranchs there are 5–7 openings on each side of the head; in bony fishes there is only one on each side (in some fishes the left and right gill openings may be continuous ventrally).
gill rakers – bony, finger-like (or lath-like) projections along the anterior edge of the gill arches. The number of gill rakers is often used to identify species.
gill slits – gill openings.
gnathostomes – vertebrates that have true jaws, or simply 'jawed vertebrates'; includes placoderms, acanthodians, chondrichthyans and osteichthyans.
gonad – the reproductive organ: ovary or testis.
gonadal sex reversal – when the gonads change from male (testicular) to female (ovarian) tissue, or the other way around.
Gondwana / Gondwanan – southern supercontinent following the break-up of Pangea, which included portions of modern South America, Africa, Arabia, Australia, Antarctica, and India, among other smaller regions; present both prior to the formation of Pangea, and following its break-up in the Jurassic.
gonochoristic – separate sexes, i.e., not hermaphroditic.
gonopodium – the modified anal-fin rays of males of certain fishes with internal fertilisation, and is used to transfer sperm bundles or spermatophores to females.
gorgonian – sea fans; a polyzoan coelenterate in which the polyps form upright branching colonies.
gravid – carrying unborn young; pregnant.

guanine – crystalline substance in dermis of fishes giving iridescent silvery or whitish colour.
gular – the area between the dentary bones; the throat.
gular bones – the median dermal bones that lie between the dentaries.
gular flap – in very large sharks the first gill slits are joined across the throat as a gular flap.

H
habitat – the place where a species normally lives.
haemal arch – the bony arch on the ventral side of a vertebra through which the dorsal aorta and caudal vein run.
haemal spine – spine on lower end of haemal arch in caudal vertebrae.
haploid – having only one chromosome (of the normally paired homologous chromosome set) and, thus, one copy of each gene present in the cell nucleus or cell organelle.
haremic mating system – a single male with a 'harem' of several females.
head length – the length of the head from the tip of the upper jaw or snout, where it projects over the upper jaw, to the posterior bony edge of the opercle.
hemibranch – a gill with filaments only on one side of gill arch.
herbivorous – feeding on plants.
hermaphrodite – having both sexes in the same individual (see also *protandrous*, *protogynous* and *synchronous hermaphrodite*).
heteracanth spines – asymmetrical dorsal-fin spines, with either the right or left side thickened.
heterocercal – caudal fin with the upper lobe larger than the lower.
heterodont – more than one kind of tooth in the same fish.
high aspect-ratio caudal fin – a caudal fin of a fish that is tall and narrow, such as that of a tuna or billfish.
histotroph – uterine secretions that provide additional nutrition to embryos in some viviparous sharks and rays.
holomorphic fossil – a fossil that is more or less 'completely' preserved; fossils that include a good portion of the skeleton and body outline.
holothurian – sea cucumber, an elongate soft-bodied relative of the starfish.
holotype – a single specimen designated as the 'type' (i.e., 'name bearer') of a new species by the author of the original description.
homeothermic = endothermic – animals that regulate body temperature.
homologous – the same structure as; e.g., a bird's wing is homologous with a foreleg or arm or bat's wing.
homology – sharing the same evolutionary origins.
homonym – two organisms with the same name, of which the younger name is invalid.
homoplasy / homoplastic – a similar feature or characteristic that has evolved independently in different groups of organisms.
humeral – relating to the pectoral girdle or shoulder region.
hyaline – translucent.
hybodonts – a diverse group of Palaeozoic and Mesozoic sharks that ranged significantly in size and morphology and that occupied many diverse habitats and niches, characterised by small cephalic spines in males, massive jaws and shoulder girdles, and characteristic fin spines and dentitions. Hybodonts are phylogenetically placed usually on the elasmobranch stem below neoselachians.
hydrophiin sea snakes – sea snakes with a tail like a fin.
hypaxial myotomes – the blocks of muscles that lie ventral to the horizontal septum.
hypermineralised tooth plates – referring to the teeth of chimaeroids that undergo significant hardening by the excessive deposition of minerals to facilitate a durophagous diet.
hyperostosis – excessive growth of bone.
hypersaline – with salinities higher than that of sea water, i.e., more than 35 parts per thousand (ppt).
hypnosqualean hypothesis – a hypothesis that proposes that the batoids (rays and skates) are derived sharks, based on many morphological phylogenetic studies (cf. Shirai 1992, 1996; Carvalho 1996).
hypobranchials – paired bones on the lower part of the gill arch.
hypocercal – caudal fin with the lower lobe larger than the upper.
hypomaxilla – small, paired, tooth-bearing bone behind the premaxilla and below the maxilla.
hyposaline – having an abnormally low salinity.
hypurals / hypural plate – the fan-shaped series of bones (sometimes fused to one or two plates) to which the caudal-fin rays are attached.

I
illicium – the 'fishing pole' of anglerfishes, developed as a greatly modified dorsal-fin ray and located on top of the head.
imbricate – overlapping evenly.
incertae sedis – a qualification to indicate that a taxon's phylogenetic affinities are uncertain within a more inclusive group of organisms, and authors do not want to guess where a taxon belongs.
incised – notched
incisor – a tooth flattened at the tip like a chisel.
Indonesian Throughflow – an ocean current important for global climate, which moves warmer freshwater from the Pacific to the Indian Ocean, where most of the water flows from north of the Equator, past the south of the Philippines, between Borneo and Sulawesi and south between Bali and Lombok, Indonesia, into the eastern Indian Ocean.
Indo-Pacific – the tropical and subtropical waters of the area of ocean from the east coast of Africa, including the Red Sea and Persian/Arabian Gulf to Easter Island in the eastern Pacific, and in which the marine fauna are of a common origin. (Note: only broad distributions of species outside the Western Indian Ocean are given)
inferior – the position of the mouth when it is on the underside of the head.
infraorbital – below the eyes.
infrapharyngobranchial tooth plate – a tooth plate on bones in the pharynx (throat) of a fish, behind the gills.
insertion (of a fin) – the anterior end of the base of the paired fins; the posterior end of the base of a dorsal or anal fin.
interarcual cartilage – a cartilage in the pharyngeal arch.
interbranchial septa – the partitions separating the gill chambers.
interdorsal – see *basidorsals*.
interhaemal bone – the bones between the haemal (ventral) spines of the vertebrae and the spines or rays of the anal fin.
internarial – between the nostrils.
interneural bone – the bones between the neural (dorsal) spines of the vertebrae and the spines and rays of the dorsal fin.

interorbital – the area between the eyes, on top of the head.
interorbital commissure of supraorbitals – the suture of the supraorbital bones between the eyes.
interpelvic process – a narrow, pointed area between the pelvic fins.
inter-radial membrane – the membrane between the rays of a fin.
interspecific – between separate species.
interspinous membrane – the membrane between the spines of a fin.
intertidal – between the high and low tide marks on a shore.
intraspecific – within one species.
iodoform – smelling of iodine, odour of flesh from a fish that feeds on sponges or tunicates rich in iodine compounds.
iridescent – with a wide range of often-changing, brilliant colours.
iris – the black part of the eye, which is not the pupil (see *pupil*).
iris lappet – a fleshy flap-like structure in the eye, which can be short and rounded, simple or branched.
isobath – a line on a map that joins all points of the same water depth in the sea.
isthmus – the lower part of the head that separates the two gill chambers
isthmus muscle – the muscle that lies between the two gill chambers.

J

jugular – located in front of the pectoral fins.
junior synonym – a younger name for a species named earlier.

K

keel – a narrow ridge on the sides of the caudal peduncle or at the base of the caudal fin, typically found in fast-swimming fishes with narrow caudal peduncle. Term is also used for sharp blade on the peduncle plates of *Naso* and *Prionurus* species; a narrow ridge-like process.
keeled scales – scales with a narrow ridge along the middle.
keratin – a protein that protects epithelial cells from damage.
keris larvae – the late post-larval stage of fishes of the genus *Naso*, which come inshore from the open ocean to metamorphose into juveniles.
***kolachi vala* nets** – a kind of a drag net.

L

labial – pertaining to the lips.
labial ossicles – small bones associated with the upper 'lips' of certain species of *Bleekeria*.
lachrymal – the anteriormost bone below the eye.
lacustrine – living in lakes.
lagerstätte – a sedimentary deposit that has extraordinarily preserved fossils, usually in abundance, and sometimes even with preserved soft tissues.
lamella (pl. lamellae) – plate-like fold of skin.
lanceolate – broad at the base and tapering to a point.
larva (pl. larvae) – the early life history stage between the time of hatching and transformation to a juvenile, the latter a miniature replica of the adult.
lateral – pertaining to, at, or towards the side.
lateral ethmoid – the bone forming the front of the eye socket.
lateral line – a system of tubes or canals containing cells sensitive to low-frequency sounds and vibrations produced by the movements of other animals in the vicinity.
lateral-line scales – the perforated or tubed scales on the body that are sensitive to changes to water pressure. These pored lateral-line scales are often counted, with the count stopping at the caudal-fin base.
lateral scale series – this is generally the number of scales from the upper end of the gill opening, often lying just above the lateral line, to the base of the caudal fin. This may vary for different fishes as not all species have the same lateral-line configuration, and where different it is explained in the family account.
Laurasia – the northern supercontinent following the break-up of Pangea, which included portions of modern North America and Asia.
lecithotrophic – where embryos receive nutrition entirely from yolk reserves.
leptocephalus – the transparent, ribbon-like, pelagic larva of eels and other elopomorph fishes.
Lessepsian migrant – an organism that moves from the Red Sea to the Mediterranean Sea via the Suez Canal, and more rarely in the opposite direction (anti-Lessepsian).
lingual lure – a worm-like lure on the tongue.
lipid – fatty substances produced by fishes as an energy store and, in some species, to provide buoyancy; may be deposited in or around the swimbladder as fat, or as oil in the liver, skeleton or body muscles.
littoral – the intertidal zone of the marine environment, delimited by the tide marks of low and high water.
lunate – sickle- or moon-shaped.
lymphocytes – small white blood cells found in the lymphatic system.

M

malar thorns – patch of thorns found on some mature male skates close to the edge of the upper surface of the disc opposite the eye.
mandible – the lower jaw.
Mascarene Plateau – an extensive WIO submarine plateau, extending from the Seychelles to Réunion in the west and to St Brandon Shoals in the east.
Mascarenes (or Mascarene islands) – Réunion, Mauritius, Rodrigues and St Brandon Shoals.
matrotrophic – in viviparous species where nutrients are transferred to the developing embryos from the mother.
maxilla (pl. maxillae) – one of the two bones that comprise each half of the upper jaw.
medial – on or towards the middle of the body.
median – on the midline or axial plane of the body.
median fins – the dorsal and anal fins.
melanophore – a pigment cell containing melanin that gives skin a black, grey or brown colour.
membranous labyrinth – the fluid-filled, adjoining canals of the inner ear housed in the bony labyrinth of the skull and responsible for the sense of equilibrium.

Mendelian inheritance – the rules of genetic inheritance in diploid organisms, as deduced by Gregor Mendel's seminal 'genetic' hypotheses based on breeding, cross-breeding and observing the phenotypes of garden peas. This work suggested that phenotypes are controlled by two factors (alleles in a genetic context), one obtained from each parent; that these factors assort or act independently of factors for other phenotypes during cell division (meiosis) and fertilisation; that these factors can be dominant or recessive with respect to influencing the phenotype and that the phenotypic outcomes can be predicted numerically/statistically, based on the phenotypes present in the population and by tracing a genealogy.
mental – pertaining to the chin.
meridional – along a meridian or in a north–south direction.
meristic – countable features (e.g., lateral-line scales, fin rays or gill rakers).
mesopelagic – the region of the oceanic zone from 200 m to 1 000 m.
microphagous detritivores – animals that feed on small particles of detritus.
mimic – an organism that closely resembles another, usually unrelated, organism which is protected from predation for some reason.
Miocene – the period of geological time from 23.03–5.33 million years ago.
mitochondrial DNA – an extranuclear (i.e., occurring outside the cell nucleus), double-stranded, circular DNA molecule found in the mitochondria of animal cells; the molecule is maternally inherited and haploid.
molar – a blunt, rounded tooth adapted for crushing shellfish.
molecular clock estimates – the estimates of time of divergence between taxa based on mutation rates of DNA.
monandric – initial-phase fish all female, terminal phase all secondary males.
mongolepids – refers to an order of early fossil sharks known from isolated dermal denticles from the Ordovician or Silurian of Colorado (USA), Mongolia and China; includes the genera *Mongolepis*, *Solinalepis*, *Rongolepis*, *Teslepis*, *Shiqianolepis*, *Xinjiangichthys*, and *Sodolepis*.
monocuspidate – teeth ending in a single point.
monophyletic – a group of organisms (a clade) comprising the most recent common ancestor and all its descendants.
monophyly of genus – all species sharing a common ancestor.
monospecific / monotypic – including only a single species.
monospondylous – having a single vertebra in each body segment.
morphology – the form and structure of organisms or the study of this subject.
mucus – a slimy substance secreted by the skin of fishes.
multicuspid – a tooth with many cusps.
multiserial – arranged in several rows or series.
myomere – a segment of the body (trunk) muscles, seen as V- or W-shaped muscle fibres, separated from its neighbours by a connective tissue septum (myosepta) and most easily seen in larval fishes; the number of myomeres is important in identifying larvae, since their number equals the number of vertebrae in the adult.
myosepta – the layer of connective tissue between myomeres.
mysids – small, shrimp-like crustaceans found in all oceans and seas.

N

nape – the part of the dorsum from the back of the head to the dorsal fin or vertical at the base of the pectoral fins.
naris (pl. nares) – nostril.
nasal fossa – the cavity or pit, containing nasal papillae, into which the nostrils open.
nasopharyngeal duct – the duct through which hagfishes take in water.
nasoral/oronasal groove – groove between the nostril and corner of mouth.
nautiloid – refers to the mostly extinct cephalopod molluscs of the group Nautiloidea, with shells that are coiled and with forward-facing concave septa, and that flourished in the Palaeozoic seas; a few genera, such as *Nautilus*, are extant.
nekton – organisms that actively swim in the water column.
neonate – newborn.
neritic – the shallow pelagic zone over the continental shelf.
neural arch – the bony arch on the dorsum of a vertebra through which the spinal cord runs (see *haemal arch*).
neural spine – the spine on the neural arch of a vertebra.
neurapophyses – the structure that forms the neural arch of vertebrae.
neurocranial – the skeletal structure surrounding the brain and cranial sensory organs.
neurocranium – skull.
neuston – small, aquatic organisms that live in the surface of the water.
niche – the habitat and role (community relationships, food habits, etc.) of an organism.
nictitating membrane (nictitans) – a clear, moveable inner eyelid found in sharks.
nocturnal – active at night.
node-based approach – an approach to defining a taxonomic group that includes all taxa that share a most recent common ancestor.
non-otolith fossil record – the fossil record based on the remains of fishes other than their otoliths; otoliths are rarely found with the remains of the animal and are often of limited value.
notochord – the cartilaginous rod in the embryo that runs from head to tail and supports the nerve cord; in most fishes the notochord is replaced in the larval stage by the developing vertebrae, but in some primitive fishes (e.g., *Latimeria*, hagfishes, chimaeras) the notochord persists in the adult and serves as the vertebral column or 'backbone' of these species.
nuchal – pertaining to the nape.
nuchal crest – a fleshy crest on top of the middle of the head.
nuchal plate – a plate of bone at the neck.
nyctoepipelagic – migrating from deeper waters to the epipelagic zone at night.

O

obligate inquiline – an inquiline is an animal that exploits the living space of another (from the Latin *inquilinus*, a tenant).
obsolete – disappearing or scarcely evident.
obtuse – broadly rounded, having a blunt end.
occipital (pertaining to the occiput) – the upper rear part of the head.

occipital fossa – depression at the rear of the skull.
oceanic – pertaining to the open ocean beyond the continental shelf.
ocellus (pl. ocelli) – pigment pattern on body or fins forming a false eye.
ocular – pertaining to the eyes.
odontoid process – a small, bony process on the dorsum of the second vertebra; also a small, tooth-like bony process on the dentary (part of the upper jaw).
olfactory – pertaining to the nasal organs or sense of smell.
oophagy / oophagous – where the embryos feed on unfertilised eggs in the uterus of viviparous species.
opercle – the large, posterior bone of the gill cover, the largest bone of the operculum.
opercular – pertaining to the operculum (gill cover).
opisthotic – a deep, endochondral bone forming the ventral element of the otic capsule, covering the ampulla of the posterior semicircular canal.
orbit – the dermal or bony eye socket.
order – the taxonomic rank that includes one or more families of organisms, all of which share a common ancestor.
origin (of a fin) – the anterior end of the base of a fin.
ossicle – bony plate.
ossified – become bone.
ostraciids – boxfishes.
otolith(s) – calcareous concretions in the ear capsules of bony fishes; also called 'ear bones' or 'ear stones'; there are three otoliths, the sagitta (largest), the astericus and the lapillus.
otophysic connection – an extension from the swimbladder to the inner ear.
oviparous – producing eggs that develop and hatch outside the body of the female.
ovocyte – a cell in the ovary that divides to form an ovum.
ovoviviparous – see *yolk-sac viviparity.*

P

Pacific Plate – that part of the Pacific Ocean floor bounded by the Aleutian Trench in the north, the trenches that extend from the Okhotsk Peninsula, past Japan, the Mariana Trench, to the Tonga and Kermadec trenches to cut through South Island, New Zealand, to the Antarctic Plate in the south. It is bounded on the east by mid-ocean ridges that extend past Easter Island to Baja California and along the west coast of North America to Alaska. It covers 103.3 million sq. km.
paired fins – the pectoral and pelvic fins.
palaeoclimatic evidence – what geological information can tell us about climates thousands to millions of years ago.
palate – the roof of the mouth.
palatines – elongate bone on each side of the palate.
palato-premaxillary – of, relating to, or connecting the palate and the premaxilla.
Pangea – the large supercontinental landmass that persisted from the late Palaeozoic to the early Mesozoic eras.
papilla (pl. papillae) – a small fleshy projection.
papillose – with many papillae.
parahypural – the last haemal spine that forms part of the hypural plate.
paralectotype – an additional specimen selected from a series of syntypes, after a lectotype has been designated.
paraphyletic – a taxonomic grouping that does not include all descendants of a most recent common ancestor.
parapophysis (pl. parapophyses) – a long, transverse process arising ventrally from the centrum of abdominal vertebrae; serves to support epipleural ribs when present and, in Gadidae, the gas bladder.
parasphenoid – a bone in the middle at the base of the skull.
paratype – a specimen, other than the holotype, on which the description of a new species is based.
parsimony analysis – a way of analysing data to give the most reasonable (or parsimonious) answer.
parturition – the process of giving birth.
pectoral-fin insertion – lower or rear end of the fin; the upper end of the fin is the origin.
pectoral fins – the anterior or uppermost of the paired fins, corresponding to the forelimbs of higher vertebrates.
pectoral girdle – the bony or cartilaginous skeletal arch supporting the pectoral fins.
pedicellate – with a stalk.
pedicle – a small, stalk-like structure connecting two structures.
pelagic – pertaining to the open ocean.
pelvic claspers – organs present in male sharks, rays and skates for introducing semen directly into the reproductive tracts of females.
pelvic fins – paired ventral fins usually located below or behind the pectoral fins.
pelvic scute – a long, pointed scale above the pelvic-fin base.
percomorph – fishes belonging to the Percomorpha, a large clade of bony fishes, mostly perciform, characterised by having bony fin spines, two dorsal fins, thoracic pelvic fins, a ductless swimbladder and ctenoid scales.
peritoneal spots – pigment spots on the peritoneum.
peritoneum – the membrane lining the abdominal cavity.
pharyngeal arch – a segment of the lateral wall of the pharynx that will form jaw and gill structures.
pharyngeal plates – the bones in the pharynx that carry teeth.
pharyngeal sulcus – a groove on either side of the pharyngobranchial chamber, part of the filter-feeding mechanism.
pharyngeal teeth – teeth located on the pharyngeal bones (modified fifth gill arches) in the throat behind the gills.
pharyngobranchial tooth plates – tooth plates on bones in the pharynx (throat) of a fish, behind the gills.
pharyngocutaneous duct – a duct between the pharynx and the skin behind the last gill of hagfishes that clears large particles from the pharynx.
phenotype – physical features of the organism or aspects of the organism's biochemistry, physiology or behaviour that can be observed and are thought to reflect variation in the genotype or the interaction of the genotype and the environment.
philopatry – the habit of many animals to return to a particular site or place for various reasons, either to spawn at the same place they were spawned (e.g., salmon and anguillid eels), to breed (many sea birds), or to associate with their own species (raggedtooth sharks gathering by the dozen in shark gutters).
photic zone – the surface layer of the ocean that is reached by sunlight, and hence where photosynthesis can take place (roughly to 80+ m depth).
photophore – a light-emitting organ.

phylogeny / phylogenetic analysis – the hierarchical evolutionary relationships among fossil and living organisms, and the process for hypothesising such relationships.
phylogenetically informative characters – characters that reveal the historical patterns of phylogenetic relationships among organisms.
physoclistous – with a closed swimbladder (i.e., without any connection between swimbladder and gut).
phytoplankton – microscopic (unicellular) plant life that floats in the open ocean.
phytoplankton bloom – a large and sudden increase in microscopic algae caused by an increase in nutrient content in an area, common in the world's oceans, and often changing the local colour of the water.
pinniform – shaped like a fin.
placentotrophic – way of feeding embryos of viviparous species where nutrients are transferred across the mother's uterine epithelium which is in close contact with foetal tissue (a placenta).
placoderms – refers to a Palaeozoic (Silurian to Devonian) gnathostome group of armoured fishes with dermal bony plates on head and trunk, and which occupied numerous habitats and niches from large pelagic predators to small benthic forms; presently considered to not be monophyletic and placed on the stem below the divergence between osteichthyans and chondrichthyans.
placoid – plate-like scales of some extinct fishes, and of sharks and rays.
planktivorous – feeding on plankton.
plankton – small floating organisms that drift more or less passively with the ocean currents.
plesiomorph / plesiomorphy / plesiomorphic – an underived or 'primitive' character that cannot be used to define a group of organisms.
pleural rib – the ribs of the 'rib cage' around the viscera.
plicate – with pleat-like folds.
poikilothermic = ectothermic – animals that do not regulate body temperature, but have body temperature of their surroundings.
polychaetes – segmented marine worms with bristles.
polygynous – a male with many females.
polyphagous – feeding on different kinds of food.
polyphyly / polyphyletic – a group of organisms (a clade) that has more than one ancestor and is defined on the basis of convergent features or characteristics.
polytomy – unresolved branches within an otherwise hierarchical hypothesis of relationships among organisms.
population – a group of organisms belonging to the same species that co-occur in a distinct area.
postcleithrum – a bone behind the cleithrum of the pectoral girdle.
posterior – at or towards the rear end of the fish.
post-interorbital knobs – bony knob posterior to the interorbital area.
postlarva – a larva after it has absorbed its yolk.
post-maxillary process – an extension posterior to the ascending process.
postocular, postorbital – that part of the head behind the eye.
post-pelvic scutes – keeled scales along the midline of the 'belly', from pelvic fin to anal fin.
precaudal pit – the notch just in front of the caudal fin in sharks.
prehensile – able to grasp, and used as an anchor around a variety of objects in the wild and coiled ventrally in preservative.
prelingual filament – the worm-like filament on the floor of the mouth.
premaxillae (premaxillaries) – the main bones of the upper jaw that carry teeth; they lie in front of and below the maxillae.
premaxillary diastema – space between the premaxillary bones.
preopercle – the falcate bone before the opercle and behind and below the eye, and constituting the fore part of the operculum; its rear edge is usually free, and may be serrated or not.
preorbital – the bone or region before and below the eye.
pre-pelvic scutes – keeled scales along the midline of the 'chest', in front of the pelvic fins.
preural vertebra – the second-last vertebra of the spine.
procumbent – lying down and pointing forwards.
produced – elongated or projecting.
prognathous jaw – the lower jaw protruding in front of the upper jaw.
propagule – a vegetative/living structure that becomes detached from a parent to give rise to a new organism; an agent of reproduction, e.g., a sucker on a plant or the eggs fishes or corals shed into the water.
protandrous hermaphrodite – hermaphroditism that functions first as a male and then changes into a female.
protocols – a set of procedures or methodology to be followed in a laboratory.
protogynous hermaphrodite – an individual that functions first as a female and then changes to a male.
protrusile, protrusible – capable of being thrust out or extended forwards.
proximal – towards/closest to the body or base of attachment.
pseudobranch (pl. pseudobranchiae) – a small, gill-like organ on the inner surface of the operculum; the reduced first gill arch.
pseudobranchial filaments – filaments of the small, gill-like organ on the inner surface of the operculum.
pseudoceanic – members of a basically oceanic group that are distributed over continental shelf and slope regions and in the neighbourhood of oceanic islands and that are associated with land-orientated food chains.
pseudoclasper – an accessory male copulatory organ, inserted into the female during spawning.
pseudocycloid scales – a few species of fishes fail to produce ctenii on their scales, and such 'secondary' cycloid scales are called pseudocycloid.
pterotic – a bone on the side of the cranium.
pterygiophore(s) – the three bones (distal, medial and proximal), sometimes some fused together, that support and articulate with the fin spines and rays.
pterygoid teeth – the teeth on the bones of the roof and walls of the mouth, behind the palatines.
pterygoids – bones of the roof and walls of the mouth in fishes, behind the palatines.
pungent – sharp-pointed.
pupil – the opening at the centre of the iris, is white or transparent, and is usually covered by the iris (see *iris*).

pyloric caecum (pl. caeca) – a variously shaped diverticulum from the junction of the stomach and intestine; the pyloric caeca may be long and numerous, or short and few, or profusely branched, or even absent.
pyriform (scales) – pear-shaped, with an extended middle posterior margin.
pyrosomes – large, free-floating colonial tunicates of the genus *Pyrosoma*.

Q

quincunx – an arrangement of five objects in a rectangle, with one on each corner and one in the middle.

R

radial – see *pterygiophore*.
ramus – a branch; one side of the lower jaw.
raptorial – adapted for seizing prey.
recumbent spine – a spine that is more or less parallel to the horizontal (lying down), rather than almost vertical.
recurved – curved backward or inward.
replacement scales – tilefishes inhabit mounds and burrows. As they move in and out of a burrow they apparently rub against the walls of the mound or burrow losing scales in the process. The scales that grow back lack the early annuli ('growth rings'), and are called replacement scales to differentiate them from the original scales.
respiratory – associated with breathing.
rete mirabile – a network of small veins and arteries that lie very close together, where heat is transferred from outgoing venous blood to incoming arterial blood.
reticulate – resembling a network.
reticulum – a network of intercellular fibres in certain tissues, with a fine, net-like appearance.
retrorse (spines) – pointing or curved backward.
rhipidion – longitudinal, elongated flap of soft tissue on the distal opening of the claspers of chondrichthyans through which sperm is dispersed.
rhomboidal – diamond-shaped.
rictus – the corner or gape of the mouth.
rocker bone – a bean-shaped bone which is drummed against the anterior end of the gas bladder to produce sound.
rostral – pertaining to the snout or rostrum; towards snout (usually anteriorly).
rostral cartilage – the cartilage on the snout.
rostral organ – an organ on the snout.
rostral process – a beak-like structure on the rostrum or 'nose'.
rostrum – a projecting snout or beak; protracted anterior part of the skull in sharks and rays.
ruga (pl. rugae) – ridge or corrugation.
rugose – with a rough or wrinkled surface.
rugosities – wrinkles and lumps on a surface.

S

saccus vasculosus – an organ associated with the hypothalamus of many jawed fishes, that seems to be able to sense the seasons.
sagitta – the largest of the otoliths or ear-bones.
Sahul Shelf – the section of continental crust which forms Australia and New Guinea.
salinity – the measure of dissolved salt content in water, usually expressed as a ratio in parts per thousand (ppt); average ocean salinity is ~35 ppt (or 3.5%, or 3.5 g of salt per litre of water).
salp (pl. salps) – a pelagic, barrel-shaped tunicate.
Sargassum – a genus of brown seaweed (macroalgae) common in temperate and tropical seas.
scapula – a bone of the pectoral girdle.
scientific name – the formal binominal name of an organism, which consists of the genus and specific names; a species has only one valid scientific name.
sclera (of eye) – the outer, protective layer of the eye; outside of the pupil and the iris; the transparent outer layer of the eye overlying the pupil (scleral cornea of pupil).
scleractinian corals – stony or hard corals that form coral reefs today.
scute (pl. scutes) – a modified (thickened) bony scale with a keel or spiny point.
scutella – the shield-shaped, bony elements between trunk and body rings; the rectangular, fused body scales of Syngnathidae.
seamount – a mountain rising from the ocean floor.
segmented ray (soft-ray) – a bilaterally paired fin ray that is marked by cross striations like the joints on a stalk of bamboo.
semicircular canal – fluid-filled canals embedded in the cranium and concerned with balance and hearing.
sensu lato – in a broad sense; the name of a taxonomic group used in such a way that it includes taxa that have been referred to a group, whether or not they have been robustly shown to share a most-recent common ancestor with that group.
sensu stricto – in the strict sense; a strictly defined taxonomic group; usually used to exclude taxa that were historically allied to a particular group but are of questionable relation to that group.
serrae – saw-like teeth or serrations.
serrate, serrated – bearing small saw-like notches or spines (serrae).
sessile – an organism that lives attached to the substrate.
sessile teeth – directly attached to jaw bones.
setae – bristles.
setiform – bristle-like.
sexual dimorphism – males and females of the same species with different body form.
sexually dichromatic – males and females of the same species with different colour patterns.
shagreen-like – rough, like shark skin.
silica – silicon dioxide, a mineral used by marine organisms such as diatoms to build the cell wall.
simple – not divided into branches.
siphonophores – colonial, free-swimming or floating pelagic hydrozoans, mostly delicate and transparent with long filamentous tentacles.
sipunculids – a group of unsegmented marine worms that live in burrows or discarded shells; some bore into rock or coral. Also called peanut worms.
sister-group relationship – two taxa of equal rank that share a common ancestor.
somites – body muscle segments.
spawning-site fidelity – returning to the same site to spawn each season.
species – groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups.

spermatogonia – cells produced early on in the formation of spermatozoa.
spine – a sharp, projecting point; a fin ray that is unpaired, unbranched, lacks segmentation and is usually stiff and sharp-pointed.
spinescent – with spines.
spinning down – losing energy, slowing down and dissipating.
spinoid (scales) – modified ctenoid scales with spines fused to the surface and/or posterior margin.
spinules – small, spine-like structures.
spinulose – with spines.
spiracle – an opening behind the eye of some elasmobranchs that leads into the mouth cavity and may serve as an incurrent opening for water entering the gill chambers.
spiral valve – a spiral structure in the intestines of some fishes.
spur and groove zone – a zone of finger-like projections of coral (the spurs) in a fringing reef that grow out towards oncoming waves, with 'valleys' or grooves in between, which together serve to break the energy of incoming waves.
squalene – oil produced in the liver of some sharks.
standard length – the length from the tip of the upper jaw or snout to the end of the hypural plate. This can usually be seen as a crease when the caudal fin is bent from side to side.
stem chondrichthyan – refers to a fossil shark that is placed very low on the chondrichthyan phylogeny, below the divergence of elasmobranchs and holocephalans.
stem elasmobranch – refers to a fossil shark that is placed very low on the elasmobranch phylogeny below the divergence of 'neoselachians', the level of more modern sharks and rays.
stem-group – the basal members of a taxon that are known exclusively as fossils, and that are hypothesised to lie outside of a crown-group taxon.
stem holocephalan – refers to a fossil holocephalan that is placed very low on the holocephalan phylogeny below the divergence of more modern chimaeroids.
stomatopods – mantis shrimps.
strangulate – close-set, dense, not sparse.
stratophenetic – relating to overall similarity in form and geologic age.
striate – marked by lines or grooves.
sub (as a prefix) – less than, not quite, approximately, below, under.
subcutaneous – under the skin.
subequal – almost, but not exactly, equal.
subjective synonym – two species/names that do not have the same type specimen.
subocular (suborbital) – beneath the eye.
subopercle – the gill-cover bone that is ventral to the opercle.
subspecies – a taxonomically and geographically distinct subgroup within one species.
substrate – the material forming the floor/bottom of the sea.
sulcus – the indentation on the inner surface of the sagitta.
superior – above; dorsal to.
supernumerary spine – an additional spine (or spines); more than the normal single spine supported by a pterygiophore.
supracleithrum – the dorsalmost bone of the pectoral girdle in bony fishes, usually articulated with the post-temporal bone of the skull.
supramaxilla – a small bone along the upper rear edge of the maxilla.
supraneural bones – unpaired bones above the neural spines of the anterior vertebrae, between the skull and the origin of the dorsal fin.
supraoccipital – a median bone at the upper rear surface of the skull, frequently bearing an expanded crest (supraoccipital process).
supraorbital crest – narrow cartilaginous ridge from the chondrocranium extending above the eyes in catsharks of the family Scyliorhinidae. The crests can usually be felt by touch without needing any dissection.
suprascapular spines – spines on the posttemporal area.
supratemporal bones – a series of 2–8 small bones bordering the posterior margin of the roof of the skull.
supratemporal commissure – the lateral-line canal that crosses the back of the cranium.
suspensorium – the bones from which the lower jaw is suspended.
suture – line where two bones join.
swimbladder – a membranous, usually gas-filled sac attached to the dorsal surface of the body cavity; in some fishes the swimbladder is filled with fat, and in a few species it is rudimentary or absent.
symmoriiforms – a diverse group of Palaeozoic sharks (or possibly basal holocephalans) known from many morphologically unique genera displaying strong sexual dimorphism.
sympatric – groups of organisms living together in the same spatial or geographic area.
symphyseal (or symphysial) – relating to a symphysis.
symphyseal teeth – teeth at the junction between the two halves of the lower jaw.
symphysis – the median point or junction of the two halves of the jaws; an immovable joint between two bones.
symplectic – a bone that lies between the hyomandibular and quadrate in the suspensorium.
symplesiomorphic – shared primitive characters, e.g., a genus of fishes where all but one species have palatine teeth; the loss of the teeth would be apomorphic (derived) and the retention of the teeth would be plesiomorphic, the original condition.
synapomorph – a shared, derived character, indicating common ancestry.
synchronous hermaphrodite – a hermaphrodite with both ovaries and testes that function at the same time.
synechodontiforms – an extinct order of sharks, mostly Mesozoic, which are phylogenetically close to living orders of elasmobranchs (sharks and rays) as they share, for example, calcified vertebral centra.
synonym – different names applied to the same taxon.
synonymy – chronological list of all scientific names that have been applied, correctly or incorrectly, to a given taxon.
syntype – one of the specimens on which a species description is based if no holotype was designated.

T

tanaids – a small order of shrimplike Crustacea, the Tanaidacea.
tandem articulation – two bones, one behind the other, that articulate with each other.
taxon (pl. taxa) – a group of organisms such as a species, genus or a family that share a common ancestor.
taxonomic – pertaining to the classification of organisms according to their natural (evolutionary) relationships; systematic.

tegument – the covering membrane of the body.
teleost – a 'modern' (advanced) bony fish (not including *Latimeria* and some other primitive fishes).
tenaculum (pl. tenacula) – an appendage on the forehead of male chimaeroid fishes, weakly differentiated to ridge-like in male juveniles (frontal tenaculum); additional small, retractable appendage on each side just in front of the pelvic fins with intromittent organs (claspers) of chimaeroid males, only partially differentiated in male juveniles, and hidden in a slit when retracted (pre-pelvic tenaculum).
teratogenic pollution – teratogens are substances that cause physical or functional defects in embryos.
terminal – pertaining to a mouth at the anteriormost part of the head.
tetrodotoxin – a potent neurotoxin found in the skin and some other organs, present in many tetraodontiforms, and also some gobiids.
thermocline – the distinct interface between warmer surface waters and cooler deeper waters.
tholichthys stage – the larval stage of a butterflyfish (Family Chaetodontidae).
thoracic – under the pectoral fins.
thorn – large denticle on the surface of a ray or skate.
time-calibrated – the use of minimum ages from the palaeontological record to constrain molecular clock analyses.
tooth file – see *tooth series*.
tooth row – in sharks, teeth arranged parallel to the jaw line that are at the same stage of development.
tooth series – in sharks, teeth at different stages of development, arranged from the front of the jaw inwards; also known as a file of teeth.
total length – the length from the tip of the snout to the end of the caudal fin.
transverse rows of scales (also transverse scale rows) – counted between a specified point along the dorsal-fin base, e.g., fin origin, and pelvic-fin insertion or anal-fin origin, depending on the fish; sometimes specified as two values—above and below the lateral line.
tricuspid – with three cusps or points.
tritor – grinding surface on a tooth, such as in Rhinochimaeridae (longnose chimaeras).
tropeic fold – ventral fold under the belly of some sharks.
truncate – having the end square-cut or even.
tunic ridges – ridges on the swimbladder.
tympanic spine – a spine near the 'ear'.
tympanum – an area of enlarged scales behind the gill opening of some Balistidae that can be vibrated to produce sound.

U
uncinate processes – a hook-shaped projection.
unicuspid – teeth with a single-point cusp.
uniserial – arranged in a single row.
urohyal – bone at anterior floor of mouth, between the two sides of the hyoid arch.
urostylar centrum – the last vertebra, and part of the caudal skeleton.

V
vegetative (or vegetal) pole – the side of an egg opposite to the 'animal' pole; cell growth is slower in the vegetal pole which contains more yolk.
vent – the external opening of the alimentary canal.
venter – relating to the underside, the abdomen.
ventral – on or towards the lower surface (underside) of the fish.
ventral fins – pelvic fins.
ventrorostrally – downwards position of rostrum.
vermiculations – a pattern of fine wavy lines; worm-like lines of colour.
vermiform – worm-like.
vertical fins – the dorsal, caudal and anal fins; median fins.
vestigial – the remaining part of an earlier, functional structure.
vicariance / vicariance biogeography – an approach to understanding the distribution of organisms related to physical or biological separation between groups of organisms (in contrast to dispersal).
villi – fine bristles.
villiform – having the appearance of velvet or fine bristles of a brush.
villose papillae – papillae (like taste buds) that look like fine bristles.
viscera – the internal organs of the body cavity.
viviparous – bringing forth living (active, free-swimming) young.
volume flux – a measure of water flow, where a particular volume (m^3) flows across a unit area (m^2) in a unit of time.
vomer – a median bone in the front of the palate that often bears teeth.

X
xanthic – yellowish.
xenacanths – a group of fossil, mostly Palaeozoic, sharks phylogenetically positioned on the chondrichthyan stem according to many authors, known for their morphological peculiarity and living mostly in freshwater habitats.

Y
yolk-sac placenta – a vascular placental-like structure in some sharks where the embryonic yolk-sac wall is closely associated with the maternal uterine or oviducal wall, providing nourishment to the embryo.
yolk-sac viviparity – producing eggs that hatch within the body of the mother, but the embryos lack a placental attachment to the oviduct.

Z
zona pellucida – see *chorion*.
zooplankton – animals (mostly microscopic) which drift freely in the water column.

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COASTAL FISHES OF THE

WESTERN INDIAN OCEAN

SYSTEMATIC ACCOUNTS

MYXINIFORMES AND PETROMYZONTIFORMES: LIVING REPRESENTATIVES OF JAWLESS FISHES, AND THEIR RELATIONSHIPS WITH OTHER VERTEBRATES

Fabio Di Dario and Michael Maia Mincarone

The living representatives of jawless fishes, the hagfishes (Myxiniformes) and lampreys (Petromyzontiformes), comprise two distinct lineages of primitive-looking yet highly specialised craniates. These two groups were first combined in the Cyclostomes (later recognised as Cyclostomi or Cyclostomata) by Duméril (1806), based on a combination of some unusual morphological characters: a cartilaginous skeleton, absence of the opercle and branchial membranes, absence of paired fins, and the presence of a round mouth, at the tip of a cylindrical, naked and slimy body. With the advance of the cladistic paradigm in the 1970s, the shared morphological attributes of hagfishes and lampreys were best interpreted as symplesiomorphies (e.g., Løvtrup 1977). In addition, comparative morphological studies also revealed that lampreys might be phylogenetically closer to the Gnathostomata, the monophyletic group that comprises all jawed vertebrates. Lampreys and gnathostomes share, for instance, the presence of arcualia (singular arcualium). In lampreys the arcualia are rudimentary, bilaterally-paired cartilaginous structures on the dorsolateral side of the notochord. Arcualia are also known as neurapophyses, interdorsals or basidorsals, and in the gnathostomes they develop into the neural arches (Richardson *et al.* 2011). Whereas a single lamprey might have up to 130 arcualia (Tretjakoff 1926), those structures are completely absent in hagfishes and more basal clades of the Chordata, leading to the conclusion that the name Vertebrata should be restricted to the clade composed by the Petromyzontiformes and Gnathostomata. In that view (e.g., Janvier 1981, 2002), hagfishes are not vertebrates but members of a more encompassing clade — the Craniata. Lampreys and gnathostomes alone also share other key morphological and physiological features, such as a lateral line, a complex adenohypophysis, extrinsic eye muscles, true lymphocytes, and the nervous-system control of the heart (Janvier 2002).

In the 18th century and during most of the 19th, hagfishes and lampreys were considered 'degenerate representatives' of the 'Ostracodermi,' a non-monophyletic assemblage of bony armoured, jawless Palaeozoic craniates (Janvier 2008). Cyclostomes and ostracoderms were first combined in the 'Agnatha' by Cope (1889), who viewed this group as ancestral to the Gnathostomata. If hagfishes and lampreys were degenerate ostracoderms, then the absence of bones, enamel and dentine in those animals would be secondary, since those mineralised tissues are present in the skeleton of most ostracoderms. During the 1970s and 1980s, however, the Myxiniformes were gradually moved to the base of the Craniata, implying that their ancestors might never have had mineralised tissues after all, whereas the Petromyzontiformes were still perceived as an offshoot of the 'Ostracodermi' (e.g., Janvier 1978).

The debate as to whether or not the Cyclostomata comprises a monophyletic lineage is one of the most interesting topics in comparative biology, because it ultimately relates to a deeper understanding of vertebrate origins. The hypothesis of Cyclostomata monophyly was revived at the beginning of the 'molecular revolution' in systematics in the 1990s (Stock & Whitt 1992; Mallatt & Sullivan 1998; Kuraku *et al.* 1999). Since then, almost all phylogenetic reconstructions based on molecular data recovered the Cyclostomata as a monophyletic assemblage (e.g., Delarbre *et al.* 2002; Kuraku & Kuratani 2006; Heimberg *et al.* 2010). As succinctly stated by Janvier (2008: 1046), "These results leave morphologists and physiologists greatly perplexed," given the amount of morphological, physiological and biochemical synapomorphies that support a closer relationship between the Petromyzontiformes and Gnathostomata (recently summarised by Near 2009). If lampreys are actually related to hagfishes, then one would expect that the Cyclostomata might be the sister group of the remaining vertebrates, including fossil ostracoderms, since the Myxiniformes have been recognised as a basal clade in the Craniata for almost 50 years. However, even that view is now under dispute: it is possible that the Cyclostomata, if monophyletic, evolved from an ancestor morphologically more similar to ostracoderms than to gnathostomes (Heimberg *et al.* 2010; Janvier 2010), implying that living lampreys and hagfishes would indeed be "offshoots" of the 'Ostracodermi' after all.

Summing up, relationships among the three major living groups of craniates – the Myxiniformes, Petromyzontiformes and Gnathostomata – are still under debate. Difficulties in accessing the phylogenetic position of hagfishes and lampreys are in part related to their highly specialised feeding mechanisms and biology.

The 87 valid species of living hagfishes have an entirely marine distribution, inhabiting the cold or deep parts of oceans of both hemispheres. Lengths typically range from ~25–100 cm. The recently described *Eptatretus goliath* from New Zealand is the largest species recorded so far, reaching at least 127 cm TL and ~6.2 kg (Mincarone & Stewart 2006).

Hagfishes usually live in burrows in soft mud-bottom habitats, in depths ranging from the surface to at least 2 743 m, but a species of *Eptatretus* was photographed below 5 000 m in the tropical Pacific (Sumich 1992). In cold waters at higher latitudes some species live in shallower depths. Recent studies also indicate that hagfishes might live in association with rocky and deep coral reef habitats (Mincarone & McCosker 2004; Fernholm & Quattrini 2008) or hydrothermal vent sites (Møller & Jones 2007). Hagfishes have a nocturnal pattern of activity both in aquaria and in the wild (Worthington 1905; Fernholm 1974). Seasonal migration in response to habitat shifts or reproductive season is apparently unusual, and has been reported only for *Eptatretus burgeri* (Kobayashi *et al*. 1972; Fernholm 1974; Tsuneki *et al*. 1983; Nozaki *et al*. 2000). The reproductive biology of hagfishes is practically unknown, but might be inferred on the basis of collected specimens and from observations made on animals held in aquaria. Hagfishes have a single gonad, which is differentiated anteriorly as an ovary and posteriorly as a testicle in immature individuals. Adult individuals are functionally males or females, however. Fertilisation is probably external. Females produce ~20–30 relatively large eggs (15–40 mm long), laid in batches. Eggs are approximately sausage-shaped, heavily yolked, and covered by a horny shell. There is little information on the development of hagfishes, but it is probably direct, without a larval stage, with young emerging at ~45 mm TL (Gorbman 1983, 1997; Helfman *et al.* 2009).

Information on other aspects of the biology of hagfishes is also scarce, simply because most species are deepsea dwellers, and thus both hard to observe and to collect. Although hagfishes are jawless vertebrates, two eversible keratinised tooth plates located in the lower mouth chamber are used in conjunction with a single, curved, horny tooth at the roof of the mouth to grasp prey or perforate the tegument of dead or dying animals (Martini & Flescher 2002; Helfman *et al.* 2009; Zintzen *et al.* 2011). Hagfishes are well known for their scavenging habits, which are particularly relevant during the onset of so-called whale fall communities (Smith & Baco 2003). They might penetrate the carcass of large whales and other animals through natural orifices on their bodies, consuming their prey from the inside out. They also use a very elaborate mechanism for perforating the tegument, which probably evolved in order to compensate for the absence of paired fins, which provide a counterforce or anchor point for the biting action in aquatic gnathostomes. This mechanism is succinctly described as follows: the eversible tooth plates are used to firmly grasp the skin of the prey; a knot, produced by twisting the posterior portion of the hagfish, moves forward along its body and reaches the head region; that knot is then pressed against the tegument of the prey as a means of levering off a piece of flesh (Helfman *et al.* 2009). A species of *Neomyxine* from New Zealand was observed in active predation using this knotting mechanism to remove live red bandfish (*Cepola hastii*) from their burrows (Zintzen *et al.* 2011). Hagfishes also prey on a large variety of invertebrates, and the force generated during their bite actually matches or exceeds that of several gnathostomes. Surprisingly, the Myxiniformes might be regarded as the oldest living lineage of chordate predators (Zintzen *et al.* 2011). It has also been recently discovered that hagfishes are able to absorb dissolved organic matter through the skin and gills. This ability probably originated as an adaptation associated with their scavenging lifestyle, allowing hagfishes to maximise sporadic opportunities for acquiring nutrients (Glover *et al.* 2011).

The eyes of hagfishes are small and subcutaneous, and also devoid of musculature and true lenses. Two pairs of sensory tentacles or barbels encircle the single nasopharyngeal duct at the tip of the head, and a third pair of barbels is located near the mouth (Janvier 2002; Martini & Flescher 2002); when searching for food, hagfishes keep their barbels in constant contact with the substrate (Zintzen *et al.* 2011). The inner ear is also relatively simplified and contains a single vertical semicircular canal. The number of branchial openings ranges from 5–14 in *Eptatretus*, to a single common opening in *Myxine.* An opening for the pharyngocutaneous duct on the left side of the body, behind the gill apertures, connects the pharynx to the exterior (Janvier 2002). A series of 57–207 ventrolateral pairs of slime glands can produce copious quantities of mucus, used mostly in defence against predation but also during hunting and probably reproduction (Gorbman 1997; Helfman *et al.* 2009; Zintzen *et al.* 2011).

Lampreys do not occur in the Western Indian Ocean or on the African continent, and for that reason only a brief summary of the group is given. The most distinctive morphological feature of an adult lamprey is the oral disc, which is a highly muscular structure. The mouth, at the centre of the oral disc, is encircled by a series of relatively well-developed keratinised teeth. The primary function of the oral disc is to provide a suction mechanism for the lamprey, which attaches itself to the skin of larger fish and, occasionally, cetaceans (Nichols & Tscherter 2011). A piston-like tongue, also covered with horny teeth, is used in conjunction with the teeth of the oral disc to abrade the skin of the prey, and blood, other body fluids and bits of skin, are ingested during the process. Adult lampreys are sometimes considered parasites, but since they harm other organisms only during feeding, they might be best regarded as highly specialised predators. Adults of about half of the known species never feed, and the Caspian lamprey *Caspiomyzon wagneri* feeds exclusively as a scavenger (Renaud 1997; Potter & Gill 2003).

Three families and ~48 species of lampreys are known (Renaud & Economidis 2010; Renaud 2011; Tutman *et al.*

2017; Riva-Rossi *et al.* 2020). Petromyzontidae is the most diverse family, with 8 genera and 43 species occurring in the Northern Hemisphere (Renaud 2011; Nelson *et al.* 2016; Tutman *et al.* 2017). Species of Geotriidae and Mordaciidae occur exclusively in the southern portions of South America and Oceania (Nelson *et al.* 2016). Two species of pouched lampreys (*Geotria australis* and *G. macrostoma*) are recognised in the Geotriidae, whereas 1 genus (*Mordacia*) with 3 species is recognised in the Mordaciidae (Renaud 2011; Riva-Rossi *et al.* 2020). Interestingly, the extinct but exquisitely preserved and fascinating *Priscomyzon riniensis* is known from the Late Devonian (~360 MYA) in a marine or estuarine environment of southern Africa (Gess *et al.* 2006).

FAMILY MYXINIDAE

Hagfishes

Michael Maia Mincarone

Body eel-like, subcylindrical and slender, slightly deeper than wide at prebranchial, branchial and trunk regions; tail strongly compressed, paddle-shaped. Mouth jawless, with 2 sets of laterally everting keratinous cusps (or 'teeth') for biting and scraping, attached to the dental plate, which is attached to anterior end of dental muscle; single tooth on roof of mouth. No paired fins and no dorsal fin; midventral finfold present on trunk; caudal fin extends onto dorsal and ventral surfaces of tail. Single nostril above mouth, which leads respiratory water through the nasopharyngeal duct to pharynx and gill pouches. Pharyngocutaneous duct (PCD) on the left side confluent with (or posterior to) the last gill aperture. Three pairs of barbels on head: the first 2 pairs adjacent to nostril, the 3rd pair immediately adjacent to oral cavity. Vestigial eyes embedded in flesh. Body naked, with mucus-secreting slime glands, in segmentally arranged row, with pores opening along ventrolateral sides of body and tail. Endoskeleton cartilaginous; cranium a simple trough below brain, and postcranial skeleton comprising a large unconstricted notochord without centra or ribs. No separate larval phase. Attains 127 cm TL.

Hagfishes have an entirely marine distribution. Usually burrow in mud-bottom habitats, and found from surface to >5 000 m deep; however, some species appear to be closely associated with deepwater rocky areas, coral reefs, or hydrothermal vent habitats. Can produce copious amounts of slime or mucus, which might have a gill-clogging effect on predatory fish. Hagfishes have an important role in their benthic ecosystems: as scavengers, they are one of the most important mechanisms for the rapid clean-up and processing of carrion-falls; likewise, in areas subject to intensive commercial fisheries, they probably play a key role in the removal and recycling of discarded bycatch.

Six genera and 87 species; 2 genera and 4 species in WIO.

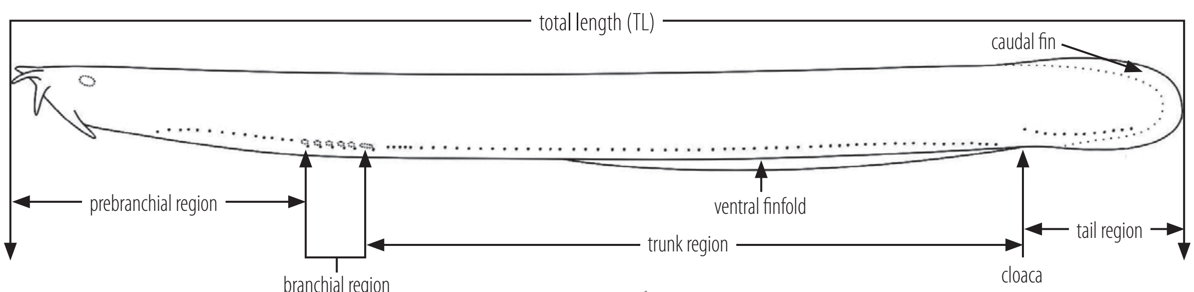
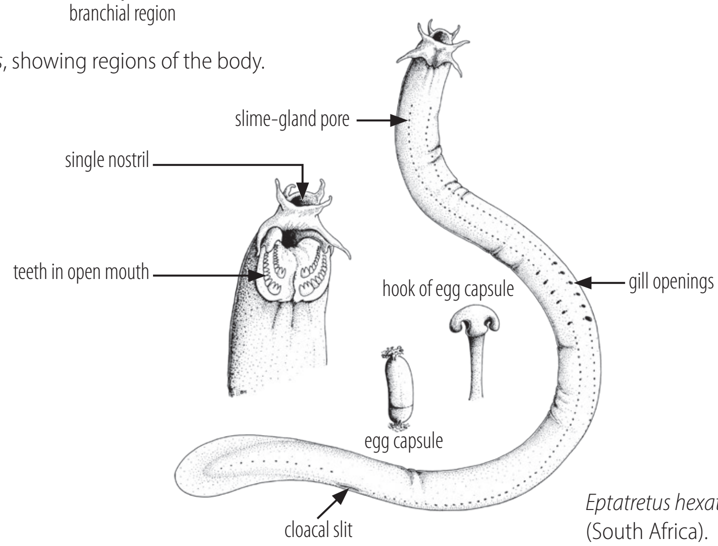


Diagram of an *Eptatretus*, showing regions of the body.



Eptatretus hexatrema, 40 cm TL, ventral view (South Africa). Source: SSF

KEY TO GENERA

1a	External gill apertures 5–8 pairs	***Eptatretus***
1b	External gill apertures 1 pair	***Myxine***

GENUS ***Eptatretus*** Cloquet 1819

External gill apertures 5–14 on each side of body; nostril short and not tubular. Distributed in all oceans, except eastern North Atlantic and Southern Ocean. About 53 species, 3 in WIO.

KEY TO SPECIES

1a	External gill apertures 5 pairs; prebranchial pores 12–15; tail pores 15–17	***E. profundus***
1b	External gill apertures ≥6 pairs; prebranchial pores 21–29; tail pores 11–14	**2**
2a	External gill apertures usually 6 pairs; anterior unicusps 8–10; total cusps 44–49; trunk pores 53–60	***E. hexatrema***
2b	External gill apertures usually 8 pairs; anterior unicusps 7; total cusps 38–40; trunk pores 63–68	***E. octatrema***

Eptatretus hexatrema (Müller 1836)

Sixgill hagfish PLATE 1

Bdellostoma hexatrema Müller 1836: 79 (Table Bay, Cape of Good Hope, South Africa).
Bdellostoma heterotrema Müller 1836: 79, Pls. 1, 3, 6–9 (Table Bay, Cape of Good Hope, South Africa).
Bdellostoma forsteri var. *heterotrema*: Müller 1838; Paepke & Schmidt 1988.
Bdellostoma forsteri var. *hexatrema*: Müller 1838; Paepke & Schmidt 1988.
Bdellostoma cirrhatum: Günther 1870 [in part], 1880; Putnam 1874 [in part].
Homea cirrhata: Garman 1899 [in part]; Dean 1904 [in part]; Fowler 1964 [in part].
Heptatretus hexatrema: Regan 1912; Barnard 1947*; Smith 1950*.
Bdellostoma (*Eptatretus*) *hexatrema*: Holly 1933*.
Eptatretus hexatrema: Strahan 1975*; SSF No. 1.1*; Bianchi *et al.* 1999*; Knapp *et al.* 2011; Mincarone 2017*.

Gill pouches 6 (rarely 7); external gill apertures 6 (rarely 7). Total cusps 44–49: anterior cusps 3 + 8–10, posterior cusps 2 + 9–10. Total slime pores 93–107: prebranchial pores 21–29, branchial pores 5–7, trunk pores 53–60, and tail pores 12–14. Percentage TL: prebranchial length 27–33%, branchial length 5–7%, trunk length 48–58%, tail length 12–14%, body depth at PCD 4–7%, body depth at cloaca 4–7%, tail depth 6–8%.

Body dark brown dorsally, paler ventrally; barbels usually with white tip; eyespots conspicuous; mouth, gill apertures and ventral finfold with pale margins; slime pores and caudal finfold the same colour as body. Attains 80 cm TL.

DISTRIBUTION Southern Africa: Namibia (Walvis Bay) in southeastern Atlantic, to South Africa (KwaZulu-Natal) in WIO.

REMARKS Common throughout its range, from shallow waters (usually associated with rocky reefs) to 400 m. Caught incidentally by baited traps, hooks and bottom trawls.

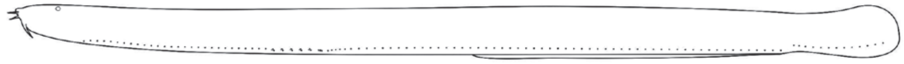
Eptatretus octatrema (Barnard 1923)

Eightgill hagfish PLATE 1

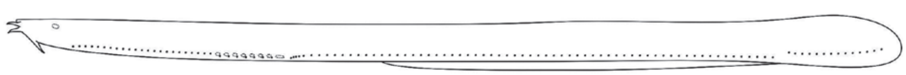
Heptatretus octatrema Barnard 1923: 439 (Agulhas Bank, off Cape St Blaize, South Africa); Barnard 1947.
Bdellostoma (*Eptatretus*) *octatrema*: Holly 1933.
Bdellostoma octatrema: Adam & Strahan 1963.
Homea octatrema: Fowler 1964.
Eptatretus octatrema: SSF No. 1.2; Knapp *et al.* 2011; Mincarone 2017*.

Gill pouches usually 8 (rarely 7); external gill apertures usually 8 (rarely 7). Total cusps 38–40: anterior cusps 3 + 7, posterior cusps 2 + 7–8. Total slime pores 104–117: prebranchial pores 22–26, branchial pores 7–13, trunk pores 63–68, and tail pores 11–14. Percentage TL: prebranchial length 22–25%, branchial length 7–9%, trunk length 55–58%, tail length 10–13%, body depth at PCD 3–4%, body depth at cloaca 3–6%, tail depth 4–7%.

Body dark brown dorsally, paler ventrally; some specimens with whitish ventral band along the body; barbels with white tip; eyespots inconspicuous; rostrum, mouth, branchial apertures, cloaca and caudal fin with pale margin. Attains at least 42 cm TL.



Eptatretus hexatrema, diagram of lateral view.



Eptatretus octatrema, diagram of lateral view.

DISTRIBUTION South Africa (Western Cape). In coastal waters of Kommetjie (near Cape Town) in Atlantic, and off Mossel Bay in WIO.

REMARKS May be naturally rare. Known only from a few specimens, caught in relatively shallow water, at 49–66 m. IUCN Red List conservation status Critically Endangered; but see Mincarone (2017) for further information.

Eptatretus profundus (Barnard 1923)

Fivegill hagfish PLATE 1

Heptatretus profundus Barnard 1923: 439 (off Cape Point, South Africa). Barnard 1947.
Bdellostoma (*Eptatretus*) *profundum*: Holly 1933.
Bdellostoma profundum: Adam & Strahan 1963.
Homea profunda: Fowler 1964.
Eptatretus profundum: Hardisty 1979.
Eptatretus profundus: Strahan 1975*; SSF No. 1.3; Knapp *et al.* 2011; Mincarone 2017*.

Gill pouches 5; external gill apertures 5. Total cusps 42–46: anterior cusps 3 + 8–9, posterior cusps 2 + 8–9. Total slime pores 81–86: prebranchial pores 12–15, branchial pores 4–5, trunk pores 48–52, and tail pores 15–17. Percentage TL: prebranchial length 19–28%, branchial length 5–7%, trunk length 53–69%, tail length 17–24%, body depth at PCD 7–10%, body depth at cloaca 6–9%, tail depth 7–11%.

Body purplish dark brown; eyespots conspicuous; tip of barbels and margin of mouth pale; gill apertures and ventral finfold variably with pale margins; caudal finfold the same colour as body. Attains 70 cm TL.

DISTRIBUTION South Africa: Lambert's Bay (Western Cape) in southeastern Atlantic to Cape Agulhas (Western Cape) in WIO.

REMARKS Poorly known; so far collected from 490–1 150 m. May be caught incidentally in bottom trawls.

GENUS *Myxine* Linnaeus 1758

One pair of external gill apertures: efferent branchial ducts coalesce to form a common aperture on each side. Occurs in all oceans, except eastern Indian Ocean and western South Pacific. About 25 species, 1 in WIO.

Myxine capensis Regan 1913

Cape hagfish PLATE 1

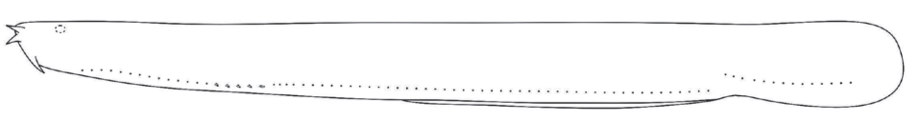
Myxine capensis Regan 1913: 398 (Cape of Good Hope, South Africa); Fernholm 1981; Lloris 1986*; SSF No. 1.4; Villanueva 1993; Bianchi *et al.* 1999*; Knapp *et al.* 2011; Mincarone *et al.* 2011*.
Myxine glutinosa (non Linnaeus 1758): Adam & Strahan 1963 [in part]; Fowler 1964; Hardisty 1979 [in part].

Gill pouches 7; external gill aperture 1 pair. Total cusps 40–44: anterior cusps 2 + 7–10, posterior cusps 2 + 7–9. Total slime pores 93–111: prebranchial pores 26–37, trunk pores 55–66, and tail pores 9–13. Percentage TL: prebranchial length 27–33%, trunk length 54–63%, tail length 11–14%, body depth at cloaca 4–6%, tail depth 3–6%.

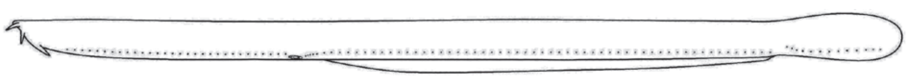
Body pinkish grey; barbels, face, slime pores, and ventral surface of prebranchial region sometimes paler; ventral finfold pale. Attains 53 cm TL.

DISTRIBUTION Southern Africa: Namibia (Walvis Bay) in southeastern Atlantic, to South Africa and Mozambique (off Maputo) in WIO.

REMARKS Females mature at ~32–33 cm TL. Considered common; known from 88–675 m. Incidentally caught by baited traps, hooks and in bottom trawls; this species accounted for ~14% of the diet in 90 specimens of *Octopus magnificus* caught in its range.



Eptatretus profundus, diagram of lateral view.



Myxine capensis, diagram of lateral view.

CLASS CHONDRICHTHYES

Cartilaginous Fishes

ORIGIN AND EVOLUTION OF THE CHONDRICHTHYES

Marcelo R de Carvalho

Sharks, rays (batoids), and chimaeras (ratfishes, ghost sharks) form the class Chondrichthyes, the cartilaginous fishes – referred to as 'sharks' – a group of jawed vertebrates (gnathostomes) whose origins extend back in time to the early Late Ordovician period, some 455 million years ago (MYA) (see geological timescale, Figure 1), as evidenced by very small dermal denticles probably of chondrichthyan affinity (Andreev *et al.* 2016; Sansom & Andreev 2019). Other fossil denticles attributed to sharks from the lower Silurian of Mongolia (Andreev *et al.* 2016) and China (Andreev *et al.* 2020) are only some 25 million years younger. The minute dermal denticles of these early sharks, collectively known as 'mongolepids', were deposited within shallow coastal marine environments. Their classification as sharks is, however, still debated and would be reinforced by the discovery of associated skeletons (Janvier & Pradel 2016; cf. Sansom & Andreev 2019).

Fossil shark teeth, among the most common vertebrate fossils, are known from the beginning of the Early Devonian (*Leonodus*, ~400 MYA). The earliest known shark skeletons appeared in the fossil record in the late Early Devonian, a little later than teeth (*Doliodus*; Maisey *et al.* 2019). Sharks are, therefore, one of the first groups of gnathostomes to have become established in early, warm Palaeozoic seas, even though the oldest 'fishes' (stem craniates, like the diminutive *Haikouichthys* and *Myllokunmingia* from China) appeared in the Early Cambrian some 65 million years earlier (Shu *et al.* 1999, 2003).

Presently, there are about 1 267 living species of chondrichthyans worldwide, comprised of some 540 species of sharks, 675 of rays (skates, guitarfishes, sawfishes, stingrays and electric rays), and 52 species of chimaeras (Last *et al.* 2016; Ebert & Dando 2021). However, a handful of new species (principally rays) are described every year, and dozens of 'known' undescribed species await scientific description. More than 20% of all valid chondrichthyan species were described in the past 20 years alone, indicating that much of their diversity may still be undetected. By comparison, the number of species of chondrichthyans described from fossils is close to twice the number of living species, with the vast majority of these known from isolated remains such as teeth, denticles or spines.

Extant sharks and rays and their immediate fossil relatives are grouped together as elasmobranchs, a group with greater modern diversity compared to any single time in their past, while living and fossil chimaeras, collectively known as holocephalans, were significantly more diverse in the Palaeozoic. Most fossil chondrichthyans are placed in either the Elasmobranchii or Holocephali, but many fossils (called stem sharks), including some very early ones, are phylogenetically placed at the base of the chondrichthyan phylogeny, before its divergence into elasmobranchs and holocephalans.

But what, exactly, is a chondrichthyan? The answer depends on whether one is referring to living species and their more closely related fossils (crown group), which includes elasmobranchs and holocephalans, or to the entire lineage, including the stem fossils, and which stretches back in time from the earliest recognisable fossil sharks to their origins.

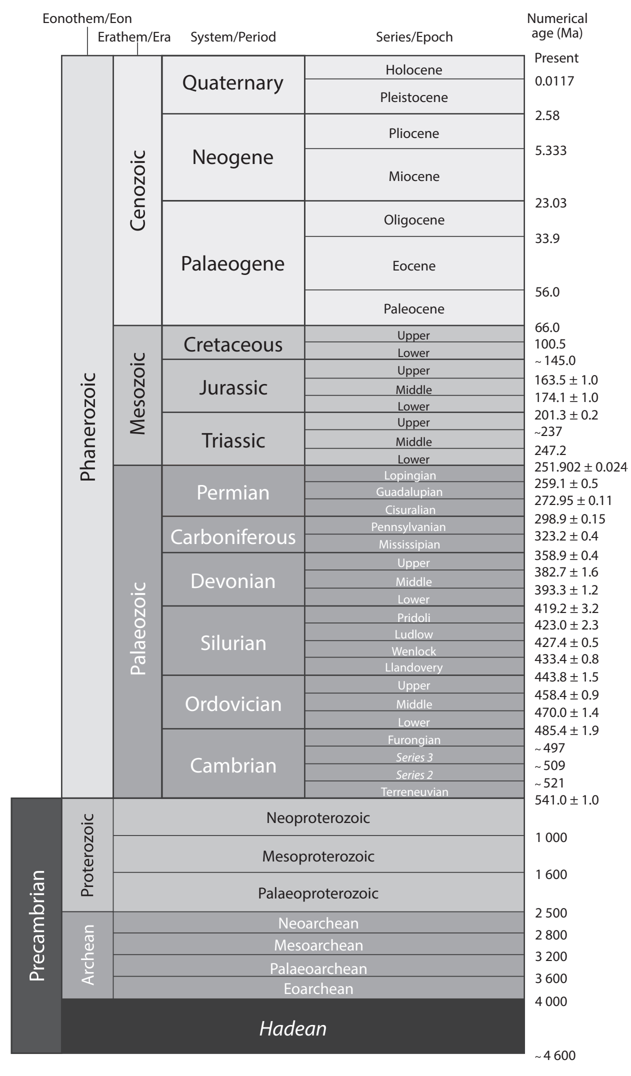


Figure 1 Geological time scale.

Answering this question is difficult because many fragmentary and transitional gnathostome, shark or shark-like fossils display a mosaic of characters, especially those discovered in the past 30 years. Phylogenetically informative characters evolved intermittently, as opposed to 'all at once', and hence defining characters present in crown chondrichthyans evolved at different times on the stem. Add to this the scarce depositional environments associated with early sharks worldwide, and the fact that their skeletons have no significant endochondral ossification (i.e., are not made of true bone; as it turns out, a unique feature of sharks as bone is present in armoured jawless fishes), and one begins to get the picture that early, somewhat complete or even partially preserved sharks are hard to come by.

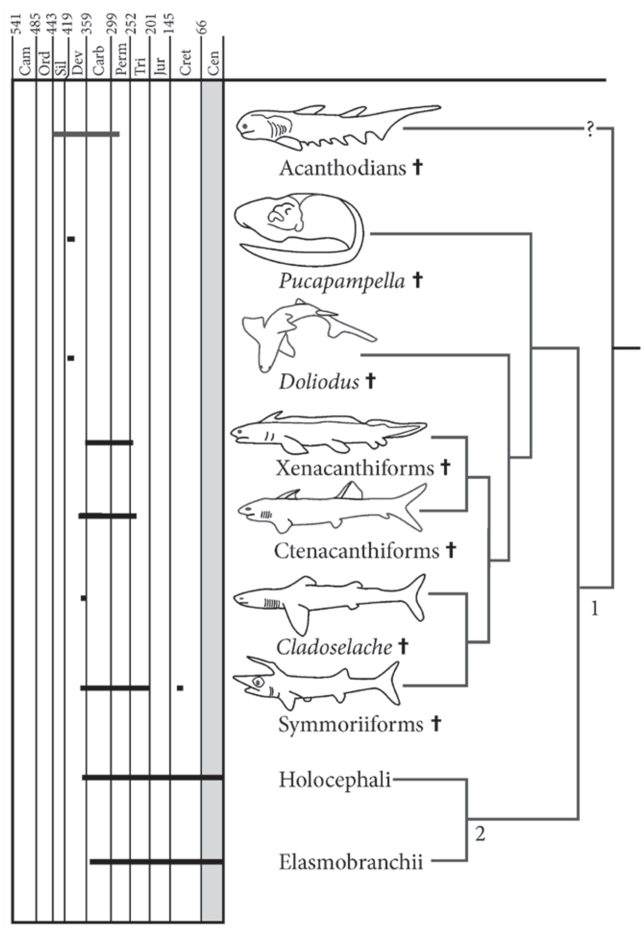


Figure 2 Time-calibrated phylogenetic relationships of early chondrichthyans (modified from Janvier & Pradel 2016). Current phylogenies differ in the relationships of stem chondrichthyans (as a larger monophyletic group here, from *Pucapampella* to symmoriiforms), as there is much disagreement concerning early chondrichthyan evolution. Note that acanthodians are placed outside Chondrichthyes as an outgroup but current understanding is that the many acanthodian genera are scattered on the chondrichthyan stem below sharks.
† denotes an extinct taxon; **1** Chondrichthyes; **2** Elasmobranchii + Holocephali. See Janvier & Pradel (2016) and the text for explanations.

There is still much debate around unequivocally defining early chondrichthyans, acanthodians and placoderms, the first gnathostome lineages dating from the Ordovician and Silurian (see Long *et al.* 2019; Maisey *et al.* 2019 – Figure 2). These three traditionally recognised early gnathostome lineages shared many generalised (plesiomorphic) features, muddling their distinctiveness. This is apparent, for example, in *Doliodus* (an early Devonian shark, known from portions of the head and pectoral-fin skeleton) that is phylogenetically placed low on the chondrichthyan stem even though it had acanthodian-like fin spines (Maisey *et al.* 2017). Early stem taxa may also have had specialisations that belie their supposed primitiveness, such as in stem sharks of the family Pucapampellidae from South America and Africa (Maisey *et al.* 2019). Phylogenetic studies attempting to answer questions about the origins of early gnathostomes have repeatedly shown that acanthodians and placoderms do not form natural groups. Acanthodian genera are scattered on the base of the chondrichthyan tree, and placoderms occupy basal positions on the gnathostome stem below the divergence of Chondrichthyes and Osteichthyes (Zhu *et al.* 2013; Brazeau & Friedman 2015; Coates *et al.* 2017; Long *et al.* 2019; but note that Long *et al.* 2015 and King *et al.* 2016 maintain placoderms as a natural group).

Current notions that acanthodians are phylogenetically scattered on the chondrichthyan stem (at the base of the chondrichthyan phylogeny), and the fact that many early shark fossils are known only from partial remains, have implications for the definition of Chondrichthyes. Given this scenario, chondrichthyans without acanthodians (the 'euchondrichthyans' of Janvier & Pradel 2016) are best characterised by tessellated mineralisation of the skeleton (Dean & Summers 2006; Janvier & Pradel 2016), in which mineral deposits form a tile-like mosaic overlying the cartilaginous matrix. This feature is present in crown- and stem-group chondrichthyans, but is not present in acanthodians phylogenetically positioned on the chondrichthyan stem (Maisey *et al.* 2021). Crown-group chondrichthyans also have pelvic claspers derived from radial pelvic-fin elements, easily observed in any living male shark, ray or chimaera, but many early fossil sharks do not have preserved pelvic fins or claspers so we cannot know exactly when this feature first evolved on the chondrichthyan stem. Claspers have also been found in placoderms, but these are differently structured and positioned and are therefore not homologous with shark claspers (Long *et al.* 2015; Trinajstic *et al.* 2015).

Many Palaeozoic sharks that are placed low on the chondrichthyan stem are known from three-dimensional remains, and their anatomy is actually better known than many Mesozoic sharks. Recognised stem sharks vary among phylogenetic studies, as do their relationships to each other. According to Janvier & Pradel (2016), these sharks include *Cladoselache* from the Devonian, the 'symmoriiforms' (e.g., *Stethacanthus*, *Falcatus* [see Figure 3], *Damocles*, *Akmonistion* [see Figure 4], *Cobelodus*, the South African

Dwykaselachus, and the recently described *Kawichthys*, *Ozarcus* and *Ferromirum*), the xenacanths (such as *Orthacanthus*, *Triodus*, *Xenacanthus*), the 'ctenacanths' (e.g., *Cladodoides*, *Tamiobatis*, *Dracopristis*), and the earliest sharks known from neurocranial remains (*Doliodus*, *Antarctilamna*, *Pucapampella* and *Gydoselache*), among a few others. But Coates *et al.* (2017, 2018) and Frey *et al.* (2020) regard *Cladoselache* and symmoriiforms as stem holocephalans, and Hodnett *et al.* (2021) don't recognise a chondrichthyan stem at all and place these sharks as stem elasmobranchs. Hence, there is still much uncertainty concerning the early evolution of chondrichthyans.

Stem chondrichthyans are mostly Devonian and Carboniferous, but some (such as *Triodus* – see Figure 5) extended into the Triassic, contemporaneous with more modern elasmobranchs and holocephalans. Most of these stem sharks were demersal or benthic littoral forms, and also rather small, measuring only up to one metre in length, but some were very large (*Orthacanthus* measured up to three metres and one ctenacanth from Texas may have been the size of a white shark). Almost all stem sharks were marine, but xenacanths lived predominantly in fresh and brackish waters. Many of these stem sharks deviated from the 'conventional' shark design, i.e., streamlined or fusiform with a heterocercal caudal fin, large, falcate pectoral fins, and multiple rows of large, sharp teeth, and some were downright bizarre compared to modern species. Stethacanthids had strange spine-brush complexes on or behind the head in mature males (in *Akmonistion* it was a massive, anvil-shaped structure larger than the head – see Figure 4), sometimes associated with enlarged denticles, possibly used either to ward off predators or to attract females; these sharks also had a whip-like extension trailing their pectoral fins. Xenacanths were eel-like, with

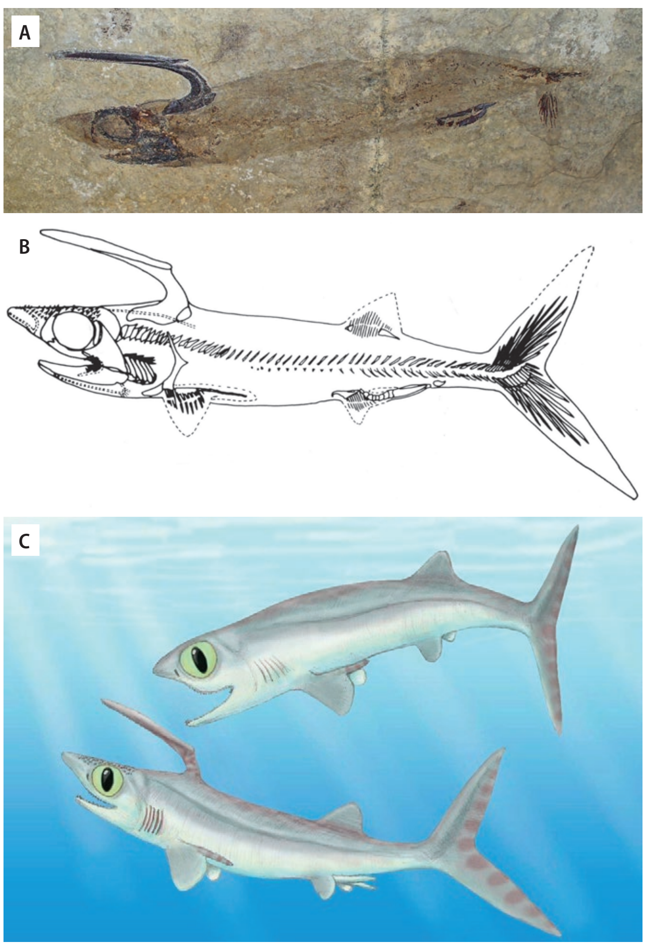


Figure 3 A *Falcatus falcatus* from the Lower Carboniferous Bear Gulch limestone of Montana, USA. A greatly modified symmoriiform shark. Notice the enlarged, forward projecting cephalic spine in specimen (indicative of a male); claspers are also present in male. **B** Reconstructed adult male specimen; notice greatly developed lower lobe of caudal fin. **C** Artist impression of a male and female possibly in a mating ritual.
(**A** H Zell, CC BY-SA 3.0; **B** from Lund 1985; **C** Smokeybjb, CC BY-SA 3.0)

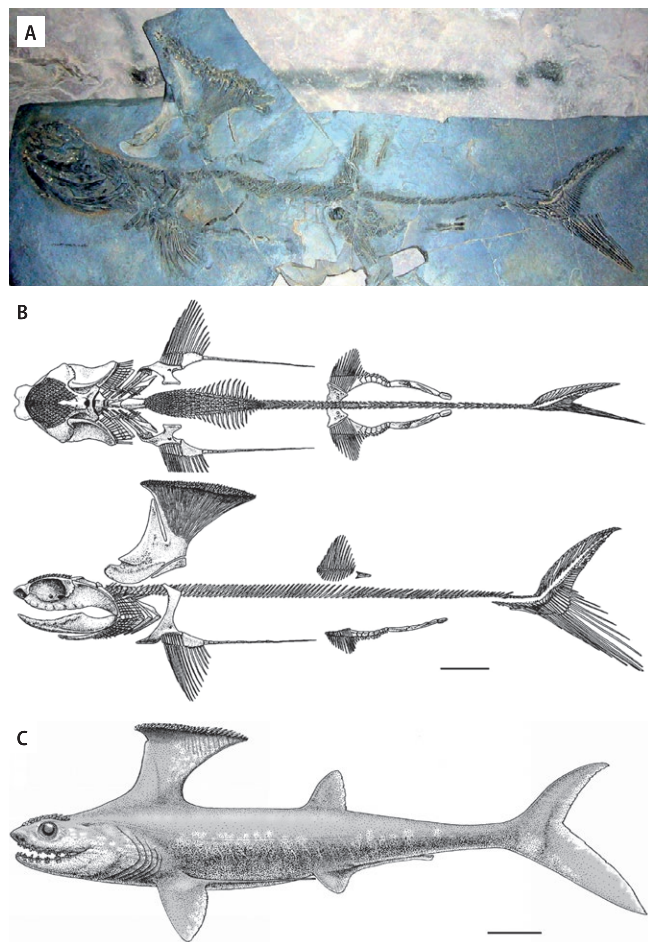


Figure 4 A *Akmonistion zangerli* from the Lower Carboniferous of Scotland. This symmoriiform shark has also been considered a stem holocephalan in some phylogenetic studies. Specimen is male as per the large spine-brush complex and claspers. Notice also the slender head and trunk, large caudal fin (with massive ventral lobe), and elongate projections from pectoral fins. **B** Reconstruction. **C** Artist impression.
(**A** USNM PAL508523; © Smithsonian Institution; **B & C** from Coates & Sequiera 2001)

elongate bodies and a low dorsal fin, sometimes with a double anal fin and diphycercal caudal fin, backward projecting cephalic or dorsal-fin spines with retrorse barbs (like a stingray tail sting), and unusual bicuspid teeth. Many Palaeozoic sharks did not survive the fateful Permian–Triassic extinction, but a few lineages that evolved in the Devonian, Carboniferous and Permian (e.g., hybodonts) flourished in the Mesozoic.

Palaeontological evidence of *bona fide* Palaeozoic holocephalans points to a Late Devonian (c. 380 million years) divergence between elasmobranchs ('euselachians' of Janvier & Pradel 2016 – see Figure 6) and holocephalans ('euchondrocephalans' of Grogan & Lund 2004; see also Grogan *et al*. 2012). The distinction between living sharks and rays (as a group) and chimaeras is morphologically straightforward, as evidenced by many characters in the neurocranium, mandibular and gill arches, claspers, sensory systems, and reproduction (Janvier 1996; Didier *et al*. 2012).

Elasmobranchs include all modern sharks and rays but also certain fossils, mostly Mesozoic, that are placed lower on the elasmobranch phylogeny and are therefore usually not classified within lower-level living groups. These sharks share with modern species features of the neurocranium, membranous labyrinth, gill arches and even fused pelvic girdles, and include the diverse hybodontiforms (e.g., *Tristychius*, *Onychoselache*, *Hybodus* [Figure 7], *Egertonodus*; Maisey *et al.* 2004; Coates & Gess 2007) that ranged from the Late Devonian to the Cretaceous, and the mostly Mesozoic (Jurassic and Cretaceous) 'synechodontiforms'.

Synechodontiforms (e.g., *Palidiplospinax*, *Paraorthacodus*, *Synechodus*) were closer to living forms than hybodonts as they had fully calcified vertebral centra (Maisey *et al.* 2004). They are often referred to as neoselachians together with living sharks and rays, and some synechodontiforms may have been closer to living galeomorph sharks (Maisey *et al.* 2004; cf. Cappetta 2012). Hybodonts comprise a morphologically diverse group that were the dominant sharks of the Triassic and Jurassic. They ranged in size from a few metres (*Asteracanthus ornatissimus*, one of the largest Jurassic sharks) to only about 15 centimetres (*Lissodus*), and occupied diverse niches from large pelagic predators to smaller bottom-feeding durophagous

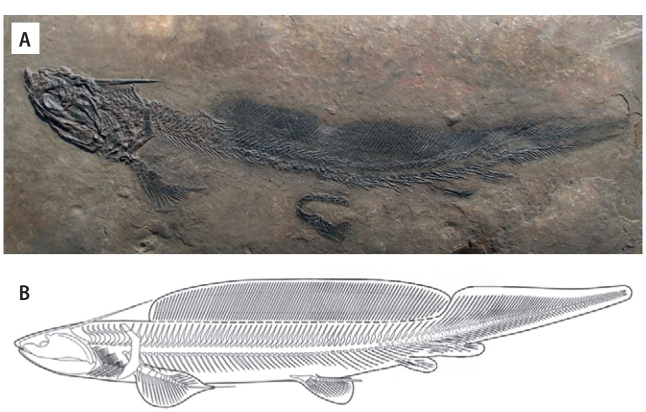


Figure 5 **A** A well-preserved specimen of a xenacanth shark, *Triodus* cf. *sessilis*, 60 cm TL, from the freshwater Permian outcrops of the Saar-Nahe basin, southwest Germany. Notice the eel-like, elongated body and dorsal fin, acute cephalic spine, claspers (specimen is an adult male), diphycercal caudal fin, and slender double anal fin. **B** Reconstruction.
(**A** © D Herr-Heidtke; **B** adapted from Brignon 2015)

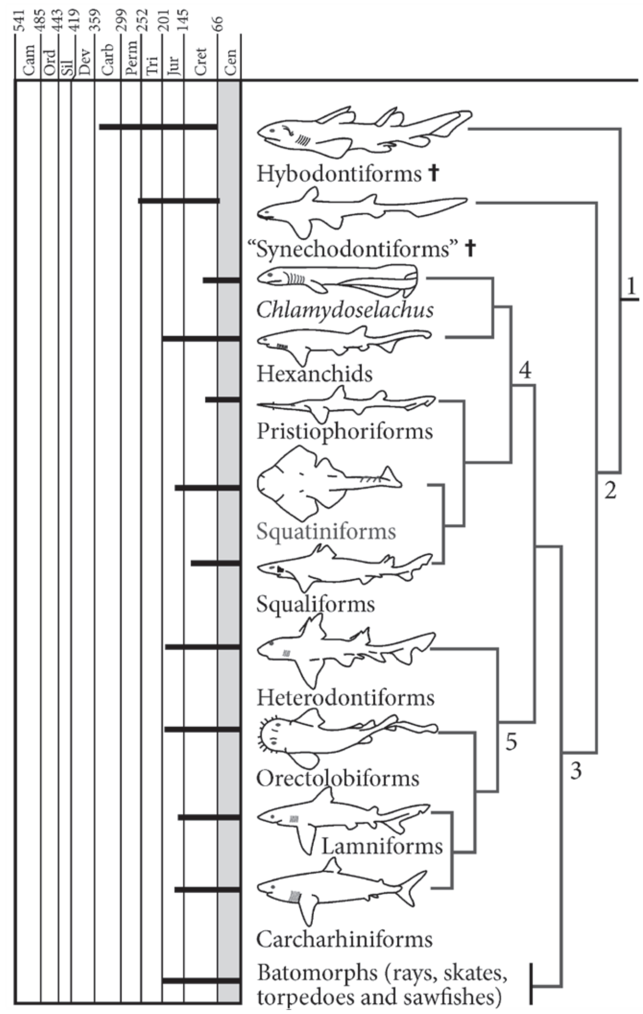


Figure 6 Time-calibrated phylogenetic relationships of Elasmobranchii (modified from Janvier & Pradel 2016). Only major groups of fossil elasmobranchs are represented, and fossils that are nested within living groups are not shown for simplicity. This phylogeny summarises current understanding based on molecular characters, in which sharks are a natural group (but note that Echinorhiniformes is not recognised as a separate order here, and squatiniforms and pristiophoriforms are usually considered to be more closely related to each other than either is to squaliforms). In contrast, morphological phylogenies place the rays ('Batomorphs' in the phylogeny) within squalomorphs, and more closely related to squatiniforms and pristiophoriforms.
† denotes an extinct taxon; **1** Elasmobranchii; **2** Neoselachi; **3** crown-group or living elasmobranchs; 4 Squalomorphi; 5 Galeomorphi. See Janvier & Pradel (2016) and the text for explanations.

forms (*Tribodus*), both freshwater and marine. Hybodonts had massive jaws, large dorsal fins with ornate fin spines (with retrorse denticles and smooth ribs), conspicuous cephalic spines in males, and are among the best-known fossil sharks.

Crown-group elasmobranchs include all living sharks and rays and fossil relatives usually placed within living groups (at the ordinal, familial or generic levels). Researchers working on living elasmobranchs usually recognise nine orders of living sharks (Heterodontiformes, Orectolobiformes, Lamniformes, Carcharhiniformes, Hexanchiformes, Echinorhiniformes, Squaliformes, Squatiniformes and Pristiophoriformes) and four orders of living rays (Rhinopristiformes, Torpediniformes, Rajiformes and Myliobatiformes) (Last *et al.* 2016; Ebert & Dando 2021). Phylogenetic studies conducted over the past 25 years, based on robust morphological and molecular datasets, vary in the recognition or placement of certain orders (e.g., in recognising a separate order for the bramble sharks, *Echinorhinus*), but more fundamentally differ in recovering two conflicting patterns of relationships centred on the evolution of the rays. Analyses of morphological datasets conclude that rays are phylogenetically positioned high among squalomorph sharks (hexanchiforms, echinorhiniforms, squaliforms, squatiniforms and pristiophoriforms), and hence sharks are not monophyletic without their inclusion. Rays and pristiophoriforms (sawsharks) are considered to be each other's closest relative, and their next closest relative are the squatiniforms (angelsharks); this is known as the hypnosqualean hypothesis (Shirai 1992, 1996; Carvalho 1996; Carvalho & Maisey 1996).

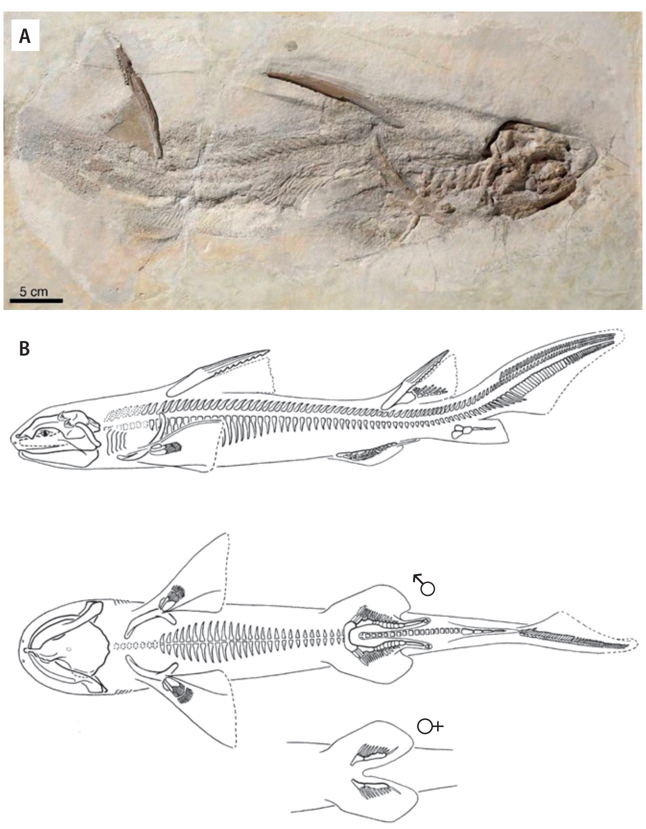


Figure 7 Specimens of hybodont sharks. **A** Photograph of *Hybodus fraasi* from the Lower Jurassic of southern Germany (caudal fin not preserved); notice enlarged dorsal-fin spines. **B** Illustrations of the Late Carboniferous *Hamiltonichthys mapesi*, male, from Kansas, USA. Reconstruction in lateral view (top) showing massive jaws, dorsal-fin spines, cephalic spines and claspers; bottom image depicting anatomy in ventral view (note differences between male and female).

(**A** from Kriwet & Klug 2004; **B** from Maisey 1989)

Molecular data, however, point to an earlier derivation of rays from sharks on the elasmobranch stem and recognise living shark orders as a monophyletic group divided into two superorders, the galeomorphs (heterodontiforms, orectolobiforms, lamniforms and carcharhiniforms) and squalomorphs, equivalent in rank to batoids (Maisey *et al.* 2004). The conflicting results, therefore, centre on *when* batoids diverged from sharks—either before the split into the two extant shark superorders (molecular phylogenetic hypothesis), or after the appearance of squalomorphs (morphological data). As characterised by the great American zoologist William King Gregory, rays are indeed 'winged sharks' (Gregory 1935).

The oldest fossils of extant elasmobranch orders are teeth from the Early Jurassic assigned to heterodontiforms, hexanchiforms, orectolobiforms and batoids (Cappetta 2012; Maisey 2012). Articulated skeletons are known from the Middle (batoids) and Late Jurassic (squatiniforms, carcharhiniforms, heterodontiforms, hexanchiforms and lamniforms; Maisey *et al.* 2004; Thies & Leidner 2011; Maisey 2012), and there is an undescribed Early Jurassic holomorphic batoid from Holzmaden (Germany). Many articulated Jurassic, Cretaceous and early Cenozoic elasmobranchs are essentially modern in morphology and easy to assign to living suprafamilial groups (e.g., stingrays such as *Asterotrygon*, *Heliobatis*, *Promyliobatis* [Carvalho *et al.* 2004]; electric rays, e.g., *Titanonarke*; angelsharks, e.g., *Pseudorhina*; sixgill sharks, e.g., *Notidanoides*), whereas other more complete fossils are placed on the stem leading to certain modern orders (e.g., the morphologically 'transitional' *Protospinax*, a Late Jurassic squalomorph positioned on the stem leading to angelsharks and sawsharks [and batoids in the hypnosqualean hypothesis; Carvalho & Maisey 1996]; *Sphenodus*, on the stem of carcharhiniforms and lamniforms; Maisey *et al.* 2004; cf. Cappetta 2012). Clearly the Mesozoic record concerning articulated remains referable to living orders is still somewhat incomplete. Articulated basal neoselachians (synechodontiforms) are also known from the Early Jurassic, such as the morphologically unique and enigmatic *Ostenoselache* from Italy. However, essentially no Triassic fossils, teeth or otherwise, can be assigned to any living elasmobranch order.

The holocephalans were far more diverse in the Palaeozoic. The three living families pale in comparison to the Carboniferous holocephalan heyday when diverse and morphologically aberrant forms were common, especially in the Bear Gulch lagerstätte of Montana, an ancient warm water embayment at the time (Grogan & Lund 2004) (Figure 8). Fossil tooth plates and some articulated remains from the Mesozoic can be assigned to the three living families (Callorhinchidae, e.g., the Jurassic holomorphic *Ischyodus*; Chimaeridae, Cretaceous; Rhinochimaeridae, Triassic), but articulated Palaeozoic specimens are assigned to several dozen genera. Some of these were eel-like with elongated cephalic tenacula (the chondrenchelyid *Hapagofututor* – see Figure 9), or were shaped like frogfishes of the genus *Antennarius* (petalodontids), but the most bizarre stem holocephalans were the eugeneodontids with symphyseal, vertical tooth-whorls on their lower jaws that perhaps acted to remove soft nautiloid animals from their shells. The Carboniferous genera of the Bear Gulch represent some of the most unusual fossil chondrichthyans known (iniopterygians had dorsally articulating pectoral fins), but *Echinochimaera*, also from Bear Gulch, clearly resembles modern holocephalans in overall appearance (Figure 10).

When we consider all the morphologically peculiar to outlandish Palaeozoic sharks and holocephalans, especially in the Carboniferous, it becomes easy to dismiss the popular notion that 'sharks have not evolved or changed in the past 400 million years'; clearly, modern chondrichthyans resemble their closer Mesozoic relatives much more. We can summarise chondrichthyan evolution by noting that, whether they originated in the Late Ordovician or Early Silurian (denticle-based forms), they began diversifying in the Devonian but truly exploded in diversity in the Carboniferous when dozens of families of sharks and holocephalans were the dominant fishes in many environments. The 'age of amphibians' was also the 'golden age of sharks'. This dominance was perhaps facilitated by major extinction events at the end of the Devonian that eliminated many competing lineages of fishes, such as placoderms, including the giant predator *Dunkleosteus*,

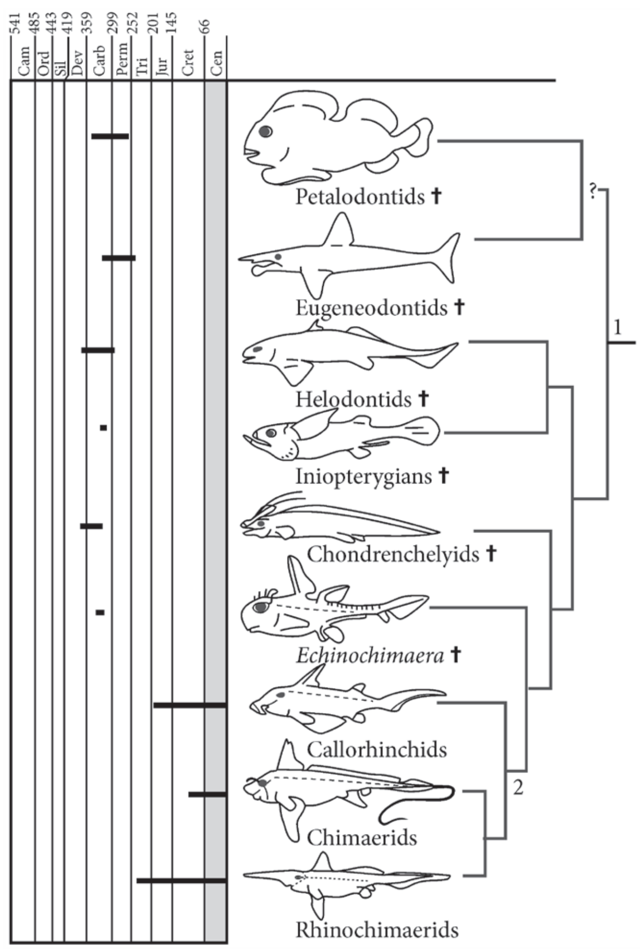


Figure 8 Time-calibrated phylogenetic relationships of Holocephali (modified from Janvier & Pradel 2016). Note that recent authors differ in the phylogenetic relationships of stem holocephalans, and that only a few groups of fossil holocephalans are represented (fossils that are nested within living groups are not shown for simplicity).

† denotes an extinct taxon; **1** Holocephali; **2** Chimaeroidea. See Janvier & Pradel (2016) and the text for explanations.

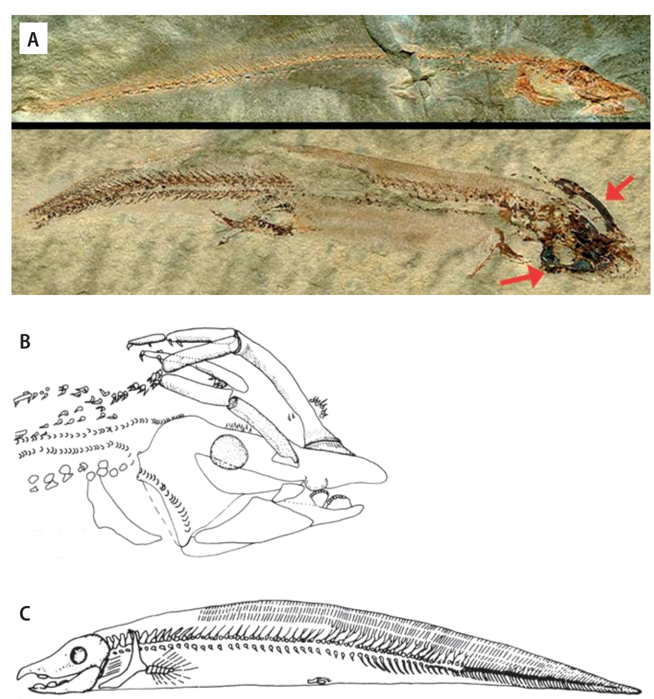


Figure 9 *Harpagofututor volsellorhinus*, a small (up to 25 cm in length) and morphologically unique holocephalan from the Early Carboniferous Bear Gulch limestone of Montana, USA. **A** Female (top) and male (bottom) specimens. Arrows point to enlarged cephalic appendages in the male (with small hooks, believed to have been used to grasp females in copulation – see **B** for more detail). **C** Eel-like body in female.

(**A** from D Chure, http://qvcproject.blogspot.com/2012/05/; **B & C** from Lund 1982) and many acanthodians and armoured jawless fishes. Extinction played a role again a little later during the Permian–Triassic extinction, but in a less favourable way to sharks and holocephalans as many were eliminated along with some 95% of marine life. Some chondrichthyan lineages survived into the Mesozoic, however, when sharks again underwent gradual but significant diversification especially with the evolution of rays sometime in the Early Jurassic (rays are more diverse than sharks at the species level even though there are fewer ray orders). As noted, the beginning of the Jurassic saw the rise of some modern orders of sharks, and almost all elasmobranch orders were established by the end of this period and the early to mid-Cretaceous (the sole exception are the electric rays that date from the Paleocene).

Holocephalan diversity gradually became reduced to the three modern families toward the end of the Mesozoic, with most fossils being massive, hypermineralised tooth plates. There are, however, some remarkable Mesozoic holocephalan articulated fossils, all from Europe, such as the Early Jurassic *Squaloraja* (a flattened, guitarfish-like chimaera with long median and lateral rostral cartridges that formed a huge, triangular snout, a very large and upward-curved cephalic spine [or frontal clasper], huge eyes and short neurocranium – see Figure 11) and *Acanthorhina* (with a sturgeon-like neurocranium and a very long dorsal fin spine). These articulated fossils, along with *Myriacanthus* (also known from Early Jurassic skeletons), are closely related to the living families (Stahl 1999). *Ischyodus*, however, known from some three dozen species, including *I. quenstedti* from articulated remains from the Late Jurassic of Bavaria, is classified as a basal callorhinchid (*Callorhinchus* has three living species).

Many elasmobranchs did not survive the end-Cretaceous extinction (e.g., sclerorhynchid sawfishes), but representatives of living orders obviously did, and elasmobranch diversity steadily increased to present-day levels shortly after in the Cenozoic. Some of the more diverse extant groups date from earlier, in the Late Cretaceous (rajiforms, scyliorhinoids, dasyatids, triakids, many squaliform families), but other species-rich families are from the Eocene (e.g., carcharhinids, narcinids) or even as recent as from the Miocene (potamotrygonins). These records, however, only indicate earliest occurrences in the fossil record and not actually when these groups achieved their present-day diversity.

In terms of modern diversity, elasmobranchs show interesting trends. For example, much speciation has occurred in cold, deep waters and not just in tropical, warm-water regions. The three most diverse families predominantly occur in cold deeper waters of the continental slope and outer shelf regions: skates (Rajidae, ~160 spp.), softnose skates (Arhynchobatidae, 111 spp.), and deepwater catsharks (Pentanchidae, ~110 spp.). These three families alone account for close to one-third of all living elasmobranch diversity. Significant speciation has also occurred in warmer, more shallow seas, as seen in the families Dasyatidae (100 spp.) and Carcharhinidae (57 spp.), and relatively rapid speciation rates are also a factor in Neotropical freshwater ecosystems (potamotrygonin stingrays; 38 spp.).

The Cenozoic rise in diversity is presently being counterbalanced by threats not from catastrophic extinction events, such as recorded at the end of the Cretaceous, but from climate change brought on by global warming, habitat degradation, and overexploitation—in other words, by factors associated with unsustainable development. Having survived the past four global mass extinctions dating back to the Devonian, chondrichthyans now face an entirely different plight.

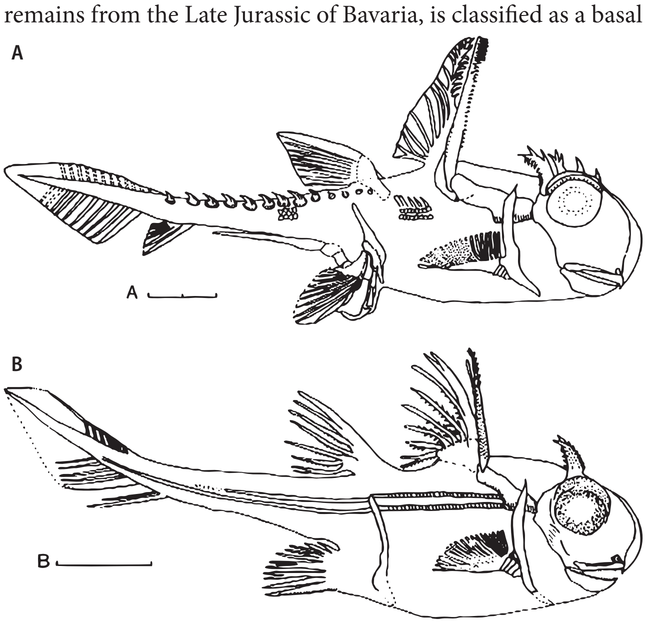


Figure 10 *Echinochimaera meltoni*, a small holocephalan from the Early Carboniferous Bear Gulch limestone of Montana, USA. Even though similar to modern chimaeras, their bodies were covered with small dermal denticles. Specimens reached about 24 cm in length. Both male (**A**) and female (**B**) specimens are shown (redrawn from Lund 1988).

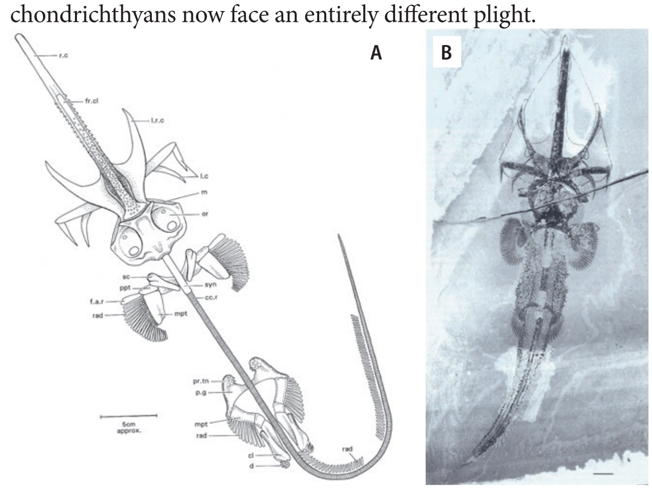


Figure 11 **A** *Squaloraja polyspondyla*, an Early Jurassic, morphologically modified holocephalan with a very enlarged and flattened head endowed with a head spine in males (frontal clasper).
B Photo of specimen from Osteno, Italy.
(**A** Illustration modified from Patterson 1965; **B** from Stahl 1999)

GLOSSARY

acanthodian – a class of early jawed vertebrates that resembled sharks in overall appearance, characterised by fin spines on their dorsal and paired fins (sometimes in between these), divided into three or four orders, and presently considered not to be monophyletic; acanthodians were entirely Palaeozoic ranging from the early Silurian to the Permian.
batoids – refers to the monophyletic group that contains all of the orders of rays.
cephalic tenacula – appendage(s) on the head in male chimaeroids, both fossil and living, used to help grasp the female during copulation (at least in living species; function in fossils possibly the same).
crown chondrichthyans – present-day sharks, rays, skates and holocephalans and their immediate fossil relatives.
ctenacanths – a group of mostly Palaeozoic sharks characterised by specific dentitions and fin spines, usually phylogenetically placed on the chondrichthyan stem below the elasmobranch/holocephalan divide.
demersal – living just above the bottom of the sea or a lake.
diphycercal – a type of caudal fin with a subtriangular shape in which both dorsal and ventral lobes are symmetrical and vertebrae continue towards the extremity of the fin.
durophagous – eating of hard-shelled (exoskeleton- bearing) organisms as a major part of the diet.
endochondral ossification – a type of ossification (formation of bony tissue) in which osteoblasts replace hyaline cartilage with bone.
galeomorphs – a diverse group of sharks that includes the orders Heterodontiformes (bullhead sharks), Orectolobiformes (carpet sharks), Lamniformes (mackerel sharks) and Carcharhiniformes (ground sharks).
gnathostomes – vertebrates that have true jaws, or simply 'jawed vertebrates'; includes placoderms, acanthodians, chondrichthyans and osteichthyans.
holomorphic fossil – a fossil that is more or less 'completely' preserved; fossils that include a good portion of the skeleton and body outline.
homologous – characters or features of organisms that have the same origins in phylogenetic history, and hence usually the same general position and structure (but not necessarily the same function, as in the swim bladder in fishes and lungs in tetrapods).
hybodonts – a diverse group of Palaeozoic and Mesozoic sharks that ranged significantly in size and morphology and that occupied many diverse habitats and niches, characterised by small cephalic spines in males, massive jaws and shoulder girdles, and characteristic fin spines and dentitions. Hybodonts are phylogenetically placed usually on the elasmobranch stem below neoselachians.
hypermineralised tooth plates – referring to the teeth of chimaeroids that undergo significant hardening by the excessive deposition of minerals to facilitate a durophagous diet.
lagerstätte – a sedimentary deposit that has extraordinarily preserved fossils, usually in abundance, and sometimes even with preserved soft tissues.
membranous labyrinth – the fluid-filled, adjoining canals of the inner ear housed in the bony labyrinth of the skull and responsible for the sense of equilibrium.
mongolepids – refers to an order of early fossil sharks known from isolated dermal denticles from the Ordovician or Silurian of Colorado (USA), Mongolia and China; includes the genera *Mongolepis, Solinalepis, Rongolepis, Teslepis, Shiqianolepis, Xinjiangichthys*, and *Sodolepis*.
monophyletic group – a group of organisms (or a clade) comprising the most recent common ancestor and all its descendants; a natural group; a group that is formally recognised in classifications.
natural group – see *monophyletic group*.
nautiloid – refers to the mostly extinct cephalopod molluscs of the group Nautiloidea, with shells that are concave (appearing coiled) and that flourished in the Palaeozoic seas; a few genera, such as *Nautilus*, are extant.
neurocranial – the skeletal structure surrounding the brain and cranial sensory organs.
neurocranium – skull.
pelvic claspers – organs present in males for introducing semen directly into the reproductive tracts of females.
phylogenetic studies – studies that aim to reveal the evolutionary relationships (i.e. the historical patterns of descent) of fossil and living organisms.
phylogenetically informative characters – characters that reveal the historical patterns of phylogenetic relationships among organisms.
placoderms – refers to a Palaeozoic (Silurian to Devonian) gnathostome group of armoured fishes with dermal bony plates on head and trunk, and which occupied numerous habitats and niches from large pelagic predators to small benthic forms; presently considered to not be monophyletic and placed on the stem below the divergence between osteichthyans and chondrichthyans.
plesiomorphic – an ancestral (also referred to as 'generalised', underived or 'primitive') character state shared by groups of organisms (homologous for the group). Such characters cannot be used to define a group of organisms. For example, the presence of vertebrae cannot be used to define sharks.
retrorse (spines) – pointing or curved backward.
stem chondrichthyan – refers to a fossil shark that is placed very low on the chondrichthyan phylogeny, below the divergence of elasmobranchs and holocephalans.
stem elasmobranch – refers to a fossil shark that is placed very low on the elasmobranch phylogeny below the divergence of 'neoselachians', the level of more modern sharks and rays.
stem holocephalan – refers to a fossil holocephalan that is placed very low on the holocephalan phylogeny below the divergence of more modern chimaeroids.
symmoriiforms – a diverse group of Palaeozoic sharks (or possibly basal holocephalans) known from many morphologically unique genera displaying strong sexual dimorphism.
symphyseal teeth – teeth at the junction between the two halves of the lower jaw.
synechodontiforms – an extinct order of sharks, mostly Mesozoic, which are phylogenetically close to living orders of elasmobranchs (sharks and rays) as they share, for example, calcified vertebral centra.
xenacanths – a group of fossil, mostly Palaeozoic, sharks phylogenetically positioned on the chondrichthyan stem according to many authors, known for their morphological peculiarity and living mostly in freshwater habitats.

COASTAL CHONDRICHTHYANS OF THE WESTERN INDIAN OCEAN

David A Ebert and James DS Knuckey

The class Chondrichthyes contains the cartilaginous fishes, which includes the sharks, batoids and chimaeras. The chondrichthyans are one of the most successful groups of fishes and are found in most marine ecosystems. Most of the species (~55%) occur on continental shelves, from the intertidal zone to 200 m deep, and to a lesser extent on insular shelves (Compagno 1990; Ebert & Winton 2010). The diversity of the shelf species is greatest in the tropics and lower in temperate seas. However, knowledge of regional chondrichthyan biodiversity is relatively uneven, with some areas, such as Australia, Europe and North America, being relatively well known, while some regions considered biodiversity hotspots, are poorly known. One of these regions is the Western Indian Ocean (WIO), which has the second most diverse chondrichthyan fauna in the world (at least 304 known species), exceeded only by Australia (with 322 species), although the former region has been comparatively little surveyed relative to the latter region (DA Ebert, personal database). The total number of WIO chondrichthyans represents about 24% of all known species in the class, with 164 shark, 131 batoid, and at least 9 chimaera species present.

Knowledge of the fauna within WIO is relatively uneven, with the number of chondrichthyan species widely differing across the five large marine ecosystems (Agulhas Current, Somali Current, Arabian Sea, Red Sea and Sri Lankan waters) as well as across the Indian Ocean offshore ecosystem. The southwestern Indian Ocean environment, primarily that affected by the Agulhas Current (including Comoros, Geyser Reef, Zélée Bank, Madagascar, Mozambique and South Africa), is the best known, with ~205 species, followed by the Arabian Sea ecosystem (including Persian/Arabian Gulf but not the Red Sea), with ~142 species (Jabado & Ebert 2015; Jabado *et al*. 2017). Faunal surveys conducted primarily off South Africa and southern Mozambique, and more recently off India, have increased our knowledge of these areas. The three other ecosystems (Somali Current, Red Sea and Sri Lankan waters) have fewer species reported to date: Somali Current has ~119 species (R Bennett, pers. comm.), Red Sea has 77 species (Bonfil & Abdallah 2004; Golani & Fricke 2015), and Sri Lankan waters (Ebert *et al*. 2017) have 124 species. The lower numbers reported for these marine ecosystems may be due to research constraints in these regions.

Despite limited scientific sampling, the coast of East Africa from Mozambique to the Arabian Sea, including the many islands and island chains in the region, has produced a remarkable number of new species. From 2001–2020 at least 50 new chondrichthyan species from WIO type localities have been described and named, and 2 new genera, with at least another dozen species awaiting formal description. The number of new species described compares well to the at least 88 species described from Australian waters during this same period. No other regions come close to the total number of species described over the past decade from Australian waters and the WIO. Furthermore, endemism is relatively high, especially among sharks and batoids, with respectively ~18.5% and 36.6% of these elasmobranchs known only from WIO. These numbers may increase with improved taxonomic resolution in some groups, especially the Myliobatiformes (devilrays, eagle rays and stingrays), Squalidae (dogfishes) and Pentanchidae (deepwater catsharks). The high degree of endemism also suggests that some of these species, especially coastal ones, may be at a high conservation risk.

Among elasmobranch species in WIO, approximately 16% have been assessed by the IUCN Red List of Threatened Species (http://www.iucnredlist.org/) as being Data Deficient, with another 2.4% not yet assessed. At the other end of the scale, at least 39 species (13.5%) are listed as Endangered and 24 species (8.3%) are considered Critically Endangered. However, the conservation assessments for many species at potential risk, especially those not considered to be charismatic, may be underestimated relative to some higher-profile, more appealing species. Many of the threatened species have a relatively restricted geographic range, which may be subject to intense anthropomorphic disturbances. Two case studies emphasise this point: *Pliotrema warreni* (sixgill sawshark) and *Holohalaelurus favus* (honeycomb catshark). *Pliotrema warreni* has a relatively restricted range, primarily from Cape Point, South Africa, to southern Mozambique, with its main distribution on the Agulhas Bank, an area of intense commercial trawl fisheries. Basic information on the biology and population structure of this species and the potential impacts of fishing, if any, are virtually unknown. Another species that may be of even more concern is *H. favus*, which was not formally named until 2006, but this once common species has not been seen in surveys since 1972.

Higher classification within the chondrichthyans has undergone considerable debate by taxonomists this century, especially with regard to the taxonomic and phylogenetic relationships of various groups (Shirai 1992; Carvalho 1996; Naylor *et al*. 2005, 2012; Aschliman *et al*. 2012; Straube *et al*. 2015). Recent classifications have suggested that the batoids are a sister group to the modern shark orders Pristiophoriformes and Squatiniformes, and share a common ancestry with the Squaliformes (e.g., the hypnosqualean hypothesis). The two hypotheses break down largely between traditional morphological dichotomy of all modern sharks and batoids (Compagno 1973, 1977, 2001, 2005; Shirai 1992, 1996; Carvalho 1996) and newer molecular evidence (Douady *et al*. 2003; Naylor *et al*. 2005, 2012). In this book the classification of orders of sharks and rays is based on phylogenetic studies mostly carried out by Naylor *et al*. (2012, 2016) in the framework of the Tree of Life program which recognises 9 orders of sharks with 37 families, and the *Rays of the World* book (Last *et al*. 2016), both of which have been adopted in *Eschmeyer's Catalog of Fishes*. The batoid classification used here recognises 4 orders and 26 families (DA Ebert, personal database). The higher classification of chimaeras follows Didier *et al*. (2012) in recognising 1 order and 3 families. Within WIO, all 13 chondrichthyan orders, and ~33 shark, 19 batoid, and 3 chimaera families occur.

The **Hexanchiformes** (cow sharks and frilled sharks) comprises 2 families, 4 genera, and 7 species of morphologically unique sharks in that they are the only group to possess six or seven paired gill slits, a single dorsal fin, and an anal fin. Members of this group of moderately sized to very large sharks mostly occupy a benthopelagic habitat. Both families, all 4 genera, and 5 species occur in WIO. The Chlamydoselachidae (frilled sharks) are sporadically distributed off South Africa, but also with scattered records from islands and seamounts, including the Maldives and Madagascar Ridge. The Hexanchidae (cow sharks) are also wide-ranging but scattered, with records throughout WIO. The hexanchoids occur mostly along the outer continental shelf and upper slope, with the exception of *Notorynchus cepedianus*, a primarily coastal continental-shelf species.

The **Echinorhiniformes** (bramble sharks) is a small group consisting of the family, Echinorhinidae, with a single genus, and 2 wide-ranging benthopelagic species with a scattered worldwide distribution. The single WIO species, *Echinorhinus brucus,* is spottily distributed over a wide range, from South Africa, Mozambique, Maldives, Gulf of Aden, Oman and India.

The **Squaliformes** (dogfish sharks) is the third largest group of chondrichthyans, with 6 families, 23 genera, and at least 143 described species. The squaloids are a morphologically diverse group that contains some of the smallest and largest known species of sharks. Morphological characteristics of this order include 2 small to moderately large dorsal fins, which may be preceded by a fin-spine in some species, the absence of an anal fin, eyes without a nictitating membrane, and five paired gill slits located anterior of the pectoral fins. In WIO, members of this group inhabit both shallow and deepwater environs, but are generally replaced by Carcharhinidae (requiem sharks) and Sphyrnidae (hammerhead sharks) in warm-temperate to tropical seas. All 6 families, 17 genera and at least 42 species occur in WIO. The members of this group occupy a wide variety of habitats and are found from inshore to depths of 4 000+ m. Individual species may be demersal or epipelagic, with some species exhibiting pronounced ontogenetic changes in habitat during their lifetime. In WIO, 36 of the species in this group occur within 4 families: Squalidae, Centrophoridae, Etmopteridae and Somniosidae. The remaining 6 species in this group are in 2 relatively small families: Dalatiidae and Oxynotidae.

The Squalidae is a wide-ranging, benthopelagic family with 2 genera and 40 species recognised worldwide; both genera and 10 species occur in WIO. This family shows a high degree of endemism, with only 1 species (*Squalus acanthias*) known to occur in multiple geographic locations. The Centrophoridae is a taxonomically challenging group, with 2 genera and 19 species recognised worldwide, although the genus *Centrophorus* is currently undergoing an extensive taxonomic revision by the lead author (DA Ebert) and WT White (CSIRO, Hobart, Australia). Both genera and at least 9 species of this family have been recorded in WIO. This group of benthopelagic sharks is most diverse off South Africa and Mozambique, with 8 species reported from that region; the Gulf of Aden has 3 species, and the Aldabra and Seychelles islands have 4 species. The Etmopteridae is the largest family of squaloid sharks, with 5 genera and 52 species worldwide. Members are benthopelagic, mostly in deep water at 200–1 500 m, though some species may range to 4 500 m (Compagno *et al*. 2005). Two genera (*Centroscyllium* and *Etmopterus*) and 11 species occur in WIO. Most species in this family are regional endemics, except for 3 species (*Etmopterus bigelowi*, *E. granulosus* and *E. pusillus*) that are known from scattered records throughout the WIO region. The Somniosidae is one of the widest-ranging groups, occurring in most seas from the tropics to polar seas. Members of this group are benthopelagic, although some are pelagic. The group consists of 7 genera and 17 species, and contains some of the smallest and largest known species of sharks; 4 genera and 6 species occur in WIO. The Oxynotidae is a morphologically distinct group of 5 small- to medium-sized sharks in a single genus. Members are benthic-dwelling, at 50–650 m; only 1 species (*Oxynotus centrina*) is found in WIO <200 m. The Dalatiidae is a small group of 7 genera and 10 species of dwarf to medium-sized, wide-ranging sharks. Members of this group are mostly pelagic or benthopelagic and occur from near surface to >1 500 m deep; 5 genera, each with a single species, are represented in WIO.

The **Pristiophoriformes** (sawsharks) is a small group of poorly known, morphologically distinct sharks within a single family (Pristiophoridae), with 2 genera and 10 described species, with 4 species occurring in WIO. These slender-bodied sharks have a long flattened saw-like snout, lateral rostral teeth, a pair of long string-like barbels in front of the nostrils, two dorsal fins, and no anal fin. Most species have 5 paired gill slits, though the WIO genus *Pliotrema* has six pairs. These benthopelagic sharks occur primarily on continental shelves in temperate seas and usually along the upper continental slope in deeper tropical seas. Both genera occur in WIO; *Pliotrema warreni* is known off South Africa and Mozambique, *P. annae* from Zanzibar, and a deepwater species *P. kajae* from the Mascarene Plateau and off Madagascar; the African dwarf sawshark *Pristiophorus nancyae* is known off southern Mozambique only in deep water (>200 m).

The **Squatiniformes** (angel sharks) is a single family (Squatinidae) and genus (*Squatina*) of small-sized, rather morphologically similar, dorso-ventrally flattened sharks which are often misidentified; they are benthic inhabitants and often seen partially buried in the sediment. There are approximately 20 described species worldwide, occurring mostly in temperate to subtropical seas, with 1 endemic species (*Squatina africana*) in WIO.

The **Heterodontiformes** (bullhead or horn sharks) is a small group with 1 family (Heterodontidae) and single genus (*Heterodontus*) of 9 similar-looking species; 2 species occur in WIO. These are the only living sharks having both a spine preceding each dorsal fin and also an anal fin. Members of this group are primarily benthic-dwelling and nocturnal, tending to rest in caves and rocky crevices during the day but becoming quite active at night. They are found mostly nearshore, from the intertidal zone to ~100 m deep, but at least 1 species (*H. ramalheira*) is known to 275 m.

The **Orectolobiformes** (carpet sharks) comprises 7 families, 13 genera and 45 species worldwide. Members of this group can be distinguished by the presence of nasal barbels, two dorsal fins which are not preceded by a spine, and an anal fin. They are primarily benthic, occurring in tropical to warm-temperate seas, from the intertidal zone to ~200 m deep, usually on rocky or coral reefs, but 1 notable species (the whale shark *Rhincodon typus*) is oceanic. Four families (Hemiscylliidae, Ginglymostomatidae, Stegostomatidae and Rhincodontidae), 5 genera and 9 species are known in WIO, with the highest diversity found in the Arabian Sea and off India and Sri Lanka.

The **Lamniformes** (mackerel sharks) is a small but diverse group of 8 very distinctive families, 10 genera and 15 species. Although each of these families appears to be morphologically distinct, they are united by several unique features, including: a pointed snout, no dorsal-fin spine, a similar type of dentition, and oophagous reproduction. These sharks occupy a wide range of nearshore, coastal, deepsea and pelagic habitats, in temperate to tropical seas. All but one species have been recorded in WIO. These generally large-sized, wide-ranging sharks are most diverse off South Africa and Madagascar and in the Persian Gulf. The Lamnidae are mostly large, actively swimming, voracious sharks, and are among the most media-publicised species. The 3 species of Alopiidae, with their distinctively long tail, and the monotypic Carchariidae, with the coastal raggedtooth shark *Carcharias taurus*, are common throughout the region, while Odontaspididae (2 species) and the monotypic families Cetorhinidae, Megachasmidae, Mitsukurinidae and Pseudocarchariidae are less common.

The **Carcharhiniformes** (ground sharks) is the most diverse and largest group of shark-like cartilaginous fishes, comprising 10 families, 52 genera and 300 species. These sharks, despite a wide range in external morphological appearances, all have two spineless dorsal fins, an anal fin, a long mouth that extends behind the eyes which are protected by nictitating lower eyelids, and usually no oronasal grooves. Nine families (Carcharhinidae, Galeocerdonidae, Hemigaleidae, Pentanchidae, Proscylliidae, Pseudotriakidae, Scyliorhinidae, Sphyrnidae and Triakidae), 35 genera and 89 species are known in WIO. Most of these (54 species) are members of either the Carcharhinidae (30 species) or Pentanchidae (28 species), and may be very common locally.

The Pentanchidae (deepwater catsharks) is the largest family of sharks, comprising 11 genera and at least 111 harmless species worldwide; 5 genera and 28 species are reported from WIO of which 16 are deepwater species. This group may be subdivided into the colourful and mostly shallower species, and the uniformly coloured deepsea forms, which mostly lack any distinctive colour patterns. The number of catshark species is likely to increase with increased exploration, especially in deepsea habitats. The Scyliorhinidae (catsharks) has 10 genera and 71 species; 4 genera and 7 species in WIO. The Proscylliidae (finback catsharks) with 3 genera and 6 species, and Pseudotriakidae (false catsharks) with 3 genera and 5 species worldwide, both have 2 genera with 3 and 2 species respectively, in WIO, where they are known only from a few scattered, mostly deepsea locations. The Triakidae (houndsharks) is a large family consisting of 9 genera and at least 47 species worldwide, of which 6 genera and 9 species are found in WIO. These are mostly coastal species, several of which are regional endemics, plus there may be numerous others that are undescribed. The Hemigaleidae (weasel sharks) is a small group, with 4 genera and 8 species, with all genera and 5 species in WIO; most species in this family, except for the snaggletooth shark *Hemipristis elongata*, are relatively uncommon and poorly known. The Carcharhinidae (requiem sharks) is one of the largest shark families, comprising 11 genera and at least 59 species worldwide. The family is most diverse in coastal warm-temperate to tropical seas; 9 genera and 30 species are known to occur in WIO. The Sphyrnidae (hammerhead sharks) is a small group, with 2 genera and 8 species, which are mostly tropical to warm-temperate; both genera and 4 species found in WIO. The Galeocerdonidae (tiger sharks) is a family with one distinctive monotypic genus; it is circumglobal in warm-temperate to tropical seas, but not present in the Mediterranean Sea.

The **Torpediniformes** (electric rays) is a group of specialised batoids characterised by a thick, flabby, oval to round disc; a short, truncated snout; soft, loose skin without dermal denticles; a relatively short, thick tail; 0–2 dorsal fins; and a well-developed caudal fin. Five families and 15 genera are recognised, of which 3 families and 7 genera occur in WIO; 2 of these genera (*Electrolux* and *Heteronarce*) are WIO endemics, and as currently known have very restricted geographic ranges. Worldwide there are ~69 species, with 19 known in WIO. Limited molecular data suggest this traditional classification is likely to change once more sampling has been undertaken.

The **Rhinopristiformes** (sawfishes, giant guitarfishes, guitarfishes, wedgefishes and banjo rays) is comprised of 5 families and 61 species; 4 families and 29 species known in WIO. The Pristidae (sawfishes) is a small group of very large batoids, having a flattened, greatly elongated rostrum with large transverse teeth along each side; 2 genera and 5 species occur worldwide, with both genera and 3 species found in the WIO. A recent global revision of the family has revealed the genus *Pristis* to have only 5 species rather than the 7 usually noted in the literature (Faria *et al*. 2013). This is likely the most critically endangered group of elasmobranchs, as their coastal habitat has been impacted from anthropogenic changes in many areas, and they are severely affected by fishing. *Pristis* are now considered locally extinct in several countries, including South Africa. The morphologically distinct Glaucostegidae (giant guitarfishes) has a single genus and 6 species worldwide, with 5 species in WIO; all species with IUCN Red List conservation status Critically Endangered. Glaucostegidae was formerly classified in Rhinobatidae, from which it differs in head shape and nasal flap configuration. The Rhinobatidae (guitarfishes) range in size from small to large, with 3 genera and 33 species worldwide, 2 genera and at least 16 species in WIO. The more shark-like, medium- to large-sized Rhinidae (wedgefishes) has 3 genera with 10 species, 2 genera and at least 4 species in WIO.

Four families are recognised within the order **Rajiformes** (skates), the Anacanthobatidae (legskates), Arhynchobatidae (softnose skates), Gurgesiellidae (pygmy skates) and Rajidae (hardnose skates). Members of this group usually have skin with prickles or thorns, often in a row along the midback; 0–2 dorsal fins; and long slender claspers in males. Worldwide, 39 genera are recognised within this order as presently arranged, with all families and 15 genera represented in WIO. This is the largest group of batoids, with 298 species, of which 32 occur in WIO, 9 of which are from deep water.

The **Myliobatiformes** (stingrays, devilrays and eagle rays) is the second-largest group of batoids and are characterised by their enlarged, expanded pectoral fins being completely fused to the head and trunk (except for the Myliobatidae), a disc ranging from diamond-shaped to subrhombic or lozenge-shaped; the presence or absence of a single dorsal fin; and a long whip-like tail in many species, with one or more stinging spines at the base. Worldwide there are 12 families, 56 genera and 244 species recognised; of these, 8 families, 22 genera and 51 species occur in WIO. It is likely that the numbers of species may increase with improved taxonomic resolution of some of these groups. In WIO, the family Dasyatidae (stingrays) is most diverse, with 27 species, followed by the Myliobatidae (eagle rays) with 6 species and Mobulidae (devilrays) with 7 species. The families Gymnuridae (butterfly rays) and Rhinopteridae (cownose rays) have 4 species and 2 species, respectively, in WIO; the family Aetobatidae (pelagic eagle rays) has 1 genus with 5 species, 3 species in WIO; while the families Hexatrygonidae (sixgill stingray) and Plesiobatidae (deepwater stingray) each have a single wide-ranging species, including in WIO.

The **Chimaeriformes** (chimaeras, ratfishes or silver sharks) is a small group of unusual chondrichthyans comprised of 3 families, 6 genera, and 57 described species. The chimaeras are readily distinguished by their elongated tapering body, filamentous whip-like tails, smooth scales, large venomous dorsal-fin spine, broad wing-like pectoral fins, single external gill opening on each side, and open lateral-line canals, which appear as grooves on the head and along the trunk. Chimaeras are sluggish-swimming species usually found along outer continental shelves and upper slopes, although some species (especially members of the Callorhinchidae) are common in nearshore coastal waters. All 3 families, 6 genera and 9 or 10 species occur in WIO. However, of the Callorhinchidae (elephantfishes) only one species is represented in WIO at depths of <200 m (*Callorhinchus capensis*, off South Africa). The Chimaeridae (shortnose chimaeras or ratfishes) is the most species-rich family, with possibly 3 of 40 described species in 2 genera occurring in WIO, but all at depths exceeding 200 m, although there are several species in this region awaiting formal descriptions. The family Rhinochimaeridae (longnose chimaeras) is a wide-ranging group, with 3 genera and 5 species found in WIO, 2 species in 2 genera known from depths of <200 m, and a 3rd species likely.

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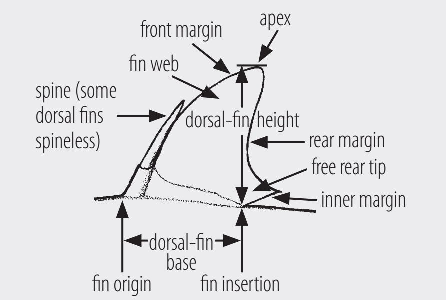
GLOSSARY

hypnosqualean hypothesis – a hypothesis that proposes that the batoids (rays and skates) are derived sharks, based on many morphological phylogenetic studies.
nictitating membrane or nictitans – a clear, moveable inner eyelid found in sharks, and some reptiles and birds.
benthopelagic – fishes that live and feed near the bottom as well as in midwater.

ANATOMY OF SHARKS, RAYS AND CHIMAERAS

The Chondrichthyes, comprising the sharks, batoids (rays and skates) and chimaeras, are characterised by a skeleton that is entirely cartilaginous. In adults the skeleton becomes more or less hardened by calcification. Shark skeletons also have far fewer components than the skeletons of bony fishes. The cranium is a single cartilaginous box to which the gill arches and jaws are not directly attached. The vertebral column consists of a series of vertebrae below an arch that protects the spinal cord. It runs from the posterior part of the skull to the tip of the upper caudal-fin lobe. The fins are variously supported by cartilaginous structures that articulate distally with keratinous, hair-like filaments, called ceratotrichia.



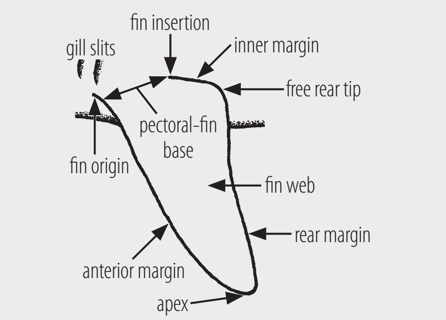
Dorsal-fin morphology and measurements

BODY FORM AND FINS

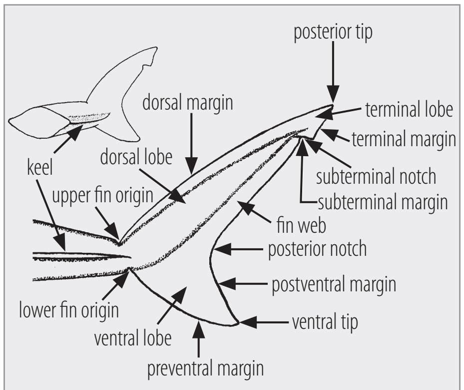
The torpedo-shaped body of most sharks and chimaeras has remained nearly the same for millions of years. They vary in length from the nearly 19-m whale sharks (Rhincodontidae) with a confirmed length of 18.8 m (McClain *et al.* 2015) to little lanternsharks (Etmopteridae), that are less than 30 cm. Rays and skates have very flattened (depressed) bodies.

The body of sharks and chimaeras is divided into three parts: head, trunk and tail. In batoids head and trunk are a single unit, their large pectoral fins stretch from the head, and tails are long, frequently thin, and sometimes very small. Several of the larger, fast-swimming sharks also have a fleshy keel on each side of the caudal peduncle to strengthen it and reduce turbulence.

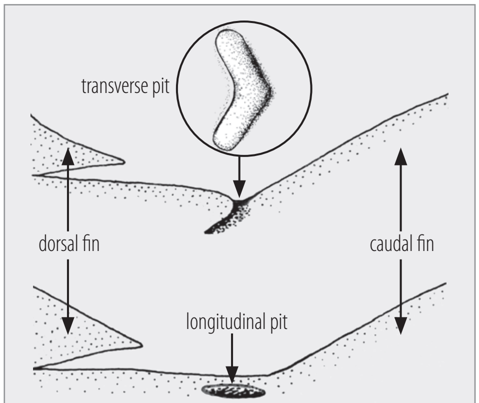
Most sharks have two rigid dorsal fins, the first usually larger than the second, and several families have a stout spine in front of each dorsal fin. The second dorsal fin is absent in cow sharks (Hexanchidae) and frilled sharks (Chlamydoselachidae). Most sharks also have an anal fin. An asymmetrical caudal fin, in which the upper lobe is longer than the lower, is the main propulsion unit. In fast-swimming sharks, like the mako and the white shark (Lamnidae), the caudal fin is almost symmetrical. The paired pectoral and pelvic fins are nearly rigid and are used to provide lift (like the wings on an aeroplane) and control pitch (the 'nose up' or 'nose down' of an aeroplane). In the batoids (rays and skates) and in chimaeras the flexible pectoral fins are used for swimming.



Pectoral-fin morphology



Caudal-fin morphology



Types of precaudal pit at caudal-fin origin

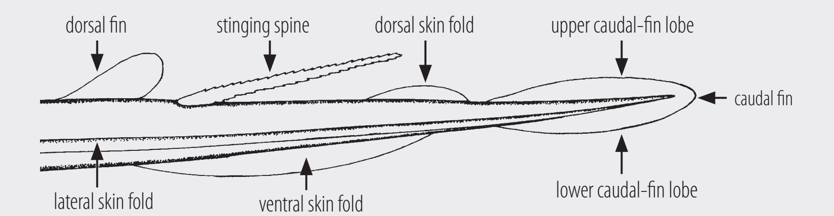
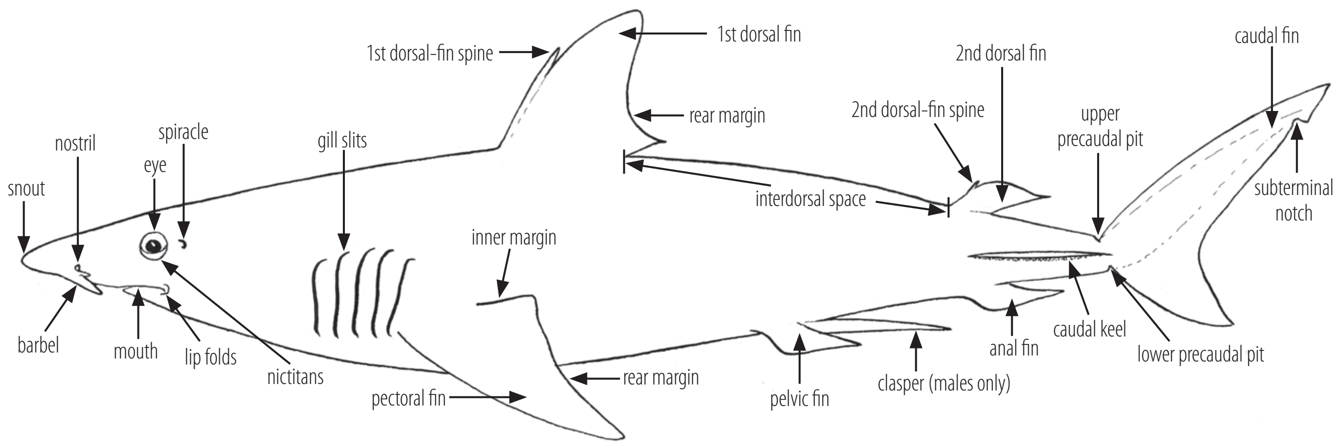
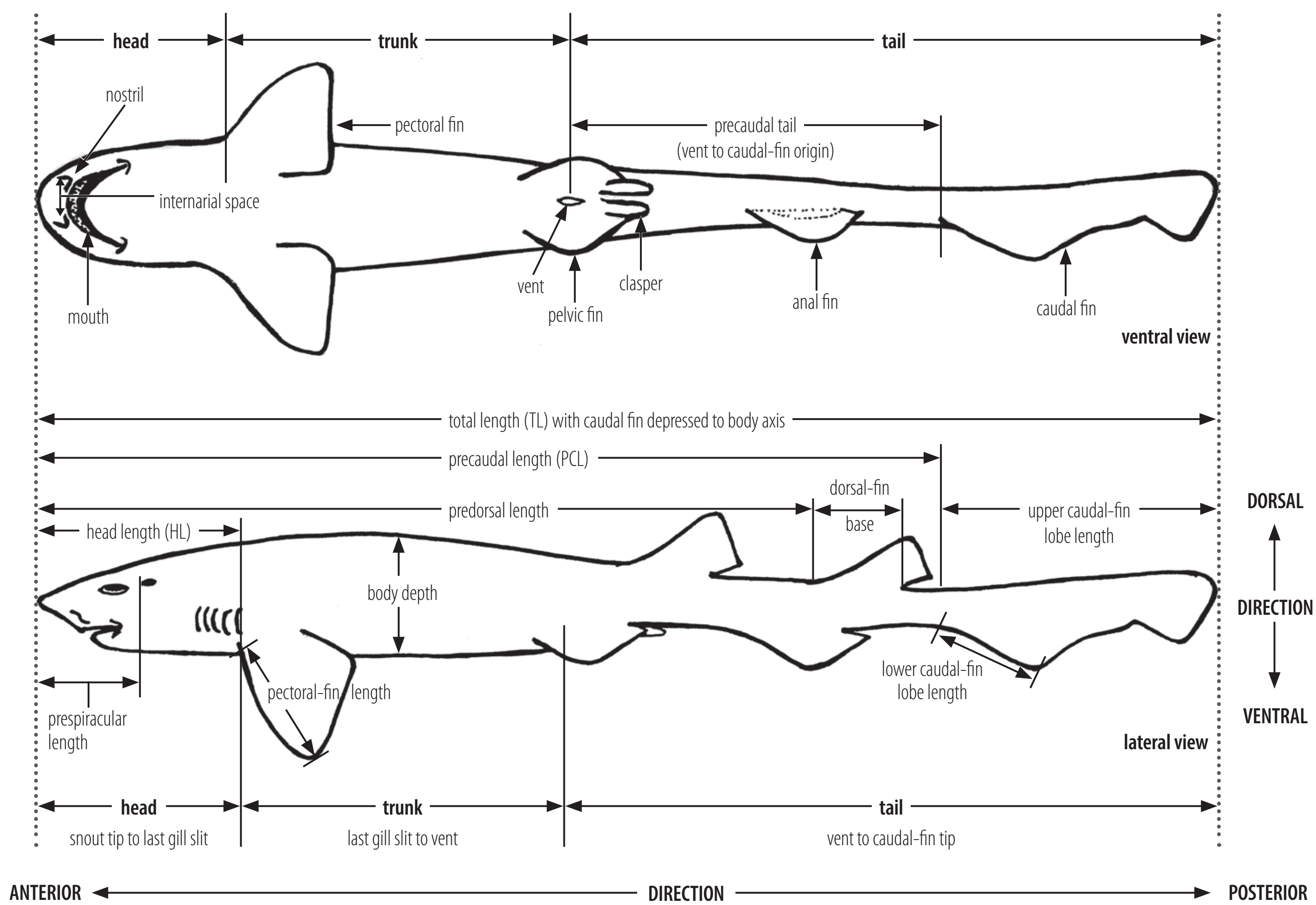


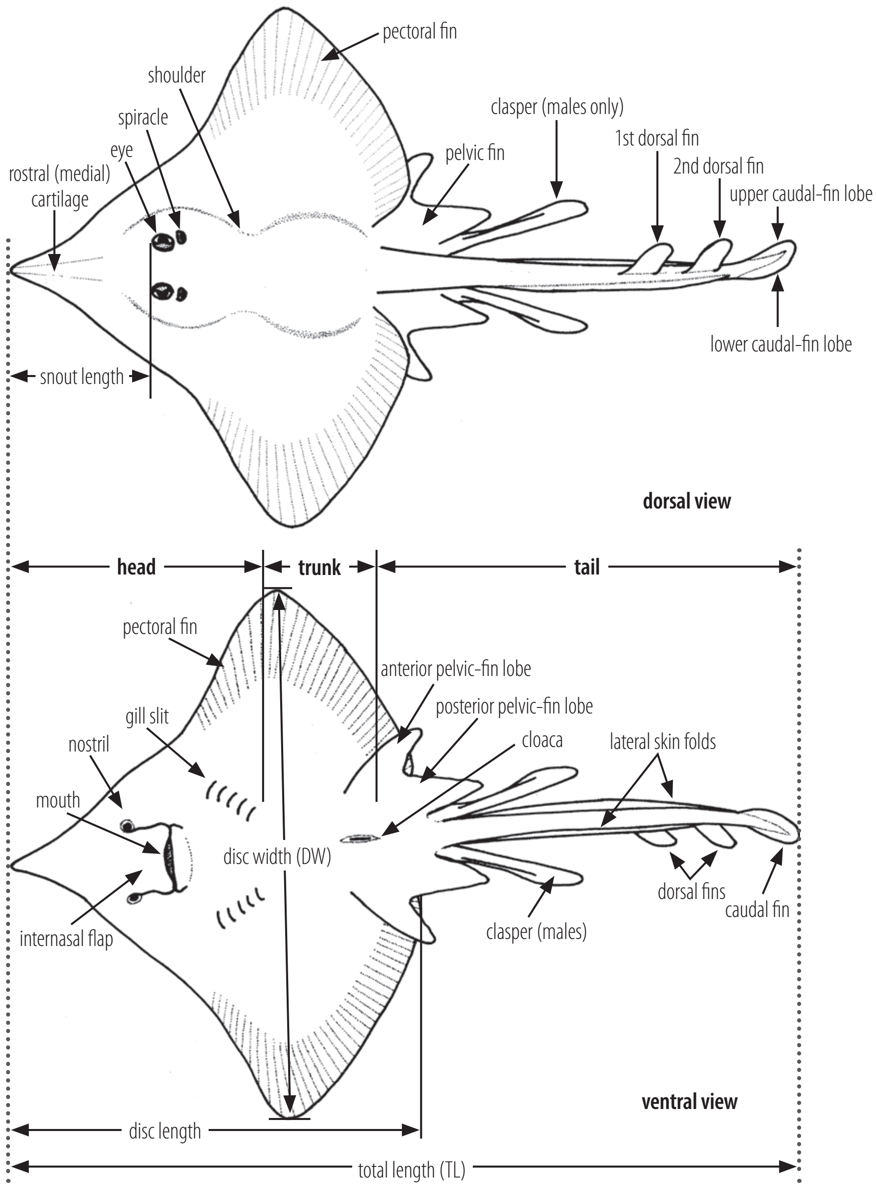
Diagram of fin and skin fold positions on a generalised batoid tail (not all features are found in any one specimen)



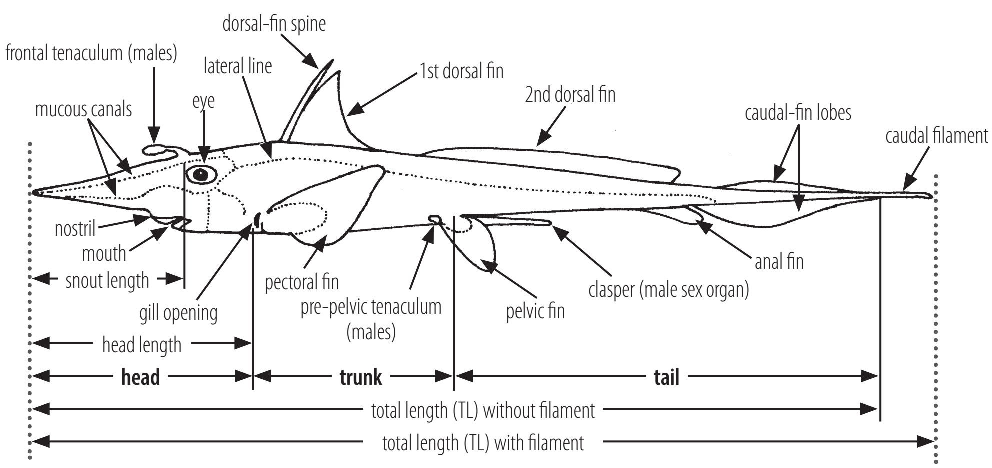
Morphology of a generalised shark



Ventral and lateral views of a generalised catshark to show morphology and measurements



Morphology and measurements of a generalised batoid

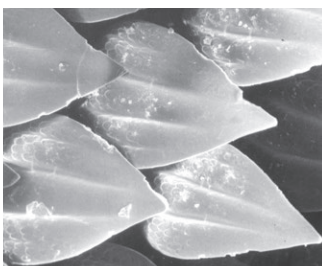


Morphology and measurements of a generalised chimaeroid

BUOYANCY

Sharks and other chondrichthyans do not have a swimbladder to compensate for a heavy bony skeleton. Many sharks store lightweight oil, called squalene, in their (large) livers for buoyancy, while species such as the raggedtooth shark swallow air at the surface and use the stomach to provide buoyancy. Most batoids are demersal and have no buoyancy requirements. Large pelagic rays, e.g., mantas, use their pectoral fins like wings to provide lift when swimming.

THE SKIN



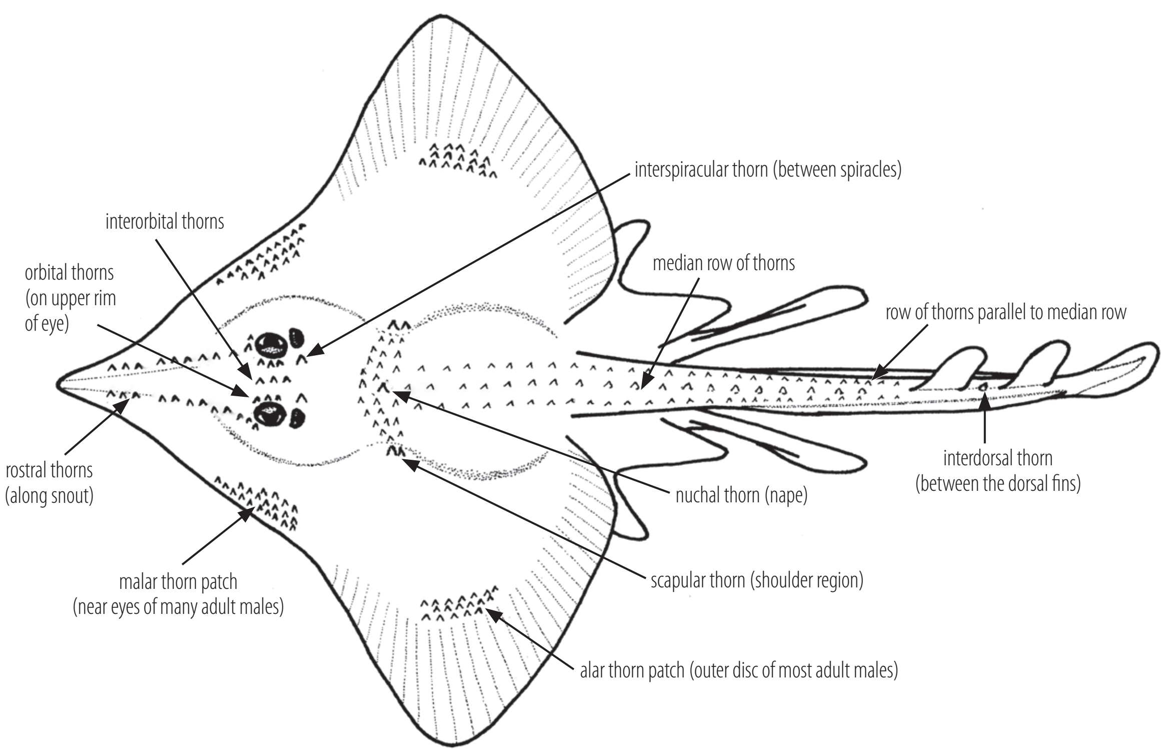
The skin of most sharks is covered with minute placoid scales or denticles, although some stingrays and electric rays lack these.

Scanning electron micrograph of shark scales (denticles) from a houndshark (Family Triakidae).

Unlike the scales of typical bony fishes, the dermal denticles of elasmobranchs (chondrichthyans that exclude the chimaeras) are essentially similar to their teeth, with a hard outer layer of enameloid over a core of dentine. Also, like the teeth, most denticles do not increase in size after they are completely formed; individual denticles and teeth are continually being replaced by newly formed and slightly larger ones during the lifespan of the shark. There is considerable variation in the shape and size of denticles. The surface of the denticles has series of tiny ridges and furrows, with the points of the denticles directed backwards. This accounts for the roughness of a shark's skin if stroked toward the head. The pattern and shape of denticles can often be used to identify certain species. However, the most important function of the ridged surface of the denticles is to produce laminar flow of water over the skin. This minimises the surface drag (or friction) of the water, and thus maximises swimming efficiency. Denticles also protect against parasites and fouling.

The skin of chimaeras is smooth and mostly covered with placoid scales.

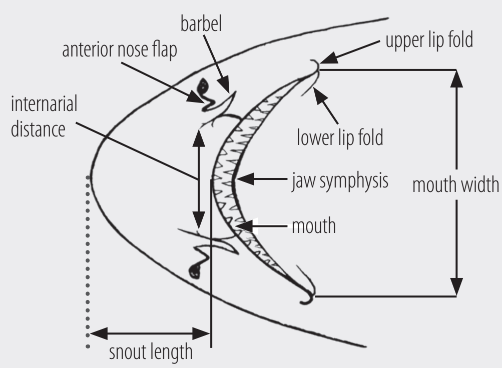
In many skates the denticles are modified as thorns of various sizes, and occur in species-specific patterns on the dorsal surface of the disc, and along the tail. In stingrays (Dasyatidae) one or two thorns have become modified into sharp, serrated, venomous stinging spines (caudal sting), situated near the base of the tail.



Thorn patterning terminology and positions

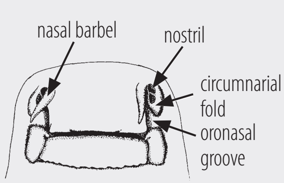
HEAD MORPHOLOGY

The mouth of nearly all elasmobranchs is situated on the underside of the head, with a pair of nostrils of varying form in front of the mouth. In whale and basking sharks the very large mouth is situated at the front of the head. Each nostril has a (generally) anterior incurrent and a posterior excurrent aperture, separated by an anterior nasal flap, which directs water into the nostril over highly sensitive olfactory membranes. In some sharks the nostrils are small, in some large, often with a barbel of varying length on the anterior margin.

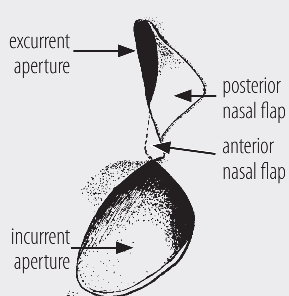


Ventral view of shark head to show morphology and measurements

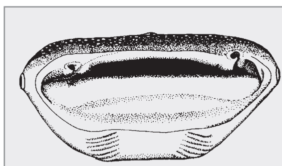
The underside of the snout and sides of the head carry many ampullae of Lorenzini, visible as small black dots, which are extremely sensitive detectors of electrical fields generated by other animals.



Ventral view of a hemiscylliid shark

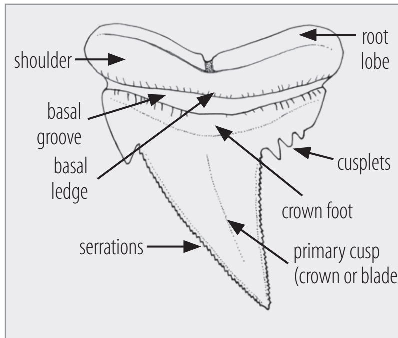


Nostril of a hemigaleid shark



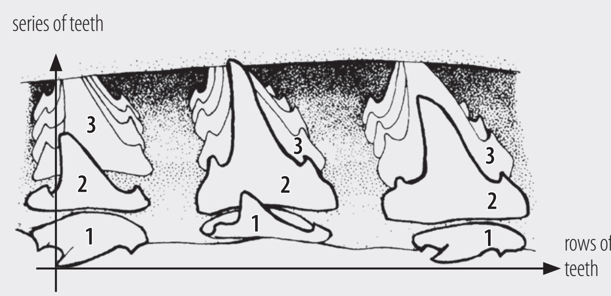
Anterior view of a whale shark (Family Rhincodontidae) with its terminal mouth partially open. Source: CFSA

Teeth

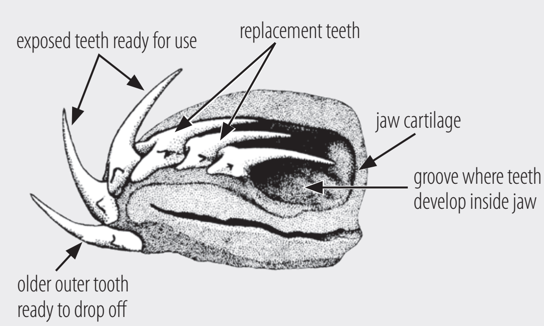


Shark tooth morphology

The teeth are thought to be modified dermal denticles. Sharks and rays have a lifetime supply of teeth, as new ones are continually being formed on the inner surface of the jaws. The teeth are firmly anchored to a layer of tough connective tissue, not fixed in sockets in the jaws (as in most bony fishes). When the outer teeth are lost, the next one in the row moves forward to take its place. In the few species in which tooth replacement rate has been measured, the outer teeth are replaced every one to two weeks; thus, a species that lives for 20 to 30 years produces thousands of teeth during a lifetime, and which is reflected in the numerous teeth in the fossil record. Chimaeras, which feed on molluscs and other invertebrates, have three pairs of large, permanent grinding plates that are worn down as they are used, and grow continuously.

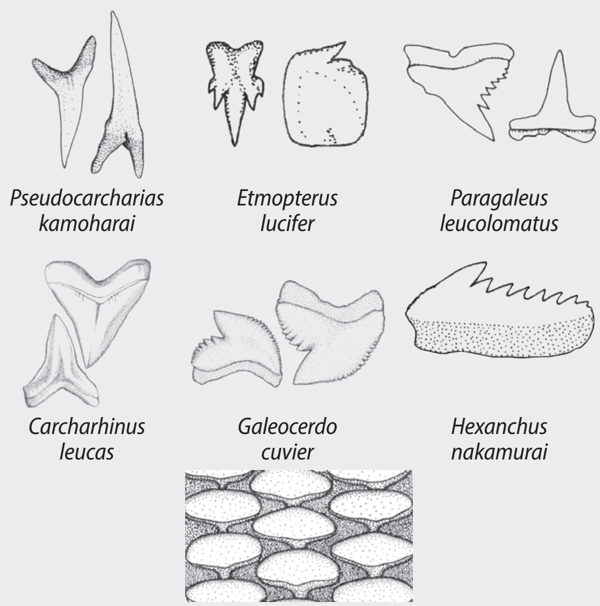


The outer row (1) of shark teeth anchored at the front of the jaw cartilage eventually falls out to be replaced by row 2. Teeth rows follow the line of the outer jaw, while a series (or file) of teeth are at right angles to the jaw.



Cross-section through the jaw of *Carcharias taurus* (Family Carchariidae) to show a single file of teeth, where older teeth drop off and are continuously replaced by new teeth forming inside the mouth/jaw. Source: CFSA

Shark teeth are a useful taxonomic character, as their number and shape are more or less distinctive. A species may sometimes be identified with certainty from a single tooth. There are three basic types of teeth with three main types of function (cutting, grabbing and crushing): broad, triangular, blade-like teeth, as in white and tiger sharks, which are well adapted for slicing pieces from large prey; slender awl-like teeth as in raggedtooth sharks, which are suited for catching and holding bite-sized fishes and squid; and the blunt, molariform, pavement-like teeth of smoothhound sharks, rays and skates, which are generally used to crush hard-shelled molluscs and crustaceans.



Shark teeth diversity

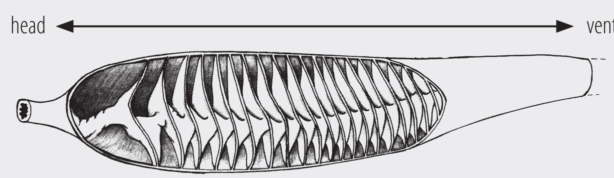
Feeding

The common belief that all sharks are scavengers is incorrect. Many species are selective feeders: many species of Carcharhinidae feed largely on fishes but the tiger and Zambezi (or bull) shark are omnivorous; whereas *Heterodontus* species (Heterodontidae) mostly eat sea urchins. However, many species are opportunistic and will feed on other prey when it is available. The megamouth, basking and whale sharks are the only sharks that feed on plankton but may also ingest small fish.

The cookiecutter shark (*Isistius brasiliensis*) ambushes an unsuspecting prey, bites it and then rolls over, removing an almost circular chunk of skin and muscle tissue from the victim. The tawny nurse shark (*Nebrius ferrugineus*) uses its pharynx as a suction pump to suck prey out of nooks and crannies in the reef. Most rays and skates are benthic animals and feed on shrimps, crabs, shellfish and other invertebrates. Skates have small, shark-like teeth while rays have plate-like teeth adapted for crushing prey. All devil and manta rays (Mobulidae) are filter feeders and rely on plankton as their main food source.

Chimaeras, elephantfishes and ghost sharks are opportunistic feeders, feeding on small fishes and benthic invertebrates such as crabs, molluscs, marine worms and sea-urchins. Like sharks they use electroreception to locate prey in the dark. Their teeth are formed into two pairs of ever-growing tooth plates in the upper jaw and one pair in the lower jaw.

All elasmobranchs (and some primitive bony fishes) have a spiral valve in their intestine. In most species the valve is like a spiral staircase; in others it looks like a series of elongated cones, one inside the other, and, in the requiem and hammerhead sharks, it resembles a scroll of rolled paper. The spiral valve provides a much greater area of absorptive intestinal surface than a straight tube.



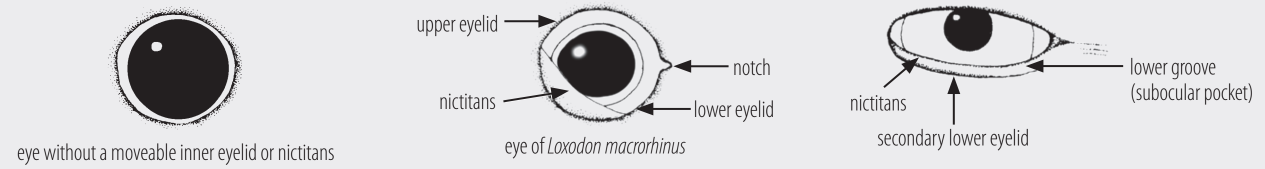
Diagrammatic representation of a spiral valve in a shark intestine

Gill slits and spiracles

All sharks have five pairs of gill slits of varying size, except for Chlamydoselachidae with 6 pairs, and Hexanchidae with 6 or 7 pairs of gill slits. In fast-swimming sharks, such as the Lamnidae, the gill slits are situated in front of the pectoral fins and are long, sometimes extending to below the fins. In demersal and generally slower-moving sharks the gill slits are shorter and sometimes lie partially above the pectoral fins.

Batoids also have five pairs of gill slits (except a single deepwater family, the Hexatrygonidae, with six pairs), which are on the ventral surface of the head. Batoids and sharks have an opening of varying size situated behind the eye, known as a spiracle. In pelagic species (Lamnidae, Carcharhinidae and Sphyrnidae) the spiracle is absent or greatly reduced, but is well developed in benthic (bottom-living) sharks and batoids. In rays it is the major inlet for water to be pumped over the gills, for the mouth of these sedentary fishes is usually submerged in sand or mud, and a respiratory current of water coming in through the mouth would soon foul the gills.

Chimaeras have only a single pair of gill slits in front of the pectoral fins and no spiracle.



eye without a moveable inner eyelid or nictitans
Family Alopiidae,
thresher sharks

eye of *Loxodon macrorhinus*
Family Carcharhinidae,
requiem sharks

Family Triakidae,
houndsharks

Ears and eyes

As in other fishes, the ear of sharks and other chondrichthyans lies behind the eye and consists of three semi-circular canals at right angles to each other and connected to a sac-like structure, the sacculus. The ear is connected to the surface of the skin by a pore, and sensitive to gravity and vibrations (sound waves) in the water.

The eye of most sharks is round, with a round pupil. The pupil can also be crescent-shaped or a vertical, diagonal or horizontal slit. Some sharks have a moveable inner lower eyelid called a nictitating membrane or nictitans, which is variously developed in different species. In sharks with a large spiracle, the nictitans is absent or represented by a rudimentary groove along the lower edge of the orbit; while those without a spiracle (or a very small one) have a well-developed nictitans that can be pulled up to cover the eye completely. The white shark and whale shark lack a nictitans and protect their eyes by rotating them in the socket, exposing the tough sclera covering to protect the eye.

In benthic dwelling rays and skates (except the Mobulidae) the eyes are located more dorsally on the head and tend to look upwards. Chimaeras have prominent, large eyes on the sides of the head, also with a nictitans.

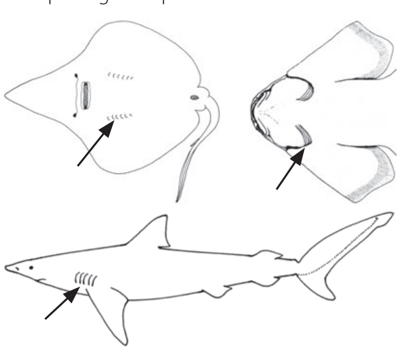
The retina of chondrichthyans contain both cones (for colour vision) and rods, which are sensitive to low light levels. They also have a reflective layer, a tapetum, behind the retina that bounces the light around inside the eye, thus improving their vision in low light and causing the eyes to glow in the dark.

REPRODUCTIVE ORGANS

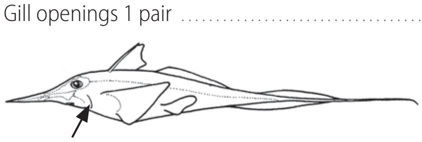
All chondrichthyans fertilise eggs internally. Males have a pair of modified pelvic fin radials that serve as intromittant organs, called claspers. These deposit sperm in a female's cloaca during mating. The claspers of chimaeras, which lie in front of the pelvic fins, can be retracted. Male chimaeras also have an additional, retractable sexual appendage on the forehead, called a tenaculum, which is thought to aid in holding onto a female during mating.

KEY TO FAMILIES OF CHONDRICHTHYANS

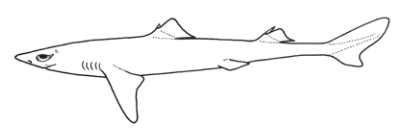
1a Gill openings 5–7 pairs 2



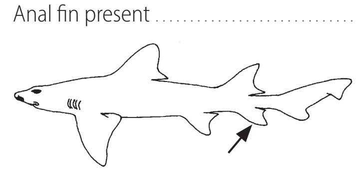
1b Gill openings 1 pair 50



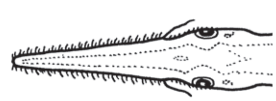
2a No anal fin 3



2b Anal fin present 29



3a Snout saw-like, with distinct lateral teeth 4



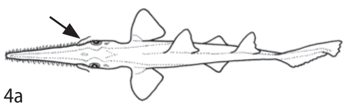
3b Snout not saw-like, without distinct lateral teeth 5

Continued ...

KEY TO FAMILIES OF CHONDRICHTHYANS

4a Gill openings lateral on head; rostral barbels present .... **PRISTIOPHORIDAE (Sawsharks)**

4b Gill openings ventral on head; no rostral barbels .... **PRISTIDAE (Sawfishes)**

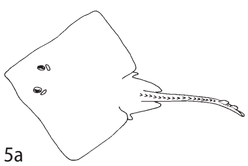


4a

4b

5a Body flat, ray-like 6

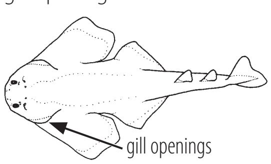
5b Body fusiform, not ray-like 23



5a

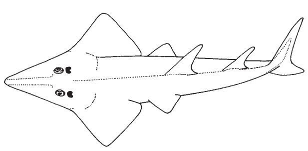
5b

6a Mouth terminal; pectoral fins not attached to head; gill openings lateral on head .... **SQUATINIDAE (Angel sharks)**



6b Mouth ventral; pectoral fins attached to head; gill openings ventral on head 7

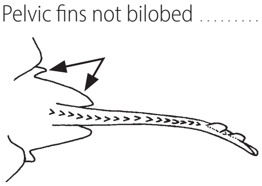
7a Dorsal fins large and strongly falcate; caudal fin prominent, with strong lower lobe ...... **RHINIDAE (Shark ray and wedgefishes)**



7b Dorsal fins, if present, not falcate, usually angular or rounded; caudal fin small and without lower lobe, or caudal fin absent.... 8

8a Pelvic fins strongly bilobed 9

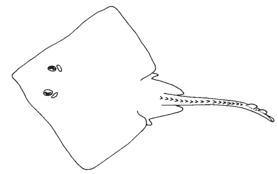
8b Pelvic fins not bilobed 11



8a

8b

9a Rostrum soft and flabby, flexible .... **ARHYNCHOBATIDAE (Softnose skates)**

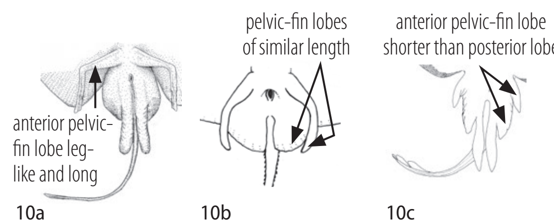


9b Rostrum semi-rigid, to rigid and stiff, inflexible 10

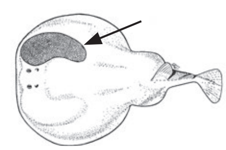
10a Tail thin and filamentous, dorsal fins absent; pelvic fins with 2 lobes, anterior lobes usually longest .... **ANACANTHOBATIDAE (Legskates)**

10b Tail thin but not filamentous, 0–2 dorsal fins; pelvic fins with single lobe, or deeply incised with 2 lobes of similar length .... **GURGESIELLIDAE (Pygmy skates)**

10c Tail not slender or filamentous, with 2 dorsal fins; pelvic fins weakly to deeply incised, with anterior lobes usually shortest............................. **RAJIDAE (Hardnose skates)**

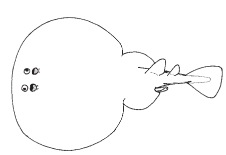


11a Disc thick and flabby, with prominent kidney-shaped electric organs visible through skin on underside 12



11b Disc relatively thin, not flabby, without prominent kidney-shaped electric organs 14

12a Disc truncated or emarginate anteriorly; rostrum reduced .... **TORPEDINIDAE (Torpedo rays)**



12b Disc rounded anteriorly; rostrum evident 13

13a Rostrum broad; jaws long and protractible; usually 2 dorsal fins .... **NARCINIDAE (Numbfishes)**

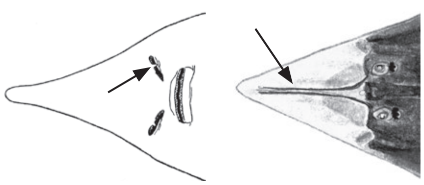
Continued ...

13b Rostrum narrow; jaws short and weakly protractible; usually 1 dorsal fin .... **NARKIDAE (Sleeper rays)**

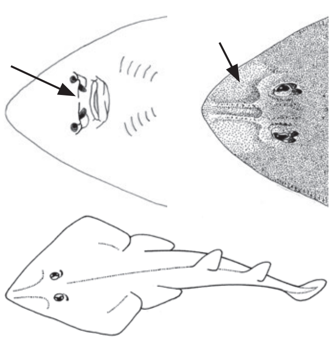
14a Tail large, thick; caudal fin large, without a stinging spine; 2 prominent dorsal fins **15**

14b Tail slender, attenuated; stinging spine usually present on tail; 1 small to moderate-sized dorsal fin, or dorsal fin absent **16**

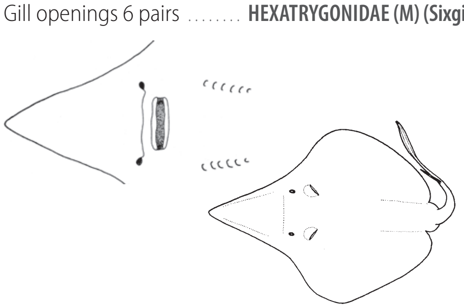
15a Anterior nasal flaps weakly developed, forming small triangular lobe inserted on front margin of nostril; pale translucent snout sharply demarcated by rostral cartilage and cranium .... **GLAUCOSTEGIDAE (Giant guitarfishes)**



15b Anterior nasal flaps well-developed and inner margins extending more or less onto internasal space; paler snout only faintly demarcated by rostral cartilage and cranium .... **RHINOBATIDAE (Guitarfishes and shovelnose rays)**



16a Gill openings 6 pairs .... **HEXATRYGONIDAE (M) (Sixgill stingray)**

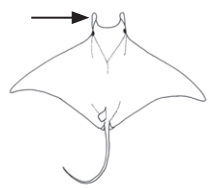


16b Gill openings 5 pairs **17**

17a Head elevated above disc; eyes and spiracles on sides of head **18**

17b Head not elevated above disc; eyes and spiracles on top of head **21**

18a Head with paired horn-like flaps at front .... **MOBULIDAE (Devilrays)**

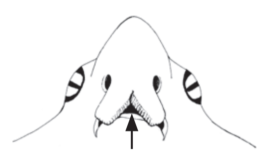


18b Head without paired flaps at front **19**

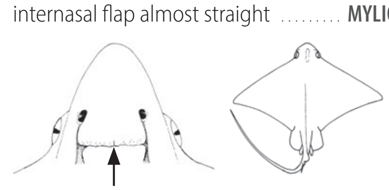
19a Sub-rostral lobe rounded **20**

19b Sub-rostral lobe with median notch .... **RHINOPTERIDAE (Cownose rays)**

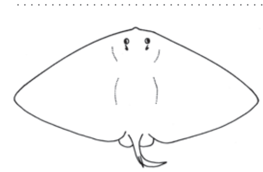
20a Spiracle openings almost completely visible in dorsal view; rear edge of internasal flap deeply notched .... **AETOBATIDAE (Pelagic eagle rays)**



20b Spiracle openings not visible in dorsal view; rear edge of internasal flap almost straight .... **MYLIOBATIDAE (Eagle rays)**



21a Disc width >1.5 times disc length; tail short, slender, less than disc length; stinging spine relatively short .... **GYMNURIDAE (Butterfly rays)**



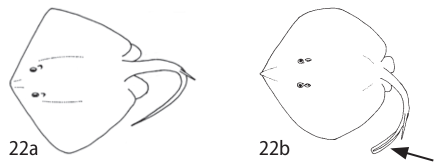
21b Disc width <1.5 times disc length; tail long and whip-like, greater than disc length; stinging spine relatively long **22**

(M) = Monotypic

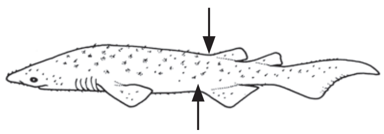
Continued …

KEY TO FAMILIES OF CHONDRICHTHYANS

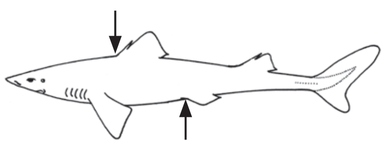
22a Caudal fin absent .... **DASYATIDAE (Stingrays)**
22b Caudal fin present .... **PLESIOBATIDAE (M) (Deepwater stingray)**



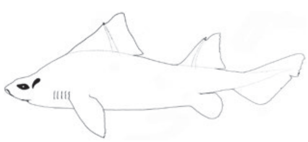
23a First dorsal-fin origin behind pelvic-fin origins .... **ECHINORHINIDAE (Bramble sharks)**



23b First dorsal-fin origin in front of pelvic-fin origins **24**

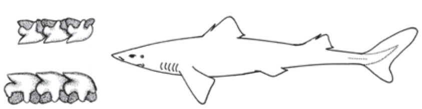


24a Body compressed, very high, nearly triangular in cross-section; dorsal fins extremely high .... **OXYNOTIDAE (Roughsharks or prickly dogfishes)**

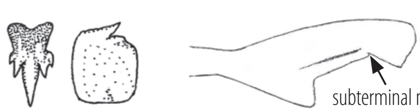


24b Body low, nearly cylindrical in cross-section; dorsal fins low .. **25**

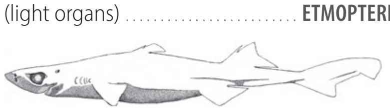
25a Teeth similar in both jaws, oblique, blade-like, with single smooth-edged cusp, without cusplets; caudal fin without subterminal notch .... **SQUALIDAE (Dogfishes)**



25b Teeth dissimilar in both jaws, with prominent single cusp, possibly flanked by lateral cusplets; caudal fin with subterminal notch **26**

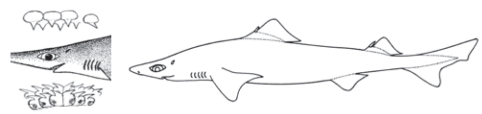


26a Flanks, underside of body and caudal fin with conspicuous black markings with photophores (light organs) .... **ETMOPTERIDAE (Lanternsharks)**



26b Flanks, underside of body and caudal fin without conspicuous black markings or photophores **27**

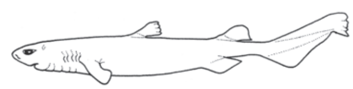
27a Upper teeth broad-based, with cusps narrow and blade-like, lower teeth low, with cusps oblique to semi-erect; dorsal-fin spines prominent .... **CENTROPHORIDAE (Gulper sharks)**



27b Upper teeth with relatively narrow bases, not blade-like, lower teeth high and wide; dorsal-fin spines short and inconspicuous or absent **28**

28a Head moderately broad and somewhat flattened or conical; dorsal-fin spines variably present or absent (depending on species) .... **SOMNIOSIDAE (Sleeper sharks)**

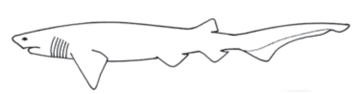
28b Head narrow and rounded conically; dorsal-fin spines absent from most genera (except *Squaliolus*) .... **DALATIIDAE (Kitefin sharks)**



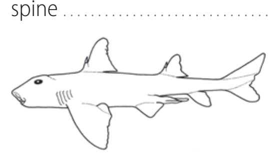
29a Gill openings 6 or 7 pairs; 1 dorsal fin **30**
29b Gill openings 5 pairs; 2 dorsal fins **31**

30a Body eel-like; mouth terminal; teeth tricuspidate, similar on both jaws; 6 paired gill openings, with first extending across throat .... **CHLAMYDOSELACHIDAE (Frilled sharks)**

30b Body fusiform; mouth subterminal; teeth not tricuspidate, dissimilar on upper and lower jaws; 6 or 7 paired gill openings, with first not extending across throat .... **HEXANCHIDAE (Cow sharks)**



31a Each dorsal fin preceded by prominent spine .... **HETERODONTIDAE (Bullhead sharks)**



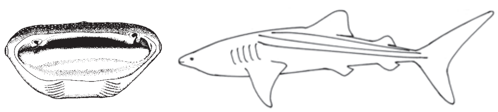
31b Dorsal fins not preceded by a spine **32**

32a Mouth does not extend behind eyes **33**
32b Mouth extends behind eyes **36**

(M) = Monotypic

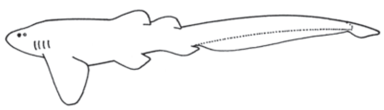
Continued ...

33a Mouth broad and terminal ... **RHINCODONTIDAE (M) (Whale shark)**



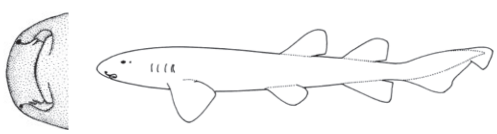
33b Mouth smaller and subterminal **34**

34a Caudal fin subequal to precaudal length .... **STEGOSTOMATIDAE (M) (Zebra shark)**

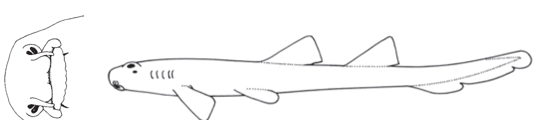


34b Caudal fin much shorter than precaudal length **35**

35a No circumnarial lobe and groove around outer edges of nostrils .... **GINGLYMOSTOMATIDAE (Nurse sharks)**

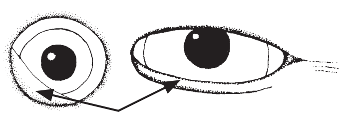


35b Circumnarial lobe and groove present around outer edges of nostrils .... **HEMISCYLLIIDAE (Bamboo sharks)**

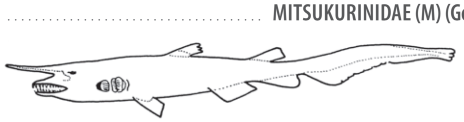


36a No nictitating eyelids **37**

36b Nictitating eyelids present **44**

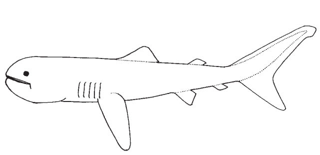


37a Snout extremely elongated, flat and blade-like; no precaudal pits and no caudal-fin lower lobe .... **MITSUKURINIDAE (M) (Goblin shark)**



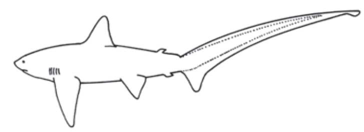
37b Snout short to moderately elongated (not greatly elongated or blade-like), and broadly rounded; precaudal pits and caudal-fin lower lobe present **38**

38a Snout short and mouth terminal .... **MEGACHASMIDAE (M) (Megamouth shark)**



38b Snout relatively long and mouth subterminal **39**

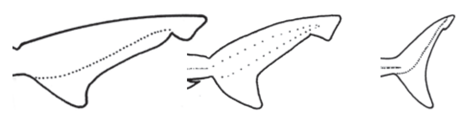
39a Caudal fin about as long as trunk of body.. **ALOPIIDAE (Thresher sharks)**



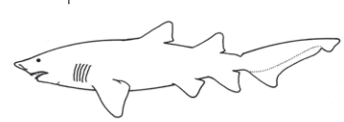
39b Caudal fin much shorter than trunk of body **40**

40a Caudal fin heterocercal, not crescent-shaped; peduncle with weak lateral keels or without keels **41**

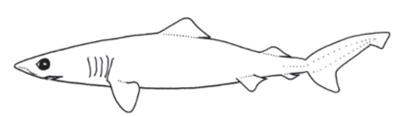
40b Caudal fin crescent-shaped; peduncle with strong lateral keels **43**



41a Body stout; eyes relatively small; anal fin broad-based, not pivoting; peduncle with upper precaudal pit, but without lower pit and lateral keels **42**



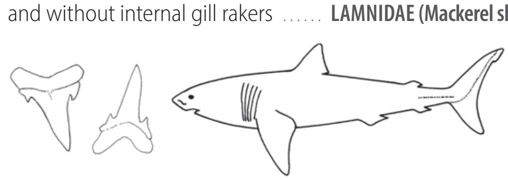
41b Body slender; eyes relatively large; anal fin narrow-based, pivoting; peduncle with upper and lower precaudal pits, and with weak lateral keels .... **PSEUDOCARCHARIIDAE (M) (Crocodile shark)**



42a Snout slightly depressed; dorsal fins subequal; 1st dorsal fin closer to pelvic-fin bases than to pectoral-fin bases .... **CARCHARIIDAE (M) (Raggedtooth shark)**

42b Snout conical; 1st dorsal fin larger than 2nd; 1st dorsal fin closer to pectoral-fin bases than to pelvic-fin bases .... **ODONTASPIDIDAE (Sandtiger sharks)**

43a Teeth large, triangular, blade-like; gill slits large, but not extending onto dorsal surface of head or nearly across throat, and without internal gill rakers ...... **LAMNIDAE (Mackerel sharks)**

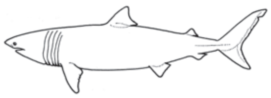


(M) = Monotypic

Continued ...

KEY TO FAMILIES OF CHONDRICHTHYANS

43b Teeth minute, hook-shaped, and not blade-like; gill slits extremely large, extending onto surface of head and the first nearly extending across the throat, and with internal gill rakers .... **CETORHINIDAE (M) (Basking shark)**

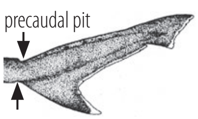


44a Head with distinctive lateral, blade- or hammer-like expansions .... **SPHYRNIDAE (Hammerhead sharks)**

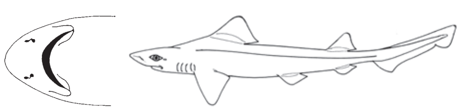
44b Head normal, without lateral expansions **45**

45a First dorsal-fin base opposite or behind pelvic-fin bases **51**
45b First dorsal-fin base in front of pelvic-fin bases **46**

46a No precaudal pits; caudal-fin dorsal margin without undulations **47**
46b Precaudal pits present; caudal-fin dorsal margin wavy or not wavy **49**

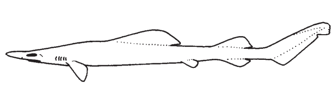


47a Labial furrows relatively long, with upper furrows extending partway or all the way anterior to level of jaw symphysis; rear teeth on dental bands not comb-like .... **TRIAKIDAE (Houndsharks)**

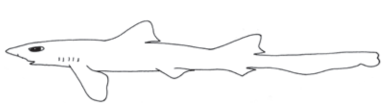


47b Labial furrows absent or very short and confined to mouth corners; rear teeth on dental bands comb-like **48**

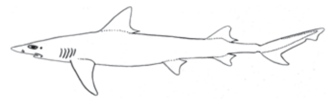
48a Snout bell-shaped in dorsoventral profile, with deep groove in front of eyes; 1st dorsal fin more or less elongated, base closer to pectoral fins than to pelvic fins .... **PSEUDOTRIAKIDAE (False catsharks)**



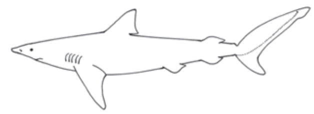
48b Snout rounded-parabolic or subangular in dorsoventral profile, without deep groove in front of eyes; 1st dorsal fin short, base closer to pelvic fins than to pectoral fins ..... **PROSCYLLIIDAE (Finback catsharks)**



49a Eyes horizontal and oval; upper lip folds at least ½ length of mouth; all fins falcate; spiracles present; caudal peduncle without keels .... **HEMIGALEIDAE (Weasel sharks)**

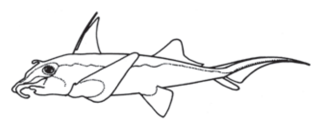


49b Eyes round; upper lip folds not extending to front edge of eyes; all fins not falcate; spiracles usually absent; caudal peduncle usually without keels (keels weak if present) .... **CARCHARHINIDAE (Requiem sharks)**



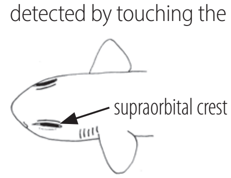
49c Eyes round; upper lip folds reaching front edge of eyes; all fins not falcate; spiracles present; caudal peduncle with low lateral keel on either side .... **GALEOCERDONIDAE (M) (Tiger shark)**

50a Snout recurved and plough-shaped; 2nd dorsal fin falcate, short and high; caudal fin heterocercal .... **CALLORHINCHIDAE (Elephantfishes)**

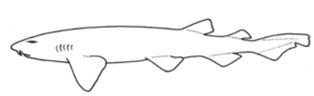


50b Snout straight, not recurved or plough-shaped; 2nd dorsal fin long and low; caudal fin not heterocercal **52**

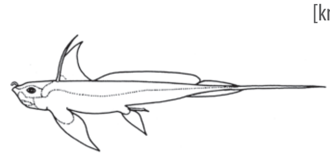
51a Narrow shelf-like cartilage extending from the chondrocranium to just above the eyes, forming a supraorbital crest (usually detected by touching the area) ....**SCYLIORHINIDAE (Catsharks)**



51b No supraorbital crest present .... **PENTANCHIDAE (Deepwater catsharks)**



52a Snout short and blunt .... **CHIMAERIDAE (Chimaeras)**
[known in WIO only from >300 m]



52b Snout elongated and tapering .... **RHINOCHIMAERIDAE (Longnose chimaeras)**

(M) = Monotypic

ORDER **HEXANCHIFORMES**

FAMILY **CHLAMYDOSELACHIDAE**

Frilled sharks

David A Ebert

Medium-sized, distinctively elongate and slender-bodied; snout extremely short with truncated tip. Six paired gill slits with enlarged frilly interbranchial septa; ventral edge of 1st gill slit extends across throat as gular flap. Nostrils opposite jaw symphyses. Mouth terminal; teeth and jaw edges exposed when mouth closed; upper lip not expanded below level of tooth bases to form prominent flange and groove; lower lip not expanded anteriorly and laterally to the teeth series. Teeth alike in both jaws, with 3 cusps and 2 cusplets on crown; no small granular posterior teeth. Dermal denticles on lateral trunk with spike-like crowns; enlarged monocuspidate denticles at edges of mouth. One dorsal fin, very low, rounded and elongated, its insertion just before upper caudal origin. Pectoral fins rounded and smaller than pelvic fins. Pelvic fins with broadly rounded anterior margin and apex, inner margin not forming expanded clasper sheath in males. Pair of longitudinal ridges or tropeic folds on ventral surface of abdomen. Anal fin broad-based and rounded, larger than dorsal fin, its insertion ending at lower caudal origin. Peduncle short, compressed. Caudal fin with vestigial subterminal notch, and ventral lobe essentially absent.

Generally considered a deepsea group, although members are well known to ascend to within ~20 m of surface. No directed fisheries for these sharks. One genus with 2 species: one species wide-ranging, but patchy, in most seas, and the other appearing more restricted to the southwestern Indian Ocean and southeastern Atlantic.

GENUS *Chlamydoselachus* Garman 1884

Diagnosis as for family. Two similar-looking species with differing vertebral counts. Unconfirmed whether both species co-occur off African coast, as records of *Chlamydoselachus* species prior to 2009 were given as if a single wide-ranging species.

KEY TO SPECIES

1a Vertebrae 147; monospondylous–diplospondylous transition at about 18th vertebrae, just behind pectoral-fin tips; spiral valve turns 26–28; HL 17–18% TL .... ***C. africana***

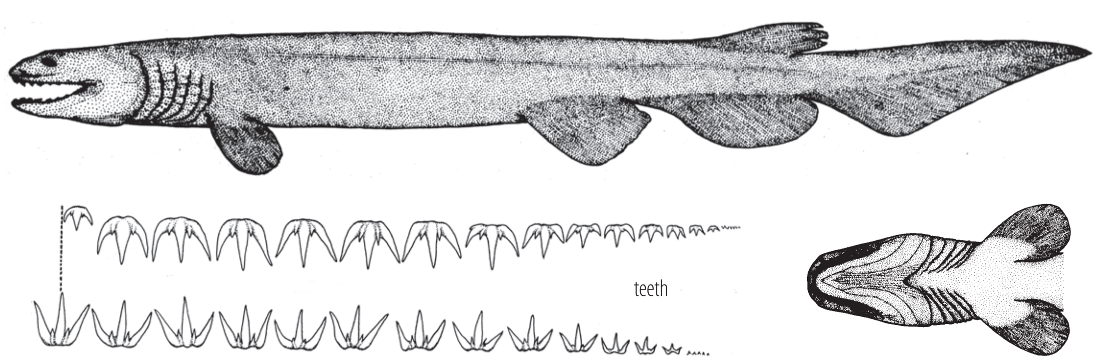
1b Vertebrae 160–171; monospondylous–diplospondylous transition between 72nd and 75th vertebrae, approximately over pelvic fins; spiral valve turns 35–49; HL 13–16% TL .... ***C. anguineus***

Chlamydoselachus africana

Ebert & Compagno 2009

Southern African frilled shark PLATE 2

Chlamydoselachus africana Ebert & Compagno 2009: 3, Figs. 1–4, 6 (off Cunene River, Namibia); Ebert 2013; Ebert *et al*. 2013*.
Chlamydoselachus anguineus: Smith 1951, 1967*; Bass *et al*. 1975; Compagno *et al*. 1989*, Compagno *et al*. 1991.
Chlamydoselachus sp. A: Ebert 1990*; Compagno *et al*. 2005*.



Chlamydoselachus africana, 102 cm TL, immature female (Namibia). Source: Bass *et al*. 1975

Slender, eel-like, with body compressed beyond pectoral-fin region; 6 paired gill slits. One dorsal fin. Mouth terminal; teeth tricuspid, similar in both jaws, with 3 long, slender, smooth-edged cusps, and small pointed cusplet between each cusp; upper jaw with paired medial teeth, shaped similar to anterolateral teeth, but reduced; lower jaw with single medial tooth undifferentiated from anterolateral teeth; teeth in both jaws curved inwards and set on broad base projecting behind and interlocking with tooth base behind it; tooth count 24–30/23–27. Dermal denticles on lateral trunk lanceolate, single-cusped, with flattened bases; crowns widely spaced and slightly projecting above body, with 4 longitudinal ridges from base to cusp. Total vertebrae 147, precaudal vertebrae 94, monospondylous vertebrae 18; spiral valve turns 26–28.

Body dark brown, but with thin membranous mucous covering, which upon being rinsed off after death reveals dark grey colour; preserved specimens pale brown to grey. Attains ~125 cm TL.

DISTRIBUTION Southern Africa: Angola to Namibia in southeastern Atlantic, and scarce records from South Africa and around Cape Peninsula in WIO.

REMARKS Externally morphologically similar to common frilled shark *C. anguineus*, but smaller, with proportionally longer head, greater head height and width, and proportionally longer pre-pectoral and predorsal-fin lengths. Viviparous with yolk sac; litters of 3 or more; size at birth 40–45 cm TL. Males mature at 92 cm TL, but female size at maturity unknown (117 cm TL for an immature female). Little-known; occupies benthic, epibenthic, and possibly pelagic habitat on upper continental slope, at 100–1 400 m. Hydrographic and substratum data collected on a specimen caught off southern Namibia found it occurred in a low-oxygen, high-nutrient zone with soft substratum; one record of note is of a frilled shark caught off a pier in South Africa (Eastern Cape). Feeds mostly on other sharks, squaloids and scyliorhinids, bony fishes and cephalopods; capable of swallowing relatively large prey (measuring ⅓–½ their own body length) in much the same way snakes are able to consume large prey items. Likely caught as bycatch in bottom-trawl and longline fisheries.

Chlamydoselachus anguineus Garman 1884

Frilled shark PLATE 2

Chlamydoselachus anguineus Garman 1884: 47, Fig. (Japanese seas [probably southeastern Honshu]); Ebert 1990, 2003, 2013*; Compagno *et al.* 2005*; Ebert & Compagno 2009; Ebert *et al.* 2013*.

Long, slender, eel-like, with compressed body beyond pelvic-fin region; 6 paired gill slits. One dorsal fin. Mouth terminal and snake-like; teeth tricuspid in both jaws. Tooth count 19–28/21–29; total vertebrae 160–171, precaudal vertebrae 93–102, monospondylous vertebrae 72–75; spiral valve turns 35–49.

Body uniformly dark brown, brownish grey or brownish black (closely resembles *C. africana*, but differs in counts and measurements). Attains 196 cm TL.

DISTRIBUTION North Atlantic and Pacific oceans (wide-ranging, patchy); unconfirmed in southwestern Indian Ocean.

REMARKS Viviparous with yolk sac; litters of 2–15 (average 6); size at birth ~55 cm TL. Males mature at 118–163 cm TL, and females at 130–150 cm TL. Reproduces all year in deep water off Japan, with mating thought to occur in springtime, from March to June; gestation period long, probably 1–2 years. Feeds on a variety of other sharks, bony fishes, and epipelagic and deepwater cephalopods. Occupies benthic, epibenthic and occasionally pelagic habitat, over offshore continental and insular shelves and upper slopes, at 20–1 440 m, but occasionally taken at surface. Harmless species of little importance to fisheries, but taken as a bycatch, especially in bottom trawls and midwater shrimp trawls; used for fishmeal and human consumption. Has been kept in aquaria in Japan.

FAMILY **HEXANCHIDAE**

Cow sharks

David A Ebert

Medium- to very large-sized (~1.4–5 m TL), elongated, moderately slender to stout cylindrical body and flattened head; snout moderately long, pointed to broadly rounded. Six or 7 paired gill slits. Eyes about opposite symphyses of mouth. Mouth subterminal; teeth dissimilar in upper and lower jaws: anterolateral teeth in lower jaw much larger, compressed and comb-like, with more cusplets than teeth in upper jaw, and posterior teeth smaller, granular. One spineless dorsal fin, relatively high, angular, short; its insertion well before upper caudal origin by at least length of dorsal-fin base. Pectoral fins angular, larger than pelvic fins. Pelvic-fin anterior margin nearly straight and apex narrowly rounded. Anal fin narrow-based and angular, its insertion well anterior to lower caudal origin. Peduncle moderately long and cylindrical. Caudal fin with well-developed subterminal notch, and lower lobe weak to moderately developed. No longitudinal keels on abdomen.

Reproductive mode yolk-sac viviparity. Mostly deepwater inhabitants of outer continental shelf and upper slope, insular shelves and slopes, and submarine canyons, to at least 2 500 m deep, and found near bottom or well above it; however, some species also occur in shallow bays, close inshore and near surface.

Worldwide in boreal and cold-temperate to tropical seas. Three genera and 4 species, all in WIO.

KEY TO GENERA

1a	Six paired gill slits	***Hexanchus***
1b	Seven paired gill slits	2
2a	Eyes very large; head extremely narrow and pointed; body plain, without spots; medium-sized, maximum ~1.4 m TL	***Heptranchias***
2b	Eyes small; head broad and rounded; body usually with scattered small black spots and sometimes white spots; large-sized, maximum ~3 m TL	***Notorynchus***

GENUS *Heptranchias* Rafinesque 1810

Head acutely pointed, compressed, and rounded or vertically oval in section at eyes. Seven paired gill slits. Eyes large. Mouth very narrow and angular-parabolic. Lower jaw with 5 rows of long and low, comb-like anterolateral teeth, with a few short mesial cusplets and an abruptly high cusp, and up to 7 or 8 distal cusplets in adults, increasing and then decreasing in size distal to cusp. Peduncle elongated. Lateral-line canal closed. No spots on body; dorsal fin and caudal-fin upper lobe with black tips (may be faded or absent in adults but prominent in young). One species.

Heptranchias perlo (Bonnaterre 1788)

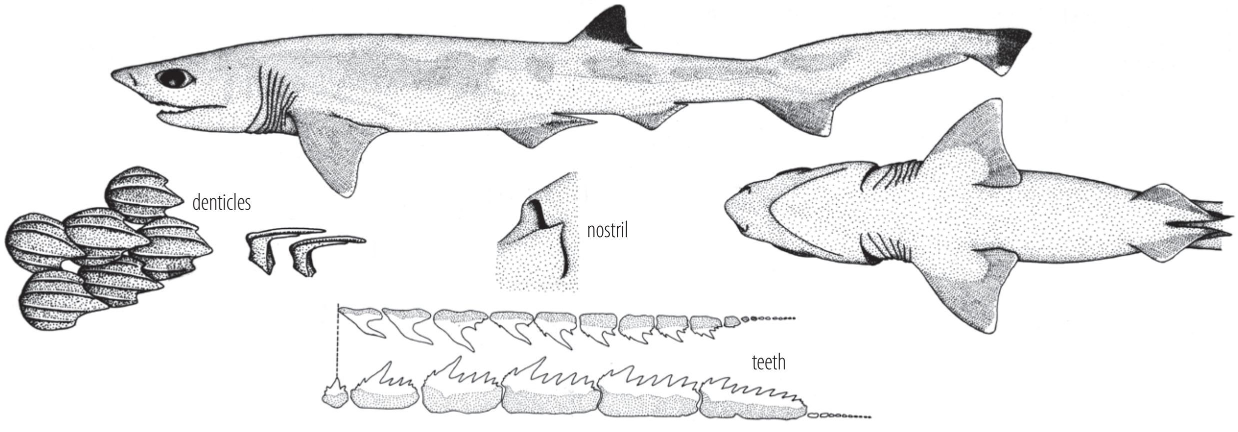
Sharpnose sevengill shark PLATE 2

Squalus perlo Bonnaterre 1788: 10 (France, Mediterranean Sea).
Heptranchias perlo: Bass *et al.* 1975*; SSF No. 2.1*; Compagno *et al.* 1989*; Ebert 1990*, 2013*; Ebert *et al.* 2013*.

Diagnosis as for genus. Medium-sized, with narrow head and large eyes. Tooth count 23–43/20–33; total vertebrae 141–159, precaudal vertebrae 72–94 (calcified and with obvious double cones); spiral valve turns 18–22.

Body uniformly pale grey to olive dorsally, paler to white ventrally; no spots on body; dorsal fin with black blotch and caudal-fin upper lobe black-tipped (prominent in young, faded or absent in adults). Attains 137 cm TL.

DISTRIBUTION All tropical and temperate seas (wide-ranging, somewhat sparse), except eastern North Pacific. WIO: South Africa (Western Cape to KwaZulu-Natal), southern Mozambique, Comoros, Madagascar, Mascarene Seamounts, Mauritius to Seychelles, Aldabra, Maldives, Gulf of Aden, southwestern India (Kollam), Sri Lanka and southwestern Mediterranean Sea.



Heptranchias perlo, 68 cm TL, immature male (S Mozambique). Source: Bass *et al.* 1975

REMARKS Litters of 6–20; size at birth ~26 cm TL. Males mature at 70–78 cm TL, and females at 89–90 cm TL. Appears reproductively active during entire year off Japan and in Mediterranean Sea. Relatively uncommon; primarily deepwater, benthic and epibenthic, over continental and insular shelves and upper slopes, at 27–720 m (mostly deeper than 100 m, and possibly to ~1 000 m), but occasionally close inshore. Probably strong-swimming as indicated by firm skin and muscles and by vigorous, agile, snake-like activity when captured. Feeds on a wide variety of small to moderately large demersal and pelagic bony fishes, small elasmobranchs such as catsharks (Pentanchidae and Scyliorhinidae), lanternsharks (*Etmopterus*, Etmopteridae), skates (Rajidae), cephalopods and crustaceans. Narrow jaws and teeth with prominent, narrow, needle-sharp cusps and cusplets suggest they are well equipped for grabbing, holding and swallowing small soft-bodied prey, but less capable of dismembering large-bodied tough-skinned prey. Of minor importance commercially, but affected by a wide variety of demersal fisheries and generally caught as bycatch of bottom-trawl fisheries or deepwater fisheries using bottom longlines. IUCN Red List conservation status Near Threatened as population declines may have occurred in some areas, such as southern Mozambique, where deepwater demersal trawling for shrimp and bony fishes has been operational during the past few decades.

GENUS *Hexanchus* Rafinesque 1810

Head narrowly or broadly parabolic in dorsoventral view, depressed and transversely oval in section at eyes. Six paired gill slits. Eyes small or large. Mouth moderately to very wide, parabolic or arcuate. Lower jaw with 5 or 6 rows of comb-like anterolateral teeth, long and low in adults but higher in young; mesial edges smooth in young but with serrations in adults; low to moderately high cusp, and 8–10 distal cusplets in adults, decreasing in size distal to cusp. Peduncle short to elongated. Lateral-line canal closed. Spiral valve turns 22–39. Body without spots or with irregular brown spots; fins not black-tipped. Size at maturity 123 cm to ~5 m TL. Two species, both in WIO.

KEY TO SPECIES

1a Snout short, blunt and broad; eyes small; lower jaw usually with 6 rows of large, comb-like anterolateral teeth; distance between dorsal-fin insertion and upper caudal origin about equal to or slightly greater than length of dorsal-fin base; very large-sized, maximum ~5 m TL .... ***H. griseus***

1b Snout long, pointed and narrow; eyes large; lower jaw usually with 5 rows of large, comb-like anterolateral teeth; distance between dorsal-fin insertion and upper caudal origin much greater than length of dorsal-fin base; medium-sized, maximum ~1.8 m TL .... ***H. nakamurai***

Hexanchus griseus (Bonnaterre 1788)

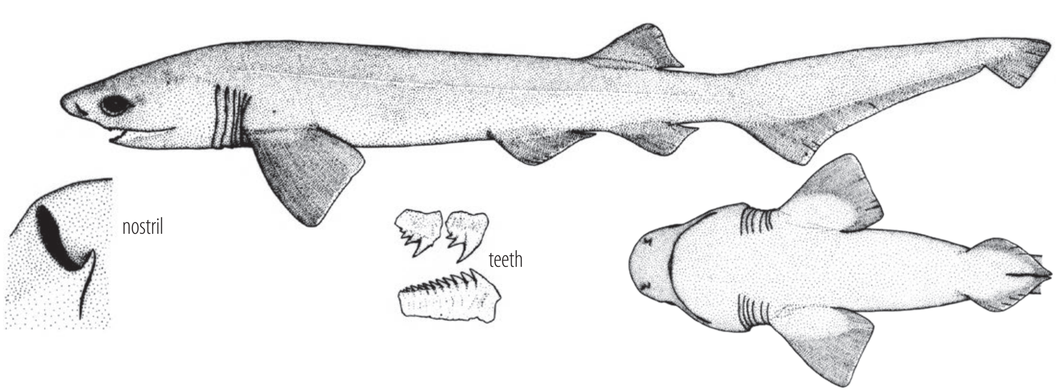
Bluntnose sixgill shark PLATE 3

Squalus griseus Bonnaterre 1788: 9 (France, Mediterranean Sea); Forster *et al.* 1970.

Hexanchus griseus: Bass *et al.* 1975*; Bass 1978; SSF No. 2.2*; Compagno *et al.* 1989*; Ebert 1990*, 1994, 2002, 2003*, 2013*; Anderson & Ahmed 1993; Ebert *et al.* 2013*.

Stout, heavy-bodied and broad-headed; snout bluntly rounded to rounded-angular in dorsoventral view; preoral length shorter, 4.3–5.4% TL. Eyes small. Mouth broad, U-shaped, its width more than twice length. Lower jaw with 6 rows of blade-like, comb-shaped anterolateral teeth. Pectoral fins broadly triangular. Peduncle short and stout. Caudal-fin postventral margin weakly concave to straight and not subdivided, and lower lobe poorly developed at all stages. Tooth count 26–46/20–36; vertebrae 118–148; spiral valve turns 35–39.

Body grey or tan to blackish, with conspicuous paler lateral line; sometimes with darker spots on flanks; underside often paler than dorsal surface in newborns, and colouration more uniform in larger juveniles and adults. Attains ~5 m TL.



Hexanchus griseus, 97 cm TL, immature male (Namibia).
Source: Bass *et al.* 1975

DISTRIBUTION Wide-ranging in boreal, temperate and tropical seas, except possibly Arctic and Antarctic oceans. WIO: Somalia, Mozambique, South Africa (Western Cape to KwaZulu-Natal), Madagascar, Comoros, Aldabra, Réunion, Maldives, India and Sri Lanka.

REMARKS Litters of 47–108 (relatively large); size at birth 61–74 cm TL. Males mature at ~3.1 m TL, and females at ~4.2 m TL. Pupping grounds apparently occur on upper slope and outer continental shelf, with one such area known from southern Namibia. Based on size, may be long-lived but it has yet to be aged. Mostly deepwater, benthic and pelagic, over continental and insular shelves and slopes and off seamounts and underwater ridges, found close to or well off bottom. Occurs at surface in tropics, and close inshore near beaches, at heads of submarine canyons, and in bays in cold-temperate waters, but down to at least 2 500 m on upper continental slope. May show equatorial submergence in tropics as with some other deepwater sharks, and may not normally penetrate warm tropical inshore waters, although it has been known to rise to surface offshore in response to fishing operations. Young of this species often found close inshore, occasionally in enclosed bays; adults, especially males, often found in water >200 m deep in temperate areas, although adults and subadults may enter shallow water in open or enclosed bays with adjacent deepwater canyons. Often associated with areas of upwelling and high biological productivity. Off southern Africa, smaller individuals (<120 cm TL) feed primarily on cephalopods, and secondarily on bony fishes and some chondrichthyans, while larger individuals (~120–200 cm TL) feed primarily on cephalopods, bony fishes and chondrichthyans, plus a small marine mammal component. Very large individuals (>200 cm TL) feed mostly on marine mammals (Cape fur seals and cetaceans) and large pelagic teleosts, with a smaller component of cartilaginous fishes and cephalopods. Apparently feeds on the bottom and well above it; may be able to take large active prey, such as eared seals, cetaceans and large pelagic bony fishes, by means of stealthy stalking, which is possibly aided by its cryptic colouration. Caught largely as a bycatch of other fisheries, but once targeted for human consumption off the Maldives where a fishery for this species peaked but subsequently collapsed. Used fresh, frozen, and dried and salted for human consumption, and for fishmeal and oil. Implicated in attacks on humans, but also the subject of ecotourism dives in some areas. IUCN Red List conservation status Near Threatened; assumed to be vulnerable to overfishing and not able to sustain intensive targeted fisheries.

Hexanchus nakamurai Teng 1962

Bigeyed sixgill shark

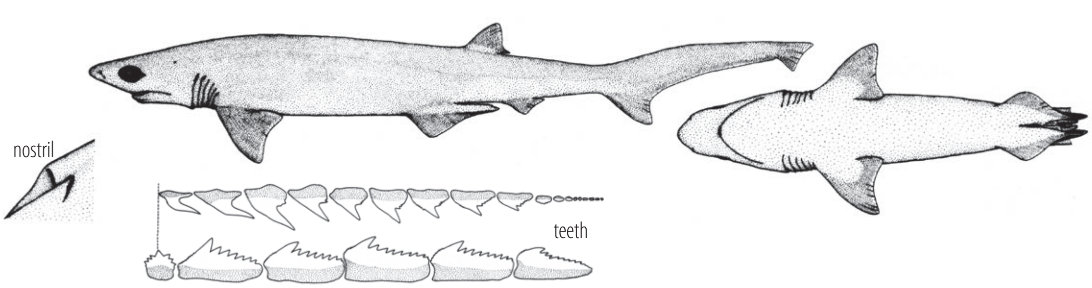
PLATE 3

Hexanchus griseus nakamurai Teng 1962: 30, Fig. 5 (Keelung [Cheng-gong], Taiwan).
Hexanchus vitulus Springer & Waller 1969: 160, Figs. 1–4 (near Bimini, Bahamas); Forster *et al.* 1970; Bass *et al.* 1975*; Compagno 1984*; SSF No. 2.3*; Compagno *et al.* 1989.
Hexanchus nakamurai: Ebert 1990*, 2013*; Compagno *et al.* 2005*; Ebert *et al.* 2013*.

Moderate-sized, slender-bodied and narrow-headed; snout narrowly rounded. Eyes large. Mouth V-shaped, narrow, its width ~1.5 times length. Lower jaw with 5 rows of blade-like, comb-shaped anterolateral teeth. Pectoral fins narrowly triangular and semi-falcate. Anal fin smaller than dorsal fin and set just behind it. Peduncle long and slender. Caudal-fin postventral margin deeply notched in adults and subdivided into upper and lower parts; lower lobe short and strong in adults but weak in young. Tooth count 25–33/9–32; vertebrae 155; spiral valve turns 22–28.

Body pale grey to brown, darker dorsally and paler ventrally; fins sometimes dusky and usually with trailing white edges. Attains 180 cm TL.

DISTRIBUTION Sparsely but widely distributed in warm-temperate and tropical seas, except possibly eastern Pacific. WIO: Kenya, South Africa (KwaZulu-Natal), northern Madagascar, Nazareth Bank, Aldabra, Mauritius, Geyser and Zélée coral banks (NE Mozambique Channel) and southwestern Mediterranean Sea (rare).



Hexanchus nakamurai, 155 cm TL, mature male (South Africa). Source: Bass *et al.* 1975

REMARKS Litters of 13–26; size at birth 40–43 cm TL. Males mature at 123–157 cm TL, and females at 142–178 cm TL; fecundity is much lower in this species than in *H. griseus*. Little-known, primarily deepwater, over continental and insular shelves and slopes, at 90–621 m, usually on or near bottom, but occasionally moving to near surface or inshore in tropics. Likely feeds on small- to medium-sized bony fishes, cephalopods and crustaceans. Uncommonly taken on line gear and in trawls; of relatively minor importance to fisheries, probably used for human consumption and as fishmeal. Apparently uncommon to rare, thus affected by a variety of bottom fisheries; often misidentified as juveniles of *H. griseus*. IUCN Red List conservation status Near Threatened.

GENUS ***Notorynchus*** Ayres 1855

Head broad, bluntly pointed, depressed and transversely oval in cross-section at eyes. Seven paired gill slits. Eyes small. Mouth wide and arcuate. Lower jaw with 6 rows of comb-shaped anterolateral teeth, with low mesial serrations and cusplets in young, and with serrations, low cusp, and 5 or 6 distal cusplets in adults, decreasing in size distal to cusp. Peduncle short. Precaudal vertebrae not calcified and without obvious double cones. One species.

Notorynchus cepedianus (Péron 1807)

Sevengill shark PLATE 4

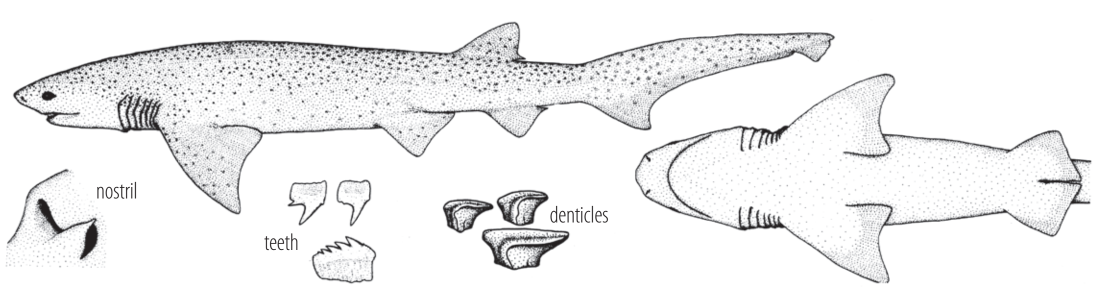
Squalus cepedianus Péron 1807: 337 (Adventure Bay, Tasmania, Australia).
Notorynchus cepedianus: Bass *et al.* 1975*; SSF No. 2.4*; Compagno *et al.* 1989*; Ebert 1990*, 1991, 1991, 1996, 2002, 2003*; Ebert *et al.* 2013*.

Diagnosis as for genus. Tooth count 21–42/20–37; vertebrae 123–130; spiral valve turns 14–17.

Body olive brown to grey, usually covered with numerous small black spots and sometimes with white spots, but occasionally plain; dorsal fin and caudal-fin dorsal lobe with black tips in young individuals, but lost in larger specimens. Attains 3 m TL.

DISTRIBUTION Wide-ranging in most temperate seas (antitropical), but not in North Atlantic and Mediterranean Sea. WIO: South Africa (Western Cape and Eastern Cape).

REMARKS Litters of 80–100; size at birth 34–45 cm TL. Males mature at 150–180 cm TL, at 4–5 years; females mature at ~220 cm TL, at 11–21 years; estimated maximum lifespan 30 years. Reproductive cycle may take 2 years, with gestation period ~1 year plus a year's recovery period during which the next batch of eggs mature. Females give birth to young in shallow bays in springtime. Neritic and benthic, over continental and insular shelves, from surfline and intertidal zone to at least 136 m deep, but mostly above 50 m, and often less than 1 m deep and at surface. Common in shallow bays and close inshore, with larger individuals ranging into deeper water offshore and deep channels in bays. Apparently coordinates its movements in bays with tidal cycle by moving in with a tidal rise and out with its fall, and moves out of shallow bays and estuaries during rainy winter season when salinities drop. Powerful, high-level predator and rather broad-spectrum in its feeding habits, concentrating on marine vertebrates (primarily chondrichthyans, bony fishes and marine mammals). Active and strong-swimming, often found cruising steadily and slowly near bottom but sometimes at surface. Apparently social, often found in groups or aggregations; most active at night, in early morning before sunrise and on overcast days, and tends to move into shallower water in low light and retreat into deeper water with increasing light. In South African waters it may aggregate in patches of turbid brown water caused by phytoplankton blooms, runoff or sediment disturbance. Its large size, local abundance, and high-quality flesh have made this species the subject of fisheries. A small-scale fishery occurred in Namibia (Lüderitz Lagoon) where it was common in the late 1980s and early 1990s. Also caught as a bycatch of various inshore fisheries, including demersal trawls targeting bony fishes and gillnet shark fisheries. Can respond vigorously and assertively when provoked; has been involved in a few unprovoked attacks on divers and swimmers, and has behaved aggressively towards spearfishers. In recent years, an ecotourism industry has sprung up in South Africa (False Bay) where sevengill sharks congregate in relatively clear water.



Notorynchus cepedianus, 209 cm TL, mature female (South Africa). Source: Bass *et al.* 1975

ORDER ECHINORHINIFORMES

FAMILY ECHINORHINIDAE

Bramble sharks

David A Ebert

Large-sized with heavy cylindrical body, covered with coarse spiky denticles or enlarged tack-like denticles; head flattened; snout short and broad. Spiracles very small and far behind eyes. Fifth gill slit much larger than preceding four. Nostrils wide-spaced, internarial width much greater than nostril width. Mouth large, broadly arched, with thin non-papillose lips; lip furrows short, confined to mouth corners, not elongated posteriorly into post-oral grooves or anteriorly into preoral grooves. Teeth in both jaws compressed, low-crowned, broad, blade-like, forming saw-like edge, not arranged in quincunx pattern but in single, flat, non-overlapping series. Two small, spineless, posteriorly placed dorsal fins; 1st dorsal-fin origin over or behind pelvic-fin origins. Pectoral fins low, broadly rounded, with anterior margin moderately large and about equal to or smaller than prespiracular length, and rear tip rounded and not elongated. Pelvic fins as large as or slightly larger than pectoral fins, and more than twice size of dorsal fins. No anal fin. Peduncle compressed, very short; no lateral keels or precaudal pits.

Found from inshore to deep water; circumglobal but sparse, in cold-temperate to tropical seas. One genus with 2 species.

GENUS *Echinorhinus* Blainville 1816

Diagnosis as for family. Body and fins with large, whitish, scattered and conspicuous thorn-like denticles. First dorsal-fin base above pelvic fins. Tooth counts 20–26/20–26; vertebrae 86–102; spiral valve turns 8–16. Body pale to medium grey, grey-brown, brownish or blackish dorsally, often paler ventrally, sometimes with red or black spots or blotches on body, and fin edges blackish. Size range ~1.5–4.5 m TL or more. Two wide-ranging species, 1 in WIO.

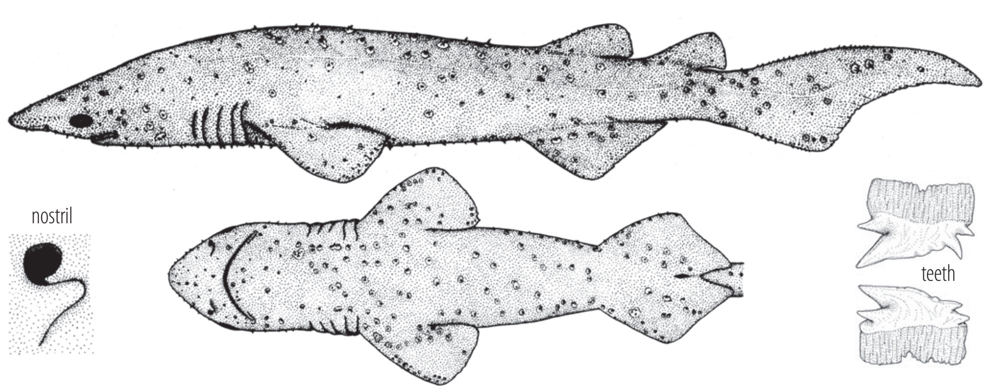
Echinorhinus brucus (Bonnaterre 1788)

Bramble shark PLATE 4

Squalus brucus Bonnaterre (ex Broussonet) 1788: 11 (L'Ocean [North Atlantic]).
Echinorhinus obesus Smith 1838 (Cape of Good Hope, South Africa).
Echinorhinus brucus: SFSA No. 44*; Nair & Lal Mohan 1971; Silas & Selvaraj 1972; Bass *et al.* 1976*; Compagno 1984*; SSF No. 6.1*; Compagno *et al.* 1989; Anderson & Ahmed 1993*; Akhilesh *et al.* 2013; Ebert 2013*; Ebert *et al.* 2013*.

Diagnosis as for genus. Dermal denticles on body and fins (in adults and juveniles >90 cm TL) varying from small to very large, with many large, widely spaced thorn- or buckler-like denticles, with bases not stellate and >1 cm wide; some groups of denticles may fuse to form plates >2.5 cm across. 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; newborns densely covered with small and high denticles with narrow semi-stellate bases. Tooth count 20–26/21–26; vertebrae 102; spiral valve turns 12–16.

Body dark purplish grey, sometimes with red or black blotches on back and sides. Attains at least 3.2 m TL, possibly 3.9 m TL.



Echinorhinus brucus, 122 cm TL, female (Namibia).
Source: Bass *et al.* 1976

DISTRIBUTION Eastern Atlantic, Indo-Pacific and Mediterranean Sea (wide-ranging but sparse). WIO: South Africa (Eastern Cape and KwaZulu-Natal), southern Mozambique, Gulf of Aden, Oman, India (southwestern coast and Gulf of Mannar) and Maldives.

REMARKS Viviparous with yolk sac; litters of 10–52; size at birth 40–54 cm TL. Males mature at 150–198 cm TL, and females at 189–230 cm TL; does not appear to have defined breeding season in Indian waters. Diet includes benthic and littoral bony fishes, smaller sharks and crustaceans. Sluggish and bottom-dwelling, rarely encountered, usually singly. Found in shallow (<18 m) water inshore in cold-temperate areas and places with upwelling, and possibly intertidal zone, but primarily in deep water on continental and insular shelves and upper slopes, at 200–900 m. Along cold-temperate west coast of South Africa and Namibia it moves inshore up submarine canyons and is regularly caught by shore anglers on rod and reel and by small-scale commercial fishers. Relatively unimportant to fisheries, except off southwestern India where it is taken in large numbers; fished in mid-19th century off Namibia in small-scale targeted line fishery; occasionally caught off South Africa as bycatch of demersal trawls. Sporadic and largely unused bycatch of other fisheries, including those for other sharks, but sometimes used for fishmeal and the liver oil used medicinally by traditional healers in South Africa. Has never been known to bite people in the water. Seldom kept in captivity. IUCN Red List conservation status Endangered.

ORDER SQUALIFORMES

FAMILY SQUALIDAE

Dogfishes

David A Ebert

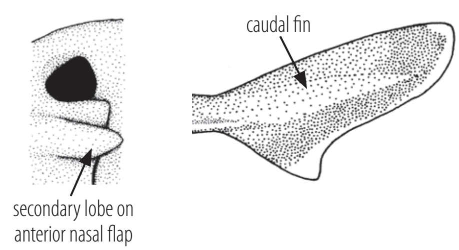
Small- to moderately large-sized with cylindrical body, and abdomen with or without inconspicuous lateral ridges; head moderately broad and flattened; snout flat and broadly to narrowly rounded or angular. Mouth nearly transverse, short, with thin non-papillose lips; lip furrows short, confined to mouth corners, extending to below eyes and elongated posteriorly into post-oral grooves. Teeth in both jaws compressed, low-crowned, broad and blade-like, forming saw-like edge and deeply overlapping series; upper teeth slightly smaller than lower teeth; tooth count 21–29/19–27. Two dorsal fins, each with strong ungrooved spine; 1st dorsal-fin origin opposite or slightly behind pectoral fins; 2nd dorsal fin strongly falcate, its origin opposite or well behind pelvic-fin inner margins; interdorsal space elongate, greater than length of 1st dorsal-fin base. Pectoral fins moderately high, angular, falcate or subtriangular; anterior margin moderately large and subequal or slightly greater than prespiracular length; free rear tip rounded to angular but not greatly elongated. Pelvic fins smaller than pectoral fins and 1st dorsal fin, and subequal to or smaller than 2nd dorsal fin. No anal fin. Peduncle with low, strong keels. Caudal fin without subterminal notch; upper precaudal pit present in *Squalus* and absent or faintly indicated in *Cirrhigaleus*. Dermal denticles small to moderately large, with leaf-shaped, tricuspidate, lanceolate or cross-shaped crowns.

Reproductive mode yolk-sac viviparity. Occur in intertidal zone and near surface of epipelagic zone to ~1 500 m on deep slopes, with most species occurring on continental shelf and uppermost slope (usually to ~600 m deep). Found close inshore and in shallow bays in cool-temperate waters, but often epipelagic well offshore in the tropics, where they tend to be replaced in inshore habitats by small species of Carcharhinidae, Sphyrnidae and other carcharhinoid families. Maximum size ~180 cm TL, except one species (*Squalus acanthias*) reportedly reaching 200 cm TL.

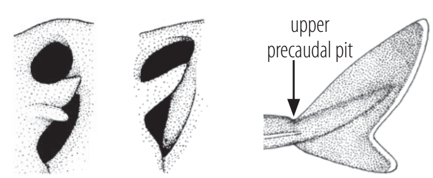
Almost circumglobal, in boreal, temperate and tropical seas (except tropical eastern Pacific), often in association with continents, islands, submarine peaks and ridges. Two genera and 40 species, although several may represent species-complexes, with additional species likely to be described; both genera and at least 10 species in WIO.

KEY TO GENERA

1a Anterior nasal flaps with secondary lobe large and broad, expanded into long or very short barbel; upper precaudal pit weak or absent; 2nd dorsal fin almost as large as 1st; caudal-fin postventral margin shallowly concave; denticles large; body surface rough .... ***Cirrhigaleus***



1b Anterior nasal flaps with secondary lobe small and narrow or absent; upper precaudal pit prominent; 2nd dorsal fin much smaller than 1st; caudal-fin postventral margin deeply notched; denticles small; body surface smooth .... ***Squalus***



GENUS *Cirrhigaleus* Tanaka 1912

Heavy-bodied with short blunt snout, and short anterior nasal flaps with broad-based, stubby to elongated medial barbels. Low blade-like cutting teeth in both jaws. Dorsal fins each with stout, high, ungrooved spine; 2nd dorsal fin about as large as 1st. Peduncle with lateral keels, but precaudal pit poorly developed or absent. Fins with conspicuous white rear margins but no black markings. Three species, 1 in WIO.

Cirrhigaleus asper (Merrett 1973)

Roughskin spurdog PLATE 5

Squalus asper Merrett 1973: 94, Pl. 1b, Fig. 1 (off Aldabra, equatorial WIO); Bass *et al.* 1976*; Compagno 1984*; SSF No. 5.25*; Compagno *et al.* 1989*.
Cirrhigaleus asper: Compagno *et al.* 2005*; Ebert 2013*; Ebert *et al.* 2013*.

Anterior nasal flaps with large medial barbel, usually as broad as distance from its base to inner edge of nostrils, but not elongated behind flaps and not reaching mouth. Oblique-cusped cutting teeth; tooth count 27/23. Dorsal fins subequal; origin of 1st dorsal-fin spine behind pectoral-fin free rear tips.

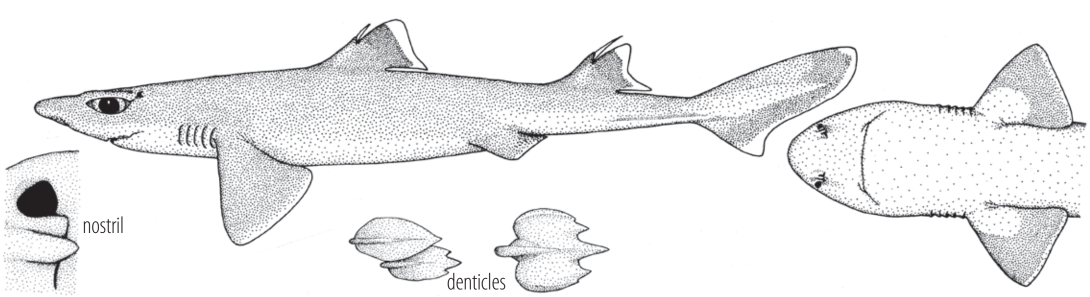
Body dark grey or brown dorsally; no white spots on flanks, but prominent white-edged fins; pale ventrally. Attains 118 cm TL.

DISTRIBUTION Peculiar disjunct distribution; known in western Atlantic, central Pacific and WIO, suggesting it may occur elsewhere. WIO: southern Mozambique, South Africa (Eastern Cape and KwaZulu-Natal), Aldabra, Comoros, Saint-Paul and Amsterdam Is., and possibly India (west and east coasts).

REMARKS Litters of 18–22 (relatively large); size at birth 25–28 cm TL. Males mature at 85–90 cm TL, and females at 89–118 cm TL. Distinctive but little-known; occurs on upper continental and insular slopes and outer continental shelf in warm-temperate to tropical seas, on or near bottom, at 73–600 m. Often caught well offshore on upper slopes at ~73–110 m, but sometimes found near bays and in river mouths (e.g., in Eastern Cape and KwaZulu-Natal, South Africa). Feeds mostly on bony fishes and squid. Interest to fisheries minimal, but probably caught incidentally and possibly a utilised bycatch of bottom-trawl and deep longline fisheries; occasionally caught by inshore line fisheries in South Africa (Eastern Cape).

GENUS *Squalus* Linnaeus 1758

Slender body with flat rounded head, angular to conical in dorsoventral view; snout flattened, rounded to narrowly pointed, short to elongate. Anterior nasal flaps short, with small, narrow medial barbels; length of upper lip furrow greater than nostril width. Teeth blade-like, with cutting edge, similar in both jaws. Skin smooth; dermal denticles small, crowns of lateral trunk denticles in adults usually <0.5 mm long, with low, pedicellate, lanceolate or tricuspid and triple-ridged, flat, leaf-shaped crowns. Pectoral-fin free rear tips narrowly rounded to acutely angular. Pelvic fins low and obtusely triangular, with anterior margin ~⅓–½ length of pectoral-fin anterior margin. Dorsal-fin spines stout; 2nd dorsal fin smaller than 1st, its base ~¾ length of 1st dorsal-fin base; 2nd dorsal-fin origin usually behind pelvic-fin rear tips, but occasionally over them. Peduncle elongated, with lateral keels and precaudal pit. Caudal fin slightly elongated, upper lobe narrower, lower lobe strong, and postventral margin usually deeply concave in adults. Body grey to pale brown, some species with white spots on flanks; fins plain or with conspicuous white or black margins or tips, but usually without continuous broad white rear margins. Worldwide, at least 24 species, some of which appear to be species-complexes, which may result in several additional species descriptions; at least 9 species in WIO, 4 species too late for inclusion.

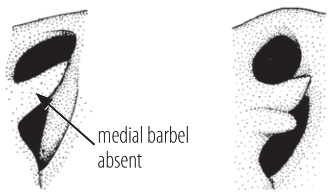


Cirrhigaleus asper, 38 cm TL, female (South Africa). Source: Bass *et al.* 1976

KEY TO SPECIES

1a First dorsal fin posteriorly set, with origin behind or sometimes over pectoral-fin free rear tips; origin of 1st dorsal-fin spine well behind pectoral-fin free rear tips; medial barbel on anterior nasal flaps minute or absent; flanks usually with white spots .... ***S. acanthias***

1b First dorsal-fin origin usually in front of pectoral-fin free rear tips; origin of 1st dorsal-fin spine usually over pectoral-fin inner margins and ahead of pectoral-fin free rear tips (but varying from just behind to well ahead of tips); medial barbel on anterior nasal flaps well-developed; no white spots on flanks 2



1a 1b

2a Distance from snout tip to inner edge of nostril shorter than distance from inner edge of nostril to front of upper lip furrow 3

2b Distance from snout tip to inner edge of nostril longer than distance from inner edge of nostril to front of upper lip furrow 4

3a Anterior nasal flaps not bifurcate; total vertebrae 93–95, precaudal vertebrae 67–69 .... ***S. lalannei***

3b Anterior nasal flaps bifurcate; total vertebrae 102–110, precaudal vertebrae 78–84 .... ***S. acutipinnis***

4a First dorsal fin high and erect, height ~80% fin length, with 1st dorsal-fin spine about as long as fin base; precaudal vertebrae 90–96 .... ***S. blainville***

4b First dorsal fin lower, height ~70% fin length or less, with 1st dorsal-fin spine shorter than fin base; precaudal vertebrae 83–89 .... ***S. mitsukurii***

Squalus acanthias Linnaeus 1758

Spotted spiny dogfish

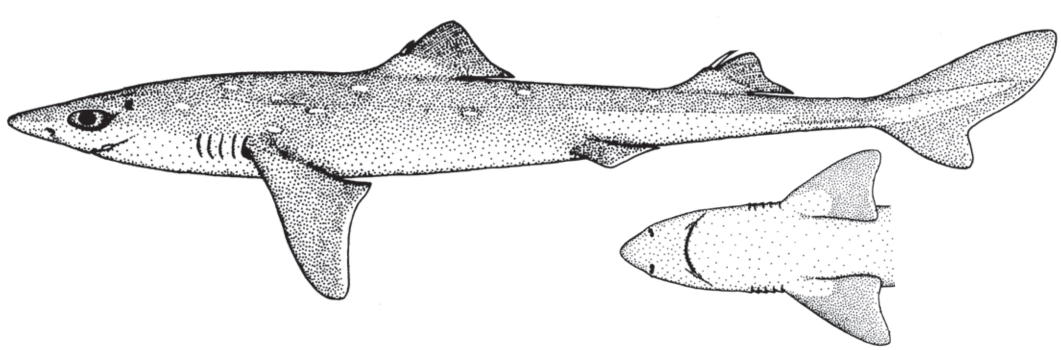
PLATE 5

Squalus acanthias Linnaeus 1758: 233 (Mediterranean Sea and northeastern Atlantic); Barnard 1925; Smith 1949*, 1965*; Bass *et al.* 1976*; Compagno 1984*; Myagkov & Kondyurin 1986; SSF No. 5.24*; Compagno, Ebert & Smale 1989*; Compagno, Ebert & Cowley 1991; Ebert, Compagno & Cowley 1992; Compagno *et al.* 2005; Ebert *et al.* 2013*.

Squalus acanthias africana Myagkov & Kondyurin 1986: 564 (SE Atlantic) (junior homonym of *Squalus africanus* Gmelin 1788 = *Poroderma africana* [Scyliorhinidae]).

Moderate- to large-sized and slender-bodied with moderately long, narrow, angular or subangular snout. Preoral length 1.1–1.4 mouth width; distance from snout tip to excurrent nostril aperture slightly greater than or approximately same as distance from excurrent aperture to front edge of upper lip furrow. Oblique-cusped cutting teeth in both jaws. Pectoral fins narrow and falcate or semifalcate, with straight to concave rear margin. First dorsal fin relatively long and low; its spine slender and short, and spine origin always behind pectoral-fin free rear tips. No subterminal notch on caudal fin. Tooth count 26–29/20–27; vertebrae 109–116; spiral valve turns 12 or 13.

Body grey, with series of white spots on flanks and dorsal surface, paler ventrally; dorsal-fin edges dusky in adults, and black in young; caudal web dusky, no blackish bar along caudal base and caudal-fin lower lobe not black. Attains ~180 cm TL (highly variable depending on population).



Squalus acanthias, 46 cm TL, female (South Africa). Source: Bass *et al.* 1976

DISTRIBUTION Nearly circumglobal, except for tropics, with apparently isolated allopatric populations or subpopulations, some of which are of uncertain taxonomic status; replaced by *S. suckleyi* (Girard 1855) in North Pacific (Ebert *et al.* 2010). WIO: South Africa (Western Cape to Eastern Cape).

REMARKS Litters of 1–32 (usually 2–12 in southern Africa); gestation period long, reported as 18–24 months, possibly varying regionally. Size at maturity varies between populations, those in southern Africa at the lower end of the range, at 52–77 cm TL for males, and 66–100 cm TL for females. Slow-growing: age at maturity may vary markedly between regions and populations, and is variously reported as 10–20 years for females and 11+ years for males. Long-lived: estimated maximum age 25–30 years, but possibly as long as 75 years. Found in boreal to warm-temperate seas, from inshore and offshore; mainly demersal but also apparently epipelagic over continental and insular shelves, and nearer surface in oceanic waters; mostly above ~600 m deep over continental shelf and upper slope (usually at 124–515 m in southern Africa), but to 1 446 m on deep slopes. Also found in open bays and estuaries, and often caught over soft substrates, and reported from brackish estuaries and freshwater of Europe and eastern United States. Most stocks are highly migratory in dense aggregations. Powerful voracious predator, feeds primarily on bony fishes and capable of dismembering largish prey with its strong jaws and clipper-like teeth; invertebrate prey includes cephalopods, crustaceans, polychaete worms, jellyfish and comb jellies. Can inflict toxins with its tail. Predators on this species include larger bony fishes, sharks and cetaceans. Naturally abundant and heavily fished in many parts of its range, especially North Atlantic and Mediterranean Sea; in WIO, mainly caught incidentally in bottom-trawl hake fisheries and usually discarded. IUCN Red List conservation status Vulnerable globally.

Squalus acutipinnis Regan 1908

Shortnose spurdog

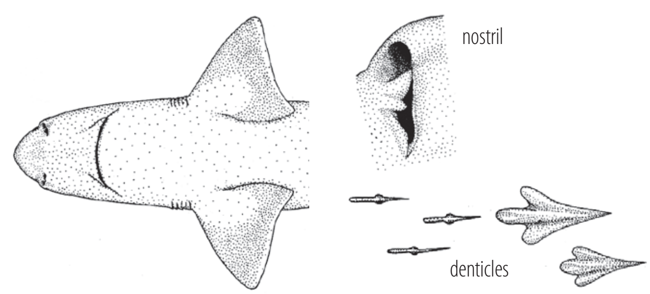
PLATES 5 & 6

Squalus acutipinnis Regan 1908: 248, Pl. 37 (SW Indian Ocean); Regan 1921; Barnard 1925, 1947*; Viana & Carvalho 2016*.

Squalus megalops (non Macleay 1881*)*: Bass *et al.* 1976*; Compagno 1984*; Myagkov & Kondyurin 1986*; SSF 5.26*; Compagno, Ebert & Smale 1989*; Muñoz-Chapuli & Ramos 1989*; Compagno, Ebert & Cowley 1991; Ebert, Compagno & Cowley 1992; Watson & Smale 1998; Compagno *et al.* 2005*; Ebert 2013; Ebert *et al.* 2013*.

Small-sized, moderately slender, with wide head and short, broad, rounded-parabolic snout; preoral length 1.2–1.4 mouth width. Anterior nasal flaps with small medial bifurcate barbel. Dorsal fins unequal-sized; 1st dorsal fin moderately high, its origin over pectoral-fin inner margins; both dorsal-fin spines slender, 1st spine low and tapering. Pectoral fins broad and falcate, with moderately concave rear margin. No subterminal notch on caudal fin. Vertebrae 107–111.

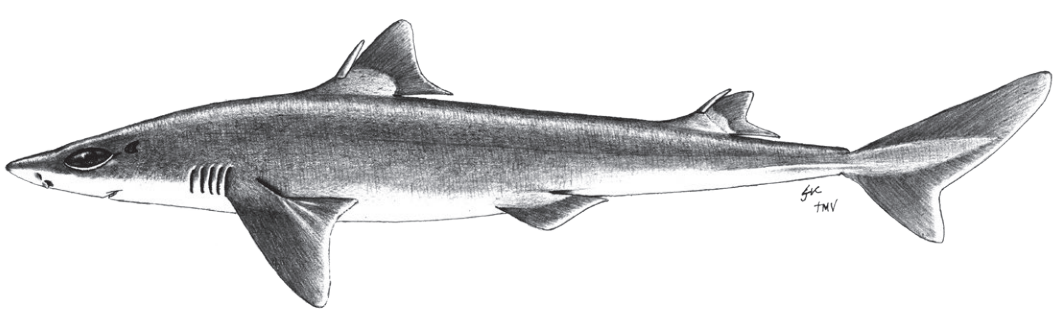
Body pale grey-brown to dark brown dorsally, paler ventrally; no white spots on flanks; dorsal fins with black tips, and white rear margins and free rear tips (but this colouration often inconspicuous or lacking in adults). Attains 77 cm TL.



Squalus acutipinnis, 40 cm TL, male, ventral head (South Africa).
Source: Bass *et al.* 1976

DISTRIBUTION Southeastern Atlantic to southwestern Indian Ocean. WIO: Mozambique to South Africa (Western Cape), Madagascar and Mauritius.

REMARKS Litters of 1–6 (usually 2 or 3); size at birth 23–28 cm TL. In populations off South Africa there appears to be no defined reproductive cycle as adult females continuously reproduce without a gap between pregnancies; estimated gestation period 2 years. Males mature at ~46 cm TL, and females at ~54 cm TL. Common to abundant in temperate



Squalus acutipinnis, 56 cm TL, female (South Africa). Source: SSF and tropical seas, on inner and outer continental shelves and upper slopes. Generally found on or near bottom, from intertidal zone and close inshore, to ~732 m deep. Off South Africa, newborns are pelagic on pupping grounds over outer continental shelf of Agulhas Bank. Feeds on a variety of bony fishes and occasionally other elasmobranchs, as well as invertebrates, including crustaceans and cephalopods. Often abundant and of considerable interest to fisheries; taken in large quantities in bottom trawls but also on line gear; a common bycatch of trawl fisheries off southern Africa, but largely discarded.

Squalus blainville (Risso 1827)

Longnose spurdog

PLATE 6

Acanthias blainville Risso 1827: 133, 478, Pl. 3, Fig. 6 (France, northwestern Mediterranean Sea).

Squalus blainville: Compagno 1984*; Myagkov & Kondyurin 1986*; Parin 1987; Muñoz-Chapuli & Ramos 1989*; Ebert *et al.* 2002; Compagno *et al.* 2005*; Ebert 2013*; Ebert *et al.* 2013*.

Large-sized, stocky to moderately slender, with broad head; oblique distance from snout tip to eyes less than interorbital space; mouth moderately long, rounded-parabolic, preoral length 1–1.3 mouth width. Oblique-cusped cutting teeth in both jaws. Dorsal fins unequal-sized, each with high ungrooved spine; 1st dorsal fin very high and short, with tall slender spine, and spine origin over pectoral-fin inner margins. Pectoral fins broad, semifalcate, with slightly concave rear margin.

Body greyish brown, without white spots on flanks; dorsal and caudal fins white-edged and without conspicuous dark markings or dusky edges or tips; caudal fin without conspicuous dark markings. Attains 100 cm TL.

DISTRIBUTION Undefined; possibly globally wide-ranging but may be species-complex with several undescribed species represented. WIO: South Africa (KwaZulu-Natal).

REMARKS Details of its biology are uncertain because of taxonomic confusion. Litters of 3–8. Males mature at ~56 cm TL, but female adult size undefined due to confusion with similar-looking *Squalus* species. Females attain ~100 cm TL, and males ~75 cm TL; a female, possibly of this species, caught off KwaZulu-Natal, South Africa, measured 96 cm TL and had 8 near-term embryos. Nominally recorded from continental shelves and upper slopes, on or near bottom, at 16–600 m, but probably occurs deeper. Feeds on bony fishes, cephalopods and crustaceans. Interest to fisheries unclear, but at minimum taken as a bycatch of other fisheries. IUCN Red List conservation status Data Deficient due to uncertain taxonomy.

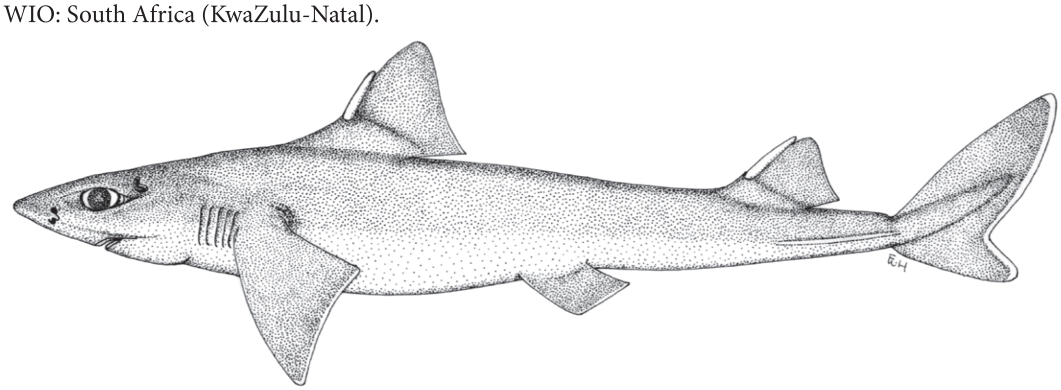
Squalus lalannei Baranes 2003

Seychelles spurdog

Squalus lalannei Baranes 2003: 42, Figs. 6–12 (Alphonse I., Seychelles).

Moderately slender-bodied with short head and snout; snout rounded; prenarial length 2–2.3 preoral length. Anterior nasal flaps not bifurcate. Mouth rounded, upper jaw concave; mouth width 1.3–1.4 preoral length; upper lip furrow longer than lower lip furrow, with groove extending to level below posterior edge of spiracle. Teeth unicuspidate, blade-like, with cusps directed laterally; teeth similar in both jaws, but upper teeth slightly larger than lower teeth; tooth count 24–26/22–24. First dorsal-fin origin over pectoral-fin free rear tips; 2nd dorsal fin smaller than 1st, with origin over pelvic-fin bases. No interdorsal ridge. Pectoral fins moderate-sized. Peduncle with lateral keels originating below 2nd dorsal-fin free rear tip and reaching past caudal-fin origin. Caudal-fin terminal margin moderately convex; tip of lower lobe narrowly rounded. Vertebrae 93–95.

Body uniformly grey, with blackish dorsal fins. Attains at least 79 cm TL.



Squalus blainville, 96 cm TL, female (South Africa).

REMARKS Known only from two specimens from the Seychelles (79-cm-TL female; 62-cm-TL male), collected from ~1 000 m. Closely resembles Australian *S. megalops*, but differs in lower number of precaudal vertebrae (67–69 versus 78–84), non-bifurcated anterior nasal flaps, and rounded pectoral-fin free rear tips (cf. more angular tips in *S. megalops*). Presumed viviparous with yolk sac. Possibly taken in deepwater longline fisheries.

Squalus mitsukurii Jordan & Snyder 1903

Shortspine spurdog PLATE 6

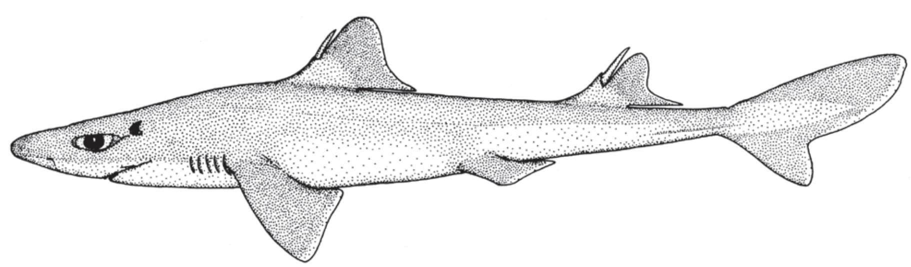
Squalus mitsukurii Jordan & Snyder *in* Jordan & Fowler 1903: 629, Fig. 3 (Misaki, Japan); Barnard 1925; Smith 1949*, 1965*; Bass *et al.* 1976*; Compagno 1984*; SSF No. 5.27*; Compagno, Ebert & Smale 1989*; Muñoz-Chapuli & Ramos 1989*; Compagno, Ebert & Cowley 1991; Ebert, Compagno & Cowley 1992; Compagno *et al.* 2005*; Ebert 2013*; Ebert *et al.* 2013*.
?*Squalus probatovi*: Myagkov & Kondyurin 1986.

Medium- to large-sized, moderately stout-bodied, with broad head; snout moderately long and rounded. Anterior nasal flaps with small medial barbel; distance from snout tip to excurrent aperture of nostril slightly greater than from excurrent aperture to front edge of upper lip furrows. Teeth broad-based, with single smooth-edged triangular cusp, and similar in both jaws; tooth count 25–29/22–25. First dorsal fin moderately high, more anteriorly situated, with origin over pectoral-fin inner margins and just behind pectoral-fin insertions. Peduncle with upper precaudal pit. Vertebrae 118–127.

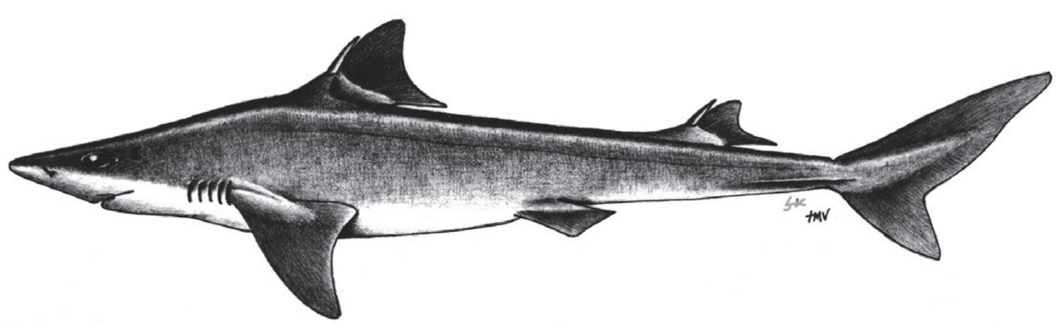
Body grey or grey-brown dorsally, white or paler grey ventrally; no white spots on flanks; pectoral fins dusky above, with white tips and rear margins. Attains 125 cm TL (variable depending on population).

DISTRIBUTION Wide-ranging in cold-temperate to tropical seas, but range only approximately known because of widespread nominal records of similar-looking species. WIO: Tanzania, Mozambique, South Africa (Eastern Cape and KwaZulu-Natal), Madagascar and India.

REMARKS Males mature at 47–85 cm TL, at 4–11 years, and attain ~18 years; females mature at 50–100 cm TL, at 15–20 years, and attain ~27 years. Litters of 2–15, correlating to size of mother; size at birth 21–30 cm TL; gestation period possibly up to 2 years. Occurs on continental and insular shelves, upper slopes, submarine ridges and seamounts, on or near bottom, at 4–954 m (mostly 100–500 m). Common to abundant, sometimes in large aggregations. Powerful predator, feeds primarily on bony fishes, cephalopods and crustaceans. Of considerable interest to fisheries in some regions; commonly caught incidentally in demersal fisheries off southern Africa.



Squalus mitsukurii, 43 cm TL, male (South Africa). Source: Bass *et al.* 1976



Squalus mitsukurii, 81 cm TL, female (S Mozambique). Source: SSF

FAMILY CENTROPHORIDAE

Gulper sharks

David A Ebert

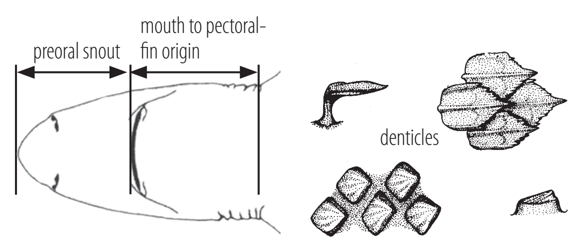
Small- to moderate-sized (~40–170 cm TL) with cylindrical or slightly compressed trunk, without lateral ridges on abdomen, and moderately broad to narrow and somewhat flattened head. Snout short or long, flattened and narrowly rounded to elongate-rounded in dorsoventral view. Nostrils wide-spaced, internarial width greater than nostril width, with simple anterior nasal flaps and no medial barbels. Spiracles large, set close behind large oval eyes. Teeth in both jaws with compressed cusp, distal blade and sometimes medial blade, and no cusplets; upper cusps narrow, erect to oblique, and broad-based; lower cusps oblique to semi-erect; tooth counts 22–45/24–35. Two dorsal fins, each with strong grooved spine; 1st dorsal-fin origin usually opposite pectoral-fin bases or inner margins or sometimes just behind free rear tips; 2nd dorsal fin not falcate, its origin usually opposite pelvic-fin bases or inner margins, but exceptionally somewhat behind pelvic-fin rear tips. Interdorsal space elongated and usually greater than length of 1st dorsal-fin base (subequal to or slightly longer than fin base in some species). Pectoral fins low, angular or rounded, and not falcate; anterior margins moderately large. Pelvic fins smaller than pectoral fins and 1st dorsal fin, and subequal to or smaller than 2nd dorsal fin. No anal fin. No keels or precaudal pit on peduncle. Caudal fin heterocercal, lower lobe poorly to strongly developed in adults, and subterminal notch strong. Dermal 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. Total vertebrae 106–131; spiral valve turns 10–25. Body plain or with pale or dark markings on fins; no black photophore markings on flanks or tail.

Reproductive mode yolk-sac viviparity, with litters of 1–12. Primarily bottom-dwelling deepwater inhabitants of continental and insular slopes, but also found on submarine ridges and seamounts, at mostly 200–1 500 m (one has been photographed on ocean floor below 4 000 m). Rarely, these sharks also occur offshore to ~50 m deep over continental and insular shelves. Geographic and bathymetric ranges are imperfectly known for most *Centrophorus* species, a result of uneven sampling of deepwater slope-dwelling sharks as well as problems in identifying these species. Social, forming small to huge aggregations, making them among the most common deep-benthic sharks in temperate and tropical seas, although their behaviour and biology are little known. Feed mostly on bony fishes and cephalopods but also crustaceans, small sharks, batoids and chimaeras. For fisheries purposes, one of the most important families of deep-benthic slope-dwelling sharks, although catches are relatively smaller and more localised than sympatric species of squalid dogfishes. In WIO (especially off India) and elsewhere, these sharks are a common component of targeted deepwater shark fisheries and also form an important bycatch of deepwater fisheries for bony fishes; however, separate fisheries statistics are seldom reported for the family or for individual species. Used for human consumption as dried-salted or fresh, for fishmeal, and for their oily squalene-rich livers, which are extremely large. The conservation status of gulper sharks is of concern because of expanding deepwater fisheries, limited knowledge of their biology, and possibly more extreme limits in life-history parameters than what occurs among well-known and more abundant species of squalid dogfishes.

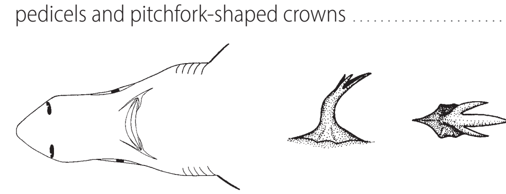
Almost circumglobal in cold-temperate to tropical seas, in association with landmasses, including continents, islands, submarine peaks and ridges. Generally absent from very high latitudes, and most diverse in warm-temperate waters and the tropics. Several species are wide-ranging, whereas a few may be localised endemics. The greatest known diversity of this family occurs in the Indo-Pacific. Two genera and 15 species; both genera and at least 9 species in WIO.

KEY TO GENERA

1a Preoral snout length less than distance from mouth to pectoral-fin origins; lateral trunk denticles leaf-shaped with pedicels, or sessile with low ridges, and without erect pitchfork-shaped crowns .... ***Centrophorus***



1b Preoral snout length greater than distance from mouth to pectoral-fin origins; lateral trunk denticles with tall, slender pedicels and pitchfork-shaped crowns .... ***Deania***



GENUS *Centrophorus* Müller & Henle 1837

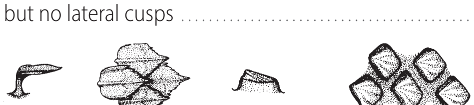
Body cylindrical, with very tough skin; snout moderately long and broad; eyes huge and iridescent green. Dermal denticles large and leaf-like, thorn-like or pebble-shaped; lateral trunk denticles with low, flat, ridged crowns, varying from leaf-shaped and with low pedicels and posterior cusps, to cuspless, block-shaped and without pedicels. Teeth similar in both jaws, blade-like and without cusplets, but lower teeth imbricated (overlapping) and much larger than upper teeth; tooth counts 30–45/24–35. Lip furrows not extended anteromedially as elongated preoral grooves. Pectoral-fin free rear tips more or less angular to attenuated. Vertebrae 106–127. Body pale grey or grey-brown to blackish grey, sometimes paler below; fin webs dusky or with pale and dark bars.

This group is extremely problematic taxonomically, with many species poorly known, and with undescribed species possibly occurring in the WIO, especially in deep waters. Worldwide, 17 species; 6 species in WIO, but 2 of these (*C. isodon* [Chu, Meng & Liu 1981] and *C. seychellorum* Baranes 2003) are known only from very deep water (off Maldives, Seychelles, South Africa, and possibly southern Mozambique), thus given the rarity of these deepwater *Centrophorus* species they are included here only in the key.

KEY TO SPECIES

1a Lateral trunk denticles with leaf-like flattened crowns on elevated narrow to broad pedicels extending above denticle bases, and crowns with strong medial and lateral cusps on their posterior edge .... ***C. squamosus***

1b Lateral trunk denticles with flat sessile crowns on denticle bases, without separate pedicels, and crowns usually with or sometimes without posterior medial cusp but no lateral cusps **2**



1a 1b

2a Second dorsal fin very small, ≤½ height of 1st dorsal fin, with origin of 2nd dorsal-fin spine usually well behind pelvic-fin rear tips .... ***C. moluccensis***

2b Second dorsal fin larger, nearly as high as 1st dorsal fin, with origin of 2nd dorsal-fin spine usually over pelvic-fin inner margins **3**

Continued …

KEY TO SPECIES

3a Snout elongated, narrowly parabolic in dorsoventral view, narrowly cuneate in lateral view; preoral length 1.4–1.8 mouth width, and 0.9–1.1 head width at mouth corners; mouth narrower, its width 5.2–7.3% TL; body usually slender **4**

3b Snout short and broad, broadly parabolic in dorsoventral view, broadly wedge-shaped in lateral view; preoral length 0.9–1.5 (usually <1.3) mouth width, and 0.6–0.9 head width at mouth corners; mouth broader, its width 6.6–9.5% TL; body usually stout **5**

4a Dorsal-caudal space relatively short, <7% TL; flank denticles block-like, widely spaced .... ***C. isodon*** [deep water]

4b Dorsal-caudal space relatively long, >8% TL; flank denticles not block-like, more pointed, close-set .... ***C. seychellorum*** [deep water]

5a Fins of adults and subadults prominently marked with black tips and margins, including pectoral fins, both dorsal fins, both caudal-fin lobes, and sometimes pelvic fins; maximum <100 cm TL .... ***C. atromarginatus***

5b Fins of adults and subadults not prominently marked, their colour pale to dusky; maximum ~170 cm TL .... ***C. granulosus***

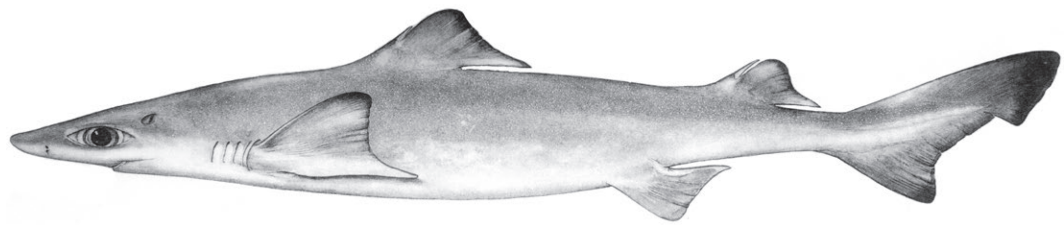
Centrophorus atromarginatus Garman 1913

Blackfin gulper shark — PLATE 7

Centrophorus atromarginatus Garman 1913: 200, Pl. 13, Figs. 1–4 (Suruga Gulf, Japan); Compagno *et al.* 2005*; Ebert 2013*; Ebert *et al.* 2013*.

Snout moderately long and thick. Teeth blade-like, monocuspidate in both jaws, with lower teeth much larger than upper teeth; tooth count 40–42/29–30. Pectoral-fin free rear tips narrowly angular and greatly elongated. First dorsal fin short, higher than 2nd; base of 2nd dorsal-fin spine over pelvic-fin inner margins or rear tips. Vertebrae 107–114; spiral valve turns 10–12.

Body grey or grey-brown dorsally, paler ventrally; prominent blackish markings on fins. Attains 94 cm TL.



Centrophorus atromarginatus, 85 cm TL (Japan). Source: Garman 1913

DISTRIBUTION Sparse records from eastern Atlantic, western Pacific and Indian oceans, but probably wider-ranging. WIO: Somalia (Gulf of Aden), India and Sri Lanka.

REMARKS Often confused with *C. granulosus* and *C. moluccensis*. Litters of 1 or 2; size at birth 30–36 cm TL. Males mature at ~56 cm TL, and females at ~75 cm TL. Occupies moderately deep water along outer continental shelf, upper slope and insular shelves, at 150–450 m. Feeds on small bony fishes and shrimps. Mostly caught as bycatch in WIO; elsewhere localised fisheries occur for its squalene-rich liver oil.

Centrophorus granulosus (Bloch & Schneider 1801)

Gulper shark PLATE 7

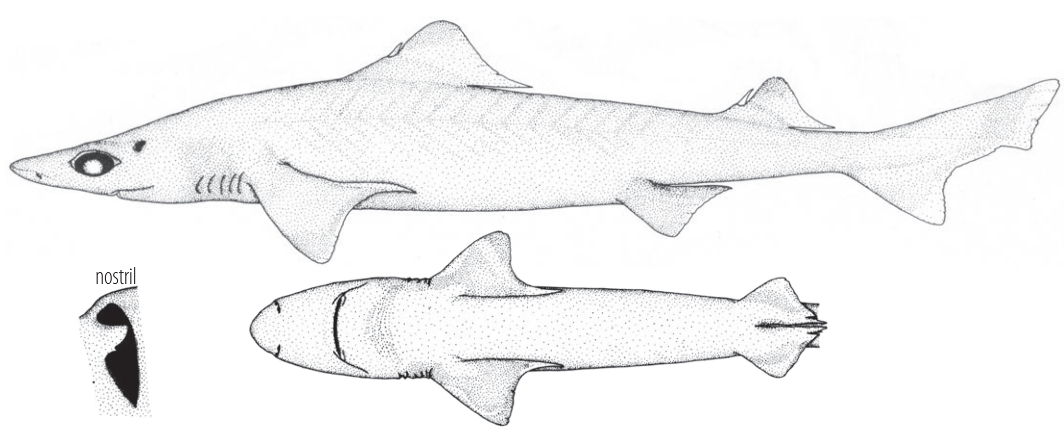
Squalus granulosus Bloch & Schneider 1801: 135 [Canary Is.].
Centrophorus lusitanicus Barbosa du Bocage & De Brito Capello 1864: 260, Fig. 1 (Portugal, North Atlantic); Compagno 1984 [in part: southern Africa]; SSF No. 5.2*; Compagno *et al.* 1989*.
Centrophorus granulosus: Bass *et al.* 1976*; SSF No. 5.1*; Compagno *et al.* 1989*; Compagno *et al.* 1991; Ebert *et al.* 1992; Compagno *et al.* 2005*; Ebert 2013*; Ebert *et al.* 2013*; White *et al.* 2013*.

Snout moderately long and thick. Teeth blade-like, monocuspidate, similarly shaped in both jaws, but lower teeth larger than upper teeth; tooth count 36–43/28–32. Pectoral-fin free rear tips narrowly angular and greatly elongated. First dorsal fin higher than 2nd; base of 2nd dorsal-fin spine over pelvic-fin inner margins. Vertebrae 113–125; spiral valve turns 11–15.

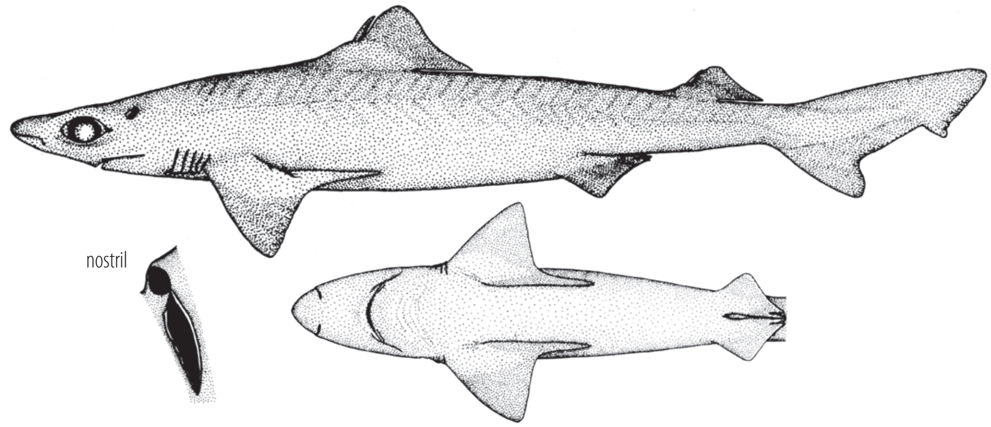
Body dark grey or grey-brown above, slightly paler below; fins with dark grey or blackish webs, but without prominent black tips or margins. Attains 170 cm TL.

DISTRIBUTION Circumglobal, including Mediterranean Sea, southeastern Atlantic, central and western Pacific (excluding eastern Pacific), and Indian Ocean. WIO: Gulf of Aden, Mozambique, South Africa (Mozambique/KwaZulu-Natal border to Orange River, Northern Cape Province), Madagascar, southern Madagascar Ridge, Aldabra, Maldives and possibly India.

REMARKS Often confused with *C. atromarginatus* and *C. moluccensis*. Litters of 1–6; size at birth 30–45 cm TL. Males mature at 110–128 cm TL, and females at >130 cm TL; size at maturity varies by region. Occurs in deep water along outer continental shelves and upper slopes, and insular shelves, at 50–1 440 m (usually 200–600 m). Feeds on bony fishes, cephalopods and crustaceans. Fished primarily in North Atlantic, and taken mostly as a bycatch in WIO; used for its meat and squalene-rich liver oil. IUCN Red List conservation status Critically Endangered in North Atlantic and Mediterranean, but Vulnerable in WIO.



Centrophorus granulosus, 85 cm TL, male (S Mozambique). Source: Bass *et al.* 1976



Centrophorus moluccensis, 78 cm TL, mature male (S Mozambique). Source: Bass *et al.* 1976

Centrophorus moluccensis Bleeker 1860

Smallfin gulper shark PLATE 7

Centrophorus moluccensis Bleeker 1860: 3 (Ambon I., Moluccas, Indonesia); Compagno 1984*; Compagno *et al*. 1989*, 2005*; Ebert 2013*; Ebert *et al*. 2013*.
Centrophorus scalpratus McCulloch 1915: 97, Pl. 13, Figs. 2–7 (off Gabo I., Victoria coast, Australia); Bass *et al*. 1976*; SSF No. 5.3*.
Atractophorus armatus Gilchrist 1922: 48, Pl. 7, Fig. 3 (KwaZulu-Natal, South Africa); SFSA No. 47*.

Snout moderately long and flat. Teeth blade-like, similar in both jaws, but lower teeth much larger than upper teeth; tooth count 36–45/29–35. Pectoral-fin free rear tips elongated into very narrow angular lobe, reaching well behind base of 1st dorsal-fin spine. First dorsal fin much higher and larger than 2nd; base of 2nd dorsal-fin spine usually behind pelvic-fin rear tips. Caudal-fin postventral margin conspicuously notched. Vertebrae 113–131; spiral valve turns 20–29.

Body grey-brown or grey dorsally, slightly paler ventrally; pectoral fins with conspicuously paler rear margins. Attains at least 100 cm TL.

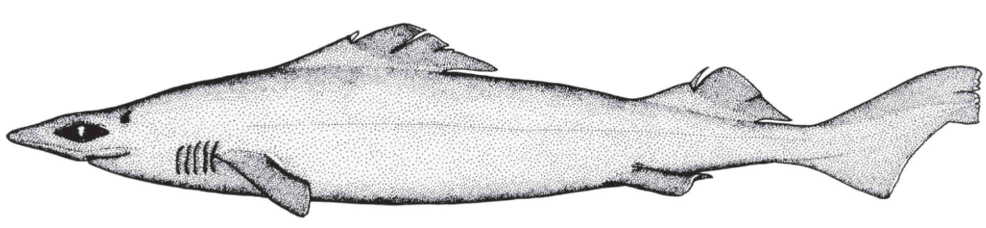
DISTRIBUTION Indo-Pacific (scattered); Indian subcontinent records of *C. atromarginatus* may be of *C. moluccensis*, thus this species likely has a more extensive range than indicated by available records. WIO: South Africa (KwaZulu-Natal) and Mozambique.

REMARKS Litters of 2; size at birth 31–37 cm TL; gestation period possibly 2 years. Males mature at ~70 cm TL, and females at ~89 cm TL. Common; occurs in deep water over outer continental and insular shelves and upper slopes, on or near bottom, at 128–823 m. Feeds primarily on bony fishes, other dogfish sharks (Order Squaliformes), cephalopods and crustaceans. Of minor to moderate fisheries importance off South Africa and Australia, along with other dogfish sharks, but little utilised; mostly taken as a bycatch of fisheries targeting shrimp and bony fishes (populations off the east coast of southern Africa may have declined markedly as a result).

Centrophorus squamosus (Bonnaterre 1788)

Leaf-scale gulper shark

Squalus squamosus Bonnaterre 1788: 12 [probably eastern North Atlantic].
Encheiridiodon hendersoni Smith 1967: 129, Pls. 24–27 (Algoa Bay, South Africa).
Centrophorus squamosus: Forster *et al.* 1970; Bass *et al*. 1976*; Compagno 1984*; SSF No. 5.4*; Compagno *et al*. 1989*; Muñoz-Chapuli & Ramos 1989; Compagno *et al*. 1991*; Ebert *et al*. 1992*; Compagno *et al*. 2005*; Last & Stevens 2009*; Ebert 2013*; Ebert *et al*. 2013*.



Centrophorus squamosus, 93 cm TL, male (South Africa). Source: Bass *et al.* 1976

Large-sized and relatively stocky; snout short, thick and somewhat flattened. Teeth blade-like, similar in both jaws, but lower teeth much larger than upper teeth; tooth count 30–38/24–32. Lateral trunk denticles high, rough, leaf-shaped, tricuspidate or multicuspidate. Pectoral-fin free rear tips hardly angular and not greatly elongated, forming angular corner to very short, narrow, angular lobe that ends well in front of 1st dorsal-fin spine. First dorsal fin long and low, usually slightly lower but larger than 2nd; base of 2nd dorsal-fin spine usually opposite pelvic-fin inner margins or rear tips. Vertebrae 106–120; spiral valve turns 12–14.

Body grey, grey-brown or reddish brown dorsally, usually similar ventrally; fin webs and margins dusky, but no prominent fin markings. Attains 165 cm TL.

DISTRIBUTION Atlantic and Indo-Pacific (wide-ranging). WIO: South Africa (Eastern Cape and KwaZulu-Natal), southern Madagascar Ridge, Seychelles (Aldabra and Assumption) and India.

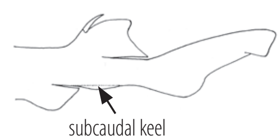
REMARKS Litters of 4–9; size at birth 30–40 cm TL. Males mature at ~100 cm TL, at ~30 years; females mature at ~120 cm TL, at ~35 years; estimated maximum age 70 years. Occurs in deep water over continental slope, at 229–2 359 m, usually on or near bottom, but has been found in epipelagic and mesopelagic zones, between the surface and ~1 250 m over water to ~3 940 m deep. (One specimen was collected by a spearfisher in water ~4 m deep off east coast of South Africa, but this shark does not normally stray onto the continental shelf.) Feeds on bony fishes, chimaeras, small dogfish sharks, cephalopods and crustaceans. Interest to fisheries limited, mostly taken as a bycatch. IUCN Red List conservation status Endangered globally.

GENUS *Deania* Jordan & Snyder 1902

Body cylindrical or compressed, with fine rough skin and large erect denticles with pitchfork-shaped crowns and 3 sharp cusps. Snout very long (>50% HL) and broad, spatulate in dorsoventral view, and appearing as thin elongated wedge in lateral view. Lip furrows elongated anteriorly as preoral grooves. Teeth without cusplets, similar in both jaws; lower teeth imbricated and somewhat larger than upper teeth; tooth counts 22–36/24–33. Pectoral-fin free rear tip rounded, not angular or attenuated. Two dorsal fins, each with strong grooved spine; 2nd dorsal-fin spine much larger than 1st. Second dorsal fin about as large as, or slightly larger than, 1st dorsal fin, its base ≤⅔ length that of 1st; 2nd dorsal-fin origin about over middle of pelvic-fin bases, with free rear tip reaching caudal-fin origin. No anal fin. Caudal fin with strong subterminal notch. Vertebrae 118–128. Body pale grey or grey-brown to blackish; fins dusky and without conspicuous markings; eyes huge and iridescent green or yellowish. Four species, 3 in WIO.

KEY TO SPECIES

1a Subcaudal keel on underside of peduncle .... ***D. profundorum***



1b No subcaudal keel on peduncle **2**

2a First dorsal fin relatively high, angular and short; distance from spine origin to free rear tip ~⅔ distance from its free rear tip to origin of 2nd dorsal-fin spine .... ***D. quadrispinosa***

2b First dorsal fin relatively low, rounded and long; distance from spine origin to free rear tip greater than distance from its free rear tip to origin of 2nd dorsal-fin spine .... ***D. calceus***

Deania calceus (Lowe 1839)

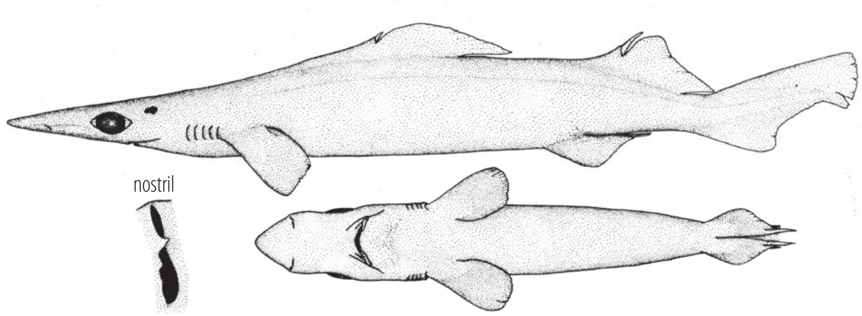
Birdbeak dogfish

PLATE 8

Acanthidium calceus Lowe 1839: 92 (Madeira, North Atlantic).

Deania calcea: Bass *et al.* 1976*; Compagno 1984*; Compagno *et al.* 1989*; Compagno *et al.* 1991; Ebert *et al.* 1992; Compagno *et al.* 2005*; Last & Stevens 2009*; Ebert 2013*; Ebert *et al.* 2013*.

Deania calceus: SSF No. 5.8*.



Deania calceus, 84 cm TL, male (South Africa). Source: Bass *et al.* 1976

Snout extremely long and flattened. First dorsal fin long and low; 2nd dorsal-fin spine much higher than 1st. No subcaudal keel on underside of peduncle. Tooth count 25–35/27–33; vertebrae 118–127.

Body varying from uniformly pale or dark grey or grey-brown to dark brown; fins darker, and fin webs dusky to blackish; juveniles also with darkened dorsal-fin margins, caudal-fin lobes, and areas above eyes and gills. Attains 122 cm TL.

DISTRIBUTION Eastern Atlantic, southeastern and western Pacific, and Indian oceans (patchy). WIO: South Africa and southern Madagascar Ridge.

REMARKS Litters of 6–17; size at birth ~30 cm TL. Males mature at ~80 cm TL, at ~14 years; females mature at ~105 cm TL, at ~22 years; estimated maximum age 35 years. Occurs in deep water over outer continental and insular shelves and upper, middle and lower slopes, on bottom to well above it, at 73–1 471 m. Common, sometimes found in large groups. Diet includes bony fishes, cephalopods and crustaceans. Interest to fisheries moderate, usually taken as a bycatch; used for its meat and squalene-rich liver oil. IUCN Red List conservation status Near Threatened.

Deania profundorum (Smith & Radcliffe 1912)

Arrow-head dogfish PLATE 8

Nasisqualus profundorum Smith & Radcliffe *in* Smith 1912: 681; Pl. 53, Fig. 3 (between Leyte and Mindanao Is., Philippines).
Acanthidium natalense Gilchrist 1922: 49, Pl. 7, Fig. 2 (off Illovo River, KwaZulu-Natal, South Africa).
Deania profundorum: Bass *et al.* 1976*; Compagno 1984*; SSF No. 5.9*; Compagno *et al.* 1989*; Compagno *et al.* 1991; Ebert *et al.* 1992; Compagno *et al.* 2005*; Ebert 2013*; Ebert *et al.* 2013.

Snout long and flattened. First dorsal fin short, moderately high; 2nd dorsal-fin spine higher than 1st dorsal-fin spine. Distinctive subcaudal keel on underside of peduncle.

Body uniformly grey or grey-brown. Attains 97 cm TL.

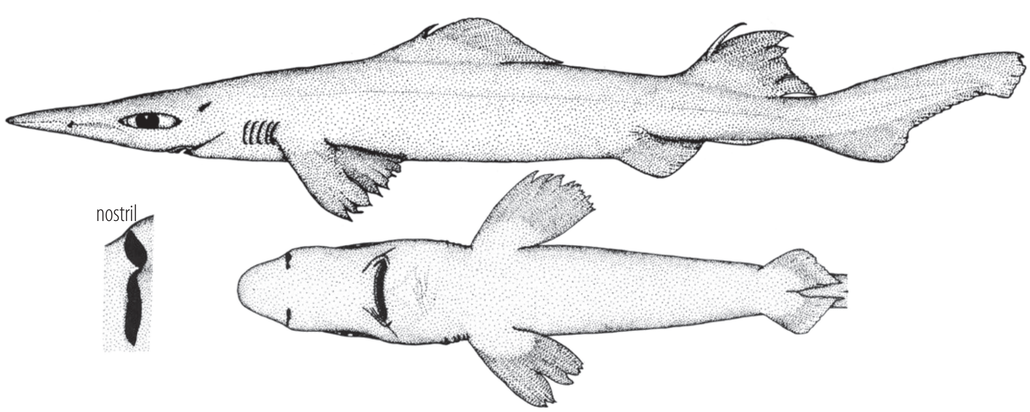
DISTRIBUTION Atlantic, western Pacific (Philippines), and Indian oceans (patchy). WIO: South Africa, southern Madagascar Ridge, Gulf of Aden and India.

REMARKS Litters of 5–7; size at birth ~31 cm TL or more. Males mature at ~43 cm TL, and females at ~60 cm TL. Little-known; occurs in deep water over upper continental and insular slopes, on or near bottom, at 205–1 800 m (Weigmann 2016). Diet includes bony fishes, cephalopods and crustaceans. No interest to fisheries, but taken as bycatch and often caught in huge aggregations.

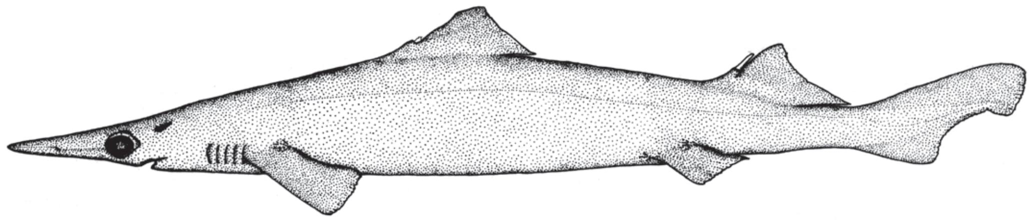
Deania quadrispinosa (McCulloch 1915)

Longsnout dogfish PLATE 8

Acanthidium quadrispinosum McCulloch 1915: 100, Pl. 14, Figs. 5–8 (Great Australian Bight, between Gabo I. and Cape Everhard).
Deania quadrispinosum: Bass *et al.* 1976*; Compagno *et al.* 1989; Compagno *et al.* 1991; Compagno 1999; Ebert 2013*; Ebert *et al.* 2013*.
Deania quadrispinosus: SSF No. 5.10*.
Deania quadrispinosa: Compagno 1984*; Last & Stevens 2009.



Deania profundorum, 33 cm TL, male syntype of *Acanthidium natalense* (South Africa). Source: Bass *et al.* 1976



Deania quadrispinosa, 110 cm TL, female (S Mozambique). Source: Bass *et al.* 1976

Snout extremely long and flattened. First dorsal fin relatively short, moderately high; 2nd dorsal-fin spine much higher than 1st dorsal-fin spine. No subcaudal keel on underside of peduncle. Tooth count 28–33/29–31; vertebrae 118–127.

Body uniformly brown, grey, grey-brown or black; sometimes with white-edged fins. Attains 118 cm TL.

DISTRIBUTION Southeastern Atlantic, western Pacific and Indian oceans. WIO: South Africa (Eastern Cape), southern Mozambique, and seamounts south of Madagascar.

REMARKS Litters of 5–17; size at birth ~24 cm TL. Males mature at ~80 cm TL, and females at ~100 cm TL. Little-known; occurs in deep water over outer continental shelves and slopes, and around seamounts, on or near bottom, at 150–1 360 m. Feeds on bony fishes. Fisheries interest minimal; a discarded bycatch of trawl fisheries off South Africa. IUCN Red List conservation status Near Threatened, because of its limited bathymetric and geographical distribution and its possible vulnerability to overfishing due to low fecundity.

FAMILY ETMOPTERIDAE

Lanternsharks

James DS Knuckey and David A Ebert

Dwarf to medium-sized (often <100 cm TL) with cylindrical to slightly depressed body; snout short or long, flat or conical, and narrow to broadly rounded. Fifth gill slit not much enlarged relative to first 4 slits (although widths may increase slightly from 1st to 5th slits). Mouth varying from broadly arched or U-shaped and elongated to nearly transverse and very short. Teeth similar in both jaws or differentiated between jaws; upper teeth with medial cusp, sometimes flanked by smaller lateral cusplets; lower teeth similar to upper teeth (*Centroscyllium*) or compressed and blade-like with cusp (*Etmopterus*). Dermal denticles small to moderately large, variable in shape, with slender to stout, pointed, wedge-shaped or hooked erect crowns without pedicels, or with low concave sessile crowns. Dorsal fins each with strong grooved spine. First dorsal fin and spine usually smaller than 2nd, its origin varying from opposite pectoral-fin inner margins to somewhat behind their free rear tips. Second dorsal fin falcate or not, its origin often opposite pelvic-fin bases or inner margins. No anal fin. Caudal fin with subterminal notch moderately strong to lacking. Body and fin bases with photophores (light organs), inconspicuous and diffuse or in black patches on ventrolateral surfaces.

Reproductive mode where known is yolk-sac viviparity. Primarily deepwater and bottom-dwelling, at ~70–2 250 m (possibly deeper); a few species are semi-oceanic in epipelagic and mesopelagic zones. Some species form schools. Of little importance to fisheries but often taken as bycatch. Circumglobal in boreal, austral, temperate and tropical seas, mostly in association with landmasses, including continents, continental and oceanic islands, or submarine peaks and ridges.

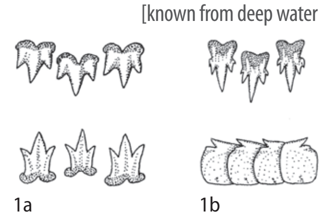
The largest family of Squaliformes, with with 4 genera and >50 species recognised; 2 genera and at least 11 species in WIO (4 of these species from deep water: *Centroscyllium ornatum* [Alcock 1889], *Etmopterus gracilispinis* Krefft 1968, *E. sculptus* Ebert, Compagno & De Vries 2011 and *E. viator* Straube 2011).

KEY TO GENERA

1a Lower teeth similar to upper teeth, not compressed or blade-like, and not overlapping or abutting one another; mouth moderately long and arcuate .... ***Centroscyllium***

1b Lower teeth dissimilar to upper teeth, compressed and blade-like, and with adjacent teeth overlapping or abutting one another; mouth short, nearly straight and transverse .... ***Etmopterus***

[known from deep water in Arabian Sea and Bay of Bengal]



GENUS *Centroscyllium* Müller & Henle 1841

Head broad and flattened, wider than deep. Snout short to moderately long, moderately rounded or slightly pointed; preoral length 0.5–1 mouth width. Teeth similar in both jaws, comb-like, with conical straight cusps and 1 or 2 pairs of cusplets, not compressed and blade-like and not imbricated. Dermal denticles on lateral trunk with bluntly conical, thorn- or bristle-like cusps and stellate bases; denticles usually sparse and well-spaced. First dorsal-fin base much shorter than interdorsal space; 1st dorsal-fin origin usually about opposite or just behind pectoral-fin free rear tips. Second dorsal fin usually larger than 1st. Photophores denser on ventral surface than on dorsal surface or else absent from dorsal surface; usually no conspicuous black photophore patches on underside of head and abdomen or on flanks and tail. Body greyish or blackish brown; fin webs varying from as dark as fin bases to abruptly white or with black and white markings; no naked patch of white skin on edge of upper eyelid. Seven species, 2 in WIO (one of which is only known from deep water).

KEY TO SPECIES

1a Pectoral-fin free rear tips ending well before origin of 1st dorsal-fin spine; 1st dorsal-fin spine lower, about half height of 2nd dorsal-fin spine .... ***C. fabricii***

1b Pectoral-fin free rear tips ending about opposite origin of 1st dorsal-fin spine; 1st dorsal-fin spine very tall, almost as high as 2nd dorsal-fin spine .... ***C. ornatum* [deep water]**

Centroscyllium fabricii (Reinhardt 1825)

Black dogfish PLATE 9

Spinax fabricii Reinhardt 1825: 3 (Julianehåb [Qaqortoq], Greenland, North Atlantic).

Centroscyllium fabricii: Bass *et al.* 1976*; SSF No. 5.5*; Compagno *et al.* 1989*; Compagno *et al.* 1991; Ebert *et al.* 1992; Compagno *et al.* 2005*; Ebert *et al.* 2013*.

Body moderately stout and compressed. Mouth moderately arched; teeth in both jaws with narrow cusps and cusplets. Skin firm; denticles high, conical and sharp-cusped, dense and numerous on dorsal and ventral surfaces. Pectoral-fin apex when laid back ending well before origin of 1st dorsal-fin spine. First dorsal fin low, subtriangular, with low subangular fin web. Second dorsal fin larger than 1st. Dorsal-fin spines grooved; 1st dorsal-fin spine ending below fin apex; 2nd dorsal-fin spine longer than 1st dorsal-fin spine, and extending to below or about height of 2nd dorsal-fin apex. Vertebrae 87–97; spiral valve turns 7–10.

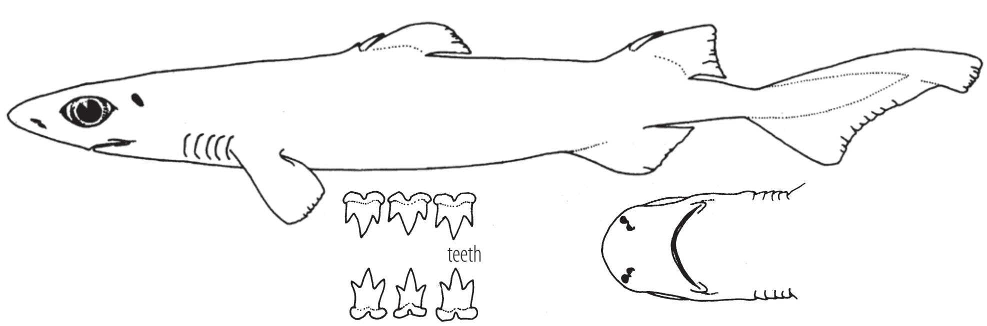
Body uniformly blackish brown, without white markings on fins or discrete black photophores on body. Attains at least 107 cm TL.

DISTRIBUTION Western and eastern North Atlantic, including West Africa and southern Africa, from Orange River mouth (Namibia/South Africa) in southeastern Atlantic, and just rounding Cape Agulhas (South Africa) into WIO.

REMARKS Viviparous with yolk sac; size at birth 15–20 cm TL. Matures at ~46 cm TL. Abundant deepwater schooling shark of outermost continental shelves and slopes, at 180–2 250 m (mostly deeper than 275 m). May move up to near surface, especially during winter and when darkest at night. Feeds primarily on crustaceans, cephalopods, jellyfish and bony fishes. Interest to fisheries limited, commonly taken as a bycatch. IUCN Red List conservation status Least Concern.

GENUS *Etmopterus* Rafinesque 1810

Head broad and flattened, wider than deep; gill slits very short. Snout moderately long, broadly rounded to slightly pointed, flattened or subconical; preoral length 0.9–1.7 mouth width. Teeth strongly differentiated in upper and lower jaws; upper teeth small, not fang-like, with strong, conical, nearly straight cusps, and 1 to several pairs of cusplets; lower-jaw dentition compressed and blade-like, with flattened cusp, no cusplets,

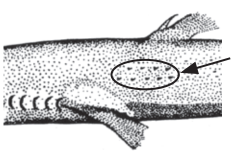


Centroscyllium fabricii, 64 cm TL, female (NW Atlantic).
Source: Bass *et al.* 1976, drawn from Bigelow & Schroeder 1948

and distal blade. Dermal denticles on lateral trunk with thorn- or bristle-like, conical or hooked cusps, or flat, truncate and without cusps; denticles usually closely spaced. First dorsal-fin base much shorter than interdorsal space; 2nd dorsal fin noticeably larger than 1st. Dorsal-fin spines usually large and strongly posteriorly curved; 2nd dorsal-fin spine usually much longer than 1st, its tip extending to 2nd dorsal-fin apex. Photophores denser on ventral surface than on dorsal surface; conspicuous black photophore patches often on underside of head and abdomen, and on flanks and tail, but obscure or absent in some species. Body varying from blackish to tan dorsally, and often black ventrally; fin webs slightly or abruptly paler than fin bases; semicircular or elongated patch of white skin on edge of upper eyelid in some species. At least 37 species; at least 8 species in WIO at depths near 200 m and 3 species from deep water (see family account).

KEY TO SPECIES

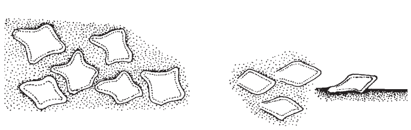
1a Two or 3 longitudinal rows of conspicuous, enlarged thorn-like denticles on flanks above pectoral fins .... ***E. sentosus***



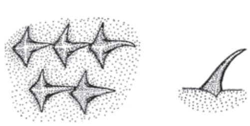
1b No enlarged thorn-like denticles on flanks above pectoral fins 2

2a Skin smooth; dermal denticles with low, flat, concave, sessile crowns atop low bases 3

2b Skin texture 'fuzzy' or rough; dermal denticles with erect, thorn-like, cuspidate crowns, more or less elevated from their bases 4



2a



2b

Continued ...

KEY TO SPECIES

3a Upper tooth cusps stout and thick; lower tooth cusps become erect with growth; 1st dorsal fin more anteriorly set; distance from pectoral-fin insertion to 1st dorsal-fin base >3 in interdorsal space; 1st dorsal-fin spine long and stout, its length equal to or longer than fin base; spiral valve turns 16–19 .... ***E. bigelowi***

3b Upper tooth cusps slender; lower tooth cusps do not become erect with growth; 1st dorsal fin more posteriorly set; distance from pectoral-fin insertion to 1st dorsal-fin base <3 in interdorsal space; 1st dorsal-fin spine short and slender, its length equal to or less than fin base; spiral valve turns 10–13 .... ***E. pusillus***

3a 3b

4a Denticles on flanks, peduncle and caudal fin in regular longitudinal lines .... ***E. granulosus***

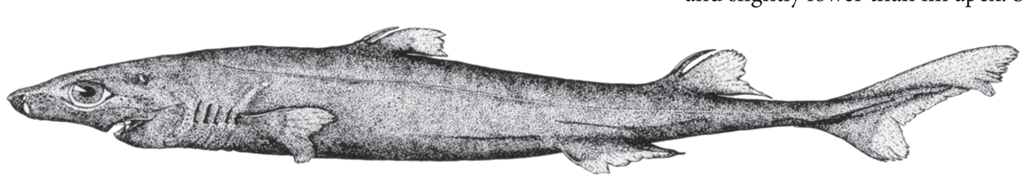
4b Denticles on flanks randomly arranged, not in regular lines .... ***E. compagnoi***

Etmopterus bigelowi Shirai & Tachikawa 1993

Blurred lanternshark

Etmopterus bigelowi Shirai & Tachikawa 1993: 487, Figs. 1b–d, 2b, 5b (off Angola); Compagno *et al*. 2005; Ebert *et al*. 2013*.

Body firm, slightly compressed and slender. Head broad and flattened, width about equal to preoral length. Snout long, broad and spatulate. Upper teeth with 1–3 or occasionally 4 pairs of lateral cusplets, with stout expanded cusps; lower teeth cusps become erect with maturity. Dermal denticles on lateral trunk flat and robust with sessile low crowns (not thorn- or bristle-like), fairly wide-spaced and not overlapping, giving skin smooth texture, and denticles not in regular longitudinal rows; no rows of enlarged denticles on flanks above pectoral fins; denticles on 2nd dorsal fin densely covering fin base but sparse or absent on fin web. First dorsal-fin origin opposite or just behind pectoral-fin free rear tips; 1st dorsal-fin spine stout and slightly lower than fin apex. Second dorsal fin larger than



Etmopterus bigelowi, 46 cm TL, mature male (Angola).
Source: Shirai & Tachikawa 1993

1st, fin apex rounded-angular, and rear margin deeply concave; 2nd dorsal-fin spine stout, with tip posteriorly curved to become diagonally vertical. Caudal fin long. Vertebrae 79–91; spiral valve turns 16–19.

Body dark brown or blackish dorsally, with underside of snout and abdomen grading to black. Flank and caudal photophores inconspicuous; flank photophore base before 2nd dorsal-fin spine, with anterior branch long and broad, and no posterior branch. Attains at least 72 cm TL.

DISTRIBUTION Tropical and subtropical waters of Atlantic and Indo-Pacific. WIO: South Africa (Cape Town to Mossel Bay, and open ocean off KwaZulu-Natal).

REMARKS Viviparous with yolk sac. Males mature at 41–67 cm TL, and females at 50–65 cm TL. Deep water, over continental shelves and slopes, island slopes and submarine ridges, at 163–1 000 m; also partly epipelagic and occurring near surface in open ocean, at 110–700 m. Feeds primarily on fishes and cephalopods. Of no importance to fisheries, although probably a discarded bycatch of commercial fisheries.

Etmopterus compagnoi Fricke & Koch 1990

Brown lanternshark PLATE 9

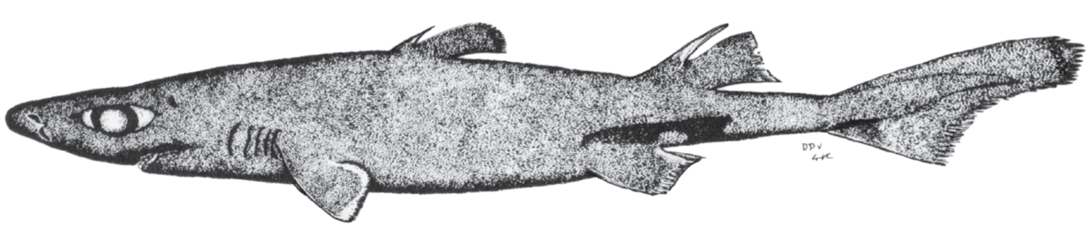
Etmopterus compagnoi Fricke & Koch 1990: 2, Figs. 1–2 (off Cape Town, South Africa); Ebert *et al*. 2013*.
Etmopterus spinax: Gilchrist 1922; Barnard 1925, 1947*; Smith 1949*; Compagno 1984*.
Etmopterus gracilispinis: Karrer 1973; Compagno 1984*; Compagno *et al*. 1989; Compagno *et al*. 1991; Ebert *et al*. 1992.
Etmopterus sp.: SSF No. 5.16*.
Etmopterus unicolor: Compagno *et al*. 2005*.

Body moderately firm, cylindrical, heavy and stout. Head broad and flattened, width about 1.1–1.3 preoral length; snout thick but broadly spatulate, not bulbous. Upper teeth generally with 1 or 2 pairs of cusplets, and expanded cusps. Denticles on 2nd dorsal fin densely covering base; lateral trunk denticles slender, close-set, and with very slender, hooked, conical crowns, giving skin velvety texture. First dorsal-fin origin well behind pectoral-fin free rear tips; 1st dorsal-fin spine stout and usually lower than fin apex. Second dorsal fin larger than 1st, fin apex more or less pointed or rounded-angular, and rear margin broadly concave; 2nd dorsal-fin spine stout with tip posteriorly curved. Caudal fin short. Vertebrae 82–90; spiral valve turns 9–12.

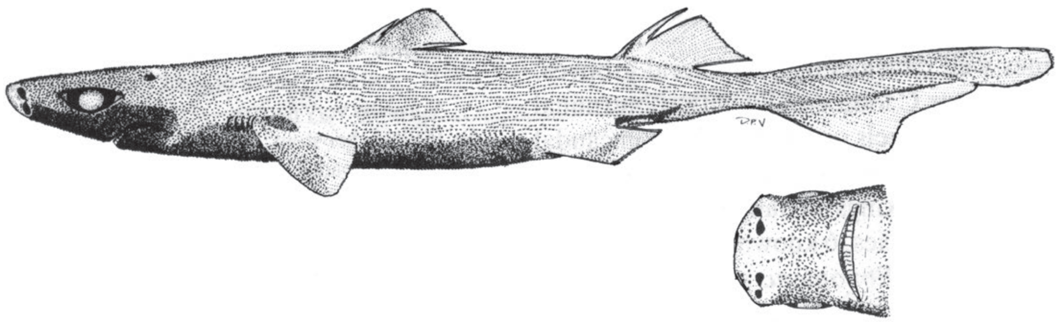
Body dark grey, dark brown or grey-brown dorsally; underside of snout and abdomen grading to blackish brown; flanks above and behind pelvic fins and underside of caudal fin with indistinct darker markings. Photophores on flank and caudal area inconspicuous, photophore base mostly behind 2nd dorsal-fin spine, with anterior branch long and slender, and longer than posterior branch. Attains 79 cm TL.

DISTRIBUTION Subtropical waters of southeastern Atlantic and Western Indian Ocean. WIO: South Africa (Western Cape to KwaZulu-Natal).

REMARKS Viviparous with yolk sac; litters of 2–21 (average 12); size at birth ~17 cm TL. Males mature at 48–68 cm TL, and females at 53–79 cm TL. Occurs in deep water over continental and insular slopes, often on bottom but sometimes well off it, at 465–1 500 m; has also been caught in epipelagic zone of open ocean in 120 m. Broadly sympatric with larger *E. granulosus*, with which it has been caught in experimental trawls on slopes off South Africa, at 383–1 300 m. Feeds on cephalopods, penaeid shrimp and fishes. Limited or no interest to fisheries, although probably an incidental bycatch of deepwater trawl fisheries.



Etmopterus compagnoi, 32 cm TL, male (South Africa). Source: SSF



Etmopterus granulosus, 31 cm TL, male holotype (Chile). Source: SSF

Etmopterus granulosus (Günther 1880)

Southern lanternshark PLATE 9

Spinax granulosus Günther 1880: 19, Pl. 2c (SW coast of South America).
Etmopterus baxteri: Compagno *et al*. 2005*.
Etmopterus granulosus: Bass *et al.* 1976*; SSF No. 5.12*; Compagno *et al.* 1989*; Compagno *et al*. 1991; Ebert *et al*. 1992; Ebert 2013*; Ebert *et al*. 2013*.

Body moderately large, firm and slightly compressed. Head broad and flattened, width greater than preoral length. Gill slits very small. Upper teeth with medial cusp and 2 or 3 pairs of lateral cusplets. No rows of enlarged dermal denticles on flanks above pectoral fins; denticles in regular longitudinal rows on peduncle, caudal fin and sometimes flanks, but no denticles on head and 2nd dorsal fin; lateral trunk denticles large and robust, with low-hooked, stout, conical crowns, and wide-spaced, giving skin very rough texture. First dorsal-fin origin well behind pectoral-fin free rear tips; 1st dorsal-fin spine stout and usually lower than fin apex. Second dorsal fin much larger than 1st, fin apex rounded-truncated, rear margin shallowly concave; 2nd dorsal-fin spine stout with tip posteriorly curved to become horizontal in adults. Caudal fin short. Vertebrae 86–94; spiral valve turns 9–13.

Body dark brown or blackish, with underside of snout and abdomen blackish, but dorsal surface not conspicuously paler than ventral surface. Flank and caudal photophores inconspicuous; flank photophore base well forward of 2nd dorsal-fin spine, with anterior branch elongated and narrow, much longer than posterior branch. Attains 88 cm TL.

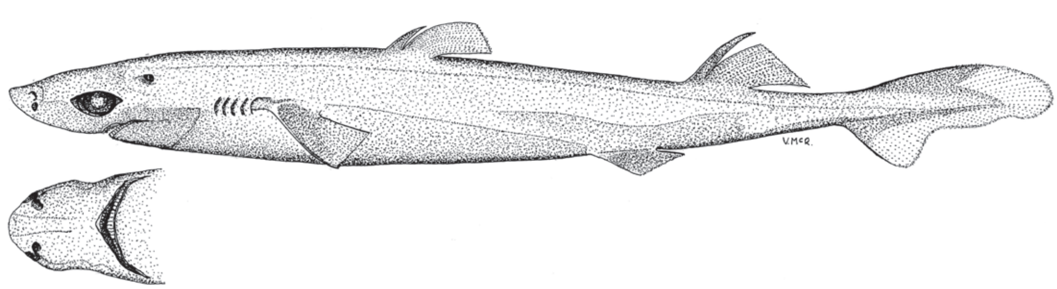
DISTRIBUTION Southeastern Pacific to southwestern Atlantic (Chile to Argentina), and Indian Ocean. WIO: South Africa (Western Cape to Eastern Cape), Madagascar Ridge (south of Madagascar); elsewhere near Marion I. (sub-Antarctic Indian Ocean).

REMARKS Viviparous with yolk sac; litters of 6–16; size at birth 16–17 cm TL. May breed all year long. Males mature at 46–68 cm TL, at ~20 years; females mature at 75–86 cm TL, at ~30 years; maximum estimated ages 48 and 57 years for males and females, respectively. Common to abundant in deep water over upper continental and insular slopes, on or near bottom, at 220–1 500 m (Weigmann 2016) (mostly deeper than 600 m). Feeds primarily on cephalopods, crustaceans and other invertebrates, and bony fishes. Of minor interest to fisheries. IUCN Red List conservation status Least Concern, although deepwater trawl and line fisheries occur in its range and habitat.

Etmopterus pusillus (Lowe 1839)

Smooth lanternshark PLATE 10

Acanthidium pusillum Lowe 1839: 91 (Madeira, North Atlantic).
Etmopterus pusillus: Bass *et al.* 1976*; SSF No. 5.14*; Compagno *et al*. 1989*; Compagno *et al*. 1991; Ebert *et al*. 1992; Compagno *et al*. 2005*; Ebert *et al*. 2013*.



Etmopterus pusillus, 33 cm TL, female (South Africa). Source: SSF

Body moderately firm, slightly compressed, and moderately slender. Head moderately broad and flattened, not deep and conical; head width 0.9–1.4 preoral length; snout flattened and broadly rounded, not bulbous. Upper teeth generally with 1 or 2 pairs of cusplets, with slender cusps. Dermal denticles on lateral trunk flat and robust, close-set but not overlapping, with sessile low crowns (not thorn- or bristle-like), giving skin smooth texture, and denticles not in regular longitudinal rows; no rows of enlarged dermal denticles on flanks above pectoral fins; denticles on 2nd dorsal fin densely covering base but absent from rear margin. First dorsal-fin origin just behind pectoral-fin free rear tips; 1st dorsal-fin spine slender, short and usually lower than fin apex. Second dorsal fin much larger than 1st, fin apex more or less pointed or narrowly rounded, rear margin usually deeply concave; 2nd dorsal-fin spine stout with tip posteriorly curved to become diagonally vertical. Caudal fin long. Vertebrae 82–88; spiral valve turns 10–13.

Body pale or dark brown to blackish dorsally; ventral surface conspicuously darker, and underside of snout and abdomen abruptly black. Flank and caudal photophores inconspicuous; flank photophore base opposite and behind 2nd dorsal-fin spine, with anterior branch long and broad, and no posterior branch. Attains 50 cm TL.

DISTRIBUTION Tropical and subtropical waters of Atlantic and Indo-Pacific. WIO: Mozambique, South Africa (KwaZulu-Natal) and Sapmer Seamount.

REMARKS Viviparous with yolk sac; litters of 1–6. Males mature at 31–48 cm TL, at 5–9 years; females mature at 38–50 cm TL, at 8–11 years. Size at maturity may vary regionally. Found on continental slopes, submarine ridges and seamounts, on or near bottom, at 0–1 500 m (Weigmann 2016). Consumes primarily fish eggs, fishes and other small dogfish sharks, and squid. Interest to fisheries limited, but often captured as a bycatch.

Etmopterus sentosus

Bass, D'Aubrey & Kistnasamy 1976

Thorny lanternshark

PLATE 11

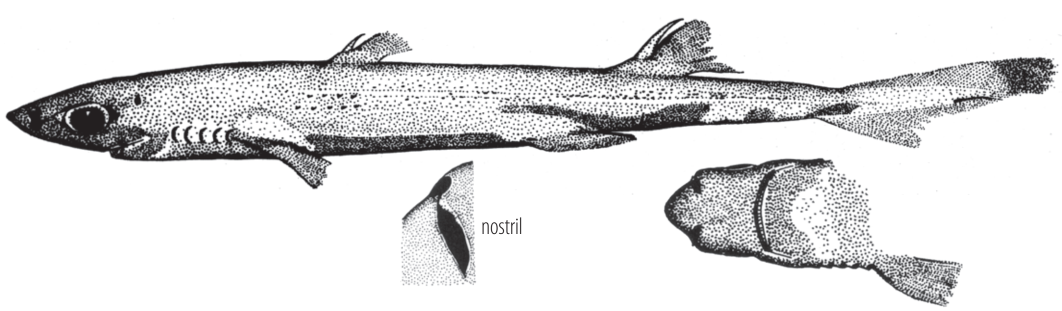
Etmopterus sentosus Bass, D'Aubrey & Kistnasamy 1976: 22, Figs. 15, 18a (southern Mozambique); SSF No. 5.15*; Compagno *et al.* 1989*; Compagno *et al.* 2005*; Ebert *et al.* 2013*.

Body small, moderately firm, cylindrical, not compressed, and slender. Head somewhat depressed, flattened and subconical; head width ~2.4 preoral length; snout flattened-conical, not bulbous. Upper teeth generally with 2–4 pairs of cusplets, with cusps greatly expanded. Two or 3 horizontal rows of greatly enlarged hook-like denticles on flanks above and slightly behind pectoral fins. Denticles on head not in longitudinal rows, but denticles on flanks and tail arranged in regular or semi-regular longitudinal rows; scattered denticles on base of 2nd dorsal fin. First dorsal-fin origin over pectoral-fin inner margins; 1st dorsal-fin spine stout, lower than fin apex. Second dorsal fin much larger than 1st, fin apex rounded-angular, and rear margin deeply concave; 2nd dorsal-fin spine stout with tip posteriorly curved to become diagonally vertical. Vertebrae 83; spiral valve turns 8 or 9.

Body greyish above and below, dorsal surface paler but ventral surface not conspicuously dark, except underside of snout and abdomen blackish; caudal-fin tip with conspicuous black bar. Flank and caudal photophores conspicuous; flank photophore base just behind 2nd dorsal-fin spine, with anterior branch long and broad, much longer than posterior branch. Attains 27 cm TL.

DISTRIBUTION WIO: Kenya to South Africa (KwaZulu-Natal) and Madagascar (off Toliara).

REMARKS Viviparous with yolk sac. Males mature at 22–27 cm TL, and females at 25–27 cm TL. Little known, dwarf-sized; found in deep water at or near bottom, at 200–500 m. No interest to fisheries but apparently caught as a bycatch. IUCN Red List conservation status Least Concern, although bottom-trawl fisheries occur in its range.



Etmopterus sentosus, 27 cm TL, male holotype (S Mozambique).
Source: Bass *et al.* 1976

FAMILY SOMNIOSIDAE

Sleeper sharks

Jenny M Kemper and David A Ebert

Small-sized to gigantic (a few >6 m TL, but most <170 cm TL) with moderately broad head and short to long, flattened snout; trunk cylindrical or slightly compressed, and abdomen often with lateral ridges. Spiracles large and close behind eyes. Nostrils wide-spaced (internarial width greater than nostril width) and with simple anterior nasal flaps. Mouth short, nearly transverse, with thin lips; lip furrows short to greatly elongated, encircling mouth or not. Upper teeth small, lanceolate, high-crowned, needle-like, and with narrow erect to semi-oblique cusps and no cusplets or blades; lower teeth large, compressed, high-crowned, narrow and blade-like, with compressed erect to oblique cusp, a distal blade, and no cusplets. Dermal denticles moderate-sized and pedicellate, with flattened, narrow to broad-keeled or smooth leaf-shaped, round or narrow thorn-like crowns, slender pedicels and low bases. Two small, broad dorsal fins, with or without spines; 1st dorsal-fin origin anterior to pelvic-fin origins; 2nd dorsal fin smaller than or subequal to 1st, its origin over to slightly anterior to pelvic-fin insertions; interdorsal space greater than length of 1st dorsal-fin base. Pectoral fins low, angular or rounded, not falcate, and free rear tips rounded and short. Pelvic fins subequal to or larger than pectoral fins and 1st dorsal fin, and subequal to or smaller than 2nd dorsal fin. No anal fin. Peduncle slightly compressed, short to moderately elongated. Caudal fin heterocercal, lower lobe weakly to strongly developed in adults, with strong subterminal notch. Body without photophores (light organs).

Reproductive mode yolk-sac viviparity, with litters of 4–59 pups. Diet includes bony fishes, chondrichthyans, cephalopods and other molluscs, crustaceans, seals, whale meat, carrion, sea birds, echinoderms and jellyfish. Targeted and taken as a bycatch in deepwater shark fisheries and caught by line gear and trawls; used for human consumption, fishmeal, and their squalene-rich liver oil. Mainly deepwater and bottom-dwelling, on continental and insular slopes, but also on submarine ridges and seamounts, at ~200–3 675 m (possibly deeper), but mainly <1 500 m. Some species are oceanic. Circumglobal in most seas, including polar to tropical regions. Seven genera and 17 species; 5 genera and 6 species in WIO.

KEY TO GENERA

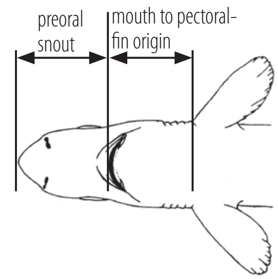
1a Dorsal fins with spines, although sometimes partially or wholly covered by skin 2

1b No dorsal-fin spines .... *Somniosus*

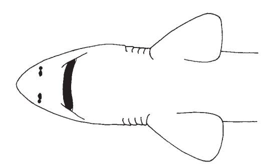
Continued …

KEY TO GENERA

2a Snout greatly elongated, preoral length about equal to distance from mouth to pectoral-fin origins; upper lip furrows greatly elongated, their length greater than distance between their anterior ends .... *Centroselachus*

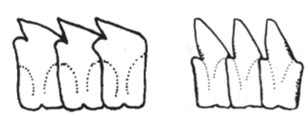


2b Snout shorter, preoral length much less than distance from mouth to pectoral-fin origins; upper lip furrows short, their length less than distance between their anterior ends 3



3a Lower teeth with relatively low and more-or-less oblique cusps 4

3b Lower teeth with relatively high and more-or-less erect cusps .... *Zameus*



3a 3b

4a Dorsal-fin spines inconspicuous, tips barely or not protruding; pectoral fins small, body not tapering beyond pectoral fins; pectoral-fin apex when laid back falling well ahead of 1st dorsal-fin spine............ *Centroscymnus*

4b Dorsal-fin spines fairly stout, tips prominent; pectoral fins large, body strongly tapering beyond pectoral fins; pectoral-fin apex when laid back approximately reaches 1st dorsal-fin spine .... *Scymnodon*

GENUS *Centroscymnus*

Barbosa du Bocage & De Brito Capello 1864

Snout flattened, short to moderately long; preoral length varying from about equal to much less than distance from mouth to pectoral-fin origins. Body not tapering beyond pectoral fins. Anterior nasal flaps short; lips thick but not pleated or suctorial. Upper teeth very slender, with acute cusps; lower teeth blade-like, interlocked, with short oblique cusps and distal blades. Dermal denticles with low, pedicellate, flat, ovoid crowns, varying from triple-ridged and tricuspid to smooth and acuspidate in adults, and triple-ridged and tricuspidate in young. Dorsal fins each with small inconspicuous spine, sometimes covered with skin. First dorsal-fin origin varying from over pectoral-fin bases to behind their free rear tips; 1st dorsal-fin insertion anterior to pelvic-fin origins and closer to pectoral- than to pelvic-fin bases. Second dorsal fin as large as or slightly smaller than 1st, its origin about over middle of pelvic-fin bases. Pectoral-fin free rear tips short, broadly rounded; fin apex when laid back not reaching 1st dorsal-fin spine. Caudal fin asymmetric, upper lobe long and lower lobe short but well-developed, with strong subterminal notch. Two species, both in WIO.

KEY TO SPECIES

1a Snout short, preoral length ~⅔ distance from mouth to 1st gill slit and less than mouth width; abdomen without lateral ridges .... ***C. coelolepis***

1b Snout moderately long, preoral length about equal to distance from mouth to 1st gill slit and about equal to mouth width; abdomen with lateral ridges .... ***C. owstonii***

Centroscymnus coelolepis

Barbosa du Bocage & De Brito Capello 1864

Portuguese dogfish

PLATE 11

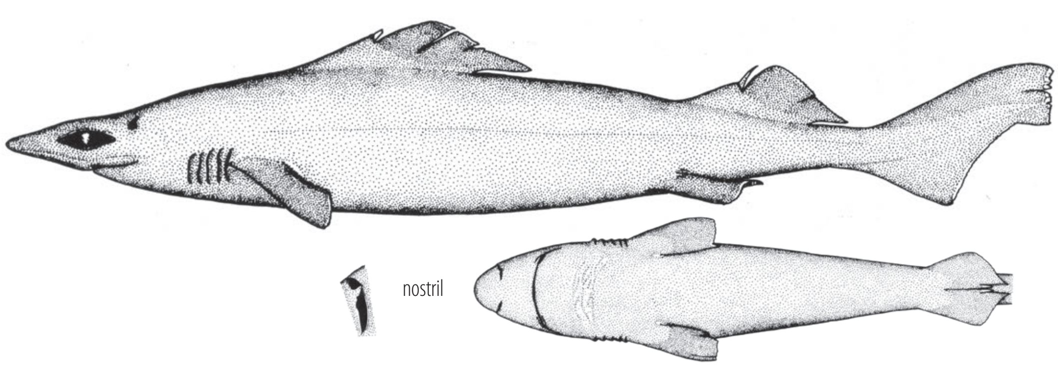
Centroscymnus coelolepis Barbosa du Bocage & De Brito Capello 1864: 263, Fig. 4 (Portugal, North Atlantic); Compagno 1984*; Compagno *et al.* 1989*; Compagno *et al.* 1991; Ebert *et al.* 1992; Last & Stevens 2009*; Ebert 2013*; Ebert *et al.* 2013*.
Centroscymnus fuscus Gilchrist & Von Bonde 1924: 2 (off St Helena Bay, South Africa, SE Atlantic); Barnard 1925; Smith 1949, 1965.
Scymnodon melas Bigelow, Schroeder & Springer 1953: 233, Fig. 5 (off Georges Bank, North Atlantic); Krefft & Tortonese 1973; Compagno 1984; McEachran & Branstetter *in* Whitehead *et al.* 1984; Castro 2011.
Centrophorus squamosus: Hulley 1971*; Bass *et al.* 1976*.
Centroscymnus macrops Hu & Li *in* Chu *et al.* 1982: 305, Fig. 4 (South China Sea); Compagno 1984; White & Last 2013.

Body stout, not strongly tapering after pectoral fins. Snout short, preoral length much less than distance from mouth to 1st gill slit and less than mouth width; lip furrows very short. Upper teeth lanceolate; lower teeth blade-like, with short oblique cusps. Dermal denticles on lateral trunk large, with smooth circular acuspidate crowns in adults and subadults. Dorsal fins about equal in size and height; each fin with very small spine with tip protruding. First dorsal-fin base not extending forward as prominent ridge; fin origin behind pectoral fins. Second dorsal-fin base shorter than space between fin insertion and upper caudal origin; free rear tip well in front of upper caudal origin. Pectoral fins moderately large; fin apex when laid back not reaching 1st dorsal-fin spine. Pelvic-fin rear tips extend beyond 2nd dorsal-fin insertion. Tooth count 43–68/29–42; vertebrae 102–114; spiral valve turns 16–21.

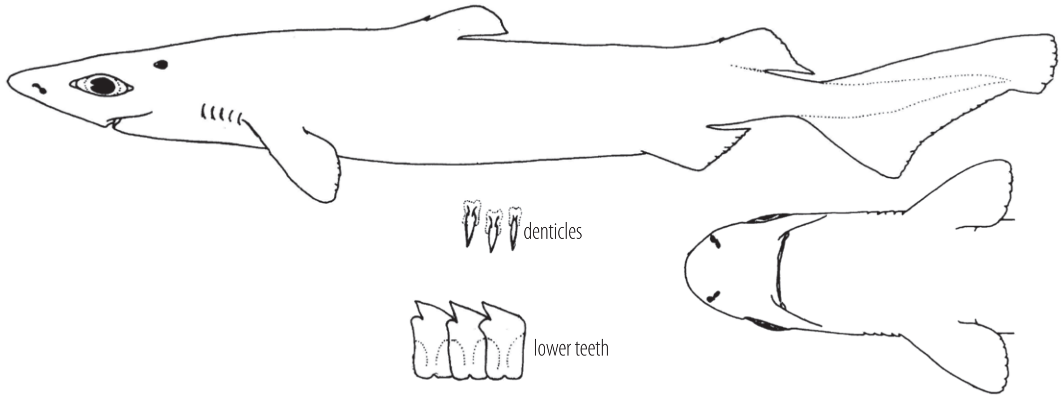
Body uniformly pale to blackish or golden brown. Attains 122 cm TL.

DISTRIBUTION Atlantic and Indo-Pacific (widespread). WIO: South Africa (Eastern Cape) and submarine seamounts, including Madagascar Ridge (south of Madagascar) and southern East Indian range (between Africa and Australia).

REMARKS Litters of 1–29 (mostly 12–14); size at birth 30–35 cm TL. Males mature at ~85 cm TL, and females at ~100 cm TL. Appears to be depth-segregated by size, sex and stage of maturity. Common on or near bottom on continental slopes and upper and middle rises, at 128–3 675 m (commonly >400 m). Prey includes bony fishes, other sharks, benthic invertebrates, and cetacean and seal meat. Limited interest to fisheries; caught by bottom trawls, fixed nets and line gear in targeted deepwater shark fisheries and as bycatch in other deepwater demersal fisheries. IUCN Red List conservation status Near Threatened globally.



Centroscymnus coelolepis, 93 cm TL, male (South Africa). Source: Bass *et al.* 1976



Centroscymnus owstonii, 58 cm TL, female (New Zealand).
Source: Bass *et al.* 1976

Centroscymnus owstonii Garman 1906

Roughskin dogfish

PLATE 11

Centroscymnus owstonii Garman 1906: 207 (Sagami Bay, Japan); Garman 1913*; Compagno 1984*; Anderson *et al.* 1998; Last & Stevens 2009*; Ebert 2013; Ebert *et al.* 2013*.
Centroscymnus cryptacanthus Regan 1906: 437 (Madeira, eastern Atlantic).

Body stout, not strongly tapering after pectoral fins. Snout moderately long, preoral length about equal to distance from mouth to 1st gill slit. Upper lip furrows very short. Upper teeth lanceolate; lower teeth blade-like. Dorsal fins each with spine covered by skin or tip barely exposed. Dermal denticles on lateral trunk large, with mostly smooth, circular, cuspidate and acuspidate crowns in adults. First dorsal fin long and low; fin origin over or behind pectoral-fin bases. Second dorsal fin taller than 1st. Pectoral fins moderately large; fin apex when laid back falling before 1st dorsal-fin spine. Pelvic-fin rear tips below or slightly before 2nd dorsal-fin insertion. Tooth count 36–39/32–40; vertebrae 96–114.

Body pale grey or brown to dark brown or black. Attains 120 cm TL.

DISTRIBUTION Atlantic and Indo-Pacific. WIO: South Africa (southern portion of Western Cape) and Madagascar.

REMARKS Litter size unknown, but 34 eggs have been observed in a female; size at birth ~30 cm TL. Males mature at 70–84 cm TL, and females at 100–104 cm TL. Found on outer continental shelves and upper continental slopes, on or near bottom, at ~150–1 500 m (commonly deeper than 600 m), sometimes in schools. Prey includes bony fishes and cephalopods. Limited and localised interest to fisheries, mainly as a bycatch.

GENUS *Centroselachus* Garman 1913

Moderately sized, fairly slender with body not strongly tapering beyond pectoral fins. Snout greatly elongated; preoral length about equal to distance from mouth to pectoral-fin origins. Lips not thick and fleshy; upper lip furrows very long, their length greater than distance between their anterior ends. Lower teeth with moderately long and semi-oblique cusps, and moderately high and fairly broad roots; upper teeth lanceolate. Dermal denticles on lateral trunk moderately large, with anteriorly smooth but posteriorly ridged, oval cuspidate crowns. Dorsal fins about equal in size and height; each with very small spine with tip protruding. First dorsal-fin base extends forward as prominent ridge; fin origin over pectoral-fin bases. Second dorsal-fin base longer than space between fin insertion and upper caudal origin; free rear tip nearly reaching upper caudal origin. Pectoral fins moderately large; fin apex when laid back not reaching 1st dorsal-fin spine. Pelvic-fin rear tips extend to about opposite 2nd dorsal-fin insertion. Tooth count 36–51/30–36; vertebrae 105–119. One species.

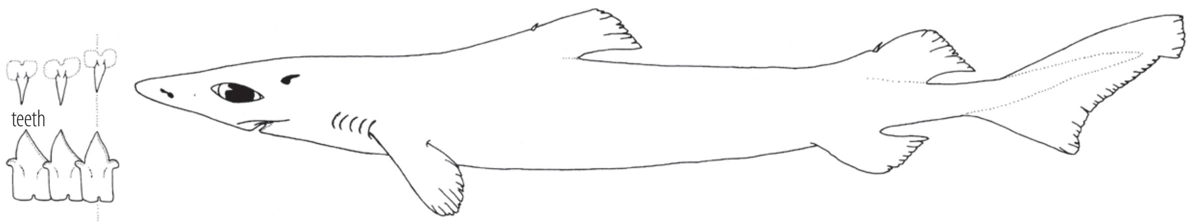
Centroselachus crepidater

(Barbosa du Bocage & De Brito Capello 1864)

Longnose velvet dogfish

PLATE 12

Centrophorus crepidater Barbosa du Bocage & De Brito Capello 1864: 262, Fig. 3 [Portugal, North Atlantic].
Centrophorus rossi Alcock 1898: 143 (off Travancore coast, India).
Centrophorus jonssonii Saemundsson 1922: 192, Pl. 5, Figs. 1–2 (Iceland, North Atlantic).
Centroscymnus furvescens De Buen 1960: 20, Fig. 7 (off Valparaíso, Chile).
Centroscymnus crepidater: Bass *et al.* 1976; Compagno 1984*; SSF No. 5.6*; Compagno *et al.* 1989*; Compagno *et al.* 1991; Ebert *et al.* 1992.
Centroselachus crepidater: Compagno *et al.* 2005*; Irvine *et al.* 2006; Last & Stevens 2009*; Ebert 2013*; Ebert *et al.* 2013*; Ebert & Stehmann 2013*; White *et al.* 2014.



Centroselachus crepidater, 90 cm TL, female (New Zealand). Source: Bass *et al.* 1976, drawn from Garrick 1959

Diagnosis as for genus. Snout very long; lip furrows nearly encircling small mouth. First dorsal-fin base extends forward as prominent ridge.

Body black or blackish brown, with narrow paler fin margins. Attains 105 cm TL.

DISTRIBUTION Eastern Atlantic and Indo-Pacific. WIO: South Africa, seamounts of the Madagascar Ridge (south of Madagascar), Aldabra Is., Seychelles and India (Travancore coast).

REMARKS Formerly placed in genus *Centroscymnus*. Litters of 1–9; size at birth 28–35 cm TL. Males mature at 60–68 cm TL, and females at 77–82 cm TL. Found on upper continental and insular slopes, on or near bottom, at 200–1 500 m (mainly below 500 m). Prey includes bony fishes and cephalopods. Limited interest to fisheries; taken as a bycatch in bottom trawls.

GENUS *Scymnodon*

Barbosa du Bocage & De Brito Capello 1864

Body robust, fusiform, and tapering after pectoral fins. Snout short to moderately long. Upper lip furrows very short. Lower teeth with short oblique cusps, and moderately high and fairly broad roots. Dermal denticles on lateral trunk large, with triple ridges and cusps. Dorsal fins subequal or 2nd slightly higher than 1st; each fin with small but prominent spine. Second dorsal-fin base about as long as space between fin insertion and upper caudal origin; free rear tip well in front of upper caudal origin. Pectoral fins large; fin apex when laid back nearly reaching 1st dorsal-fin spine. Pelvic-fin rear tips fall well in front of 2nd dorsal-fin insertion. Four species, 1 in WIO.

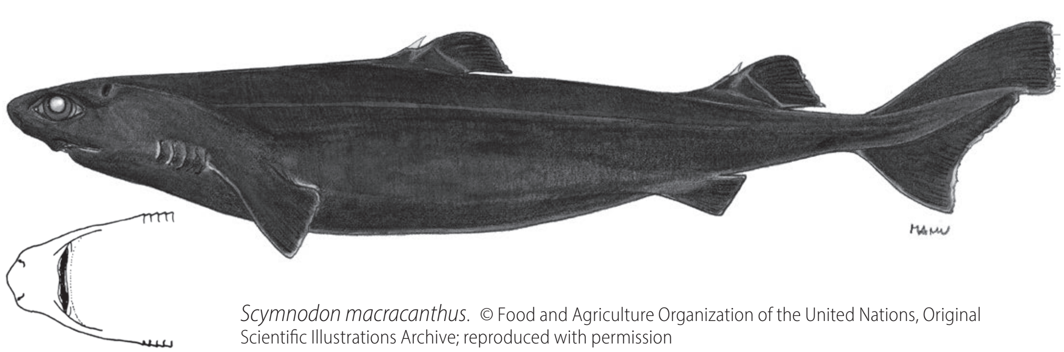
Scymnodon macracanthus (Regan 1906)

Largespine velvet dogfish PLATE 12

Centroscymnus macracanthus Regan 1906: 436 (Strait of Magellan).
Centrophorus plunketi Waite 1910: 384, Pl. 37 (South Island, New Zealand); Compagno 1984*.
Centroscymnus plunketi: Compagno 1984*.
Proscymnodon plunketi: Compagno *et al.* 2005*; Last & Stevens 2009*; Ebert 2013*; Ebert *et al.* 2013*.
Scymnodon plunketi: White *et al.* 2015*.
Scymnodon macracanthus: Weigmann 2016.

Large-bodied with very short snout. Upper teeth lanceolate and dagger-like; lower teeth with short oblique cusps. Dermal denticles on lateral trunk moderately large. Dorsal fins about equal in size and height; each fin with very small spine with tip slightly protruding. First dorsal-fin base extends forward as prominent ridge; fin origin behind pectoral fins. Pectoral fins moderately large. Tooth count 48/32–35; vertebrae 114–115.

Body uniformly dark grey-brown. Attains 170 cm TL.



Scymnodon macracanthus. © Food and Agriculture Organization of the United Nations, Original Scientific Illustrations Archive; reproduced with permission

DISTRIBUTION Southwestern Atlantic and Indo-Pacific. WIO: Madagascar Ridge and Melville Ridge (south of Madagascar).

REMARKS Litters of up to 36; size at birth 32–36 cm TL. Males mature at 100–131 cm TL, and females at 129–170 cm TL. Inhabits continental and insular slopes of temperate seas, near bottom, at 219–1 550 m (commonly 550–732 m). Occurs in large schools, segregated by size and sex. Prey includes bony fishes and cephalopods. Caught by longlines and demersal trawls; discarded or utilised. IUCN Red List conservation status Near Threatened.

GENUS *Somniosus* Le Sueur 1818

Moderately large-sized to gigantic with snout short to fairly long, broadly rounded to pointed, and somewhat flattened. Anterior nasal flaps short; lips thin, and not fringed, pleated or suctorial. Upper teeth small, with narrow, acute, erect cusps; lower teeth much larger, blade-like, interlocked, with low to moderately high oblique or semi-erect cusps and distal blade, edges serrated or not. Dermal denticles with oblique to erect, hooked, cuspidate narrow crowns. Dorsal fins spineless; 1st dorsal fin set on midback and behind pectoral fins, its insertion before pelvic-fin origins; 2nd dorsal fin slightly smaller than 1st, its origin over front half of pelvic-fin bases to posterior of their rear tips. Pectoral fins with short, narrowly to broadly rounded free rear tips and inner margins. Caudal fin semi-symmetrical and paddle-shaped, with relatively short upper lobe and long lower lobe, and strong subterminal notch.
Five species, 1 in WIO.

Somniosus antarcticus Whitley 1939

Southern sleeper shark PLATE 12

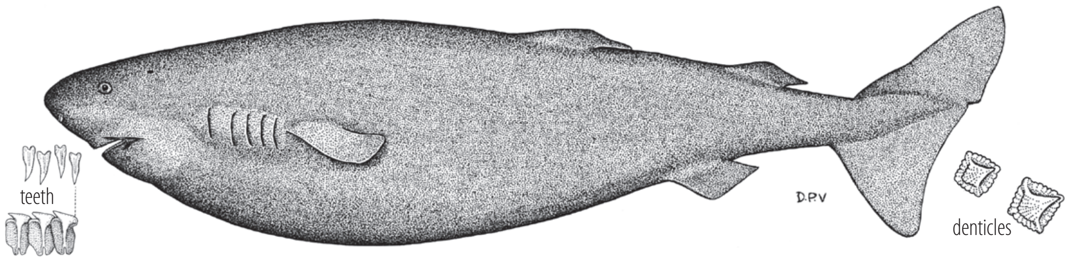
Somniosus antarcticus Whitley 1939: 242 (Macquarie I., south of Tasmania); Yano *et al.* 2004*, 2007; Compagno *et al.* 2005*; Murray *et al.* 2008; Last & Stevens 2009*; Ebert 2013; Ebert *et al*. 2013.
Somniosus microcephalus: Bass *et al.* 1976*; Duhamel & Hureau 1982; Compagno 1984*; Duhamel & Compagno 1985; Gushchin *et al.* 1986; Compagno *et al*. 1989; Compagno 1990*.

Gigantic, heavy cylindrical body; snout short, rounded; precaudal fins very small. Upper teeth lanceolate; lower teeth with short, low, strongly oblique cusps. Dermal denticles on lateral trunk with narrow erect crowns and hooked cusps, giving skin rough texture. Equal-sized dorsal fins; 1st dorsal fin very low, slightly closer to pelvic fins than to pectoral fins; interdorsal space greater than distance from snout to 2nd gill slit. Peduncle short, with lateral keels. Tooth count 37–48/ 49–59; vertebrae 36–38; spiral valve turns 36–41.

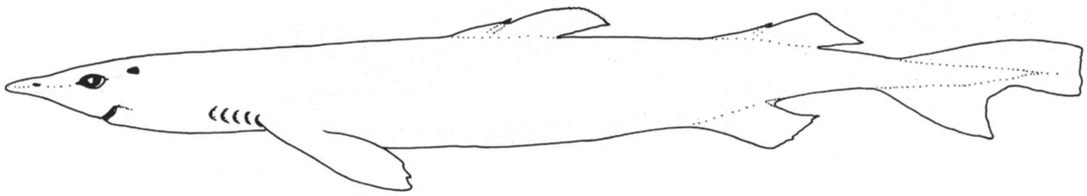
Body uniformly grey to pinkish. Attains ~6 m TL.

DISTRIBUTION Southern Ocean to Antarctica, and spotty records from southernmost Indian Ocean. WIO: Madagascar Ridge (south of Madagascar), South Africa and Kerguélen Is. and Heard I. (between Madagascar and Antarctica).

REMARKS Size at birth ~40 cm TL; males mature at ~4 m TL, and females at ~4.3 m TL. Coastal and epibenthic, on continental and insular shelves and upper slopes, to ~1 440 m deep. Prey includes fishes, pinnipeds, cetaceans and cephalopods. Not commercially important, but taken as a bycatch in trawl and longline fisheries.



Somniosus antarcticus, 4.4 m TL, female (South Africa). Source: FSO



Zameus squamulosus, 59 cm TL, female (NW Africa). Source: Bass *et al.* 1976 (drawn from Vaillant 1888)

GENUS ***Zameus*** Jordan & Fowler 1903

Small- to moderate-sized and slender, with low flattened head, and long to short but narrow snout. Eyes moderately large. Mouth short, narrow, transverse; upper lip furrows short. Upper teeth small and spear-like; lower teeth larger, highly erect, and knife-like. Dermal denticles on lateral trunk with or without tricuspid ridges. First dorsal-fin spine relatively large; 2nd dorsal-fin spine slightly shorter than 1st; length of 1st dorsal-fin base greater than 2nd. Pectoral fins small, narrow to moderately broad, leaf-shaped to round. Pelvic fins small, subequal to 2nd dorsal fin. Peduncle long; length of 2nd dorsal-fin base about equal to distance from fin insertion to upper caudal origin. Caudal fin with strong subterminal notch and short lower lobe. Tooth count 42–60/28–38; vertebrae 93–105; spiral valve turns 12–16. One species. The only bioluminescent sleeper shark known at present.

Zameus squamulosus (Günther 1877)

Velvet dogfish PLATE 12

Centrophorus squamulosus Günther 1877: 433 (off Enoshima, Japan).
Centroscymnus obscurus: Vaillant 1888; SSF No. 5.7*.
Scymnodon ?obscurus: Bass *et al.* 1976*
Scymnodon obscurus: Compagno 1984*.
Scymnodon niger: Chu & Meng 1982.
Scymnodon squamulosus: Compagno *et al.* 1989*; Compagno *et al.* 1991; Ebert *et al.* 1992.
Zameus squamulosus: Compagno *et al.* 2005; Last & Stevens 2009*; Ebert 2013*; Ebert *et al.* 2013*; White *et al.* 2015.

Small-sized, slender-bodied, with fairly long, narrow snout, and post-oral grooves very long, much longer than upper lip furrows. Dermal denticles on lateral trunk with cross-ridges on crowns. Second dorsal fin slightly larger than 1st, and subequal to pelvic fins. Pectoral fins narrow to moderately broad and leaf-shaped; fin apex when laid back falling well in front of 1st dorsal-fin spine. Tooth count 47–60/32–38; vertebrae 93–105; spiral valve turns 16.

Body uniformly black to dark brown. Attains 89 cm TL.

DISTRIBUTION Wide-ranging but patchy in most seas. WIO: South Africa (KwaZulu-Natal), Melville Ridge south of Madagascar, Réunion, Mauritius and India.

REMARKS Size at birth ~20 cm TL; males mature at 47–51 cm TL, and females at 59–69 cm TL. Inhabits continental and insular slopes, on or near bottom, at 0–1 511 m (Weigmann 2016). Prey includes bottom-dwelling fishes and invertebrates. Minor interest to fisheries as a bycatch in bottom fisheries.

FAMILY **OXYNOTIDAE**

Roughsharks or prickly dogfishes

David A Ebert

Unmistakable small- to moderate-sized (up to ~150 cm TL) with strongly compressed body, extremely rough skin, 2 sail-like, spined dorsal fins, and no anal fin. Body humpbacked, very high and triangular in cross-section; lower abdomen with strong lateral ridges between pectoral fins and pelvic fins. Head moderately broad and somewhat flattened; snout blunt. Spiracles large to enormous. Gill slits about subequal. Mouth nearly transverse, very short, small, with thick papillose lips, and more or less encircled by lip folds. Teeth with dignathic heterodonty well-developed; upper teeth spear-like, much smaller than lower teeth; lower teeth compressed, forming saw-like edge; tooth counts 9–18/9–15. Dermal denticles on lateral trunk large and close-set, pedicellate with flattened, broad-keeled, erect or semi-erect trident-like crowns with medial and lateral cusps, slender tall pedicels, and low bases. Dorsal fins very large, broad, angular, high, and often falcate, each with strong stout spine nearly completely buried in fin but with smooth exposed tip. Pectoral fins high, narrow, distally lanceolate, leaf-shaped, subangular or falcate; length of anterior margins varying from about equal to prespiracular length to equal to head length; free rear tips rounded and not elongated. Pelvic-caudal space short, subequal to less than twice length of pelvic-fin bases. Peduncle slightly compressed, short; no lateral keels or precaudal pit. Caudal fin with subterminal notch. Vertebrae 84–95; spiral valve turns 9–11.

Mostly bottom-dwelling, on outer continental shelf, upper continental slope and insular slopes, at 40–1 067 m. Wide-ranging but disjunct, in temperate to tropical seas. One genus, *Oxynotus* Rafinesque 1810, with 5 species, 1 in WIO.

Oxynotus centrina (Linnaeus 1758)

Angular roughshark PLATE 13

Squalus centrina Linnaeus 1758: 233 (Mediterranean Sea).
Oxynotus shubnikovi Myagkov *in* Gubanov, Kondyurin & Myagkov 1986: 171, Fig. 59b (Cunene River mouth, Namibia).
Oxynotus centrina: Bass *et al.* 1976*; SSF No. 5.21*; Compagno *et al.* 1989*, 1991, 2005*; Ebert *et al.* 2013*.

Snout short and blunt; knob-like ridges over eyes, covered with enlarged denticles; spiracles vertically elongated. Upper teeth lanceolate; lower teeth blade-like; tooth count 10/9. First dorsal-fin spine inclined forward.

Body uniformly grey or grey-brown, with darker blotches on head and flanks (sometimes obscure, particularly in adults); paler horizontal line separating dark areas on head and another crosses cheeks below eyes. Attains 150 cm TL (most records <100 cm TL).

DISTRIBUTION Eastern Atlantic (Norway to England and Mediterranean Sea, and southward to South Africa [Cape Town]); possibly Mozambique in WIO (needs confirmation).

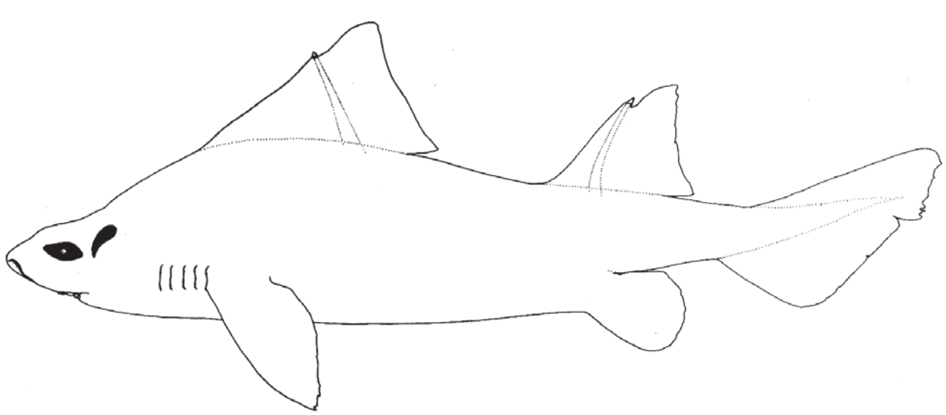
REMARKS Bass *et al.* (1976) noted that records of *O. centrina* from Angola, Namibia and South Africa may be of an undescribed species, differing in having a much shorter interdorsal space. Myagkov (in Gubanov, Kondyurin & Myagkov 1986) named the Namibian rough shark as a new species, *O. shubnikovi*, which was recognised by Compagno *et al.* (1991). However, subsequent examination of southern African specimens of *Oxynotus* and comparison with specimens from Namibia and the North Atlantic indicates the supposed differences are due to allometric and ontogenetic changes and individual variation (Yano & Matsuura 2002). Biology sketchily known, despite being widely known in European waters. Viviparous with yolk sac; litters of 7–23; size at birth 21–24 cm TL. In the Mediterranean Sea, mating reportedly occurs in February, with parturition possibly 3–12 months later. Males mature at ~60 cm TL, and females at ~65 cm TL. Bottom-dwelling on continental shelf and upper slope, at 50–660 m (mostly deeper than 100 m), usually over coralline algal and muddy bottoms. Appears to be a weak swimmer and a suction feeder, based on a diet that includes primarily polychaetes. A minor bycatch in bottom-trawl fisheries in North Atlantic. IUCN Red List conservation status Vulnerable because of its occurrence in areas with intense demersal fisheries.

FAMILY DALATIIDAE

Kitefin sharks

Kelsey C James and David A Ebert

Small- to moderately large-sized (to ~180 cm TL) with cylindrical body, narrow conical head and snout, and no anal fin. Spiracles large, close behind eyes. Nostrils widely to narrowly spaced, with simple anterior nasal flaps; internarial width equal to or much greater than nostril width. Mouth nearly transverse, short, with lips thin and smooth or thickened and fringed or pleated; lip folds short to moderately long, thin or thickened, and not encircling mouth. Upper teeth small, lanceolate, with narrow erect cusps; lower teeth highly compressed, broad and blade-like. Dermal denticles small, usually with low-ridged sessile crowns. Two dorsal fins, small- to moderate-sized, angular or rounded-angular, most often without spines. First dorsal fin small- to medium-sized, its base usually over pectoral–pelvic space or partially over pelvic fins. Second dorsal fin subequal



Oxynotus centrina, 55 cm TL, female (Namibia). Source: Bass *et al.* 1976 to, or slightly or much larger than 1st dorsal fin; 2nd dorsal-fin base over or just behind pelvic-fin bases. Pectoral-fin anterior margin rounded-angular or rounded-lobate, and mostly shorter than or sometimes subequal to prespiracular length; pectoral-fin free rear tip short and broadly rounded. Pelvic fins subequal to or smaller than pectoral fins. Claspers with or without lateral spine. Caudal fin markedly heterocercal to almost diphycercal, and subterminal notch weak to strong. Body usually dark brown or blackish, with pale fins and fin margins; ventral surface with luminous organs (photophores) in some species.

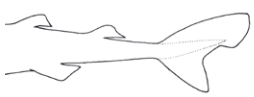
Reproductive mode yolk-sac viviparity, with litters of 6–16, although reproduction is not known for all species. Diet includes bony and cartilaginous fishes, crustaceans, cephalopods, polychaetes, siphonophores and tunicates. One species (*Isistius brasiliensis*) is ectoparasitic on larger pelagic marine vertebrates. Limited fisheries interest exists for these sharks due to their small sizes, but one species (*Dalatias licha*) is caught by longlines and trawls and used for human consumption, fish meal, leather and its squalene-rich liver oil.

Primarily oceanic and mesopelagic, but with some benthic deepwater members, over continental and insular shelves and slopes, at 20–1 800 m (mostly 200–1 000 m). Some species seem to be diel vertical migrators. Nearly circumglobal in warm-temperate to tropical seas. Seven genera and 10 species; 5 genera and 5 species in WIO.

KEY TO GENERA AND SPECIES

1a First dorsal-fin insertion about over pelvic-fin origins; cusps of lower teeth covering entire crown foot, without convex accessory blade separated from cusp by notch .... ***Isistius brasiliensis***

1b First dorsal-fin insertion well before pelvic-fin origins; cusps of lower teeth covering part of crown foot, with convex distal blade separated from cusp by notch 2



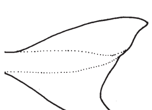
1a

1b

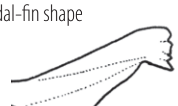
2a Second dorsal-fin base at least twice length of 1st; caudal fin paddle-shaped and upper lobe shortened 3

2b Second dorsal-fin base equal to or shorter than 1st; caudal fin not paddle-shaped and upper lobe not shortened 4

caudal-fin shape



2a



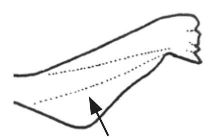
2b

3a First dorsal fin with small spine (sometimes concealed by skin) and fin set closer to pectoral fins than to pelvic fins; 2nd dorsal-fin base about twice length of 1st; snout more elongated and pointed, ~½ HL .... ***Squaliolus laticaudus***

3b First dorsal fin spineless and set closer to pelvic fins than to pectoral fins; 2nd dorsal-fin base ~4 times longer than 1st; snout shorter and more bluntly rounded, ~⅖ HL .... ***Euprotomicrus bispinatus***

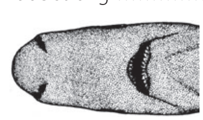
4a Preoral snout length very short, <⅓ HL; lips thick and pleated; lower teeth with strongly serrated edges; caudal-fin lower lobe weak .... ***Dalatias licha***

preoral snout length

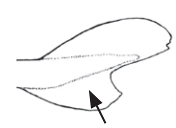


weak caudal-fin lower lobe

4b Preoral snout length long, >⅓ HL; lips thin and not pleated; lower teeth with smooth edges; caudal-fin lower lobe strong .... ***Heteroscymnoides marleyi***



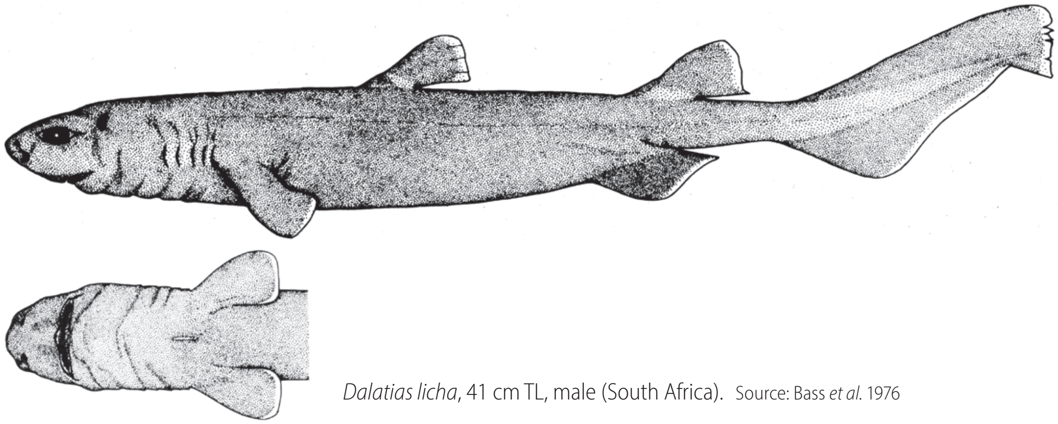
preoral snout length



strong caudal-fin lower lobe

GENUS *Dalatias* Rafinesque 1810

Moderately sized with short, broadly conical snout. Gill slits moderately broad and about equal in width. Anterior nasal flaps short, not expanded into barbels. Lips thick, and fringed or pleated. Upper teeth small, with narrow, hooked, needle-shaped cusps and no cusplets; lower teeth very large, blade-like, interlocked, with broad, erect, triangular cusps, small distal blades and serrated edges. Dermal denticles with low, flat, ridged, unicuspid crowns. Dorsal fins without spines; 2nd dorsal fin slightly larger than 1st, its base <1.5 length of 1st. First dorsal-fin origin behind pectoral-fin free rear tips, and fin insertion before pelvic-fin origins. Second dorsal-fin origin midway over pelvic-fin bases. No precaudal pit or lateral keels on peduncle. Caudal fin asymmetric, upper lobe long and lower lobe very short or virtually absent; subterminal notch well-developed. Cloaca without luminous gland. One species.



Dalatias licha, 41 cm TL, male (South Africa). Source: Bass *et al.* 1976

Dalatias licha (Bonnaterre 1788)

Kitefin shark PLATE 13

Squalus licha Bonnaterre (ex Broussonet) 1788: 12 (Cape Breton I., Nova Scotia, Canada).
Scymnorhinus brevipinnis: Smith 1936.
Scymnorhinus licha: SSF No. 5.22*.
Dalatias licha: Bass *et al.* 1976*; Compagno *et al.* 1989*; Compagno *et al.* 2005*; Ebert 2013*; Ebert *et al.* 2013*.

Diagnosis as for genus. Tooth count 16–21/17–20.

Body greyish to black or blackish brown, sometimes violet with black spots; posterior margins of most fins translucent. Attains 159 cm TL, possibly 182 cm TL.

DISTRIBUTION Mediterranean Sea, Atlantic, western and central Pacific, and Indian oceans. WIO: South Africa (Eastern Cape and KwaZulu-Natal) and Mozambique.

REMARKS Litters of 3–16; size at birth 30–40 cm TL. Males mature at ~100 cm TL, and females at ~120 cm TL. Primarily solitary with wide depth range, found on outer continental and insular shelves and slopes, at 37–1 800 m (mainly >200 m). Prey includes deepwater bony fishes, some elasmobranchs, cephalopods, crustaceans, polychaetes and siphonophores. Has been found with pieces of large fish in its stomach, suggesting that it bites chunks from live fish prey in a 'cookie-cutter' fashion. Of some interest to commercial fisheries. IUCN Red List conservation status Vulnerable globally, Endangered in European waters.

GENUS *Euprotomicrus* Gill 1865

Small-sized with cylindrical body and ventral photophores. Snout moderately long and bulbously conical; anterior nasal flaps very short. Gill slits very small and uniform. Lips thin, not fringed, pleated or suctorial. Upper teeth small, not blade-like, with narrow, acute, erect cusps and no cusplets; lower teeth much larger, blade-like, interlocked, with high, broad, nearly erect cusp and distal blade, edges not serrated. Dermal denticles flat and block-like, no posterior cusps on flat depressed crowns. Dorsal fins without spines; 1st dorsal-fin tiny, fin origin far behind pectoral-fin free rear tips, fin insertion closer to pelvic fins than to pectoral fins; 2nd dorsal-fin base much longer than 1st, its origin over rear of pelvic-fin bases. Pectoral fins with short, broadly rounded free rear tips and inner margins, not expanded, and acute or lobate. No precaudal pit; peduncle with low lateral keels and no midventral keel. Caudal fin nearly symmetrical, paddle-shaped, with short strong upper lobe and long lower lobe; subterminal notch well-developed. One species.

Euprotomicrus bispinatus (Quoy & Gaimard 1824)

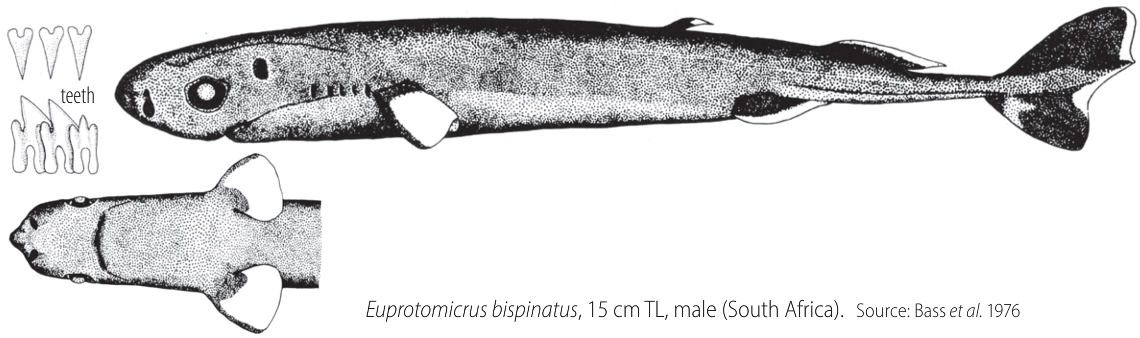
Pygmy shark PLATE 13

Scymnus bispinatus Quoy & Gaimard 1824: 197, Pl. 44 (Mauritius, Mascarenes).
Euprotomicrus bispinatus: Hubbs *et al.* 1967*; Bass *et al.* 1976*; SSF No. 5.18*; Compagno *et al.* 1989*; Compagno *et al.* 2005*; Ebert 2013*; Ebert *et al.* 2013*.

Diagnosis as for genus. Tiny, with bulbous snout and large eyes; peduncle with low lateral keels; ventral photophores; tooth count 19–21/19–23.

Body blackish, with conspicuously pale-edged fins. Attains 27 cm TL.

DISTRIBUTION Oceanic and amphitemperate, throughout central South Atlantic, central South and North Pacific, and southern Indian oceans. WIO: South Africa (KwaZulu-Natal), Madagascar and Mauritius.



Euprotomicrus bispinatus, 15 cm TL, male (South Africa). Source: Bass *et al.* 1976

REMARKS Litters of ~8; size at birth 6–10 cm TL. Males mature at 17–19 cm TL, and females at 22–23 cm TL. Pelagic, from 1 829–9 938 m, but occurs at or near surface at night, apparently descending to midwater or well below 1 500 m during daytime. Prey includes deepwater squid, bony fishes and some crustaceans.

GENUS *Heteroscymnoides* Fowler 1934

Small-sized with very long bulbously conical snout. Anterior nasal flaps very short. Gill openings very small and uniform. Lips thin, unpleated. Upper teeth small, with narrow, acute, erect cusps and no cusplets; lower teeth much larger, blade-like, interlocked, with high, moderately broad semi-erect cusp and distal blade, edges not serrated. Dermal denticles flat, but with pedicels with lanceolate, ridged, wedge-shaped, monocuspidate crowns. Dorsal fins without spines; 1st dorsal fin set far forward, fin origin over pectoral-fin bases, fin insertion closer to pectoral fins than to pelvic fins; 2nd dorsal fin slightly larger than 1st but with equal base length, its origin midway over pelvic-fin bases. Pectoral fins with short, narrowly rounded free rear tips and inner margins, not expanded, and acute or lobate. No precaudal pit or lateral or midventral keels on peduncle. Caudal fin semi-symmetrical, almost paddle-shaped, with moderately long upper lobe and well-developed lower lobe; subterminal notch strong. One species.

Heteroscymnoides marleyi Fowler 1934

Longnose pygmy shark PLATE 14

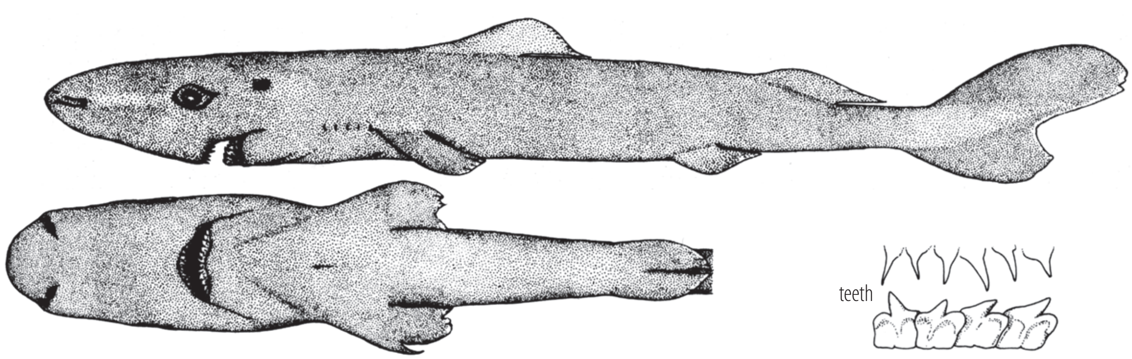
Heteroscymnoides marleyi Fowler 1934: 240, Fig. 4 (Durban, KwaZulu-Natal, South Africa); Bass *et al.* 1976*; SSF No. 5.19*; Compagno *et al.* 1989*; Compagno *et al.* 2005*; Ebert 2013*; Ebert *et al.* 2013*.

Diagnosis as for genus. Tooth count 22/23.

Body dark brown, with conspicuous dark-and-pale-banded fin margins. Attains at least 36.5 cm TL.

DISTRIBUTION Likely circumglobal, but limited, in cold sub-Antarctic waters and current systems of Southern Hemisphere: records from southeastern Atlantic (Walvis Ridge), southeastern Pacific (Chile) and southwestern Indian Ocean (KwaZulu-Natal, South Africa).

REMARKS Rare, known only from six specimens. Presumably viviparous with yolk sac; probably has few young; size at birth ~13 cm TL. Oceanic and epipelagic, from surface to ~502 m deep, over waters 830–4 000 m deep. Likely feeds on pelagic fishes and invertebrates.



Heteroscymnoides marleyi, 13 cm TL, female holotype, ventral view and dentition (South Africa). Source: Bass *et al.* 1976

GENUS *Isistius* Gill 1865

Cigar-shaped body with long abdomen and short tail. Snout short and bulbously conical. Anterior nasal flaps very short. Gill slits small and uniform. Lips expanded, fleshy and suctorial. Upper teeth small, with narrow, acute, erect cusps and no cusplets; lower teeth very large, blade-like, interlocked, with high, broad, erect cusp, edges not serrated; tooth counts 29–43/17–31. Dermal denticles flat and block-like, no posterior cusps on flat depressed crowns. Dorsal fins without spines; 1st dorsal fin set far back, its origin far behind pectoral fins; 2nd dorsal fin slightly larger than 1st, its origin over pelvic-fin rear tips. Pectoral fins with short rounded free rear tips and inner margins, not expanded, and acute or lobate. No precaudal pit; peduncle with low lateral keels and no midventral keel. Caudal fin asymmetrical to nearly symmetrical, with short upper lobe and short to long lower lobe; strong subterminal notch. Two species, 1 in WIO.

Isistius brasiliensis (Quoy & Gaimard 1824)

Cookiecutter shark PLATE 14

Scymnus brasiliensis Quoy & Gaimard (ex Cuvier) 1824: 198 (Brazil).
Isistius brasiliensis: Bass *et al.* 1976*; SSF No. 5.20*; Jahn & Haedrich 1987; Compagno *et al.* 1989*; Compagno *et al.* 2005*; Ebert 2013*; Ebert *et al.* 2013*.

Small-sized, with large anteriorly set eyes and suctorial lips. Pectoral fins subquadrate. Pelvic fins larger than dorsal fins. Second dorsal-fin height about equal to 1st; space between 2nd dorsal-fin insertion and caudal-fin origin long. Caudal fin large and nearly symmetrical, with long lower lobe. Tooth count 30–37/25–31.

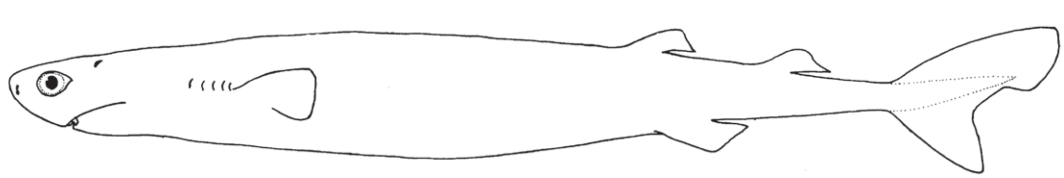
Body medium grey or grey-brown, with pale-edged fins; prominent dark collar-marking around branchial region; tips of caudal-fin lobes blackish. Photophores on lower abdomen allow it to glow bright green. Attains 56 cm TL.

DISTRIBUTION Circumtropical (patchy), in Atlantic, Pacific and Indian oceans. WIO: South Africa, Madagascar and Mauritius.

REMARKS Little known. Litters of ~6–12; size at birth 14–15 cm TL. Males mature at 31–37 cm TL, and females at 38–44 cm TL. Inhabits epipelagic and bathypelagic zones in tropical regions, at 85–3 500 m. Poor swimmer; makes diel vertical migrations, ascending to midwater or near surface at night. Prey includes squid, gonostomatid fishes and crustaceans; an ecoparasite on large marine organisms, attaching itself to sides of elasmobranchs, bony fishes, phocid seals, dolphins and other cetaceans, and then twisting to cut out conical plug of flesh. Of little interest to fisheries; occasionally caught in bottom trawls.

GENUS *Squaliolus* Smith & Radcliffe 1912

Head cylindrical, snout long and slightly pointed. Upper margin of orbit nearly straight to broadly arched or angular and chevron-shaped. Anterior nasal flaps very short. Gill slits very small and uniform. Lips thin, and not fringed, pleated or suctorial; upper lip with or without paired lateral papillae. Upper teeth small, with narrow, acute, erect cusps and no cusplets; lower teeth much larger, blade-like, interlocked, with high, moderately broad, nearly erect cusp and distal blade, edges not serrated. Dermal denticles on lateral body flat, block-like, with no posterior cusps on flat depressed crowns. First dorsal fin with small spine; fin anteriorly set, its origin about opposite pectoral-fin inner margins or free rear tips. Second dorsal-fin base about twice length of 1st; fin origin over front half of pelvic-fin bases. Pectoral fins with short, narrowly rounded free rear tips and inner margins. No precaudal pit; peduncle with low lateral keels but no midventral keels. Caudal fin nearly symmetrical, paddle-shaped; strong subterminal notch. Cloaca normal, not expanded as luminous organ. These are among the smallest known species of living sharks. Two species, 1 in WIO.



Isistius brasiliensis, 43 cm TL, female (Gulf of Mexico). Source: Bass *et al.* 1976, drawn from from Bigelow & Schroeder 1948

Squaliolus laticaudus Smith & Radcliffe 1912

Spined pygmy shark PLATE 14

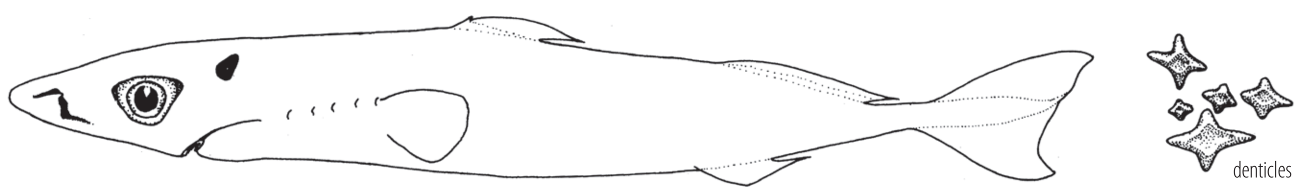
Squaliolus laticaudus Smith & Radcliffe *in* Smith 1912: 684, Pls. 50, 54, Fig. 4 (Batangas Bay, Luzon I., Philippines); Compagno *et al*. 2005*; Ebert 2013; Ebert *et al*. 2013*.

Eyes large, upper margin of orbit nearly straight. Upper lip without pair of lateral papillae; tooth count 22–23/16–21. First dorsal-fin spine sometimes covered by skin. Vertebrae 55–62.

Body blackish or blackish brown, with conspicuously pale fin margins; ventral surface densely covered with photophores. Attains ~28 cm TL.

DISTRIBUTION Nearly circumtropical, in Atlantic and Indo-Pacific. WIO: Somalia.

REMARKS Little known. Size at birth <10 cm TL; litter size probably small, but 12 mature eggs observed in single ovary of a mature female. Males mature at ~15 cm TL, and females at 17–20 cm TL. Epipelagic, near continental and island land masses, at 200–500 m; possibly occurs in aggregations as well as solitarily. Makes diel vertical migrations, ascending at night only to the upper limit of its depth range (avoids surface). Prey includes deepwater squid and bony fishes.



Squaliolus laticaudus, 14 cm TL, female (Philippines). Source: Bass *et al.* 1976

ORDER PRISTIOPHORIFORMES

FAMILY PRISTIOPHORIDAE

Sawsharks

David A Ebert

Distinctive small- to medium-sized (up to ~150 cm TL, but a few <70 cm TL) with slender, cylindrical body; head greatly flattened and somewhat expanded laterally; snout greatly elongated, flattened, laterally expanded, with close-set lateral and ventral 'sawteeth' and pair of string-like ventral rostral barbels before nostrils. Eyes dorsolateral on head; no nictitans, secondary lower eyelids or subocular pouches, but upper eyelid not fused to eyeball. Spiracles large and set just behind eyes. Five or 6 paired gill slits (in *Pristiophorus* and *Pliotrema*, respectively), lateral on head, posteriormost just before pectoral-fin origins. Nostrils longitudinal on snout and separate from mouth; no barbels, oronasal grooves or circumnarial grooves; anterior nasal flaps short and not reaching mouth. Mouth small, subterminal, broadly arched and short, extending slightly behind eyes; lip folds short on both jaws; teeth weakly differentiated, no enlarged teeth. Dermal denticles covering entire body, but not enlarged as thorns or spines. Two spineless dorsal fins; 1st dorsal-fin origin behind pectoral-fin free rear tips and well before pelvic-fin bases. Pectoral fins rather large, not fused to head. Pelvic fins small, and vent continuous with their inner margins. Peduncle with long, thick lateral ridges. No anal fin. Caudal-fin axis nearly straight, with long upper lobe and no lower lobe. Total vertebrae 132–157, precaudal vertebrae 90–108; spiral valve turns 6–10.

Reproductive mode yolk-sac viviparity, with litters of 5–17. Food habits of this group are poorly known, but known prey includes small fishes, crustaceans and squid. No directed fisheries for these sharks in WIO, but taken incidentally in groundfish trawl fisheries; elsewhere, especially in Australia, directed sawshark fisheries occur. Sometimes found in aggregations. Harmless to people, unlike the larger sawfishes (Pristidae).

Found in temperate and tropical benthic and epibenthic waters, over continental and insular shelves and upper slopes, from close inshore to ~950 m deep. Some temperate-water species occur in shallow bays and estuaries, near intertidal zone or on offshore sand and gravel banks, down to upper continental slope; tropical species occur mainly on upper continental and insular slopes. Sporadic, disjunct distribution in western North Atlantic, eastern South Atlantic, Indian, and western Pacific oceans. Fossil records indicate a formerly almost worldwide distribution during the Tertiary, including into the eastern Pacific and eastern Atlantic oceans (including the Tethys-Mediterranean Sea). Two genera and 10 species; both genera and 4 species occur in WIO in depths <200 m (*Pristiophorus nancyae* Ebert & Cailliet 2011 only known from deep water and not included here).

GENUS *Pliotrema* Regan 1906

Six paired gill slits. Barbels posteriorly situated on snout, snout length 64–67% preoral length. Larger rostral sawteeth with 2–8 mesially directed barbs along posterior edges; teeth with transverse ridges on basal ledges. Dermal denticles on lateral trunk widely spaced and only semi-imbricated in large specimens, usually separated by distance greater than crown lengths. Three species, one described here; see key (from Weigmann *et al.* 2020) for *P. annae* (from 20–35 m; too late for inclusion of species account), and a 3rd species *P. kajae* from deep water.

KEY TO SPECIES

1a Barbels ~⅔ way from rostral tip to mouth, prebarbel length about twice distance from barbel origin to upper-jaw symphysis; rostrum not constricted between barbel origin and nostrils; pronounced longitudinal yellowish stripe on dorsal surface .... ***P. warreni*** [South Africa, S Mozambique]

1b Barbels about halfway from rostral tip to mouth, prebarbel length subequal to distance from barbel origin to upper-jaw symphysis; rostrum constricted between barbel origin and nostrils; dorsal surface with or without 2 longitudinal stripes **2**

Continued ...

KEY TO SPECIES

2a Snout long, head length 38.3–40.4% TL, preorbital length 25.7–27.3% TL, preoral length 28.6–31.3% TL, prebarbel length 14.8–16.2% TL, barbel origin to upper-jaw symphysis 13.7–15.0% TL; 21–31 large lateral rostral teeth; 38–43 upper-jaw tooth rows, jaw teeth with sharp basal folds; pale to light brown dorsally with two yellowish stripes, uniform white ventrally, posterior fin margins with narrow white edges .... ***P. kajae*** [deep water; Madagascar, Mascarene Ridge; Plate 15]

2b Snout short, head length 34.2–34.5% TL, preorbital length 21.7–22.0% TL, preoral length 24.6–25.1% TL, prebarbel length 12.6–12.7% TL, barbel origin to upper-jaw symphysis 12.1–12.3% TL; 16–17 large lateral rostral teeth; 35–37 upper-jaw tooth rows, jaw teeth without basal folds; medium to dark brown dorsally without longitudinal stripes, white ventrally with some indistinct dark blotches on belly, posterior fin margins conspicuously white-edged ...... ***P. annae*** [Tanzania (Zanzibar); Plate 15]

Pliotrema warreni Regan 1906

Sixgill sawshark

PLATE 15

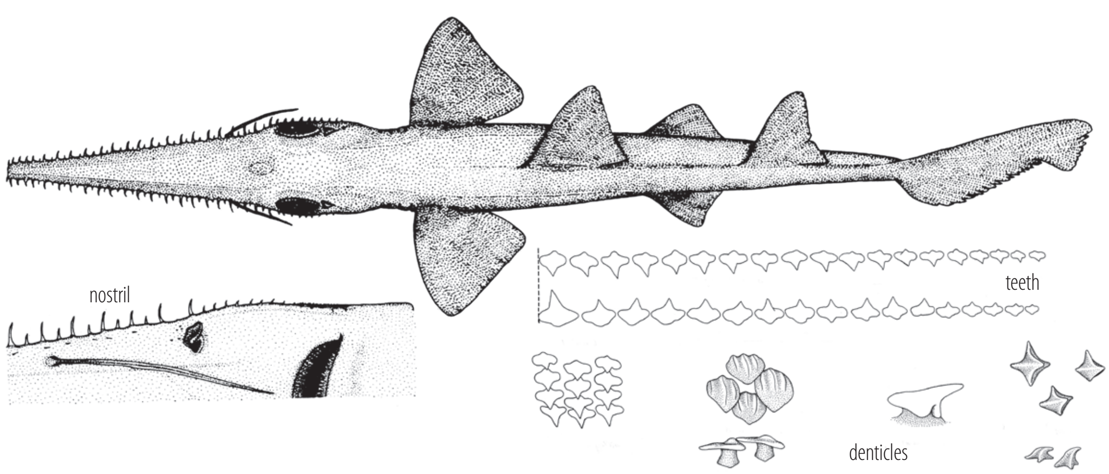
Pliotrema warreni Regan 1906: 1, Pl. 1 (KwaZulu-Natal, South Africa; False Bay, South Africa); Bass *et al.* 1975*; Compagno 1984*; SSF No. 20.1*; Compagno, Ebert & Smale 1989*; Compagno, Ebert & Cowley 1991; Compagno, Dando & Fowler 2005*; Ebert 2013*; Ebert *et al.* 2013*.

Small-sized with 6 paired gill slits; barbs on posterior edges of larger rostral teeth, and barbels positioned closer to mouth as compared with other species; teeth in mouth small, unicuspid. Tooth count 36–43/31–38; vertebrae 146–157; spiral valve turns 7 or 8.

Body pale brown dorsally, paler to white ventrally. Attains at least 136 cm TL.

DISTRIBUTION Southern Africa: southeastern Atlantic (Table Bay, South Africa) and eastwards in WIO, from South Africa (False Bay to KwaZulu-Natal) to southern Mozambique and southeastern Madagascar.

REMARKS Litters of 5–17; size at birth 35–37 cm TL. Males mature at ~83 cm TL, and females at ~110 cm TL. Benthic and epibenthic in offshore areas; partially segregates by depth, with young in shallower water. Neonates, small juveniles, and females with full-term foetuses have been collected in WIO off South Africa, suggesting pupping grounds there; larger individuals, including adult males, appear wider-ranging. Most records from warm-temperate and subtropical waters along southern Cape coast of South Africa, at 60–290 m, but recorded to 500 m. Feeds on small fishes, crustaceans and squid. Larger individuals may have pale-coloured parallel cuts and scratches, suggestive of combat scars inflicted by the oral and rostral teeth of other sawsharks. Predators include the tiger shark *Galeocerdo cuvier*. Taken as bycatch of demersal fisheries off South Africa, but not utilised. Has not been kept in captivity. This species requires study as it is endemic to southern Africa with a relatively restricted geographic, bathymetric and possibly habitat distribution, and displays morphological vulnerability to net gear while intensive offshore trawl fisheries occur in its known range.



Pliotrema warreni, 36 cm TL, immature male (South Africa). Source: Bass *et al.* 1975

ORDER SQUATINIFORMES

FAMILY SQUATINIDAE

Angel sharks

David A Ebert

Medium-sized sharks (~90–240 cm TL) with uniquely shaped flattened and batoid-like body with pectoral fins not attached to head but the triangular anterior portion of fins covering underside of head in area of gill slits. Head greatly depressed and laterally expanded; snout extremely short and truncated, without lateral sawteeth or rostral barbels. Five paired gill slits, laterally placed, posteriormost before pectoral-fin origins. Nostrils terminal on snout and separate from mouth, but anterior nasal flaps overlap mouth; anterior nasal flaps with barbels; no oronasal grooves or circumnarial grooves. Eyes dorsal on head; spiracles large. Mouth large, terminal, broadly arched and subangular, terminating about opposite or slightly behind eyes; lip folds very large, on both jaws. Teeth moderately differentiated, with slightly enlarged anterior teeth and no enlarged molars, and no gap or small intermediate teeth between anterior and lateral teeth in upper jaw. Dermal denticles covering entire body or absent from underside; some denticles on head and midline of back more or less enlarged as thorns or spines. Pectoral fins very large, expanded and ray-like; pelvic fins very large, inner margins lateral to vent. Two spineless dorsal fins set rearwards on tail; 1st dorsal-fin origin over or behind pelvic-fin rear tips. No anal fin. Peduncle with short thick keels on caudal base, but no elongated lateral dermal ridges. Caudal fin with high rounded upper lobe and expanded lower lobe. Vertebrae 119–146; intestinal valve of conicospiral type.

Reproductive mode yolk-sac viviparity, with litters of 1–25. Some species are heavily patterned dorsally, and most are uniformly pale ventrally. Angel sharks (also known as monkfish) occur in cool-temperate to tropical continental waters, from close inshore to ~1 300 m depth. Ambush predators that lie mostly buried in sand and mud bottoms with only eyes and spiracles protruding; many species are intensively fished.

Globally wide-ranging throughout Atlantic and Pacific oceans, but absent from most of Indian Ocean and central Pacific. One genus.

GENUS *Squatina* Duméril 1806

Diagnosis as for family. At least 20 species, several of these undescribed; 1 species known in WIO (specimens from East Africa should be compared with southern African material to determine whether a single species is represented).

Squatina africana Regan 1908

African angel shark PLATE 16

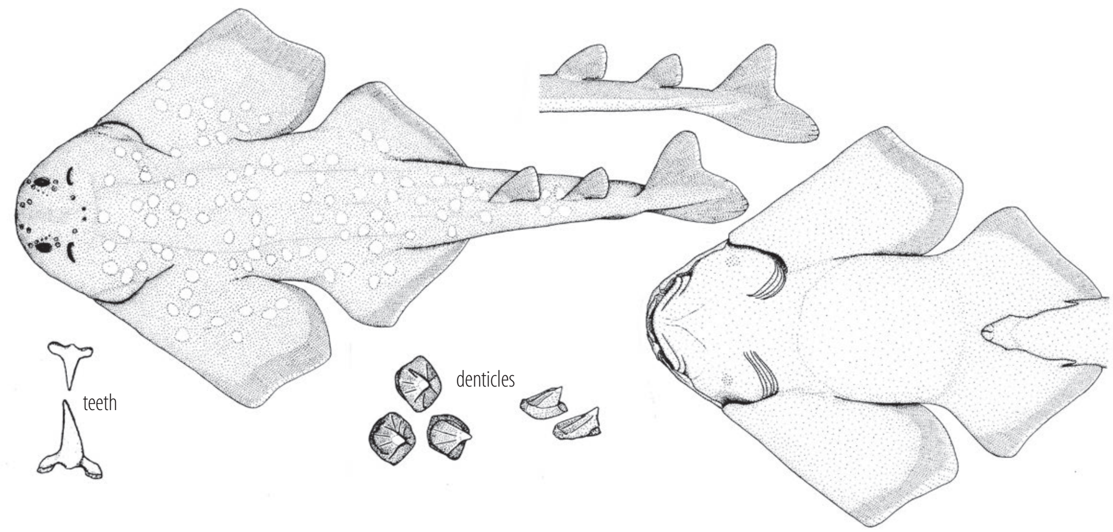
Squatina africana Regan 1908: 248, Pl. 38 (Durban Bay, KwaZulu-Natal, South Africa); Bass *et al.* 1975*; Compagno 1984; SSF No. 21.1*; Compagno *et al.* 1989*; Compagno *et al.* 2005*; Ebert 2013*; Ebert *et al.* 2013*.

Head greatly depressed and interorbital space concave. Spiracles with 14 pseudobranchial folds; spiracle width 1.2–1.4 eye length. Nasal barbels simple, flat, with fairly narrow, tapering or spatulate tips and weakly fringed bases. Anterior nasal flaps smooth or moderately fringed, and tips expanded as simple narrow-based lobe; posterior nasal flaps greatly enlarged and moderately fringed. Moderately large thorns on snout and interorbital space above and medial to eyes, and pair of thorns between spiracles in young individuals, but clusters of numerous large denticles in adults; no enlarged predorsal thorns on midline of back; adult males with enlarged alar thorn patch and a few thorns on apices of pelvic fins. Dermal denticles closely spaced but not imbricated, forming rough surface; denticles with slender (in young) to thick (in adults) posteriorly hooked cusp, and with 4 ridges and distal scalloping; ventral surface smooth. Pectoral-fin apex angular, posterior margin somewhat concave, and free rear tip usually closer to pelvic-fin origin than to pelvic-fin apex (sometimes equidistant). First dorsal-fin origin about opposite or slightly after pelvic-fin rear tips. Caudal-fin postventral margin oblique. Vertebrae 121–143; tooth count 20–22/18–20.

Body greyish or reddish brown dorsally, white ventrally; numerous pale and dark spots on dorsal surface, often with large ocelli with granular centres, and symmetrical darker bands or blotches. Attains 122 cm TL.

DISTRIBUTION Tropical and warm-temperate waters of WIO: South Africa (Western Cape to KwaZulu-Natal [commonest]), Mozambique, southern Madagascar, Mauritius (Mascarenes), Tanzania and possibly Socotra.

REMARKS Benthic and epibenthic on continental shelf and uppermost slope, from surfline to ~494 m deep, but mostly 60–300 m. Litters of 1–12 (average 6); size at birth 28–30 cm TL; gestation period probably ~12 months. Males mature at 77–95 cm TL, and females at 82–107 cm TL. Mating appears to take place in February and March, with embryos of various sizes present from April through January, and the largest embryos typically found in October. Off KwaZulu-Natal, South Africa, it occurs inshore along open beaches, near river mouths, and on offshore banks, but not in estuaries; the Thukela Bank appears to be a nursery ground as neonates are commonly taken as a bycatch in the prawn trawl fishery. Feeds on small bony fishes (mainly Carangidae, Haemulidae and Sparidae), cephalopods and large shrimp. Limited interest to fisheries, often captured as bycatch of bottom trawls and in anti-shark gillnets; not used as far as known. IUCN Red List conservation status Near Threatened; population trends should be monitored because of its occurrence in areas off South Africa and Mozambique subjected to intensive demersal trawling.



Squatina africana, 44 cm TL, immature male (South Africa). Source: Bass *et al.* 1975

ORDER HETERODONTIFORMES

FAMILY HETERODONTIDAE

Bullhead sharks

Kelsey C James and David A Ebert

Small- to medium-sized and stout-bodied with blunt pig-like snout. Eyes slightly elongated, with very prominent supraorbital ridge; spiracles small, set below and behind eyes. Anterior nasal flap J-shaped, encircling most of nostril, or lobate. Mouth small; lip folds moderately long to long. Teeth similar in both jaws; anterior teeth small and raptorial with 0–3 cusp pairs, and posterior teeth molariform. Two dorsal fins, each with stout spine. First dorsal fin triangular, medium to large, elongated in some species, and larger than 2nd dorsal fin; 1st dorsal-fin base well ahead of pelvic fins and sometimes over pectoral-fin bases. Anal fin midway between pelvic fins and caudal fin. No precaudal pit. Caudal-fin lower lobe moderately or well developed. Vertebrae 103–123; spiral valve turns 7. Body colouration includes dark saddles, spots or intricate stripes.

Mostly coastal in warm and temperate seas, but also found over outer continental shelf, to ~245 m deep, and almost always closely associated with the bottom. Commonly found in rocky habitats or on sandy bottom, most bullhead sharks are nocturnal and hide in crevices and caves during daytime. Reproductive mode oviparity, with large screw-shaped egg cases laid in pairs. Oviposition can be seasonal, in spring or summer, or year round; gestation period 6–12 months, depending on water temperature. Most species mature at >55 cm TL. Most feed predominantly on hard benthic invertebrates, including sea urchins, crustaceans and molluscs, and occasionally on small demersal fishes. No species are important to fisheries but several are a common bycatch in trawl nets, bottom gillnets and traps; catches are generally discarded but occasionally used for human consumption, fishmeal, or for their skin. Some species keep well in public aquariums, and small individuals are sometimes caught for the aquarium trade. None of the species are dangerous to people.

One genus, *Heterodontus* Blainville 1816, with 9 species, 2 in WIO.

KEY TO SPECIES

1a	Body tan or brown, with 4 or 5 brown saddles; pectoral fins, dorsal fins and caudal fin black-tipped, and dorsal-fin tips also with white apical spots	***H. omanensis***
1b	Body reddish brown with white spots, or with darker indistinct saddles in juveniles	***H. ramalheira***

Heterodontus omanensis Baldwin 2005

Oman bullhead shark — PLATE 17

Heterodontus omanensis Baldwin 2005: 262, Figs. 1–2 (Gulf of Masira, Oman, Arabian Sea).
Heterodontus sp. A: Randall 1995*; Compagno 2001*, 2005*; Ebert *et al.* 2013*.

Medium-sized with moderately low supraorbital ridges. Anterior teeth with cusp and pair of cusplets in adults; posterior molars unknown. Lateral trunk denticles fairly rough. First dorsal-fin low, rounded-angular, with free rear tip; fin origin before pectoral-fin insertion, and fin insertion well forward of pelvic-fin origin. Second dorsal fin nearly as large as 1st. Anal fin subangular. Vertebrae 106.

Body tan or brown, with 4 or 5 broad, diffuse-edged brown saddles distributed from snout tip to caudal-fin origin (no pale or dark spots or harness-type marking); dorsal fins, caudal fin and pectoral fins with black tips, and dorsal-fin tips also with white spot; single dark blotch under eyes. Colour of hatchlings possibly differs from adults. Attains 61 cm TL.

DISTRIBUTION WIO: Arabian Sea (Oman).

REMARKS Apparently common in northern Indian Ocean, but little known. Egg cases screw-shaped with two full turns and long tendrils extending from base. Males mature at ~52 cm TL, and females at ~61 cm TL. Caught by commercial trawlers off southern Oman: the type specimen was taken at ~72 m over soft bottom.

Heterodontus ramalheira (Smith 1949)

Whitespotted bullhead shark

PLATE 17

Gyropleurodus ramalheira Smith 1949: 367, Fig. 1 (off Inhambane, Mozambique).
Heterodontus ramalheira: SFSA No. 4a*; Pinchuk 1969; SSF No. 4.1*; Van der Elst & Vermeulen 1986; Compagno *et al*. 1989*; Compagno 2001*; Compagno *et al*. 2005*; Ebert 2013*; Ebert *et al*. 2013*.

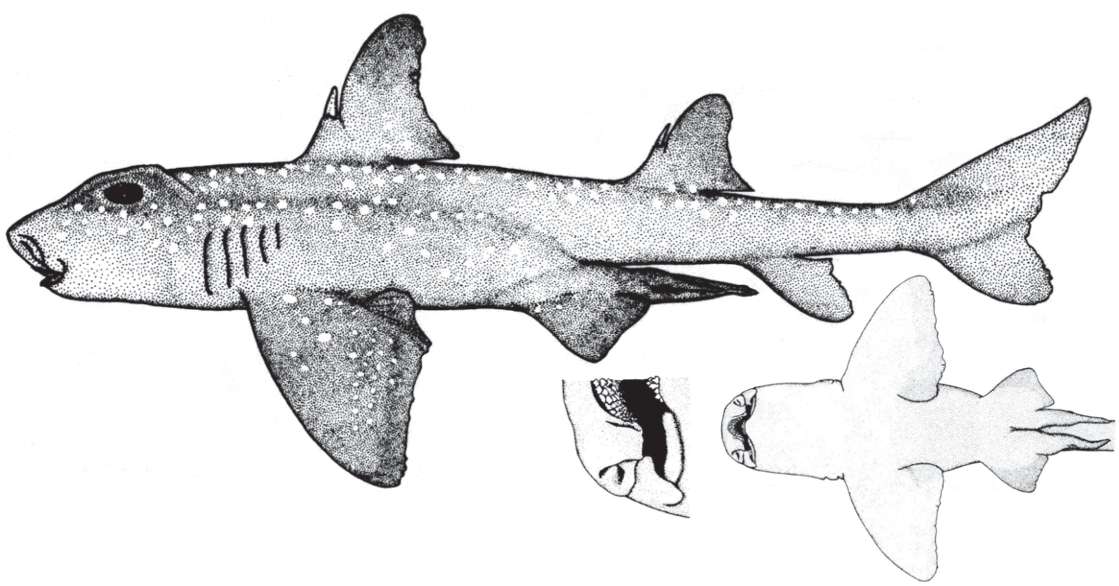
Medium-sized with moderately high supraorbital ridges. Anterior teeth in adults with cusp and pair of cusplets; posterior molars strongly ridged and not greatly expanded or rounded. Lateral trunk denticles large and rough. First dorsal-fin triangular, its origin far before pelvic fins. Second dorsal fin smaller than 1st, its origin over pelvic fins. Anal fin angular and falcate. Vertebrae 104–116.

Body dark red-brown with white spots; hatchlings paler and without dark harness-type marking but with darker, indistinct saddles. Attains at least 85 cm TL.

DISTRIBUTION WIO: South Africa (KwaZulu-Natal) to south-central Mozambique, Somalia, eastern Arabian Peninsula and southern Oman.

REMARKS Apparently uncommon or rare and little-known; benthic on outer continental shelf and upper slopes of East Africa. An unusually deepwater species for the family, at 40–275 m, with most records from >100 m. Egg cases not described, but hatchlings ~18 cm TL. Males mature at ~60 cm TL, and females at 75–83 cm TL. Diet mostly unknown, but crabs found in stomach of two individuals. Occasionally taken as a bycatch in commercial bottom trawls, such as for shrimp, off Mozambique and South Africa.

Heterodontus ramalheira, 37 cm TL, juvenile (Mozambique). O Alvheim © IMR



Heterodontus ramalheira, 64 cm TL, male (S Mozambique). Source: Bass *et al*. 1975

ORDER ORECTOLOBIFORMES

FAMILY HEMISCYLLIIDAE

Bamboo sharks

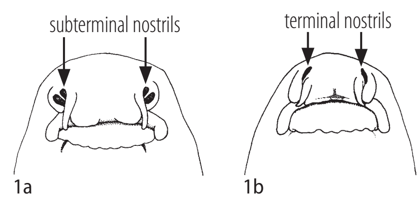
Brett A Human

Small-sized (to ~110 cm TL) and slender with cylindrical to slightly depressed body, with or without dorsal or lateral ridges, and with very long tail. Head length 12–14% TL; 5 paired gill slits, small and lateral on body, with 5th slit overlapping 4th; snout broadly to acutely rounded, not depressed, and with nasal barbels, circumnarial folds and grooves, and oronasal groove. Eyes dorsolateral, with strong subocular ridges, and no nictitans; spiracles large, set just below eyes. Mouth small, transverse or nearly so, subterminal to inferior, with well-developed lip folds fused medially into a complete post-oral fold. Teeth similar in both jaws, with strong median cusp and 1 or no lateral cusps; tooth counts 26–35/21–32. Fins rounded to angular or weakly falcate. Two spineless equal-sized dorsal fins, set far back; 1st dorsal fin over or slightly behind pelvic-fin bases. Pectoral fins small and rounded, gill slits extending well over pectoral-fin bases; pelvic fins subequal to pectoral fins. Anal fin low, moderate to long, smaller than 2nd dorsal fin, and more or less contiguous with caudal fin but separated by notch; anal-fin origin after 2nd dorsal-fin insertion. Peduncle long, cylindrical, without ridges or pits; distance from cloaca to anal fin >26% TL. Caudal fin elongated, weakly heterocercal, and without lower lobe. Vertebrae 151–192; spiral valve turns 12–20. Juveniles and adults typically with very different colour patterns.

Strongly associated with coral and rocky reefs. Also known as longtailed carpetsharks, as they possess muscular pectoral and pelvic fins that allow them to clamber over reef bottoms. Often seen in very shallow water and tidal pools, their preferred habitat makes them highly susceptible to human-induced habitat degradation. Oviparous where known, with conflicting reports as to whether oviparity is single or multiple. Common to rare, and all species are poorly known biologically and taxonomically; poorly represented in fish collections and more specimens are needed to clarify taxonomic identities and distributions. Although not targeted in any fishery they can be common bycatch species and are often exploited in the aquarium trade due to their colourful patterns and hardiness. Two genera and 15 species, plus several undescribed species; one genus and at least 5 species in WIO.

KEY TO GENERA

1a Nostrils subterminal; snout length >3% TL; mouth closer to eyes than to snout tip .... ***Chiloscyllium***
1b Nostrils terminal; snout length <3% TL; mouth closer to snout tip than to eyes .... ***Hemiscyllium***
[tropical Australasian distribution, reports from WIO unsubstantiated]



GENUS *Chiloscyllium* Müller & Henle 1837

Predorsal and interdorsal ridges variably developed, and lateral body ridges present or not. Mouth closer to eyes than to snout tip. Eyes and supraorbital ridges weakly elevated. Length of nasal barbels >1.3% TL. Cloaca to anal fin <38% TL. No large dark spot over pectoral fins. Found mostly in shallow water, but ranging to 100 m deep. Indo-Pacific distribution, primarily tropical but with a few species extending into subtropical or temperate waters. At least 7 species, 5 in WIO.

KEY TO SPECIES

1a Lateral body ridges present 2
1b No lateral body ridges 3

2a Length of anal-fin base equal to or greater than distance from lower caudal origin to subterminal notch; anal-fin origin far behind 2nd dorsal-fin free rear tip .... ***C. indicum***
2b Length of anal-fin base less than distance from lower caudal origin to subterminal notch; anal-fin origin behind 2nd dorsal-fin free rear tip .... ***C. plagiosum***

3a First dorsal-fin origin above or behind rear half of pelvic-fin bases 4
3b First dorsal-fin origin before or above front half of pelvic-fin bases .... ***C. punctatum***

Continued ...

KEY TO SPECIES

4a First dorsal-fin base shorter than, rarely equal to, 2nd dorsal-fin base; predorsal and interdorsal ridges well-developed .... ***C. arabicum***

4b First dorsal-fin base longer than 2nd dorsal-fin base; predorsal and interdorsal ridges not well-developed .... ***C. griseum***

Chiloscyllium arabicum Gubanov 1980

Arabian bamboo shark PLATE 18

Chiloscyllium arabicum Gubanov *in* Gubanov & Shleib 1980: 14, Figs. 6–7 (Persian/Arabian Gulf); Compagno 1984*, 2001*; Randall 1995*; Carpenter *et al.* 1997*; Al-Shuaily & Henderson 2003*; Compagno *et al.* 2005*; Ebert *et al*. 2013*.
Chiloscyllium confusum: Dingerkus & DeFino 1983*; Goto 2001; Eschmeyer 2010.

Predorsal and interdorsal ridges well-developed. First dorsal-fin base shorter than 2nd dorsal-fin base, rarely equal; 1st dorsal-fin origin above rear half of pelvic-fin bases. Length of anal-fin base less than distance from lower caudal origin to subterminal notch; anal-fin origin not far behind 2nd dorsal-fin free rear tip. Cloaca to tail tip 61–68% TL. Vertebrae 141–175.

Adults uniformly tan dorsally, paler ventrally; juveniles identical to adult colouration but with pale spots on fins. Attains 70 cm TL.

DISTRIBUTION WIO: Arabian Sea, Persian/Arabian Gulf, Oman, Pakistan and India.

REMARKS Goto (2001) and Eschmeyer (2010) recognised *C. confusum* as a valid species, but without supporting evidence; Compagno (2001) found *C. confusum* agreed with *C. arabicum*, however, and this has been followed by most subsequent authors. Confusion with *C. griseum* may have resulted in some erroneous distribution and abundance data. Lays up to 4 egg cases on coral reefs, hatching after 70–80 days; also found on rocky shores and in mangrove estuaries and lagoons. Has reproduced in captivity. Feeds on shelled molluscs, squid, crustaceans and fishes. IUCN Red List conservation status Near Threatened.

Chiloscyllium griseum Müller & Henle 1838

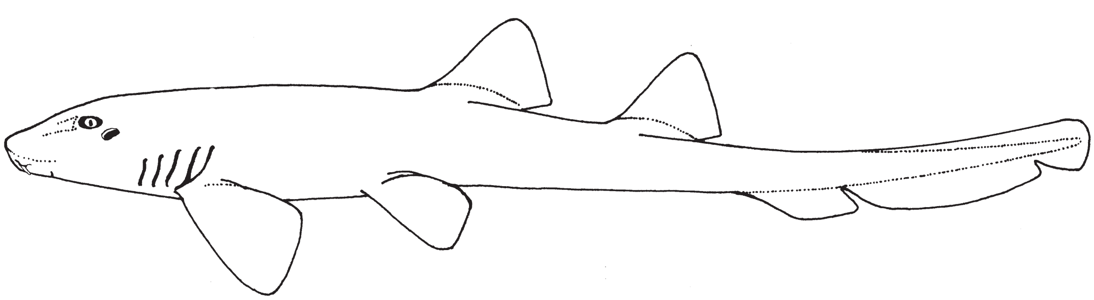
Grey bamboo shark PLATES 18 & 19

Chiloscyllium griseum Müller & Henle 1838: 19, Pl. 4 (Puducherry, India; Japan); Smith 1949*; Dingerkus & DeFino 1983*; Compagno 1984*, 2001*; Carpenter *et al.* 1997*; Morón *et al.* 1998; Al-Shuaily & Henderson 2003*; Compagno *et al.* 2005*; Ebert *et al*. 2013*.
Chiloscyllium indicum: Thompson 1914.

No predorsal or interdorsal ridges. First dorsal-fin base longer than 2nd dorsal-fin base; 1st dorsal-fin origin above rear half of pelvic-fin bases. Length of anal-fin base less than distance from lower caudal origin to subterminal notch; anal-fin origin not far behind 2nd dorsal-fin free rear tip. Tail long, thick; cloaca to tail tip 58–64% TL. Vertebrae 156–170; spiral valve turns 15–19.

Adults pale brown dorsally, paler ventrally; juveniles with distinct pale to dark grey-brown bands without black margins. Attains 77 cm TL.

Chiloscyllium arabicum, ~40 cm TL, subadult (Persian/Arabian Gulf).



Chiloscyllium griseum, adult (WIO). Composite

DISTRIBUTION Indo-Pacific. WIO: Arabian Sea, Persian/Arabian Gulf, Oman, Pakistan, India and Sri Lanka; elsewhere to Indonesia and southern Japan.

REMARKS Müller & Henle's (1838) illustration on Pl. 4, labelled *C. griseum*, is actually based on a specimen referable to *C. punctatum*. Westernmost records of this species may be confused with *C. arabicum*, and easternmost records may be partly based on *C. hasseltii*. Very poorly known despite being reportedly common within its distribution. Occupies inshore rocky habitat and lagoons; lays oval-shaped egg cases. Assumed to feed mostly on invertebrates. Commonly caught in fisheries and used for human consumption in Pakistan, India and Thailand, and also exploited in the aquarium trade. IUCN Red List conservation status Vulnerable.

Chiloscyllium indicum (Gmelin 1789)

Slender bamboo shark PLATE 19

Squalus indicus Gmelin 1789: 1503 (East Indies [Indian Ocean]).
Chiloscyllium indicum: Gilchrist 1902; Thompson 1914; Barnard 1925, 1927*; Smith 1949*; Dingerkus & DeFino 1983*; Compagno 1984*, 2001*; Compagno *et al.* 2005*; Ebert *et al.* 2013*.

Very slender body, with well-developed predorsal and interdorsal ridges. First dorsal-fin base longer than 2nd dorsal-fin base; 1st dorsal-fin origin above rear half of pelvic-fin bases. Length of anal-fin base equal to or greater than distance from lower caudal origin to subterminal notch; anal-fin origin far behind 2nd dorsal-fin free rear tip. Cloaca to tail tip 62–67% TL. Vertebrae 166–170; spiral valve turns 14 or 15.

Adults pale brown dorsally, with many small dark spots, saddles and bars; juveniles with many large dark saddles and bands without dark margins, which fade and separate to create adult patterning. Attains 65 cm TL.

DISTRIBUTION Indo-Pacific. WIO: Pakistan, India and Sri Lanka; elsewhere to Thailand, Indonesia, China and Japan.

REMARKS Despite a long history in southern African literature, this species has not been definitively recorded from there; the confusion seems to have arisen from specimens probably collected in India or Asia, deposited in South Africa, and mislabelled in the early 19th century. Biology virtually unknown, but commonly caught in fisheries in India, Sri Lanka and Thailand and used for human consumption. Found inshore on bottom; also reported from brackish water in Malaysia. IUCN Red List conservation status Vulnerable.

Chiloscyllium plagiosum

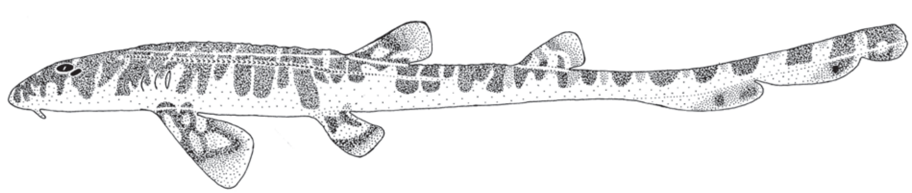
(Anonymous [Bennett] 1830)

Whitespotted bamboo shark PLATE 19

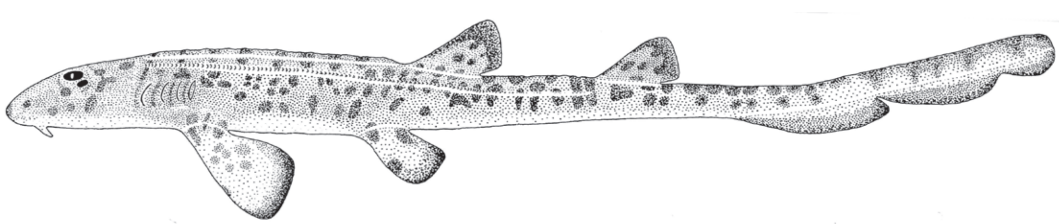
Scyllium plagiosum Anonymous [Bennett] 1830: 694 (Java Sea, Sumatra, Indonesia).
Chiloscyllium indicum: Gilchrist 1902; Thompson 1914.
Chiloscyllium caerulopunctatum: Bass *et al.* 1975*; Bauchot & Bianchi 1984*; Compagno 1984*; SSF No. 7.1*.
Chiloscyllium plagiosum: Dingerkus & DeFino 1983*; Compagno 1984*, 2001*; Compagno *et al.* 2005*; Ebert *et al.* 2013*.

Predorsal and interdorsal ridges well-developed. First dorsal-fin base longer than 2nd dorsal-fin base; 1st dorsal-fin origin above rear half of pelvic-fin bases. Length of anal-fin base less than distance from lower caudal origin to subterminal notch; anal-fin origin behind 2nd dorsal-fin free rear tip. Cloaca to tail tip 61–67% TL. Vertebrae 161–185; spiral valve turns 16 or 17.

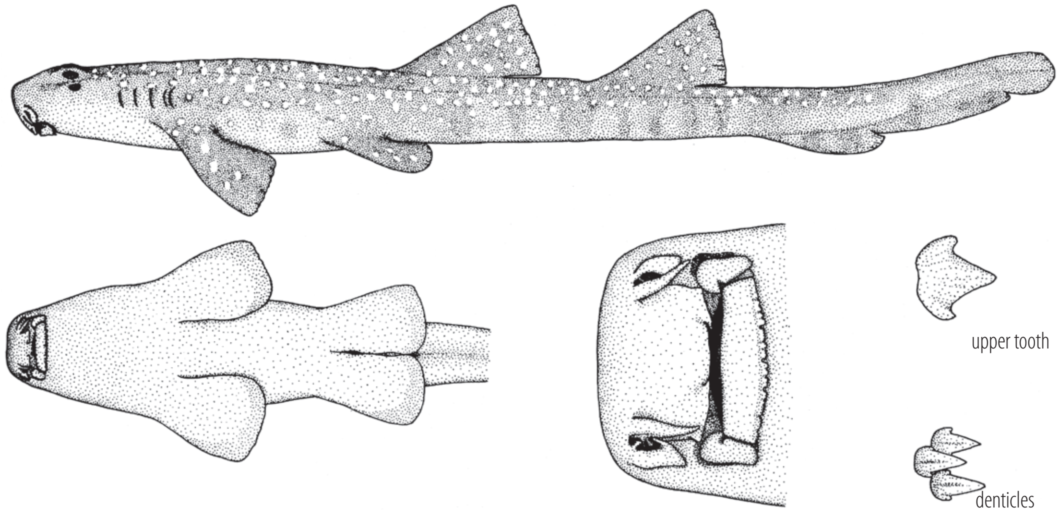
Adults with blotchy, pale to medium brown background, prominent dark saddles and many dark and white or bluish spots; juveniles dark, almost black, or with patterning similar to adults. Attains 95 cm TL.



Chiloscyllium indicum, 32 cm TL, juvenile female. Source: Dingerkus & DeFino 1983



Chiloscyllium indicum, 43 cm TL, adult female. Source: Dingerkus & DeFino 1983



Chiloscyllium plagiosum, 67 cm TL, female (S Madagascar). Source: Bass *et al.* 1975

DISTRIBUTION Indo-Pacific. WIO: Madagascar, India and Sri Lanka; elsewhere to Indonesia, Philippines, Japan and New Guinea.

REMARKS *C. plagiosum* recorded from Madagascar is probably a distinct species; however, it is synonymised here due to a lack of published diagnostic characters (although blue spots are noted as present only on specimens from Madagascar). Common, but biology virtually unknown. Nocturnally feeds on bony fishes and crustaceans. Frequently caught in fisheries in Madagascar, India, Thailand and China, and used for human consumption. A popular aquarium species that has reproduced in captivity. IUCN Red List conservation status Near Threatened.

Chiloscyllium punctatum Müller & Henle 1838

Brownbanded bamboo shark

PLATES 19 & 20

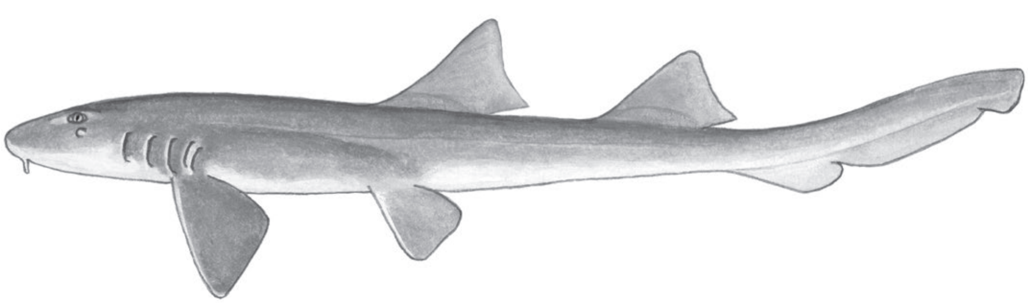
Chiloscyllium punctatum Müller & Henle 1838: 18, Pl. 3 (off Jakarta, Java, Indonesia); Dingerkus & DeFino 1983*; Compagno 1984*, 2001*; Compagno *et al.* 2005*; Ebert *et al.* 2013*.

Predorsal and interdorsal ridges not well developed. Dorsal-fin rear margins concave, and free rear tips elongated. First dorsal-fin base longer than 2nd dorsal-fin base; 1st dorsal-fin origin above or before front half of pelvic-fin bases. Length of anal-fin base less than distance from lower caudal origin to subterminal notch; anal-fin origin below posterior half of 2nd dorsal-fin base. Tail long, thick; cloaca to tail tip 61–64% TL. Vertebrae 136–170; spiral valve turns 20.

Adults with pale to medium brown background, paler ventrally, and usually without other markings, but with pale gill-slit margins; juveniles with prominent broad dark bands on very pale background, fading with maturity to small dark spots on darker background. Attains 132 cm TL.

DISTRIBUTION Indo-Pacific. WIO: Arabian Sea and southern India; elsewhere to Thailand, Indonesia, Philippines, Japan, New Guinea and Australia.

REMARKS Biology virtually unknown despite relatively wide distribution and abundance. Lays rounded egg cases. Diet includes invertebrates and fishes. Common but cryptic, regularly taken in fisheries in India and South East Asia for human consumption. A common species in aquaria, where it has reproduced. IUCN Red List conservation status Near Threatened.



Chiloscyllium punctatum, 63 cm TL, adult female (Indian Ocean).

FAMILY STEGOSTOMATIDAE

Zebra shark

David A Ebert

Distinctively large-bodied, somewhat stout, with prominent longitudinal ridges; head broad, conical and somewhat flattened; snout broadly rounded. Nostrils short, with small pointed barbels; oronasal groove long and well-developed. Eyes lateral, without strong subocular ridges; spiracles large. Mouth small, nearly transverse. Five paired short gill slits, the last three behind pectoral-fin origins; 4th and 5th gill slits very close, often giving the impression of one slit. First dorsal fin larger than 2nd, its origin well before pelvic-fin origins. Pectoral fins large, broadly rounded. Anal-fin origin about opposite upper caudal origin. Caudal fin greatly elongated, broad, equal to half TL, with strong terminal lobe and subterminal notch. Body with distinct spotting, it is also known as the leopard shark.

Monotypic genus *Stegostoma* Müller & Henle 1837.

Stegostoma tigrinum (Forster 1781)

Zebra shark — PLATE 20

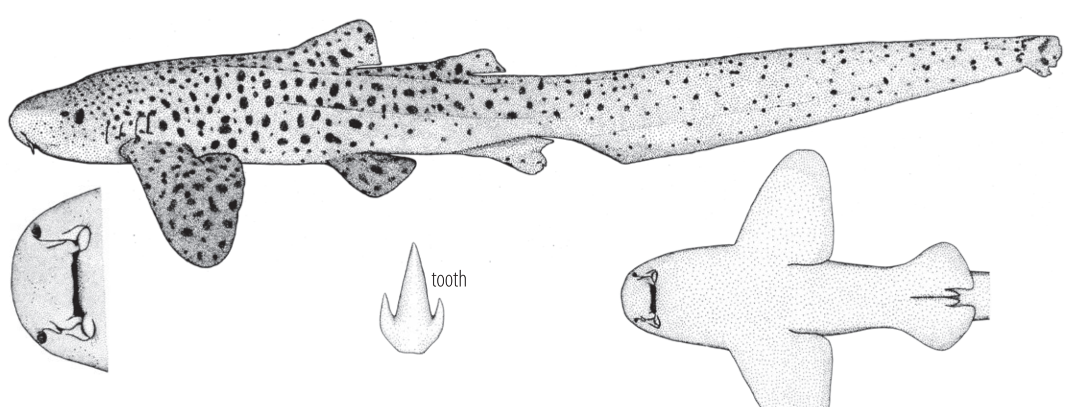
Squalus tigrinus Forster 1781: 24, Fig. 2, Pl. 13 (Sri Lanka).
Stegostoma tigrinum Barnard 1937; Dahl *et al.* 2019.
Stegostoma fasciatum: SFSA No. 30*; Compagno 1984*; SSF No. 7.4*; Compagno *et al.* 1989*; Compagno 1999; Compagno 2001*; Heemstra & Heemstra 2004*; Ebert *et al.* 2013*; Ebert & van Hees 2015; Weigmann 2016.
Stegostoma varium: Bass *et al.* 1975*.

Diagnosis as for family. Teeth small and tricuspidate, similar in both jaws; tooth count 28–33/22–34. Vertebrae 207–243; spiral valve turns 18.

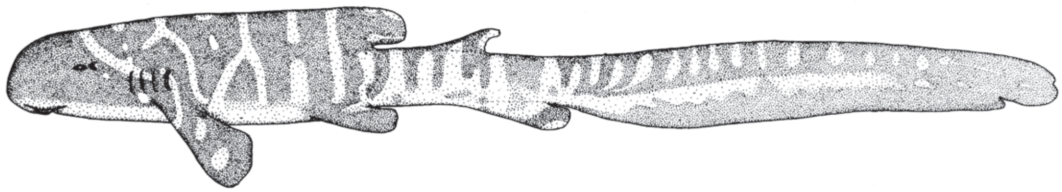
Body yellowish with distinctive pattern of dark brown spots in adults, or with dark saddles and black spots alternating with vertical white or yellowish stripes in juveniles. Attains 250 cm TL (possibly >3.5 m TL).

DISTRIBUTION Indo-Pacific (widespread). WIO: Persian/Arabian Gulf, Red Sea, Gulf of Aden to South Africa (Eastern Cape and KwaZulu-Natal), Madagascar, Mauritius, Maldives, India and Sri Lanka; elsewhere to Indonesia, southern Japan, Marshall Is., Australia New Caledonia and Samoa.

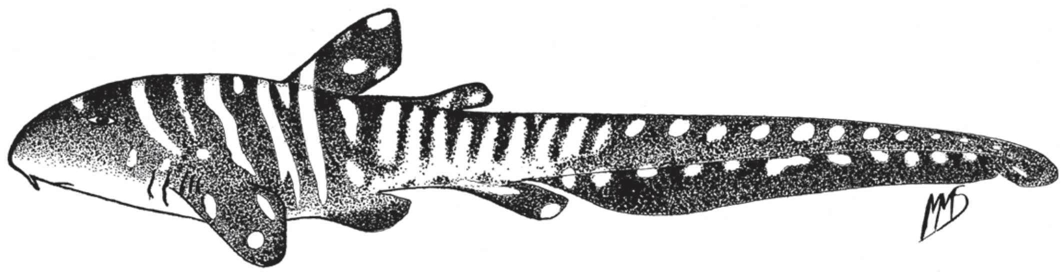
REMARKS Oviparous, with large dark brown to purplish black egg cases with fine hair-like fibres that anchor to substrate; egg dimensions approximately 13–17 cm long, 8 cm wide, 5 cm thick. Litter size likely >2, as multiple egg cases have been found in a single oviduct. Inshore shark of tropical continental and insular shelves, from intertidal zone, coral reefs and offshore sediments, to ~62 m deep. Usually solitary, but also found in large aggregations (up to ~50) over sand near reefs, but young seldom seen. Slow but strong-swimming; probably nocturnal, feeds mostly on molluscs (gastropods and bivalves) but also small bony fishes and crustaceans. Commonly taken throughout its range in nearshore fisheries by bottom trawls or longlines, and often sold in local fish markets; captured in smaller numbers by prawn trawls in Australia. Also kept in public aquaria. IUCN Red List conservation status Endangered due to fishing and coral reef degradation, but assessed as Least Concern in Australia where it is abundant.



Stegostoma tigrinum, 128 cm TL, immature male (South Africa). Source: Bass *et al.* 1975



Stegostoma tigrinum, 37 cm TL, immature male (South Africa). Source: Bass *et al.* 1975



Stegostoma tigrinum, 51 cm TL, juvenile (South Africa). Source: SFSA

FAMILY GINGLYMOSTOMATIDAE

Nurse sharks

Brett A Human

Moderately sized (up to ~3 m TL) and robust with thick cylindrical or depressed body; head short, broad and depressed (HL 19–27% TL). Five paired gill slits, small, lateral on body, with 4th nearly overlapping 5th. Eyes tiny, lateral or dorsolateral on head, set posterior to mouth; no nictitans; spiracles minute, posterior to and level with eyes, <⅓ eye diameter. Mouth transverse, subterminal, not extending behind eyes, with well-developed lip folds. Teeth moderately sized, similar in both jaws, with strong median cusp and 1–7 lateral cusps; tooth counts 24–38/22–32. Nasal flaps small, with short to moderately long nasal barbels, and well-developed oronasal grooves. Fins rounded or falcate. Two spineless dorsal fins; 1st dorsal fin over or slightly anterior to pelvic fins; 2nd dorsal fin subequal to 1st. Pectoral fins rounded or falcate, fin origin under 4th gill slit. Pelvic fins smaller than pectoral fins. Anal fin large and high, equal in size to 2nd dorsal fin; anal-fin origin under or slightly posterior to 2nd dorsal-fin origin. Peduncle short, compressed, without ridges or pits. Tail large, elongated, slightly elevated, heterocercal and lower lobe poorly developed. Vertebrae 135–195; spiral valve turns 15–24.

Reproductive mode yolk-sac viviparity, except *Pseudoginglymostoma* which is possibly oviparous. Distributed throughout tropical and subtropical oceans, found inshore and close to bottom, from intertidal zone to at least 70 m deep, and abundant where recorded. Nurse sharks are a common catch in artisanal and commercial fisheries, and used for human consumption, liver oil and leather products.

Three monotypic genera; 2 genera and 2 species in WIO.

KEY TO GENERA AND SPECIES

1a Fin tips angular; 1st dorsal fin larger than 2nd; body depressed; tail length >25% TL .... ***Nebrius ferrugineus***

1b Fin tips rounded; dorsal fins equal-sized; body cylindrical; tail length <20% TL .... ***Pseudoginglymostoma brevicaudatum***

GENUS *Nebrius* Rüppell 1837

Head U-shaped in dorsal view; snout moderately elongated, preoral length ~63% mouth width; eye diameter >1% TL. Nasal barbels elongated, reaching past mouth; teeth with 3 or more lateral cusps either side of median cusp; lower lip trilobate. One species.

Nebrius ferrugineus (Lesson 1831)

Tawny nurse shark PLATES 20 & 21

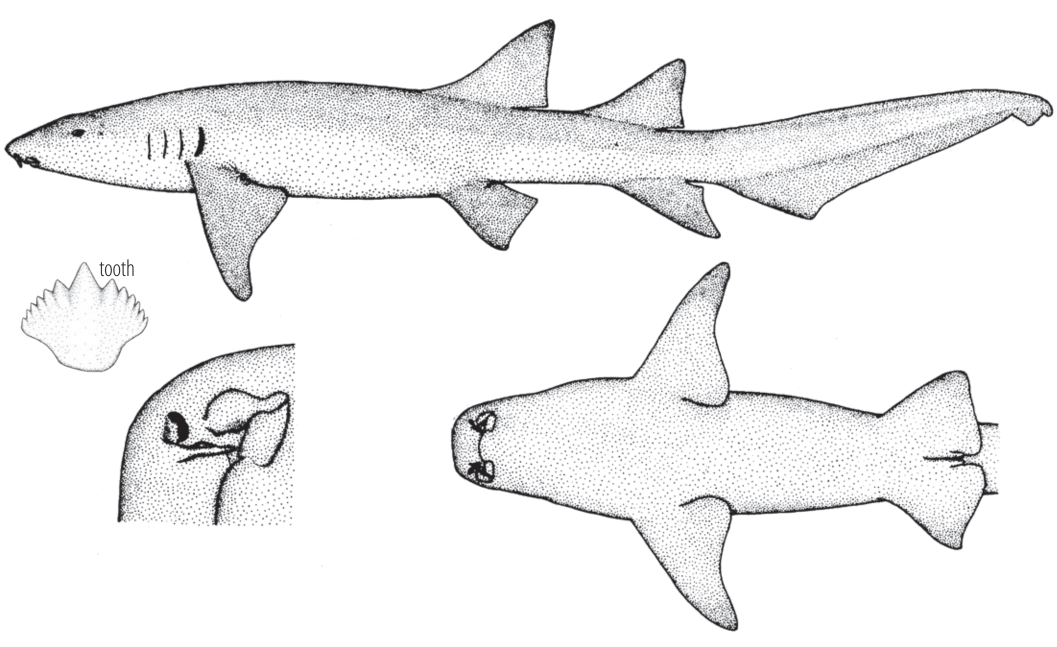
Scyllium ferrugineum Lesson 1831: 95 (New Ireland, Bismarck Archipelago; Waigeo I., Moluccas, Indonesia).
Nebrodes macrurus Garman 1913: 58, Pl. 8, Figs. 7–10 (Mauritius, Mascarenes).
Nebrius concolor: Bass *et al*. 1975*; Dingerkus 1986; SSF No. 7.3*; Taniuchi & Yanagisawa 1987.
Nebrius ferrugineus: Compagno 1984*, 2001*; Stevens 1984; Compagno *et al.* 1989*; Randall & Anderson 1993; Randall 1995*; Carpenter *et al.* 1997*; Marine Research Section [Maldives] 1997; Winterbottom & Anderson 1997; Al-Shuaily & Henderson 2003*; Compagno *et al.* 2005*; Ebert *et al.* 2013*.

Diagnosis as for genus. Fins angular; 1st dorsal fin larger than 2nd, its base over pelvic-fin bases. Nasal barbels fairly long. Tooth count 29–33/26–28; vertebrae 189–195; spiral valve turns 23 or 24.

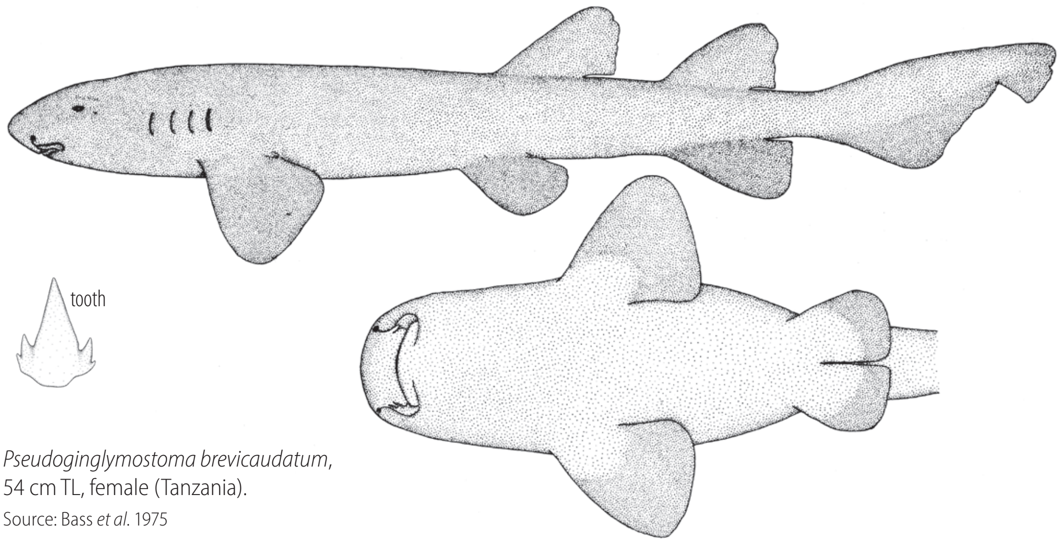
Body uniformly brown, but may slowly change to yellowish or greyish depending on habitat, and paler ventrally; albinism recorded. Attains 3.2 m TL.

DISTRIBUTION Tropical and subtropical waters of Indo-Pacific (widespread). WIO: Persian/Arabian Gulf, Red Sea, Gulf of Aden, Arabian Sea, Mozambique, South Africa (KwaZulu-Natal), Madagascar, Aldabra, Mauritius, Seychelles, Chagos, Maldives, India and Sri Lanka; elsewhere to Indonesia, southern Japan, Australia, New Caledonia, Society Is. and Marquesas Is.

REMARKS Its wide distribution has given rise to multiple synonyms, with those pertaining to WIO discussed in Bass *et al*. (1975). Viviparous with yolk sac; the only orectolobiform shark known to be intrauterine oophagous. Found on continental and insular shelves, on or near bottom, mainly at 5–30 m. Maintains limited home range; nocturnal and often found resting during daylight hours, sometimes with individuals positioned atop others, although active during day in some regions. Large pharynx and small mouth capable of powerful suction for feeding on invertebrates (crustaceans, cephalopods, echinoderms) and reef fishes; may squirt water from mouth when caught and reportedly makes a grunting sound. Caught frequently in commercial and artisanal nearshore fisheries. Individuals of this species from Japan and Taiwan have been reported missing their 2nd dorsal fin, possibly due to teratogenic pollution. Docile and popular with divers, and common in public aquaria. IUCN Red List conservation status Vulnerable due to high fishing pressure and habitat loss, but assessed as Least Concern in Australia.



Nebrius ferrugineus, 118 cm TL, immature male (N Mozambique). Source: Bass *et al.* 1975



Pseudoginglymostoma brevicaudatum,
54 cm TL, female (Tanzania).
Source: Bass *et al.* 1975

GENUS *Pseudoginglymostoma*

Dingerkus 1986

Head broadly rounded and parabolic in dorsal view; snout bluntly rounded, preoral length 34.5–42% mouth width; eye diameter <1% TL. Nasal barbels very short, not reaching mouth; teeth with 1 or 2 lateral cusps either side of median cusp; lower lip not trilobate. Tail length <¼ TL. This genus (and the subfamily Pseudoginglymostomatinae, Compagno 2001) may warrant separation from Ginglymostomatidae, based on morphology, and could be placed in its own family pending a review. One species.

Pseudoginglymostoma brevicaudatum (Günther 1867)

Shorttail nurse shark PLATE 21

Ginglymostoma brevicaudatum Günther *in* Playfair & Günther 1867: 141, Pl. 21 (Zanzibar, Tanzania); Garman 1913; Bass *et al.* 1975*; Compagno 1984*; SSF No. 7.2*.
Pseudoginglymostoma brevicaudatum: Dingerkus 1986; Compagno 2001*; Ebert *et al.* 2013*.

Diagnosis as for genus. Fins rounded; dorsal fins equal-sized. Tooth count 24–27/22–27; vertebrae 135–143; spiral valve count 15.

Body uniformly dark brown, but paler ventrally. Attains 75 cm TL.

DISTRIBUTION WIO: Kenya to Mozambique, Madagascar, and possibly Seychelles and Mauritius.

REMARKS Reportedly common off East Africa, but poorly known. Assumed oviparous, as one female that lived for at least 33 years in an aquarium laid infertile egg cases. Nocturnal in captivity; diet presumably similar to other members of the family. Probably landed in inshore artisanal and commercial fisheries.

FAMILY RHINCODONTIDAE

Whale shark

David A Ebert

Enormous, heavy-bodied and fusiform, with wide depressed head and huge terminal transverse mouth. Gill slits huge and internally modified for filter-feeding; nostrils rudimentary; spiracles larger than eyes. Teeth hook-shaped with single cusp; ~300 tooth rows in each jaw. First dorsal fin very large, posteriorly set, with insertion over pelvic fins; 2nd dorsal fin smaller, with insertion over anal-fin base; pectoral fins falcate; caudal fin crescent-shaped, unnotched. Prominent ridges along flanks, with lowest ending in keel on peduncle.

Monotypic.

Rhincodon typus Smith 1828

Whale shark

PLATES 21 & 22

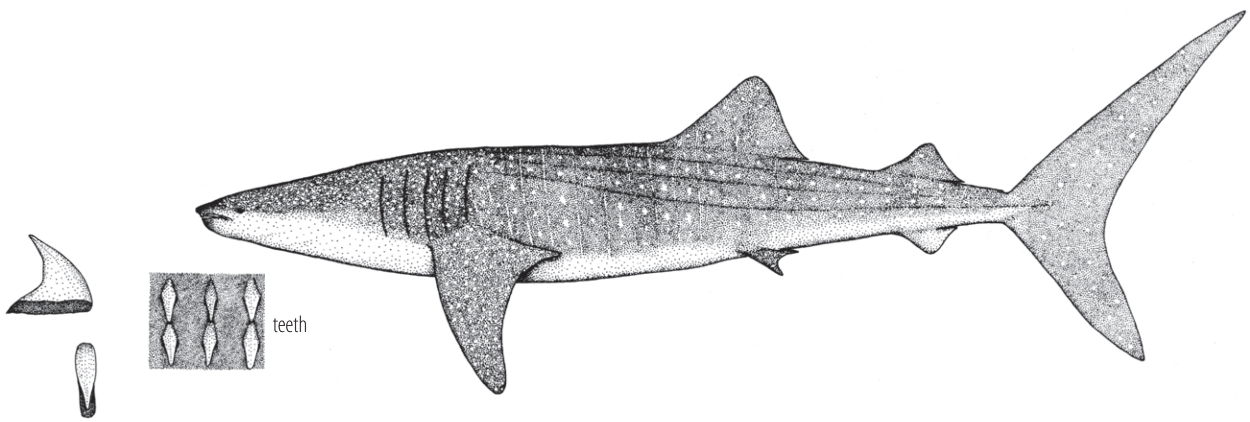
Rhincodon typus Smith 1828: 2 (Table Bay, South Africa); Bass *et al.* 1975*; SSF No. 8.1*; Compagno *et al.* 1989*; Anderson & Ahmed 1993; Beckley *et al.* 1997; Wintner 2000; Ebert 2003*; Ebert *et al.* 2013*.

Diagnosis as for family. Vertebrae 153–174; spiral valve turns 68–73.

Body with prominent pattern of white or yellow spots between vertical and horizontal stripes reminiscent of checkerboard pattern, offset by background colour of dark grey, bluish or brown above, becoming white below. The largest living fish, attains at least 18 m TL.

DISTRIBUTION Circumglobal in tropical to temperate seas, including Red Sea. WIO: South Africa (Western Cape) to Sri Lanka and northwards to Pakistan.

REMARKS Viviparous with yolk sac, without placenta; litters large, up to 300 embryos; size at birth 55–64 cm TL; gestation period and pupping grounds unknown. Males mature at 7–9 m TL, at ~20 years; females mature at ~10 m TL, at 27 years or more. Diet of this huge filter-feeding shark includes plankton, copepods, jellyfish, and pelagic crustaceans such as crabs. Gulps and feeds, often while hanging vertically, by drawing in water at high velocity by expansion of gill cavity, unlike the more passive method of basking sharks. Oceanic, to >700 m deep, but usually found at or near the surface, from close inshore, including bays and lagoons, to far out at sea. Prefers areas of mixing layers of cool upwelled oceanic waters. Highly migratory, often making long-term transoceanic migrations. A docile species that has at times been the subject of regional artisanal fisheries; has become a popular attraction for ecotourism in recent years. IUCN Red List conservation status Endangered; currently protected under CITES.



Rhincodon typus, 4.4 m TL, immature female; lateral and dorsal tooth from 8-m-TL specimen, and natural appearance of teeth with all but tips covered by skin (South Africa). Source: Bass *et al.* 1975

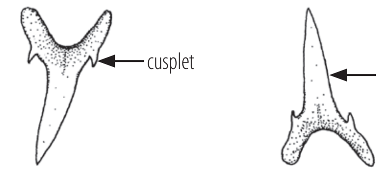
ORDER LAMNIFORMES

FAMILY CARCHARIIDAE

Raggedtooth shark

Brett A Human

Large-sized (to at least 3.2 m TL) with stout cylindrical body and long head (HL ~25% TL); snout short, slightly depressed and pointed; snout length less than mouth length; preorbital length 0.3–0.5 times mouth width; eye diameter 0.9–1.4% TL. Five paired gill slits, large, lateral and not extending dorsally, with all slits before pectoral-fin origins. Eyes small, to ~1.4% TL, set dorsolaterally on head over mouth, with prominent lateral head ridge underneath; no nictitating eyelid; spiracles minute. Mouth parabolic, subterminal, extending behind eyes, with lip folds. Teeth large, similar in both jaws, although identifiable as symphysials, anteriors, intermediates, laterals and posteriors; teeth erect with elongated medium cusp and a much shorter lateral cusplet either side of median cusp, becoming compressed posteriorly; tooth counts 40–42/38–42. Vertebrae 156–186. Nasal flaps small, without nasal barbels; no oronasal grooves. Fins angular and broad; dorsal fins, pelvic fins and anal fin subequal. Two spineless low dorsal fins, 1st dorsal-fin base closer to pelvic-fin base than to pectoral-fin base. Pectoral fins medium-sized and broad; pectoral-fin origin behind 5th gill slit. Anal-fin base under 2nd dorsal fin. Peduncle compressed, without lateral keels, and with upper crescentic precaudal pit, but no lower pit. Caudal fin heterocercal, its dorsal margin <⅓ precaudal length. Intestinal valve of ring type.



Reproductive mode oophagous, the only shark species where adelphophagy has been verified. Near global distribution in inshore tropical and temperate waters, except for central and eastern Pacific. Occur close inshore to oceanic, generally littoral or epipelagic, to ~230 m, but reported to 500 m. Common to rare, they have proven to be largely innocuous, are popular in public aquaria, and have become the subject of dive ecotourism. Monotypic genus *Carcharias* Rafinesque 1810.

Carcharias taurus Rafinesque 1810

Raggedtooth shark PLATE 22

Carcharias taurus Rafinesque 1810: 10, Pl. 14, Fig. 1 (Sicily, Mediterranean Sea); Barnard 1925, 1927*; Smith 1949*; D'Aubrey 1964*, 1969; Forster *et al.* 1970; Compagno & Follett 1986; Compagno *et al.* 1989*; Cliff & Wilson 1994*; Randall 1995*; Pradervand 2000; Compagno 2001*; Smale 2002; Al-Shuaily & Henderson 2003*; Bonfil & Abdallah 2004*; Heemstra & Heemstra 2004*; Compagno *et al.* 2005*; Dicken *et al.* 2007; Moore *et al.* 2007*; Ebert *et al.* 2013*; Weigmann 2016; Stone & Shimada 2019*.
Odontaspis americanus: Gilchrist 1902; Thompson 1914.
Carcharias tricuspidatus: Smith 1949* [in part]; Compagno 1984* [in part].
Odontaspis taurus: Bass *et al.* 1975*; Buxton *et al.* 1984; Wallace *et al.* 1984.
Eugomphodus taurus: Compagno 1984*, 1986*; SSF No. 19.1*.

Carcharias taurus, 103 cm TL, immature male (South Africa).
Source: Bass *et al.* 1975

Diagnosis as for family.

Body pale brown to grey, often darker brown or bronzy dorsally, with large dark blotches spread over body; abruptly white ventrally. Attains at least 3.2 m TL, possibly 4.3 m TL.

DISTRIBUTION Warm-temperate and tropical coastal waters of Atlantic, Indo-Pacific and western Mediterranean Sea. WIO: northern India, Pakistan, Gulf of Oman, Red Sea, Tanzania (Zanzibar), Mozambique and South Africa (KwaZulu-Natal to southeastern Atlantic).

REMARKS Some literature cites Pl. 44 in Rafinesque's original description as an illustration of this species; however, it is Pl. 14 that illustrates the species. Able to gulp air into its stomach and hover motionlessly, it is often found aggregating in so-called shark gutters, demonstrating philopatry for those sites, sometimes numbering dozens of individuals. More active at night, feeds on a wide range of fishes and invertebrates. Known to migrate seasonally in South Africa, Australia and United States, apparently between mating and pupping grounds. Historical persecution by spearfishers has resulted in dramatically reduced populations in eastern Australia, and to a lesser extent in South Africa; commercially fished throughout its range, particularly in Pakistan and India. Historically common in many parts of its range, and a familiar shark due to its popular use in public aquaria as well as supporting dive tourism operations globally. Not usually dangerous to people. IUCN Red List conservation status Vulnerable to Critically Endangered, depending on population, but the health of most populations is unknown. Given the declines reported in most areas where the population status of the species is known, as well as its philopatric habit, it can be assumed to be Near Threatened.

FAMILY ODONTASPIDIDAE

Sandtiger sharks

Brett A Human

Large-sized (to at least 4.5 m TL) with stout cylindrical to compressed body and long head (HL ~25% TL); snout moderately elongate, slightly depressed and bluntly conical; 5 paired gill slits, large, lateral and not extending dorsally, with all slits before pectoral-fin origins. Eyes moderately large, 1.6–2.8% TL, set laterally on head over mouth without lateral head ridges underneath; no nictitating eyelid; spiracles minute. Mouth parabolic, subterminal, extending behind eyes, with lip folds. Teeth large, similar in both jaws, although identifiable as symphysials, anteriors, intermediates, laterals and posteriors; teeth erect with long cusps and 1–3 lateral cusplets either side of median cusp, becoming compressed posteriorly; tooth counts 34–56/36–46. Nasal flaps small, without nasal barbels; no oronasal grooves. Fins angular and weakly falcate or rounded. Two spineless dorsal fins; 2nd dorsal fin smaller than 1st. Pectoral fins medium-sized and broad; pectoral-fin origin behind 5th gill slit. Pelvic fin smaller than 1st dorsal fin. Anal fin subequal to 2nd dorsal fin; anal-fin base slightly posterior to 2nd dorsal-fin base. Peduncle compressed, without lateral keels, and with upper crescentic precaudal pit, but no lower pit. Caudal fin heterocercal, its dorsal margin <⅓ precaudal length.

Reproductive mode presumed yolk-sac viviparous with oophagy. Patchily distributed throughout tropical and temperate oceans. Occur close inshore to oceanic, generally littoral or epipelagic, but known to 1 600 m deep. Common to rare. One genus and 2 species, both in WIO.

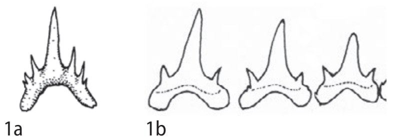
GENUS *Odontaspis* Agassiz 1838

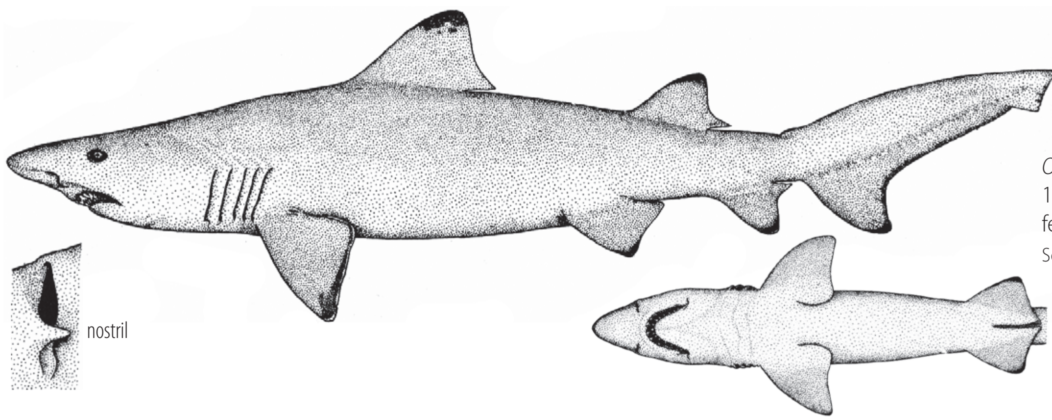
Snout relatively long, preorbital length 0.8–1.2 times mouth width. Fins angular and weakly falcate or rounded; 1st dorsal fin larger than 2nd dorsal fin, pelvic fins and anal fin; 1st dorsal-fin origin closer to pectoral fins than to pelvic fins. Teeth erect, with elongated median cusp and 1–3 much shorter cusplets on either side. Scattered distribution in tropical and temperate waters. Two species, both in WIO.

KEY TO SPECIES

1a Dorsal fins angular and weakly falcate; bump on leading edge of caudal-fin upper lobe before precaudal pit; teeth with 2 or 3 pairs of lateral cusps either side of median cusp .... ***O. ferox***

1b Dorsal fins rounded; no bump on leading edge of caudal-fin upper lobe; teeth with single pair of lateral cusps either side of median cusp .... ***O. noronhai***





Odontaspis ferox,
110 cm TL, immature
female (South Africa).
Source: Bass *et al.* 1975

Odontaspis ferox (Risso 1810)

Smalltooth sandtiger PLATE 23

Squalus ferox Risso 1810: 38 (Nice, France, Mediterranean Sea).
Odontaspis herbsti: Bass *et al.* 1975*.
Odontaspis ferox: D'Aubrey 1969*; Bauchot & Bianchi 1984*; Compagno 1984*, 2001*; Gubanov 1985; SSF No. 19.2*; Compagno *et al.* 1989*; Randall & Anderson 1993; Marine Research Section [Maldives] 1997*; Winterbottom & Anderson 1997; Adam *et al.* 1998*; Morón *et al.* 1998; Heemstra & Heemstra 2004; Compagno *et al.* 2005*; Ebert 2013*; Ebert *et al.* 2013*; Stone & Shimada 2019.

Diagnosis as for genus. Teeth erect, with elongated median cusp and 2 or 3 pairs of lateral cusps; 2 rows of symphysial teeth in upper and lower jaws, and 2–5 rows of intermediate teeth in upper jaw; gill filaments not protruding from gill slits; tooth count 46–56/36-46. Vertebrae 177–183; spiral valve turns 32–34.

Body grey or grey-brown dorsally, paler ventrally; variably with or without large darker spots; no pale blotch on 1st dorsal fin; extreme piebald colour variant recorded in Mediterranean Sea. Attains ~4.5 m TL.

DISTRIBUTION Probably circumglobal, fragmented populations, in warm-temperate to tropical deep water of open ocean, including Mediterranean Sea. WIO: Tanzania (Pemba I.), South Africa (KwaZulu-Natal and possibly Transkei region), Melville Bank, southern Madagascar, Chagos, Maldives and Sri Lanka.

REMARKS Uncommon to rare, and rarely encountered. Mostly known from deep inshore coastal waters, on or near bottom and near reef gullies, but possibly epipelagic. Feeds on small bony fishes, shrimp and squid. Incidentally caught in commercial fisheries by gillnets, longlines and trawl gear, particularly in Mediterranean Sea, Japan and Australia. The subject of ecotourism dives off Colombia (Malpelo I.) and Lebanon; has been exhibited in public aquaria with limited success. IUCN Red List conservation status Vulnerable, but listed as possibly Endangered in Mediterranean Sea, and protected in parts of Australia.

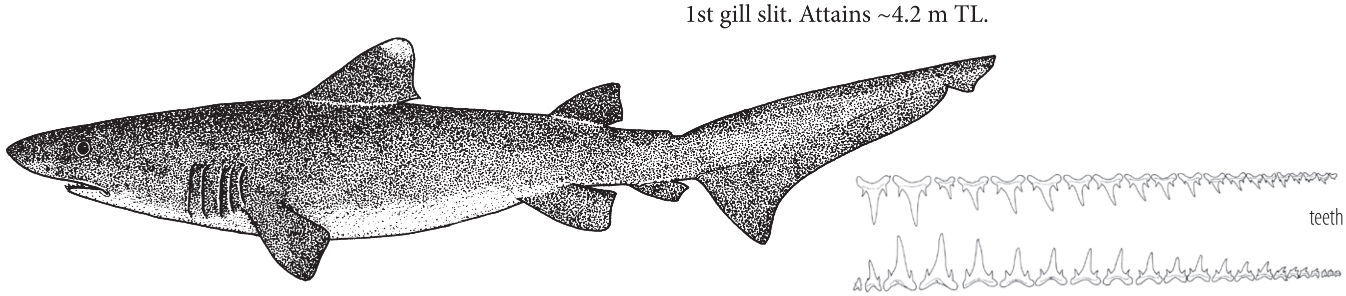
Odontaspis noronhai (Maul 1955)

Bigeye sandtiger PLATE 23

Carcharias noronhai Maul 1955: 3, Figs. 1–4 (Madeira, North Atlantic).
Odontaspis noronhai: Compagno 1984*, 2001*; Morón *et al.* 1998; Compagno *et al.* 2005*; Ebert 2013; Ebert *et al.* 2013*; Stone & Shimada 2019.

Diagnosis as for genus. Large eyes. Teeth erect with elongated central cusp and pair of lateral cusps; 1 or no rows of symphysial teeth in upper jaw, and 2–4 rows of symphysial teeth in lower jaw; 1 or 2 rows of intermediate teeth in upper jaw; tooth count 34–43/37–46. Spiral valve turns 30.

Body dark reddish brown, sometimes greyish or purplish to black, without darker spots; sometimes with white blotch on 1st dorsal-fin apex; bright red gill filaments may protrude from 1st gill slit. Attains ~4.2 m TL.



Odontaspis noronhai

DISTRIBUTION Possibly circumglobal in deep warm waters, but with disjunct populations: scattered records from Atlantic (Brazil and Mexico), central Pacific (including Hawaii) and Indian oceans. WIO: India, Sri Lanka and possibly Seychelles.

REMARKS Rare and poorly known from very few records. Oceanic; primarily mesopelagic, but also epipelagic to demersal. May undergo diurnal vertical migrations, inhabiting deep water by day and near surface at night; some evidence of seasonality in Brazilian waters, indicating the species may also be migratory. Very rare bycatch of oceanic longline fisheries. IUCN Red List conservation status Data Deficient, although a prohibited catch in the United States.

FAMILY MITSUKURINIDAE

Goblin shark

David A Ebert

Body soft, somewhat flabby, and slender, with unmistakable snout flattened as long blade-like rostrum; head nearly as long as body. Eyes small, spiracles very small; 5 paired gill slits, broad, with exposed filaments. Mouth large, broadly arched, with highly protrusible jaws; anterior teeth very long and slender with single cusp; tooth count 35–53/31–62. Dermal denticles small, with erect narrow cusps, making skin rough. Two dorsal fins, small, rounded, nearly equal in size, and smaller than pelvic fins and anal fin; pectoral fins small and broad; caudal-fin dorsal margin elongate, but <½ body length, and no lower lobe.

Monotypic.

Mitsukurina owstoni Jordan 1898

Goblin shark PLATE 24

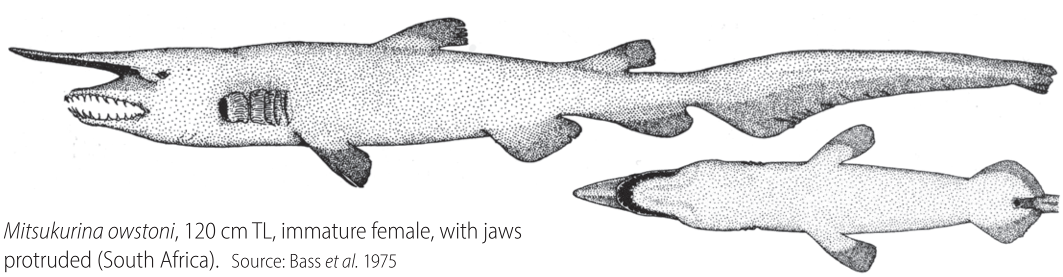
Mitsukurina owstoni Jordan 1898: 200, Pls. 11–12 (Sagami Sea, Japan); Bass, D'Aubrey & Kistnasamy 1975*; Piotrovsky & Prut'ko 1980; SSF No. 17.1*; Compagno *et al.* 1989*; Compagno 2001*; Compagno *et al.* 2005*; Yano *et al.* 2007; Last & Stevens 2009*; Ebert 2013*; Ebert *et al.* 2013*.

Diagnosis as for family. Vertebrae 122–125; spiral valve turns 18–23.

Colour in life spectacular pinkish white, with bluish fins; preserved specimens uniformly grey or brown. Attains at least 5.5 m TL, possibly 6.2 m TL.

DISTRIBUTION Circumglobal in temperate to tropical seas (patchy), with records from western and eastern Atlantic, western Pacific (Taiwan, Japan, Australia, New Zealand), eastern Pacific (southern California), and Indian Ocean. WIO: South Africa (Western Cape to KwaZulu-Natal) and Mozambique seamount range.

REMARKS Very poorly known; occurs over outer continental shelf and upper slope, to at least 1 300 m deep, and off seamounts. Its soft body and the prey items it consumes suggest it is poor-swimming and mesopelagic. Reproduction presumed oophagous; gestation period and litter size unknown; size at birth 80–90 cm TL. Males mature at ~265 cm TL, and females at >400 cm TL. Diet includes small pelagic fishes, pelagic crabs and cephalopods. Infrequent bycatch of deepwater fisheries, the jaws are sought by collectors.



Mitsukurina owstoni, 120 cm TL, immature female, with jaws protruded (South Africa). Source: Bass *et al.* 1975

FAMILY **PSEUDOCARCHARIIDAE**

Crocodile shark

Brett A Human

Small-sized (diminutive among lamniforms), with slender, cylindrical body and long head (HL ~⅓ TL); snout long and broadly conical. Nostrils small, with small nasal flaps. Five paired gill slits, broad and lateral on body, extending onto dorsal surface of head, with all gill slits anterior to pectoral-fin origin. Eyes huge (diameter 3.6–4.9% TL), lateral on head, above front of mouth; no nictitans; spiracles very small, level with eyes and approximately over angle of mouth. Mouth large, subterminal, parabolic and extending well behind eyes, with highly protrusible jaws. Teeth large, monocuspidate, and similar in both jaws, although identifiable as anteriors, intermediates and laterals; anterior teeth elongate, becoming short and compressed posteriorly; teeth sexually dimorphic: females with longer and broader teeth. Fins small, low and broadly angular. Two spineless dorsal fins; 1st dorsal fin low, larger than 2nd, and about equally spaced between pectoral and pelvic fins. Pectoral fins much shorter than HL, origin behind 5th gill slit. Pelvic fins smaller than pectoral fins; pelvic-fin bases before 2nd dorsal-fin origin. Anal fin minute, smaller than 2nd dorsal fin; anal-fin origin opposite 2nd dorsal-fin insertion. Peduncle short, cylindrical to slightly depressed, with poorly developed lateral keel, and weak upper and lower precaudal pits (but upper pit better developed). Caudal fin heterocercal; upper lobe long, but dorsal margin <⅓ TL. Monotypic genus *Pseudocarcharias* Cadenat 1963.

Pseudocarcharias kamoharai (Matsubara 1936)

Crocodile shark PLATE 24

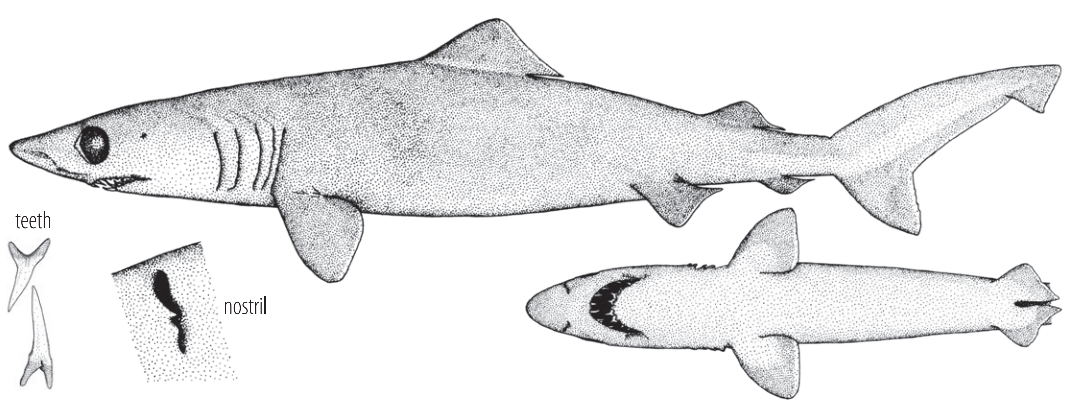
Carcharias kamoharai Matsubara 1936: 380 (Kôti fish market, Japan); D'Aubrey 1964*.
Odontaspis kamoharai: Bass *et al*. 1975*.
Pseudocarcharias kamoharai: Compagno 1984*, 2001*; SSF No. 18.1*; Compagno *et al*. 1989*; Romanov & Samorov 1994*; Anderson *et al*. 1998; Morón *et al*. 1998; Compagno *et al*. 2005*.

Diagnosis as for family. Tooth count 22–29/21–26; vertebrae 146–158; spiral valve turns 24–27.

Body dark grey, brown or lilac above, paler below, and snout sometimes greyish underneath; fin margins white and translucent; white blotch between mouth and gill slits in some Pacific specimens. Attains 120 cm TL.

DISTRIBUTION Circumtropical to subtropical in all seas, although patchily recorded. WIO: South Africa, Mozambique, Madagascar, Seychelles, Chagos, Maldives and Sri Lanka; not known from Red Sea and Persian/Arabian Gulf.

REMARKS D'Aubrey (1964) compared a specimen captured off Cape Town, South Africa, to all other known synonyms for this species, concluding that only a single species exists worldwide. Biology poorly known; its morphology suggests a strong-swimming, active, predatory shark. Reproduction mode yolk-sac viviparity and oophagy, potentially adelphophagy given low litter size of 2–4. Diet includes small pelagic fishes, shrimp and squid. Uncommon (except previously locally common in Mozambique Channel); predominately oceanic, epipelagic and possibly mesopelagic, seldom found close inshore; recorded to 590 m deep. A bycatch of pelagic longlines.



Pseudocarcharias kamoharai, 81 cm TL, mature female. Source: Bass *et al*. 1975

FAMILY MEGACHASMIDAE

Megamouth shark

Brett A Human

Gigantic filter-feeding shark with cylindrical, relatively flabby body tapering towards caudal fin, and massive head (HL ~⅓ TL). Snout short and broadly rounded, giving head bulbous appearance; nostrils small, with small nasal flaps; 5 paired gill slits, moderately large and lateral on body; gill rakers finger-like, cylindrical, on internal gill arches. Eyes moderately large, diameter <⅓ length of largest gill slit, set laterally on head, above and before corners of mouth; no nictitans; spiracles minute. Mouth huge, terminal, broadly arched, and extending behind eyes. Teeth small, numerous, hook-shaped, unicuspid, similar in both jaws, with >100 rows in each jaw, but with toothless gap at symphyses. Pectoral fins long and narrow, but shorter than HL, origin under 4th gill slit. Other fins small: 2 spineless, triangular dorsal fins; 1st dorsal fin nearly twice size of 2nd, and closer to pectoral fins than to pelvic fins; pelvic fins smaller than 1st dorsal fin; anal fin behind and smaller than 2nd dorsal fin. Peduncle short, compressed, with upper precaudal pit and no ridges. Caudal fin hypercercal: upper lobe very long, <½ body length, and lower lobe short but well-developed.

Monotypic.

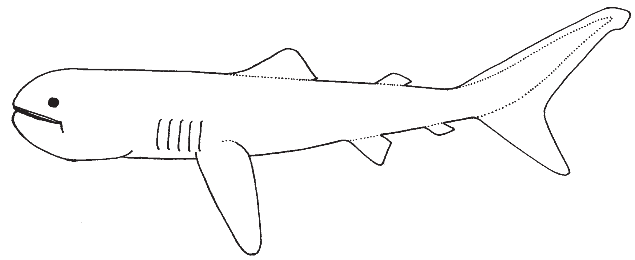
Megachasma pelagios Taylor, Compagno & Struhsaker 1983

Megamouth shark PLATE 24

Megachasma pelagios Taylor, Compagno & Struhsaker 1983: 96, Figs. 2–5 (off Oahu I., Hawaii); Compagno 1990*, 2001*; Nelson *et al.* 1997*; Smale *et al.* 2002*; Ebert 2003*; Compagno *et al.* 2005*; Last & Stevens 2009*; Ebert *et al.* 2013*.

Diagnosis as for family. Vertebrae 139–151; spiral valve turns 23 or 24.

Body grey to dark grey, paler below; lower jaw often with numerous large dark spots, and luminous bar visible above upper lip when jaw extended; pale margins on tips and posterior edges of pectoral fins and pelvic fins. Attains 5.5+ m TL.



Megachasma pelagios, 190 cm TL, juvenile (Atlantic Ocean).

DISTRIBUTION All tropical and some temperate seas, but few records, mostly from the Pacific (Taiwan, Philippines, Japan and Hawaii). WIO: one specimen found washed ashore in South Africa (Nature's Valley, Western Cape).

REMARKS Reproduction assumed yolk-sac viviparity, possibly with intrauterine cannibalism. One of three species of filter-feeding sharks; jaw morphology suggests it uses gulping action to feed on plankton, mainly euphausiids, copepods and jellyfish; a band of luminescent tissue on the upper lip may attract prey. Oceanic and coastal over very deep water; primarily tropical but may stray into temperate water following warm ocean currents. Epipelagic, with evidence that it migrates vertically in diurnal cycle following migrations of euphausiid shrimps (krill), which migrate from 5–40 m at night to ~600 m during the day. Specimens often found scarred by attacks from cookiecutter shark *Isistius brasiliensis*. Known since 1976, rarely seen and presumed rare throughout its (possibly fragmented) range; an extremely rare incidental bycatch of various coastal and high-seas fisheries, and some specimens found washed ashore.

FAMILY ALOPIIDAE

Thresher sharks

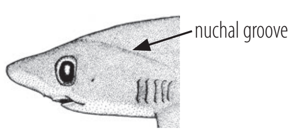
Brett A Human

Large- to very large-sized (to ~6 m TL) with stout, cylindrical body; HL <⅛ TL; snout moderately long and conical; 5 paired gill slits, short and lateral, not extending onto dorsal surface of head, with 4th and 5th gill slits over pectoral fins. Eyes large, 1.8–4.3% TL, lateral to dorsolateral and above mouth; no nictitans; spiracles minute, level with eyes, and posterior to eyes by about twice snout length. Nostrils small, with small nasal flaps and no oronasal groove. Mouth small, subterminal, parabolic to broadly arching, extending behind eyes; and lip folds present or absent. Teeth small to moderate, similar in both jaws, although identifiable as symphysials (absent in *Alopias superciliosus*), anteriors, intermediates and laterals; unicuspid, erect, slender and elongated to oblique and compressed, with small secondary cusp posterior to primary cusp; tooth counts 19–52/20–50. Fins large or small and falcate. Two spineless dorsal fins; 1st dorsal fin high and falcate, 2nd dorsal fin minute. Pectoral fins large, long and narrow, broadly to narrowly pointed. Pelvic fins moderately large, falcate, approximately size of 1st dorsal fin. Anal fin low, minute, equivalent in size to 2nd dorsal fin; anal-fin base behind 2nd dorsal-fin base. Peduncle short, slightly compressed, without lateral keels, and with crescentic upper and lower precaudal pits. Caudal fin strongly heterocercal; upper lobe extremely long, equal to body length; lower lobe moderately developed.

Wide-ranging in tropical to cold-temperate seas. Reproductive mode yolk-sac viviparity with oophagy. All are active swimmers and popular game fish. Use their enormous tails to corral and stun smaller fish for feeding, behaviour that is confirmed by the high numbers of thresher sharks caught by their tails in longline fisheries due to the sharks whipping the live bait on the hooks. One genus, *Alopias* Rafinesque 1810, with 3 species, all in WIO.

KEY TO SPECIES

1a Deep nuchal groove from above eye to over gill slits; eyes huge, encroaching onto nearly flat interorbital space ...... ***A. superciliosus***



1b Nuchal groove rudimentary or absent; interorbital space strongly convex **2**

2a Pectoral fins falcate and sharply pointed; lip folds present; teeth elongate and unicuspid ...... ***A. vulpinus***

2b Pectoral fins nearly straight and narrowly rounded; no lip folds; teeth oblique with secondary cusp ...... ***A. pelagicus***

Alopias pelagicus Nakamura 1935

Pelagic thresher

PLATE 25

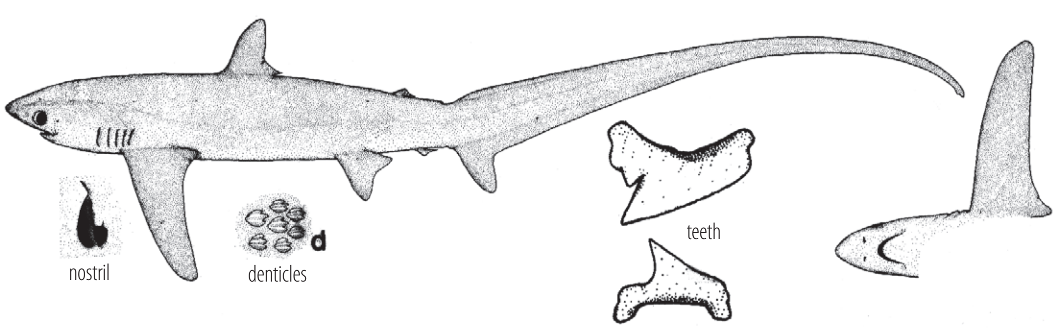
Alopias pelagicus Nakamura 1935: 2, Pl. 1, Fig. 1 (Taiwan); Gubanov 1972; Bass *et al.* 1975*; Compagno 1984*, 1986*, 2001*; SSF No. 16.1*; Compagno *et al.* 1989*; Cliff & Wilson 1994*; Randall 1995*; Anderson *et al.* 1998; Morón *et al.* 1998; Bonfil & Abdallah 2004*; Compagno *et al.* 2005*; Ebert *et al.* 2013*.

Pectoral fins nearly straight and narrowly rounded. Mouth parabolic, without lip folds; teeth oblique, with small secondary cusp posterior to primary cusp, and with symphysial teeth; tooth count 41–45/37–48. Vertebrae 453–477.

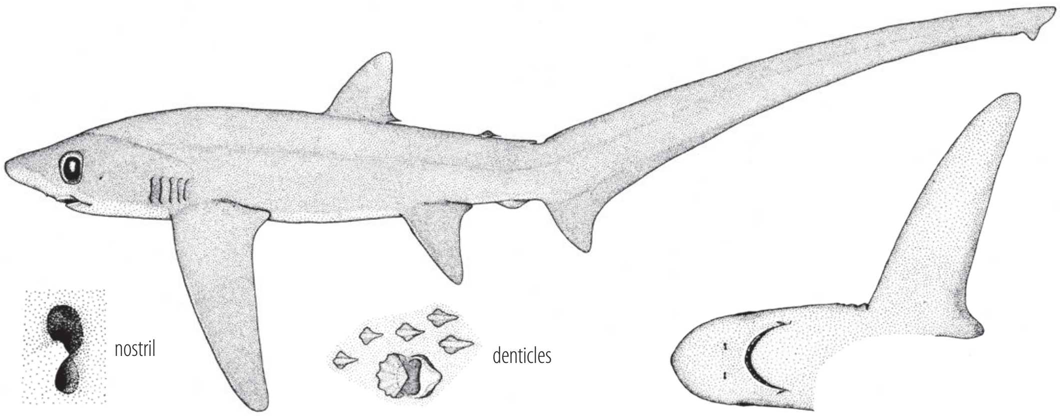
Body metallic pale blue to dark blue or grey, above and on fins, changing to white below level of pectoral fins. Attains 3.8 m TL.

DISTRIBUTION Tropical to temperate waters of Indo-Pacific. WIO: Gulf of Oman, Red Sea, Gulf of Aden, Arabian Sea, Kenya, Tanzania, South Africa (KwaZulu-Natal), Maldives and Sri Lanka.

REMARKS Historically confused with thresher shark *A. vulpinus* in the Indian Ocean, resulting in few reliable records of this species from the region. Oceanic, epipelagic, and apparently rare in inshore waters of Indian Ocean. Behaviour and biology poorly known, and virtually unknown in WIO. Reproduction in the Pacific is possibly aseasonal; gestation <1 year, with litters of 2; the Gulf of Aden may be used as pupping grounds. Taken as a bycatch in longline fisheries where it occurs. IUCN Red List conservation status Endangered globally.



Alopias pelagicus, 2.8 m TL, immature female (South Africa). Source: Bass *et al.* 1975



Alopias superciliosus, 1.6 m TL, immature female (South Africa). Source: Bass *et al.* 1975

Alopias superciliosus (Lowe 1841)

Bigeye thresher PLATE 25

Alopecias superciliosus Lowe 1841: 39 (Madeira, North Atlantic).
Alopias superciliosus: Gubanov 1972, 1978; Bass *et al.* 1975*; Gruber & Compagno 1981; Compagno 1984*, 1986*, 2001*; SSF No. 16.2*; Compagno & Smale 1986; Compagno *et al.* 1989*; Randall & Anderson 1993; Cliff & Wilson 1994*; Marine Research Section [Maldives] 1997*; Morón *et al.* 1998; Bonfil & Abdallah 2004*; Heemstra & Heemstra 2004; Compagno *et al.* 2005*; Ebert *et al.* 2013*.

Pectoral fins weakly falcate and somewhat pointed. Eyes huge, with deep nuchal groove above eye to over gill slits. Mouth broadly rounded, without lip folds. Teeth erect and unicuspid, slender and elongate (as compared with thresher shark *A. vulpinus*), without secondary cusps, and no symphysial teeth; tooth count 22–27/20–24. Vertebrae 219–319.

Body dark grey, varying from purplish to brownish dorsally and on fins, changing to white below level of pectoral-fin bases. Attains 4.8 m TL.

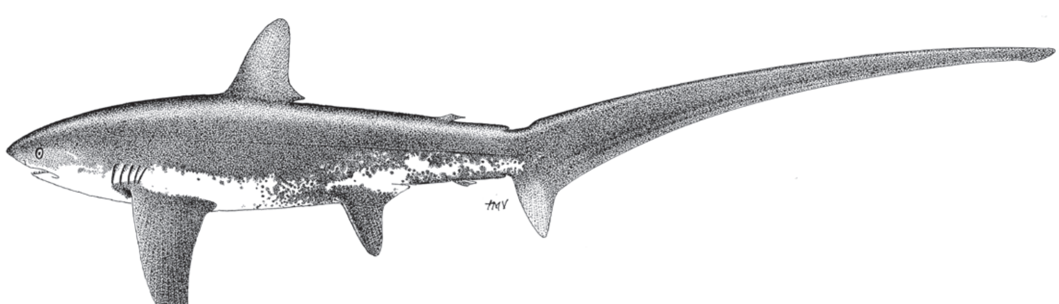
DISTRIBUTION Circumglobal in tropical to temperate seas, including western Mediterranean Sea. WIO: Red Sea, Gulf of Aden to Tanzania, South Africa (KwaZulu-Natal; Cape Peninsula), Madagascar, Maldives and Sri Lanka.

REMARKS Readily identifiable from other thresher sharks by the arrangement of the eyes which give this species dorsal binocular vision. Reproduction probably aseasonal, with litters of 2–4. Epipelagic and neritic, oceanic to close inshore, and more common in inshore waters than pelagic thresher *A. pelagicus*. Feeds largely on pelagic fishes, but also demersal fishes and squid. Caught as a bycatch primarily in longline fisheries, but also by gillnets and trawls. IUCN Red List conservation status Vulnerable globally.

Alopias vulpinus (Bonnaterre 1788)

Thresher shark PLATE 25

Squalus vulpinus Bonnaterre 1788: 9 (Mediterranean Sea).
Alopecias vulpes: Bleeker 1878; Sauvage 1891; Gilchrist 1902.
Alopias vulpes: Thompson 1914; Barnard 1925.
Alopias pelagicus: D'Aubrey 1964*.
Alopias vulpinus: Smith 1949*; Gubanov 1972, 1978; Bass *et al.* 1975*; Compagno 1984*, 1986*, 2001*; SSF No. 16.3*; Compagno *et al.* 1989*; Compagno *et al.* 1991; Randall & Anderson 1993; Cliff & Wilson 1994*; Marine Research Section [Maldives] 1997*; Winterbottom & Anderson 1997; Bonfil & Abdallah 2004*; Heemstra & Heemstra 2004*; Compagno *et al.* 2005*; Ebert *et al.* 2013*.



Alopias vulpinus, 3.5 m TL, female (South Africa). Source: SSF

Pectoral-fin tips acute; 1st dorsal-fin height greater than peduncle depth; caudal-fin upper lobe nearly equal to body length. Mouth parabolic, with lip folds. Teeth erect, unicuspid, relatively broad-based and compressed (as compared with bigeye thresher *A. superciliosus*), without secondary cusps, and with symphysial teeth; tooth count 32–52/25–50. Vertebrae 230–364.

Body dark grey or bluish dorsally and on fins, flanks sometimes silvery or coppery, and white below; white on at least part of gill region and over pectoral-fin bases; pectoral-fin tips sometimes white dorsally. Attains at least 5.8 m TL, possibly 6.3 m TL.

DISTRIBUTION Nearly circumglobal in tropical to cold-temperate seas, including throughout Mediterranean Sea. WIO: Pakistan, Gulf of Oman, Red Sea, Gulf of Aden to Tanzania, South Africa (Western Cape to KwaZulu-Natal), Madagascar, Mauritius, Chagos, Maldives, India and Sri Lanka.

REMARKS Litters of 2–4 (occasionally 6); gestation period (in NE Pacific) 9 months. Wide-ranging, oceanic, epipelagic to neritic, although most common near land and in temperate waters. Behaviour poorly known, but populations in various oceans may be distinct with differing demographics; horizontal and vertical sexual segregation occurs in northern WIO, and seasonally migratory in NE Pacific. Diet includes small pelagic and schooling fishes, some demersal and benthic fishes, cephalopods, shrimp and pelagic crabs; uses its tail to corral and stun fish prey. A bycatch of pelagic longlines and gillnets; in WIO, commonly caught 350–800 km off Somalia and NE of Maldives. IUCN Red List conservation status Vulnerable globally, with several differing regional assessments.

FAMILY CETORHINIDAE

Basking shark

David A Ebert

Unmistakably huge, stout, fusiform body; head moderately long; snout large, pointed and conical; gill slits enormous, nearly encircling head. Eyes small; spiracles very small. Mouth huge, subterminal; teeth minute, with single smooth-edged hook-shaped cusps, and >200 tooth rows on upper and lower jaws. Dermal denticles large, with hook-shaped cusps, very rough to touch. First dorsal fin very large, triangular, high and erect, its origin behind pectoral-fin free rear tips; 2nd dorsal fin smaller, <½ height of 1st dorsal fin, its origin before anal fin. Pectoral fins very large and broad, but their length less than HL. Pelvic fins smaller, less than 1st dorsal-fin height, but larger than 2nd dorsal fin. Peduncle depressed, with strong lateral keels, and with upper and lower crescent-shaped precaudal pits. Caudal fin large, lunate. Monotypic genus *Cetorhinus* Blainville 1816.

Cetorhinus maximus Gunnerus 1765

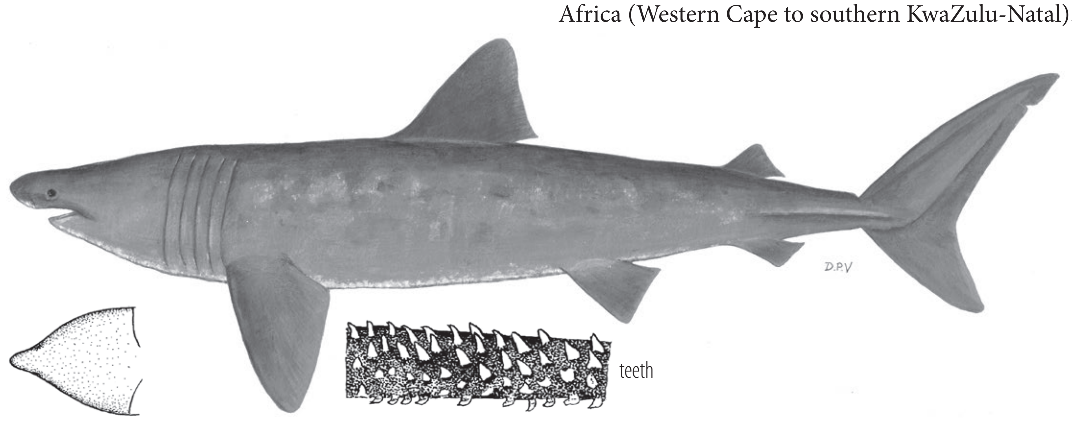
Basking shark PLATE 26

Cetorhinus maximus Gunnerus 1765: 33, Pl. 2 (northern Norway); Bass *et al.* 1975*; SSF No. 15.1*; Compagno *et al.* 1989*; Compagno *et al.* 2005*; Natanson *et al.* 2008; Ebert *et al.* 2013*.

Diagnosis as for family. Vertebrae 107–116; spiral valve turns 47–51.

Body colour dark and variable, often with mottling on flanks and back; white blotches under head. Attains >10 m TL.

DISTRIBUTION Circumglobal in all warm- to cold-temperate seas, known to make transoceanic migrations. WIO: South Africa (Western Cape to southern KwaZulu-Natal).



Cetorhinus maximus, ~7.5 m TL, adult female (South Africa). Source: SSF; dorsal view of head, and teeth (South Africa). Source: SFSA

REMARKS Oophagous, with litters of 1–6; size at birth ~1.5–2 m TL; gestation period unknown. Exceeded in size only by the whale shark (*Rhincodon typus*); males mature at ~4–5 m TL, and females at ~8–9 m TL. Juveniles >3 m TL rarely encountered, suggesting pupping and nursery grounds located in planktonic-rich oceanic waters far from populated coastal areas. Previous age estimates for this species are known to be erroneous as vertebral bands are associated with growth and not age. Oceanic, coastal and pelagic, will dive to several hundred metres and remain at depth as they migrate between hemispheres. Docile and often seen cruising slowly ('basking') at surface in cooler waters, these enormous filter-feeding sharks consume vast quantities of zooplankton, including copepods and planktonic larvae. When feeding, adults swim at ~2 knots and will pass ~2 000 tons of water over the gills per hour as they close their mouth every 30–60 seconds to ingest filtered plankton trapped in their gill rakers; an individual may have half a ton of food in its stomach at any time. Sometimes found swimming in large groups. A target fishery for this species has occurred in the northeastern Atlantic and North Pacific; occasionally indirectly caught in other fisheries. IUCN Red List conservation status Endangered globally, due to regional fishing pressure.

FAMILY LAMNIDAE

Mackerel sharks

Brett A Human and David A Ebert

Large- to very large-sized (to 6+ m TL) with slender to stout fusiform body, and conical head (HL 20–30% TL). Five paired gill slits, lateral on body and extending dorsally, with all gill slits anterior to pectoral-fin origins. Snout relatively long, bluntly to sharply conical. Eyes lateral or dorsolateral on head, over mouth; eye diameter 0.7–3.1% TL; no nictitans; spiracles minute or absent. Nasal flaps small, without nasal barbels or oronasal grooves. Mouth broadly arched, subterminal, extending behind eyes, with poorly developed lip folds. Teeth large to very large, similar in both jaws, although identifiable as anteriors, intermediates, laterals and posteriors; teeth varying from long and elongate with strong median cusp, with or without lateral cusplets, to compressed, triangular and blade-like with serrated margins; tooth counts 22–31/20–29. Fins triangular or rounded to falcate. Two spineless dorsal fins; 1st dorsal fin high, much larger than 2nd, its origin over pectoral-fin bases or rear margins. Pectoral fins long and narrow; pectoral-fin origin behind 5th gill slit. Pelvic fins much smaller than pectoral fins. Anal fin tiny, equivalent in size to 2nd dorsal fin; anal-fin base under or slightly posterior to 2nd dorsal-fin base. Peduncle moderately long and strongly depressed, with 1 or 2 well-developed lateral keels, and with upper and lower crescentic precaudal pits. Caudal fin lunate. Vertebrae 153–197; spiral valve turns 38–55.

Reproductive mode yolk-sac viviparity, with oophagy. All lamnids are warm-blooded and maintain a body temperature higher than the ambient water temperature, facilitating their highly active and predatory habits, with the family containing some of the swiftest fishes known. Found close inshore to oceanic, generally littoral or epipelagic, but known to ~1 280 m deep. Lamnid species are either common, uncommon or endangered, with some particularly susceptible to high-seas longline fisheries; all are regarded as game fish. Distributed throughout all tropical, temperate and subpolar oceans (absent only from icepack regions in polar oceans).

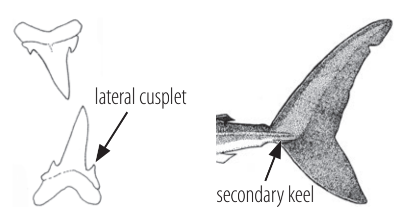
Three genera and 5 species; all genera and 4 species in WIO.

KEY TO GENERA

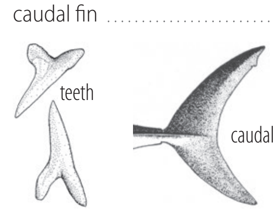
1a Teeth broadly triangular and serrated .... ***Carcharodon***

1b Teeth long, narrow, and without serrations 2

2a Teeth with small lateral cusplets; 1st dorsal-fin origin over pectoral-fin bases or inner margins; secondary keel on caudal fin .... ***Lamna***



2b Teeth without small lateral cusplets; 1st dorsal-fin origin behind pectoral-fin free rear tips; no secondary keel on caudal fin .... ***Isurus***



GENUS *Carcharodon* Smith 1838

Body cylindrical and moderately stout; peduncle with single well-developed lateral keel; eye diameter 0.7–1.8% TL. Teeth triangular, compressed, broad, and with serrations. One species.

Carcharodon carcharias (Linnaeus 1758)

White shark PLATE 26

Squalus carcharias Linnaeus 1758: 235 (western and northeastern Atlantic, and Mediterranean Sea).
Carcharodon capensis Smith 1849: no page no., Pl. 4 (Cape Seas, South Africa).
Carcharodon rondeletii: Gilchrist 1902; Thompson 1914.
Carcharodon carcharias: Barnard 1925; Fowler 1925; Smith 1949*; Farquhar 1963; D'Aubrey 1964*; SFSA No. 26*; Bass *et al.* 1975*; Compagno 1984*, 1986*, 2001*; SSF No. 14.1*; Compagno *et al.* 1989*; Cliff & Wilson 1994*; Smale & Heemstra 1997*; Cliff *et al.* 2000; Zuffa *et al.* 2002; Heemstra & Heemstra 2004*; Compagno *et al.* 2005*; Ebert *et al.* 2013*.

Diagnosis as for genus. First dorsal-fin origin over pectoral-fin inner margins; 2nd dorsal fin minute. Tooth count 20–28/ 20–28; vertebrae 170–187.

Body grey to dark blue-grey, sometimes brownish, blackish or bronzy dorsally, and abruptly white ventrally; eyes very black; pectoral fins black-tipped underneath, with or without black axillary spot on body near rear edge of pectoral fins; albinism recorded. Attains 6.4 m TL, but most adults <6 m TL.

DISTRIBUTION Worldwide in most temperate and tropical seas. WIO: Kenya to South Africa, Madagascar, Seychelles, Réunion, Mauritius, southern India and Sri Lanka, and possibly Red Sea; records from Arabian Sea and Persian/ Arabian Gulf need confirmation.

REMARKS One of the greatest known distributions for a shark; this wide geographic and habitat distribution has given rise to multiple synonyms. Generally uncommon but locally common in some areas; principally pelagic, but known from surfline to >1 250 m deep. Individuals are known to make transoceanic movements: in the Indian Ocean, tagged white sharks have travelled from South Africa to Australia and back within a span of months. Litters of 2–13; size at birth 110–160 cm TL; gestation period assumed >1 year. Feeds on a variety of bony fishes and elasmobranchs, other vertebrates (seabirds, pinnipeds and cetaceans), cephalopods and crustaceans. Larger individuals are a spectacular ambush predator of marine mammals, patrolling close to bottom and then launching upwards to strike prey close to surface, sometimes becoming airborne in the process. Relentlessly sensationalised in the media, particularly regarding infrequent but dangerous interactions with humans; paradoxically now the subject of dive tourism. IUCN Red List conservation status Vulnerable; a protected species in South Africa and in other countries outside the region due to historical persecution and its highly valued jaws and teeth.

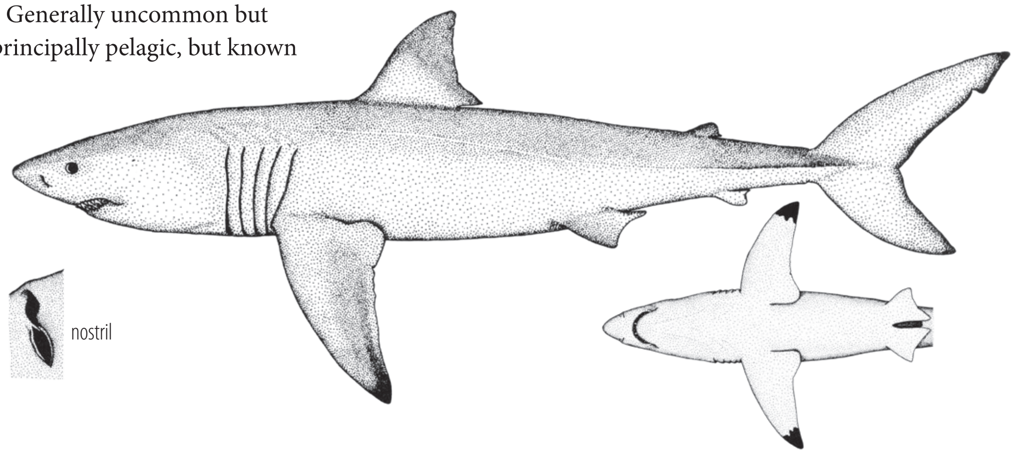
GENUS *Isurus* Rafinesque 1810

Body slender to robust, fusiform, and with single well-developed lateral keel on peduncle; eye diameter 1–3% TL. Teeth long, slender, and somewhat protrude from mouth; anterior teeth enlarged, with single, large, robust, smooth-edged cusp; upper and lower teeth similarly shaped. Two species, both in WIO.

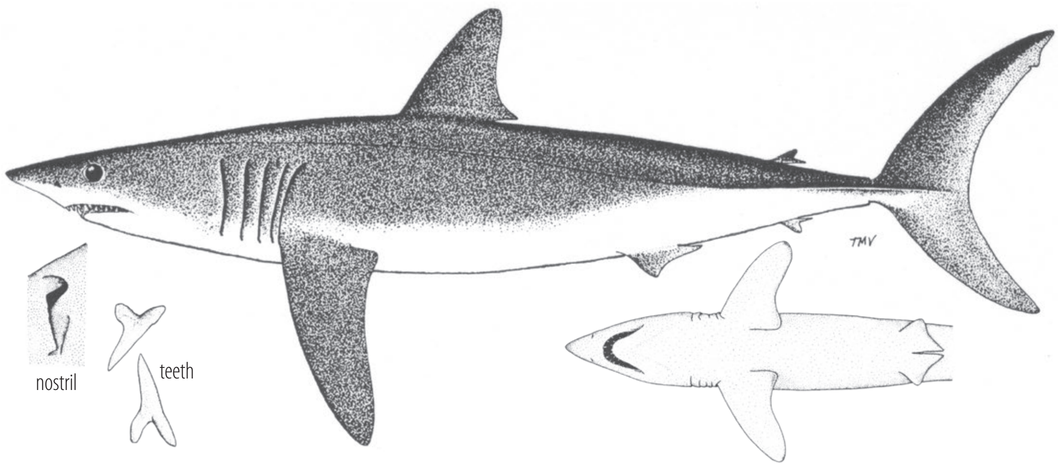
KEY TO SPECIES

1a	Ventral surface of snout and mouth white; anterior tooth cusps recurved forward; pectoral fins much shorter than HL; anal-fin origin below 2nd dorsal-fin base	***I. oxyrinchus***
1b	Ventral surface of snout and mouth dusky; anterior tooth cusps straight; pectoral fins long, about equal to HL; anal-fin origin below or behind 2nd dorsal-fin insertion	***I. paucus***

Carcharodon carcharias, jaws of a large specimen (South Africa).



Carcharodon carcharias, 177 cm TL, immature female (South Africa). Source: Bass *et al.* 1975



Isurus oxyrinchus, 250 cm TL, female; ventral view, ~100 cm TL, immature female (both South Africa). Source: SSF (lateral view); Bass *et al.* 1975 (ventral view)

Isurus oxyrinchus Rafinesque 1810

Shortfin mako PLATE 26

Isurus oxyrinchus Rafinesque 1810: 12, Pl. 13, Fig. 1 (Sicily, Mediterranean Sea); Smith 1957*; Bass *et al.* 1975*; Compagno 1984*, 1986*, 2001*; SSF No. 14.2*; Compagno *et al.* 1989*; Cliff *et al.* 1990; Anderson & Ahmed 1993*; Randall & Anderson 1993; Cliff & Wilson 1994*; Randall 1995*; Marine Research Section [Maldives] 1997; Winterbottom & Anderson 1997; Ebert 2001, 2003*; Al-Shuaily & Henderson 2003; Bonfil & Abdallah 2004; Heemstra & Heemstra 2004*; Compagno *et al.* 2005*; Last & Stevens 2009*; Ebert *et al.* 2013*.
Lamna glauca: Gilchrist 1902; Thompson 1914.
Isurus glauca: Barnard 1925.
Isurus glaucus: Smith 1949*, 1957*; D'Aubrey 1964*.
Isurus tigris africanus: Smith 1957*.

Body fusiform and relatively robust; snout long, acutely pointed; eye diameter <33% snout length. Teeth with single, large, smooth-edged cusps, similar in both jaws. First dorsal-fin origin behind pectoral-fin free rear tips; pectoral fins shorter than HL; anal-fin origin under midbase of 2nd dorsal fin; caudal fin crescent-shaped. Peduncle with strong keel. Tooth count 24–26/22–32; vertebrae 183–196; spiral valve turns 47–48.

Body brilliant blue or purplish dorsally, becoming paler blue along flanks and white ventrally. Attains ~4 m TL, but most adults <3 m TL.

DISTRIBUTION Widespread in most tropical to warm-temperate seas, including Mediterranean Sea, Red Sea and coastal and oceanic waters throughout WIO.

REMARKS Litters of 4–25; size at birth 60–70 cm TL. Males mature at ~195 cm TL, at ~4 years; females mature at 270–300 cm TL, at 7–8 years. Reproductive cycle may be up to 3 years, including 15–18 month gestation period followed by 18 month resting stage; juveniles grow rapidly during first 2 years, nearly doubling their length. Coastal and oceanic, from surface to at least 500 m deep. Possibly the fastest swimming shark, known for its spectacular jumping ability when feeding on schools of fish or hooked by an angler. Feeds primarily on fishes, including other sharks, rays, mackerel, yellowtail, sea bass and swordfish, as well as squid; larger individuals will feed on sea turtles and small cetaceans. Has been implicated in attacks on people, particularly when provoked. The subject of directed fisheries worldwide and a popular big-game fish; highly valued for its meat and fins. IUCN Red List conservation status of most populations Endangered; Critically Endangered in Mediterranean Sea.

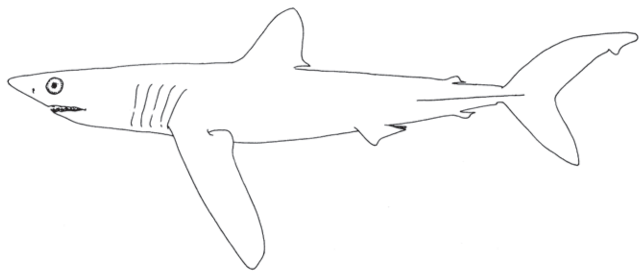
Isurus paucus Guitart Manday 1966

Longfin mako PLATE 27

Isurus paucus Guitart Manday 1966: 3, Figs. 1–3 (Cuba, western Atlantic); Compagno 1984*, 2001*; SSF No. 14.3*; Ebert 2001*, 2003*; Compagno *et al.* 2005*; Last & Stevens 2009*; Ebert *et al.* 2013*.

Body fusiform and relatively slender; snout narrow to bluntly pointed; eye diameter >33% snout length. Teeth with single, large, robust, smooth-edged cusp; shape similar in both jaws. Pectoral-fin length subequal to HL. Anal-fin origin slightly behind 2nd dorsal-fin origin. Peduncle with long, strong keel. Tooth count 24–26/22–24; vertebrae 195–197; spiral valve turns 54.

Body blue above and below, except for white midventral undersurface; underside of snout distinctly dusky, except in small juveniles. Attains 4.3 m TL.



Isurus paucus, 123 cm TL, immature male. Drawn from Garrick 1967

DISTRIBUTION Circumglobal in tropical to warm-temperate seas, but poorly recorded; commonly western Atlantic and central Pacific. WIO: Mozambique Channel, Madagascar and possibly off South Africa, but probably occurs throughout the region.

REMARKS Poorly known and infrequently encountered species, often misidentified as the better-known shortfin mako *I. oxyrinchus*. Litters of 2–8; size at birth 92–97 cm TL. Males mature at ~190 cm TL, and females at ~245 cm TL. Probably epipelagic, off continental shelf and over deep water in open ocean, but depth range unknown. Feeds primarily on schooling fishes and pelagic cephalopods. Despite its large size, has never been implicated in attacks on people. Of little commercial value as the flesh is soft and of poor quality.

GENUS *Lamna* Cuvier 1816

Body stout and fusiform, with 2 well-developed lateral keels on peduncle. Eyes 1.6–2.8% TL. Teeth elongate, with single small lateral cusps either side of median cusp. Global, in temperate to subpolar seas. Two species, 1 in WIO.

Lamna nasus (Bonnaterre 1788)

Porbeagle PLATE 27

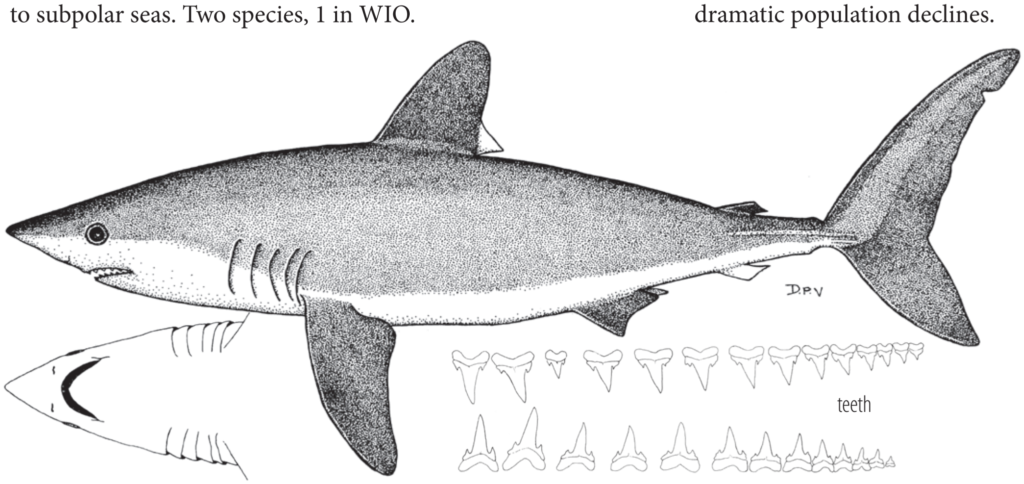
Squalus nasus Bonnaterre 1788: 10, Pl. 85, Fig. 350 (Cornwall, England).
Lamna nasus: Smith 1949*; Farquhar 1963; Nakaya 1971*; Bass *et al.* 1975*; Compagno 1984*, 1986*, 1990*, 2001*; SSF No. 14.4*; Compagno *et al.* 1989*; Compagno *et al.* 2005*; Last & Stevens 2009*; Ebert *et al.* 2013*.

Diagnosis as for genus. First dorsal-fin origin over pectoral-fin bases or inner margins. Tooth count 28–31/26–29; vertebrae 150–162.

Body grey to dark grey, sometimes bluish or blackish, abruptly changing to white ventrally, but no white patch above pectoral fins; 1st dorsal fin with distinctive white free rear tip; underside of head dusky in adults; abdomen blotched in some Southern Hemisphere adults as compared with no blotching and with white underside of head in Northern Hemisphere specimens. Attains 3.5 m TL.

DISTRIBUTION Antitropical and amphitemperate. In Northern Hemisphere: mostly North Atlantic and Mediterranean Sea, and absent from North Pacific. In Southern Hemisphere: most commonly found south of the region covered here and apparently only strays into the region. WIO: South Africa (south coast) and eastwards, but perhaps circumglobal in southern temperate seas.

REMARKS Swift and active shark, although its behaviour is poorly known. Coastal and oceanic on continental shelf, in littoral and epipelagic habitats, but recorded to 700 m deep. Migratory, moving inshore to surface waters in summer and offshore to deeper waters in winter. Mediterranean Sea appears to be a nursery ground. Feeds primarily on small pelagic and demersal bony fishes, but also sharks and squid. Heavily caught in both hemispheres as secondary target or in directed fisheries, especially by longline. Not dangerous to people. IUCN Red List conservation status Vulnerable globally, due to dramatic population declines.



Lamna nasus, 94 cm TL, immature male (South Africa); ventral head; teeth from larger specimen.
Source: FSO (lateral view); Bigelow & Schroeder 1948 (head); SSF (teeth)

ORDER CARCHARHINIFORMES

FAMILY PENTANCHIDAE

Deepwater catsharks

Brett A Human and David A Ebert

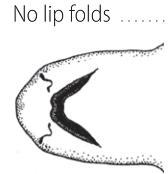
Generally small-sized, long and slender (most WIO species <69 cm TL), but a few are relatively stocky. Head length typically 20% TL; 5 pairs of gill slits, small to greatly enlarged, the last gill slit over or behind pectoral-fin origins. Snout broadly to acutely rounded, not depressed to strongly depressed and laterally expanded compared to rest of head, and tip upturned or not. Anterior nasal flaps not expanded, or short or extending to mouth, and separate or fused; nasal barbels absent; oronasal grooves present or absent. Eyes slit-like and dorsolateral, with rudimentary nictitans and strong subocular ridges, but no supraorbital crest; spiracles moderately large, set just behind eyes. Mouth inferior, long and arched, and with or without lip folds. Teeth multicuspidate (except monocuspidate in adult males of one species of *Apristurus* not known from WIO) and in multiple functional rows in both jaws. Fins rounded or weakly falcate. Two spineless dorsal fins (except one dorsal fin in *Pentanchus* from western Pacific), usually subequal; 1st dorsal fin above or behind pelvic-fin bases. Pectoral fins moderately sized and paddle-shaped. Pelvic fins moderately long and low. Anal fin long and low to high, its base usually longer than 2nd dorsal-fin base. Peduncle and caudal fin slender; peduncle without pits or keels; caudal fin heterocercal, lower lobe poorly developed. Sexual dimorphism of TL absent to extreme (with males attaining greater lengths than females) and also apparent in dentition of some species. Tooth counts 28–130/28–111; vertebrae 85–183; spiral valve turns 5–23.

Reproductive mode mostly oviparous, with females depositing egg cases on the substrate where the embryos develop and eventually hatch out. However, for some species the egg cases are retained *in utero* until the embryos are nearly completely developed. A few species are viviparous with a yolk sac whereby the embryos fully develop internally prior to the mother giving live birth to fully developed, free-swimming neonates. Deepwater catsharks are found worldwide in tropical to cold-temperate seas, with preferred temperatures likely contributing to a high degree of endemism. Most shallow-water species occur in tropical to warm-temperate regions and tend to be brightly coloured, whereas deep-sea forms tend to be more uniformly coloured. Sluggish, poor swimmers, and generally deep-dwelling on or near bottom, although some deep-sea species are known to migrate far off the bottom into the water column; in the WIO they are found from intertidal zone to deep-sea (>1 500 m), over soft bottom, on rocky or coral reefs and in kelp beds, and are rarely locally abundant. Some species may have become recently extirpated from parts of the WIO. Harmless to people. Generally not targeted in fisheries but often comprise a bycatch where abundant; some of the more colourful species are displayed and bred in aquariums.

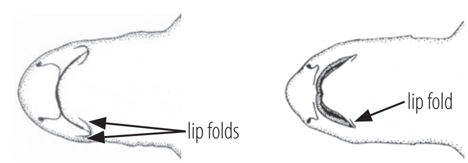
A large family of diverse sharks, with 11 genera and ~111 species; 5 genera (2 in >200 m) and 16 species in WIO in <200 m, with several additional deep-sea species awaiting formal description. The genera *Apristurus* Garman 1913 and *Bythaelurus* Compagno 1988 are both deep-sea groups, and the former is included here only in the key. Previous records of a species of *Parmaturus* Garman 1906 from the southwestern Indian Ocean are now known to be a *Bythaelurus* species (see Ebert [2013] for more information on the deep-sea genera).

KEY TO GENERA

1a No lip folds .... ***Holohalaelurus***



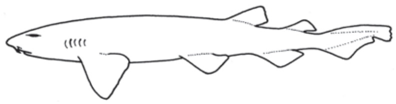
1b Lip folds on one or both jaws **2**



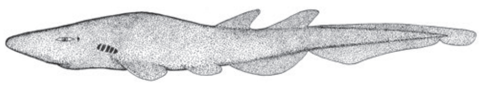
Continued …

KEY TO GENERA

2a Body firm; snout not strongly depressed or laterally expanded as compared to rest of head 3

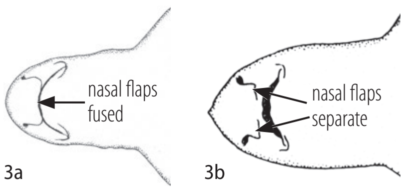


2b Body flaccid; snout strongly depressed and laterally expanded as compared to rest of head .... ***Apristurus*** [deep-sea group]



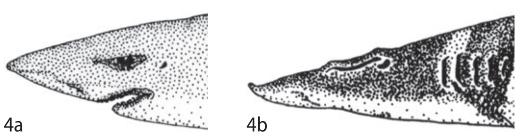
3a Nasal flaps extend to mouth, fused .... ***Haploblepharus***

3b Nasal flaps short, separate 4



4a Eyes not noticeably elevated; snout broadly rounded .... ***Bythaelurus*** [deep-sea group]

4b Eyes noticeably elevated; snout acutely rounded and tip pointed .... ***Halaelurus***



GENUS *Bythaelurus* Compagno 1988

Body usually slender; head moderately depressed. Eyes not noticeably elevated. Snout broadly rounded and not coming to a point, not strongly depressed, and tip not upturned. Upper and lower lip folds short. Nasal flaps weakly expanded, separate and not fused; no nasal barbels. Fins more or less rounded. Dorsal and anal fins more or less subequal. Pelvic fins more or less fused but never forming pelvic curtain; claspers stout to elongate, outer length 5–6 times width. No crest of enlarged denticles along upper peduncle or dorsal caudal margin. Stomach not inflatable. Tooth counts 62–99/63–101; vertebrae 117–142; spiral valve turns 7–10. Presumed size range 29–76 cm TL.

Genus was separated from *Halaelurus*. Patchily distributed in all oceans; recorded from 220–1 262 m. At least 12 species, with 9 species in WIO, but all recorded at depths of >200 m. *Bythaelurus lutarius* is included here nonetheless as it is likely to be trawled from shallower depths in the future. The other deepwater WIO species are: *B. alcockii* (Garman 1913) (resembling *B. hispidus*, but only tentatively placed in this genus), *B. bachi* Weigmann *et al*. 2016, *B. clevai* (Séret 1987) (Plate 27), *B. hispidus* (Alcock 1891), *B. naylori* Ebert & Clerkin 2015 (Plate 28), *B. stewarti* Weigmann *et al.* 2018, *B. tenuicephalus* Kaschner *et al*. 2015, and *B. vivaldii* Weigmann & Kaschner 2017.

Bythaelurus lutarius (Springer & D'Aubrey 1972)

Mud catshark

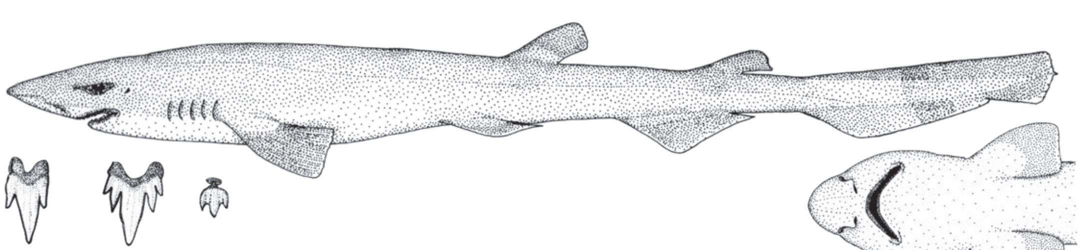
Halaelurus lutarius Springer & D'Aubrey 1972: 6, Fig. 1 (off Maputo Bay, Mozambique); Bass 1973; Bass *et al.* 1975*; Springer 1979*; Compagno 1984*, 1988; SSF No. 11.6*; Compagno *et al.* 1989*; Howe & Springer 1993; Sommer *et al.* 1996*.
Bythaelurus lutarius: Compagno 1999; Compagno *et al.* 2005*.

Anal-fin base twice length of 2nd dorsal-fin base; prenarial length equal to internarial distance. Tooth count 74/86; vertebrae 132; spiral valve turns 10.

Body uniformly drab grey, but sometimes with dusky saddles beneath dorsal-fin bases, and slightly paler ventrally. Attains 39 cm TL.

DISTRIBUTION WIO: Mozambique (patchy), Somalia, Socotra and Oman.

REMARKS Reportedly viviparous with yolk-sac placenta; litters of 2; size at birth 10–14 cm TL. Abundant where caught in Oman; recorded from 220–813 m, on continental slope, over mud bottom. Feeds on cephalopods, crustaceans and small bony fishes. Probably a bycatch of trawl fisheries.



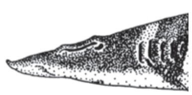
Bythaelurus lutarius, 24 cm TL, immature male (S Mozambique). Source: Bass *et al.* 1975

GENUS *Halaelurus* Gill 1862

Body slender; head moderately depressed. Eyes noticeably elevated. Snout acutely rounded and tip pointed, upturned or not upturned, and with or without knob; upper and lower lip folds short to minuscule; nasal flaps somewhat expanded, separate; no nasal barbels. Fins rounded to weakly falcate. Dorsal fins and anal fin more or less subequal. Pelvic fins sometimes partially fused, but never forming pelvic curtain; claspers stout to elongate, outer length 5–6 times width. No crest of enlarged denticles along upper peduncle and dorsal caudal margin. Stomach not inflatable. Tooth counts 54–60/41–55; vertebrae 117–142; spiral valve turns 7–10. Abundant to rare on continental shelf, inshore or offshore, in Indo-Pacific. At least 7 species, 4 in WIO.

KEY TO SPECIES

1a	Snout tip upturned	2
1b	Snout tip not upturned	3



1a

1b

2a	Mouth width 6–7% TL; saddle markings dusky with thin dark edges, and numerous small dark spots on body	***H. lineatus***
2b	Mouth width 7–9% TL; saddle markings prominent with broad dark edges, and no spots on body	***H. natalensis***
3a	Snout tip without knob	***H. boesemani***
3b	Snout tip with knob	***H. quagga***

Halaelurus boesemani Springer & D'Aubrey 1972

Speckled catshark

PLATE 32

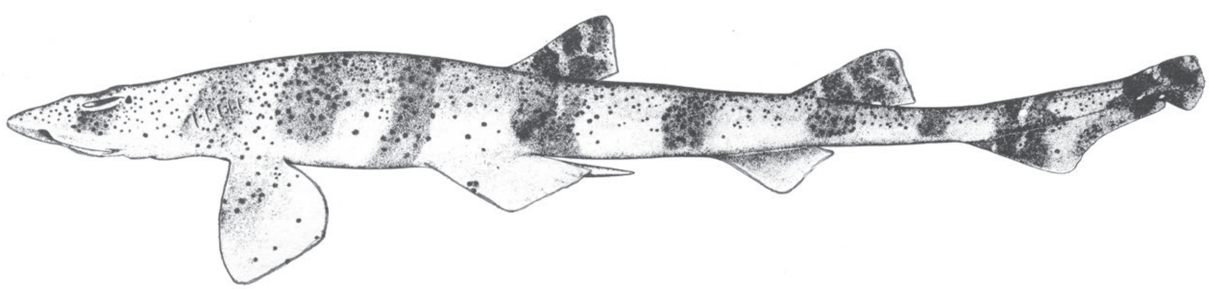
Halaelurus boesemani Springer & D'Aubrey 1972: 11, Fig. 1 (Somalia); Springer 1979*; Compagno 1984*, 1988; Bonfil & Abdallah 2004*; Compagno *et al*. 2005*; White *et al*. 2007.
Scyliorhinus buergeri: Regan 1908.
Scyliorhinus quagga: Norman 1939*.

Head broad; snout tip pointed (but not upturned) and without knob; mouth width 6–8% TL, mouth length 3–4% TL. Tooth count 57/55; vertebrae 135–139; spiral valve turns 6.

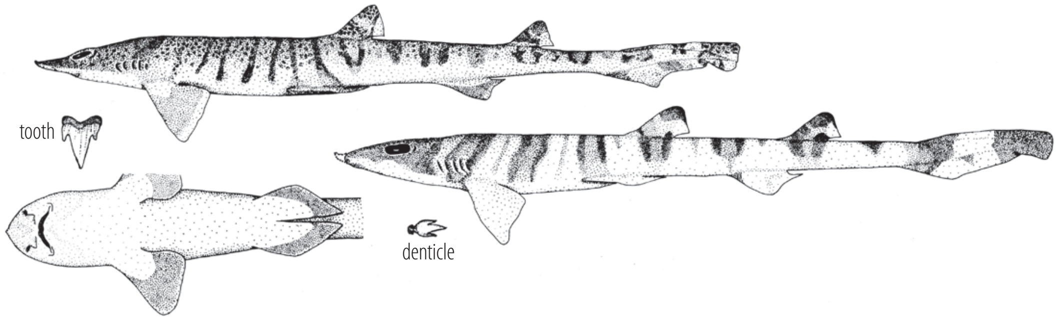
Body pale brown to yellowish brown background dorsally, with ~8 darker brown bands or saddle markings; numerous small dark spots scattered over body, dorsal and caudal fins, and large dark blotches on dorsal fins and caudal fin; paler ventrally and on pelvic and anal fins. Attains 48 cm TL.

DISTRIBUTION Indo-Pacific (range uncertain). WIO: Somalia and Gulf of Aden.

REMARKS Poorly known; previously confused with the western Pacific *H. buergeri* until it was separated as distinct by Springer & D'Aubrey (1972). Its presence beyond WIO needs to be reassessed as species recently described from Australia and Indonesia/Philippines were previously recorded as this species, and thus records of *H. boesemani* from Australia are erroneous and its presence in Indonesia is now questionable. Retained oviparity, with up to 4 egg cases per uterus. Probably uncommon with restricted range, on continental and insular shelves, at 37–91 m. Presumably subject to bycatch in demersal trawl and artisanal net fisheries.



Halaelurus boesemani (Somalia). Source: Springer & D'Aubrey 1972



Halaelurus lineatus, 48 cm TL, mature female (top); 13 cm TL, immature male paratype (bottom) (both South Africa). Source: Bass *et al.* 1975

Halaelurus lineatus Bass, D'Aubrey & Kistnasamy 1975

Banded catshark PLATES 28 & 32

Halaelurus lineatus Bass, D'Aubrey & Kistnasamy 1975: 12, Figs. 8, 20e (Durban shoreline, KwaZulu-Natal, South Africa); Springer 1979*; Compagno 1984*, 1988; SSF No. 11.5*; Compagno *et al.* 1989*; Heemstra & Heemstra 2004; Compagno *et al.* 2005*; White *et al.* 2007.
Scylliorhinus natalensis: Gilchrist & Thompson 1911; Gilchrist 1922.
Scyliorhinus natalensis: Fowler 1934.
Halaelurus natalensis: Smith 1950.

Head narrow; snout tip pointed and upturned with knob; mouth width 6–7% TL, mouth length 2% TL. First dorsal fin slightly larger than 2nd. Caudal-fin postventral margin concave. Tooth count 56–60/53–55; vertebrae 124–142; spiral valve turns 7.

Body pale brown background dorsally, with ~15 thin, prominent dark brown bands arranged in pairs outlining dusky saddles, and blanketed with many small dark spots; cream ventrally. Attains 56 cm TL.

DISTRIBUTION WIO: South Africa (Eastern Cape) to Mozambique (Beira).

REMARKS Relatively common, although with restricted range; previously confused with *H. natalensis*. Retained oviparity, with up to 8 egg cases per uterus; hatched in captivity at ~8 cm TL after 23–36 days, although young may be live born in the wild. Segregated, with gravid females predominating in northern regions of its range, and a larger proportion of males and juveniles occurring southwards and by depth. Found on continental shelf and upper slope, from surf zone to ~290 m deep. Feeds mostly on crustaceans, but also small bony fishes and cephalopods. A frequent bycatch of prawn trawl fishery.

Halaelurus natalensis (Regan 1904)

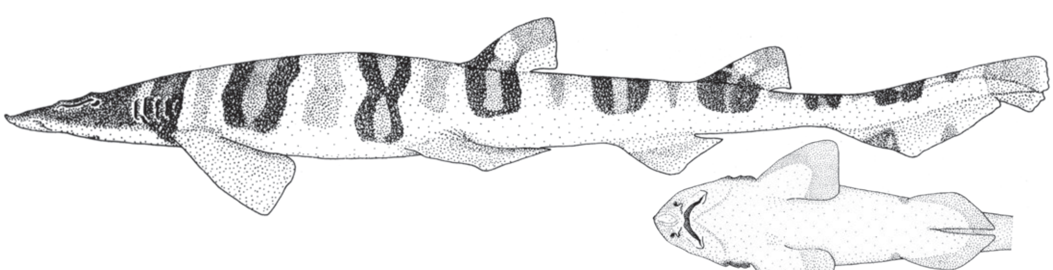
Tiger catshark PLATES 28 & 32

Scyllium natalense Regan 1904: 128 (KwaZulu-Natal, South Africa).
Scyliorhinus natalensis: Regan 1908; Fowler 1934, 1935.
Scylliorhinus natalensis: Gilchrist & Thompson 1911, 1914; Thompson 1914; Gilchrist 1922; Von Bonde 1923; Barnard 1925.
Halaelurus natalensis: Smith 1949*, 1950; Bass *et al.* 1975*; Springer 1979*; Compagno 1984*, 1986*, 1988*; SSF No. 11.7*; Compagno *et al.* 1989*; Compagno *et al.* 1991; Heemstra & Heemstra 2004*; Compagno *et al.* 2005*; Human *et al.* 2006; White *et al.* 2007.

Head broad; snout tip pointed and upturned with knob; mouth width 7–9% TL, mouth length 2–3% TL. First dorsal fin slightly larger than 2nd. Tooth count 54/41; vertebrae 123–133.

Body yellow-brown background dorsally, with ~10 conspicuous broad red-brown saddles with thick darker brown margins, and no spots; creamy ventrally. Attains 50 cm TL.

DISTRIBUTION WIO: endemic to South Africa (Cape Agulhas to southern KwaZulu-Natal).



Halaelurus natalensis, 44 cm TL, mature female (South Africa). Source: Bass *et al.* 1975

REMARKS Although originally described from KwaZulu-Natal, South Africa, large-scale trawl surveys since the mid-1980s have shown this species to be most common south of East London in the Eastern Cape. Also, historical confusion between this species and *H. lineatus* makes it difficult to attribute records from KwaZulu-Natal to *H. natalensis*, and records from Mozambique are almost certainly attributable to *H. lineatus* instead. Retained oviparity, with 6–11 egg cases per uterus; embryos ~4.5 cm TL when eggs are laid. Found on continental shelf, from surf zone to at least 172 m deep (most commonly <100 m). Feeds predominantly on bony fishes and crustaceans, but also cephalopods and other small sharks. Frequently caught by recreational anglers, in commercial crayfish traps, and a discarded bycatch of bottom trawlers.

Halaelurus quagga (Alcock 1899)

Quagga catshark

PLATES 29 & 32

Scyllium quagga Alcock 1899: 17 (Laccadive Sea [Lakshadweep], Malabar coast, India).
Scyliorhinus quagga: Regan 1908.
Halaelurus quagga: Springer & D'Aubrey 1972*; Springer 1979*; Compagno 1984*, 1988*; White *et al.* 2007; Akhilesh *et al.* 2011.

Small-sized and extremely slender. Head narrow; snout tip pointed and with knob, but not upturned; mouth width 6–9% TL, mouth length 4% TL. Second dorsal-fin base longer than 1st. Tooth count 55–59/54–55; vertebrae 123–125.

Body pale brown dorsally, with 20+ narrow, equally spaced dark brown bands (those under dorsal fins forming slight saddle markings) and no spots; paler ventrally. Attains at least 35 cm TL.

DISTRIBUTION WIO: Somalia, Socotra, Maldives, Lakshadweep and India (Kerala and southwards).

REMARKS Poorly known from only a few specimens. Differences in colour patterns (Springer 1979) between specimens from India and Somalia may indicate population substructuring. Uncommon; occurs in tropical offshore waters of outer continental shelf, at 54–220 m. Presumably taken as bycatch of demersal fisheries.

GENUS *Haploblepharus* Garman 1913

Body slender to moderately stocky; head not depressed. Eyes moderately elevated or not elevated. Snout broadly rounded, or narrowly rounded and coming to a point, and tip not upturned; nostrils very large; nasal flaps expanded, fused and extending to mouth; oronasal grooves deep; no nasal barbels. Upper and lower lip folds short. Fins rounded. Dorsal fins and anal fin more or less equally sized. Pelvic fins not fused; claspers long and robust, outer length 3–8 times width. No crest of enlarged denticles along upper peduncle and dorsal caudal margin. Stomach not inflatable. Tooth counts 40–90/46–92; vertebrae 93–141; spiral valve turns 6–9. Inshore, abundant to rare, found primarily in kelp forests and on rocky reefs, but also along sandy shores; all members are poorly represented in museum collections. At least 4 species, all in WIO.

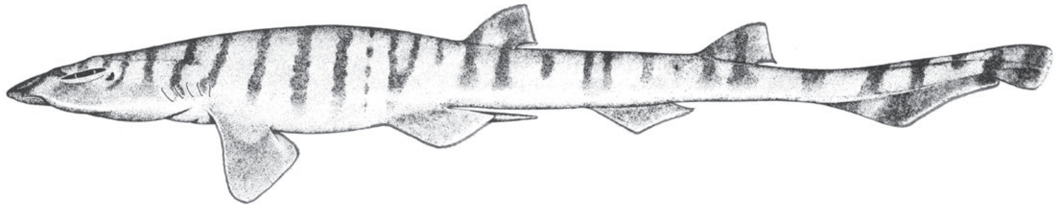
KEY TO SPECIES

[Excludes juveniles]

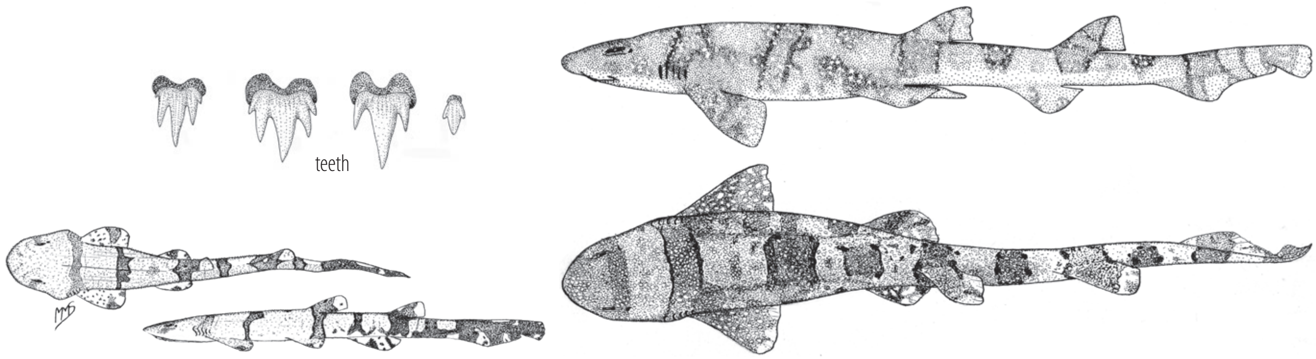
1a Body slender, compressed to moderately depressed; snout acutely rounded; teeth in upper jaw <70 in total **2**
1b Body stocky, moderately to greatly depressed; snout broadly rounded, not acutely pointed; teeth in upper jaw ≥75 in total **3**

2a Head width ≥1.3 times head height at pectoral-fin origins .... ***H. edwardsii***
2b Head width ≤1.3 times head height at pectoral-fin origins .... ***H. kistnasamyi***

3a Saddle markings and sparse white spots obvious (these markings usually occur together) .... ***H. pictus***
3b Saddle markings obscure, and black or white spots inconspicuous or absent (saddles and spots rarely occur together) .... ***H. fuscus***



Halaelurus quagga, 35 cm TL, adult male (Somalia). Source: Springer 1979



Haploblepharus edwardsii, 49 cm TL, mature male (top right); 13 cm TL, juvenile, dorsal and lateral views (bottom left); 53 cm TL, female, dorsal view (bottom right) (all South Africa). Source: Bass *et al.* 1975 (male); Smith 1953 (juvenile); SFSA (female)

Haploblepharus edwardsii (Schinz 1822)

Happy Eddie PLATE 29

Squalus edwardsii Schinz 1822: 504 (False Bay, Western Cape, South Africa).
Catulus edwardii: Smith 1837.
Scyllium edwardsii: Müller & Henle 1838*; Gilchrist 1902.
Scyliorhinus edwardsii: Regan 1908.
Scylliorhinus edwardsi: Thompson 1914; Gilchrist & Thompson 1916; Barnard 1925.
Scylliorhinus edwardsii: Gilchrist 1922.
Haploblepharus edwardsii: Smith 1950*; Bass 1973; Bass *et al.* 1975*; Springer 1979*; Compagno 1984*, 1986*, 1988; SSF No. 11.8*; Compagno *et al.* 1989*; Van Oijen 2001; Heemstra & Heemstra 2004; Compagno *et al.* 2005*; Human & Compagno 2006*; Human *et al.* 2006; Human 2007*.

Trunk moderately depressed; head rounded, head height at rear edge of orbit 5–7% TL; snout short. Eyes moderately elevated. Claspers slender, inner length 3–6 times width. Tooth count 51–68/46–60; vertebrae 121–139; spiral valve turns 7.

Body pale brown to pale or dark grey-brown background dorsally, with numerous small white spots, and 8–10 prominent saddles with brilliant orange or orange-brown centres and dark brown to almost black margins; paler ventrally. Attains 60 cm TL.

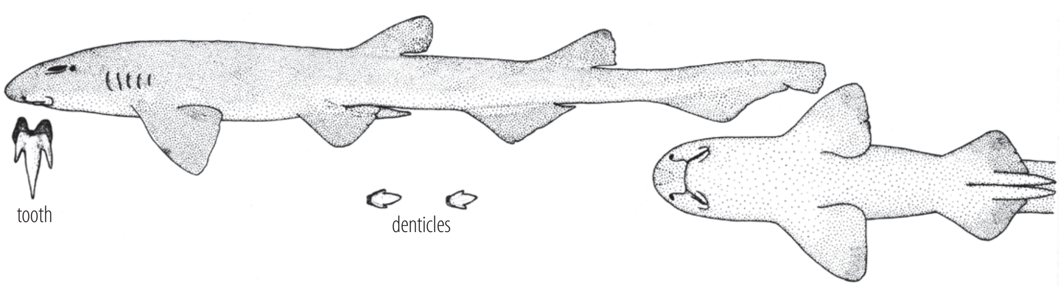
DISTRIBUTION WIO: endemic to South Africa (Langebaan Lagoon in Western Cape to Algoa Bay in Eastern Cape), with possibly severely fragmented populations.

REMARKS Historically confused with other *Haploblepharus* species (particularly *H. pictus*), resulting in confused distributional and biological reports, and probably leading to overestimations in its abundance and range. Oviparous, pairs of egg cases laid aseasonally, hatching after 3 months. Matures at ~7 years; maximum age at least 22 years. Occurs over continental shelf and slope, at 30–130 m; found in kelp forests and along rocky shores (western part of its range), and on sandy bottom in deeper water (eastern part of its range); possibly separate populations in deeper water attain greater sizes than inshore populations. Social, frequently aggregating and resting in groups; if disturbed these sharks will curl up with their caudal fin over their eyes, hence the common name shyshark. Feeds on small bony fishes, worms, crustaceans, squid and octopus. Treated as a nuisance catch by recreational anglers; also used in aquariums. IUCN Red List conservation status Endangered.

Haploblepharus fuscus Smith 1950

Brown shyshark PLATES 29 & 32

Haploblepharus fuscus Smith 1950: 883, Fig. 2 (East London, Eastern Cape, South Africa); Bass *et al.* 1975*; Springer 1979; Compagno 1984*, 1986*, 1988*; SSF No. 11.9*; Compagno *et al.* 1989*; Compagno *et al.* 2005*; Human & Compagno 2006; Human *et al.* 2006; Human 2007*.
Haploblepharus edwardsii: Smith 1949*.



Haploblepharus fuscus, 43 cm TL, immature male (South Africa). Source: Bass *et al.* 1975

Body stocky; head broad, head height at rear edge of orbit 5–8% TL; nostrils large. Eyes moderately elevated. Claspers stout, inner length 3–4 times width. Tooth count 40–90/48–92; vertebrae 128–141; spiral valve turns 9.

Body uniformly brown or dull grey-brown dorsally, with slightly darker saddle markings variably present (more conspicuous in smaller specimens); rarely with inconspicuous black spots or inconspicuous white spots (never both); white ventrally. Attains 73 cm TL.

DISTRIBUTION WIO: endemic to South Africa (site-specific, fragmented population: Storms River mouth, Western Cape, to near Durban, KwaZulu-Natal).

REMARKS Biology unknown, assumed singly oviparous. Very restricted, close inshore range, from surf zone to ~35 m deep. Adults are locally common over rocky reefs; juveniles possibly use unknown habitat as nursery areas, and are rare in collections. Presumably feeds on small bony fishes and crustaceans. Treated as a nuisance catch by rock and surf anglers. IUCN Red List conservation status Vulnerable.

Haploblepharus kistnasamyi

Human & Compagno 2006

Happy chappie PLATE 32

Haploblepharus kistnasamyi Human & Compagno 2006: 44, Figs. 2–5 (Park Rynie, KwaZulu-Natal, South Africa); Human 2007*.
Haploblepharus edwardsii: Smith 1949 [in part], 1950* [in part]; Bass *et al.* 1975* [in part]; Compagno 1984* [in part], 1988 [in part]; SSF No. 11.8* [in part]; Compagno *et al.* 1989* [in part].
Haploblepharus sp. A: Compagno *et al.* 2005*; Human *et al.* 2006.

Stocky body, trunk not depressed; head slightly depressed, head height at rear edge of orbit 6–11% TL. Nasal flaps with slight median indentation and reaching to upper lip. Claspers stout, inner length 5 times width. Tooth count 55–81/53–74; vertebrae 121–133; spiral valve turns 6.

Body with 8 or 9 dark brown, loosely H-shaped saddle markings, the centres darker than background, and white spots only on these saddles (giving blotchy effect over body and fins); saddle markings in juveniles conspicuous, with orange-brown centres and dark brown margins; interspaces between saddles and on fins with dark mottling on brown background; abruptly white ventrally. Attains 50 cm TL.

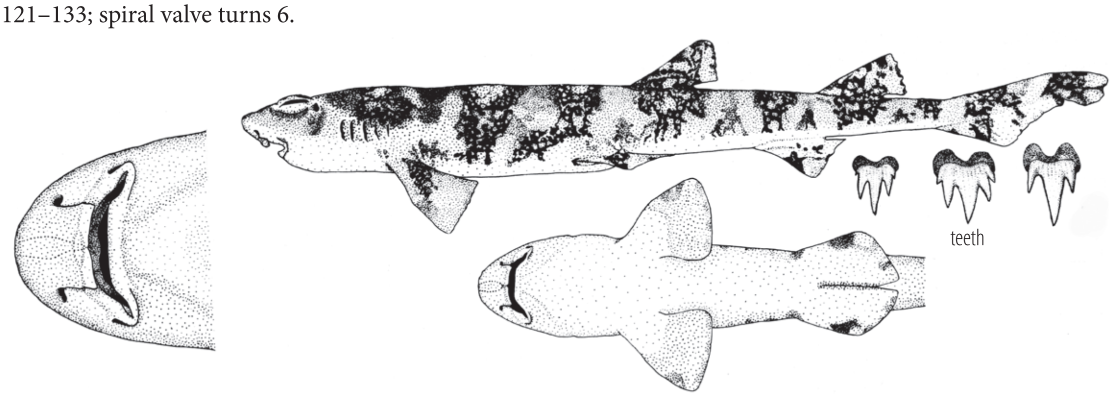
DISTRIBUTION WIO: endemic to southern Mozambique and South Africa (eastern Western Cape to KwaZulu-Natal).

REMARKS Superficially resembles *H. edwardsii*; first recognised as distinct by Bass *et al.* (1975) who described it as the Natal form and *H. edwardsii* proper as the Cape form. Biology unknown, presumably singly oviparous. Rarely seen, with very a restricted range and possibly a single population: so far, adults found only from southern Mozambique (Techobanine) (to ~100 m deep) to KwaZulu-Natal (Park Rynie), South Africa (collected from 40–50 m), and juveniles tentatively assigned to this species only found further south, to Mossel Bay in South Africa. Usually close inshore, from surf zone to ~30 m deep. IUCN Red List conservation status Vulnerable.

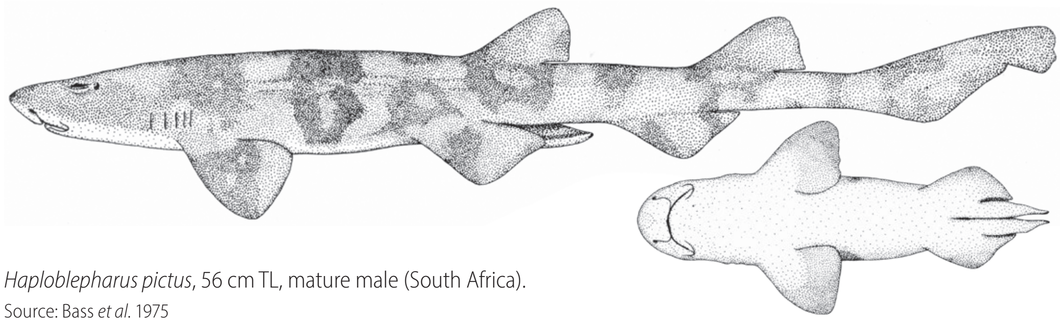
Haploblepharus pictus (Müller & Henle 1838)

Pretty happy PLATE 32

Scyllium pictum Müller & Henle 1838: 4 (Cape of Good Hope, South Africa).
Scyliorhinus edwardsii: Regan 1908.
Scylliorhinus edwardsi: Thompson 1914; Gilchrist & Thompson 1916.
Haploblepharus edwardsii: Smith 1950.
Haploblepharus pictus: Bass *et al.* 1975*; Springer 1979*; Compagno 1984*, 1988*; SSF No. 11.10*; Compagno *et al.* 1989*, 2005*; Van Oijen 2001; Heemstra & Heemstra 2004; Human & Compagno 2006*; Human *et al.* 2006; Human 2007*.



Haploblepharus kistnasamyi, 48 cm TL, mature female (South Africa). Source: Bass *et al.* 1975



Haploblepharus pictus, 56 cm TL, mature male (South Africa).
Source: Bass *et al.* 1975

Head and trunk moderately depressed; head broad, height at rear edge of orbit 6–8% TL. Eyes moderately elevated. Claspers stout, inner length 3–5 times width. Tooth count 45–83/47–75; vertebrae 93–133.

Body pale to dark brown (tawny coloured) or almost black, grey, grey-brown or red-brown background dorsally; 6–8 faint saddle markings, the centres variously orange, brown or dark brown to almost black, and the margins often indistinct; irregular large white spots absent or present on saddles or on and between saddles (never just between saddles); abruptly white or creamy ventrally. Attains 60 cm TL.

DISTRIBUTION Endemic from Namibia in southeastern Atlantic, to South Africa (Storms River mouth, Eastern Cape) in WIO.

REMARKS Long considered a synonym of *H. edwardsii* and largely ignored until it was resurrected by Bass *et al.* (1975), and hence recognised as *H. pictus* by subsequent authors. However, misidentification with *H. edwardsii* and other species continued largely due to its highly variable patterning. Oviparous, single egg case laid aseasonally; hatched in captivity after 3.5–10 months. Matures at ~15 years; maximum age at least 25 years. Has a greater range than previously thought; common to abundant in shallow inshore waters, in kelp forests and along rocky reefs and shores, to ~35 m deep. Feeds on small bony fishes, worms, crustaceans, cephalopods, molluscs (snails), echinoderms and occasionally algae. A common bycatch in recreational fishing and generally treated as a nuisance catch; regularly seen by divers.

GENUS *Holohalaelurus* Fowler 1934

Body slender; head strongly depressed; tail long; some with enlarged denticles on mid-back, but no crest of denticles on dorsal caudal margin. Eyes dorsolateral on head, very broad subocular ridges below eyes. Snout short, broadly rounded; no lip folds; nasal flaps short, separate; no nasal barbels. Dorsal fins subequal and higher than anal fin, but anal fin much longer than dorsal-fin lengths. Pelvic fins partially fused but never forming pelvic curtain; claspers elongate, their outer length 4–8 times width. Anal fin long and low. Tail long and slender. Stomach not inflatable. Tooth counts 40–68/38–78; vertebrae 85–132; spiral valve turns 7. All species have conspicuous black sensory pores ventrally (fresh specimens). Males appear to attain greater sizes than females.

Although *Holohalaelurus* sharks have long been known from East Africa, their biology is poorly known; their taxonomy was revised by Human (2006), although they remain poorly represented in collections. Historically abundant but now mostly rare, over the continental shelf and slope; some species and populations from southwestern WIO are possibly extinct in the region. Reports of *Holohalaelurus* from Somalia are likely valid but require confirmation. At least 5 species, all in WIO. Of these, *H. melanostigma* is known only from four male specimens collected from 607–658 m, off Tanzania and Kenya, and is distinguished by a tear-line marking on the snout forward of the eyes.

KEY TO SPECIES

[Excludes juveniles]

1a No enlarged denticles on midback; small white spot at origin of both dorsal fins, and C- or V-shaped mark on each dorsal fin .... ***H. punctatus***

1b Denticles on dorsal midline, moderately or greatly enlarged; small white spot absent or variably present at origin of either dorsal fin (never at origin of both fins) **2**

2a Anal-fin base ≤1.5 times pelvic-fin base; club-shaped papillae on tips of claspers; several white spots distributed on upper body, and short horizontal bar on each dorsal fin .... ***H. grennian***

2b Anal-fin base >1.8 times pelvic-fin base; no papillae on tips of claspers; no white spots anywhere on body **3**

Continued …

KEY TO SPECIES

3a No enlarged denticles on dorsal surface of snout, and no enlarged denticles on dorsal surface of pectoral fins in adults; 'tear-line' markings present from front edge of eyes to anterior margin of snout ...... ***H. melanostigma***
[known only from >600 m off East Africa]

3b Enlarged denticles present on dorsal surface of snout and on dorsal surface of pectoral fins in adults; no 'tear-line' markings from front edge of eyes to anterior margin of snout **4**

4a Markings on body resembling honeycomb pattern; at most 1 symphysial tooth in each jaw ...... ***H. favus***

4b Irregular horseshoe-shaped markings on body; up to 6 symphysial teeth in each jaw ...... ***H. regani***

Holohalaelurus favus Human 2006

Honeycomb Izak

PLATE 32

Holohalaelurus favus Human 2006: 36, Figs. 11–12 (KwaZulu-Natal, South Africa); Human 2007, 2010.
Holohalaelurus regani (*non* Gilchrist 1922): Bass *et al.* 1975*; Compagno 1984; SSF No. 11.12*; Compagno *et al.* 1989; Richardson *et al.* 2000; Compagno *et al.* 2005*.

Head broad; 1st dorsal fin rounded, 2nd dorsal fin angular. Slightly enlarged denticles on midback from snout to 2nd dorsal-fin, and denticles on dorsal surface of pectoral fins greatly enlarged in adults. Buccal papillae large and prominent on upper and lower surfaces in mouth; no papillae on tips of claspers. Tooth count 65–68/53–70; vertebrae 104–124.

Body yellowish brown background dorsally, covered with relatively regular checkerboard-like spots resembling honeycomb pattern; rarely with inconspicuous white spots above pectoral fins; paler grey-brown ventrally. Attains ~52 cm TL.

DISTRIBUTION WIO: South Africa (KwaZulu-Natal) to southern Mozambique.

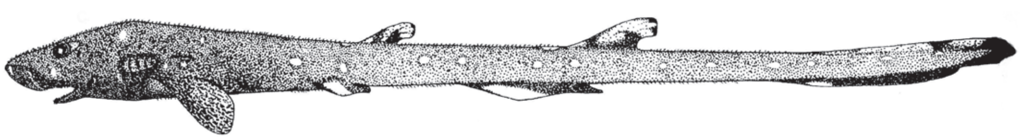
REMARKS Long confused with *H. regani* (sometimes referred to as the north-eastern subspecies) and illustrated several times under that name. First recognised as distinct by Bass *et al.* (1975) who referred to it as the Natal form rather than the Cape form of true *H. regani*, and subsequent authors recognised the two forms. Oviparous, probably pairs of egg cases laid. Possibly a single population, with estimated depth range of 200–1 000 m on upper to mid slope, with juveniles preferring deeper water than adults. Probably feeds on small bony fishes, cephalopods and crustaceans. Previously a common bycatch off South Africa (KwaZulu-Natal) and southern Mozambique, but now rarely recorded as bycatch in the KwaZulu-Natal prawn trawling fishery. IUCN Red List conservation status Endangered.

Holohalaelurus grennian Human 2006

Grinning Izak

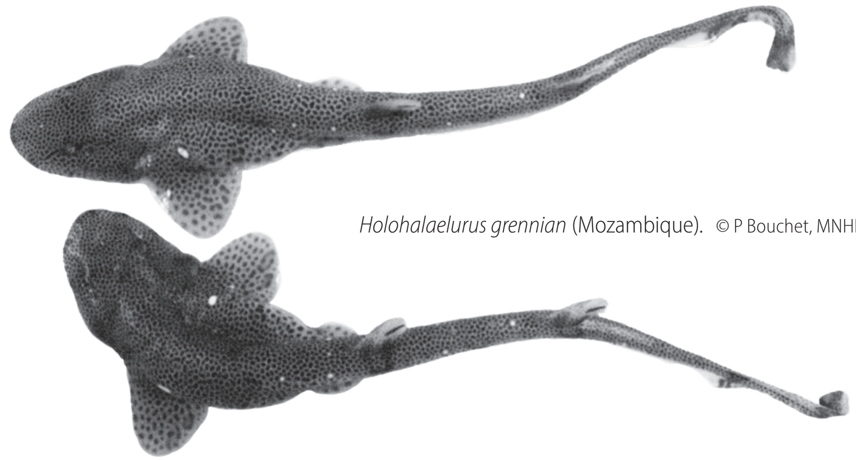
PLATE 30

Holohalaelurus grennian Human 2006: 44, Figs. 14–16 (off Ras Ngomeni, Kenya); Human 2007, 2010*.
Holohalaelurus punctatus (*non* Gilchrist 1914): Bass *et al.* 1975; Springer 1979; Compagno 1984, 1988*; SSF No. 11.11*; Compagno *et al.* 1989; Compagno *et al.* 1991.
Holohalaelurus sp. A: Compagno *et al.* 2005*.



Holohalaelurus favus, 13 cm TL, immature male (South Africa).
Source: Bass *et al.* 1975

Holohalaelurus favus, 52 cm TL, holotype (South Africa).
© BA Human



Holohalaelurus grennian (Mozambique). © P Bouchet, MNHN

Head broad; dorsal fins subequal. Slightly enlarged denticles on midback from above pectoral-fin origins to 1st dorsal fin, and denticles on dorsal surface of pectoral fins not enlarged. Buccal papillae inconspicuous; club-shaped papillae on tips of claspers. Tooth count 40–43/38–41; vertebrae 90–112.

Body yellow-brown to grey-brown background dorsally, with numerous small brown spots; characteristic horizontal dark bar or C-shaped mark on both dorsal fins; white spot absent or variably present at origin of either dorsal fin (never at origin of both fins); large pale or white spots above pectoral fins; paler ventrally. Attains at least 27 cm TL.

DISTRIBUTION WIO: northern Tanzania, Zanzibar, southern Kenya (few records) and southern Mozambique.

REMARKS Smallest of the *Holohalaelurus* sharks. A single female specimen, along with several male specimens, was included in the original description of *H. melanostigma*, with differences between male and female specimens attributed to sexual dimorphism. However, additional male specimens were later collected and readily identifiable with the female specimen previously collected, thus justifying the separation of this species from *H. melanostigma*. Very rare, known only from five museum specimens; biology unknown, presumably singly oviparous. Possibly a single population, recorded from 238–353 m, on upper slope.

Holohalaelurus punctatus (Gilchrist 1914)

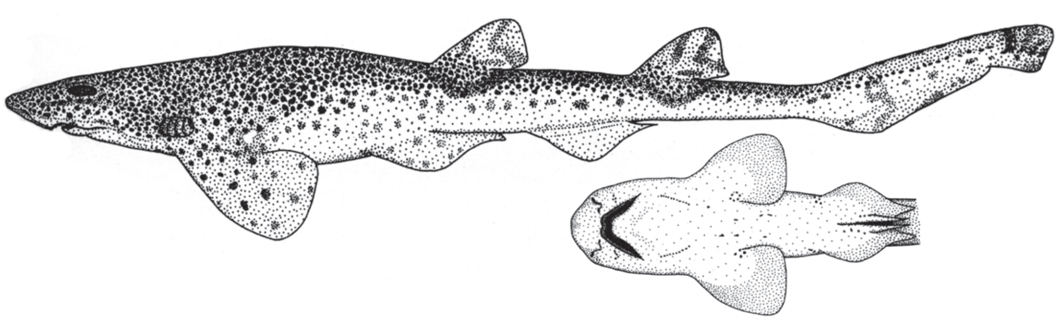
White-spotted Izak

PLATE 30

Scylliorhinus punctatus Gilchrist 1914: 129, Fig. (off Bazaruto, Mozambique); Thompson 1914; Gilchrist 1922; Barnard 1925; Norman 1939.
Scyliorhinus (*Halaelurus*) *polystigma* Regan 1921: 413 (KwaZulu-Natal, South Africa); Norman 1939*.
Halaelurus punctatus: Fowler 1934, 1935*.
Holohalaelurus punctatus: Smith 1949*; Bass 1973; Bass *et al.* 1975*; Springer 1979*; Compagno 1984*, 1988*; SSF No. 11.11*; Séret 1987; Compagno *et al.* 1989*; Compagno *et al.* 1991; Compagno *et al.* 2005*; Human 2006*, 2007, 2010.

Head broad; dorsal fins angular. No enlarged denticles on midback or dorsal surface of pectoral fins in adults. Buccal papillae large and prominent on upper and lower surfaces of mouth; no papillae on tips of claspers. Tooth count 42–52/40–47; vertebrae 85–120.

Body golden brown to dark brown background dorsally, densely covered with irregularly shaped dark brown spots (but no reticulations, blotches or horizontal stripes); few white spots scattered on back and at origins of both dorsal fins; C- or V-shaped marking on each dorsal fin; paler ventrally, and sometimes with tiny dark dots and dashes under head. Attains 34 cm TL.



Holohalaelurus punctatus, 24 cm TL, immature male (South Africa).
Source: Bass *et al.* 1975

DISTRIBUTION WIO: South Africa (KwaZulu-Natal) to Mozambique and Madagascar; its occurrence off Cape Point, South Africa (as stated in literature), is highly unlikely.

REMARKS Oviparous, pairs of egg cases laid. May be comprised of two distinct populations, one off South Africa and Mozambique, and the other off Madagascar. Estimated depth range of 219–420 m off Mozambique and South Africa, and 280–600 m off Madagascar; juveniles may live in deeper water than adults. Probably feeds on bony fishes, crustaceans and cephalopods. Previously a common bycatch in fisheries off South Africa and Mozambique, but now rarely recorded off KZN; records require confirmation due to confusion with *H. favus*; the status of the Madagascan population is unknown. IUCN Red List conservation status Endangered; Data Deficient in Madagascar.

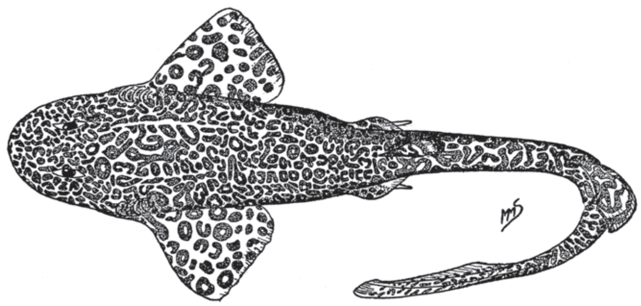
Holohalaelurus regani (Gilchrist 1922)

Izak PLATES 30, 31 & 32

Scylliorhinus regani Gilchrist 1922: 45 (SE of Hondeklip Bay, Northern Cape, South Africa); Barnard 1925.
Holohalaelurus regani: Smith 1949*; Bass 1973; Bass *et al.* 1975*; Springer 1979*; Compagno 1984*, 1986*, 1988*; SSF No. 11.12*; Compagno *et al.* 1989*; Compagno *et al.* 1991; Ebert *et al.* 1996; Richardson *et al.* 2000*; Compagno *et al.* 2005*; Human 2006*, 2007, 2010; Human *et al.* 2006.

Snout short, mouth long. Slightly enlarged denticles on midback from snout to 2nd dorsal fin, and denticles on dorsal surface of pectoral fins greatly enlarged in adults. Buccal papillae large and prominent on upper and lower surfaces of mouth; no papillae on tips of claspers. Tooth count 55–72/27–78; vertebrae 106–132; spiral valve turns 7.

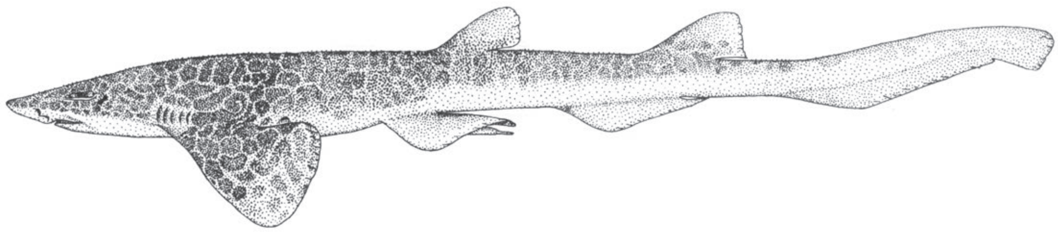
Body pale yellow to yellow-brown background dorsally, with bold reticulations and irregular horseshoe-shaped markings and virtually no spots, and never with white spots in adults; whitish ventrally; juveniles darker, with irregularly shaped larger dark brown spots, and also row of white spots along each side. Attains 69 cm TL (males reach larger sizes than females).



Holohalaelurus regani, 61 cm TL, mature male (South Africa). Source: SFSA

DISTRIBUTION Southern Africa: Namibia in southeastern Atlantic, to South Africa (Eastern Cape, possibly KwaZulu-Natal and southern Mozambique) in WIO.

REMARKS Oviparous and highly fecund, with pairs of egg cases laid aseasonally; size at hatching 8–10 cm TL. Found over continental shelf, at 40–910 m (mostly 100–500 m). Abundant in southern and western parts of its distribution, where continental shelf is broadest. Most records of *H. regani* in the eastern part of its distribution are referable to *H. favus* (once considered a subspecies). Minor seasonal migrations occur in at least part of its range, and depth segregation is apparent, with females dominant above 200 m and males occurring deeper; juveniles most commonly found in shallow water. Males attain ~20% greater length than females, and juveniles are much more elongate than adults (possibly true for all *Holohalaelurus* species). Active and demersal, feeds on small bony fishes, crustaceans, cephalopods, polychaetes, kelp and possibly fishing discards. A regular discard of demersal hake trawl fishery throughout its range.



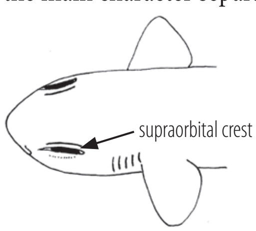
Holohalaelurus regani, 57 cm TL, mature male (South Africa). Source: Bass *et al.* 1975

FAMILY SCYLIORHINIDAE

Catsharks

Brett A Human and David A Ebert

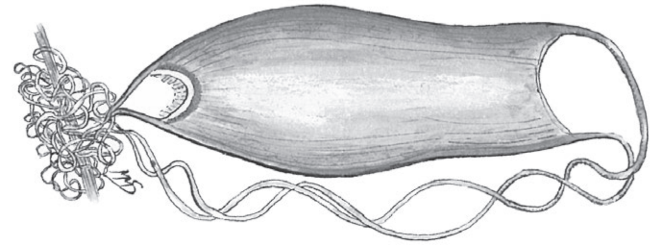
Generally small-sized, long and slender (most WIO species <80 cm TL), but a few are relatively large and stocky. Head length typically 20% TL; 5 pairs of gill slits, small to greatly enlarged, the last gill slit over or behind pectoral-fin origins. Snout broadly to narrowly rounded, not depressed to moderately depressed and laterally expanded compared to rest of head, and tip not upturned. Anterior nasal flaps short or extending to mouth, and separate or fused; nasal barbels present or absent; oronasal grooves absent. Eyes slit-like and dorsolateral, with rudimentary nictitans and strong subocular ridges; spiracles moderately large, set just behind eyes. Supraorbital crest present (usually detected by touch), and is the main character separating the catshark families.



Mouth inferior, long and arched, and with or without lip folds. Teeth multicuspidate (except monocuspidate in one species of *Schroederichthys* not known from WIO) and in multiple functional rows in both jaws. Fins rounded, angular or weakly falcate. Two spineless dorsal fins, usually subequal; 1st dorsal fin above or behind pelvic-fin bases. Pectoral fins moderately sized and paddle-shaped. Pelvic fins moderately long and low. Anal fin long and low to high, its base usually longer than 2nd dorsal-fin base. Peduncle and caudal fin slender; peduncle without pits or keels; caudal fin heterocercal, lower lobe poorly developed. Sexual dimorphism in TL absent to extreme (with males attaining greater lengths than females) and also apparent in dentition of some species. Tooth counts 40–116/38–110; vertebrae 100–183; spiral valve turns 6–14.

Reproductive mode oviparous, with females depositing egg cases on the substrate where the embryos develop and eventually hatch out. However, for some species the egg cases are retained *in utero* until the embryos are nearly completely developed. Scyliorhinids are found worldwide in tropical to cold-temperate seas, with preferred temperatures likely contributing to a high degree of endemism. Most shallow-water species occur in tropical to warm-temperate regions and tend to be brightly coloured, whereas deep-sea forms tend to be more uniformly coloured. Sluggish, poor swimmers, and generally deep-dwelling (<1 000 m) on or near bottom, although some deep-sea species are known to migrate far off the bottom into the water column; in the WIO they are found from intertidal zone to deep-sea (<700 m), over soft bottom, on rocky or coral reefs and in kelp beds, and may be rarely seen to locally abundant. Harmless to people. Generally not targeted in fisheries but often comprise a bycatch where abundant; some of the more colourful species are displayed and bred in aquariums.

This family has 7 genera and ~50 species; 4 genera and 7 species in the WIO, with one of the species from deep water.



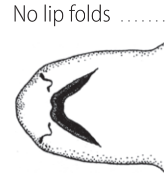
Typical catshark egg case. Source: SFSA

GLOSSARY

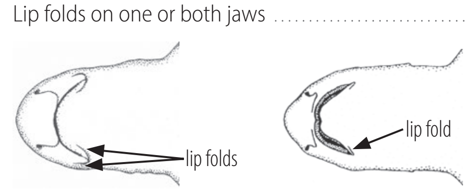
supraorbital crest – narrow cartilaginous ridge from the chondrocranium extending above the eyes in catsharks of the family Scyliorhinidae. The crests can usually be felt by touch without needing any dissection.

KEY TO GENERA

1a No lip folds .... ***Cephaloscyllium***



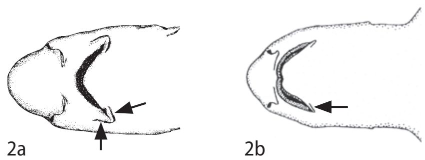
1b Lip folds on one or both jaws **2**



Continued …

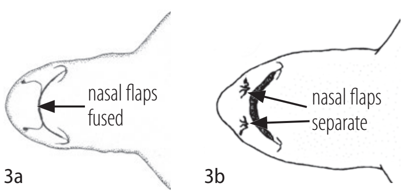
KEY TO GENERA

2a Lip folds on both jaws **3**
2b Lip folds on lower jaw only .... ***Scyliorhinus***



2a 2b

3a Nasal flaps extend to mouth, separate or fused; nasal barbels absent .... ***Atelomycterus***
3b Nasal flaps short, separate; nasal barbels well developed .... ***Poroderma***



3a 3b

GENUS ***Atelomycterus*** Garman 1913

Body slender; head narrow and slightly depressed. Eyes not noticeably elevated. Supraorbital crest present. Snout narrowly rounded and coming to a point, not depressed, and tip not upturned; upper and lower lip folds long; nasal flaps long, extending to mouth, and separate or fused; no nasal barbels. Fins rounded to weakly falcate. Dorsal fins subequal, and dorsal fins much larger than anal fin. Pelvic fins not fused; claspers elongate, outer length 5–11 times width. No crest of enlarged denticles along upper peduncle or dorsal caudal margin. Stomach not inflatable. Tooth counts 56–89/50–74; vertebrae 147–183; spiral valve turns 11–14. Predominantly Australasian distribution; strongly associated with coral reefs and frequently found in very shallow water, otherwise poorly known. At least 5 species, 1 in WIO.

Atelomycterus marmoratus

(Anonymous [Bennett] 1830)

Coral catshark PLATE 32

Scyllium marmoratum Anonymous [Bennett] 1830: 693 (Sumatra, Indonesia); Smith 1837.
Scyllium maculatum: Müller & Henle 1838; Day 1878*.
Scyliorhinus marmoratus: Regan 1908.
Atelomycterus marmoratus: Springer 1979*; Compagno 1984*, 1988*; Yamakawa *et al*. 1995*; Compagno *et al*. 2005*; White *et al*. 2005; Jacobsen & Bennett 2007.

Tooth count 74/74; vertebrae 157–162; spiral valve turns 7.

Body grey to dark grey background dorsally, with many large white spots and dash and bar marks over body and fins, some bordered by thick black margins and spots, giving mottled appearance but no clear saddle markings; both dorsal fins conspicuously white-tipped, and pectoral and pelvic fins with white margins; abruptly pale ventrally. Attains 70 cm TL.

DISTRIBUTION Indo-Pacific. WIO: Pakistan to southern India; elsewhere to Malaysia, Indonesia, New Guinea, Philippines, Taiwan and southern China.

REMARKS Wide-ranging, but poorly known. Oviparous, egg cases laid in pairs; size at hatching 10–13 cm TL. Inshore, common on coral reefs, often found in crevices and holes; nocturnal. Feeds on crustaceans and small fishes. Common bycatch of artisanal fisheries, and a hardy aquarium species. IUCN Red List conservation status Near Threatened due to habitat degradation.

Atelomycterus marmoratus, 65 cm TL (Philippines). PC Heemstra © NRF-SAIAB

GENUS *Cephaloscyllium* Gill 1862

Body moderate to stocky; head moderately depressed. Eyes not elevated, dorsolateral on head, broad subocular ridges present below eyes. Supraorbital crest present. Snout broadly to narrowly rounded, tip not upturned; no lip folds; nasal flaps generally short and lobate, separate, and not reaching mouth (except in *C. silasi*); no nasal barbels. Fins rounded to weakly falcate. First dorsal fin larger than 2nd. Pelvic fins not fused; claspers short and stubby to elongate, outer length 4–7 times width. Anal fin subequal to 1st dorsal fin and larger than 2nd dorsal fin. No crest of enlarged denticles on dorsal caudal margin. Stomach inflatable (often highly inflatable). Tooth counts 48–116/45–110; vertebrae 100–140; spiral valve turns 7–12.

Members of this genus are also referred to as swellsharks because of their ability to swallow water or air when aggravated, thus distending their abdomen as an anti-predator tactic. Generally with restricted ranges, but common to uncommon locally and found in a wide range of habitats in Indo-Pacific. Recent descriptions of new species have more than doubled the number of species in the genus, with ~18 species now recognised, plus possibly additional species yet to be described; at least 2 species in WIO. *Cephaloscyllium silasi* (Talwar 1974), a dwarf species (attains 36 cm TL), collected from ~300 m deep off Kollam, India, in WIO (specimens from Andaman Sea off Myanmar may represent a different species), is distinguishable from *C. sufflans* by nasal flaps that reach to mouth.

KEY TO SPECIES

1a	Dorsal colour pattern with indistinct dusky saddles present or absent	***C. sufflans***
1b	Dorsal colour pattern of 7 well-defined dark saddles or transverse bands [known only from ~300 m] [see Plates 31 & 32]	***C. silasi***

Cephaloscyllium sufflans (Regan 1921)

Balloon shark

PLATES 31 & 32

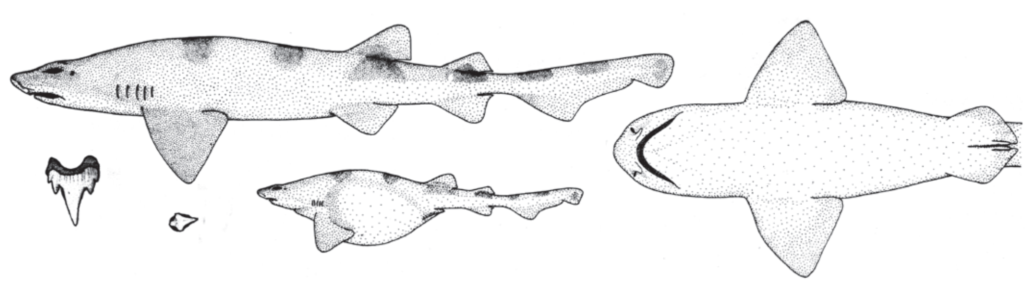
Scyliorhinus (*Cephaloscyllium*) *sufflans* Regan 1921: 413 (KwaZulu-Natal, South Africa); Norman 1939.
Scylliorhinus sufflans: Gilchrist 1922; Barnard 1925.
Cephaloscyllium sufflans: Fowler 1935*; Smith 1949*; Bass *et al*. 1975*; Springer 1979; Compagno 1984*; SSF No. 11.3*; Compagno *et al*. 1989*; Compagno *et al*. 2005*.

Body robust. Ridges over eyes. Nasal flaps end well before mouth. Vertebrae 124–140.

Body pale grey background dorsally, with dusky grey-brown saddle markings which fade with age and may be absent in adults; paler and unspotted ventrally. Attains 110 cm TL.

DISTRIBUTION Indian Ocean: South Africa (KwaZulu-Natal), Mozambique and Comoros in WIO (patchy); records from Kenya and Gulf of Aden may be of a separate species (cf. Springer 1979; Heemstra *et al.* 2006); elsewhere, records from Vietnam appear to be of an undescribed species.

REMARKS Oviparous, pairs of egg cases laid; size at hatching ~20–22 cm TL; matures at 70–80 cm TL. Common, found on continental shelf and upper slope, over sand and mud bottom, at 40–600 m. Ontogenetic segregation, with immature individuals reported to be a relatively common bycatch in KwaZulu-Natal prawn trawls in South Africa; adults may live deeper or north of the trawl grounds. Feeds primarily on crustaceans (shrimp and lobsters) and cephalopods, but also bony fishes and elasmobranchs. Known prey item of the coelacanth (*Latimeria chalumnae*) in Comoros. A discarded bycatch of bottom trawlers.



Cephaloscyllium sufflans, 42 cm TL, immature male (South Africa). Source: Bass *et al.* 1975

GENUS *Poroderma* Smith 1837

Body moderate to stocky; head only slightly depressed. Eyes moderately elevated. Supraorbital crest present. Snout broadly to narrowly rounded, and not strongly depressed; nasal flaps separate; nasal barbels well developed. Mouth short; upper and lower lip folds short. Dorsal fins posteriorly set; 1st dorsal fin larger than 2nd. Pelvic fins not fused; claspers short and stubby, their outer length 2–4 times their width. No crest of enlarged denticles along upper peduncle and dorsal caudal margin. Stomach not inflatable. Tooth counts 38–57/28–51; vertebrae 102–137; spiral valve turns 8–13. Common to abundant, inshore, often in kelp beds and on rocky reefs. Two species, both in WIO.

KEY TO SPECIES

1a Nasal barbels <½ preoral snout and not reaching mouth; prenarial length slightly less than mouth length; body with several dark longitudinal stripes and no spots .... ***P. africanum***

1b Nasal barbels >½ preoral snout and reaching upper lip; prenarial length slightly more than mouth length; dorsal surface with dense leopard-like rosettes and spots in irregular longitudinal rows .... ***P. pantherinum***

Poroderma africanum (Gmelin 1789)

Pyjama shark

PLATES 33 & 34

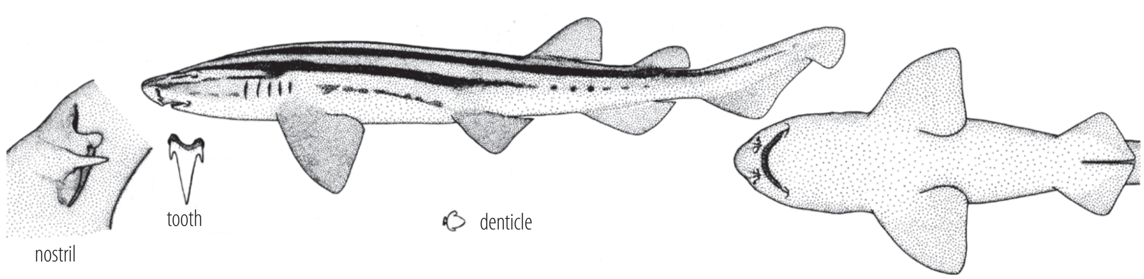
Squalus africanus Gmelin 1789: 1494 (South Africa).
Scyllium africanum: Smith 1849*; Bleeker 1878; Sauvage 1891; Gilchrist 1902, 1914.
Scyliorhinus africanus: Regan 1908.
Scylliorhinus africanus: Thompson 1914; Gilchrist & Thompson 1916; Gilchrist 1922; Barnard 1925, 1927, 1948.
Poroderma africanum: Fowler 1925, 1934; Smith 1949*; Bass 1973; Bass *et al.* 1975*; Springer 1979*; Compagno 1984*, 1986*, 1988*; SSF No. 11.13*; Compagno *et al.* 1989*; Heemstra & Heemstra 2004*; Compagno *et al.* 2005*; Human 2006*; Human *et al.* 2006.

Body stocky; snout narrowly rounded. Nasal barbels prominent but short, not reaching mouth. Tooth count 41–49/30–47; vertebrae 115–137; spiral valve turns 9–12.

Body creamy to grey background, with several striking longitudinal dark brown to black stripes and no spots; albinism reported. Attains 109 cm TL.

DISTRIBUTION Endemic to South Africa, from Northern Cape in southeastern Atlantic to southern Cape and KwaZulu-Natal (rare) in WIO; records from Madagascar, Seychelles and Mauritius are erroneous.

REMARKS Oviparous, pairs of large (5 × 10 cm) egg cases laid aseasonally, hatching after 4–5+ months. Matures at ~11 years; maximum age at least 22 years. Readily identifiable, common, inshore waters of continental shelf to upper slope, from intertidal zone to ~100 m deep, often along rocky shores, in caves and in kelp beds, with individuals apparently keeping a confined home range. Generally nocturnal. Feeds mostly on squid and octopus, but also bony fishes, other sharks and egg cases, hagfishes, molluscs, crustaceans, worms and echinoderms. Observed lying in squid egg beds to ambush mating squid during their spawning season. A common bycatch in various commercial, unregulated and sport fisheries; sometimes used for lobster bait; also a minor target of aquarium trade and hardy in captivity.



Poroderma africanum, 72 cm TL, mature female (South Africa). Source: Bass *et al.* 1975

Poroderma pantherinum (Müller & Henle 1838)

Leopard catshark PLATES 33 & 34

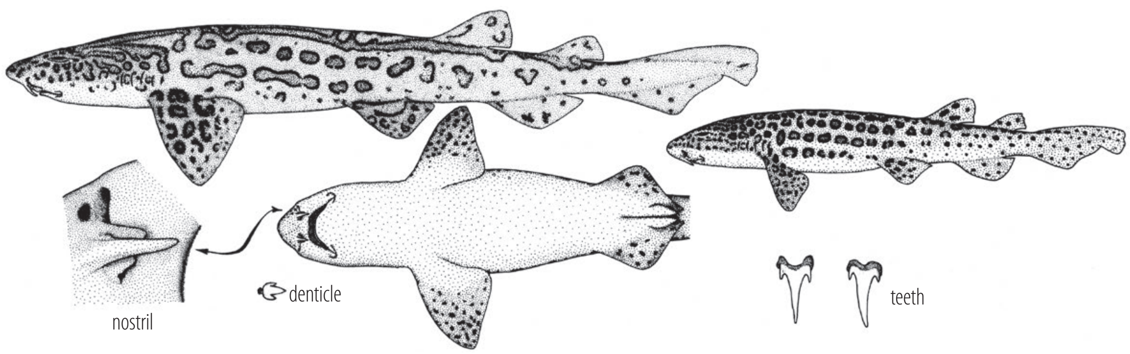
Scyllium pantherinum Müller & Henle (ex Smith) 1838: 14 (Cape of Good Hope, South Africa).
Poroderma pantherinum Smith 1838: 85 [name only]; Fowler 1925, 1934; Bass *et al.* 1975*; Springer 1979*; Compagno 1984*, 1986*, 1988*; SSF No. 11.15*; Compagno *et al.* 1989*; Heemstra & Heemstra 2004; Compagno *et al.* 2005*; Human 2006*; Human *et al.* 2006.
Poroderma submaculatum Smith 1838: 85 [name only].
Poroderma variegatum: Smith 1838.
Scyllium leopardinum Müller & Henle 1838: 13 [name only].
Scyllium maeandrinum Müller & Henle (ex Von Rapp) 1838: 13 [name only].
Scyllium variegatum Müller & Henle (ex Smith) 1838: 14 (Cape of Good Hope, South Africa); Bleeker 1878; Sauvage 1891.
Scyllium pantherinum Smith 1845: no page number, Pl. 25, Fig. 3 (near Algoa Bay, Eastern Cape, South Africa); Bleeker 1878; Sauvage 1891.
Scyliorhinus pantherinus: Regan 1908.
Scylliorhinus pantherinus: Thompson 1914; Gilchrist & Thompson 1916; Gilchrist 1922; Barnard 1925*, 1927*.
Scyliorhinus regani [misidentification of *Poroderma pantherinum*]: Fowler 1925*, 1926*.
Poroderma marleyi Fowler 1934: 234 (KwaZulu-Natal, South Africa); Smith 1949*; Bass *et al.* 1975*; Springer 1979; Compagno 1984*, 1986*; SSF No. 11.14*.
Scyliorhinus leopardus: Fowler 1935.

Body moderate; snout broadly rounded. Nasal barbels reach mouth. Tooth count 38–57/28–51; vertebrae 102–124; spiral valve turns 8–13.

Body generally pale grey to charcoal grey background dorsally, with dense leopard-like spots or rosettes in irregular longitudinal rows; paler ventrally (and sometimes strongly demarcated). Colour pattern highly variable within a continuum of four colour morphs: 1) 'typical' morph with large black blotches, whole or broken rosettes, with spots sometimes fused into short thin broken lines to long thin lines; 2) 'salt and pepper' morph usually pale grey dorsal background with numerous small black spots; 3) 'marleyi' morph with pale grey dorsal background and few large black spots; and 4) 'melanistic' morph with faint longitudinal stripes and/or spots, or without patterning, and glossy jet black. Attains 84 cm TL.

DISTRIBUTION Endemic to South Africa (possibly fragmented populations), from Northern Cape in southeastern Atlantic, to KwaZulu-Natal in WIO, and possibly Mozambique; records from Madagascar and Mauritius need confirmation.

REMARKS Highly variable colour patterning in this species has led to taxonomic confusion, resulting in numerous synonyms. In particular, *P. marleyi* has been shown to be an extreme colour variant of adults of this species. Interestingly, nearly all hatchlings emerge with the '*marleyi*' patterning, which usually develops into one of the other colour morphs, depending in part on its geographic range, possibly indicating multiple populations. While the 'typical' morph and its intermediates are found throughout its range, the 'salt and pepper' and 'marleyi' morphs are found only in the Eastern Cape of South Africa, and the 'melanistic' morph only in False Bay, Western Cape. Oviparous, pairs of egg cases laid aseasonally. Matures at ~10 years; maximum age ~19 years. Common, inshore, with biology and habitat similar to *P. africanum*, but also caught near sandy shores; recorded from shore to ~50 m deep. Taken by inshore commercial line fisheries and by recreational fishers and often persecuted by them; also heavily targeted for the aquarium trade; frequently seen by divers.



Poroderma pantherinum, 56 cm TL, immature female (top); 53 cm TL, immature male, ventral view (bottom left); 34 cm TL, immature male (right) (all South Africa). Source: Bass *et al.* 1975

GENUS *Scyliorhinus* Blainville 1816

Body slender to stocky; head moderately depressed. Eyes not elevated. Supraorbital crest present. Snout broadly to narrowly rounded and not depressed; lip folds on lower jaw only; nasal flaps separate or fused; nasal barbels absent to moderately developed. Fins rounded or angular, but not falcate. First dorsal fin larger than 2nd. Pelvic fins partially to completely fused to form pelvic curtain; claspers short and stubby, their outer length 4–8 times width. Anal fin more or less subequal to 1st dorsal fin and larger than 2nd dorsal fin. No crest of enlarged denticles on dorsal caudal margin. Stomach not inflatable. Tooth counts 40–70/38–65; vertebrae 108–144; spiral valve turns 6–12. Estimated size range 32–162 cm TL. Rare to abundant; occur mainly in the Atlantic and are infrequent in the Indo-Pacific. At least 15 species, 2 in WIO.

KEY TO SPECIES

1a Preoral length <5% TL; nasal flaps small, separate .... ***S. capensis***

1b Preoral length >5.5% TL; nasal flaps fused and extend to mouth .... ***S. comoroensis***

Scyliorhinus capensis (Müller & Henle 1838)

Yellowspotted catshark PLATE 33

Scyllium capense Müller & Henle 1838: 11 (Cape of Good Hope, South Africa); Day 1875*; Gilchrist 1902.

Scyliorhinus capensis: Regan 1908; Smith 1949*; Bass 1973; Bass *et al.* 1975*; Springer 1979*; Compagno 1984*, 1986*, 1988*; SSF No. 11.16*; Compagno *et al.* 1989*; Compagno *et al.* 1991*; Ebert *et al.* 1996; Richardson *et al.* 2000; Compagno *et al.* 2005*; Ebert *et al.* 2006*; Human *et al.* 2006.

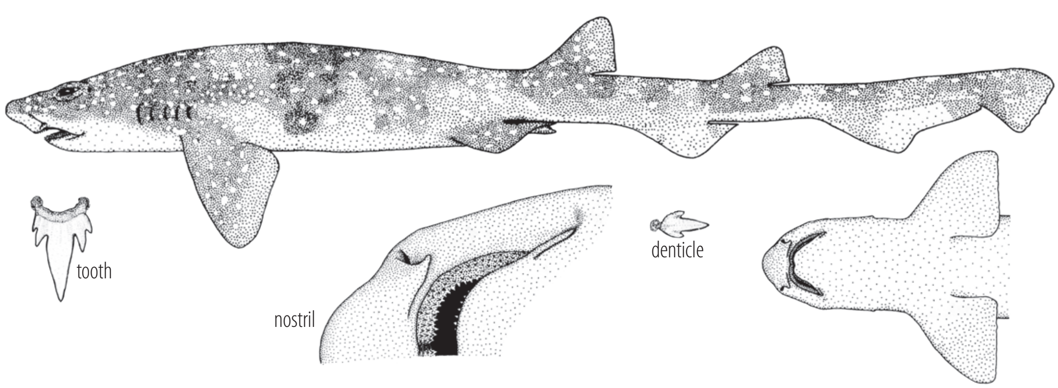
Scylliorhinus capensis: Thompson 1914; Gilchrist 1922; Von Bonde 1922; Barnard 1927.

Relatively large-bodied. Nasal flaps small, separate, and end before mouth; no oronasal grooves. Pelvic fins completely fused to form pelvic curtain. Tooth count 65–70/55–65; vertebrae 130–144; spiral valve turns 8–12.

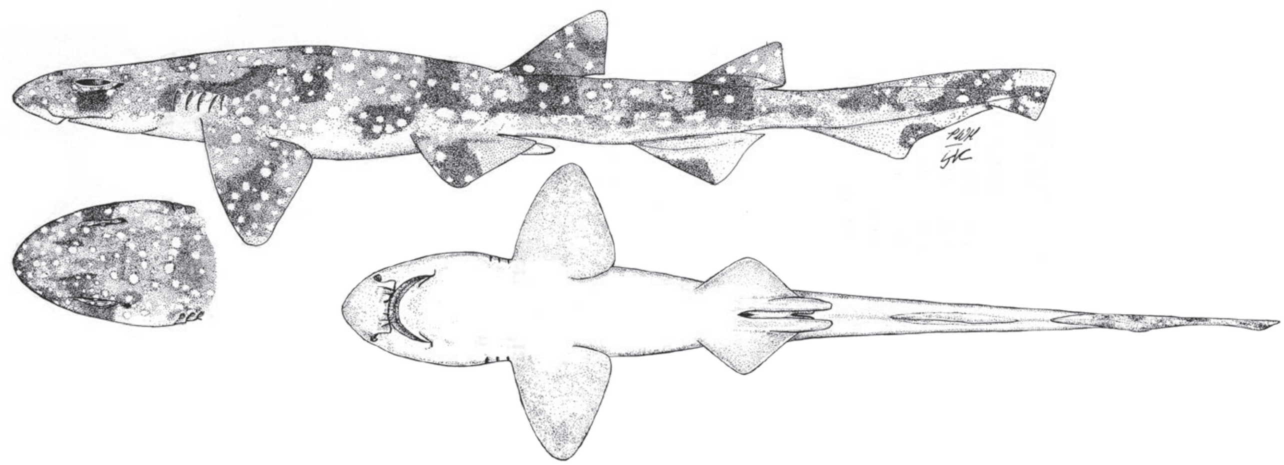
Body grey-brown background dorsally, with 8 or 9 darker brown or grey-brown saddle markings (sometimes poorly defined) and numerous small bright yellow or whitish spots (no dark spots); cream ventrally. Attains 122 cm TL.

DISTRIBUTION Southern Africa: Namibia in southeastern Atlantic, to South Africa (KwaZulu-Natal) in WIO; records from India are of a separate species.

REMARKS Oviparous, pairs of egg cases laid, possibly only during winter; hatches at 25–27 cm TL. Males mature at ~84 cm TL, and females at ~75 cm TL; males attain larger sizes than females. Bottom-dwelling over continental shelf and upper slope, at 26–695 m (mostly 200–400 m), and ventures deeper in warmer water; prefers rocky reef habitat. Coils tightly when disturbed or caught. Feeds on bony fishes and various invertebrates, especially crustaceans and worms. Common bycatch of commercial trawls, typically discarded. IUCN Red List conservation status Near Threatened.



Scyliorhinus capensis, 86 cm TL, adult male (South Africa). Source: Bass *et al.* 1975



Scyliorhinus comoroensis, 47 cm TL, adult male holotype (Comoros). Source: Compagno 1988

Scyliorhinus comoroensis Compagno 1988

Comoro catshark PLATE 33

Scyliorhinus comoroensis Compagno 1988: 609, Figs. 1, 3–8 (Moroni, Grande Comore I.); Compagno *et al.* 2005*; Heemstra *et al.* 2006.

Holotype: snout broadly rounded; nasal flaps large, fused and reach to mouth; no nasal barbels; no oronasal groves. Pelvic fins partially fused to form pelvic curtain. Tooth count 50/50; vertebrae 137; spiral valve turns 8.

Body pale grey-brown background dorsally, with distinct broad darker grey-brown saddles, and scattered with small to moderate-sized white spots (no small dark spots); dark bar under eyes; paler ventrally. Attains at least 60 cm TL.

DISTRIBUTION WIO: Comoros.

REMARKS Described from one specimen captured at ~400 m, but other individuals were subsequently photographed from a submersible in coelacanth (*Latimeria chalumnae*) habitat, on insular slope off Grande Comore I., at ~270 m deep. Bottom-dwelling; estimated depth range 200–400 m.

FAMILY PROSCYLLIIDAE

Finback catsharks

Jenny M Kemper and David A Ebert

Dwarf- to small-sized with elongated fusiform body, narrowly rounded head; eyes slit-like with rudimentary nictitans, but no deep groove in front of eyes; spiracles moderately large. Nostrils without barbels or oronasal grooves; internarial space 0.5–1.9 nostril width; anterior nasal flaps broadly angular. Mouth long and angular, arched, and reaching vertical at front edge of eyes; small papillae inside mouth and on edges of gill arches; lip furrows very short or absent. Teeth small, with acute narrow cusps, often with lateral cusplets, and strong basal ledges and grooves, not blade-like, and similar in both jaws; posterior teeth comb-like. Two spineless dorsal fins, each much shorter than caudal fin; 1st dorsal-fin base well ahead of pelvic fins and usually closer to pelvic-fin bases than to pectoral-fin bases. Pectoral fins with radials confined to fin bases. Anal fin small. Caudal-fin lower lobe very weak or absent, no undulations or ripples on dorsal margin, and no precaudal pits.

Poorly known; bottom-dwelling on outer continental and insular shelves and upper slopes, at 50–766 m. Reproductive mode appears to be viviparity with yolk-sac placenta (except for oviparous *Proscyllium habereri* from western Pacific); most species feed on small fishes and invertebrates. A few species are taken as bycatch in commercial bottom trawls, but their small adult size (15–65 cm TL) makes them unsuitable for fisheries utilisation. Disjunct distributions, mainly in Indo-Pacific but also tropical northwestern Atlantic.

Three genera and at least 6 species; 2 genera and 3 species in WIO.

KEY TO GENERA

1a	Caudal fin broad, not ribbon-like, its length subequal to HL; colour pattern of spots, saddles and bars on body and fins	***Ctenacis***
1b	Caudal fin narrow, ribbon-like, and longer than head; no colour pattern except vertical barring on caudal fin	***Eridacnis***

GENUS *Ctenacis* Compagno 1973

Relatively stout body and stout tail; head and snout not bell-shaped in dorsoventral view; preoral length ~⅔ mouth width. Anterior nasal flaps small, with rear edges not reaching mouth; internarial space ~1.2 nostril width. Mouth triangular, with short lip furrows. Dorsal fins subequal; 1st dorsal-fin origin before pectoral-fin free rear tips. Anal-fin origin slightly behind 2nd dorsal-fin origin. Caudal fin relatively broad, short, not ribbon-like, its dorsal margin ~23% TL. One species.

Ctenacis fehlmanni (Springer 1968)

Harlequin catshark

Triakis fehlmanni Springer 1968: 614, Figs. 1–4 (SW of Cape Guardafui, Somalia).
Ctenacis fehlmanni: Bass *et al.* 1975*; Compagno 1984*, 1988*; SSF No. 10.1*; Henderson & Reeve 2011; Ebert 2013*; Ebert *et al.* 2013*.

Diagnosis as for genus. Tooth count 86/88; vertebrae 136; spiral valve turns 10.

Body with unique pattern of large, reddish brown, irregular dorsal saddle blotches, interspersed with smaller round spots and vertical bars, as well as spots on fins. Attains at least 52 cm TL.

DISTRIBUTION WIO: Somalia and Oman.

REMARKS Females mature at ~52 cm TL (large, thin-walled egg cases in each uterus of the holotype suggests the species is viviparous with yolk-sac placenta); size at birth uncertain, but smallest free-swimming specimen was 17 cm TL.

Bottom-dwelling in tropical waters of outer continental shelf, usually deeper than 300 m. Likely feeds on very small invertebrates.

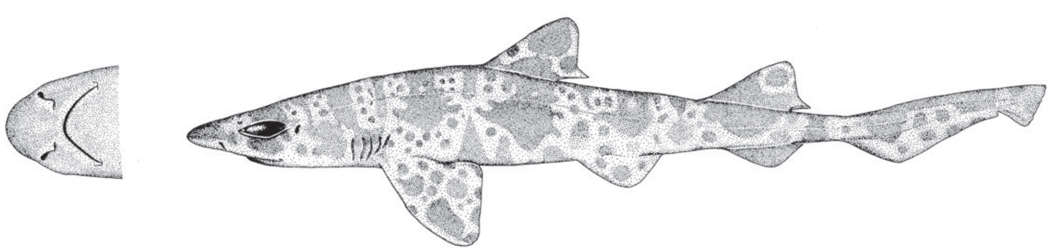
GENUS *Eridacnis* Smith 1913

Small-sized, slender body, with narrow and moderately long head. Head and snout not bell-shaped in dorsoventral view; preoral length subequal to ~⅔ mouth width. Anterior nasal flaps small, with rear edges well in front of mouth; internarial space 0.7–1.3 times nostril width. Lip furrows extremely short to vestigial or absent. Teeth exhibit sexual heterodonty: males with slightly larger, lanceolate teeth. First dorsal-fin origin well anterior to slightly posterior to pectoral-fin free rear tips. Pectoral fins with straight or convex posterior margin. Anal-fin origin slightly anterior to, under, or slightly posterior to 2nd dorsal-fin origin. Caudal fin narrow, long and ribbon-like, its dorsal margin 25–30% TL. Tooth counts 55–78/63–77; vertebrae 113–144; spiral valve turns 6–8. Three species, 2 in WIO.

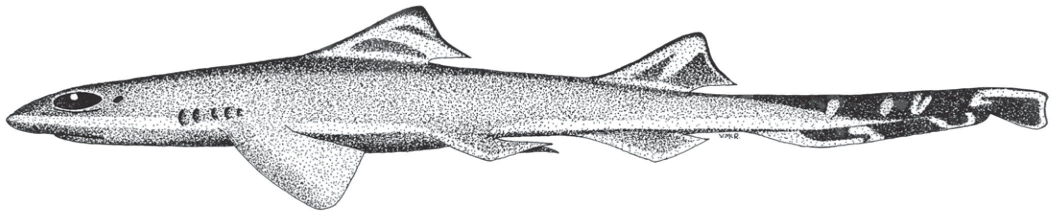
KEY TO SPECIES

1a Preoral length more than twice mouth length; lateral dermal denticles broad, with short, wide cusps .... ***E. sinuans***

1b Preoral length <1.5 mouth length; lateral dermal denticles narrow, with narrow, long cusps .... ***E. radcliffei***



Ctenacis fehlmanni, 46 cm TL, adult female (Somalia). Source: Springer 1968; © *Proc. Biol. Soc. Wash.*, Allen Press Publ. Services



Eridacnis radcliffei, 19 cm TL, male (Philippines). Source: SSF

Eridacnis radcliffei Smith 1913

Pygmy ribbontail catshark PLATE 34

Eridacnis radcliffei Smith 1913: 599, Figs. 1–3 (Jolo I., Sulu Archipelago, Philippines); Nair & Appukuttan 1973, 1974; Nair & Lal Mohan 1973; Compagno 1984*, 1988*; SSF No. 10.2*; Ebert 2013*; Ebert *et al*. 2013*.

Preoral length <1.5 mouth length; mouth triangular, lip furrows rudimentary or absent. Lateral dermal denticles narrow-crowned and with long, narrow cusps. Dorsal fins subequal, moderate and high; 1st dorsal-fin anterior margin at low angle to body axis. Anal-fin height <½ height of dorsal fins. Caudal fin narrow, long and ribbon-like; junction of caudal-fin pre- and post-ventral margins broadly rounded. Tooth count 72–78/65–77; vertebrae 113–130; spiral valve turns 6–8.

Body brown, with dark markings on dorsal fins, and prominent dark banding on caudal fin. Attains 24 cm TL.

DISTRIBUTION Indo-Pacific (patchy). WIO: Tanzania, Gulf of Aden (scattered) and southern India (common).

REMARKS Litters of 1 or 2; size at birth ~11 cm TL. Males mature by 18–19 cm TL, and females at 15–16 cm TL. Wide-ranging in tropical waters on upper continental and insular slopes and outer shelves, often over mud bottom, at 71–766 m. Feeds on small bony fishes and crustaceans, with squid a lesser component of diet. Interest to fisheries minimal; taken in commercial bottom trawls in Philippines.

Eridacnis sinuans (Smith 1957)

African ribbontail catshark PLATE 35

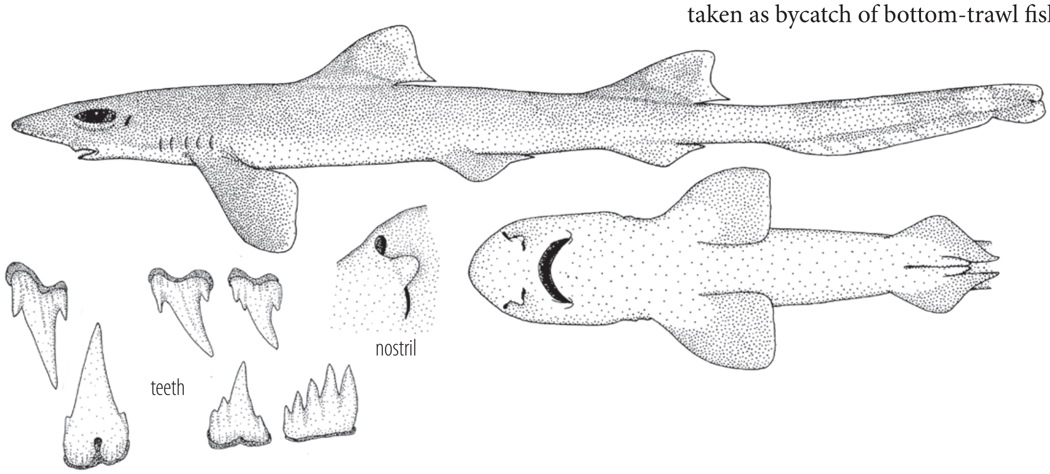
Neotriakis sinuans Smith 1957: 262, Fig. 2 (off Durban, KwaZulu-Natal, South Africa).
Eridacnis sinuans: Bass *et al.* 1975*; Compagno 1984*, 1988*; SSF No. 10.3*; Compagno *et al*. 1989*; Ebert 2013; Ebert *et al*. 2013*.

Preoral length more than twice mouth length; mouth triangular, lip furrows very short. Lateral dermal denticles broad-crowned and with short broad cusps. Dorsal fins subequal, moderately large and high; 1st dorsal-fin anterior margin at high angle to body axis. Anal-fin height <½ height of dorsal fins. Caudal fin narrow, long and ribbon-like; junction of caudal-fin pre- and post-ventral margins broadly rounded. Tooth count typically 64/50; vertebrae 132–144; spiral valve turns 7.

Body brownish grey, with pale margins on dorsal fins, and faint dark banding on caudal fin. Attains 37 cm TL.

DISTRIBUTION WIO: Tanzania to South Africa (KwaZulu-Natal).

REMARKS Litters of 2; size at birth 15–17 cm TL. Males mature at 29–30 cm TL, and females at ~37 cm TL. Bottom-dwelling in warm-temperate and tropical waters of upper continental slope and outer shelf, at 180–500 m. Apparent geographic or bathymetric segregation of populations by sex occurs, as most specimens taken off South Africa (KwaZulu-Natal) are males. Prey includes small bony fishes, crustaceans and cephalopods. Of no importance to fisheries but sometimes taken as bycatch of bottom-trawl fisheries in parts of its range.



Eridacnis sinuans, 28 cm TL, immature male (South Africa). Source: Bass *et al.* 1975

FAMILY **PSEUDOTRIAKIDAE**

False catsharks

David A Ebert

Distinctive small- to large-sized with slender body, narrowly rounded, depressed head, with more or less elongated bell-shaped snout, and deep groove in front of elongated slit-like eyes. Nictitans rudimentary; spiracles large. Anterior nasal flaps broadly angular and not barbel-like; internarial space >1.5 times nostril width. Mouth long, angularly arched, and extending posteriorly to below spiracles; no papillae inside mouth or on edges of gill arches; lip folds short and always present. Teeth small, similar in both jaws, with acute narrow cusps, lateral cusplets, and strong basal ledges and grooves, and not blade-like; posterior teeth comb-like; tooth rows numerous, 94–294/81–335. Pectoral fins with radials confined to bases. First dorsal fin elongated, base closer to pectoral-fin bases than to pelvic-fin bases. Caudal-fin lower lobe weak or absent; no undulations or ripples on dorsal margin; no precaudal pits. Vertebrae 140–186; spiral valve turns 11–17. Body usually grey to brown or blackish.

Small group of poorly known deepwater sharks, found on outer continental and insular shelves and slopes, on or near bottom, at ~130–1 890 m. At least two species are oophagous. Three genera and at least 5 species; 2 genera and at least 2 species in WIO, but only 1 of these at depths of ~200 m. The pygmy false catshark *Planonasus parini* Weigmann, Stehmann & Thiel 2013, was described from off Socotra I. (Arabian Sea), collected at 1 000–1 120 m.

GENUS ***Pseudotriakis*** De Brito Capello 1868

Large-sized, bulky and soft-bodied, with short snout and wide angular mouth. Anterior nasal flaps broadly angular, not barbel-like. Teeth numerous, small, cuspidate, with >200 rows in each jaw. First dorsal fin long, low and keel-like; 2nd dorsal fin higher than 1st; anal fin small; caudal-fin lower lobe weak, no undulations on dorsal margin, and no precaudal pits. One species.

Pseudotriakis microdon De Brito Capello 1868

False catshark PLATE 35

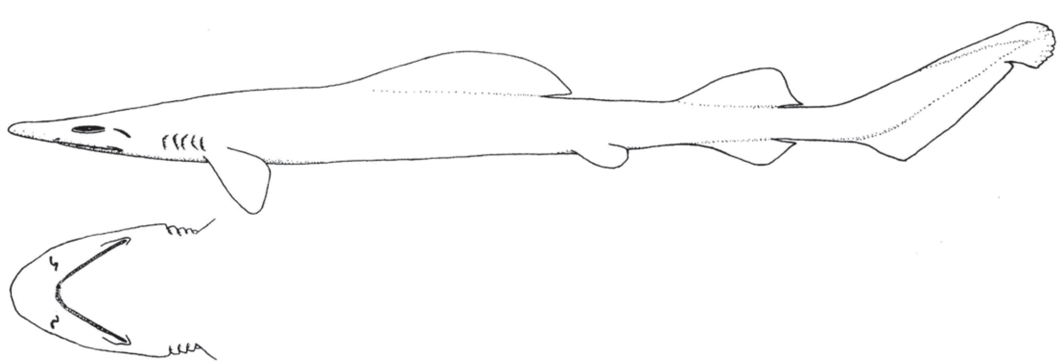
Pseudotriakis microdon De Brito Capello 1868: 316, Pl. 5, Fig. 1 (Setúbal, Portugal); Forster *et al.* 1970; Compagno 1984*; SSF No. 12.1*; Compagno *et al.* 2005*; Ebert 2013*; Ebert *et al.* 2013*.

Diagnosis as for genus. Vertebrae 180–186; spiral valve turns 17.

Body dark brown to blackish, with darker fins. Attains ~3 m TL.

DISTRIBUTION All seas (patchy) except southern Atlantic and eastern Pacific. WIO: Aldabra and Seychelles.

REMARKS Poorly known; exhibits a unique form of oophagy: in early development the embryos are nourished by a yolk sac, but oophagy commences as development proceeds. Litters of 2, possibly more; smallest free-swimming specimen measured 96 cm TL. Large body cavity, soft fins, and soft skin and musculature suggest it is relatively inactive and sluggish and can hover over the bottom at virtually neutral buoyancy. Wide-ranging, with scattered records; found on continental and insular slopes at 200–1 890 m, but occasionally wandering onto continental shelf and into shallower water; seemingly uncommon to rare wherever it occurs. Diet consists mostly of fishes, including other elasmobranchs, and cephalopods and crustaceans: small, sharp, cuspidate teeth, combined with very large mouth may allow it to capture considerably large prey items. Interest to fisheries minimal, taken incidentally in surveys and in fisheries by deep longlines and less commonly bottom trawls, but likely not impacted.



Pseudotriakis microdon, 93 cm TL, immature specimen (Atlantic). Drawn from Bigelow & Schroeder 1948

FAMILY **TRIAKIDAE**

Houndsharks

Kelsey C James and David A Ebert

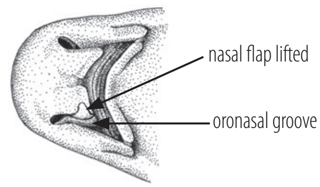
Small- to medium-sized with fusiform body. Eyes elongated and horizontally oval, or slit-like; nictitans external, transitional or internal; spiracles small to large. Anterior nasal flaps elongated to lobe-like or vestigial; lip folds moderate to very long. Teeth small to moderately large, with acute and narrow to moderately large cusps, and with lateral cusplets in some species but these structures reduced or absent in others; cuspidate and not blade-like or compressed, or else blade-like or thickened and molariform; teeth usually similar in both jaws, but differentiated in a few species; tooth counts 18–42/27–106. Two medium to large spineless dorsal fins; 1st dorsal fin large to very large but not keel-like, usually much shorter than caudal fin, and its base well ahead of pelvic-fin bases, usually closest to pectoral-fin bases. Caudal-fin lower lobe well-developed to absent; no undulations on dorsal margin, and no precaudal pits. Spiral valve turns 4–11. Some species with spots or variegated patterns, and others uniformly coloured.

Reproductive mode viviparity with yolk sac or yolk-sac placenta, with litter sizes ranging from 1 or 2 to 52. Many are fairly strong swimmers, occurring in small to large schools or singly, and others rest on the bottom. Feed primarily on bottom-dwelling and midwater bony fishes and invertebrates, with some species taking mainly fishes, others largely crustaceans, and a few primarily cephalopods. Houndshark genera that are especially important to fisheries include *Galeorhinus*, *Iago*, *Mustelus* and *Triakis*; all these are fairly common to very abundant in coastal waters where they occur but are relatively small-sized, and hence important mostly to small commercial and artisanal fisheries which are limited in their gear and movements, as well as to sports fisheries; used primarily for their meat, but also for liver oil, fishmeal, and in the shark-fin trade. None of the species are dangerous to people.

Although a motley assemblage, one of the largest families of sharks. Occur in warm- to cold-temperate seas, most often on continental and insular shelves, from shoreline and intertidal areas, to outermost shelf, often close to bottom; a few deepwater species occur on continental slope to considerable depths, possibly >2 000 m. None are coral-reef specialists or oceanic, but mainly inhabit sandy, muddy or rocky inshore areas, including enclosed bays. A few species have been recorded from river mouths, but apparently none can tolerate freshwater for an extended period. Nine genera and at least 47 species, plus many undescribed species; 6 genera and 9 species in WIO.

KEY TO GENERA

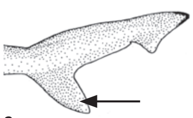
1a Anterior nasal flaps very large, nearly meeting at midline of snout and overlapping mouth posteriorly; oronasal grooves present ..... ***Scylliogaleus***



1b Anterior nasal flaps moderately large to very small, well-separated and not reaching mouth; no oronasal grooves **2**

2a Caudal-fin lower lobe very long at all stages; 2nd dorsal fin markedly smaller than 1st (<½ its area) **3**

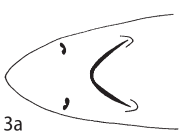
2b Caudal-fin lower lobe absent to short in adults, weak or absent in young; 2nd dorsal fin subequal to 1st (~⅔ its area) **4**

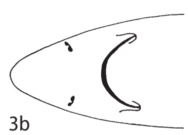

2a


2b

3a Mouth angular; 2nd dorsal fin considerably larger than anal fin; caudal-fin terminal lobe ~⅓ length of caudal-fin dorsal margin ..... ***Hypogaleus***

3b Mouth broadly arched; 2nd dorsal fin subequal to anal fin; caudal-fin terminal lobe ~½ length of caudal-fin dorsal margin ..... ***Galeorhinus***

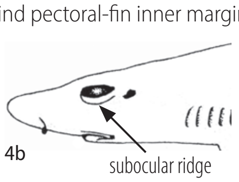

3a


3b

4a Eyes lateral, subocular ridges rudimentary; 1st dorsal-fin origin anteriorly set, over pectoral-fin bases ..... ***Iago***

4b Eyes dorsolateral, subocular ridges strong; 1st dorsal-fin origin posteriorly set, over or behind pectoral-fin inner margins **5**


4a

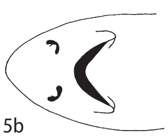


4b

5a Snout bluntly rounded in dorsoventral view; mouth arcuate, lower jaw with convex edges ..... ***Triakis***

5b Snout parabolic to subangular in dorsoventral view; mouth angular, lower jaw with straight or nearly straight edges ..... ***Mustelus***


5a


5b

GENUS *Galeorhinus* Blainville 1816

Slender-bodied with snout moderately long and parabolic in dorsoventral view, preoral length about equal to mouth width. Eyes horizontally oval and lateral; subocular ridges obsolete. Anterior nasal flaps vestigial, formed as small, low, angular points; no oronasal grooves. Mouth broadly arched and long; lip folds moderately long, upper furrows ending well behind level of upper symphysis. Teeth blade-like, compressed and cuspidate, similar in both jaws; anteroposterior teeth with oblique cusps and cusplets; medial teeth well-differentiated from anteroposterior teeth. First dorsal fin moderately large, its origin over or slightly behind pectoral-fin free rear tips; 2nd dorsal fin much smaller, <½ height of 1st. Anal fin about equal to 2nd dorsal fin. Caudal-fin lower lobe strong; terminal lobe very long, ~2 times into caudal-fin dorsal margin. One species.

Galeorhinus galeus (Linnaeus 1758)

Tope PLATES 36 & 38

Squalus galeus Linnaeus 1758: 234 (Mediterranean Sea and NE Atlantic).
Galeorhinus galeus: Bass *et al*. 1975*; SSF No. 9.20*; Compagno *et al*. 1989*; Compagno *et al*. 1991; Heemstra & Heemstra 2004*; Compagno *et al*. 2005*; Ebert *et al*. 2013*.

Diagnosis as for genus. Nictitans internal; no interdorsal ridge. Tooth count 32–46/31–38; vertebrae 123–146; spiral valve turns 4–6.

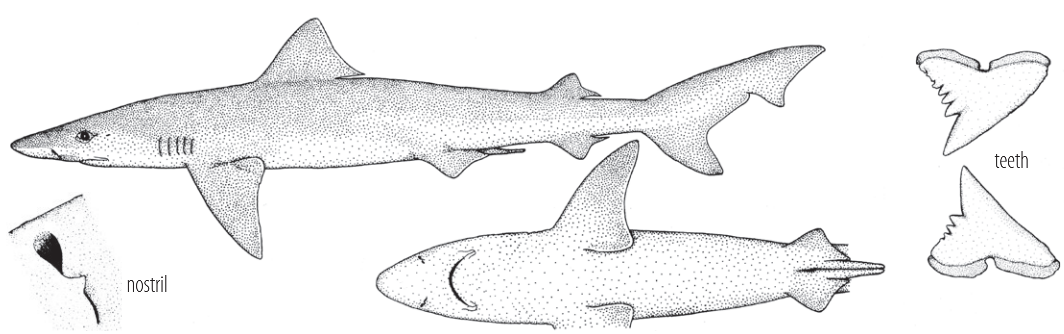
Body greyish above, white below; fins plain, but with black markings in young. Attains 195 cm TL.

DISTRIBUTION Worldwide in temperate seas, including Mediterranean Sea. WIO: South Africa (Western Cape and Eastern Cape).

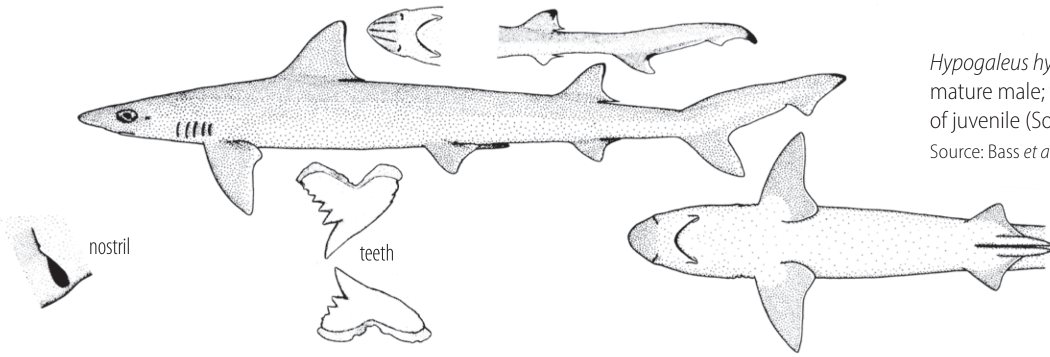
REMARKS Viviparous with yolk sac; litters of 6–52; size at birth 30–40 cm TL, with pups born in late spring and early summer in enclosed bays and estuaries. Males mature at 120–170 cm TL, at ~8 years; females mature at 130–185 cm TL, at ~11 years; maximum age possibly 60 years. Coastal-pelagic, in temperate continental and insular waters, often near bottom, at 2–471 m; strong-swimming and seasonally migratory. Feeds on large variety of demersal bony fishes and midwater schooling fishes, also cephalopods. High fisheries interest throughout its distribution, with its meat excellent for human consumption; the principal target species of the South African directed shark fishery. Different stocks may occur worldwide. IUCN Red List conservation status Critically Endangered.

GENUS *Hypogaleus* Smith 1957

Slender-bodied with snout moderately long, broadly pointed and parabolic in dorsoventral view; preoral length about equal to mouth width. Eyes horizontally oval and lateral; subocular ridges obsolete. Anterior nasal flaps vestigial, well separated from each other and mouth; no oronasal grooves. Mouth angular and long; lip folds moderately long, upper furrows ending well behind level of upper symphysis. Teeth blade-like, compressed and cuspidate, similar in both jaws; anteroposterior teeth with oblique cusps and cusplets; medial teeth well differentiated from anteroposterior teeth. First dorsal fin moderately large, its origin over or slightly behind pectoral-fins free rear tips; 2nd dorsal fin smaller than 1st. Anal fin smaller than 2nd dorsal fin. Caudal-fin lower lobe strong, and terminal lobe relatively short. One species.



Galeorhinus galeus, 134 cm TL, mature male (South Africa). Source: Bass *et al.* 1975



Hypogaleus hyugaensis, 130 cm TL, mature male; tail and ventral head of juvenile (South Africa).
Source: Bass *et al.* 1975

Hypogaleus hyugaensis (Miyosi 1939)

Blacktip tope PLATE 38

Eugaleus hyugaensis Miyosi 1939: 91, Fig. 1 (off Hyūga Nada, Miyazaki Prefecture, Japan).
Hypogaleus zanzibarensis: Smith 1957*.
Hypogaleus hyugaensis: Bass *et al.* 1975*; SSF No. 9.22*; Compagno *et al.* 1989*; Compagno *et al.* 2005*; Ebert *et al.* 2013*.

Diagnosis as for genus. Nictitans internal; no interdorsal ridge. Tooth count ~50/44.

Body bronzy to grey-brown above, paler below; dorsal and caudal fins with dusky tips (especially in young). Attains 130 cm TL.

DISTRIBUTION Indo-Pacific (patchy). WIO: Persian/Arabian Gulf, South Africa (KwaZulu-Natal) to Tanzania (Zanzibar) and Kenya.

REMARKS Viviparous with yolk-sac placenta; litters of 2–15 (average ~10); size at birth 33–35 cm TL; gestation period <12 months. Matures at ~95 cm TL. Found in relatively deep tropical and warm-temperate seas, along continental shelf and upper slope, at 40–230 m. Diet includes bony fishes and cephalopods. A bycatch of numerous fisheries, especially the trawl fisheries in WIO region.

GENUS *Iago* Compagno & Springer 1971

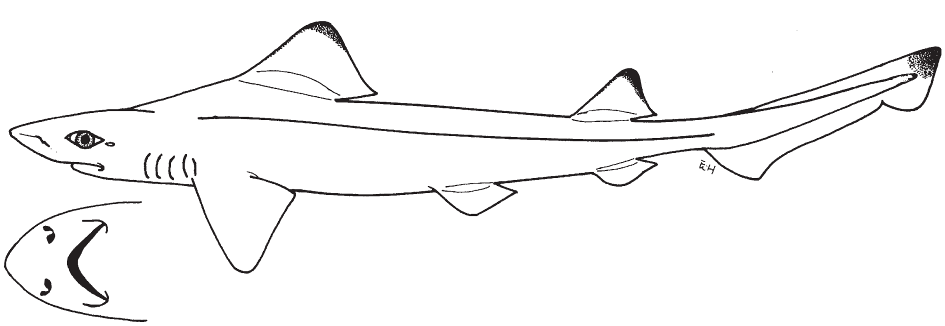
Slender-bodied with snout moderately long and subangular in dorsoventral view. Eyes horizontally oval; vestigial lateral subocular ridges. Anterior nasal flaps formed as low, rounded or angular lobes, well-separated from each other and from mouth; no oronasal grooves. Mouth angular and moderately long; lip folds short to moderately long. Teeth blade-like, compressed and cuspidate; anteroposterior teeth with oblique cusps and cusplets or blades; medial teeth well-differentiated from anteroposterior teeth. First dorsal fin moderately large, anteriorly set, its origin over pectoral-fin bases; 2nd dorsal fin somewhat smaller than 1st. Anal fin considerably smaller than 2nd dorsal fin. At least 2 species, 1 in WIO.

Iago omanensis (Norman 1939)

Bigeye houndshark PLATE 38

Eugaleus omanensis Norman 1939: 11, Fig. 3 (Gulf of Oman).
Iago omanensis: Compagno & Springer 1971*; Compagno 1984*; Compagno *et al.* 2005*; Ebert 2013*; Ebert *et al.* 2013*.

Snout moderately broad; gill slits large. Eyes large, length nearly equal to longest gill slit. Lip folds relatively short, with upper furrows falling well behind level of lower symphysis.



Iago omanensis, ~40 cm TL (Red Sea).

Body brownish or greyish above, paler below; no conspicuous markings, but dorsal-fin margins sometimes darker. Attains 58 cm TL.

DISTRIBUTION WIO: Red Sea, Gulf of Oman, and Pakistan to southwestern India.

REMARKS Viviparous with yolk-sac placenta; litters of 2–10; size at birth ~17 cm TL; females attain larger sizes than males. Found in deep, tropical waters of continental shelf and slope, at 110–1 000 m or more (particularly in Red Sea); tolerates warmer, oxygen-poor conditions. Segregates by sex, with females occurring in shallower waters. Feeds primarily on bony fishes (especially lanternfishes) and cephalopods. Limited fisheries interest; taken in gillnet fisheries in India and in small-scale and longer-range fisheries in Red Sea.

GENUS *Mustelus* Linck 1790

Slender-bodied with long, parabolic, subangular snout. Eyes horizontally elongated or oval and dorsolateral; subocular ridges strong. Anterior nasal flaps elongated and lobate, well-separated from each other and mouth; no oronasal grooves. Mouth angular and moderately long; lip folds moderately long, upper folds ending well behind level of upper-jaw symphysis. Teeth forming a pavement, similar in both jaws, but varying from compressed and with short erect cusps and cusplets, to rounded, molariform and without cusps and cusplets. First dorsal fin moderately large, its origin over pectoral-fin inner margins or slightly behind free rear tips; 2nd dorsal fin subequal to 1st. Anal fin much smaller than 2nd dorsal fin. Caudal-fin lower lobe poorly developed to short and strong. About 27 species, 4 in WIO.

KEY TO SPECIES

1a Small white spots on dorsal surface and flanks 2
1b No small white spots on dorsal surface and flanks 3

2a Pectoral fins larger, rear margin 12–16% TL .... *M. palumbes*
2b Pectoral fins smaller, rear margin 7.5–14% TL .... *M. manazo*

3a Denticles on tongue extend to level of 1st gill-arch lower limb; 2nd dorsal-fin base to caudal-fin origin 1.7–2 times length of caudal-fin upper lobe; precaudal vertebrae 62–76 .... *M. mosis*
3b Denticles on tongue not extending to level of 1st gill-arch lower limb; 2nd dorsal-fin base to caudal-fin origin 1.9–2.4 times length of caudal-fin upper lobe; precaudal vertebrae 81–95 .... *M. mustelus*

Mustelus manazo Bleeker 1854

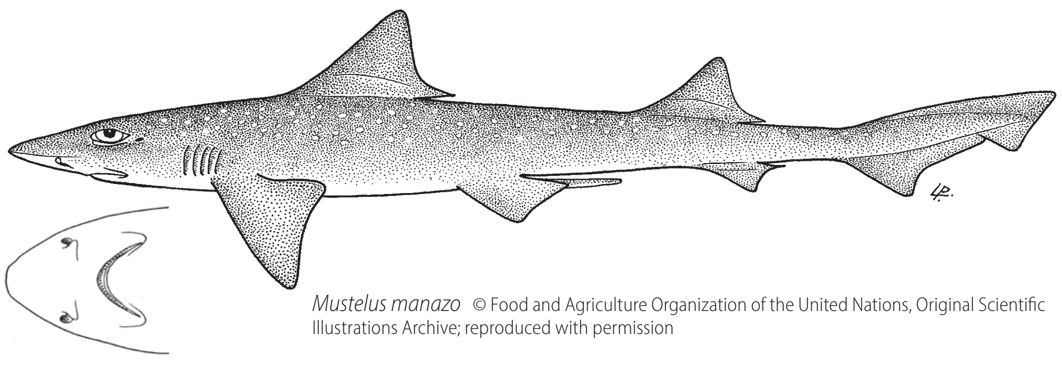
Starspotted smoothhound

PLATE 36

Mustelus manazo Bleeker 1854: 126 (Nagasaki, Japan); Compagno *et al*. 2005*; Ebert *et al*. 2013*.

Medium-sized with slender body, short head, and snout moderately long and bluntly angular in lateral view; internarial space narrow. Eyes large; interorbital space narrow. Mouth short, upper lip folds longer than lower folds. Teeth molariform and asymmetric, with cusps reduced to low point. Paired fins moderately sized. Trailing edges of dorsal fins denticulate, without bare ceratotrichia. First dorsal fin broadly triangular, with posteroventrally sloping rear margin, and midbase closer to pelvic-fin bases than to pectoral-fin bases. Anal-fin to caudal-fin space greater than 2nd dorsal-fin height. Caudal-fin lower lobe not falcate in adults. Vertebrae 129–142.

Body grey or grey-brown above, paler below; usually many white spots on dorsal surface, but no dark spots or bars. Attains 117 cm TL.



Mustelus manazo © Food and Agriculture Organization of the United Nations, Original Scientific Illustrations Archive; reproduced with permission

DISTRIBUTION Northwestern and western central Pacific and Indian oceans. WIO: Kenya.

REMARKS Viviparous with yolk sac; litters of 1–22 (mostly 2–6), varying with geographic region and mother's size; size at birth 20–35 cm TL; gestation period 10–12 months. Matures at 60–80 cm TL, depending on region. Wide-ranging, but reports may represent more than one species. Occurs in temperate to tropical continental waters, from intertidal and subtidal areas, and commonly close inshore, especially over mud or sand bottoms. Feeds on bottom-dwelling crustaceans, fishes, polychaetes and sipunculid worms. Considerable fisheries interest, especially off Japan; used for its meat and oil.

Mustelus mosis Hemprich & Ehrenberg 1899

Hardnose smoothhound PLATES 36 & 38

Mustelus mosis Hemprich & Ehrenberg 1899: 8, Pl. 7, Fig. 3a–d (Red Sea); Van der Elst 1981*; SSF No. 9.26*; Compagno *et al.* 1989*; Fricke 1999; Bonfil & Abdallah 2004; Heemstra & Heemstra 2004; Compagno *et al.* 2005*; Ebert *et al.* 2013*.

Large-sized with fairly slender body, short head, and snout moderately long, bluntly angular in lateral view, with expanded bulbous tip in adults (hypercalcified rostral cartilages). Eyes large; interorbital space narrow. Internarial space broad. Mouth moderately long; upper lip folds about equal to lower folds. Teeth molariform and asymmetric, with cusp reduced to low point. Trailing edges of dorsal fins without bare ceratotrichia. First dorsal fin somewhat falcate, with rear margin nearly vertical from apex, midbase closer to pectoral-fin bases than to pelvic-fin bases. Pectoral fins medium-sized. Pelvic fins small. Anal-fin to caudal-fin space greater or subequal to 2nd dorsal-fin height. Caudal-fin lower lobe more or less falcate in adults. Vertebrae 122.

Body tan to greyish-tan above, paler below; no white or dark spots or dark bars, but South African specimens generally have white-tipped 1st dorsal fin and black-tipped 2nd dorsal fin and caudal fin. Attains 150 cm TL.

DISTRIBUTION Indian Ocean. WIO: South Africa (KwaZulu-Natal) to Red Sea, Persian/Arabian Gulf, Pakistan, India, Mascarenes, Maldives and Sri Lanka; elsewhere to east coast of India and Bay of Bengal.

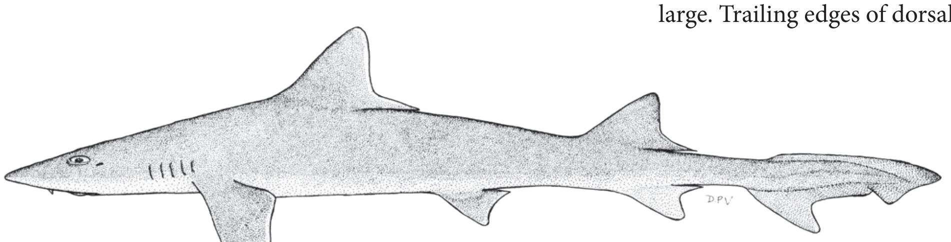
REMARKS Viviparous with yolk-sac placenta; litters of 6–10. Males mature at 63–67 cm TL. Occurs in continental waters and common in its range; bottom-dwelling, found inshore and offshore, occasionally on coral reefs. Feeds mostly on small bottom-dwelling fishes, molluscs and crustaceans. Caught in multiple gears; targeted in fisheries off Pakistan and India.

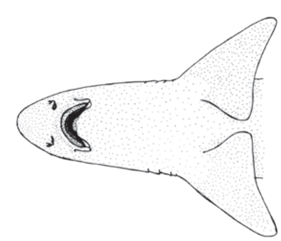
Mustelus mustelus (Linnaeus 1758)

Smoothhound PLATE 38

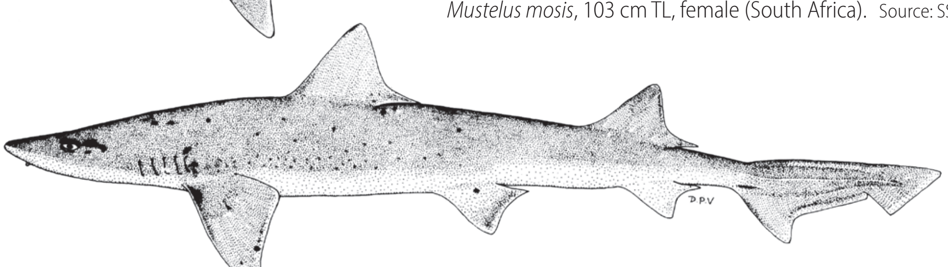
Squalus mustelus Linnaeus 1758: 235 (Mediterranean Sea).
Mustelus mustelus: SSF No. 9.27*; Compagno *et al.* 1989*; Compagno *et al.* 1991; Heemstra & Heemstra 2004*; Compagno *et al.* 2005*; Ebert *et al.* 2013*.

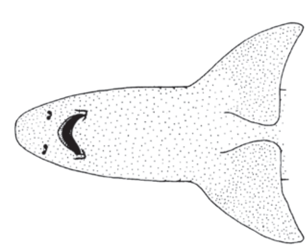
Large-sized with short slender head, and snout moderately long and bluntly angular in lateral view. Eyes fairly large; interorbital space narrow. Internarial space broad. Mouth fairly short; upper lip folds usually slightly longer than lower furrows. Teeth molariform and asymmetric, with cusps reduced to low point; cusplets absent except in very young individuals. Buccopharyngial denticles confined to tongue tip and extreme anterior end of palate. Crowns of lateral dermal denticles lanceolate or weakly tricuspidate, with longitudinal ridges extending their entire length. Paired fins moderately large. Trailing edges of dorsal fins denticulate, without





Mustelus mosis, 103 cm TL, female (South Africa). Source: SSF





Mustelus mustelus, 142 cm TL (South Africa). Source: Bass *et al.* 1975 bare ceratotrichia. First dorsal fin falcate, with rear margin almost vertical, midbase closer to pectoral-fin bases than to pelvic-fin bases. Caudal-fin lower lobe more or less falcate. Vertebrae 131–137.

Body grey to grey-brown above, paler below; no white spots or dark bars, but occasionally few irregular, small dark spots. Attains 164 cm TL.

DISTRIBUTION North Sea, Mediterranean Sea, eastern Atlantic (British Isles to West Africa), to South Africa (KwaZulu-Natal) in WIO.

REMARKS Viviparous with yolk-sac placenta; litters of 4–15; size at birth ~39 cm TL; gestation period 10–11 months. Males mature at 70–74 cm TL, and females at ~80 cm TL. Occurs on continental shelf and uppermost slope, most commonly in shallow depths of ~5–50 m, but also intertidal areas and ranging to at least 350 m deep; swims near bottom but sometimes in midwater. Feeds primarily on crustaceans, but also cephalopods and bony fishes. Considerable fisheries interest in European waters, Mediterranean Sea and off West Africa; taken in bottom trawls, fixed bottom nets and with line gear; used for human consumption. IUCN Red List conservation status Vulnerable.

Mustelus palumbes Smith 1957

Whitespotted smoothhound

PLATES 37 & 38

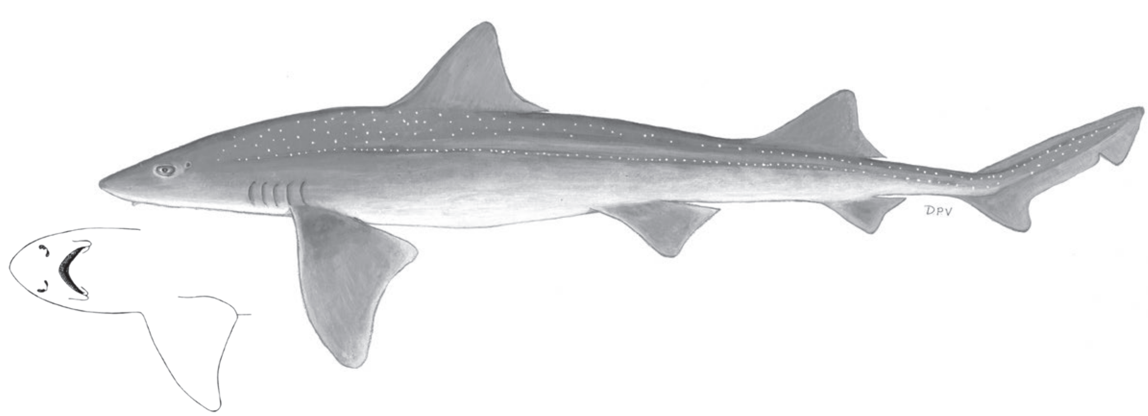
Mustelus palumbes Smith 1957: 358, Fig. 1e–f (Knysna Estuary, Western Cape, South Africa); SSF No. 9.28*; Compagno *et al*. 1989*; Compagno *et al*. 1991; Heemstra & Heemstra 2004; Compagno *et al*. 2005*; Ebert *et al*. 2013*.

Slender-bodied with short head, and snout moderately long and bluntly angular in lateral view. Eyes fairly large; interorbital space moderately narrow. Internarial space broad. Mouth short, subequal to eye length; upper lip folds longer than lower folds. Teeth molariform and asymmetric, with cusps reduced to low point. Buccopharyngial denticles covering almost entire palate and floor of mouth. Trailing edges of dorsal fins denticulate, without bare ceratotrichia. Interdorsal space moderately long; 1st dorsal fin broadly triangular, with posteroventrally sloping rear margin, and midbase closer to pectoral-fin bases than to pelvic-fin bases. Pectoral fins large. Pelvic fins high and broadly rounded. Anal-fin to caudal-fin space greater than 2nd dorsal-fin height. Caudal-fin lower lobe somewhat expanded and sometimes semifalcate.

Body grey or grey-brown above, paler below; numerous small white spots, distinct or faint. Attains 120 cm TL.

DISTRIBUTION Southern Africa: Namibia in southeastern Atlantic, to South Africa and southern Mozambique in WIO.

REMARKS Viviparous with yolk sac; litters of 3–8. Males mature at 76–88 cm TL, and females at 79–102 cm TL. Occurs in temperate seas, on continental shelf and upper slope, inshore and offshore, on or near bottom, from intertidal to at least 360 m deep; prefers sand or gravel bottoms. Feeds on crabs and probably other invertebrates. Limited fisheries interest, often taken by sports anglers and as bycatch of commercial bottom trawls.



Mustelus palumbes, 88 cm TL, mature male holotype, ventral head; lateral view of 99-cm-TL specimen (both South Africa). Source: SSF

GENUS *Scylliogaleus* Boulenger 1902

Medium-sized with short and broadly rounded snout. Eyes horizontally elongated with strong subocular ridges. Anterior nasal flaps triangular and overlapping mouth; oronasal grooves broad and shallow; internarial width half nostril width. Mouth broadly arched, short, with long lip folds. Teeth small, blunt-crowned, molariform and without cusps and cusplets. First dorsal fin moderately large, its origin over pectoral-fin inner margins or free rear tips; 2nd dorsal fin as large as 1st, its height at least three-quarters as high as 1st dorsal fin. Anal fin smaller than 2nd dorsal fin. One species.

Scylliogaleus quecketti Boulenger 1902

Flapnose houndshark PLATE 37

Scylliogaleus quecketti Boulenger 1902: 51, Pl. 4 (off Umkomaas, KwaZulu-Natal, South Africa); Bass *et al*. 1975*; SSF No. 9.34*; Compagno *et al*. 1989*; Compagno *et al*. 2005*; Ebert *et al*. 2013*.

Diagnosis as for genus. Distinguished by large fused nasal flaps expanded over mouth; nictitans transitional. Interdorsal ridge present. Caudal-fin lower lobe very short in adults, barely developed in young; caudal-fin terminal lobe moderately long. Tooth count 51/50; vertebrae 139–149; spiral valve turns 7.

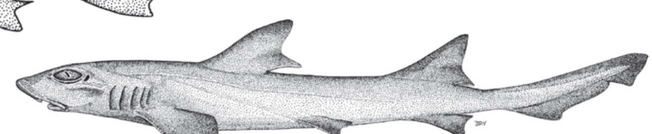
Body grey above, paler below; fins plain in adults, but median fins with white rear edges in newborns. Attains 102 cm TL.

DISTRIBUTION WIO: endemic to South Africa (Eastern Cape and KwaZulu-Natal).

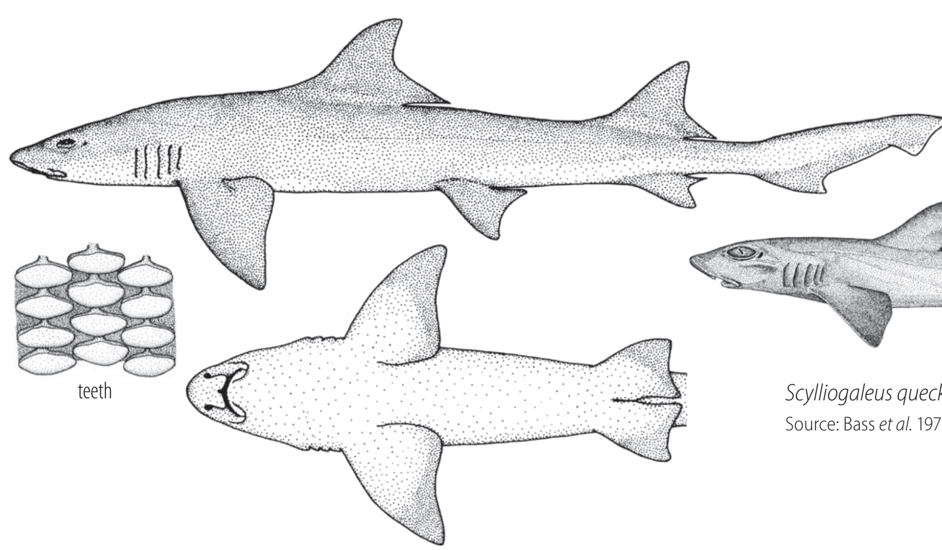
REMARKS Little known and uncommon; occurs in warm-temperate or subtropical waters of continental shelf, inshore, from surfline and intertidal areas to close offshore. Viviparous, but presence or absence of placenta unknown; litters of 2–4; size at birth ~34 cm TL; gestation period 9–10 months. Feeds primarily on crustaceans, also squid. Minimal fisheries interest; occasionally caught by shore anglers. IUCN Red List conservation status Vulnerable.

GENUS *Triakis* Müller & Henle 1838

Stout-bodied with short, broadly rounded snout. Eyes horizontally elongated with strong subocular ridges. Anterior nasal flaps elongated and lobate; no oronasal grooves. Mouth broadly arched and moderately short; lip folds long, upper furrows nearly reaching level of upper symphysis. Teeth semi-blade-like, somewhat compressed, with erect or oblique cusps variably developed, and similar in both jaws; medial teeth not differentiated from anteroposterior teeth. First dorsal fin moderately large, its origin over pectoral-fin inner margins; 2nd dorsal fin nearly as large as 1st. Anal fin smaller than 2nd dorsal fin. Five species, 1 in WIO.



Scylliogaleus quecketti, 34 cm TL, pup (South Africa). Source: Bass *et al.* 1975



Scylliogaleus quecketti, 94 cm TL, mature female (South Africa). Source: Bass *et al.* 1975

Triakis megalopterus (Smith 1839)

Spotted gullyshark PLATES 37 & 38

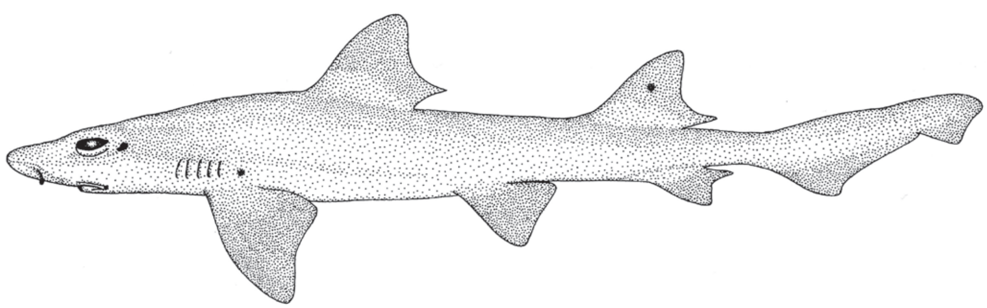
Mustelus megalopterus Smith 1839: 4, Pl. 2 (Cape Town, South Africa).
Mustelus natalensis: Steindachner 1866*; Smith 1957*.
Mustelus nigropunctatus: Smith 1952*.
Triakis megalopterus: Bass *et al.* 1975*; Van der Elst 1981*; SSF No. 9.36*; Compagno *et al.* 1989*; Heemstra & Heemstra 2004*; Compagno *et al.* 2005*; Ebert *et al.* 2013*.

Anterior nasal flaps lobate, not reaching mouth and far separated from each other; upper lip folds reaching level of lower symphysis of mouth. Teeth with strong erect cusps on at least the middle two-thirds of dental band, cusplets low or absent on almost all teeth, semi-molariform but not blade-like. Unusually high interdorsal ridge; 1st dorsal fin with abrupt vertical rear margin. Pectoral fins broadly falcate in adults. Caudal-fin lower lobe barely developed in young, but short and strong in adults; caudal-fin terminal lobe moderately long. Tooth count 48–52/44; vertebrae 162–166; spiral valve turns 6.

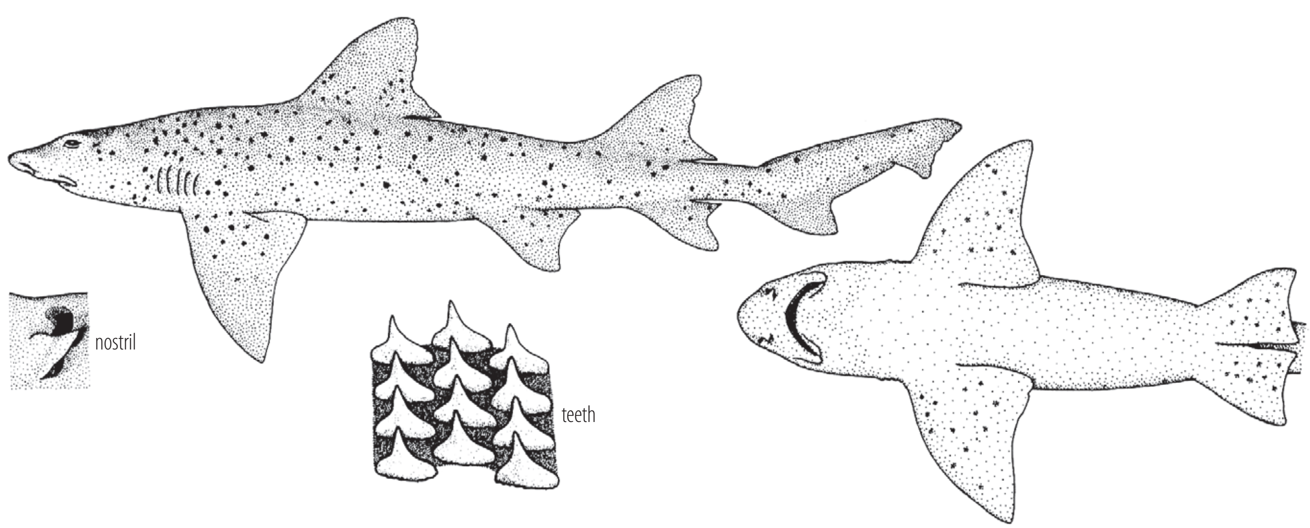
Body grey, with few to numerous small black spots in adults, and few or no spots in young, although plain adults have been recorded. Attains 208 cm TL.

DISTRIBUTION Southern Africa: southern Angola in southeastern Atlantic, to South Africa (Cape Peninsula and eastwards, but rarely to southern KwaZulu-Natal) in WIO.

REMARKS Viviparous with yolk sac; litters of 5–15; size at birth 40–45 cm TL; gestation may last 19–21 months, with reproductive cycle of 2 or 3 years, depending on time between pregnancies. Males mature at 125–135 cm TL, and females at 145 cm TL. Inshore, bottom-dwelling, in temperate continental waters, usually in shallow depths to surfline. Prefers rocky reefs at <10 m. Congregates in schools in summer (False Bay, South Africa). Diet changes with growth: small sharks <100 cm consume primarily Cape rock crabs (*Plagusia chabrus*), sharks 100–140 cm consume cephalopods in addition to Cape rock crabs, and larger sharks feed mostly on bony fishes. Hardy and keeps well in captivity. Limited fisheries interest; commonly caught by shore anglers.



Triakis megalopterus, 41 cm TL, immature male (South Africa). Source: Bass *et al.* 1975



Triakis megalopterus, 145 cm TL, mature female (South Africa). Source: Bass *et al.* 1975

FAMILY **HEMIGALEIDAE**

Weasel sharks

James DS Knuckey and David A Ebert

Small- to moderate-sized, with horizontally oval eyes, internal nictitans and small spiracles. Mouth short to long, arched and reaching past anterior edge of eyes; lip folds moderately long; no oronasal grooves or barbels. Teeth not compressed; upper teeth small to moderately large and blade-like, lower teeth more or less cuspidate. Two moderately-sized spineless dorsal fins; 1st dorsal fin much shorter than caudal fin, its base well ahead of pelvic-fin bases; 2nd dorsal fin ~⅔ size of 1st. Anal fin subequal to 2nd dorsal fin. Caudal-fin lower lobe well-developed, acute; caudal-fin dorsal margin with lateral undulations or ripples; precaudal pits present. Spiral valve turns 4–6.

Reproductive mode viviparity with yolk-sac placenta. Commonly occurring in tropical coastal waters, over continental and insular shelves, to ~100 m deep but usually shallower. Of modest importance to artisanal and small commercial inshore and near offshore fisheries where they occur, and used mostly for their meat for human consumption, although larger species are used for their liver oil and in the shark-fin trade.

Limited to the eastern Atlantic and continental Indo-Pacific, and not far into the central Pacific. Four genera and ~8 species; all genera and 5 species in WIO.

KEY TO GENERA

1a Lower anterolateral teeth with long hooked cusps; lower teeth protrude prominently when mouth closed **2**

1b Lower anterolateral teeth with short, straight or weakly hooked cusps; lower teeth concealed or protrude only slightly when mouth closed **3**

2a Snout obtusely wedge-shaped in dorsoventral view; lower jaw rounded at symphysis; diastema at midline of both jaws; mesial edges of teeth smooth, sometimes a few cusplets on mesial edges of lower teeth; pectoral fins not falcate; rear margins of 2nd dorsal fin and anal fin moderately concave; rear margins of pectoral fins and pelvic fins straight or slightly concave .... ***Chaenogaleus***

2b Snout bluntly rounded in dorsoventral view; lower jaw truncated at symphysis; diastema at midline of both jaws; mesial edges of upper teeth and most lower teeth serrated or with a few cusplets (but smooth edges in young <55 cm TL); pectoral fins strongly falcate; rear margins of 2nd dorsal fin, anal fin, pectoral fins and pelvic fins deeply concave .... ***Hemipristis***

Continued …

KEY TO GENERA

3a Upper anterolateral teeth with short cusps; no cusplets on lower teeth; roots and crown feet deeply arched, giving teeth inverted Y-shape; tooth counts 25–34/37–43, and 6–20 more lower rows than upper rows; dorsal fins, pectoral fins, pelvic fins, and caudal-fin lower lobe strongly falcate .... ***Hemigaleus***

3b Upper anterolateral teeth with long cusps; distal and sometimes mesial cusplets on some lower anterolateral teeth; roots and crown feet hardly arched, giving teeth inverted T-shape; tooth counts 26–30/27–33, with 1 less to 5 more lower rows than upper rows; dorsal fins, pelvic fins, and caudal-fin lower lobe not falcate, but only pectoral fins falcate .... ***Paragaleus***

GENUS ***Chaenogaleus*** Gill 1862

Snout moderately long and wedge-shaped in dorsoventral view. Gill slits long, about twice or more eye length. Mouth parabolic and very long, its length 66–82% width; lower teeth protrude prominently when mouth closed; ends of upper lip folds behind rear edge of eyes; lower jaw rounded at symphysis. No diastema at midline of jaws. Upper anterolateral teeth with smooth mesial edges and very long cusps; lower anterolateral teeth with very long, stout, strongly hooked cusps, and no cusplets; lower crown feet and roots deeply arched, giving teeth inverted Y-shape. Second dorsal fin at least three-fifths height of 1st dorsal fin. Pectoral fins not falcate. One species.

Chaenogaleus macrostoma (Bleeker 1852)

Hooktooth shark PLATE 38

Hemigaleus macrostoma Bleeker 1852: 46, Pl. 2, Fig. 10 (Coromandel coast, India).
Chaenogaleus macrostoma: Compagno *et al.* 2005*; Ebert *et al.* 2013*.

Diagnosis as for genus. Tooth count 33–38/34–36; vertebrae 131–139; spiral valve turns 5 or 6.

Body pale grey or bronzy, and without prominent markings, but sometimes black-tipped 2nd dorsal fin and caudal-fin terminal lobe. Attains ~100 cm TL.

Chaenogaleus macrostoma (Oman). © M Harris

DISTRIBUTION Indo-Pacific. WIO: Persian/Arabian Gulf to Pakistan, India and Sri Lanka.

REMARKS Common but little known; found in tropical inshore waters of continental and insular shelves, to at least 59 m deep. Litters of 4; size at birth at least 20 cm TL; males mature at 68–97 cm TL, and females at ~86 cm TL. Probably feeds on small fishes, cephalopods and crustaceans. Commonly landed in inshore and offshore artisanal fisheries, with drifting bottom gillnets, longlines and other line gear; meat used fresh for human consumption, and offal processed into fishmeal. IUCN Red List conservation status Vulnerable.

GENUS *Hemigaleus* Bleeker 1852

Snout rounded in dorsoventral view. Gill slits short. Mouth broadly arched and very short, its length 31–43% width; lower teeth not protruding when mouth closed; ends of upper lip folds extend below eyes; lower jaw rounded at symphysis. No diastema at midline of jaws. Upper anterolateral teeth with smooth mesial edges and very short cusps; lower anterolateral teeth with short, slender, unhooked cusps and no cusplets; lower crown feet and roots deeply arched, giving teeth inverted Y-shape; tooth counts 25–34/37–52. Second dorsal fin 0.4–0.6 times height of 1st dorsal fin. Dorsal fins, pectoral fins, pelvic fins and caudal-fin lower lobe strongly falcate. Vertebrae 112–150. Body pale grey to brown or bronzy dorsally, paler to white ventrally. Two species, 1 in WIO.

Hemigaleus microstoma Bleeker 1852

Sicklefin weasel shark PLATE 39

Hemigaleus microstoma Bleeker 1852: 46, Pl. 2, Fig. 6 (Jakarta, Java, Indonesia); Compagno *et al.* 2005*; Ebert *et al.* 2013*.

Small-sized with rounded, moderately long snout. Gill slits short, ~1.3 times eye length in adults. Mouth very short, arched, with teeth not protruding. Upper teeth with distal cusplets but no serrations; lower teeth inverted Y-shape, with short, straight, smooth-edged cusps, no cusplets, and highly arched roots. Fins distinctly falcate. Second dorsal fin about two-thirds size of 1st dorsal fin. Anal fin smaller than 2nd dorsal fin; no preanal ridges. Precaudal pits crescentic. Tooth count 25–34/37–43; vertebrae 137–150; spiral valve turns 4–6.

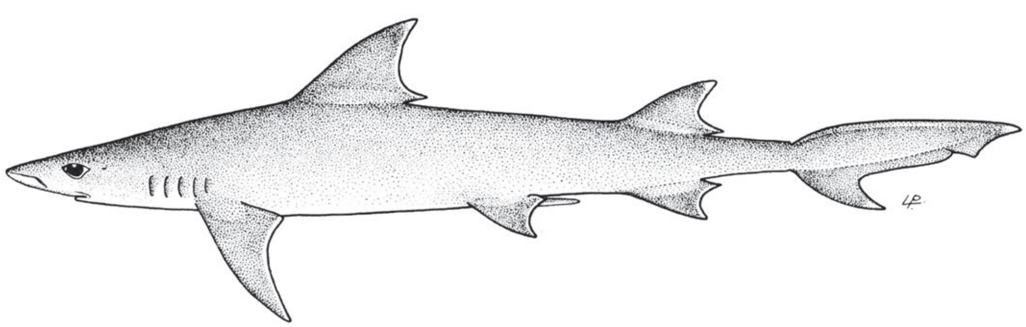
Body pale grey or bronzy dorsally, paler ventrally; sometimes with pale dorsal-fin margins and tips, and white spots on sides. Attains 111 cm TL.

DISTRIBUTION Indo-Pacific. WIO: Red Sea, and southern India to Sri Lanka.

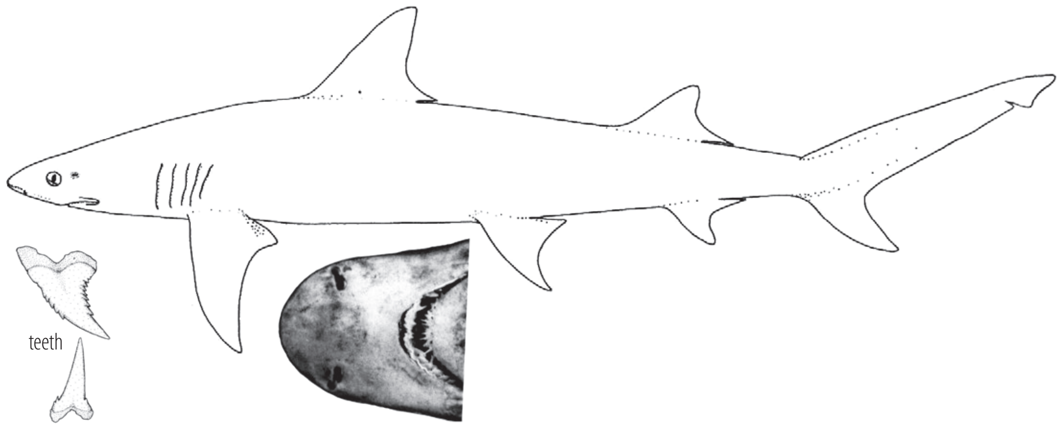
REMARKS Appears naturally uncommon; found in tropical inshore waters of continental shelf, on or near bottom, at 12–167 m. Litters of 4–14; size at birth 26–28 cm TL; males mature at 72–91 cm TL, and females at ~85 cm TL. Specialist feeder on cephalopods, but also crustaceans and echinoderms. Taken regularly in inshore artisanal fisheries in gillnets and probably on line gear; meat used fresh for human consumption. IUCN Red List conservation status Vulnerable.

GENUS *Hemipristis* Agassiz 1843

Moderately large-sized and fairly slender, with snout broadly rounded in dorsoventral view. Gill slits very long. Mouth trapezoidal-parabolic and long, its length 50–70% width; lower teeth protrude prominently when mouth closed; ends of upper lip folds behind rear edge of eyes; lower jaw truncated at symphysis. Diastema at midline of both jaws. Upper anterolateral teeth with short cusps and serrated mesial edges (but smooth edges in young); lower anterolateral teeth with very long, stout, strongly hooked cusps, and serrations and cusplets variably developed on crown feet; lower crown feet and roots deeply arched, giving teeth inverted Y-shape. Second dorsal fin ⅖–⅗ height of 1st dorsal fin. Pectoral fins strongly falcate. Rear margins of 2nd dorsal fin, pectoral fins, pelvic fins and anal fin deeply concave. Precaudal pits crescentic, transverse. One species.



Hemigaleus microstoma, 90 cm TL.



Hemipristis elongata, 137 cm TL, immature female; ventral head (Tanzania). Source: Bass *et al.* 1975 (lateral view); © NRF-SAIAB (head)

Hemipristis elongata (Klunzinger 1871)

Snaggletooth shark PLATE 39

Dirrhizodon elongatus Klunzinger 1871: 665 (Al-Qusayr, Egypt, Red Sea).
Hemipristis elongatus: Bass *et al.* 1975*; Compagno *et al.* 1989*; Compagno *et al.* 2005*; Ebert *et al.* 2013*.
Hemipristis elongata: SSF No. 9.21*.

Diagnosis as for genus. Tooth count 26–30/30–36.

Body bronzy to pale grey-brown above, paler below; no prominent markings, but sometimes tips of pectoral fins, pelvic fins, anal fin and caudal fin prominently white, and 2nd dorsal fin, anal fin, and caudal-fin terminal lobe with dusky blotch, especially in juveniles. Attains 240 cm TL.

DISTRIBUTION Indo-Pacific. WIO: Persian/Arabian Gulf, Pakistan to India, Red Sea to South Africa (KwaZulu-Natal), Madagascar and Maldives.

REMARKS Found in tropical coastal waters, inshore and offshore on continental and insular shelves, at 1–132 m. Litters of 2–11, with larger females having larger litters; size at birth 45–52 cm TL; males mature at 110–145 cm TL, and females at 110–170 cm TL. Feeds on prawns, shrimp, cephalopods and a variety of fishes. Moderate fisheries interest and a common catch in some areas; regularly taken in artisanal and commercial fisheries, with floating and fixed bottom gillnets, floating longlines, trawls and probably on hook and line; used fresh for its meat, the liver processed for vitamin oil, the fins in the shark-fin trade, and offal and spoiled carcasses for fishmeal. IUCN Red List conservation status Vulnerable.

GENUS *Paragaleus* Budker 1935

Snout rounded or slightly pointed in dorsoventral view. Gill slits short. Mouth broadly arched or parabolic and short to moderately long, its length 44–64% width; lower teeth not protruding or else slightly protruding when mouth closed; ends of upper lip folds reach below eyes; lower jaw rounded at symphysis. No diastema at midline of jaws. Upper anterolateral teeth with smooth mesial edges and moderately long cusps; lower anterolateral teeth with short, fairly stout, unhooked or slightly hooked cusps with distal cusplets; roots and crown feet hardly arched, giving teeth inverted T-shape; tooth counts 26–30/27–33. Pectoral fins narrow and falcate. Interdorsal ridge present; 2nd dorsal fin at least three-fifths height of 1st dorsal fin. Body pale to dark grey or grey-brown above, whitish below; some species variously with paired blackish marks or dusky blotches on underside of snout, longitudinal bands, or fins with pale rear margins. Four species, 2 in WIO.

KEY TO SPECIES

1a Five or more rows of lower anterolateral teeth with distal cusplets; lower anterior teeth mostly with oblique cusps .... ***P. randalli***

1b Two or 3 rows of lower anterolateral teeth with distal cusplets; lower anterior teeth mostly with erect cusps ...... ***P. leucolomatus***

Paragaleus leucolomatus Compagno & Smale 1985

Whitetip weasel shark

PLATE 39

Paragaleus leucolomatus Compagno & Smale 1985: 9, Figs. 2–8 (SE of Kosi Bay, KwaZulu-Natal, South Africa); SSF No. 9.30*; Compagno *et al*. 2005*; Ebert *et al*. 2013*.

Slender-bodied, with long snout with bluntly rounded tip in lateral view. Eyes oval; gill slits twice eye length. Mouth long; jaw symphyses extending well anterior to upper lip folds; teeth small and serrated. Lower jaw relatively deep (prominently visible in lateral view); lower anterolateral teeth mostly erect-cusped and without distal cusplets, except for last 2 or 3 rows. Pectoral fins strongly falcate. Dorsal fins and anal fin with deeply concave rear margins. Tooth count 28/30; vertebrae 180; spiral valve turns 5.

Body dark grey dorsally, white ventrally, but underside of prenarial snout with broad dusky patches; 2nd dorsal fin with black apical spot; most fins with conspicuous white tips and rear margins. Attains at least 103 cm TL.

DISTRIBUTION WIO: Southern Mozambique to northeastern South Africa (type locality); records of *Paragaleus* species from Madagascar may be this or a different species.

REMARKS Known from one formally described female specimen, with 1 pup in each uterus, taken from shallow, tropical water, at ~20 m; plus photographs from Mozambique (Plate 39). Assumed viviparous with yolk-sac placenta. The species may be subject to bycatch by coastal line fishers. IUCN Red List conservation status Vulnerable.

Paragaleus randalli

Compagno, Krupp & Carpenter 1996

Slender weasel shark

PLATE 40

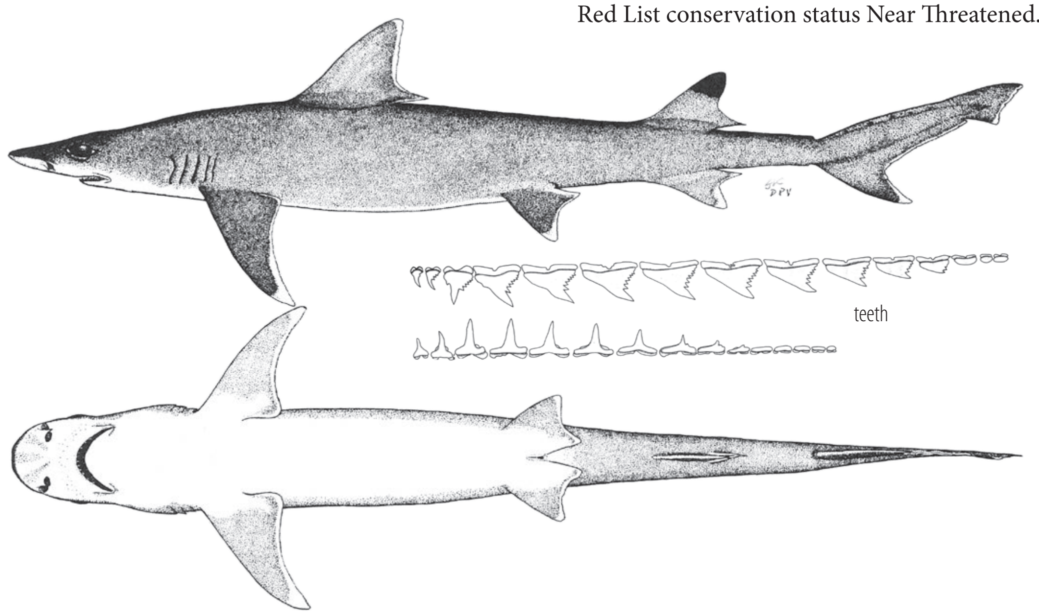
Paragaleus randalli Compagno, Krupp & Carpenter 1996: 393 (Bahrain, Persian/Arabian Gulf); Compagno *et al*. 2005*; Ebert *et al*. 2013*.

Snout with narrowly rounded tip in lateral view. Gill slits about equal to eye length. Mouth long, lower jaw relatively deep (prominently visible in lateral view); jaw symphyses extending well anterior to upper lip folds. Upper and lower teeth not strongly differentiated; lower anterolateral teeth mostly oblique-cusped, with 1 or 2 distal cusplets on 5 or more rows. Pectoral fins falcate. Dorsal fins and anal fin with deeply concave rear margins. Tooth count 28–30/28–33; vertebrae 165–187; spiral valve turns 4 or 5.

Body grey-brown dorsally (head, trunk and caudal fin), becoming paler on flanks, and whitish ventrally (from snout to caudal-fin origin); underside of prenarial snout with pair of narrow black lines (but no dark patches); most fins with dark web and inconspicuous pale rear margin (but no abruptly white or black fin tips). Attains at least 81 cm TL.

DISTRIBUTION Indian Ocean: Persian/Arabian Gulf, Gulf of Oman, India and Sri Lanka in WIO; elsewhere to Bay of Bengal (India and possibly Myanmar).

REMARKS Poorly known; patchy records from shallow inshore tropical waters of continental shelf, to at least 18 m deep. Probably litters of 1 or 2; size at birth ~29 cm TL; males mature at 62–72 cm TL, and females at 70–80 cm TL. IUCN Red List conservation status Near Threatened.



Paragaleus leucolomatus, 96 cm TL, gravid female holotype, upper and lower teeth from middle of right side of jaw (South Africa). Source: Compagno & Smale 1985

FAMILY **GALEOCERDONIDAE**

Tiger shark

Megan V Winton and David A Ebert

Body fairly stout, and head large and broad; snout short and bluntly rounded. Eyes fairly large, without posterior notch; spiracles relatively large, slit-like. Anterior nasal flaps short, broadly triangular, and not tubular. Mouth large; lip folds very long, and upper folds at least twice as long as lower folds and reaching forward to nearly below eyes. Teeth in both jaws characteristically cockscomb-shaped and heavily serrated (saw-like). Pectoral fins moderately broad and semifalcate. Interdorsal ridge prominent; 2nd dorsal fin much smaller than 1st; dorsal-fin free rear tips long. Anal fin approximately subequal to 2nd dorsal fin; preanal ridges short; rear margin deeply concave. Peduncle with low lateral keels; upper precaudal pit transverse and crescentic. Caudal fin slender with acutely pointed tip. Viviparous without yolk-sac placenta. One species.

GENUS ***Galeocerdo*** Müller & Henle 1837

Diagnosis as for family. One species, previously placed in the family Carcharhinidae.

Galeocerdo cuvier (Péron & Lesueur 1822)

Tiger shark PLATE 49

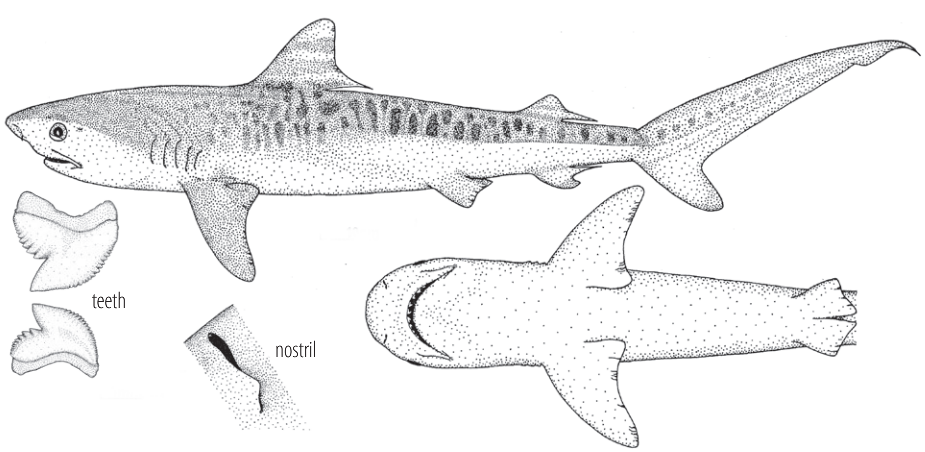
Squalus cuvier Péron & Lesueur *in* Lesueur 1822: 351 (northwestern Australia).
Galeocerdo cuvier: Bass *et al.* 1975*; Van der Elst 1981*; SSF No. 9.19*; Compagno *et al.* 1989*; Cockcroft 1991; Smale & Cliff 1998; Dudley *et al.* 2000; Ebert 2003*; Compagno *et al.* 2005*; Ebert *et al.* 2021.

Diagnosis as for family. Tooth count 18–26/18–25; vertebrae 216–234.

Body grey dorsally, with characteristic pattern of dark grey to black vertical bars and spots, present as bold reticulations in young and progressively fainter in adults; white ventrally. Attains 7.4 m TL but individuals larger than 5 m TL rarely seen.

DISTRIBUTION Circumglobal in warm-temperate to tropical seas, but not known from Mediterranean Sea. WIO: South Africa (Eastern Cape) to Red Sea, Persian/Arabian Gulf, India and Sri Lanka, as well as Socotra, Madagascar, Comoros and Seychelles.

REMARKS Relatively large litters of 10–82 (mean ~30–35); size at birth 51–76 cm TL; gestation period 13–16 months with a triennial reproductive cycle in some regions. Fast-growing in early life; males mature at 226–290 cm TL, aged 7–10 years; females mature at 250–350 cm TL, aged 8–10 years. Maximum age possibly 27–37 years. Common worldwide, on or adjacent to continental and insular shelves; coastal-pelagic, from surface and intertidal zone to at least 140 m deep. Often occurs in estuaries, harbours, coral atolls and lagoons, and may be resident or semi-resident around oceanic islands, preferring turbid areas near volcanic islands and large island groups where a large volume of freshwater runoff may contribute to higher densities of prey organisms. Strong swimmer known to make excursions far offshore into open ocean and capable of long-distance migrations over short periods, with seasonal movements noted in continental waters. A formidable predator and true scavenger; perhaps the most omnivorous of sharks, feeds on a huge variety of bony fishes, elasmobranchs (including tiger shark pups), marine reptiles, sea birds, marine mammals, invertebrates, carrion and even garbage. Caught in numerous coastal and offshore fisheries, as target species or bycatch, and by recreational anglers. One of the potentially most dangerous sharks, with more confirmed attacks on divers, swimmers and boats recorded for this species than for any other shark except the white shark (*Carcharodon carcharias*), and thus a target of many shark control programmes, yet often nonaggressive when encountered underwater and valuable for dive tourism. IUCN Red List conservation status Near Threatened.



Galeocerdo cuvier, 107 cm TL, immature female (S Mozambique). Source: Bass *et al.* 1975

FAMILY CARCHARHINIDAE

Requiem sharks

Megan V Winton and David A Ebert

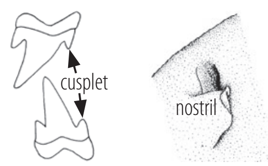
Small- to large-sized (~70 cm to 7 m TL, but most 1–3 m TL) with long arched mouth reaching past front edge of eyes, 2 spineless dorsal fins, and anal fin well separated from caudal fin. Five pairs of gill slits, lateral on body, the last over or behind pectoral-fin origin. Eyes circular, vertically oval, or horizontally oval; nictitans internal, and moveable lower eyelid well-developed; spiracles usually absent or minute. Nostrils without oronasal grooves or barbels; anterior nasal flaps vary from vestigial or weakly expanded to tube-shaped. Mouth long and arched; lip folds moderately long and conspicuous to short and confined to corners of mouth. Teeth small to large, with acute and narrow to moderately broad cusps, sometimes with lateral cusplets, and basal ledges and grooves low to absent; teeth variably differentiated in both jaws, but posterior teeth not comb-like; upper teeth often more compressed and blade-like, lower teeth often cuspidate and not compressed; tooth counts 18–60/18–56. Pectoral fins with radials extending into distal web of fins. First dorsal fin moderately sized to very large, its base well ahead of pelvic-fin bases. Second dorsal fin usually much smaller than 1st. Upper and lower precaudal pits present; peduncle usually without lateral keels. Caudal fin non-lunate, but lower lobe distinct and strong; undulations on upper caudal margin. Vertebral centra with strong, wedge-shaped intermedial calcifications. Intestinal valve scrolled. Colour variable and generally without distinctive patterns.

All species for which reproductive information is available are viviparous with yolk-sac placenta; litter sizes range from 1 to 135. Generally strong, active swimmers, occurring singly, in loose aggregations, or socially schooling. Major predators, feeding on a wide variety of prey, including bony fishes, elasmobranchs, cephalopods and crustaceans, as well as sea birds, turtles, sea snakes, marine mammals, benthic invertebrates, carrion and flotsam. By far the most important shark family for fisheries in the tropics, with numerous species prominent in artisanal, commercial and sports fisheries; used for their meat and often highly valued fins, and also the hide and liver oil. Several of the species are among the most dangerous sharks to humans, yet most of the species pose relatively little danger to swimmers and divers, while several are popular subjects of ecotourism, and some are popularly displayed in public aquaria.

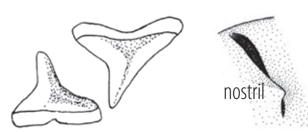
One of the largest groups of living sharks. Found in all warm and temperate seas, and the dominant sharks in tropical waters. Many species are common and wide-ranging. Mainly neritic, over continental and insular shelves, coral reefs and reef flats; only a few species are truly oceanic. Several carcharhinid species regularly enter brackish-water river mouths, estuaries or lagoons, and a very few are the only shark species able to live in freshwater for an extended period. None are truly specialised deepwater sharks, although some may be found below ~400 m. Eleven genera and at least 59 species; 9 genera and 30 species in WIO.

KEY TO GENERA

1a High proximal and distal cusplets on most teeth in both jaws; expanded anterior nasal flaps and mesonarial flaps form tube for excurrent aperture .... ***Triaenodon***

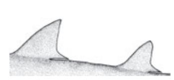


1b Cusplets low or absent on upper teeth, and usually absent on lower teeth; anterior nasal flaps do not form tube for excurrent aperture **2**



2a Second dorsal fin nearly as large as 1st dorsal fin **3**

2b Second dorsal fin smaller than 1st dorsal fin **4**


2a

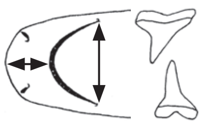

2b

Continued ...

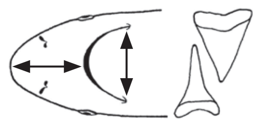
KEY TO GENERA

3a Snout short, preoral length less than mouth width; upper and lower teeth with narrow smooth-edged cusps .... ***Negaprion***

3b Snout long, preoral length about equal to mouth width; upper teeth with broad triangular cusps with serrations, and lower teeth with narrow smooth-edged cusps .... ***Lamiopsis***

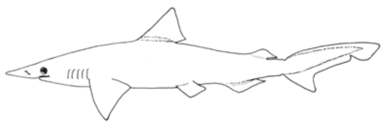


3a



3b

4a Head depressed and trowel-shaped; pectoral fins broadly triangular, distance from fin origin to free rear tip about equal to length of anterior margin; 1st dorsal-fin free rear tip about over midbase of pelvic fins; anal-fin rear margin nearly straight .... ***Scoliodon***



4b Head conical to slightly depressed; pectoral fins narrow, distance from fin origin to free rear tip at most four-fifths length of anterior margin; 1st dorsal-fin free rear tip usually before pelvic-fin origins; anal-fin rear margin concave to deeply concave **5**

5a Second dorsal-fin origin well behind anal-fin origin (but sometimes over or slightly before it); preanal ridges long and prominent, and subequal to or greater in length than anal-fin base; anal-fin rear margin straight or shallowly concave **7**

5b Second dorsal-fin origin near or well before anal-fin origin or midbase (but sometimes after it); anal-fin rear margin concave to deeply concave **6**

6a Rear edge of eyes with distinct notch; lip folds short and confined to corners of mouth; 1st dorsal-fin base 2–3 times into distance between pectoral- and pelvic-fin bases .. ***Loxodon***

6b Rear edge of eyes without notch; lip folds usually conspicuous and long (but reduced in some); 1st dorsal-fin base no more than 2 times into distance between pectoral- and pelvic-fin bases .... ***Rhizoprionodon***

7a Papillose gill rakers; weak lateral keels on peduncle; 1st dorsal-fin base closer to pelvic-fin bases than to pectoral-fin bases; body brilliant dark blue dorsally .... ***Prionace***

7b Gill rakers without papillae; no lateral keels on peduncle; 1st dorsal-fin base usually closer to pectoral fins, or equidistant between pectoral- and pelvic-fin bases; body pale to dark grey, grey-brown, brown or grey-black dorsally **8**

8a Cusps of lower teeth not prominently protruding when mouth closed; 2nd dorsal fin at most two-fifths height of 1st dorsal fin; precaudal pits transverse and crescentic .... ***Carcharhinus***

8b Cusps of lower teeth prominently protruding when mouth closed; 2nd dorsal fin at least half height of 1st dorsal fin; precaudal pits longitudinal and not crescentic .... ***Glyphis***

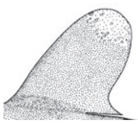
GENUS *Carcharhinus* Blainville 1816

Fairly slender to very stout-bodied; snout very short to long, narrowly parabolic or subangular to bluntly rounded or nearly truncate in dorsoventral view. Eyes small to large; no spiracles. Nostrils small and wide-spaced; anterior nasal flaps short or vestigial, and narrowly or broadly triangular, but not tubular. Lip folds confined to corners of mouth. Teeth highly variable, and anteroposterior teeth similar or strongly differentiated in both jaws; upper teeth usually with more or less erect, broad to narrow cusps, with variably developed cusplets or blades, and usually with serrations; lower teeth with oblique to erect cusps, serrations, and blades present or absent, and no cusplets; tooth counts 24–37/23–35. Pectoral fins moderately broad and semifalcate to narrow and falcate or broad-tipped, origins under 3rd to 5th gill slits; distance from fin origin to free rear tip ~⅓–⅔ length of anterior margin. Interdorsal ridge absent, low or prominent. First dorsal-fin origin over or slightly before pectoral-fin insertions to slightly behind their free rear tips; midbase closer to pectoral-fin bases than to pelvic-fin bases but sometimes equidistant between them; free rear tip usually well in front of pelvic fins but occasionally opposite their origins. Second dorsal fin much smaller than 1st (at most two-fifths height of 1st dorsal fin); origin about opposite anal-fin origin. Anal fin as large as to much larger than 2nd dorsal fin; preanal ridges short or absent; rear margin concave to deeply concave. No keels on peduncle; upper precaudal pit transverse and crescentic. Body grey, bronzy or brownish dorsally, usually without distinct colour patterns, but pale and dark fin markings and pale band on flanks variably present. Small- to very large-sized, <1 m to ~4 m TL. Thirty species, 21 in WIO.

KEY TO SPECIES

1a Pectoral fins and 1st dorsal fin very broad and rounded, tapering slightly only towards apices; most fin tips conspicuously mottled white in adults, and some fins black-tipped in juveniles; black patches on peduncle .... ***C. longimanus***

1b Pectoral fins and 1st dorsal fin tapering and pointed or narrowly rounded; fins not mottled white, but often black-tipped; no black patches on peduncle **2**



1a

1b

2a First dorsal fin, pectoral fins, pelvic fins and caudal fin with conspicuous white rear margins .... ***C. albimarginatus***

2b Fins plain, without conspicuously white rear margins or tips, but sometimes with pale edges or black tips **3**

3a Second dorsal fin with conspicuous black tip, but all other fins plain **4**

3b Second dorsal fin either plain or with white or black tip, but never the only fin with markings **5**

4a First dorsal fin triangular with posteroventrally sloping rear margin; pectoral-fin length 1.4–1.8 in pectoral-fin anterior margin; usually 13/13 rows of anteroposterior teeth, and 28/28 total rows of teeth; upper anterolateral teeth moderately broad, with strongly serrated cusps and distal cusplets; mouth width 6.4–8.3% TL. Precaudal centra 54–74 .... ***C. dussumieri***

4b First dorsal fin falcate with almost vertical (although slightly concave) rear margin (apart from free rear tip); pectoral-fin length 1.7–2 in pectoral-fin anterior margin; usually 12/12 rows of anteroposterior teeth, and 26/25 total rows of teeth; upper anterolateral teeth with smooth-edged distal cusplets; mouth width 4.2–6.6% TL. Precaudal centra 74–85 .... ***C. humani***

5a Caudal-fin posterior margin prominently black-edged and 1st dorsal fin either plain or with white tip, but never black-tipped .... ***C. amblyrhynchos***

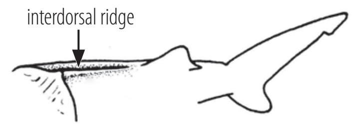
5b Caudal-fin posterior margin plain or with prominent black edge: if black, 1st dorsal fin with prominent black tip **6**

6a Upper anterolateral teeth with bent, hooked, narrow cusps .... ***C. brachyurus***

upper anterolateral tooth

6b Upper anterolateral teeth variably shaped, and broad or narrow, but with nearly straight cusps **7**

7a Interdorsal ridge present **8**



7b No interdorsal ridge **14**

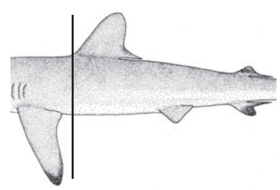
8a Second dorsal fin, pectoral fins, and caudal-fin lower lobe strikingly black-tipped **9**

8b Fins plain or with dusky tips, but not strongly black-tipped **10**

9a Second dorsal fin low, with long inner margin over twice fin height; upper anterolateral teeth with strongly serrated cusps; usually only 12 rows of upper anteroposterior teeth .... ***C. sorrah***

9b Second dorsal fin high, with shorter inner margin (margin ~1.5 times fin height); upper anterolateral teeth with weakly serrated or smooth-edged cusps; 14 or 15 rows of upper anteroposterior teeth .... ***C. hemiodon***

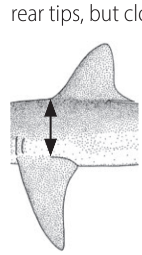
10a First dorsal-fin origin well behind pectoral-fin free rear tips; 2nd dorsal-fin inner margin very long, usually >2 times fin height (but down to 1.6 times fin height); crown feet of upper anterolateral teeth relatively narrow and with coarse serrations or small cusplets .... ***C. falciformis***



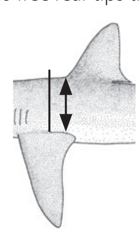
10b First dorsal-fin origin over or before pectoral-fin free rear tips; crown feet of upper anterolateral teeth with small (not coarse) serrations; 2nd dorsal-fin inner margin short, usually <2 times fin height **11**

11a First dorsal-fin origin above or slightly after pectoral-fin insertions, but nearer to insertions than to free rear tips **12**

11b First dorsal-fin origin above or slightly before pectoral-fin free rear tips, but closer to free rear tips than to insertions **13**



11a



11b

Continued ...

KEY TO SPECIES

12a Shortest distance from nostrils to mouth >2.4 in mouth width; upper anterolateral teeth moderately high, and usually in 14 rows; interdorsal ridge low; 1st dorsal fin very high, erect, its height about half predorsal length .... ***C. plumbeus***

12b Shortest distance from nostrils to mouth <2.4 in mouth width; upper anterolateral teeth very high, and usually in 15 rows; interdorsal ridge prominent; 1st dorsal fin relatively low, its height much less than half predorsal length .... ***C. altimus***

13a Upper anterolateral teeth relatively long and narrow; pectoral fins large, semifalcate; 1st dorsal fin high, erect; precaudal centra 103–109 .... ***C. galapagensis***

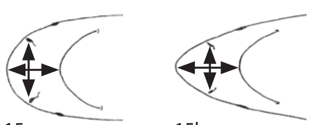
13b Upper anterolateral teeth relatively low and broadly triangular; pectoral fins moderately sized, curved; 1st dorsal fin relatively low; precaudal centra 89–95 .... ***C. obscurus***

14a Entire dorsal and ventral caudal margin with narrow but obvious black edge; 1st dorsal fin and caudal-fin lower lobe with obvious black tips, and smaller black tips to all other fins .... ***C. melanopterus***

14b Margin of caudal fin not black, or only partly dusky or black; fins black-tipped or not **15**

15a Snout short and broadly rounded; internarial space usually less than preoral length; upper anterolateral teeth with broad, triangular cusps **16**

15b Snout long and parabolic or wedge-shaped to pointed; internarial space less than or equal to preoral length; upper anterolateral teeth with narrow cusps **17**

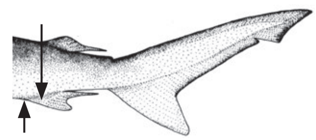


15a 15b

16a Usually 11 lower anteroposterior teeth, with extremely broad cusps; 1st dorsal fin >3 times height of 2nd dorsal fin, and 2nd dorsal-fin posterior margin nearly straight; angle of notch in anal-fin rear margin acute, usually less than right angle; precaudal centra 89–95 .... ***C. amboinensis***

16b Usually 12 lower anteroposterior teeth, with moderately broad cusps; 1st dorsal fin <3 times height of 2nd dorsal fin; 2nd dorsal-fin posterior margin slightly concave; angle of notch in anal-fin rear margin obtuse, usually right angle or more; precaudal centra 101–123 .... ***C. leucas***

17a Second dorsal-fin origin well behind anal-fin origin, opposite its midbase to insertion .... ***C. macloti***



17b Second dorsal-fin origin about over anal-fin origin **18**

18a Upper lip folds prominent; usually at least 16 rows of upper anteroposterior teeth; 1st dorsal fin relatively low, its height >2.2 in interdorsal space, and its origin over or behind pectoral-fin free rear tips .... ***C. brevipinna***

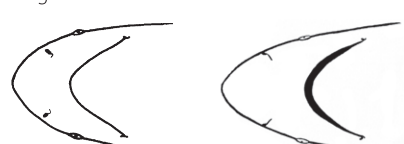
18b Upper lip folds short and inconspicuous; usually 15 or fewer rows of upper anteroposterior teeth; 1st dorsal fin relatively high, its height <2.2 in interdorsal space, and its origin over or just behind pectoral-fin insertions **19**

19a Teeth in both jaws with smooth edges, except some upper teeth weakly and irregularly serrated in adults .... ***C. leiodon***

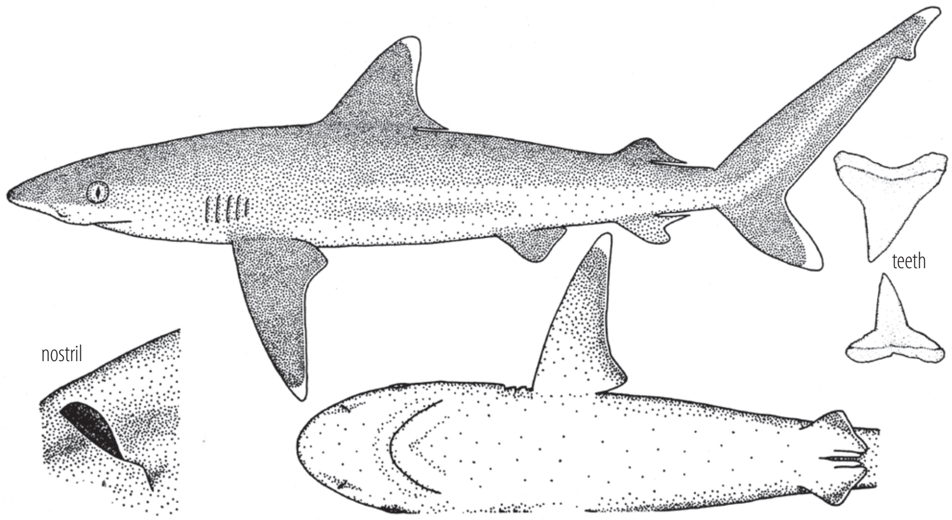
19b Teeth in both jaws with serrated edges **20**

20a Snout wedge-shaped, shorter; internarial space <1.2 into preoral length .... ***C. amblyrhynchoides***

20b Snout pointed, longer; internarial space 1.3–1.7 into preoral length .... ***C. limbatus***



20a 20b



Carcharhinus albimarginatus, 83 cm TL, male (central Mozambique). Source: Bass *et al.* 1973

Carcharhinus albimarginatus (Rüppell 1837)

Silvertip shark PLATES 40 & 41

Carcharias albimarginatus Rüppell 1837: 64, Pl. 18, Fig. 1 (Ras Muhammad, Sinai, Egypt, Red Sea).
Carcharhinus albimarginatus: Bass *et al.* 1973*; Garrick 1982*; SSF No. 9.1*; Compagno *et al.* 1989*; Compagno *et al.* 2005*; Last & Stevens 2009*; Voigt & Weber 2011*; Ebert *et al.* 2021.

Large-sized, fusiform body; snout moderately long and broadly rounded. Upper lip folds inconspicuous. Upper teeth broad, with erect to moderately oblique triangular cusps, with strong serrations and coarser serrations basally; lower teeth broad but with erect, more slender cusps, and no serrations. Pectoral fins large, semifalcate. Interdorsal ridge present. First dorsal fin moderately large, semifalcate; origin usually over or slightly before pectoral-fin free rear tips. Second dorsal-fin origin over or slightly behind anal-fin origin. Tooth count 12–14/12–14; vertebrae 216–231.

Body bronzy, dark grey or brown dorsally; inconspicuous white band on flanks; all fins (except 2nd dorsal fin) with distinctive white tips and rear margins; white ventrally. Attains 3 m TL.

DISTRIBUTION Indo-Pacific (widespread but fragmented). WIO: Red Sea, Kenya to South Africa (KwaZulu-Natal), Madagascar, Comoros, Aldabra, Seychelles, Mascarenes and Chagos.

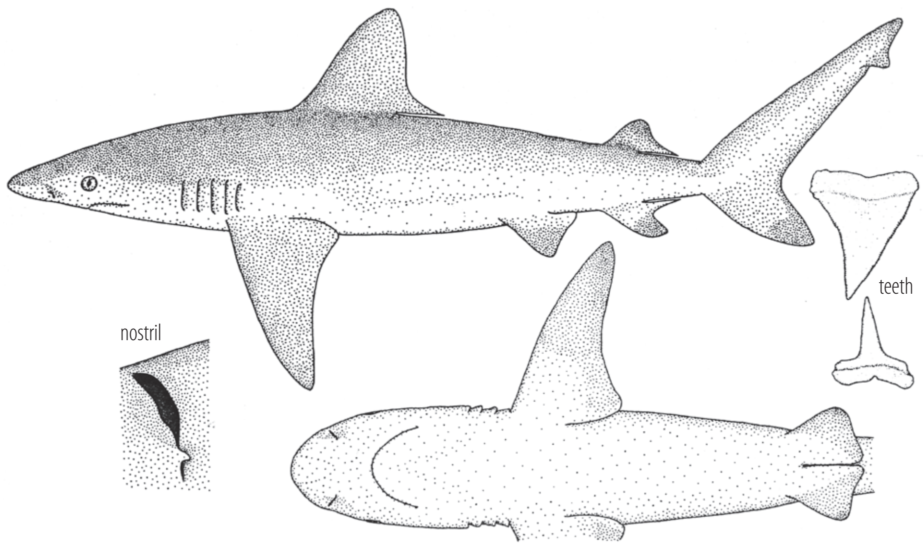
REMARKS Litters of 1–11 (average 6); size at birth 63–81 cm TL; gestation period ~12 months; biennial reproductive cycle. Males mature at 160–180 cm TL, and females at 160–199 cm TL. Occurs in tropical waters over continental and insular shelves, from surface to ~800 m deep. Has localised movements, with strong preference for offshore islands, coral reefs and offshore banks, but also found in lagoons and well offshore; young are restricted to shallower water close to shore. Feeds on a variety of midwater and bottom fishes and cephalopods. A known bycatch in areas where it occurs, especially around the WIO islands where it is abundant. Potentially dangerous to humans (although few, if any, attacks have been attributed to it). IUCN Red List conservation status Vulnerable.

Carcharhinus altimus (Springer 1950)

Bignose shark PLATE 41

Eulamia altima Springer 1950: 9 (off Cosgrove Reef, Key West, Florida).
Carcharinus radamae Fourmanoir 1961: 24, Figs. 14–17, Pls. 6–7 (west coast of Madagascar).
Carcharhinus altimus: Bass *et al.* 1973*; Compagno 1984*; SSF No. 9.2*; Compagno *et al.* 1989*; Heemstra & Heemstra 2004; Compagno *et al.* 2005*; Fricke *et al.* 2007; Last & Stevens 2009*; Voight & Weber 2011*; Ebert 2013*; Ebert *et al.* 2021*.

Large-sized, fairly slender cylindrical body; snout moderately long and bluntly pointed. Eyes circular and moderately large. Anterior nasal flaps short, broadly triangular. Upper lip folds short and inconspicuous. Upper teeth high, triangular, usually with fine serrations and no cusplets; lower teeth with erect, narrow cusps, with serrations. Gill slits moderately long. Pectoral fins large, straight, with pointed or narrowly rounded apices. Interdorsal ridge prominent. First dorsal fin relatively tall, falcate; apex bluntly pointed; origin over pectoral-fin insertions to midlength of inner margins, fin height



Carcharhinus altimus, 130 cm TL, female (South Africa).
Source: Bass *et al.* 1973

<½ predorsal length. Second dorsal-fin origin slightly before anal-fin origin. Tooth count 15/15; vertebrae 194–206.

Body pale grey, sometimes bronzy dorsally; faint white marking on flanks; fin tips (except pelvic fins) dusky; white ventrally. Attains 3 m TL.

DISTRIBUTION Circumglobal in all warm-temperate to tropical seas (patchy), including western Mediterranean Sea (rare). WIO: Red Sea, South Africa (Eastern Cape), Madagascar, Maldives, southern India and Sri Lanka.

REMARKS Litters of 3–15; size at birth 60–90 cm TL; biennial reproductive cycle. Males mature at 190–267 cm TL, and females at 205–282 cm TL. Common in deep water near edge of continental and insular shelves and on upper slope, at 80–430 m, but young are occasionally found in shallower water (up to 25 m depth). Diurnally vertically migrating: mostly bottom-dwelling by day and nearer surface at night. Feeds on a variety of bony fishes, elasmobranchs and cephalopods (cuttlefish). Interest to fisheries localised; often a utilised bycatch in pelagic longline, gillnet and bottom-trawl fisheries. Not regarded as dangerous to humans due to its deepwater habitat. IUCN Red List conservation status Near Threatened.

Carcharhinus amblyrhynchoides (Whitley 1934)

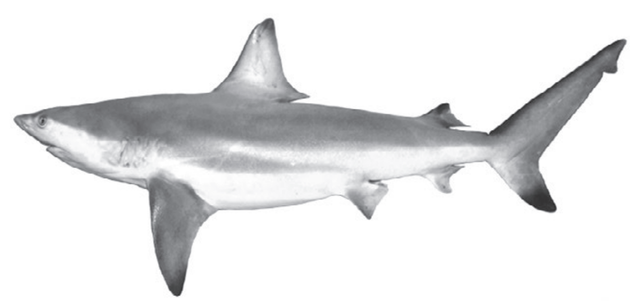
Graceful shark

PLATE 40

Gillisqualus amblyrhynchoides Whitley 1934: 189, Fig. 4 (Queensland, Australia).
Carcharhinus amblyrhynchoides: Compagno *et al.* 2005*; Last & Stevens 2009*; Voight & Weber 2011*; Ebert *et al.* 2021*.

Moderately large-sized and stout-bodied; snout fairly short and pointed, wedge-shaped; internarial width 1–1.2 times preoral length. Eyes circular and moderately large. Upper lip folds short and inconspicuous. Teeth in both jaws with erect, narrow cusps, with serrations and no cusplets. Gill slits long. Pectoral fins rather large, falcate. No interdorsal ridge. First dorsal fin rather large, broadly triangular, semifalcate; origin over or slightly after pectoral-fin insertions. Second dorsal-fin origin over or slightly before anal-fin origin. Tooth count 15/15; vertebrae 168–193.

Body grey dorsally; conspicuous white band on flanks; most fins black-tipped, and caudal-fin upper lobe usually with dusky edges (dark fin markings may fade in adults); paler ventrally. Attains at least 178 cm TL.



Carcharhinus amblyrhynchoides, 70 cm TL, male (Pakistan).
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DISTRIBUTION Indo-Pacific. WIO: Gulf of Aden, Pakistan, southwestern India and Sri Lanka (but possibly continuous from Somalia to India, including Red Sea and Persian/Arabian Gulf).

REMARKS Poorly known. Litters of 1–9 (average 3); size at birth 50–60 cm TL. Both sexes mature at 110–115 cm TL; gestation period ~9–10 months. Coastal-pelagic in tropical waters on continental and insular shelves. Feeds primarily on fishes, but also cephalopods and crustaceans. Taken in gillnet and longline fisheries where it occurs, but not targeted. Considered harmless to humans. IUCN Red List conservation status Near Threatened.

Carcharhinus amblyrhynchos (Bleeker 1856)

Grey reef shark

PLATES 41 & 42

Carcharias (*Prionodon*) *amblyrhynchos* Bleeker 1856: 467 (Java Sea near Solombo I., Indonesia).

?*Carcharhinus wheeleri* Garrick 1982: 111, Figs. 50–51 (Red Sea).

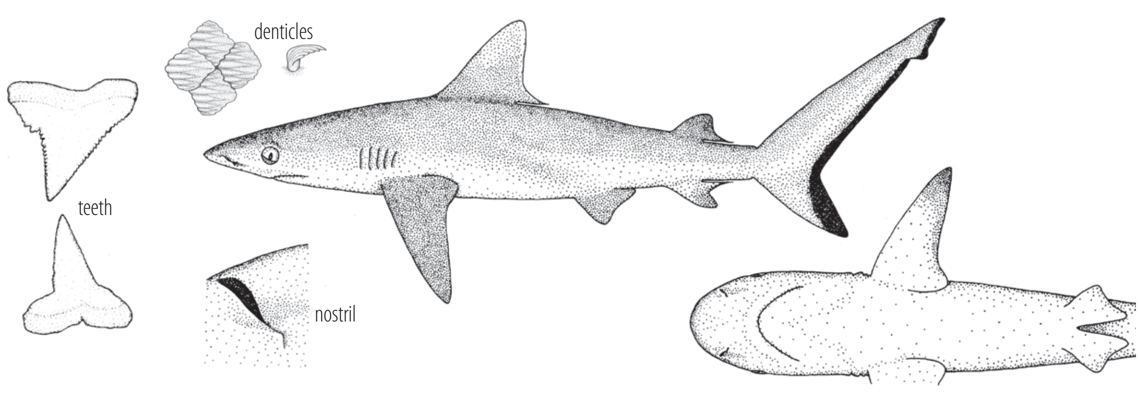
Carcharhinus amblyrhynchos: Bass *et al.* 1973*; Compagno 1984*; SSF No. 9.3*; Compagno *et al*. 2005*; Last & Stevens 2009*; Voight & Weber 2011*; Ebert *et al*. 2021*.

Moderate-sized, fairly stocky body; snout moderately long and broadly rounded. Eyes usually round and fairly large. Anterior nasal flaps weakly expanded, low triangular lobes. Upper lip folds short and inconspicuous. Upper anteroposterior teeth with narrow cusps, with serrations, and crown feet with coarser serrations and often low distal cusplets. Gill slits moderate-sized. Pectoral fins moderately large, narrow and falcate. Interdorsal ridge weak or absent. First dorsal fin relatively tall and semifalcate; origin usually over or just before pectoral-fin free rear tips. Second dorsal-fin origin roughly over anal-fin origin. Tooth count 28–30/27–29 (usually 28/28); vertebrae 211–221, precaudal vertebrae 110–119.

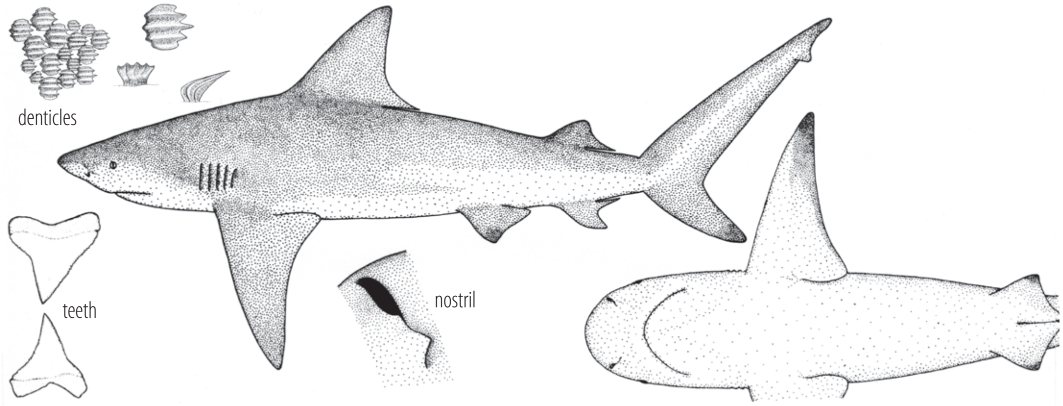
Body grey dorsally; 1st dorsal fin plain or irregularly white-edged; pectoral fins, 2nd dorsal fin, pelvic fins and anal fin with dusky tips; caudal-fin rear margin with conspicuous broad black edge; white ventrally. Attains 255 cm TL.

DISTRIBUTION Indo-Pacific. WIO: Red Sea, Gulf of Aden, Kenya to South Africa, Madagascar, Seychelles, Mauritius and India.

REMARKS Litters of 1–6; size at birth 45–60 cm TL; gestation period 12–14 months. Males mature at 130–145 cm TL, aged 7–9 years; females mature at 122–137 cm TL, aged 7.5–11 years; maximum age 25 years or more. Coastal-pelagic, on continental and insular shelves and in adjacent oceanic waters, from surface and intertidal zone to at least 100 m. Common on coral reefs, often in deeper areas near drop-offs to open sea, in atoll passes, and in shallow lagoons adjacent to areas of strong current. Active, strong swimming, social species found in groups or individually; prefers clear water and shows site fidelity, forming daytime schools or aggregations in favoured areas. Feeds mostly on small bony fishes, but also cephalopods (squid and octopus) and crustaceans. Can be aggressive to humans, yet a very popular subject of dive ecotourism. Caught in multi-species tropical fisheries. IUCN Red List conservation status Endangered.



Carcharhinus amblyrhynchos, 68 cm TL, female (NW Madagascar). Source: Bass *et al.* 1973



Carcharhinus amboinensis, 144 cm TL, female (South Africa). Source: Bass *et al.* 1973

Carcharhinus amboinensis (Müller & Henle 1839)

Pigeye shark PLATE 41

Carcharias (*Prionodon*) *amboinensis* Müller & Henle 1839: 40, Pl. 19 [teeth] (Ambon I., Maluku Is., Indonesia).
Triaenodon obtusus Day 1878: 720, Pl. 189, Fig. 3 (Karachi, Pakistan).
Carcharhinus amboinensis: D'Aubrey 1964, 1971; Bass *et al.* 1973*; Compagno 1984*; SSF No. 9.4*; Compagno *et al.* 1989*; Bonfil & Abdallah 2004*; Heemstra & Heemstra 2004; Compagno *et al.* 2005*; Last & Stevens 2009*; Voight & Weber 2011*; Ebert *et al.* 2021*.

Large-sized, stocky body and thick head; snout short and bluntly rounded, internarial width 0.9–1 in preoral length. Eyes circular and small. Anterior nasal flaps short, broadly triangular. Upper lip folds short and inconspicuous. Upper teeth broadly triangular, with serrations and no cusplets; lower teeth slightly narrower, with serrations and arched roots. Gill slits moderately long. Pectoral fins large and broad, triangular to semifalcate, with narrow, pointed apices. No interdorsal ridge. First dorsal fin large, broadly triangular or somewhat falcate, with pointed or sharply rounded apex; origin over or just behind pectoral-fin insertions; its height >3 times 2nd dorsal fin. Second dorsal-fin origin before anal-fin origin. Tooth count 11–13/10–12; vertebrae 185–195, precaudal vertebrae 89–95.

Body grey dorsally; inconspicuous white band on flanks; fin tips dusky, especially in young; pale ventrally. Attains 280 cm TL.

DISTRIBUTION Northeastern Atlantic (Nigeria) and Indo-Pacific (patchy). WIO: Pakistan, Gulf of Aden, Persian/Arabian Gulf, South Africa (KwaZulu-Natal), Madagascar and Sri Lanka.

REMARKS Similar in appearance to bull shark *C. leucas*. Litters of 3–13; size at birth 60–75 cm TL; gestation period ~12 months. Males mature at 195–210 cm TL, and females at 198–223 cm TL. Occurs near bottom in shallow inshore waters over continental and insular shelves, from near surfline to ~60 m deep, and occasionally enters brackish water; usually solitary. Feeds primarily on bottom fishes, crustaceans, cephalopods and molluscs. Caught in small numbers in longline and gillnet fisheries. Considered potentially dangerous to humans. IUCN Red List conservation status Data Deficient globally; Near Threatened for southwestern Indian Ocean subpopulation.

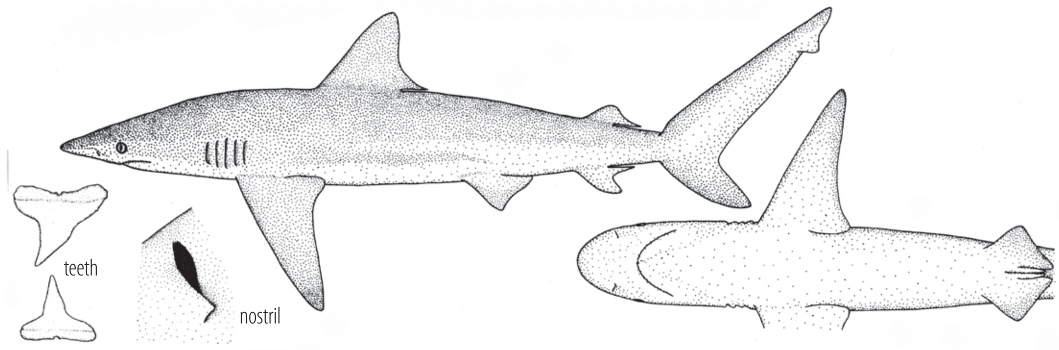
Carcharhinus brachyurus (Günther 1870)

Bronze whaler PLATE 41

Carcharias brachyurus Günther 1870: 369 (off Wanganui, New Zealand).
Carcharhinus improvisus Smith 1952: 761, Fig. 1 (Algoa Bay, South Africa).
Carcharhinus brachyurus: Bass *et al.* 1973*; Van der Elst 1981*; Compagno 1984*; SSF No. 9.5*; Compagno *et al.* 1989*; Walter & Ebert 1991; Heemstra & Heemstra 2004*; Compagno *et al.* 2005*; Last & Stevens 2009*; Voight & Weber 2011*; Ebert *et al.* 2021*.

Large-sized; snout moderately broad, long and bluntly pointed, internarial width 1.1–1.4 in preoral length. Eyes circular and moderately large. Anterior nasal flaps low and poorly developed. Upper lip folds short and inconspicuous. Upper anterolateral teeth with narrow bent cusps, with serrations and no cusplets; teeth in both jaws with transverse notch at root. Gill slits moderately long. Pectoral fins moderately large and falcate. Usually no interdorsal ridge. First dorsal fin large, falcate; origin over or slightly before pectoral-fin free rear tips. Second dorsal-fin origin over or slightly after anal-fin origin. Tooth count 14–16/14–15; vertebrae 179–203.

Body bronzy grey to olive-grey dorsally; fairly prominent white band on flanks; most fins with inconspicuous darker edges and dusky to black tips; white ventrally. Attains 295 cm TL.



Carcharhinus brachyurus, 143 cm TL, male (South Africa). Source: Bass *et al.* 1973

DISTRIBUTION Atlantic (Gulf of Mexico and West Africa), Pacific and Indian oceans, and Mediterranean Sea. WIO: South Africa (Cape of Good Hope to KwaZulu-Natal).

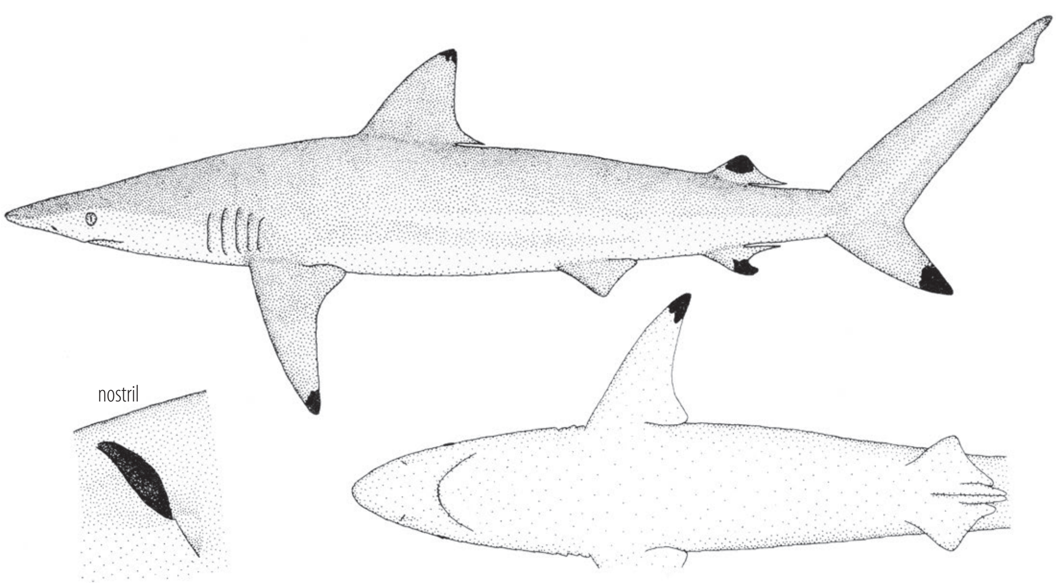
REMARKS Often confused with other large *Carcharhinus* species. Litters of 7–24; size at birth 59–70 cm TL; gestation period 15–21 months. Males mature at 200–229 cm TL, age 13–19 years; females mature at 240–292 cm TL, age 19–20 years; maximum age 25–30 years. Found in subtropical and temperate waters, close inshore and occasionally offshore, from surfline to at least 100 m deep, and enters lower reaches of large rivers; occurs singly and in loose schools. Apparently migratory in northern parts of its range, moving northwards in spring and summer and southwards in fall and winter; also segregates by size and sex, and uses inshore bays and open coastline as nursery grounds. Feeds on a wide variety of bottom-dwelling and pelagic fishes and cephalopods. Taken as bycatch and in directed fisheries, mostly by gillnets and bottom longlines, as well by recreational anglers and in anti-shark nets. Several provoked and unprovoked encounters with swimmers and divers have been ascribed to this species. IUCN Red List conservation status Vulnerable globally.

Carcharhinus brevipinna (Valenciennes 1839)

Spinner shark

PLATE 41

Carcharias (*Aprion*) *brevipinna* Valenciennes *in* Müller & Henle 1839: 31, Pl. 9 (Java, Indonesia).
Carcharinus johnsoni Smith 1951: 88, Figs. 1–2 (Port Elizabeth, Eastern Cape, South Africa).
Carcharhinus brevipinna: Bass *et al.* 1973*; Compagno 1984*; SSF No. 9.6*; Compagno *et al.* 1989*; Allen & Cliff 2000; Allen & Wintner 2002; Heemstra & Heemstra 2004*; Compagno *et al.* 2005*; Fricke *et al.* 2009; Last & Stevens 2009*; Voight & Weber 2011*; Ebert *et al.* 2021*.



Carcharhinus brevipinna, 179 cm TL, male (South Africa). Source: Bass *et al.* 1973

Large-sized, fairly slender body; snout long and pointed, internarial width 1.5–1.8 in preoral length. Eyes small and circular. Anterior nasal flaps low and inconspicuous. Upper lip folds usually long and conspicuous. Teeth fairly small; upper anterolateral teeth mostly erect, with narrow cusps, serrated or partly serrated, and no cusplets; lower teeth with narrow cusps and no serrations. Gill slits long. Pectoral fins falcate. No interdorsal ridge. First dorsal fin relatively large, semifalcate; height >2.2 in interdorsal space; origin over or slightly after pectoral-fin free rear tips. Second dorsal-fin origin over or slightly after anal-fin origin. Tooth count 15–18/14–17 (usually 16/16); vertebrae 155–185.

Body greyish to bronzy dorsally; inconspicuous white band on flanks; all fins (except pelvic fins) black-tipped in large juveniles and adults, and plain in young (<80 cm TL); white ventrally. Attains 3 m TL.

DISTRIBUTION Circumglobal, including Mediterranean Sea, except not eastern Pacific. WIO: Pakistan, Gulf of Oman, Gulf of Aden, Red Sea, Mozambique, South Africa (southwestern Cape), Madagascar, Comoros (Mayotte I.), Amirante Bank, Seychelles, Réunion, India and Sri Lanka; not known from Persian/Arabian Gulf.

REMARKS Litters of 3–15; size at birth 60–75 cm TL; gestation period 12–15 months; biennial reproductive cycle. Males mature at 159–203 cm TL, and females at 170–200 cm TL, aged 8–10 years for both sexes; maximum age 17–19 years. Common, coastal-pelagic, in warm-temperate to tropical waters, close inshore off beaches, in bays and off river mouths, from surface to at least 75 m deep offshore (but usually above 30 m). Some segregation by size and sex. Active, schooling shark that often leaps ‘spinning’ from water as part of its frenzied feeding run. Feeds mostly on a variety of fishes, but also cephalopods. Captured frequently in commercial and recreational fisheries. Not considered dangerous to people, but possibly troublesome to divers when spearfishing. IUCN Red List conservation status Vulnerable.

Carcharhinus dussumieri (Valenciennes 1839)

Whitecheek shark

PLATE 41

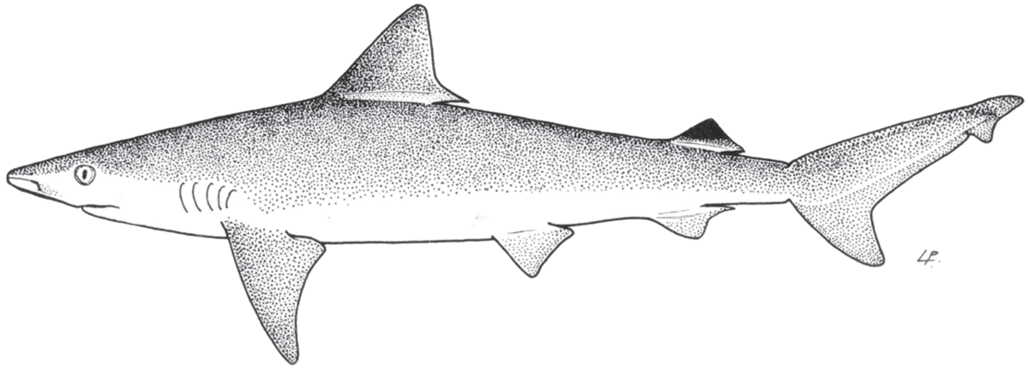
Carcharias (*Prionodon*) *dussumieri* Valenciennes *in* Muller & Henle 1839: 47, Pl. 19 [teeth] (Puducherry, India).
Carcharhinus dussumieri: Fowler 1941; Compagno 1984*; Compagno *et al*. 2005*; Last & Stevens 2009*; Voigt & Weber 2011*; White 2012*; Ebert *et al*. 2021*.

Small-sized; snout moderately long and rounded. Eyes fairly large, horizontally oval. Anterior nasal flaps conspicuous, triangular. Mouth width 6.4–8.3% TL; upper lip folds short and inconspicuous. Upper teeth with oblique triangular cusps, with serrations and cusplets; lower teeth smaller, with erect narrow cusps. Pectoral fins small and semifalcate, with narrow angular apices. Interdorsal ridge low, if present. First dorsal fin moderately large, broadly triangular, not strongly falcate; origin over rear half of pectoral-fin inner margins. Second dorsal-fin origin over or slightly after anal-fin origin. Tooth count 12–14/11–15 (usually 13/13); vertebrae 109–150, precaudal vertebrae 54–74.

Body grey, grey-brown or bronzy dorsally; inconspicuous pale band on flanks; 2nd dorsal fin with black or dusky tip, other fins with pale trailing edges; paler ventrally. Attains 100 cm TL.

DISTRIBUTION Indo-Pacific. WIO: Persian/Arabian Gulf, Gulf of Oman, Pakistan, India and Sri Lanka.

REMARKS Common but poorly known. Litters of 1–4 (usually 2); size at birth 28–38 cm TL. Males mature at 65–70 cm TL, and females at 70–75 cm TL. Occurs in inshore tropical waters, over continental and insular shelves, to ~170 m deep. Feeds mostly on small bony fishes, but also cephalopods and crustaceans. Commonly caught in inshore fisheries, including artisanal and small-scale commercial fisheries; used for its meat and fins. Harmless to humans. IUCN Red List conservation status Endangered globally.



Carcharhinus dussumieri. © Food and Agriculture Organization of the United Nations, Original Scientific Illustrations Archive; reproduced with permission

Carcharhinus falciformis (Müller & Henle 1839)

Silky shark PLATE 41

Carcharias (*Prionodon*) *falciformis* Müller & Henle (ex Bibron) 1839: 47 (Cuba, western Atlantic).
Carcharhinus falciformis: Compagno 1984*; SSF No. 9.7*; Compagno *et al*. 2005*; White *et al*. 2006*; Last & Stevens 2009*; Voigt & Weber 2011* [as *falciformes*]; Ebert *et al*. 2021*.

Large-sized, fairly slender body; snout moderately long and rounded. Eyes circular and moderately large. Upper lip folds short and inconspicuous. Teeth in both jaws with erect to semi-oblique, fairly narrow, triangular cusps; upper teeth with strong serrations, and lower teeth smooth-edged. Pectoral fins long and narrowly falcate. Interdorsal ridge narrow. First dorsal fin low, falcate, with moderately rounded apex and curved rear margin; origin behind pectoral-fin free rear tips. Second dorsal fin low; inner margin very long, usually more than twice fin height; origin over or slightly after anal-fin origin. Skin smooth, with tightly packed, small, overlapping denticles. Tooth count 14–16/13–17; vertebrae 199–215.

Body dark bronzy grey-brown dorsally, sometimes nearly blackish; inconspicuous white band on flanks; tips of all fins (except 1st dorsal fin) dusky but not black-tipped; white ventrally. Attains 3.7 m TL.

DISTRIBUTION Circumglobal in tropical seas (widespread). WIO: Mozambique to Red Sea, Persian/Arabian Gulf, Pakistan, India and Sri Lanka.

REMARKS Litters of 2–18; size at birth 65–81 cm TL; gestation period ~12 months. Males mature at 180–230 cm TL, age 5–13 years; females mature at 180–246 cm TL, age 6–15 years. Oceanic and coastal-pelagic; common near edge of continental and insular shelves, but also found far from land in open sea, from surface to at least 500 m. Segregates by size; young occur in coastal nursery areas and move offshore as subadults. Feeds mostly on bony fishes, but also cephalopods and crustaceans (pelagic crabs). Dominates as a bycatch or target species in tropical pelagic fisheries; often associated with schools of tuna. Active, swift and inquisitive, and can be aggressive to divers. IUCN Red List conservation status Vulnerable.

Carcharhinus galapagensis

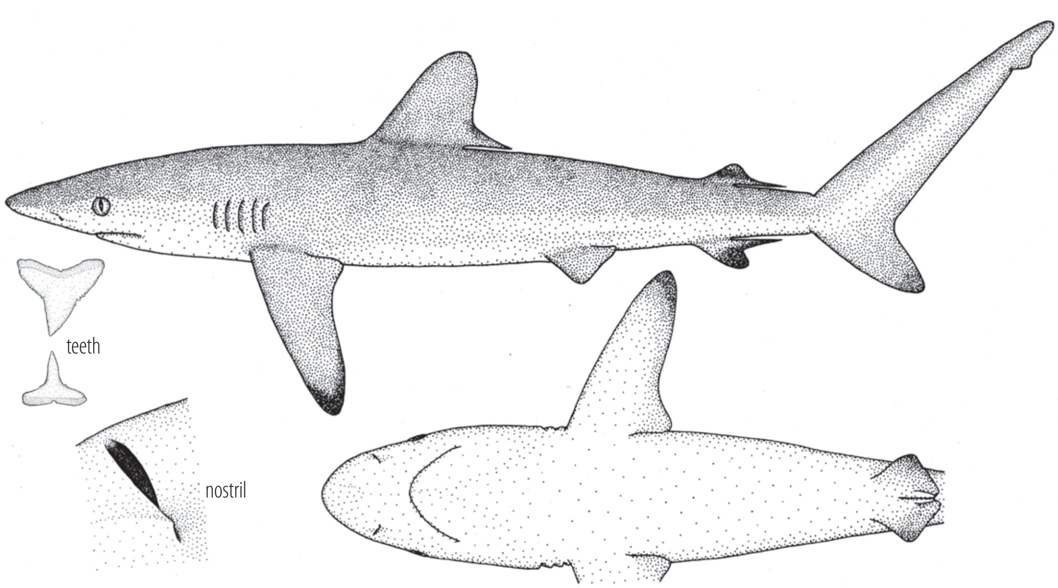
(Snodgrass & Heller 1905)

Galapagos shark PLATE 41

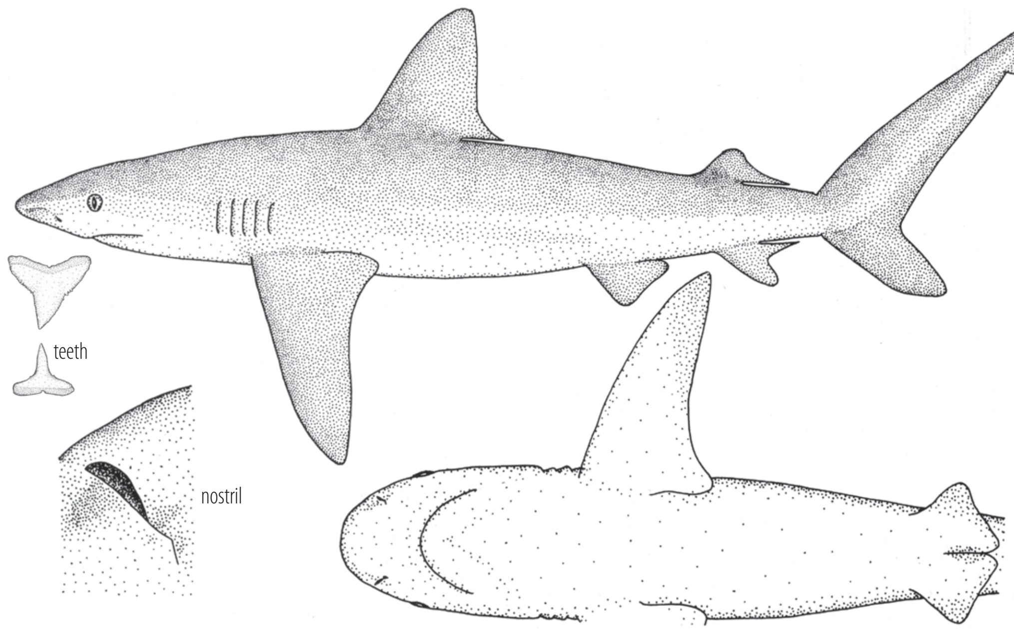
Carcharias galapagensis Snodgrass & Heller 1905: 343 (Galápagos Is.).
Carcharhinus galapagensis: Bass *et al.* 1973*; Compagno 1984*; SSF No. 9.8*; Compagno *et al*. 2005*; Last & Stevens 2009*; Voight & Weber 2011*; Ebert *et al*. 2021*.

Large-sized, fairly slender body; snout moderately long and broadly rounded, internarial width 1–1.3 in preoral length. Eyes circular and moderately large. Anterior nasal flaps low and poorly developed. Upper lip folds short and inconspicuous. Upper teeth with broad, triangular, erect to semi-oblique cusps, with strong serrations; lower teeth with erect and narrow cusps. Pectoral fins large and long, narrowly falcate. Interdorsal ridge low. First dorsal fin moderately large, falcate; origin over slightly before pectoral-fin free rear tips. Second dorsal-fin inner margin long (cf. *C. obscurus*); origin over or slightly before anal-fin origin. Tooth count usually 14/14; vertebrae 200–215, precaudal vertebrae 103–109.

Body brownish grey to dark grey dorsally; inconspicuous white band on flanks; fin tips may be dusky but not black or white; white ventrally. Attains 3.7 m TL.



Carcharhinus falciformis,
94 cm TL, male (S Mozambique).
Source: Bass *et al.* 1973



Carcharhinus galapagensis, 114 cm TL, female (Walters Shoals). Source: Bass *et al.* 1973

DISTRIBUTION Circumglobal in tropical to warm-temperate seas: patchy records from widely separated oceanic islands and some coastal sites. WIO: Walters Shoals (south of Madagascar).

REMARKS This shark and the dusky shark *C. obscurus* may prove to be the same species as they are currently differentiated only by their habitat. Litters of 4–16 (average 9); size at birth 57–80 cm TL; gestation period ~12 months. Males mature at 170–250 cm TL, and females at ~205–250 cm TL. Coastal-pelagic, from close inshore to well offshore near or on insular or continental shelves, especially around offshore islands, from surface to at least 285 m. Can be locally abundant; favours rugged substrates and clear water, and possibly strong currents; swims near bottom, frequently in aggregations. Feeds primarily on bottom fishes and cephalopods. Potentially aggressive to divers.

Carcharhinus hemiodon (Valenciennes 1839)

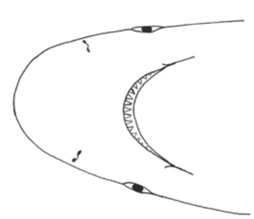
Pondicherry shark

PLATE 41

Carcharias (*Hypoprion*) *hemiodon* Valenciennes *in* Müller & Henle 1839: 35, Pl. 19 [teeth] (Puducherry, India).
Carcharhinus hemiodon: Garrick 1985*; Compagno *et al.* 2005*; Voigt & Weber 2011*; Ebert *et al.* 2013*; Ebert *et al.* 2021*.

Small-sized, somewhat stocky body; snout moderately long and bluntly pointed, internarial width 1–1.4 in preoral length. Eyes circular and moderately large. Anterior nasal flaps low and poorly developed. Upper lip folds short and inconspicuous. Upper teeth with narrow, oblique, high cusps, with low cusplets; lower teeth with semierect, narrow cusps, with no serrations. Pectoral fins moderately small and broad. Interdorsal ridge present. First dorsal fin large, falcate; origin just behind pectoral-fin insertions. Second dorsal-fin inner margin short, 1.4–1.6 times fin height; origin over or slightly after anal-fin origin. Tooth count 14 or 15/13 or 14; vertebrae 147–155.

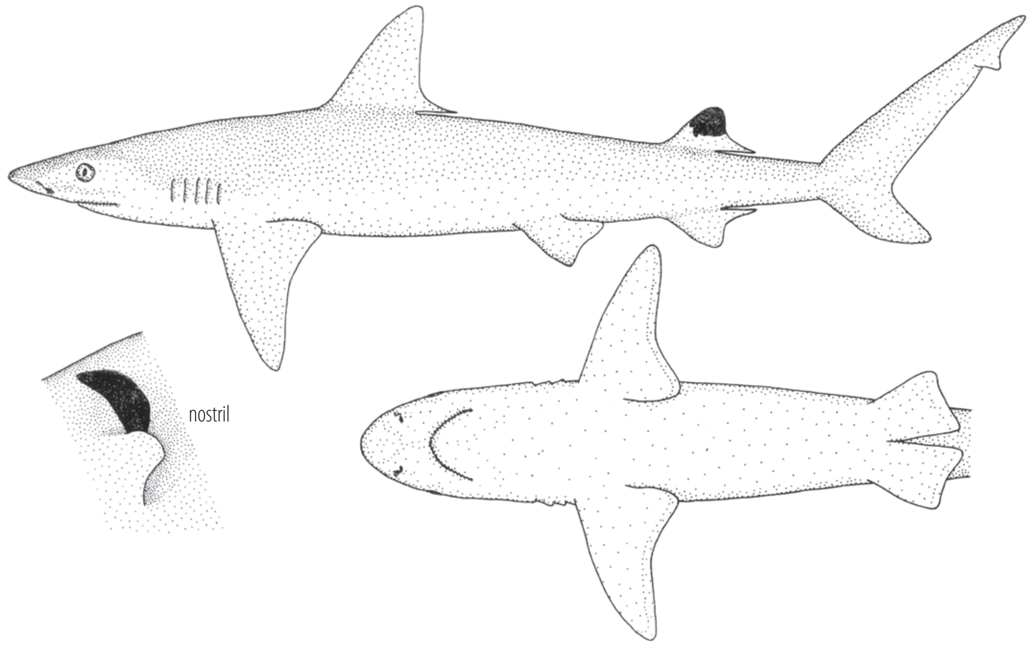
Body grey dorsally; conspicuous white band on flanks; black tips on pectoral fins, 2nd dorsal fin, and caudal-fin upper and lower lobes; white ventrally. Attains at least 102 cm TL.



Carcharhinus hemiodon, 44 cm TL, female, ventral head (India).

DISTRIBUTION Indo-Pacific. WIO: Gulf of Oman to Pakistan, India, Sri Lanka and Lakshadweep.

REMARKS Rare, possibly extinct; last recorded in India in 1979, and now known only from ~20 museum specimens collected from heavily fished, widely separated sites. Size at birth <32 cm TL. Coastal, over continental and insular shelves; also reported from river mouths and upriver in freshwater, but these records may have been based on species of *Glyphis* or other *Carcharhinus*. IUCN Red List conservation status Critically Endangered.



Carcharhinus humani, 91 cm TL, female (South Africa).
Source: Bass *et al.* 1973

Carcharhinus humani White & Weigmann 2014

Human's whaler shark PLATE 42

Carcharhinus humani White & Weigmann 2014: 71, Fig. 1 (Socotra).
Carcharias sealei Pietschmann 1913: 172, Pl. 1 (Sandakan fish market, Sabah, Borneo, Indonesia).
Carcharhinus sealei: Bass *et al.* 1973*; Van der Elst 1981*; SSF No. 9.16*; Compagno *et al.* 1989*; Compagno *et al.* 2005*; Voigt & Weber 2011*; White 2012*; Ebert *et al.* 2021*.

Small-sized body; snout moderately long and rounded. Anterior nasal flaps moderately elongate and broadly triangular. Eyes large and oval. Mouth width 4.2–6.6% TL; upper lip folds short and inconspicuous. Teeth in both jaws with oblique cusps, with coarse serrations or low cusplets basally. Pectoral fins small and strongly falcate; distance from origin to free rear tip 1.7–2 into length of anterior margin. Interdorsal ridge low, if present. First dorsal fin falcate; origin over or slightly after pectoral-fin free rear tips. Second dorsal-fin origin after anal-fin origin. Tooth count 24–28/23–27; vertebrae 148–167, precaudal vertebrae 74–85.

Body grey or tan dorsally; inconspicuous pale band on flanks; 2nd dorsal fin with conspicuous black or dusky tip, other fins with pale rear edges and no dark markings; paler ventrally. Attains 95 cm TL.

DISTRIBUTION Indo-Pacific. WIO: west coast of Madagascar, Seychelles, South Africa (KwaZulu-Natal) to Somalia, Socotra, Oman to Pakistan, India and Sri Lanka.

REMARKS Litters of 1 or 2; size at birth 33–45 cm TL; gestation period ~9 months. Males mature at 70–80 cm TL, and females at 68–75 cm TL, at ~1 year for both sexes; maximum age at least 5 years. Occurs on continental and insular shelves, in shallow water, from surf line and intertidal zone to ~40 m deep. Feeds on small fishes, cephalopods (squid) and crustaceans (prawns). Commonly taken with line gear and gillnets in artisanal and small-scale commercial fisheries and by sport anglers where it occurs. Harmless to humans.

Carcharhinus leiodon Garrick 1985

Smoothtooth blacktip shark

Carcharhinus leiodon Garrick 1985: 11, Figs. 7–8 (Gulf of Aden [probably at Yemen]); Manilo & Bogorodsky 2003; Compagno *et al.* 2005*; Voigt & Weber 2011*; Moore *et al.* 2011, 2013; Ebert *et al.* 2021*.

Body somewhat stocky; snout moderately long and bluntly pointed. Eyes large and circular. Upper lip folds short and inconspicuous. Upper teeth narrow, smooth-edged, erect near centre of mouth and slightly oblique laterally; lower teeth narrow, erect, and smooth-edged. Gill slits relatively long, 3rd gill slit 4.5% TL and >⅓ length of 1st dorsal-fin base. Pectoral fins relatively small, weakly falcate, and apices pointed. No interdorsal ridge. First dorsal fin moderately high, triangular, not falcate, with pointed apex; origin over midlength of pectoral-fin inner margins. Second dorsal fin relatively large and high, height ~4% TL; origin above anal-fin origin. Both dorsal fins with short free rear tips.

Upper precaudal pit strongly developed, and lower pit weakly developed. Tooth count 35/33; vertebrae 198, precaudal vertebrae 115 (holotype).

Body greyish green to greenish yellow dorsally, paler to whitish ventrally; all fins with conspicuous black tips. Attains 165 cm TL.

DISTRIBUTION WIO: Gulf of Aden to Oman and Persian/Arabian Gulf.

REMARKS Similar in appearance to the grey reef shark *C. amblyrhynchoides* (which has serrated upper teeth). Until recently only known from holotype (immature male, 75 cm TL). Litters of 4–6; size at birth ~35–53 cm TL. Males mature at ~120 cm TL, and females at ~131 cm TL. Feeds on bony fishes. Habitat likely inshore. IUCN Red List conservation status Endangered.

Carcharhinus leucas (Valenciennes 1839)

Bull shark

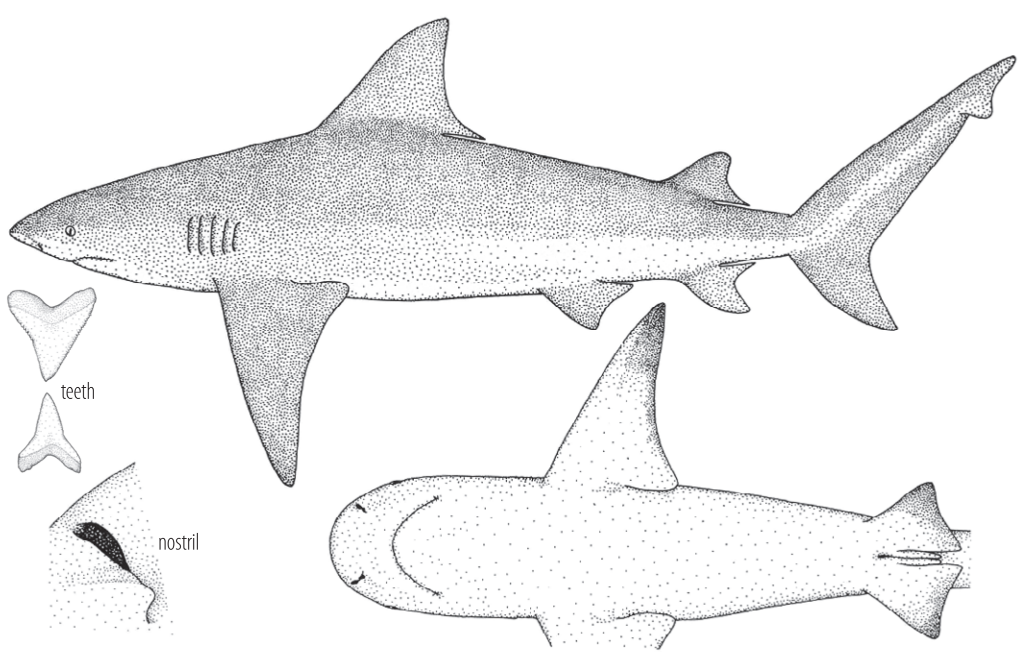
PLATE 43

Carcharias (*Prionodon*) *leucas* Valenciennes *in* Müller & Henle 1839: 42 (Antilles, western Atlantic).
Carcharias (*Prionodon*) *zambezensis* Peters 1852: 276 (Zambezi River, Mozambique); Bonfil & Abdallah 2004*; Voigt & Weber 2011*.
Carcharhinus vanrooyeni Smith 1958: 12, Fig. (St Lucia, KwaZulu-Natal, South Africa).
Carcharhinus leucas: D'Aubrey 1964, 1971; Bass *et al.* 1973*; Van der Elst 1981*; SSF No. 9.9*; Compagno *et al.* 1989*; Cockcroft 1991; Wintner *et al.* 2002; Heemstra & Heemstra 2004*; Compagno *et al.* 2005*; Last & Stevens 2009*; Voigt & Webber 2011*; Ebert *et al.* 2021*.

Large-sized, heavy-bodied; snout very short and bluntly rounded, internarial width 0.7–1 in preoral length. Eyes circular and small. Upper lip folds short and inconspicuous. Upper teeth large, broad and triangular, and saw-like with serrations and no cusplets; lower teeth triangular and narrower, erect to slightly oblique, and with weak serrations. Pectoral fins large and broad, triangular to semifalcate. No interdorsal ridge. First dorsal fin large and broadly triangular, its height up to 3 times 2nd dorsal fin; origin over or slightly after pectoral-fin insertions (sometimes nearer their free rear tips). Second dorsal fin relatively high; origin before anal-fin origin. Inconspicuous caudal keels. Tooth count 25–29/25–29; vertebrae 198–227, precaudal vertebrae 101–123.

Body grey to grey-brown dorsally; inconspicuous white band on flanks; juveniles with dusky to black fin tips, and adults with indistinct fin markings; caudal-fin upper lobe with dusky anterior and posterior margins, whitish between. Attains 3.4 m TL.

DISTRIBUTION Cosmopolitan in most tropical seas and commonly enters freshwater rivers and lakes. WIO: Persian/Arabian Gulf, Somalia to South Africa (Eastern Cape), Zanzibar (Tanzania), east coast of Madagascar, Seychelles, Lakshadweep and India; regional range includes great distance up Zambezi River (Mozambique).



Carcharhinus leucas, 166 cm TL, male (South Africa).
Source: Bass *et al.* 1973

REMARKS Often confused with the pigeye shark *C. amboinensis* or Ganges shark *Glyphis gangeticus*. Litters of 1–13 (mostly 6–8); gestation period 10–11 months; size at birth 56–81 cm TL. Males mature at 157–226 cm TL, age ~25 years; females mature at 180–230 cm TL, aged 14–22 years; maximum age 29–32 years, possibly >50 years. Coastal, estuarine, riverine, and lacustrine tropical and subtropical; usually close inshore, from surfline to usually <30 m but recorded to 152 m. Commonly occurs in hyposaline and hypersaline lagoons and bays, river mouths, and near surfline; the only wide-ranging shark that penetrates far into freshwater and is able to exist there for long periods. Migrates seasonally in some portions of its range; uses estuaries and river mouths as pupping grounds. A versatile and opportunistic predator with a varied diet comprising bony fishes, elasmobranchs, sea turtles, birds, dolphins, whale offal, terrestrial mammals and invertebrates. Caught in fisheries throughout its range, but rarely targeted. Lives well in public aquaria displays, for which there is increasing demand. May be the most dangerous species of tropical shark (particularly in warm turbid waters), and one of the three most dangerous sharks by number of recorded attacks on people. IUCN Red List conservation status Near Threatened.

Carcharhinus limbatus (Valenciennes 1839)

Blacktip shark

PLATES 43 & 44

Carcharias (*Prionodon*) *limbatus* Valenciennes *in* Müller & Henle 1839: 49, Pl. 19 [teeth] [Martinique I., West Indies].

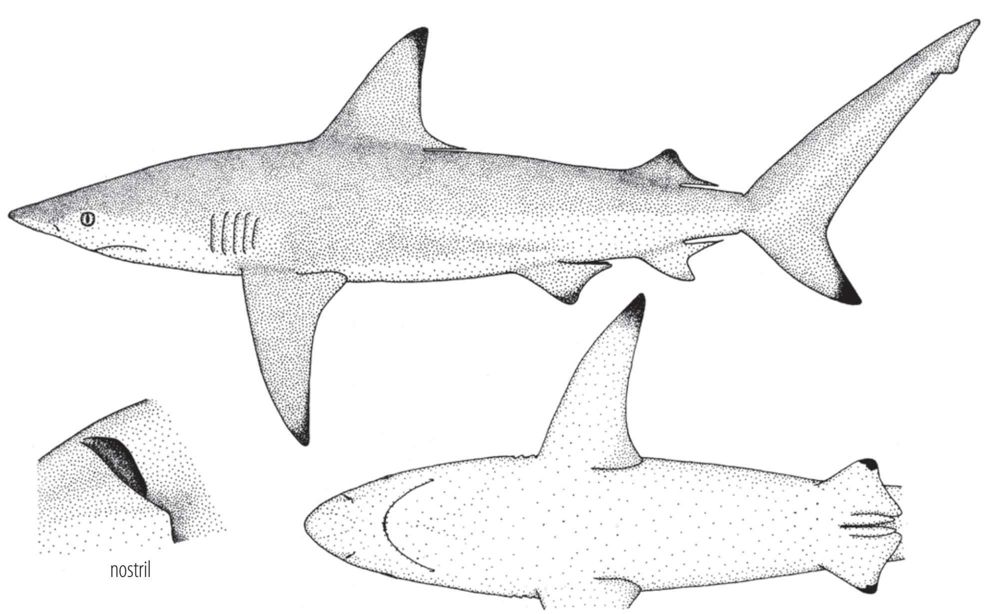
Carcharhinus limbatus: Bass *et al.* 1973*; Van der Elst 1981*; SSF No. 9.10*; Compagno *et al.* 1989*; Dudley & Cliff 1993; Wintner & Cliff 1996; Heemstra & Heemstra 2004; Compagno *et al.* 2005*; Last & Stevens 2009*; Voigt & Weber 2011*; Ebert *et al.* 2021*.

Large-sized, fairly stocky body; snout long, narrow and pointed. Anterior nasal flaps low, triangular. Upper lip folds short and inconspicuous. Upper anterolateral teeth with narrow, mostly erect cusps, with serrations and no cusplets; lower teeth with narrow cusps, usually with fine serrations. Gill slits long. Pectoral fins moderately large and falcate. No interdorsal ridge. First dorsal fin large, falcate, its height 1.5–2 in interdorsal space; origin just after pectoral-fin insertions (exceptionally nearer pectoral-fin free rear tips). Second dorsal-fin origin over or slightly before anal-fin origin; free rear tip long. Tooth count 29–35/27–33; vertebrae 174–203.

Body bronzy to grey-brown dorsally (fades to grey after death); conspicuous white band on flanks; black tips usually present on pectoral fins, dorsal fins and caudal-fin lower lobe, and sometimes on pelvic fins and anal fin (but anal fin often plain in individuals >80 cm TL), and black edges usually present on 1st dorsal fin (from tip to posterior margin) and caudal-fin upper lobe (anterior margin to tip); juveniles with stronger fin markings, and adults with less distinct fin markings; white ventrally. Attains 255 cm TL.

DISTRIBUTION Circumglobal in tropical to warm-temperate seas (widespread), including Mediterranean Sea. WIO: Persian/Arabian Gulf, Red Sea, Arabian Sea, Socotra to South Africa (Eastern Cape), Madagascar, Comoros, Seychelles and Sri Lanka.

REMARKS Litters of 1–11 (usually 4–7); size at birth 38–72 cm TL; gestation period 10–12 months, reproductive cycle biennial. Males mature at 135–180 cm TL, aged 4–5 years; females mature at 120–190 cm TL, aged 6–7 years; maximum age at least 12 years. Common close inshore and rarely deeper than 30 m; found off river mouths and in



Carcharhinus limbatus, 115 cm TL, male (South Africa).
Source: Bass *et al.* 1973

estuaries (not far into freshwater), in shallow muddy bays, the more saline parts of mangrove swamps, island lagoons, and along coral reef drop-offs, as well as offshore around some oceanic islands. Seasonally migratory in some parts of its range. Active and fast-swimming, often in loose aggregations near surface, and may leap from the water while feeding (often confused with the spinner shark, *C. brevipinna*, for this behaviour). Feeds mostly on bony fishes, also cephalopods, crustaceans and small elasmobranchs. Caught in recreational, artisanal and directed commercial fisheries with a variety of gear; its meat and fins are highly marketable. Poses little threat to humans unless stimulated by food, with only a few attacks recorded. IUCN Red List conservation status Near Threatened.

Carcharhinus longimanus (Poey 1861)

Oceanic whitetip shark PLATE 44

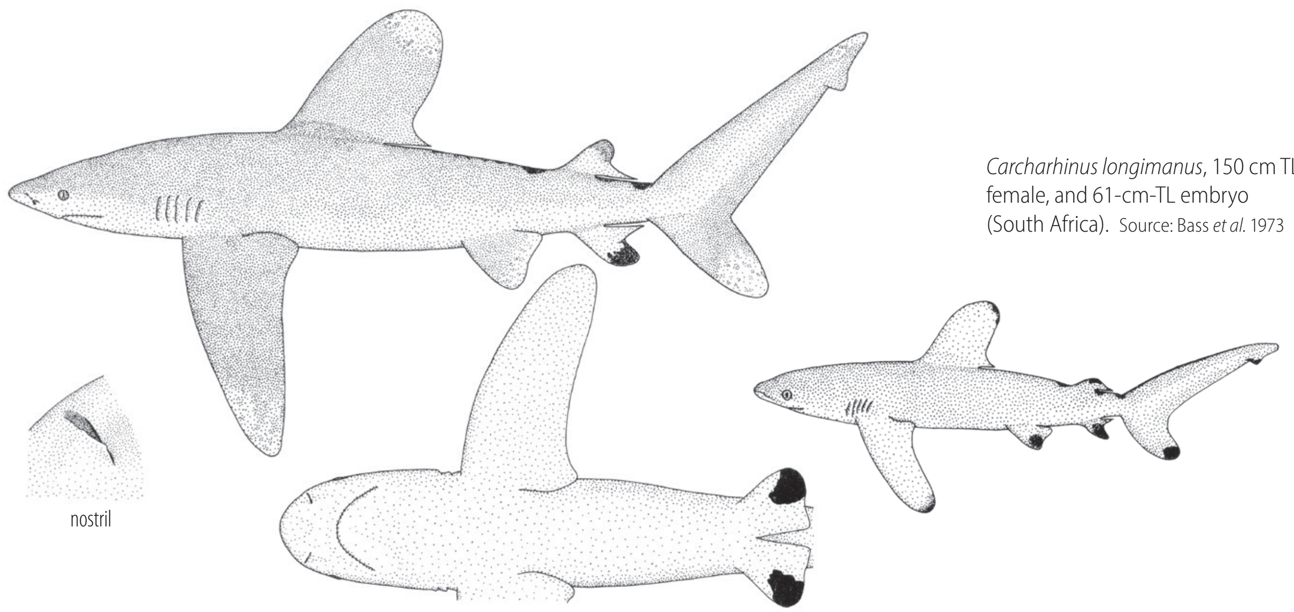
Squalus longimanus Poey 1861: 338, Pl. 19, Figs. 9–10 (Cuba).
Pterolamiops magnipinnis Smith 1958: 132, Pl. 1, Fig. 1 (off Port Elizabeth, Eastern Cape, South Africa).
Pterolamiops budkeri Fourmanoir 1961: 76 (Mozambique Channel).
Carcharhinus longimanus: Bass *et al.* 1973*; SSF No. 9.11*; Compagno *et al.* 1989*; Ebert 2003*; Compagno *et al.* 2005*; Last & Stevens 2009*; Voigt & Weber 2011*; Ebert *et al.* 2021*.

Body stocky; snout short and blunt. Upper lip folds short and inconspicuous. Upper teeth broad and triangular, erect to slightly oblique, and with strong serrations; lower teeth somewhat smaller and narrower, erect to slightly oblique, and with serrations and no cusplets. Pectoral fins distinctly long and broadly rounded (paddle-shaped), length of anterior margin 19–29% TL. Interdorsal ridge low, if present. First dorsal fin very long and large, with distinctly broadly rounded apex; origin just before pectoral-fin free rear tips. Second dorsal-fin origin over or slightly before anal-fin origin. Inconspicuous caudal keels. Tooth count 27–32/27–33; vertebrae 228–244.

Body grey-bronze dorsally; inconspicuous white band on flanks; white mottling usually present on fins (particularly pectoral fins, 1st dorsal fin, pelvic fins, and caudal-fin tips); young with additional black blotches or tips on most fins, as well as black saddles at 2nd dorsal-fin origin, upper caudal-fin origin, and sometimes between dorsal fins, and fading in adults; white ventrally. Attains 3.9 m TL, but most adults <3 m TL.

DISTRIBUTION Circumglobal in tropical to warm-temperate seas (widespread), including Mediterranean Sea. WIO: South Africa (KwaZulu-Natal) to Red Sea, and eastwards to India and Sri Lanka, including Socotra, Zanzibar, Madagascar, Comoros, Seychelles, Mascarenes, Chagos, Maldives and Lakshadweep; not known from Persian/Arabian Gulf.

REMARKS Litters of 1–15; size at birth 55–77 cm TL; gestation period ~12 months; reproductive cycle likely biennial. Males mature at 168–198 cm TL, and females at 175–224 cm TL; matures at 4–7 years. Oceanic and epipelagic, from surface to at least 152 m over deep water, but occasionally coastal in shallow water off oceanic islands or where continental shelf is very narrow. Feeds mostly on oceanic bony fishes and cephalopods, but also stingrays, crustaceans, sea birds, turtles, marine mammals and flotsam. Caught in large numbers as bycatch and in directed oceanic shark fisheries, particularly by longline and driftnet; the fins have high value in international trade. Slow-moving near surface, yet very active and inquisitive; dangerous to humans, but sought by ecotourism divers in the Red Sea and Indo-Pacific. IUCN Red List conservation status Critically Endangered globally.



Carcharhinus longimanus, 150 cm TL, female, and 61-cm-TL embryo (South Africa). Source: Bass *et al.* 1973

Carcharhinus macloti (Müller & Henle 1839)

Hardnose shark PLATE 44

Carcharias (*Hypoprion*) *macloti* Müller & Henle 1839: 34, Pl. [10] (New Guinea).
Carcharhinus macloti: Compagno 1984*; SSF No. 9.12*; Compagno *et al.* 2005*; Last & Stevens 2009*; Voigt & Weber 2011*; Ebert *et al.* 2021*.

Small-sized slender body; snout long, pointed, and noticeably stiff (rostrum hypercalcified, easily detectable by pinching or cutting into snout). Eyes large and circular. Anterior nasal flaps short and nipple-like. Upper lip folds short and inconspicuous. Upper anterolateral teeth with large basal serrations; lower teeth with oblique, moderately high, narrow cusps, with no serrations. Pectoral fins small and falcate. No interdorsal ridge. First dorsal fin moderate-sized, falcate; origin over or slightly before pectoral-fin free rear tips. Second dorsal fin low; origin near anal-fin midbase. Inner margin of both dorsal fins extremely long, at least two-thirds length of fin bases. Tooth count 29–32/26–29; vertebrae 151–156.

Body bronzy grey-brown dorsally; inconspicuous pale band on flanks; 2nd dorsal fin and upper caudal fin sometimes dark-edged, and pectoral fins and lower caudal fin sometimes pale-edged, but fins not conspicuously marked; white ventrally. Attains 110 cm TL.

DISTRIBUTION Indo-Pacific. WIO: Tanzania to Gulf of Aden, Socotra, Oman, Pakistan, India, Lakshadweep and Sri Lanka; not known from Persian/Arabian Gulf.

REMARKS Litters of 1 or 2; size at birth 45–50 cm TL (relatively large); gestation period ~12 months. Males mature at ~69 cm TL, and females at 76–89 cm TL. Coastal, in tropical waters over continental and insular shelves, from close inshore to 170 m deep. Forms large aggregations segregated by sex. Feeds primarily on small bony fishes, also cephalopods and crustaceans. Regularly caught in subsistence, artisanal and commercial fisheries, using longlines, gillnets and trawls. Harmless to humans. IUCN Red List conservation status Near Threatened globally; Least Concern in Australia.

Carcharhinus melanopterus

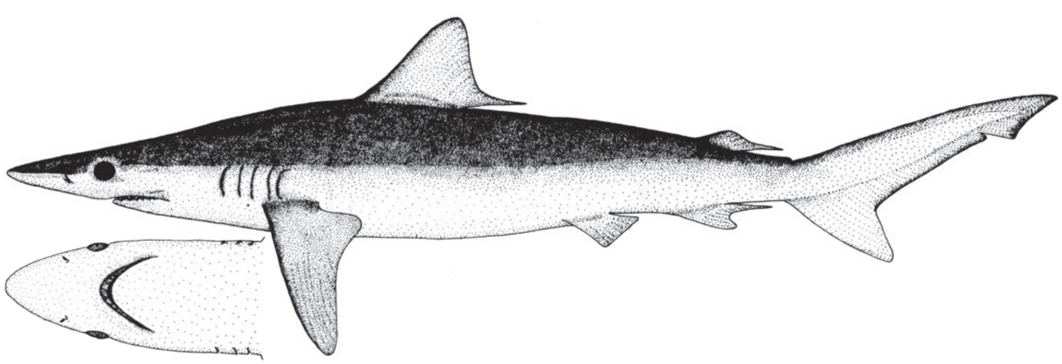
(Quoy & Gaimard 1824)

Blacktip reef shark PLATE 45

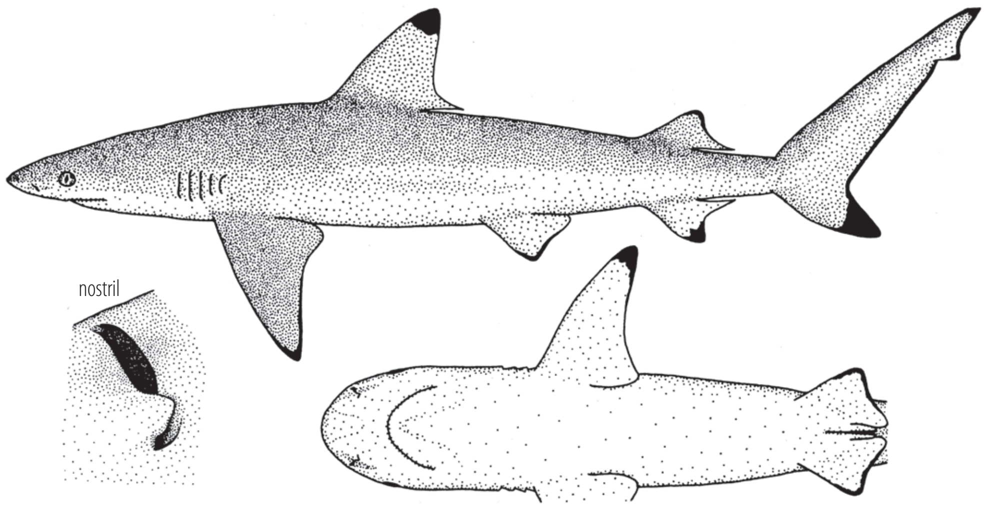
Carcharias melanopterus Quoy & Gaimard 1824: 194, Pl. 43, Figs. 1–2 (Papua Barat, Indonesia).
Carcharhinus melanopterus: Bass *et al.* 1973*; Compagno 1984*; SSF No. 9.13*; Compagno *et al.* 1989*; Compagno *et al.* 2005*; Last & Stevens 2009*; Voigt & Weber 2011*; Ebert *et al.* 2021*.

Moderate-sized; snout short and bluntly rounded, internarial width 0.9–1.1 in preoral length. Eyes horizontally oval. Anterior nasal flaps nipple-shaped. Upper lip folds short and inconspicuous. Upper teeth narrowly triangular, erect to oblique, and with coarse serrations basally; lower teeth erect, with narrower cusps, with fine serrations. Pectoral fins moderately large, narrow, and falcate. No interdorsal ridge. First dorsal fin large, falcate; origin usually over pectoral-fin free rear tips. Second dorsal fin relatively large; origin about over anal-fin origin. Tooth count 23–28/21–27; vertebrae 193–214.

Body pale brownish grey dorsally; conspicuous white band on flanks; 1st dorsal fin and caudal-fin lower lobe with large black apical blotch and brilliantly highlighted proximally with white, and other fins generally with less prominent black tips or thin edges; white ventrally. Attains 180 cm TL.



Carcharhinus macloti, 77 cm TL (Kenya).
Source: SSF



Carcharhinus melanopterus, 70 cm TL, male (St Brandon Shoals).
Source: Bass *et al.* 1973

DISTRIBUTION Indo-Pacific. WIO: South Africa (KwaZulu-Natal) to Red Sea, Persian/Arabian Gulf, Pakistan, India and Sri Lanka, as well as Madagascar, Comoros, Seychelles, Mauritius, St Brandon Shoals, Maldives and Lakshadweep; possibly enters eastern Mediterranean Sea through Suez Canal.

REMARKS Litters of 2–4; size at birth 33–52 cm TL. Males mature at 91–100 cm TL, and females at 96–112 cm TL; biennial reproductive cycle. Occurs in tropical and subtropical waters; common in very shallow inshore areas on or near coral reefs and reef flats, but also found in mangroves, near reef drop-offs and occasionally close offshore. Occurs singly or in small groups or aggregations, but not strongly schooling. Feeds on small fishes, also crustaceans, molluscs and cephalopods. Predators of this species include large groupers and other sharks. Not a major target but regularly caught in fisheries where it occurs. Not regarded as dangerous to humans yet has bitten people swimming or wading in the vicinity of reefs; a popular subject of ecotourism and aquarium displays. IUCN Red List conservation status Vulnerable.

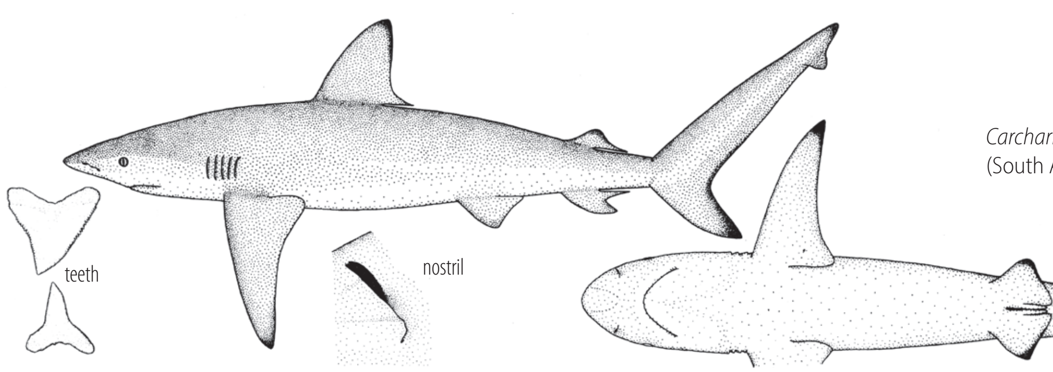
Carcharhinus obscurus (Lesueur 1818)

Dusky shark

PLATE 45

Squalus obscurus Lesueur 1818: 223, Pl. 9 [east coast of USA].
Carcharhinus iranzae Fourmanoir 1961: 40, Pl. 13, Fig. C (west coast of Madagascar).
Carcharhinus obscurus: Bass *et al.* 1973*; Van der Elst 1981*; Compagno 1984*; SSF No. 9.14*; Compagno *et al.* 1989*; Cockcroft 1991; Natanson & Kohler 1996; Ebert 2003*; Heemstra & Heemstra 2004*; Compagno *et al.* 2005*; Last & Stevens 2009*; Voigt & Weber 2011*; Ebert *et al.* 2021*.

Large-sized; snout fairly short and broadly rounded. Anterior nasal flaps low and poorly developed. Upper lip folds short and inconspicuous. Upper anterolateral teeth broad, triangular, rather low, erect to semi-oblique, with fine serrations and no cusplets; lower teeth erect, with narrow cusps. Gill slits long. Pectoral fins large, falcate. Interdorsal ridge low. First dorsal fin moderate-sized, semifalcate; origin over or slightly after pectoral-fin free rear tips. Second dorsal fin small and erect; inner margin moderately long, 1.6–2 times fin height



Carcharhinus obscurus, 165 cm TL, male (South Africa). Source: Bass *et al.* 1973 (cf. *C. galapagensis*); origin roughly over anal-fin origin. Tooth count 29–33/27–32; vertebrae 173–194, precaudal vertebrae 89–95.

Body grey or grey-brown dorsally; inconspicuous white band on flanks; most fin tips dusky but not black or white; white ventrally. Attains 4 m TL.

DISTRIBUTION Circumglobal in tropical to warm-temperate seas (patchy), including western Mediterranean Sea. WIO: Red Sea to South Africa (strays to southwest coast, but mostly KwaZulu-Natal and Eastern Cape), as well as Socotra and Madagascar.

REMARKS Notably slow-growing and late-maturing. Litters of 2–18; size at birth 70–100 cm TL; gestation period 16–22 months, reproductive cycle biennial or triennial. Males mature at 265–290 cm TL, age 17–24 years; females mature at 257–310 cm TL, age 21–32 years; maximum age 40–53 years. Coastal-pelagic, over continental and insular shelves and adjacent oceanic waters, from surf zone to far out to sea, from surface to 400 m. Adults undertake long temperature (seasonal) migrations. Feeds throughout water column on bony fishes, elasmobranchs, cephalopods, crustaceans, and other marine vertebrates and invertebrates; the young are preyed upon by other large sharks. Regularly caught as a bycatch and target species by longline, hook and line, and set bottom nets; the fins are highly valued and among the most sought-after for shark fin soup. Large individuals considered dangerous to humans. IUCN Red List conservation status Endangered.

Carcharhinus plumbeus (Nardo 1827)

Sandbar shark

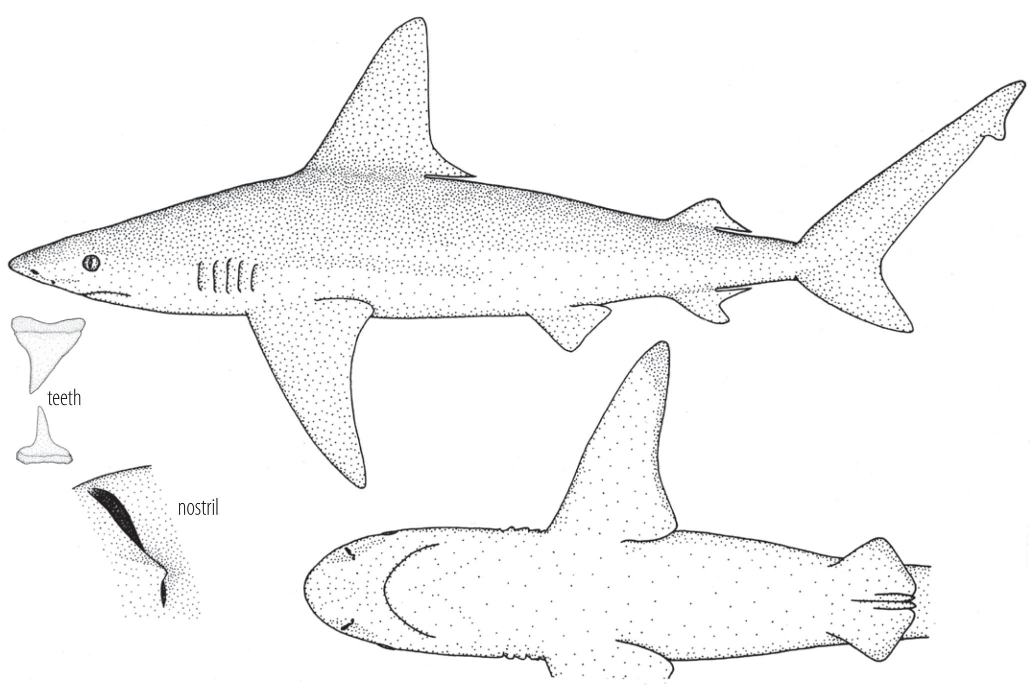
PLATE 45

Squalus plumbeus Nardo 1827: 26, 35; also Nardo 1827: 477, 483 (Adriatic Sea).
Carcharhinus plumbeus: Bass *et al.* 1973*; SSF No. 9.15*; Compagno *et al.* 1989*; Heemstra & Heemstra 2004; Compagno *et al.* 2005*; Last & Stevens 2009*; Voigt & Weber 2011*; Ebert *et al.* 2021*.

Medium-sized, stout body; snout short and rounded, shortest distance from nostrils to mouth >2.4 in mouth width. Anterior nasal flaps short, nipple-like. Upper lip folds short and inconspicuous. Upper teeth broad and triangular with high cusps, with serrations and no cusplets; lower teeth smaller, with narrow, erect, serrated cusps. Pectoral fins large, semifalcate. Interdorsal ridge narrow. First dorsal fin very large and triangular, semifalcate; origin over or slightly before pectoral-fin insertions. Second dorsal-fin inner margin short, 1–1.6 times fin height; origin over or slightly before anal-fin origin. Tooth count 27–32/25–32; vertebrae 152–189.

Body grey-brown dorsally; inconspicuous white band on flanks; fin tips and rear edges often dusky; white ventrally. Attains 240 cm TL.

DISTRIBUTION Circumglobal in tropical to warm-temperate seas (widespread), including Mediterranean Sea, but possibly not eastern Pacific. WIO: South Africa (Eastern Cape) to Red Sea, Gulf of Oman, Persian/Arabian Gulf, Pakistan and India, as well as Socotra, Madagascar, Seychelles, Mauritius and Lakshadweep.



Carcharhinus plumbeus, 118 cm TL, male (South Africa). Source: Bass *et al.* 1973

REMARKS Litters of 1–14; size at birth 56–75 cm TL; gestation period 9–12 months, reproductive cycle possibly every 2 or 3 years. Males mature at 131–178 cm TL, age ~14 years; females mature at 144–183 cm TL, age ~16 years; maximum age 19–25 years. Coastal-pelagic, over continental and insular shelves, adjacent oceanic waters and oceanic banks, from intertidal zone to 280 m deep (typically above 100 m). Also common in shallow muddy or sandy bays, harbours and estuaries but does not enter freshwater; tends to avoid sandy beaches, the surf zone, coral reefs, rough bottom and the surface. Seasonally migratory in some portions of its range. Feeds near seabed on relatively small bony fishes, elasmobranchs, cephalopods, molluscs and crustaceans. A large component of coastal shark fisheries, caught with longlines, hook and line, set bottom nets, and rod-and-reel. Not considered dangerous to humans. IUCN Red List conservation status Vulnerable.

Carcharhinus sorrah (Valenciennes 1839)

Spottail shark PLATE 46

Carcharias (*Prionodon*) *sorrah* Valenciennes *in* Müller & Henle 1839: 45, Pl. 16 (Java, Indonesia).

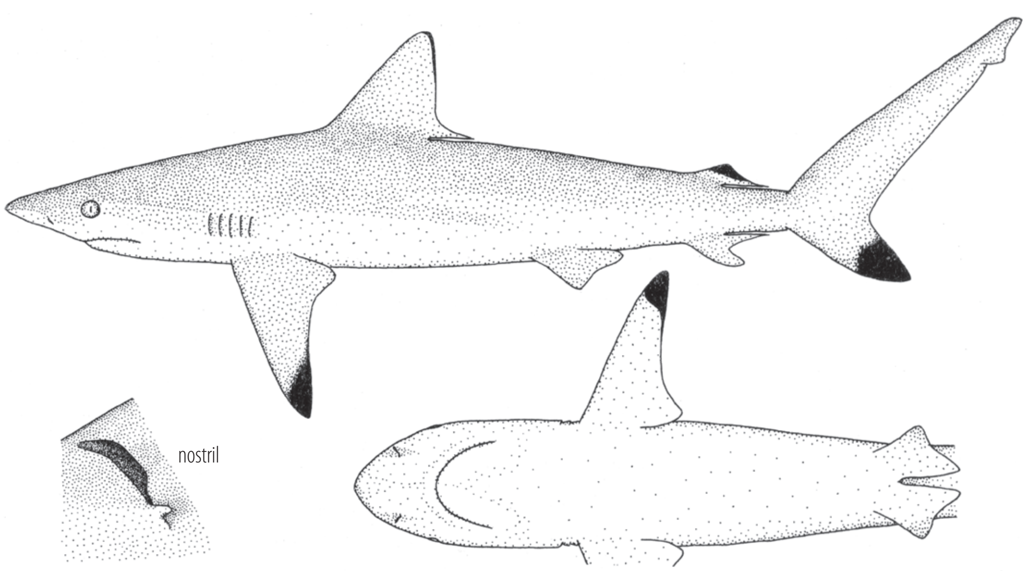
Carcharhinus sorrah: Bass *et al.* 1973*; Compagno 1984*; SSF No. 9.17*; Compagno *et al.* 1989*; Anderson & Ahmed 1993; Compagno *et al.* 2005*; Fricke *et al.* 2009; Last & Stevens 2009*; Voigt & Weber 2011*; Ebert *et al.* 2021*.

Moderately-sized spindle-shaped body; snout moderately long and rounded. Eyes large and circular. Anterior nasal flaps nipple-shaped. Upper lip folds short and inconspicuous. Upper teeth with oblique, moderately narrow cusps, with strong serrations basally, usually only 24–26 rows of upper anteroposterior teeth; lower teeth slightly oblique, narrower, smooth cusps. Pectoral fins fairly small and falcate. Interdorsal ridge low. First dorsal fin moderate-sized, falcate; origin from slightly before to after pectoral-fin free rear tips. Second dorsal fin small and low; inner margin very long, 0.9–1.1 times fin height; origin about opposite anal-fin base. Tooth count 24–26/22–25; vertebrae 153–160.

Body grey dorsally; conspicuous white band on flanks; conspicuous black tip on pectoral fins, 2nd dorsal fin and caudal-fin lower lobe, but 1st dorsal fin with black edge at most; white ventrally. Attains 160 cm TL.

DISTRIBUTION Indo-Pacific (patchy). WIO: Persian/Arabian Gulf, Red Sea to South Africa (KwaZulu-Natal), Madagascar, Seychelles, Mascarenes and Maldives.

REMARKS Litters of 1–8; size at birth 35–45 cm TL; gestation ~10 months with a reproductive periodicity of 1 year. Males and females mature at 2–3 years. Common; occurs on continental and insular shelves in tropical waters. Feeds mostly on bony fishes and cephalopods (octopus). Regularly caught with line gear and gillnets by artisanal and small-scale commercial fisheries where it occurs. Not dangerous to humans. IUCN Red List conservation status Near Threatened.



Carcharhinus sorrah, 111 cm TL, female (W Madagascar).
Source: Bass *et al.* 1973

GENUS *Glyphis* Agassiz 1843

Large-sized stocky body; snout short and broadly rounded, preoral length much less than mouth width. Eyes tiny; no spiracles. Nostrils small; anterior nasal flaps short, triangular. Lip folds short, confined to corners of mouth. Teeth strongly differentiated in upper and lower jaws; upper teeth usually erect, broad, triangular, with finely serrated cusps and no cusplets; lower teeth with or without cusplets or blades, but with variably oblique to erect long cusps, generally with no serrations, and cusps prominently protruding when mouth closed; tooth counts 29–37/28–34. Pectoral fins moderately broad, falcate or semifalcate. No interdorsal ridge. First dorsal-fin origin far anterior, over rear half of pectoral-fin bases, its free rear tip well before pelvic fins. Second dorsal fin smaller than 1st, its origin slightly before anal-fin origin. Anal fin slightly smaller than 2nd dorsal fin; preanal ridges very short or absent; rear margin concave to deeply concave. No lateral keels on peduncle; upper precaudal pit longitudinal and not crescentic. Body grey or brownish dorsally, white ventrally, and without conspicuous markings. Found in turbid brackish freshwater of rivers, estuaries and possibly adjacent marine areas. Possibly 5 species, all with small, fragmented populations in Indo-Pacific; 1 species in WIO.

Glyphis gangeticus (Müller & Henle 1839)

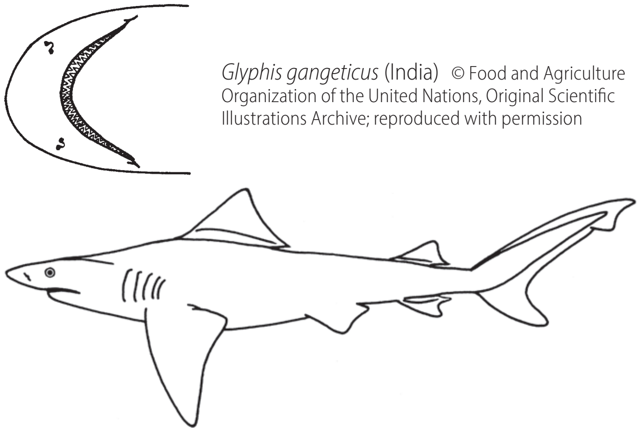
Ganges shark

Carcharias (*Prionodon*) *gangeticus* Müller & Henle 1839: 39, Pl. 13 (Ganges River at Hooghly, India [Lower Sundarbans, Bangladesh]).
Glyphis gangeticus: Compagno 1984*; Compagno *et al.* 2005*; Ebert *et al.* 2021*.

Preorbital snout rather long; preoral snout much shorter than mouth width. First dorsal-fin origin over rear of pectoral bases. Second dorsal fin ~½ height of 1st dorsal fin. First few anterior teeth in lower jaw with cutting edges along entire cusp, giving cusps claw-like shape, and with low cusplets. Tooth count 30–37/31–34; vertebrae 169.

Body grey dorsally, without markings; white ventrally. Attains at least 204 cm TL.

DISTRIBUTION India (east coast) and Bangladesh (lower reaches of Ganges-Hooghly river system, West Bengal), but may occur in other river systems or shallow estuaries in the area, and possibly in Pakistan (vicinity of Karachi) and northern India in WIO.

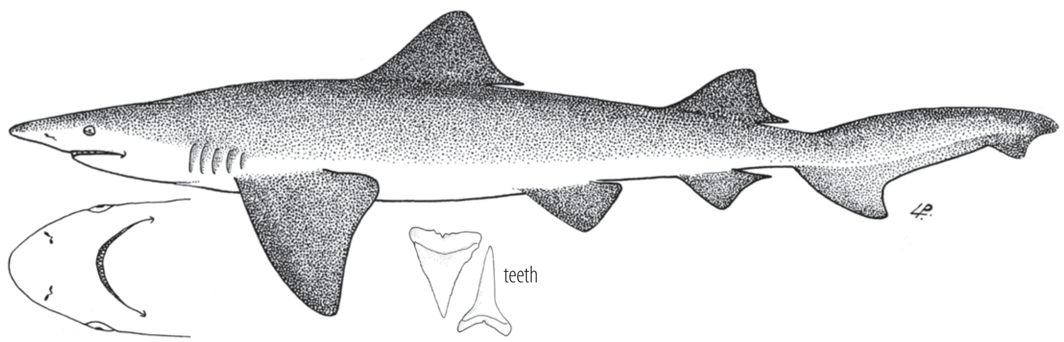


Glyphis gangeticus (India) © Food and Agriculture Organization of the United Nations, Original Scientific Illustrations Archive; reproduced with permission

REMARKS Biology little known, but probably viviparous; newborn specimens 56–61 cm TL. Rare, elusive; freshwater riverine and possibly inshore marine and estuarine habitat. Apparently fished in the Ganges-Hooghly river system. Reputed to have attacked humans, but such incidents most likely involved the Zambezi shark (*Carcharhinus leucas*) which occurs in the same area. IUCN Red List conservation status Critically Endangered.

GENUS *Lamiopsis* Gill 1862

Moderate-sized, rather stocky body; snout moderately long, preoral length nearly equal to or slightly greater than mouth width. Eyes fairly small; no spiracles. Nostrils small; anterior nasal flaps short, broadly triangular. Lip folds confined to corners of mouth. Teeth generally differentiated in upper and lower jaws; upper anteroposterior teeth with more or less erect, broad, triangular cusps, with irregular serrations and no cusplets or blades; lower teeth with oblique to erect, long, hooked cusps, with no serrations, and cusps slightly protruding when mouth closed. Pectoral fins very broad and triangular; origins under 4th or 5th gill slits; distance from origin to free rear tip >¾ length of anterior margin. No interdorsal ridge. First dorsal-fin origin over pectoral-fin inner margins; midbase slightly closer to pectoral-fin bases than to pelvic-fin bases; free rear tip over or slightly before or after pelvic-fin origins. Second dorsal fin >¾ height of 1st; origin about opposite anal-fin origin. Anal fin smaller than 2nd dorsal fin; preanal ridges very short or absent; rear margin slightly concave. No lateral keels on peduncle; upper precaudal pit longitudinal and not crescentic. Tooth counts 29–37/28–34. Two species, 1 in WIO.



Lamiopsis temminckii. © Food and Agriculture Organization of the United Nations, Original Scientific Illustrations Archive; reproduced with permission

Lamiopsis temminckii (Müller & Henle 1839)

Broadfin shark

Carcharias (*Prionodon*) *temminckii* Müller & Henle 1839: 48, Pl. [18] (India).
Lamiopsis temminckii: Setna & Sarangdhar 1949; Compagno 1984* [as *temminicki*]; Manilo & Bogorodsky 2003 [as *temminicki*]; Compagno *et al.* 2005*; White *et al.* 2010*; Ebert *et al.* 2021*.

Fifth gill slit ~½ length of 1st gill slit. Upper teeth with broad triangular cusps, with uneven serrations, and usually 5–7 posterior rows of molariform teeth; lower teeth hook-shaped, with narrow cusps and no serrations; tooth count 29–37/28–34.

Body pale grey or brownish dorsally; pale ventrally. Attains 168 cm TL.

DISTRIBUTION Indo-Pacific. WIO (patchy): Pakistan, India, Lakshadweep and Maldives, but not known from off Sri Lanka in Gulf of Mannar.

REMARKS Litters of 4–8; size at birth 40–60 cm TL; gestation period 8 months. Occurs mostly close inshore, in brackish and marine waters. Likely feeds on small fishes and invertebrates. Rare throughout most of its range, but once common off west coast of India. Taken by local fishermen in bottom and floating gillnets and with line gear; used for its meat, fins and liver oil. Not dangerous to humans. IUCN Red List conservation status Endangered.

GENUS *Loxodon* Müller & Henle 1838

Small-sized, slender body with distinctly long snout. Head fairly narrow and moderately depressed; snout narrowly parabolic in dorsoventral view, preoral length greater than internarial space and mouth width. Eyes large, with posterior notch; spiracles minute. Anterior nasal flaps very short and narrowly triangular. Lip folds short, confined to corners of mouth. Pectoral fins relatively short, moderately broad and triangular, slightly falcate; distance between pectoral- and pelvic-fin bases 2–3 times that of 1st dorsal-fin base. Interdorsal ridge absent or rudimentary. First dorsal-fin origin behind pectoral-fin free rear tips, its midbase roughly equidistant between pectoral- and pelvic-fin bases, and its free rear tip usually before pelvic-fin origins (but occasionally over them). Second dorsal fin much smaller than 1st (<¼ height of 1st dorsal fin); origin roughly over anal-fin insertion. Anal fin larger than 2nd dorsal fin; preanal ridges long; rear margin concave. No keels on peduncle; upper precaudal pit transverse and crescentic. One species.

Loxodon macrorhinus Müller & Henle 1839

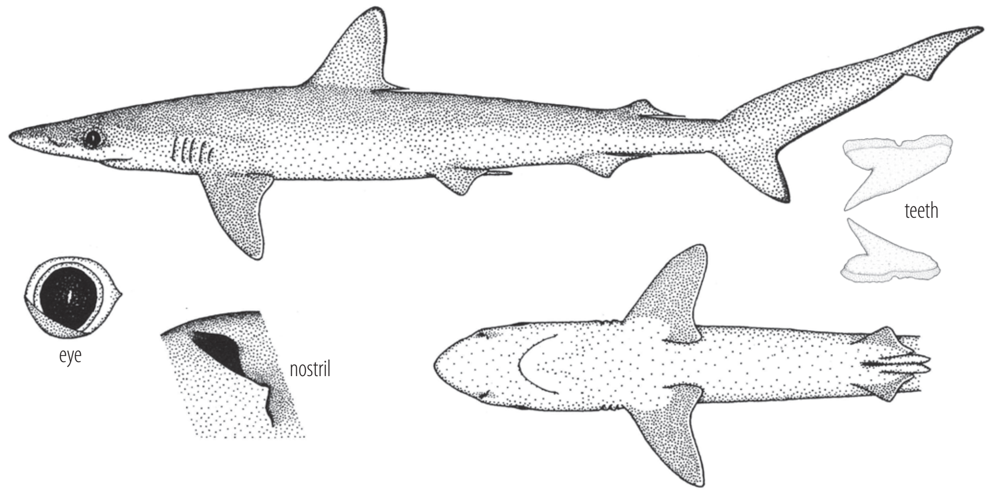
Sliteye shark

PLATE 46

Loxodon macrorhinus Müller & Henle 1839: 61, Pl. [25] [probably Indian Ocean]; Springer 1964*; Bass *et al.* 1975*; Compagno 1984*; Compagno *et al.* 1989*; Compagno *et al.* 2005*; Last & Stevens 2009*; Ebert *et al.* 2021*.
Scoliodon ceylonensis: Setna & Sarangdhar 1946; Bonfil & Abdallah 2004*.

Diagnosis as for genus. Teeth smooth-edged, similar in both jaws; anteroposterior teeth with fairly slender, highly oblique cusps, with distal blades but no cusplets or serrations. Tooth count 25–28/24–28; vertebrae 148–191.

Body grey to brownish dorsally; 1st dorsal fin and caudal fin with thin black margins, and pectoral fins with pale posterior margins; pale ventrally. Attains 99 cm TL.



Loxodon macrorhinus, 75 cm TL, adult male (S Mozambique). Source: Bass *et al.* 1975

DISTRIBUTION Indo-Pacific. WIO: South Africa (KwaZulu-Natal) to Red Sea, Oman, Pakistan, India and Sri Lanka, as well as Socotra, Madagascar, Seychelles and Maldives; not known from Persian/Arabian Gulf.

REMARKS Litters of 2–4; size at birth 40–45 cm TL. Males mature at 62–66 cm TL, and females at 79–99 cm TL. Occurs in moderately shallow, clear waters of continental and insular shelves, at 7–100 m. Feeds on small bony fishes, crustaceans (shrimp) and occasionally cephalopods (cuttlefish). Commonly caught in artisanal and small-scale commercial fisheries by gillnets and longlines; used for its meat and fins. Harmless to people.

GENUS ***Negaprion*** Whitley 1940

Large-sized, moderately stout, fusiform body; snout short, broadly rounded or angular; preoral length subequal to internarial space and much less than mouth width. Eyes small; no spiracles. Lip folds confined to corners of mouth. Teeth strongly differentiated in upper and lower jaws; upper anteroposterior teeth with more or less erect, moderately slender cusps, with mostly smooth edges and generally low cusplets; lower teeth with mostly erect, fairly long, slightly hooked cusps, with smooth edges and no cusplets, and cusps not protruding when mouth closed. Pectoral fins broad and triangular or falcate; distance from origin to free rear tip >⅔ length of anterior margin. No interdorsal ridge. First dorsal-fin origin over or behind pectoral-fin free rear tips; midbase closer to pelvic-fin bases than to pectoral-fin bases; free rear tip more or less over pelvic-fin origins. Second dorsal fin at least four-fifths height of 1st dorsal fin; origin about opposite anal-fin origin. Anal fin somewhat smaller than 2nd dorsal fin; preanal ridges hardly developed; rear margin deeply concave. No lateral keels on peduncle; upper precaudal pit longitudinal and not crescentic. Tooth counts 27–33/27–33. Two species, 1 in WIO.

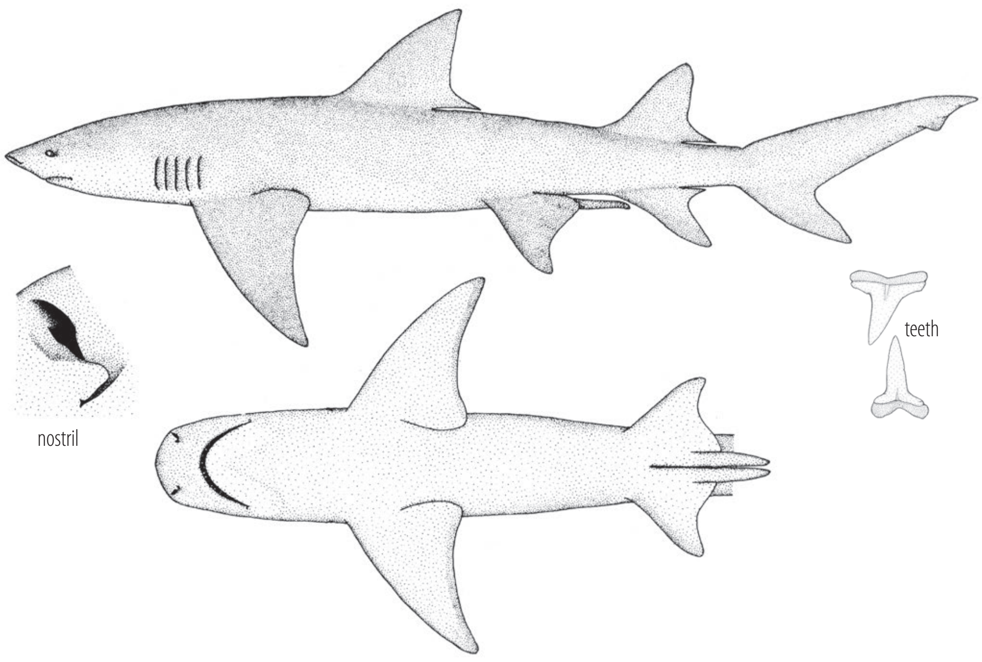
Negaprion acutidens (Rüppell 1837)

Sharptooth lemon shark — PLATE 46

Carcharias acutidens Rüppell 1837: 65, Pl. 18, Fig. 3 (Jeddah, Saudi Arabia, Red Sea).
Odontaspis madagascariensis Fourmanoir 1961: 15, Pl. 3 (Madagascar).
Negaprion acutidens: Gohar & Mazhar 1964; Bass *et al.* 1975*; SSF No. 9.29*; Compagno *et al.* 1989*; Compagno *et al.* 2005*; Last & Stevens 2009*; Ebert *et al.* 2021*.

Snout broad and blunt. Pectoral fins falcate. Tooth count 28–32/28–30; vertebrae 217–229.

Body yellowish brown to pale brown or grey dorsally; whitish ventrally. Attains 3.1 m TL.



Negaprion acutidens, 243 cm TL, mature male (South Africa). Source: Bass *et al.* 1975

DISTRIBUTION Indo-Pacific. WIO (widespread): South Africa (KwaZulu-Natal) to Red Sea, Pakistan, India and Sri Lanka, as well as Socotra, Madagascar, Seychelles, Mauritius, Maldives and Lakshadweep; not known from Persian/Arabian Gulf.

REMARKS Litters of 1–14; size at birth 45–80 cm TL; gestation period 10–11 months. Matures at 220–240 cm TL. Occurs on continental and insular shelves in tropical waters, on or near bottom, from intertidal zone to at least 30 m deep. Prefers bays, estuaries, sandy plateaus, outer-reef shelves at moderate depths, reef lagoons and mangrove estuaries; young commonly found on very shallow reef flats. Sluggish, slow swimmer, often found in turbid, still water; shy, but potentially dangerous to humans if provoked. Feeds on benthic bony fishes, elasmobranchs (stingrays) and cephalopods. Caught in Pakistan and India with longlines and gillnets; used for its meat, fins and liver oil. IUCN Red List conservation status Vulnerable globally; Southeast Asian subpopulation Endangered.

GENUS ***Prionace*** Cantor 1849

Large-sized, slender body, with long head and very long, conical snout; preoral length greater than internarial space and mouth width. Eyes large; no spiracles. Nostrils small; internarial space ~2.5–3 times nostril width; anterior nasal flaps very short and broadly triangular, and not tubular. Lip folds minute. Pectoral fins long and narrow (scythe-like); origins under 3rd and 4th gill slits. No interdorsal ridge. First dorsal fin well behind pectoral-fin free rear tips, its midbase closer to pelvic-fin bases, and its free rear tip slightly before pelvic-fin origins. Second dorsal fin much smaller than 1st (<½ height of 1st dorsal fin). Anal fin slightly larger than 2nd dorsal fin; preanal ridges short; rear margin deeply concave. Peduncle with weak keels; upper precaudal pit transverse and crescentic. Caudal fin narrow, and lower lobe long. One species.

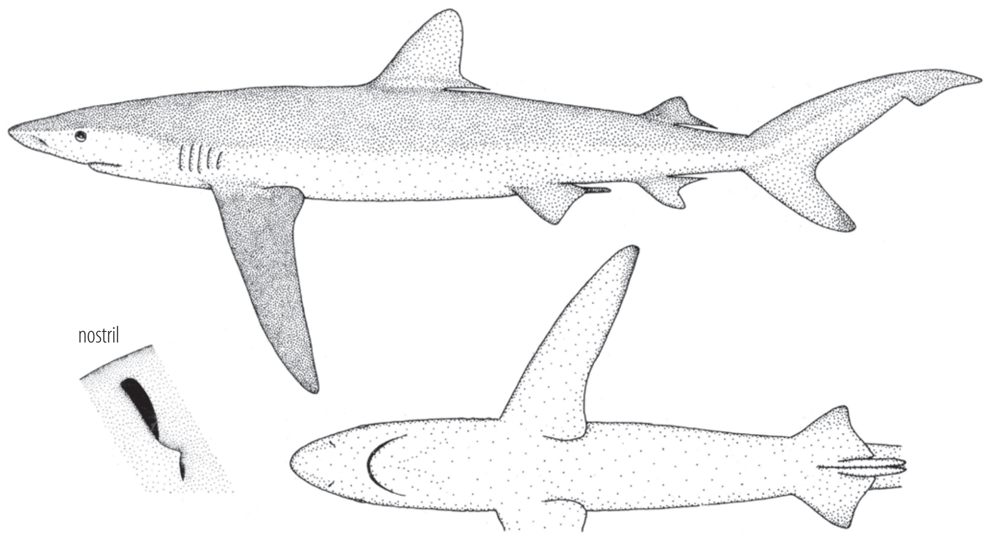
Prionace glauca (Linnaeus 1758)

Blue shark PLATE 47

Squalus glaucus Linnaeus 1758: 235 (Mediterranean Sea and NE Atlantic).
Prionace glauca: Fourmanoir 1961; Bass *et al.* 1975*; Gubanov & Grigor'yev 1975; Compagno 1984*; SSF No. 9.32*; Compagno *et al.* 1989*; Ebert 2003*; Heemstra & Heemstra 2004*; Compagno *et al*. 2005*; Last & Stevens 2009*; Ebert *et al.* 2021*.

Diagnosis as for genus. Teeth well-differentiated in upper and lower jaws; upper anteroposterior teeth triangular, curved, with erect to oblique cusps, with serrations and no blades or cusplets (except in very young specimens); lower teeth with slender cusps, no blades or cusplets, and serrations variably developed, and cusps not prominently protruding when mouth closed. Tooth count 24–31/25–34.

Body deep blue dorsally, with bright blue to silvery blue flanks (fades to grey soon after death), and pure white ventrally; pectoral-fin tips dusky. Attains 4 m TL, possibly more.



Prionace glauca, 279 cm TL, mature male (South Africa). Source: Bass *et al.* 1975

DISTRIBUTION Cosmopolitan in tropical to temperate seas, including Mediterranean Sea and throughout WIO, but not known from Red Sea and Persian/Arabian Gulf.

REMARKS Litters of 4–135 (average ~35); size at birth 35–60 cm TL; gestation period 9–12 months. Males mature at 183–218 cm TL, and females at 183–221 cm TL; fecund and fast-growing, matures at 4–8 years; maximum age ~20 years. Females have much thicker skin and often bear bite wounds as mating scars. Possibly the most wide-ranging shark, with complex movements; oceanic and pelagic, from surface to ~1 000 m deep, but occasionally ventures inshore (where continental shelf is narrowest); also makes long migrations by swimming slowly with major transoceanic currents. Graceful swimmer, observed cruising at surface with dorsal- and caudal-fin tips out of the water, and may form large aggregations to feed. Feeds on relatively small bony fishes and sharks, cephalopods (squid) and other invertebrates (pelagic red crabs), and occasionally seabirds and cetacean carrion. Heavily fished and used mostly for its fins; taken mainly as a bycatch with pelagic longlines, driftnets, and occasionally bottom trawls. Often timid, but potentially dangerous to humans. IUCN Red List conservation status Near Threatened.

GENUS *Rhizoprionodon* Whitley 1929

Small-sized, fairly slender to moderately stout, fusiform body; head moderately depressed; snout long, narrowly to broadly parabolic or obtusely wedge-shaped in dorsoventral view. Eyes large, without posterior notch; no spiracles. Nostrils small, wide-spaced; preoral length greater than internarial space and mouth width; anterior nasal flaps very short, narrowly triangular. Lip folds short to rather long; upper and lower folds unequal in length. Teeth similar in both jaws; anteroposterior teeth with relatively slender, oblique cusps, and with distal blades, no cusplets, and serrations variably developed. Pectoral fins relatively short, moderately broad and triangular, slightly falcate. Interdorsal ridge absent or rudimentary. First dorsal-fin origin over pectoral-fin free rear tips; midbase about equidistant between pectoral- and pelvic-fin bases or closer to pectoral fins; free rear tip slightly before pelvic-fin origins. Second dorsal fin much smaller than 1st (<⅓ height of 1st dorsal fin); origin just before or over anal-fin insertion. Anal fin larger than 2nd dorsal fin; preanal ridges very long; rear margin shallowly to deeply concave. No keels on peduncle; upper precaudal pit transverse and crescentic. Body pale grey, yellowish or brownish grey dorsally, pale ventrally, and without colour patterns. Tooth counts 23–31/21–28; vertebrae 121–170. Seven species, 2 in WIO.

KEY TO SPECIES

1a Upper lip folds long and rather prominent (usually as long as or longer than lower folds); tooth rows more numerous on average: mostly >25/24 .... ***R. acutus***

1b Upper lip folds reduced and often inconspicuous (usually shorter than lower folds); tooth rows fewer on average: mostly <25/24........ ***R. oligolinx***

Rhizoprionodon acutus (Rüppell 1837)

Milk shark

PLATE 47

Carcharias acutus Rüppell 1837: 65, Pl. 18, Fig. 4 (Jeddah, Saudi Arabia, Red Sea).
Rhizoprionodon acutus: Springer 1964; Bass *et al.* 1975*; Van der Elst 1981*; Compagno 1984*; SSF No. 9.33*; Compagno *et al.* 1989; Heemstra & Heemstra 2004*; Compagno *et al.* 2005*; Last & Stevens 2009*; Ebert *et al.* 2021*.

Upper lip folds long and prominent (as long as or longer than lower folds); prenarial snout long, 4–5.4% TL; usually >8 enlarged hyomandibular pores on each side of head just behind angle of mouth. Teeth generally smooth-edged, but with some irregular low cusplets. Tooth count 23–27/23 or 24; vertebrae 121–162.

Body greyish or bronzy dorsally; pectoral fins with pale margins, and 1st dorsal fin and caudal-fin upper lobe sometimes dark-edged; white ventrally. Attains 178 cm TL.

DISTRIBUTION Eastern Atlantic, Mediterranean Sea (one record off Italy) and Indo-Pacific (widespread). WIO: South Africa (KwaZulu-Natal) and Madagascar to Red Sea, Socotra, Persian/Arabian Gulf, Pakistan, India, Sri Lanka, Lakshadweep and Maldives.

REMARKS Litters of 1–8 (usually 2–5); size at birth 25–39 cm TL; gestation period ~12 months. Males mature at 68–72 cm TL, and females at 70–81 cm TL, both sexes at ~2 years; maximum age at least 8 years. Abundant, inshore and offshore over continental shelf, from shore to ~200 m deep; often found off sandy beaches, at midwater or near bottom, and sometimes in estuaries, but does not tolerate low salinities or range into freshwater. Feeds primarily on bony fishes, but also squid and crustaceans. Often preyed on by larger sharks. One of the most common sharks in inshore waters where it occurs; taken by artisanal and small-scale commercial fisheries and offshore fishing fleets by longline, hook and line and bottom trawl; used for its meat and fins, and as fish meal. Harmless to people. IUCN Red List conservation status Vulnerable.

Rhizoprionodon oligolinx Springer 1964

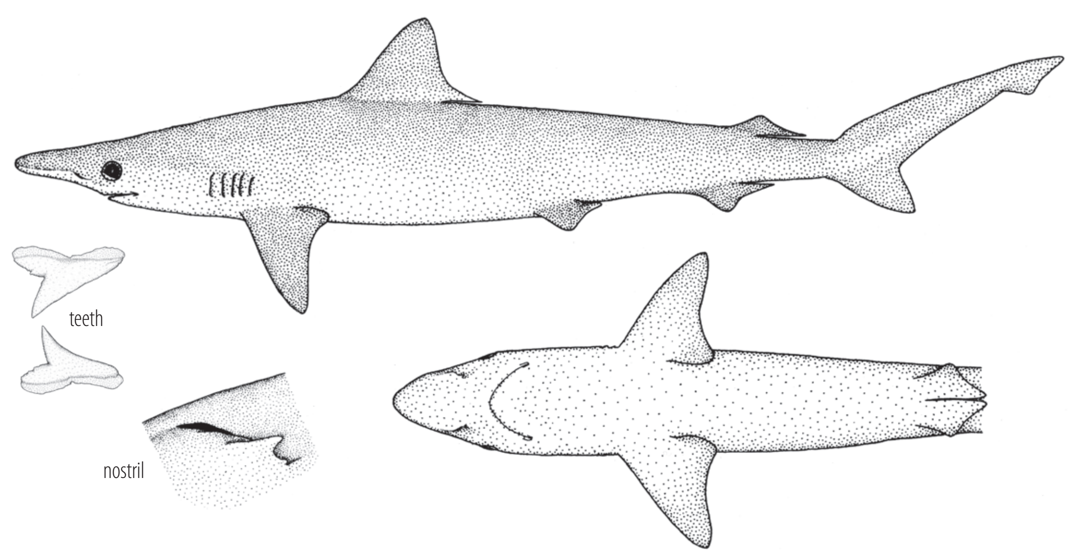
Grey sharpnose shark

PLATE 48

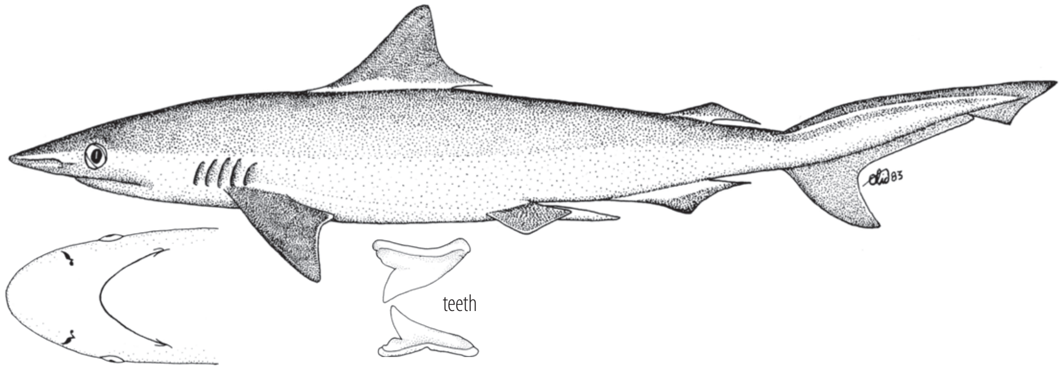
Rhizoprionodon oligolinx Springer 1964: 621, Pl. 2, Figs. 12–13 (Gulf of Thailand); Nair *et al.* 1974; Compagno *et al.* 2005*; Last & Stevens 2009*; Ebert *et al.* 2021*.

Interdorsal ridge sometimes present. Upper lip folds often inconspicuous, usually shorter than lower folds; prenarial snout short, 3.7–4.7% TL; 3–8 enlarged hyomandibular pores on each side of head just behind angle of mouth. Teeth small, with oblique cusps, with no serrations; tooth count 23–25/21–24. Vertebrae 151–164, precaudal vertebrae 84–91.

Body grey to bronzy grey dorsally; fins with inconspicuous dusky edges; pale ventrally. Attains 70 cm TL.



Rhizoprionodon acutus, 99 cm TL, mature female (South Africa). Source: Bass *et al.* 1975



Rhizoprionodon oligolinx. © Food and Agriculture Organization of the United Nations, Original Scientific Illustrations Archive; reproduced with permission

DISTRIBUTION Indo-Pacific. WIO: Arabian Sea and Persian/Arabian Gulf to Pakistan, India, Sri Lanka and Maldives.

REMARKS Common but poorly known. Litters of 3–5; size at birth 21–26 cm TL. Males mature at 29–38 cm TL, and females at 32–41 cm TL. Abundant, inshore and offshore, over continental and insular shelves. Likely feeds on small bony fishes, cephalopods and crustaceans. Probably commonly taken in subsistence, artisanal and commercial fisheries throughout its range, by gillnet, longline and trawl; used for its meat and fins.

GENUS *Scoliodon* Müller & Henle 1837

Small-sized, stocky body with compressed head; snout long and flattened, laterally expanded and trowel-shaped, preoral length greater than internarial space and mouth width. Eyes small; no spiracles. Anterior nasal flaps short and narrowly triangular. Lip folds short to rudimentary. Teeth similar in both jaws; anteroposterior teeth small, with very slender, oblique cusps, with distal blades but no cusplets or serrations. Pectoral fins very short, broad and triangular. Interdorsal ridge absent or rudimentary. First dorsal-fin origin over or behind pectoral-fin free rear tips; midbase closer to pelvic-fin bases than to pectoral-fin bases; free rear tip approximately over pelvic-fin midbase. Second dorsal fin much smaller than 1st (<⅓ height of 1st dorsal fin); origin behind anal-fin midbase. Anal fin much longer than 2nd dorsal fin; preanal ridges short; rear margin straight or slightly concave. No keels on peduncle; upper precaudal pit transverse and crescentic. Two species, 1 in WIO.

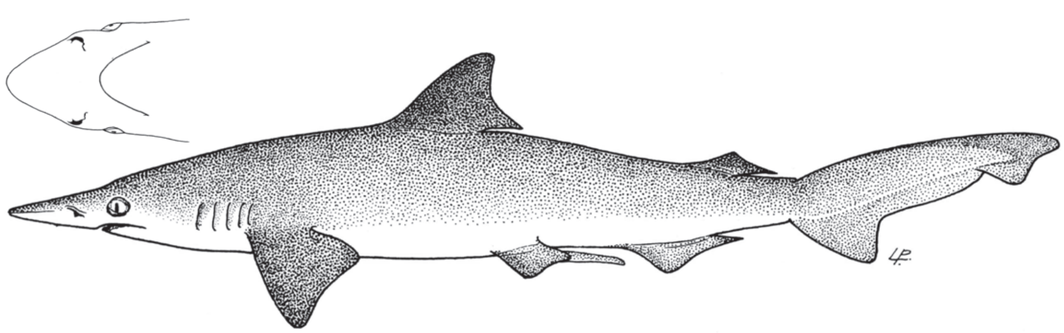
Scoliodon laticaudus Müller & Henle 1838

Spadenose shark PLATE 48

Scoliodon laticaudus Müller & Henle 1838: 27, 28, Pl. [8] (India); Müller & Henle 1839*; Compagno 1984*; Compagno *et al.* 2005*; White *et al.* 2006*; Ebert *et al.* 2021*.

No interdorsal ridge; 1st dorsal-fin origin behind pectoral-fin free rear tips. Anal fin very long, and rear margin nearly straight. Tooth count 25–33/24–34; vertebrae 148–171.

Body pale grey, yellowish or bronzy grey dorsally; white ventrally. Attains 74 cm TL.



Scoliodon laticaudus. © Food and Agriculture Organization of the United Nations, Original Scientific Illustrations Archive; reproduced with permission

DISTRIBUTION Indo-Pacific. WIO: Tanzania to Somalia, Socotra, Arabian Sea, Persian/Arabian Gulf, Pakistan, India, Lakshadweep and Sri Lanka; not known to enter Gulf of Aden and Red Sea.

REMARKS Litters of 1–14; size at birth 12–15 cm TL. Males mature at 24–36 cm TL, and females at 33–35 cm TL, at age 1–2 years for both sexes; maximum age 5–6 years. Occurs close inshore over continental and insular shelves, often in large schools; enters upper reaches of rivers in parts of Southeast Asia. Feeds on small pelagic schooling or benthic bony fishes, crustaceans (mantis shrimp, crabs) and cephalopods (cuttlefish). Abundant and heavily fished; commonly taken in Pakistan and India in artisanal and commercial fisheries by trawl lines, longlines, gillnets and traps; used for its meat. IUCN Red List conservation status Near Threatened.

GENUS *Triaenodon* Müller & Henle 1837

Moderate-sized, fairly slender body with relatively broad head; snout short and bluntly rounded, preoral length subequal to internarial space and much less than mouth width. Spiracles usually absent (may be present as minute pores or slit-like openings). Nostrils small; internarial space ~3 times nostril width; anterior nasal flaps slightly elongated, distally truncated, and forming distinct tubes with mesonarial flaps. Lip folds confined to corners of mouth. Pectoral fins fairly broad and triangular. No interdorsal ridge. First dorsal-fin origin well behind pectoral-fin free rear tips; midbase much closer to pelvic-fin bases than to pectoral-fin bases; free rear tips end slightly after pelvic-fin origins. Second dorsal fin large but distinctly smaller than 1st (½–¾ height of 1st dorsal fin); origin about opposite anal-fin origin. Anal fin approximately subequal to 2nd dorsal fin; preanal ridges short; rear margin deeply concave. No lateral keels on peduncle; upper precaudal pit transverse and crescentic. One species.

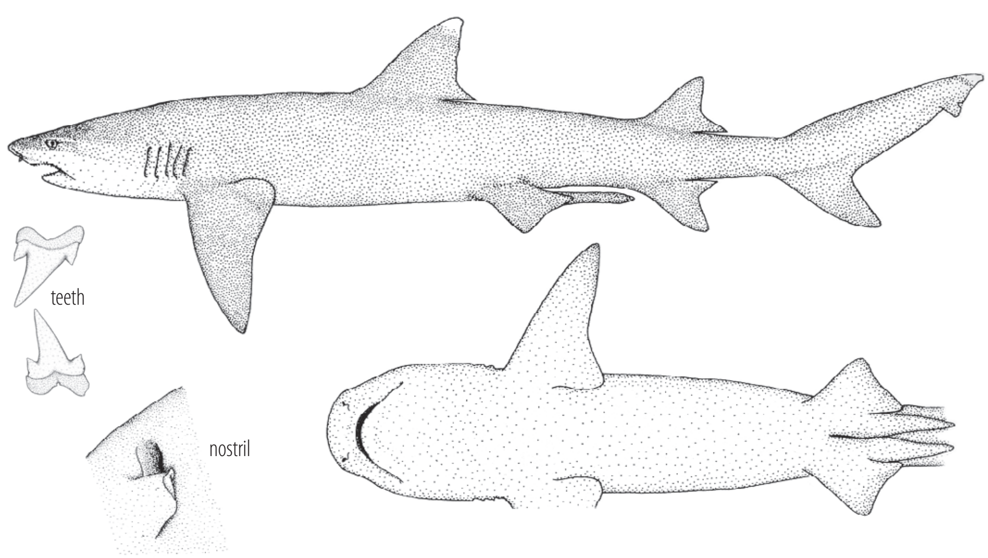
Triaenodon obesus (Rüppell 1837)

Whitetip reef shark PLATE 48

Carcharias obesus Rüppell 1837: 64, Pl. 18, Fig. 2 (Jeddah, Saudi Arabia, Red Sea).
Triaenodon obesus: Klausewitz 1960*; Fourmanoir 1961; Gohar & Mazhar 1964; Bass *et al.* 1975*; Compagno 1984*; SSF No. 9.35*; Compagno *et al.* 1989*; Compagno *et al.* 2005*; Ebert *et al.* 2021*.

Diagnosis as for genus. Mouth slanted downward in lateral view. Eyes horizontally oval. Teeth similar in both jaws, with erect to semi-oblique, triangular central cusps, flanked by pair of conspicuous cusplets or pointed blades, and no serrations; tooth count 42–50/42–48. Vertebrae 208–214.

Dorsal and lateral surfaces of head, trunk and tail greyish brown, becoming paler ventrally; flanks usually with few scattered dark spots; conspicuous white tip on 1st dorsal fin and caudal-fin upper lobe, and sometimes 2nd dorsal fin and caudal-fin lower lobe, as well as underside of pectoral-fin tips. Attains 213 cm TL.



Triaenodon obesus, 139 cm TL, mature male (South Africa). Source: Bass *et al.* 1975

DISTRIBUTION Indo-Pacific. WIO: South Africa (KwaZulu-Natal) to Red Sea, Gulf of Oman, Pakistan, India and Sri Lanka, as well as Madagascar, Comoros, Aldabra, Seychelles, Maldives and Lakshadweep; not known from Persian/Arabian Gulf.

REMARKS Litters of 1–5; size at birth 52–60 cm TL. Matures at 104–109 cm TL, with mating having been observed in the wild; maximum age at least 25 years. Occurs on continental and insular shelves, to ~330 m deep (commonly <40 m); associated with reefs and coral lagoons, in clear waters, on or near bottom and resting in caves and crevices, and occupies a small home range. Feeds on small bony fishes, cephalopods (octopus) and crustaceans. Caught in line and net trawl fisheries near shallow reef areas; used for its fins. Popular subject of ecotourism, may be curious and approach divers, and occasionally aggressive towards humans when food stimulus present. IUCN Red List conservation status Vulnerable.

FAMILY SPHYRNIDAE

Hammerhead sharks

Neil C Aschliman and Dave A Ebert

Small- to large-sized with distinctive laterally expanded head shaped like double mallet in profile. Eyes circular or nearly so, with internal nictitans; no spiracles. Anterior nasal flaps short and triangular, not barbel-like; internarial width usually 7–14 times nostril width (but <1.3 times nostril width in *Eusphyra*, which has greatly expanded nostrils). Lip folds vestigial or absent. Teeth small to moderately large, more or less blade-like, with acute and narrow to moderately broad cusps and no lateral cusplets; teeth weakly differentiated in upper and lower jaws; tooth counts 24–37/25–37. First dorsal fin moderate to large, tall, not keel-like, and much shorter than caudal fin; 1st dorsal-fin base ahead of pelvic-fin bases, varying from equidistant between pectoral- and pelvic-fin bases to closer to pectoral fins. Second dorsal fin much smaller than 1st, its size equal to or slightly smaller than anal fin. Pectoral fins with transverse radials extending into distal web. Caudal-fin lunate, lower lobe strong; undulations or ripples in caudal-fin dorsal margin; precaudal pits present. Intestinal valve scrolled.

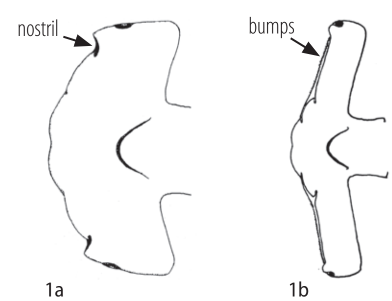
The unique flattened and laterally expanded prebranchial head (cephalofoil) of hammerhead sharks has been interpreted as a bow plane that greatly increases their manoeuverability and may also increase their sensory capacity, as the wide-spaced eyes enhance binocular vision, the expanded nasal capsules allow more acute and directional olfaction, and the increased head area allows more extensive lateral-line canals and ampullae of Lorenzini for pressure and electromagnetic senses.

Reproductive mode viviparity with yolk-sac placenta. Size range ~1.5–6 m TL. Found from surface, including surfline and intertidal zone, to at least 275 m deep. Common and wide-ranging in all warm-temperate to tropical seas, in continental and insular waters, on or adjacent to continental shelf, but none truly oceanic; some may enter estuaries. Considered potentially dangerous to people, but rare unprovoked attacks have been attributed to only a few of the species; most are shy and difficult to approach. Two genera and 8 species; both genera and 4 species in WIO.

KEY TO GENERA

1a Lateral blades of head broad anteroposteriorly, not wing-like; nostrils short, nostril width 7–14 times internarial width and less than half mouth width; no bumps along front margin of head .... ***Sphyrna***

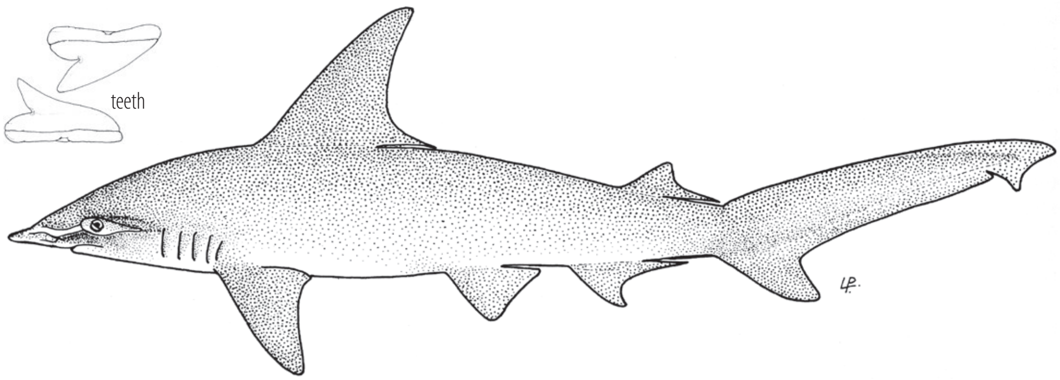
1b Lateral blades of head narrow and wing-like; nostrils enlarged, nostril width 0.8–0.9 times internarial width and nearly twice mouth width; bumps along front margin of head opposite nostrils .... ***Eusphyra***



Drawing 1b sourced from Compagno 1984, © FAO

GENUS *Eusphyra* Gill 1862

Head immensely laterally expanded and arrow-shaped in dorsoventral view, with bumps along front margin opposite nostrils; lateral blades of head narrow, wing-like; head width 40–50% TL. Nostrils enlarged. Teeth small, smooth-edged, oblique and similar in both jaws. First dorsal fin anteriorly set, its origin over pectoral-fin insertions. Anal-fin rear margin shallowly concave. Upper precaudal pit longitudinal, not crescentic. One species.



Eusphyra blochii

Eusphyra blochii (Cuvier 1816)

Winghead shark PLATE 49

Zygaena blochii Cuvier 1816: 127 [no locality given] [based on Bloch 1785: Pl. 117 and brief description].
Eusphyra blochii: Compagno 1984*; Compagno *et al.* 2005*.

Diagnosis as for genus. Nostril width 0.8–0.9 times internarial width and nearly twice mouth width. Tooth count 30–31/29; vertebrae 108–124.

Body grey or grey-brown dorsally, paler ventrally; no dark fin markings. Attains 186 cm TL.

DISTRIBUTION Indo-Pacific. WIO: Persian/Arabian Gulf to India and Sri Lanka.

REMARKS Common, distinctive, but poorly known. Litters of 6–25; size at birth 32–45 cm TL; gestation period 8–11 months. In Indian waters, young are born just before monsoon season, in April and May, and mating appears to occur from June to August. Males mature at ~108 cm TL, and females at ~120 cm TL. Found in shallow tropical waters of continental and insular shelves. Diet includes small fishes, cephalopods and crustaceans. Commonly fished throughout its range; caught with gillnets, stake nets, seines, floating and bottom longlines, and probably on hook and line; exploited for its meat and fins. Relatively harmless to people. IUCN Red List conservation status Endangered.

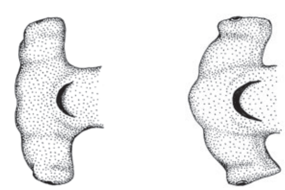
GENUS *Sphyrna* Rafinesque 1810

Moderately broad, spade-, mallet- or axe-shaped head in dorsoventral view, and without bumps along front margin; lateral blades of head broad, not wing-like; head width ⅙–⅓ TL. Nostrils short, nostril width 7–14 times internarial width and less than half mouth width. First dorsal-fin origin over or behind pectoral-fin insertions. Upper precaudal pit transverse and crescentic. Circumglobal in all warm-temperate and tropical seas. Seven species, 3 in WIO.

KEY TO SPECIES

1a Front margin of head nearly straight in adults; prenarial grooves absent or weakly developed; teeth strongly serrated at all sizes; 1st dorsal fin markedly falcate; 2nd dorsal fin very high, with short inner margin and deeply concave rear margin; pelvic fins high and falcate .... ***S. mokarran***

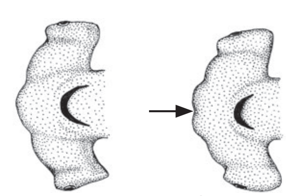
1b Front margin of head moderately convex in adults, strongly so in young; prenarial grooves well-developed; teeth weakly serrated in adults, smooth-edged in young; 1st dorsal fin usually semifalcate; 2nd dorsal fin low, with long inner margin and deeply concave rear margin; pelvic fins low and not falcate, with nearly straight posterior margins **2**



1a 1b

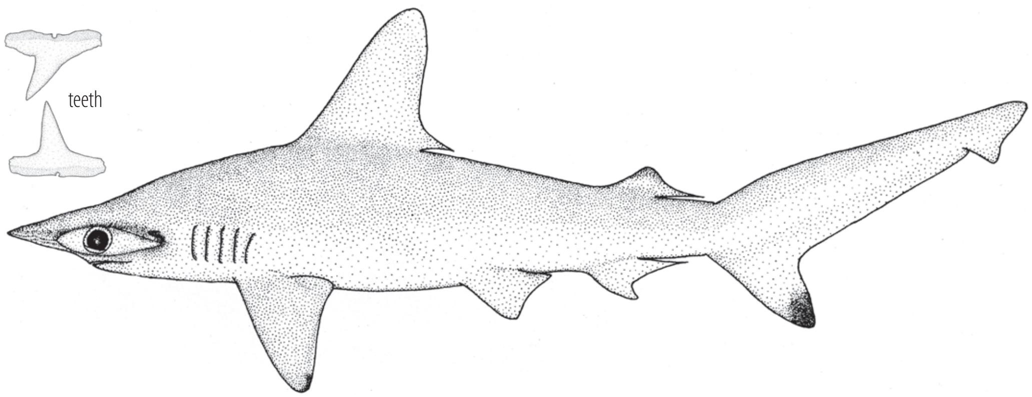
2a No median indentation on front margin of head; 2nd dorsal-fin free rear tip well ahead of upper caudal origin; anal-fin base about as large as 2nd dorsal-fin base .... ***S. zygaena***

2b Prominent median indentation on front margin of head; 2nd dorsal-fin free rear tip nearly reaching upper caudal origin; anal-fin base noticeably larger than 2nd dorsal-fin base .... ***S. lewini***



2a 2b

Drawings sourced from CFSA



Sphyrna lewini, 47 cm TL, immature female (South Africa).
Source: Bass *et al.* 1975

Sphyrna lewini (Griffith & Smith 1834)

Scalloped hammerhead PLATE 50

Zygaena lewini Griffith & Smith 1834: 640, Pl. 50 (south coast of New Holland [southern Australia]).
Sphyrna lewini: Bass *et al.* 1975*; Compagno 1984*; SSF No. 13.1*; Compagno *et al.* 1989*; Smale & Cliff 1998.

Large-sized, with front margin of head curved, and with prominent median and lateral indentations; rear margins of head long, angled posterolaterally, and generally broader than mouth width. Preoral snout length ⅕–⅓ head width; well-developed prenarial grooves in front of nostrils. Rear edge of eyes slightly ahead of upper symphysis of mouth. Anterior teeth with moderately long, smooth or occasionally weakly serrated cusps; posterior teeth mostly cuspidate and not keeled or molariform. First dorsal fin moderately falcate, its origin above or slightly behind pectoral-fin insertions, and free rear tip anterior to pelvic-fin origins. Second dorsal fin low, less than anal-fin height, with shallowly concave rear margin, and inner margin long, about twice fin height, and ending slightly before upper caudal origin. Pelvic fins not falcate, with straight to slightly concave rear margins. Anal fin larger than 2nd dorsal fin, and moderately long, its base 4.3–6.4% TL; anal-fin origin well ahead of 2nd dorsal-fin origin, and rear margin deeply concave. Tooth count 30–36/30–35; vertebrae 174–209.

Body pale grey-brown to bronzy dorsally, white ventrally; pectoral-fin tips dusky to black. Attains 4.2 m TL.

DISTRIBUTION Circumglobal in warm-temperate to tropical seas. WIO: South Africa (KwaZulu-Natal) northwards to Red Sea, Persian/Arabian Gulf and Gulf of Oman, and eastwards to Seychelles, Maldives, India and Sri Lanka.

REMARKS Genetic evidence suggests multiple subpopulations. Litters of 15–31; size at birth 42–55 cm TL. Males mature at 140–165 cm TL, at ~10 years; females mature at ~212 cm TL, at ~15 years; maximum age ~35 years. Coastal-pelagic and semioceanic, over continental and insular shelves and in adjacent deep water, from intertidal zone and surface to at least 275 m deep, but often approaching close inshore and entering enclosed bays and estuaries. Forms large schools at different stages of its lifecycle, though solitary individuals of both young and adults also occur. Feeds on a wide variety of fishes, but also invertebrates (especially cephalopods). Perhaps the most common hammerhead shark in the tropics and once abundantly available to inshore artisanal and small commercial fisheries as well as offshore operations; caught as a bycatch and in target fisheries (including illegally targeted) with a variety of gear; used less often for its meat than for its highly valued fins. Young and sometimes adults are displayed at large aquaria. IUCN Red List conservation status Critically Endangered globally, due to heavy fishing pressure in many regions.

Sphyrna mokarran (Rüppell 1837)

Great hammerhead PLATE 50

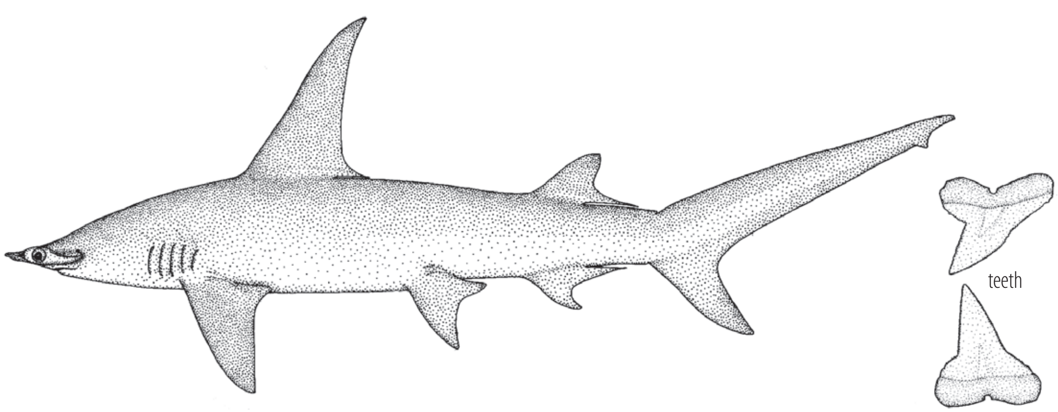
Zygaena mokarran Rüppell 1837: 66, Pl. 17, Fig. 3 (Massawa, Eritrea, Red Sea).
Sphyrna mokarran: Bass *et al.* 1975*; Compagno 1984*; SSF No. 13.2*; Compagno *et al.* 1989*; Cliff 1995; Smale & Cliff 1998.

Large-sized to gigantic, with front margin of head nearly straight in adults (but broadly arched in young), and with prominent median and lateral indentations; rear margins of head long, and transverse in adults but inclined posterolaterally in young, and about as broad as mouth width. Preoral snout length <⅓ head width; prenarial grooves absent or weakly developed. Rear edge of eyes before upper symphysis of mouth. Anterior teeth with moderately long, stout cusps and strongly serrated edges. First dorsal fin strongly falcate, origin over or slightly behind pectoral-fin insertions, free rear tip before pelvic-fin origins. Second dorsal fin moderately high, about equal to anal-fin height, with strongly concave rear margin, and short inner margin (about equal to fin height) ending slightly in front of upper caudal origin. Pelvic fins strongly falcate, with strongly concave rear margins. Anal fin moderately long, about as large as 2nd dorsal fin, its base 5.6–7.3% TL; anal-fin origin ahead of 2nd dorsal-fin origin, and rear margin deeply concave. Tooth count 36–37/34–35; vertebrae 197–212.

Body bronzy to grey-brown dorsally, pale ventrally; no fin markings except 2nd dorsal fin dark-tipped in juveniles. Attains 6.1 m TL, possibly more.

DISTRIBUTION Circumtropical and some warm temperate waters. WIO: South Africa (KwaZulu-Natal) to Red Sea, Persian/Arabian Gulf, Gulf of Oman, Madagascar, Comoros, Seychelles, Mauritius, Maldives, India and Sri Lanka.

REMARKS Litters of 6–42; gestation period at least 7 months, with birth occurring in late spring or summer in the Northern Hemisphere; size at birth 50–70 cm TL. Males mature at 234–269 cm TL, and females at 250–300 cm TL. Most adults of either sex do not exceed ~3.6 m TL, but a small percentage of the population (mainly or entirely females) attain a size much greater than the adult average. Apparently nomadic and seasonally migratory, and generally regarded as solitary. Coastal-pelagic and semi-oceanic, found from close inshore to well offshore, over continental shelf and island terraces, in passes and lagoons of coral atolls, and over deep water near land; often favours continental and insular coral reefs, from near surface to >80 m deep. Feeds on a variety of prey, especially stingrays and other batoids, groupers and sea catfishes. Interest to fisheries more limited than occurs for other large hammerhead sharks; although less abundant than *S. lewini* (which forms large schools) it is regularly caught in the tropics, especially by longline, and is favoured for its large-sized fins. Believed to be potentially more dangerous to people than other hammerhead sharks, though few if any unprovoked attacks have been definitely attributed to it because of the difficulty in distinguishing the species involved in encounters with people. IUCN Red List conservation status Critically Endangered, due to fishing pressure in some regions.



Sphyrna mokarran, 187 cm TL, immature male (South Africa). Source: Bass *et al.* 1975

Sphyrna zygaena (Linnaeus 1758)

Smooth hammerhead PLATE 51

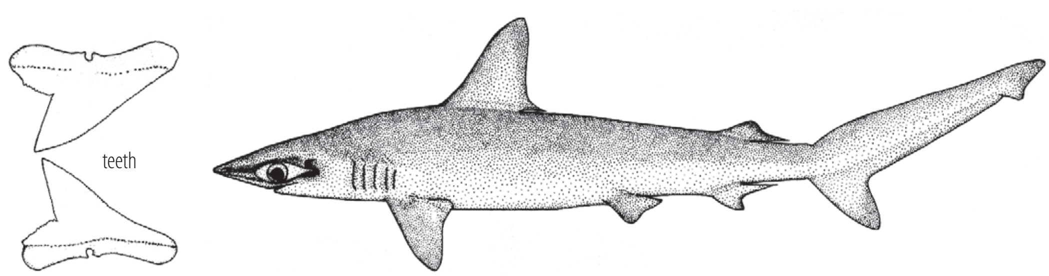
Squalus zygaena Linnaeus 1758: 234 (Mediterranean Sea and North Atlantic).
Sphyrna zygaena: Bass *et al.* 1975*; Compagno 1984*; SSF No. 13.3*; Compagno *et al.* 1989*; Cliff 1995; Smale & Cliff 1998.

Large-sized with front margin of head curved forward, and with prominent lateral indentations but no median indentation; rear margins of head long, angled posterolaterally, and generally broader than mouth width. Preoral snout ⅕–⅓ head width; well-developed prenarial grooves anteromedially to nostrils. Rear edge of eyes slightly behind upper symphysis of mouth. Teeth relatively small; anterior teeth with moderately long, very stout cusps, and smooth or weakly serrated edges. First dorsal fin moderately falcate, origin over pectoral-fin insertions, and free rear tip well anterior to pelvic-fin origins. Second dorsal fin low, less than anal-fin height, with shallowly concave rear margin and long inner margin (about twice fin height) ending in front of upper caudal origin. Pelvic fins not falcate; rear margins straight or slightly concave. Anal fin long, slightly larger than 2nd dorsal fin, base 4.3–5.7% TL; anal-fin origin slightly ahead of 2nd dorsal-fin origin, and rear margin deeply concave. Tooth count 30–32/29–30; vertebrae 193–206.

Body dark grey-brown or olive dorsally, white ventrally; pectoral-fin tips dusky. Attains 4 m TL.

DISTRIBUTION Circumglobal in mostly warm-temperate and occasionally tropical seas. WIO: South Africa (Western Cape to KwaZulu-Natal) to southern Mozambique, Persian/Arabian Gulf, southern India to Sri Lanka and Maldives.

REMARKS Widespread, but little known of its biology. Litters of 20–50, born in spring or early summer; size at birth 50–61 cm TL; gestation period 10–11 months. Matures at 210–240 cm TL; females attain greater size than males. Coastal-pelagic and semi-oceanic, with a wider range than other members of its family; found close inshore and in shallow water, over continental and insular shelves, to well offshore, from surface to at least 200 m deep, and probably much deeper. Enormous schools of young sharks may occur in some areas (such as off Eastern Cape of South Africa). Feeds on a variety of mostly bony fishes, but also on small sharks, skates and stingrays, as well as invertebrates (mostly squid). Common to abundant, taken in a variety of artisanal and commercial fisheries and in numerous shark fisheries with a wide variety of gears; targeted mostly for its highly valued fins. IUCN Red List conservation status Vulnerable.



Sphyrna zygaena, 71 cm TL, immature female (South Africa). Source: Bass *et al.* 1975

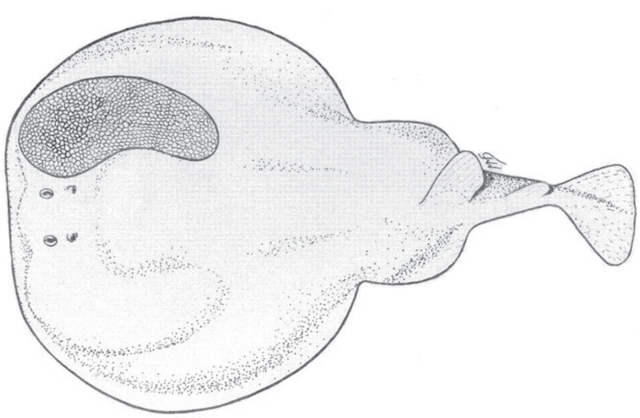
ORDER TORPEDINIFORMES

FAMILY TORPEDINIDAE

Torpedo rays

Marcelo R de Carvalho

Small- to moderately large-sized (to ~180 cm TL, but mostly <100 cm TL) with greatly expanded pectoral fins fused with head and trunk to form depressed and nearly circular disc; pectoral-fin margins thick and fleshy; well-developed electric organs; and tail stout and shark-like, shorter than disc length. Anterior margin of head straight, truncated or only slightly arched; snout reduced. Eyes small and bulging or somewhat depressed; spiracles smooth or with papillae on rear and lateral margins, and with pseudobranchial folds on inside anterior wall. Five pairs of small gill slits on front half of underside of head. Nostrils subcircular and relatively large; oronasal grooves present; internasal flap with smooth posterior edge, and sometimes with small medial indentation or lobe. Mouth moderately sized, highly arched, without lip folds but sometimes with grooves at corners. Teeth monocuspidate, relatively sharp, small and numerous (adults with 25–70 tooth rows in upper and lower jaws), set in quincunx along each jaw. Skin smooth, devoid of dermal denticles, thorns, spines and tubercles. Pair of electric organs lateral to head at mid-disc, kidney-shaped and visible through skin on underside, with irregular honeycomb appearance due to stacked electric plates.



Position of electric organ. Source: SSF

Pelvic fins fleshy, broad and rounded, comprised of a single lobe. Tail slightly depressed in cross-section, with lateral skin folds, and no caudal-region electric organs. Two prominent dorsal fins, fin apices rounded to angular; 1st dorsal fin larger than 2nd, and 1st dorsal-fin base partially or totally above pelvic-fin bases. Caudal fin subtriangular, larger than each dorsal fin, with more or less equal-sized upper and lower lobes and continuous around end of vertebral column, but lobes sometimes separated by small indentation. Body typically uniformly brown, dark grey, reddish brown or blackish background dorsally, often with various pale and dark markings (ocelli, spots, mottling, vermiculation); usually paler or white ventrally, but disc margins and pelvic fins often darker.

Reproductive mode yolk-sac viviparity. Worldwide in temperate and tropical seas, on continental shelf in shallow coastal regions or open waters of pelagic zone, often to ~100 m deep; some species may also inhabit estuaries and/or deeper waters of continental slope, but none enter freshwater. Slow-swimming, on or well off the bottom, and often found resting on mud or sandy substrates. Some larger pelagic species may undertake long migrations. The powerful electric organs can discharge up to 45 volts, depending on size of the individual ray, and are used to stun prey and for defence against predation. Feed on bony fishes and benthic invertebrates and can ingest large prey items, close to their own disc length, as their jaws and mouths have a wide gape and are highly protrusile. Prey items are grasped by their discs which aid in pushing them into their gaping mouths, and then swallowed whole. Caught principally as a bycatch in trawls, but also by hook and line, and by longlines; not regularly consumed as food. Harmless to people unless interfered with, and able to stun through strong shocks if handled alive after capture. The IUCN Red List conservation status of *Torpedo adenensis* is Endangered, but all other WIO species are Data Deficient.

Two genera and 18 species recognised, but many are in need of revision, and several undescribed species have been recently discovered (including one in the Red Sea). Furthermore, distributions among members of this species-complex may be more restricted than so far noted, with the possibility that high endemicity will be discovered in the course of revisions or new species descriptions. Large series of preserved specimens are scarce, however, and thus consistent, useful variation in specimens is difficult to find. Both genera and 6 species in WIO.

KEY TO GENERA

1a Spiracle margins smooth, without any knobs or papillae .... ***Tetronarce***

1b Spiracle margins with a few to many knobs or papillae .... ***Torpedo***

GENUS *Tetronarce* Gill 1862

Large-sized rays (to ~180 cm TL) that appear very soft, flabby and oily when captured. Distinguished from *Torpedo* by spiracles with smooth margins, devoid of papillae or similar structures. Disc round or transversely oval, and large; snout truncate or emarginate. Mouth markedly arcuate; no lip folds or circumoral grooves; teeth small, sharp, monocuspidate. Tail short and strong, with 2 prominent dorsal fins; caudal fin broad, more or less symmetrical, fan-shaped, and larger than dorsal fins. Circumglobal, in warm-temperate to temperate waters, including off distant and isolated oceanic islands and over seamounts. Primarily pelagic hunters, swimming in water column, usually at night, where they over-swim prey items that they can quickly immobilise with an electric discharge.

This genus is in need of revision, having been treated as a subgenus of *Torpedo* or else its species included in *Torpedo* without distinct supraspecific recognition. *Tetronarce* is considered a full genus here based on its consistent morphological distinctiveness. Past authors have relied on relative distances between the dorsal fins and between the 2nd dorsal fin and caudal fin as taxonomically reliable characters, but caution is necessary as these ratios are variable and not necessarily helpful. Currently, 8–10 species recognised, but many remain poorly characterised, and intermediate and unidentified specimens abound in collections; 1 species in WIO.

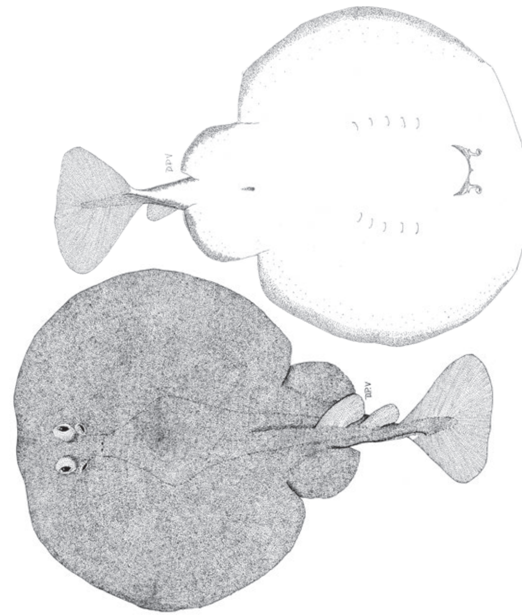
Tetronarce cowleyi Ebert, Haas & Carvalho 2015

Cowley's torpedo ray PLATE 52

Torpedo hebetans: Thompson 1914; Von Bonde & Swart 1923.
Narcobatus nobilianus: Barnard 1925, 1947*; Norman 1935.
Torpedo nobiliana: Fowler 1936*, 1941; Smith 1949*, 1965*; Lloris 1986*; Turon *et al.* 1986; Compagno *et al.* 1989*; Compagno *et al.* 1991; SSF No. 23.2* [1995].
Tetronarce cowleyi Ebert, Haas & Carvalho 2015: 237, Figs. 2–6 (South Africa, SE Atlantic); Carvalho *et al.* 2016.

Disc broad, subcircular, wider than long and thick anteriorly; snout short with rounded median protuberance. Eyes and spiracles small and close together; spiracle margins smooth, without papillae. Mouth greatly arched; teeth small and sharp, in up to 32 rows. Dorsal fins rounded to broadly oval; 1st dorsal fin taller than 2nd. Tail short, thick; caudal fin huge, paddle-shaped, with straight or rounded posterior margin. Electric organs clearly visible in ventral view. Claspers with distal integumental flap.

Disc mostly uniformly purplish black, dark brown or dark grey dorsally, but disc margins and pelvic fins sometimes darker; whitish ventrally. Attains at least 68 cm TL.



Tetronarce cowleyi, 42 cm TL (South Africa). Source: SSF

DISTRIBUTION Southern Africa: Namibia (Walvis Bay) in southeastern Atlantic, to South Africa (Algoa Bay, Eastern Cape) in WIO.

REMARKS Previously recognised in the region as *Torpedo nobiliana* (the occurrence of which needs verification in WIO). Known from 110–457 m. Feeds on (relatively large) bony fishes and possibly small sharks. Capable of delivering a powerful shock even after capture. Occasionally caught as bycatch, but typically discarded.

GENUS *Torpedo* Houttuyn 1764

Small- to medium-sized rays (to ~150 cm TL) distinguished from *Tetronarce* by spiracles with margins that are rugose or with papillae of varying dimensions and arrangement (but papillae often less conspicuous in larger specimens). Disc round or transversely oval, and large; snout usually more or less straight across, sometimes with small median bulge or even truncate. Mouth markedly arcuate; no lip folds or circumoral grooves; teeth small, sharp, monocuspidate. Tail short and strong, with 2 prominent dorsal fins; caudal fin broad, more or less symmetrical, fan-shaped, and larger than dorsal fins. Mostly benthic, sluggish rays, covering themselves with sand or mud to ambush prey (mostly fishes) which are stunned and immobilised by discharges from their electric organs. Occur predominantly in insular waters of continental shelf (in contrast to *Tetronarce*, which can occur on deeper slopes); most diverse in tropical waters of eastern Atlantic Ocean.

As with *Tetronarce*, *Torpedo* has been referred to at the subgeneric level; however, it is considered here as a full genus and separate from *Tetronarce*. At least 15 species, plus several recently discovered undescribed species; at least 5 species in WIO.

KEY TO SPECIES

1a Disc uniformly reddish brown or orange-brown dorsally, without distinctive spots, blotches, reticulations or other patterns ..... ***T. adenensis***
1b Disc not uniformly reddish brown or orange-brown dorsally, but with specific patterns formed by spots, blotches or reticulations **2**

2a Dorsal background grey to brown, and with closely packed brownish black spots, but no whitish or cream-coloured patterns; dorsal fins brownish black ..... ***T. fuscomaculata***
2b Dorsal background reddish, greyish or brown, and with paler patterns of irregular spots, rosettes or vermiculations **3**

3a Dorsal surface of disc with few but large (greater than eye diameter) brown spots ..... ***T. suessii***
3b Dorsal surface of disc with pale patterns of irregular spots, rosettes or vermiculations, but no large brown spots **4**

4a Dorsal surface includes small whitish spots that do not form broad vermiculate pattern ..... ***T. panthera***
4b Dorsal surface of disc, pelvic fins, and tail with strong creamy to whitish and dense vermiculate pattern, and anterior and lateral disc regions with many irregular whitish spots (no larger than eye diameter) ..... ***T. sinuspersici***

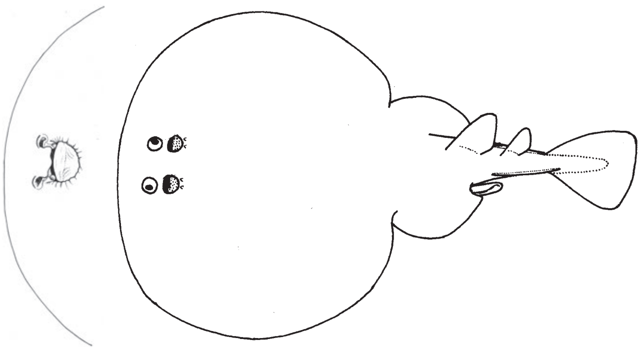
Torpedo adenensis Carvalho, Stehmann & Manilo 2002

Aden torpedo

Torpedo adenensis Carvalho, Stehmann & Manilo 2002: 5, Figs. 1–7 (close to shore of Yemen, Gulf of Aden); Manilo & Bogorodsky 2003; Carvalho *et al.* 2016.

Disc broad, slightly wider than long; anterior disc margin relatively straight, with small median protuberance. Eyes and spiracles close together; spiracle margins with a few (3–8) inconspicuous knob-like papillae. Teeth small, in up to 47/39 rows. Dorsal-fin apices rounded; 1st dorsal fin larger than 2nd, its base extending just posterior to level of pelvic-fin axil (not entirely positioned over pelvic-fin bases); distance between 2nd dorsal fin and caudal fin greater than distance between dorsal fins. Males with fleshy skin flap in clasper glans region.

Disc uniformly reddish brown or orange-brown dorsally, without any distinctive spots, blotches or reticulations; whitish ventrally. Attains at least 41 cm TL.



Torpedo adenensis, 41 cm TL, male holotype (Yemen). Drawn from photograph

DISTRIBUTION WIO: Gulf of Aden.

REMARKS Known only from a few specimens collected from three distinct but adjacent localities in eastern Gulf of Aden, close to Yemen; recorded from 26–140 m. Presumably a bycatch of shrimp trawl fisheries. IUCN Red List conservation status Endangered, due to its restricted known range.

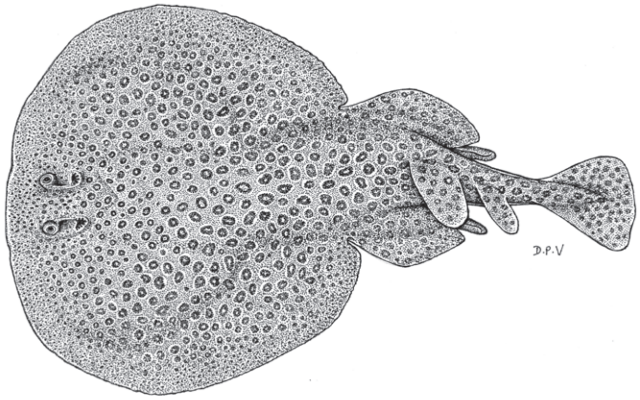
Torpedo fuscomaculata Peters 1855

Blackspotted torpedo PLATE 53

Torpedo fuscomaculata Peters 1855: 466 (Ibo, Mozambique); Playfair & Günther 1866; Fraser-Brunner 1949; Smith 1961*; Smith & Smith 1963; Wallace 1967*; Compagno *et al.* 1989*; Debelius 1993*; SSF No. 23.1* [1995]; Sommer *et al.* 1996; Carvalho *et al.* 2002*; Manilo & Bogorodsky 2003; Carvalho *et al.* 2016.
Torpedo smithii Günther 1870: 451 [probably South Africa].
Torpedo sp.: Fourmanoir 1963.

Disc slightly wider than long, widest near midlength; anterior margin truncated, sometimes with median bulge. Teeth small, in up to 50 rows. Dorsal fins rounded at apices; 1st dorsal fin larger than 2nd. Tail short, stout; lateral skin fold on tail usually ridge-like, extending from about midbase of 2nd dorsal fin to lower peduncle. Caudal fin broad, with slightly sloping upper lobe. Males without skin flap in clasper glans region.

Disc grey, yellowish to reddish brown background dorsally, with close-set brownish black spots; dorsal fins brownish black with white edges. (Colour variation in this species needs more study, as the number, size and arrangement of darker spots on the dorsal surface vary, such as no spots in specimens from South Africa, but smaller and more regularly arranged spots in specimens from Mauritius.) Attains 65 cm TL.



Torpedo fuscomaculata, 27 cm TL (South Africa). Source: Whitfield 1998

DISTRIBUTION WIO: South Africa (Eastern Cape) to southern Mozambique, Tanzania (Zanzibar), Madagascar, Seychelles and Mauritius.

REMARKS Specimens ~25 cm TL almost sexually mature. Recorded from intertidal zone to ~440 m deep, and also from estuaries in South Africa. Feeds on fishes and cuttlefish.

Torpedo panthera Olfers 1831

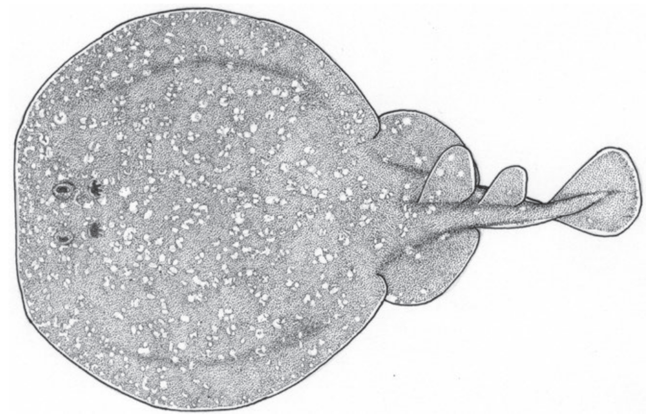
Leopard torpedo

PLATE 53

Torpedo panthera Olfers 1831: 15–16 (Red Sea); Blegvad & Løppenthin 1944; Qureshi 1972*; Dor 1984; Compagno *et al.* 1989*; Baranes & Golani 1993; Debelius 1993*; Randall 1995*; Sommer *et al.* 1996*; Carpenter *et al.* 1997*; Hennemann 2001*; Carvalho *et al.* 2002*; Manilo & Bogorodsky 2003; Carvalho *et al.* 2016.

Disc broadly circular, slightly wider than long, and widest just before mid-disc; anterior margin usually straight. Eyes and spiracles similarly sized, but separated by wide gap; spiracles with ~7 short papillae. First dorsal fin larger than 2nd and rounder at apex; interdorsal distance roughly equal to distance between 2nd dorsal fin and caudal fin. Tail short and moderately stout. Caudal-fin upper lobe larger and more sloping than lower lobe. Males with median skin flap in clasper glans region.

Disc brown, reddish brown or tan background dorsally; clusters of more or less isolated and sometimes blurry whitish spots over disc, pelvic fins, tail and even dorsal fins, with spots varying in density, size and arrangement. Attains ~60 cm TL.



Torpedo panthera, 35 cm TL (Red Sea).

DISTRIBUTION Indian Ocean. WIO: Red Sea, Gulf of Oman and shallow areas of Arabian Sea, to Bay of Bengal; reports from Persian/Arabian Gulf and south of Somalia probably erroneous.

REMARKS Biology virtually unknown other than males mature by ~28 cm TL, and feeds on invertebrates and fishes. Occurs on continental shelf, over muddy and sandy bottoms, usually to ~110 m deep.

Torpedo sinuspersici Olfers 1831

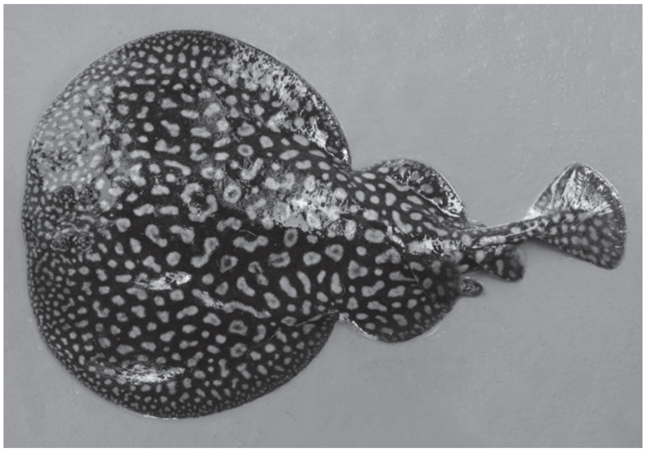
Marbled torpedo

PLATE 53

Torpedo sinuspersici Olfers 1831: 15, 17 [presumably Persian/Arabian Gulf]; Fowler 1941, 1956; Wallace 1967*; Bianchi 1985; SSF No. 23.3*; Compagno *et al.* 1989*; Van der Elst 1993*; Debelius 1993*, 1999*; Randall 1995*; Sommer *et al.* 1996*; Carpenter *et al.* 1997*; Hennemann 2001*; Carvalho *et al.* 2002*; Manilo & Bogorodsky 2003; Heemstra & Heemstra 2004*; Carvalho *et al.* 2016.
Torpedo polleni: Bleeker 1865.

Disc broad, slightly wider than long, fleshy at margins. Eyes and spiracles subequal, separated by clear gap. Spiracles rounded, their margins usually with 9 or 10 short papillae. First dorsal fin with rounded apex, larger than 2nd; distance between 2nd dorsal fin and caudal fin usually greater than interdorsal distance. Caudal-fin upper lobe larger and more sloping than lower lobe; fin margin straight or slightly rounded. Distinguished by dorsal surface with strong vermiculate colour pattern.

Disc russet to blackish background dorsally, and brightly patterned with strong creamy to whitish and rather thick vermiculations or rosettes over entire disc, pelvic fins and tail, and decreasing in size towards disc margins, plus many cream-coloured and irregular spots (no larger than eye diameter) on anterior and lateral regions of disc; whitish ventrally. Attains 130 cm TL (commonly ~80 cm TL).



Torpedo sinuspersici, 26 cm DW (Mozambique). O Alvheim © IMR

DISTRIBUTION Indian Ocean. WIO: South Africa (Eastern Cape), Mozambique to Red Sea, Persian/Arabian Gulf, Gulf of Oman to India and Sri Lanka.

REMARKS Litters of 9–22; matures at ~40 cm TL. Found over sandy bottom and near reefs, to ~300 m deep. Feeds on invertebrates and fishes. Seemingly widespread in WIO (often seen by divers), but probably a species-complex. Has been misidentified as *T. fuscomaculata* from Madagascar and Seychelles, and as *T. marmorata* from Lakshadweep; Smith & Smith's (1963) *T. fuscomaculata* from Seychelles may have also included *T. sinuspersici* (see Carvalho *et al.* 2002). Jones & Kumaran (1980) illustrated a specimen from Lakshadweep labelled *T. marmorata* but which resembles *T. sinuspersici*; other misidentifications of this species as *T. marmorata* occur in the literature.

Torpedo suessii Steindachner 1898

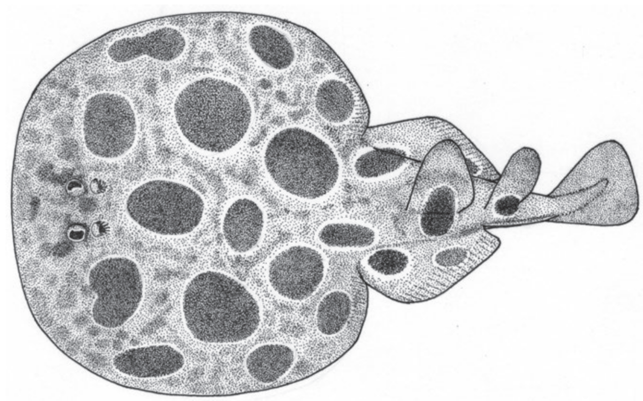
Red Sea torpedo

PLATE 54

Torpedo suessii Steindachner 1898: 784, Pl. 2 (Yemen, Red Sea); Carvalho *et al.* 2002* [as *suessi*]; Carvalho *et al.* 2016.
?*Torpedo* sp. 1: Michael 1993*.

Small-sized with ornate colour pattern. Disc broadly circular, slightly wider than long, and widest near mid-disc; snout short, anterior margin usually straight. Spiracle margins with short papillae. First dorsal fin larger and more broadly rounded at apex than 2nd. Caudal-fin upper lobe larger and more slanted than lower lobe. Claspers slender, elongate, and without skin flap in clasper glans region (versus skin flap present in *T. adenensis* and *T. panthera*).

Dorsal background bright brown, with large dark brown spots with pale outlines (ocelli), slender reticulations over disc and disc edges, and smaller dark spots on front of disc, pelvic fins and dorsal-fin bases. Attains at least 35–40 cm TL.



Torpedo suessii, ~30 cm TL (Yemen). Composite

DISTRIBUTION WIO: southern Red Sea.

REMARKS Biology virtually unknown; inhabits shallow water and probably feeds on fishes and benthic invertebrates. Almost all authors have placed this species as a junior synonym of *T. sinuspersici*, but Carvalho *et al.* (2002) presents evidence for its recognition. Its colouration easily separates it from congeners in the Red Sea and adjacent gulfs.

FAMILY NARCINIDAE

Numbfishes

Marcelo R de Carvalho

Small-sized rays (to ~86 cm TL, commonly <50 cm TL) with oval, rounded, heart-shaped or distinctively shovel-shaped disc; stout shark-like tail equal to or greater than disc length or width. Electric organs large, bean-shaped, paired at pectoral-fin bases, and visible through skin on underside. Trunk and head depressed; head relatively broad. Snout moderately elongated, broadly rounded to angular. Eyes small or minute (vestigial in *Benthobatis*), and larger or smaller than spiracles; spiracles circular to oval, margins with or without papillae, and with or without elevated rims. Five pairs of small gill slits on underside near front half of pectoral-fin bases. Nostrils circular, small; oronasal grooves broad; internasal flap overlaps mouth slightly. Mouth relatively small and transverse, surrounded by prominent groove and with strong lip folds. Teeth small, rounded-oval, with short cusps, and in 12–45 rows in each jaw. Skin smooth, without dermal denticles or thorns. Pectoral-fin insertions opposite pelvic-fin origins. Pelvic fins low, subangular or rounded, not divided into anterior and posterior lobes. Tail broad but abruptly narrower than trunk, moderately depressed and long, and usually with lateral skin folds. Two dorsal fins, moderately large and clearly separated, usually subequal (1st dorsal fin slightly larger than 2nd in some species of *Narcine*), and angular or rounded-angular; 1st dorsal-fin origin just behind mid-total length and pelvic-fin insertions. Caudal fin usually large and broadly rounded, but upper lobe slightly more angular. Dorsal surface varies from whitish, yellowish, brownish, grey-brown, greenish, reddish or black (blackish in deepwater species), either without spots or with dark spots, blotches, bars or lines, or with white spots and lines sometimes forming complex ocelli on disc and pectoral fins.

Reproductive mode yolk-sac viviparity, as far as known. Feed mostly on benthic invertebrates; their jaws and mouths are highly protrusile, forming a tubular mechanism that enables them to extract prey organisms from the substrate, especially polychaetes. Slow-swimming bottom-dwellers of upper continental slope, over sandy, muddy or occasionally rocky substrates, including off sandy beaches, in muddy enclosed bays and on coral reefs, from intertidal zone to deeper than 1 000 m; apparently unable to penetrate freshwater to any extent. Caught as minor bycatch of small local inshore fisheries and offshore trawl fisheries. Numbfishes can deliver a moderate shock when disturbed or captured, but are otherwise harmless to people. The IUCN Red List conservation status of most species is Data Deficient or Least Concern; one species from the Caribbean Sea is listed as Critically Endangered.

Almost circumglobal in tropical to warm-temperate seas, but conspicuously absent from Mediterranean Sea, eastern Atlantic, eastern South Pacific and Pacific Plate region, and so far unrecorded from the Red Sea and Persian/Arabian Gulf in WIO, despite good collections from those waters. Four genera and ~36 species recognised, but many species are in need of revision and several species are undescribed; 2 genera and 7 species in WIO (the one genus and species, *Benthobatis moresbyi* [Plate 54], known only from 524–1 071 m in the Arabian Sea and off SW India).

KEY TO GENERA

1a	Eyes extremely reduced, concealed by integument, and barely visible as faint spots anterior to spiracles; dorsal surface dark purplish brown; caudal-fin length (as measured from cloaca) >⅓ tail length; lateral skin folds on tail occur as low, inconspicuous ridges; dorsal fins fleshy, about equal in height and base length	***Benthobatis*** **[one deepwater species]**
1b	Eyes developed, functional and evident; ventral surface white to yellowish; caudal-fin length <⅓ tail length; lateral skin folds on tail wide and not ridge-like; dorsal fins translucent distally, their height greater than base length	***Narcine***

GENUS ***Narcine*** Henle 1834

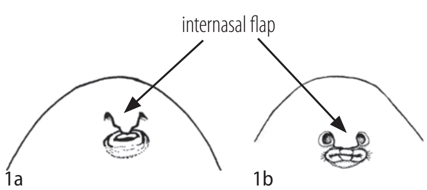
Disc oval, somewhat rounded to shovel-shaped; greatest width at ~⅔ disc length. Snout rounded to broadly angular; preorbital snout ~¼ disc length. Eyes larger than spiracles (and bulging in fresh specimens); spiracles circular to ovoid, usually with thick elevated rims; some species (not in WIO) with warty papillae on entire spiracular margin. Nostrils small and circular; internasal flap wider than long, reaching upper tooth band. Mouth protrusile. Electric organs bean-shaped, extending on underside from opposite eyes to rear fifth of disc. Tail stout at base, its length greater than disc width or length; lateral skin folds usually prominent. Dorsal fins similarly shaped, usually subequal (either fin may be slightly taller than other). Caudal fin usually tall, fan-shaped, with broadly rounded ventral margin and slightly angular upper lobe.

Distinguished from other narcinid genera by internasal flaps with relatively straight posterior edge (except trilobed in *Discopyge*); nostrils not subdivided into two distinct compartments by bridge of stiff integument; both upper and lower tooth bands exposed when mouth closed; eyes functional and evident anterior to spiracles, usually about same size as spiracles; pelvic fins posteriorly separated and not joined to form continuous pelvic curtain; claspers laterally joined to pelvic fins, and not dorsally covered and concealed by pelvic fins; and lateral skin folds on tail generally well-developed, extending from level of 1st dorsal fin to peduncle (much reduced, ridge-like folds in *Benthobatis*).

Common inshore component of Indian Ocean fauna (less so in southwestern Indian Ocean, but very common in eastern Arabian Sea). Relatively common off Pakistan, but apparently these species have not dispersed into the Persian/Arabian Gulf and are also absent from the Red Sea. Probably fairly stationary with limited individual ranges. A revision of this genus is needed, especially of species occurring in the northern Indian Ocean. Previous accounts of batoids in the Arabian Sea have usually misidentified numbfish species. With the exception of *N. lingula* and *N. timlei*, all WIO species are known from only a few specimens. Furthermore, many doubts linger concerning the number of valid species of *Narcine* from this region. For example, *N. maculata* is known from the Bay of Bengal and eastwards; it may also be present in the Arabian Sea but has not yet been found west of Sri Lanka, and thus is not included here. About 20 species; at least 6 species (possibly 2 others undescribed) in WIO.

KEY TO SPECIES

1a Internasal flap longer than wide .... ***N. rierai***
1b Internasal flap wider than long 2



2a Uniformly pale or purplish brown dorsally, and without spots, reticulations or other markings .... ***N. timlei***
2b Dorsal colouration composed of reticulations, spots or other mottled patterns, not uniformly pale or purplish brown 3

3a Preorbital snout length about equal to preoral snout length; 2nd dorsal fin about equal to or taller than 1st dorsal fin .... ***N. lingula***
3b Preoral snout length greater than preorbital snout length; 1st dorsal fin taller than 2nd dorsal fin 4

4a Dorsal colouration composed of numerous small dark spots scattered over disc, tail, fins and within spiracles .... ***N. atzi***
4b Dorsal colouration devoid of small dark spots 5

5a Mean disc width and length <45% TL; branchial basket length (distance between 1st and 5th gill slits) clearly greater than transverse distance between last pair of gill slits .... ***N. oculifera***
5b Mean disc width and length ~48% TL; branchial basket length about equal to transverse distance between last pair of gill slits .... ***N. insolita***

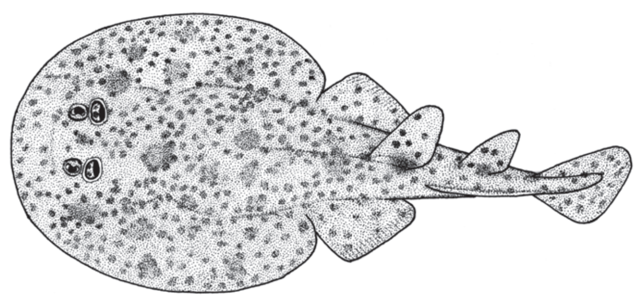
Narcine atzi Carvalho & Randall 2003

Atz's numbfish

Narcine atzi Carvalho & Randall 2003: 60, Figs. 1–2 (off Khalil, Oman, Gulf of Oman); Carvalho & Last 2016.

Disc subcircular to broadly oval, widest just posterior to its midlength; preorbital snout length shorter than preoral snout length. Spiracles wider than long, with elevated, smooth rims without papillae. Upper and lower tooth bands broadly circular and subequal in width (upper tooth band wider than lower band), visible with closed mouth; teeth in up to 20 rows. Dorsal fins large, with rounded apices, and 1st dorsal-fin height and base greater than that of 2nd dorsal fin; caudal fin tall, rounded at apex and posterior margin; lateral skin folds wide.

Disc tan dorsally, with numerous small dark brown spots (equal to or smaller than eye diameter) over disc and tail and within spiracular walls, coupled with fewer faint, large blotches on disc; creamy white ventrally, with grey margins on disc and pelvic fins, and blotches on tail. Attains at least 36 cm TL.



Narcine atzi, ~30 cm TL, female (Oman). Composite

DISTRIBUTION Northern Indian Ocean: Gulf of Oman in WIO, to Bay of Bengal and Andaman Sea.

REMARKS Poorly known from only a few specimens, collected in shallow water (~30 m). Size at birth ~11 cm TL; females mature by ~31 cm TL. Incidental bycatch in trawls.

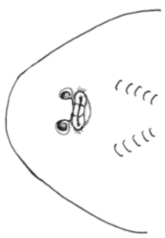
Narcine insolita Carvalho, Séret & Compagno 2002

Madagascar numbfish

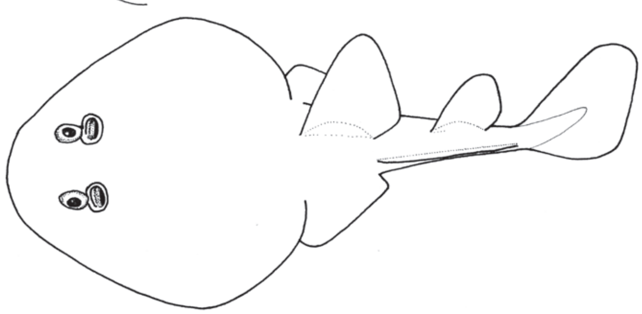
Narcine insolita Carvalho, Séret & Compagno 2002: 140, Figs. 1–5 (NW Madagascar); Carvalho & Randall 2003*; Carvalho & Last 2016.

Disc oval or heart-shaped, its greatest width just posterior to its midlength; disc fleshy, with thick margins. Eyes large and bulging; spiracles large, conspicuously rounded, with elevated rims all around; interspiracular distance much smaller than interorbital distance. Teeth in up to 24 rows; upper and lower tooth bands equal in width and broadly circular in outline. Internarial flap short and wide. First dorsal fin very large, conspicuously taller and with longer base than 2nd dorsal fin; caudal fin with well-developed upper and lower lobes, and rounded-oval apex; lateral skin folds wide.

Disc yellowish brown dorsally, with irregular darker brown to reddish brown blotches on disc margins, posterior disc and front margin of snout; darker brown blotches on front part of dorsal fins and caudal-fin apex, and laterally on tail beneath dorsal fins; creamy white ventrally. Attains at least 27 cm TL.



Narcine insolita, 27 cm TL (Madagascar).



DISTRIBUTION WIO: Madagascar (west coast).

REMARKS Known only from seven specimens collected from two localities off northwestern and southwestern Madagascar, at 150–175 m. Another specimen from southern Mozambique, collected at ~69 m, is very close in morphology to *N. insolita* but with dorsal fins of subequal proportions, and may represent an undescribed species. Occurs predominantly over muddy substrates. An unutilised bycatch of shrimp trawl fisheries.

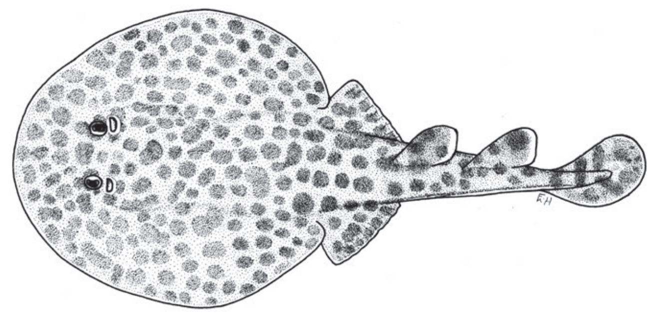
Narcine lingula Richardson 1846

Chinese numbfish PLATES 54 & 55

Narcine lingula Richardson 1846: 196 (China Seas, off Canton; Indian Ocean, off Chennai, India); Carvalho & Randall 2003*; Carvalho & Last 2016.
Narcine timlei: Qureshi 1972*; Carvalho *et al.* 1999*.

Disc oval-rounded, widest near its midlength. Preorbital length about equal to preoral length, and much greater than prenarial length. Eyes and spiracles moderately sized, subequal; spiracles with slender, elevated rims. Internarial flap short and wide. Tooth bands rounded, broad, subequal in width; up to 22 rows of teeth. Dorsal fins subequal, rounded-oval at apex; caudal fin rounded, slightly larger than dorsal fins; lateral skin folds slender.

Disc brown dorsally, with dark brown spots (usually larger than eye diameter); whitish ventrally. Attains probably 33 cm TL.



Narcine lingula (W India).

DISTRIBUTION Indo-Pacific. WIO: Arabian Sea (Pakistan and India); occurrence in Persian/Arabian Gulf needs confirmation; elsewhere to east coast of India, Indonesia (Java) and East China Sea.

REMARKS Very similar to *N. maculata* from western Pacific Ocean, thus the separation of these species is provisional. Matures at ~25 cm TL. Found inshore and offshore, in shallow tropical continental waters, but depth range unknown. A bycatch of demersal trawl fisheries.

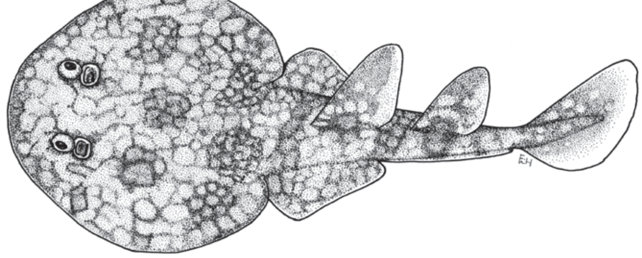
Narcine oculifera Carvalho, Compagno & Mee 2002

Big-eye numbfish PLATE 55

Narcine oculifera Carvalho, Compagno & Mee 2002: 137, Figs. 1–4 (Muscat, Oman, Gulf of Oman); Carvalho & Randall 2003*; Manilo & Bogorodsky 2003; Carvalho & Last 2016.
Narcine indica: Norman 1939; Baranes & Randall 1989.
Narcine sp.: Debelius 1993*; Randall 1995*.

Disc oval to heart-shaped, widest posterior to its midlength, with thick margins. Eyes large, bulging; spiracles large and circular with elevated rims; interorbital distance greater than interspiracular distance. Internarial flap short and wide. Teeth with small lateral cusplets; upper and lower tooth bands roughly equal in width, broadly rounded in profile. Dorsal fins tall, with rounded to oval apices, and 1st dorsal-fin height slightly greater than 2nd; caudal fin tall, with oval apex; lateral skin folds wide.

Striking dorsal colouration with reticulated pale brown to reddish brown patterning over disc, pelvic fins and tail, demarcating white or creamy oval, reniform and circular spots of variable sizes over disc, and with small white spots on dorsal fins and caudal fin; white to yellowish white ventrally. Attains at least 35 cm TL.



Narcine oculifera, 24 cm TL (Oman).

DISTRIBUTION WIO: Gulf of Oman (off Oman) and Gulf of Aden (off Somalia).

REMARKS Distinctive and not easily confused with other numbfishes. Males mature by ~24 cm TL, and females by ~32 cm TL. Known from few specimens collected mostly from shallow water (<25 m), but recorded to deeper than 100 m. Observed resting on rocky surfaces. A rare bycatch of trawls.

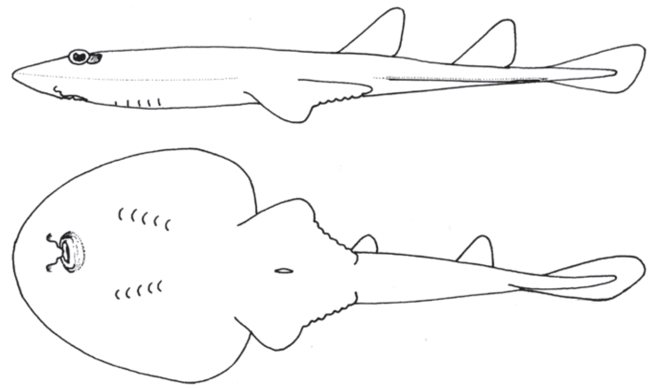
Narcine rierai (Lloris & Rucabado 1991)

Mozambique numbfish PLATE 55

Heteronarce rierai Lloris & Rucabado 1991: 327, Figs. 1–3 (Mozambique); SSF No. 24a.1* [1995].
Narcine rierai: SSF No. 24a.1* [1995]; Carvalho & Randall 2003*; Compagno & Heemstra 2007; Carvalho & Last 2016.

Disc markedly shovel-shaped; tail elongated, much longer than disc length. Eyes larger than spiracles; spiracles elliptical, without elevated rims or papillae. Internasal flap longer than wide, and with pores; nostrils slit-like. Mouth small. Tooth bands slender and subtriangular in outline; up to 16 rows of teeth. Dorsal fins wide-set, subequal; caudal fin low and elongate; lateral skin folds low ridges.

Disc uniformly medium or pale brown to golden-brown or reddish brown dorsally; uniformly whitish ventrally. Attains at least 30 cm TL.



Narcine rierai, 11 cm DW, 31 cm TL (Mozambique).

DISTRIBUTION WIO: Somalia to Mozambique and possibly South Africa.

REMARKS Size at birth >7 cm TL; matures at 23–27 cm TL. Occurs over lower continental shelf, with most specimens collected from 169–255 m, but one specimen from Tanzania collected from 300–500 m.

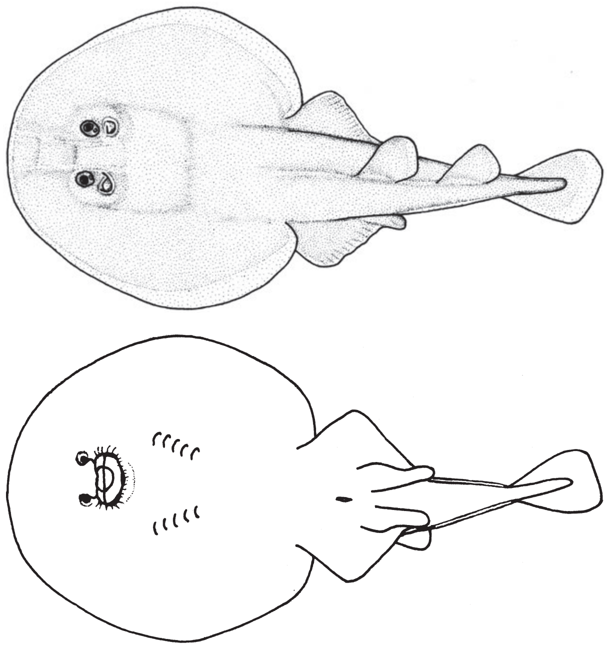
Narcine timlei (Bloch & Schneider 1801)

Brown numbfish PLATE 55

Raja timlei Bloch & Schneider 1801: 359 (Tharangambadi, India, Bay of Bengal).
Narcine indica Henle 1834: 315, Pl. 2 (Tharangambadi coast, India).
Narcine microphthalma Duméril (ex Valenciennes) 1852: 275 (Malabar coast, India).
Narcine macrura Valenciennes *in* Duméril 1852: 277 ('Sea of the Indies').
Narcine brunnea Annandale 1909: 45, Pl. 3a (Bay of Bengal); Garman 1913; Qureshi 1972*; Carvalho *et al.* 1999*; Manilo & Bogorodsky 2003.
Narcine timlei: Carvalho & Randall 2003*; Carvalho & Last 2016.

Disc oval to subtrapezoidal (usually oval in preserved specimens); snout broadly rounded. Eyes very small, smaller than spiracles; spiracles rounded, with smooth low rims. Internarial flap much wider than long. Tooth bands wide, rounded; teeth in up to 25 rows. Pelvic fins wide; dorsal fins small, rounded, subequal; caudal-fin margin usually rounded; lateral skin folds low.

Disc uniformly purplish brown, pale or dark brown or tan dorsally, and devoid of any specific markings; creamy white ventrally. Attains at least 38 cm TL.



Narcine timlei, male (India).

DISTRIBUTION Indo-Pacific. WIO: Pakistan, India and Sri Lanka; elsewhere to Bay of Bengal, Indonesia and South China Sea.

REMARKS Males mature >24 cm TL; free-swimming by ~5.5 cm TL. Inshore and offshore in tropical continental waters. Probably frequently captured by trawls.

FAMILY **NARKIDAE**

Sleeper rays

Marcelo R de Carvalho

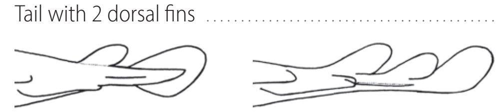
Small-sized (~8–52 cm TL; most attain <35 cm TL) with disc proportionally large, circular to oval, and with thick margins in some species. Head depressed, broad, not raised above disc; snout broadly rounded, short to moderately elongate. Pectoral-fin origins lateral to snout, ending just behind pelvic-fin origins. Pair of large bean-shaped electric organs visible through skin on underside at pectoral-fin bases. Eyes generally small (vestigial or externally absent in *Typhlonarke*), relatively close together and contiguous to spiracles; spiracles subcircular, margins with papillae (*Electrolux*) or without papillae (*Heteronarce*, *Narke*), usually with low rims. Five pairs of very small gill slits on ventral front half of disc; no gill rakers on internal gill slits. Nostrils slender, elongated or circular, slightly oblique, just in front of mouth and connected to it through broad oronasal grooves; internasal flap overlapping mouth, usually studded with pores, and posterior edge with or without small knob (trilobed). Mouth narrow and transverse, nearly straight across, with strong lip folds and weak peripheral grooves or pleats. Teeth small, similar in shape, oval, and with low transverse ridge or single cusps on crowns, not laterally expanded and plate-like; maximum ~25 tooth rows in each jaw. Skin smooth, completely devoid of denticles, spines, thorns or tubercles. Pelvic fins elongate, low, broadly rounded or subangular, and not subdivided into distinct lobes (except anterior lobes separate and leg-like in *Typhlonarke*). Tail abruptly narrower than trunk, stout and shark-like, slightly depressed, and with or without lateral skin folds. Tail either with 1 dorsal fin (*Narke*, *Typhlonarke*), 2 usually subequal-sized dorsal fins (*Electrolux*, *Heteronarce*), or no dorsal fin (*Temera*); dorsal fin(s) rounded to angular, with confluent apex and margin; 1st dorsal-fin origin behind pelvic-fin insertions or above rear part of pelvic fins. Caudal fin broadly rounded to oval, nearly symmetrical, and larger than dorsal fins, but not shark-like; lower lobe small. Dorsal colour usually brownish, greyish or reddish brown, either plain or with few markings and usually without complex patterns (except ornate in *Electrolux*); white, greyish or brownish ventrally, sometimes with darker outer disc margins or pelvic fins. Many narkids have their proportions distorted by post-mortem bloating and desiccation, usually compounded after fixation; typically, the disc, pelvic fins and eyes shrink significantly, and many other proportions such as dorsal-fin shape are also affected.

Reproductive mode yolk-sac viviparity. Shallow inshore to deepwater offshore rays of outer continental shelf and upper slope, usually found over soft bottom, to ~330 m deep; not known from freshwater. Slow-swimming bottom-dwellers which feed on small benthic invertebrates (especially polychaetes); their small mouths restrict their diet, and whether sleeper rays prey on fishes is unknown. Caught as a minor bycatch of shallow trawl fisheries and some inshore artisanal net fisheries, but typically not used. All species can deliver a moderately strong shock when disturbed or captured. IUCN Red List conservation status of most species is Data Deficient, but several are considered Vulnerable.

Occur in temperate to tropical waters of Indo-Pacific (surprisingly absent from around Australia). Six genera and ~12 species; 3 genera and 6 species in WIO.

KEY TO GENERA

1a Tail with 1 dorsal fin .... ***Narke***
1b Tail with 2 dorsal fins 2



1a 1b

Continued …

KEY TO GENERA

2a Spiracle margins with elongate, slender finger-like papillae; total tooth count 32/34; dorsal colouration ornate, with many small yellowish and/or white spots .... ***Electrolux***

2b Spiracle margins smooth, without papillae; total tooth count 20/24; dorsal colouration mostly uniformly greyish, with some large darker blotches .... ***Heteronarce***

GENUS *Electrolux* Compagno & Heemstra 2007

Disc subcircular (about as long as wide), disc length roughly half TL, and anterior margin broadly rounded; head small; snout very short and nearly straight. Eyes well-developed, close to front edge of disc, but mostly hidden by loose skin; eyes and spiracles contiguous; spiracle length slightly longer than eye diameter; spiracle margins with relatively large stiff papillae. Mouth and nostrils project ventrally from disc in lateral view; lower lip folds and grooves short, ending far lateral to mouth. Pelvic fins not divided into anterior and posterior lobes; claspers in adult males short and flat, not extending beyond pelvic-fin rear tips. Tail stout, with broad lateral skin folds. Two dorsal fins; 1st dorsal-fin origin over pelvic-fin rear tips, and only slightly larger than 2nd dorsal fin. One species.

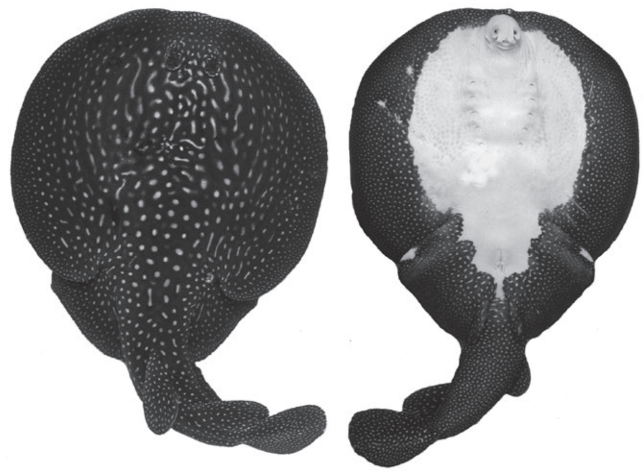
Electrolux addisoni Compagno & Heemstra 2007

Ornate sleeper ray PLATE 55

Electrolux addisoni Compagno & Heemstra 2007: 22, Figs.1–9, 11–19 (off Margate, KwaZulu-Natal, South Africa); Carvalho 2016.

Diagnosis as for genus; distinguished from other narkid species by its spiracles, oronasal region, and colouration. Spiracle margins with low ridge-like rims, 5 or 6 long, slender, stiff papillae, and 2 or 3 short soft papillae, including 1 minute papilla on eye; incurrent apertures of nostrils circular with broad trumpet-like flaps; internasal flap deeply incised, with prominent lateral lobes and very small medial lobe (trilobed). Tooth count 15 or 16/17 or 18.

Unique elaborate colour pattern of dark brown or greenish brown background, and small yellowish spots over dorsal surface of disc and fins (spots largest on middle region of disc; spots white in preserved specimens), and with several curved, somewhat concentric black stripes on disc (less evident in preserved specimens); ventral surface abruptly white in centre of disc and at pelvic-fin bases, forming pear-shaped white blotch. Attains at least 52 cm TL.



Electrolux addisoni, 51 cm TL, male (South Africa).
Source: Compagno & Heemstra 2007

DISTRIBUTION WIO: endemic to South Africa (Coffee Bay, Eastern Cape to Virginia Beach, KwaZulu-Natal).

REMARKS Apparently rare but long known and photographed by divers before it was described; the original description is based on specimens collected from a short strip of South African coastline, from <50 m deep. Inhabits sandy and gravelly patches of shallow-water reefs. Relatively large-sized; only adult male specimens collected to date; males mature by 50 cm TL. Diurnal forager; apparently feeds on small crustaceans and polychaetes. The striking colour pattern may represent an aposematic adaptation as these rays seem to enact threat displays. This species is protected in South Africa.

GENUS *Heteronarce* Regan 1921

Disc subcircular (slightly longer than wide), anterior margin oval to broadly rounded, head somewhat small, and snout relatively short (longest in *H. garmani*). Eyes and spiracles contiguous; spiracles circular, and margins with low ridge-like rim without papillae. Incurrent apertures of nostrils slit-like, elongated; internasal flap usually without pores (pores in *H. bentuviai*), and with median groove but posterior edges nearly straight. Lower lip folds and grooves relatively short. Tooth count 10–16/10–16. Claspers in adult males extend slightly beyond pelvic-fin rear tips (less so in *H. bentuviai*). Two dorsal fins, usually subequal (1st dorsal fin much larger than 2nd in *H. bentuviai*); 1st dorsal-fin origin over pelvic-fin rear tips; 2nd dorsal-fin apex usually more rounded than that of 1st. Lateral skin folds on tail only moderately broad. Colour usually greyish, reddish or brownish dorsally, sometimes with darker undefined markings or more defined spots, and usually creamy ventrally.

Poorly known genus, but easily distinguished from other narkid genera by the combination of two dorsal fins and plain dorsal colouration. Specimens of *Heteronarce* are rare in collections, which precludes a better understanding of species limits. A review by Talwar (1981) recognised *H. mollis*, *H. garmani* and *H. prabhui* (*H. bentuviai* was described later), but was based on few specimens from a small area (off Kerala, India). Even the separation of *H. garmani* and *H. mollis* (including *H. prabhui*) is in need of revision. Four species recognised in the literature, but the validity of *H. prabhui* is not accepted here; 3 species in WIO.

KEY TO SPECIES

1a Dorsal colouration with dark spots anterodorsal to pectoral-fin insertions and on 1st dorsal fin and caudal-fin upper lobe; 1st dorsal fin triangular .... ***H. bentuviai***

1b Dorsal colouration generally uniformly grey, brownish red or pale brown, without conspicuous dark spots on pectoral-fin insertions, 1st dorsal fin or caudal-fin upper lobe; 1st dorsal fin broadly rounded **2**

2a Eyes and spiracles similar in size, with spiracles relatively small (interspiracular distance about 3 times spiracle length or width); body mostly creamy white ventrally .... ***H. garmani***

2b Spiracle diameter greater than eye diameter, relatively large (interspiracular distance only about twice spiracle length or width); body greyish ventrally .... ***H. mollis***

Heteronarce bentuviai (Baranes & Randall 1989)

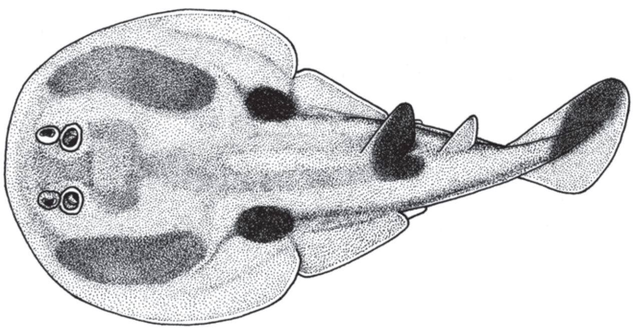
Eilat electric ray

PLATE 56

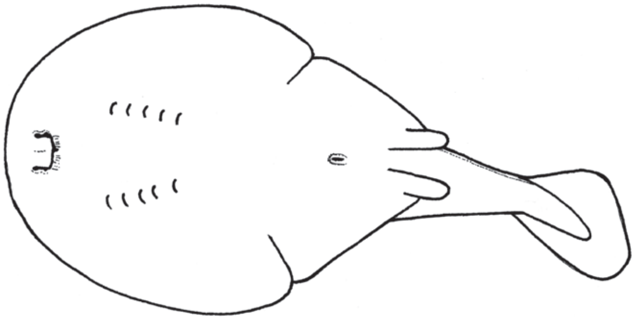
Narcine bentuviai Baranes & Randall 1989: 87, Pl. 1, Figs. 1–9 (Gulf of Aqaba, Red Sea); Carvalho 2016.
Heteronarce bentuviai: Hennemann 2001*; Compagno & Heemstra 2007.

Disc broadly rounded anteriorly, disc length ~½ TL; spiracles larger than eyes. Internasal flap with numerous pores, and more or less straight posterior margin. Teeth in up to 11 rows, not visible externally. Pelvic fins posteriorly rounded, broad; 1st dorsal-fin origin over pelvic-fin midlength, much larger than 2nd dorsal fin and apex more angular; caudal fin larger than dorsal fins; tail short and broad. Males with relatively short claspers (compared to *H. garmani*).

Conspicuous, bold colour pattern, including clearly delimited dark brown to blackish spots or blotches just anterodorsal to pectoral-fin insertions and covering 1st dorsal fin and caudal-fin upper lobe, and with poorly defined darker streaks dorsally over region of electric organs. Attains at least 19 cm TL.



Heteronarce bentuviai, 15 cm TL (Red Sea).



Heteronarce bentuviai, 18 cm TL, male paratype (Red Sea).

DISTRIBUTION WIO: northern Red Sea, including Gulf of Aqaba.

REMARKS Males mature by ~15 cm TL. Small-sized, conspicuous-looking narkid known only from Red Sea, at 80–200 m (specimens from off Socotra in Gulf of Aden were morphologically similar to *H. bentuviai* but differed in details of dorsal colouration and dorsal-fin proportions). Found on sandy and muddy bottoms; probably feeds on soft bottom-dwelling invertebrates, such as polychaetes and crustaceans, as do other narkids. A discarded bycatch of trawl and gillnet fisheries.

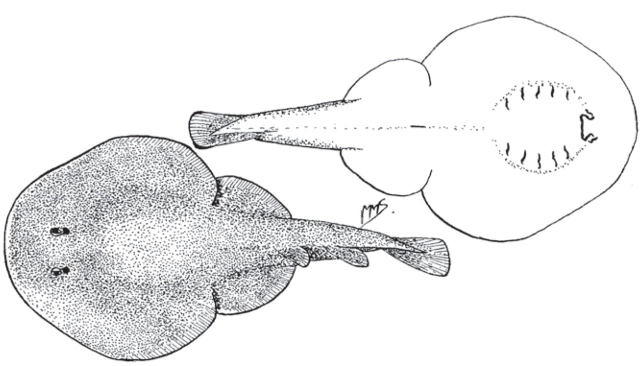
Heteronarce garmani Regan 1921

Natal electric ray PLATE 56

Heteronarce garmani Regan 1921: 414 (off Umvoti River, KwaZulu-Natal, South Africa); Gilchrist 1922; Barnard 1925, 1927; Fowler 1941; SFSA No. 90*; Wallace 1967*; Hulley 1972*; ?Talwar 1981; SSF No. 24.1*; Compagno *et al*. 1989*; Lloris & Rucabado 1991; Compagno & Heemstra 2007*; Ebert 2014*; Carvalho 2016.
Heteronarce regani Von Bonde & Swart 1923: 14, Pl. 22, Fig. 2 (KwaZulu-Natal, South Africa).
Narcine natalensis Fowler 1925: 198, Fig. 2 (KwaZulu-Natal, South Africa).

Disc subcircular, shovel-shaped, slightly longer than wide; anterior margin broadly oval or subcircular; preorbital snout length slightly greater than interspiracular distance; snout slightly longer than in congeners. Eyes and spiracles contiguous, relatively small, and subequal in diameter; spiracles with slender elevated rims. Posterior margin of internasal flap broadly rounded to straight, slightly fringed. Teeth in up to 12 rows, barely visible externally. Pelvic fins and tail slender; 2nd dorsal fin slightly larger and more rounded than 1st; 1st dorsal-fin origin over pelvic-fin free rear tips; caudal fin larger than dorsal fins.

Disc pale to dark brown dorsally, sometimes with small indistinct darker markings; creamy white ventrally, but disc margin sometimes brown posteriorly. Attains at least 27 cm TL.



Heteronarce garmani, 20 cm TL (South Africa). Source: SFSA

DISTRIBUTION WIO: South Africa and Mozambique.

REMARKS Males mature by ~17 cm TL. Occurs on outer shelf and upper slope, at 154–329 m. Specimens are rare; records from the Arabian Sea and off Kerala, India (Talwar 1981), probably refer to *H. mollis*; specimens identified as *H. garmani* from Madagascar are *Narcine insolita* (Narcinidae). Wallace (1967) considered *H. garmani* distinct from *H. mollis* by its longer snout and smaller eyes and spiracles, and proportions of the mouth, nostrils and internasal flap appear to be greater in *H. mollis*, yet its separation from *H. mollis* requires further clarification. IUCN Red List conservation status Near Threatened.

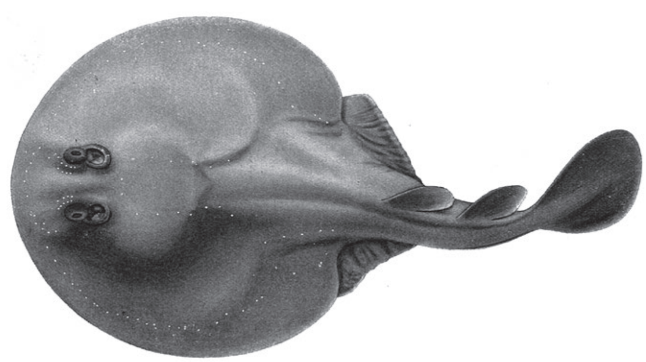
Heteronarce mollis (Lloyd 1907)

Soft electric ray

Narcine mollis Lloyd 1907: 8 (Gulf of Aden); Annandale 1909*; Lloyd 1909*; Garman 1913.
?*Heteronarce prabhui* Talwar 1981: 149, Fig. 1 (off Kollam, India).
Heteronarce mollis: Norman 1939; Fowler 1941; Talwar 1981; Lloris & Rucabado 1991; Compagno & Heemstra 2007*; Ebert 2014*; Carvalho 2016.

Disc subcircular, broad, slightly wider than long; snout broadly rounded, relatively short, preorbital snout length less than twice interspiracular distance (in preserved specimens). Spiracle diameter clearly greater than eye diameter. Internasal flap about equal in length and width, with a small notch at mid-width, and sometimes with pores. Teeth small, in up to 16 rows, not visible externally. Pelvic fins broad; dorsal fins broadly rounded, subequal or else 2nd dorsal fin slightly larger than 1st; 1st dorsal-fin origin over pelvic-fin free rear tips; lateral skin folds moderately broad; caudal fin larger than dorsal fins, with broadly rounded posterior margin.

Body dark brown to greyish dorsally, sometimes with small irregular paler and darker markings; pale brown, tan or greyish ventrally. Attains at least 25 cm TL.



Heteronarce mollis (Yemen). Source: Annandale 1909

DISTRIBUTION WIO: Somalia, Socotra, Gulf of Aden and India.

REMARKS Known from very few specimens collected mostly in Gulf of Aden from 73–346 m. Males mature at 17–20 cm TL. Recognition of *H. prabhui* (Quilon electric ray) as a synonym of *H. mollis* needs further scrutiny as the former has been accepted as valid but without supporting evidence (cf. Compagno 1999, 2005; Compagno & Heemstra 2007), and Talwar's (1981) original description of *H. prabhui* (collected from ~300 m) is remarkably similar to Lloyd's (1909) original illustration of *H. mollis* and to material examined from Somalia (moreover, the characters used to separate the species are features that typically vary with preservation: slight differences in disc width and length, and the relative proportions of spiracles and eyes). Lloyd (1909) provided the first illustration of this species (in entire dorsal aspect and ventral anterior disc), and Annandale (1909) illustrated the mouth and teeth, but no new data have been published since Norman's (1939) brief record (also from Gulf of Aden). Thus, a conservative approach is adopted here, and *H. prabhui* is therefore regarded as a junior synonym of *H. mollis*. And, with the synonymy of *H. prabhui* with *H. mollis*, its range can be extended to the eastern Arabian Sea.

GENUS ***Narke*** Kaup 1826

Disc circular to subcircular (slightly longer than wide); anterior margin broadly rounded to slightly convex; head region small, and eyes close to front edge of disc. Eyes and spiracles closely adjacent; spiracles circular, slightly greater than eye diameter, and margins with low ridge-like rims (least prominent in *N. dipterygia*) and without papillae. Incurrent apertures of nostrils slit-like, elongated; internasal flap usually without pores, and with median groove, and posterior edge nearly straight. Lower lip folds and grooves relatively short. One dorsal fin, its origin over pelvic-fin rear tips. Tail with moderately broad lateral skin folds. Claspers in adult males extend beyond pelvic-fin rear tips. Body usually greyish, reddish or brownish dorsally, without markings (*N. capensis*) or with darker spots and irregular blotches on disc margins (*N. japonica*), or with paired white spots on disc posteriorly and white bars on tail laterally (*N. dipterygia*); usually creamy white or grey ventrally.

Easily separated from other narkid genera in the region by its single dorsal fin and pelvic fins not bilobed. Biology poorly known, even as the best-known genus in the family. Specimens of *Narke* are rare in collections, impeding revisionary studies. Almost nothing known concerning variation in species. *Narke dipterygia*, however, shows significant variation over its extensive range and may require subdivision. Three species, 2 in WIO.

KEY TO SPECIES

1a Dorsal colour uniformly yellowish brown to brown, without conspicuous spots or other markings; yellowish or creamy ventrally, but outer margins brownish; spiracle margins elevated as low ridge-like rims; pelvic fins broad and slightly rounded .... ***N. capensis***

1b Dorsal colour uniformly brownish to reddish brown, with pair of large white spots on disc posteriorly, and white bars on tail laterally and extending to above pelvic-fin bases; uniformly white to creamy ventrally; spiracle margins faintly or not distinctly elevated as rims above disc; pelvic fins angular .... ***N. dipterygia***

Narke capensis (Gmelin 1789)

Cape sleeper ray

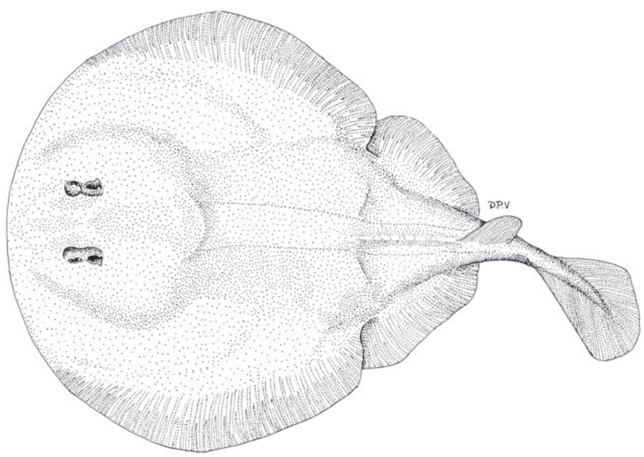
PLATE 56

Raja capensis Gmelin 1789: 1512 (Cape of Good Hope, South Africa).
Astrape capensis: Müller & Henle 1841; Günther 1870.
Narke capensis: Garman 1913; Von Bonde & Swart 1923; Barnard 1925; SFSA No. 89*; Smith 1964*; Wallace 1967*; SSF No. 24.2*; Compagno *et al.* 1989*; Compagno & Heemstra 2007; Carvalho 2016.

Disc circular, ~3/5 TL; anterior margin usually broadly rounded; snout region short. Spiracles circular, slightly larger than eyes, margins with prominent rims and ~3 small papillae. Internasal flap short, with few pores. Teeth small, usually in 10–12/11–13 rows. Pelvic fins broad and long; dorsal-fin origin slightly posterior to pelvic-fin insertions; dorsal fin and caudal fin relatively low and broadly rounded; caudal fin larger than dorsal fin;

Disc brown dorsally, and pelvic fins with darker margins; yellowish or creamy ventrally, with brownish outer margins; some specimens with yellowish, brownish or whitish spots towards end of tail. Attains 38 cm TL.

Narke capensis, 23 cm TL, adult female (South Africa).
Source: Compagno & Heemstra 2007



Narke capensis, 25 cm TL, adult female (South Africa). Source: SSF

DISTRIBUTION Southern Africa: Namibia in southeastern Atlantic, to South Africa (Cape Point to KwaZulu-Natal) and possibly Mozambique and Madagascar in WIO.

REMARKS Males mature at 17.5–23 cm TL, and females at ~16 cm TL. Occurs on continental shelf, to ~180 m deep (usually in <100 m), most commonly on muddy bottom and in bays along south Cape coast of South Africa. Feeds primarily on polychaetes. A bycatch of inshore trawls.

Narke dipterygia (Bloch & Schneider 1801)

Spottail sleeper ray

PLATE 56

Raja dipterygia Bloch & Schneider 1801: 359 (Tharangambadi, India).
Bengalichthys impennis Annandale 1909: 48, Fig. 6, Pl. 3a (Balasore Bay, Odisha coast, India); Annandale 1910; Rao 1974*.
Astrape dipterygia: Müller & Henle 1841; Günther 1870; Annandale 1909*.
Narke dipterygia: Garman 1913; Fowler 1941; Munro 1955*; Bianchi 1985*; Compagno & Last 1999*; Kapoor *et al.* 2002; Compagno & Heemstra 2007; Carvalho 2016.

Disc circular (usually longer than wide in preserved specimens); anterior margin usually broadly rounded; snout short. Spiracles larger than eyes, with low rims. Internasal flap short and wide, with pores. Teeth small, in ~16–18 rows, not visible externally. Dorsal-fin origin over pelvic-fin insertions; dorsal fin and caudal fin broadly rounded, caudal fin larger than dorsal fin.

Body brownish, reddish brown or dark brown dorsally, with pair of whitish spots on disc posteriorly, and creamy blotches on disc above pelvic-fin bases and laterally on base of tail; creamy to whitish ventrally. Attains 35 cm TL.

DISTRIBUTION Indo-Pacific. WIO: Oman to India and Sri Lanka; elsewhere to Malaysia and Japan.

REMARKS Biology mostly unknown; litters of 4–6, and males mature at 15–18 cm TL. Occurs inshore and offshore on continental shelf, in tropical to temperate waters, over sandy and muddy bottoms; reportedly locally common and widespread at just 5–36 m deep. A bycatch in bottom-trawl and gillnet fisheries, but probably not used.

ORDER RHINOPRISTIFORMES

FAMILY PRISTIDAE

Sawfishes

Marcelo R de Carvalho and Bernard Séret

Distinctive, extremely large-sized rays (up to 5 m TL; possibly >7 m TL) with blade-like hypertrophied rostrum (rostral saw) that extends forward from head and reaches ⅕–⅓ TL; body shark-like, stout, and moderately depressed; gill openings, mouth and nostrils entirely ventral; 5 small paired gill slits on underside of head (at front half of pectoral-fin bases). No paired ventral barbels on snout. Rostrum with perpendicular lateral rostral teeth (modified dermal denticles) that grow continuously but are not replaced when broken or lost (unlike the much smaller deepwater sawsharks of family Pristiophoridae), and without smaller rostral teeth between large ones; posteriormost rostral teeth well ahead of nostrils. Eyes dorsolateral on head and well anterior to spiracles. Mouth transverse and straight, without knobs or depressions. Nostrils anteriorly set, well-separated from each other and completely separate from mouth, without oronasal grooves; anterior nasal flaps short, not connected to each other, and not reaching mouth. Teeth small, rounded-oval, in numerous (up to 60) rows in each jaw and set in pavement-like bands, and without cusps. Pectoral fins relatively small, somewhat disjunct from head and not forming complete or continuous disc, inner rear tips free; pectoral-fin origins well posterior to mouth, attached to rear part of head over gill slits, and fins ending well ahead of pelvic-fin origins. Pelvic fins angular, not subdivided into anterior and posterior lobes. Two large, equal-sized and widely separated dorsal fins, tall, with similar angular or rounded-angular shape and with distinct apices and anterior, posterior and inner margins, and well-developed free rear tips varying from triangular to strongly falcate; 1st dorsal fin over or partially in front of pelvic fins. No anal fin. Peduncle moderately depressed and with keels. Tail not abruptly narrower than trunk. Caudal fin large, angular, shark-like and strongly asymmetrical, with vertebral axis raised above body axis; caudal-fin lower lobe well-developed or poorly developed. Body yellowish, brownish, grey-brown or greenish dorsally and on flanks, and pale or white ventrally, and without prominent markings although fins may be slightly dusky.

Reproductive mode yolk-sac (lecithotrophic) viviparity, with litters of 1–23 (usually 6–9), but the reproductive cycle of most species is poorly known; some species reach maturity only after ~20 years. Relatively sluggish; benthic, found predominantly over muddy and sandy bottoms. Widely distributed in tropical and subtropical inshore coastal waters, to only ~10 m deep, and frequently present in estuaries, river mouths and inland freshwater (some populations may breed in freshwater). Feed on benthic organisms and small schooling bony fishes, using the saw-like rostrum to dislodge benthic prey items or to slash at schooling fishes. Mostly caught as a bycatch of small local inshore and freshwater fisheries and by recreational anglers. Sawfishes can inflict injuries to their captors when struggling individuals are removed from nets or line gear; occasional, but largely provoked, attacks on people have occurred in shallow water. One of the most at-risk groups of sharks or rays due to the degradation of the limited inshore marine, brackish and inland freshwater habitats they occur in, and extreme vulnerability to gillnets and bottom trawls, with numerous local extinctions having already occurred. IUCN Red List conservation status of all species is Endangered or Critically Endangered globally, and all species are listed on Appendix I of CITES, banning their trade.

Sawfishes are sometimes confused with sawsharks of family Pristiophoridae, but can be easily distinguished from them by a much larger size, ventrally situated gill slits, and lacking long barbels on underside of rostrum. Two genera and 5 species currently recognised as valid (of 23 available nominal species names, as these are usually applied solely on a geographical basis); both genera and 3 species in WIO.

KEY TO GENERA

1a Rostral teeth not reaching base of rostrum, dorsoventrally compressed, and with single posterior edges; nostrils long, narrow, oblique; anterior nasal flaps small and narrow; pectoral fins narrow-based, high and short; 1st dorsal-fin origin posterior to level of pelvic-fin insertions .... ***Anoxypristis***

1b Rostral teeth reach base of rostrum, triangular in cross-section, and posteriorly double-edged; nostrils short, broad, transverse; anterior nasal flaps large and broad; pectoral fins broad-based, low and long; 1st dorsal-fin origin anterior to level of pelvic-fin insertions .... ***Pristis***

GENUS *Anoxypristis* White & Moy-Thomas 1941

Rostral teeth in 16–29 pairs, and not present on basal portion of rostrum, irregularly spaced, greatly flattened, blade-like, narrowly triangular, and with single posterior edges. Rostrum relatively slender, narrowing slightly near base. Lateral edges of head and incurrent apertures of nostrils connected by broad incurrent grooves on underside of snout. Nostrils narrow, long, oblique. Pectoral-fin bases narrow, and fins shark-like. First dorsal fin posteriorly situated, its origin slightly behind pelvic-fin insertions. Peduncle with secondary keel below main keel. Caudal fin with shallow subterminal notch, lower lobe prominent, and posterior margin deeply concave. One species currently recognised.

Anoxypristis cuspidata (Latham 1794)

Narrow sawfish PLATE 51

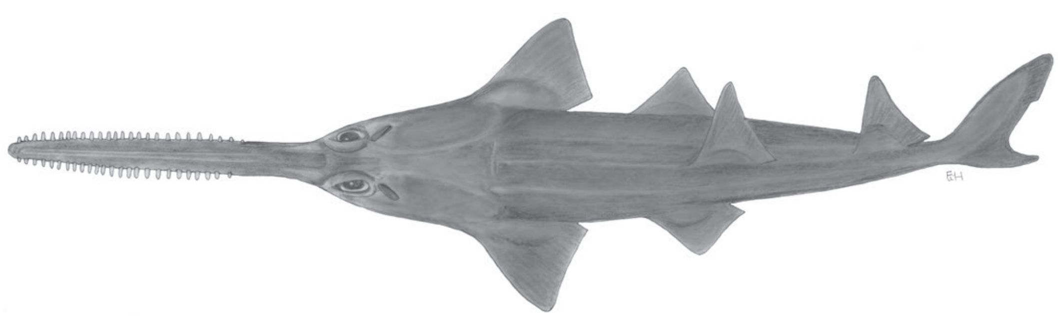
Pristis cuspidatus Latham 1794: 279, Pl. 26, Fig. 3 (Malabar, India); Klunzinger 1871; Annandale 1909*; Blegvad & Løppenthin 1944*; Munro 1955*; Qureshi 1972*.
?*Squalus semisagittatus* Shaw 1804: 361 (Visakhapatnam, India) [based on Russell 1803: Pl. 13].
Anoxypristis cuspidata: Debelius 1993*; Randall 1995*; Compagno & Last 1999*; Last & Stevens 2009*; Faria *et al.* 2013; Last *et al.* 2016.

Diagnosis as for genus. Regional and individual variation noted in pairs of rostral teeth (males usually with lower tooth counts than females); rostrum length >12 times its width at level of posteriormost lateral teeth.

Adults greyish, greyish blue or slightly greenish dorsally, and young darker grey; paler ventrally; fins dusky or pale. Attains 4.7 m TL, possibly 6.1 m TL.

DISTRIBUTION Indo-Pacific. Historic range uncertain; current populations are rare and fragmented. WIO: Red Sea, Gulf of Aden, Persian/Arabian Gulf to India and Sri Lanka.

REMARKS Viviparous with large yolk sac retained until about birth; uterine eggs enclosed in soft egg cases, and uterine wall frilly, glandular, and reported to produce histotroph (uterine secretions). Litters of 6–23 (average 12–15); size at birth (free-swimming neonates) 50–60 cm TL; gestation period 4–5 months. Males mature at ~4 years, and females at ~5 years, at 2.5–4.7 m TL. Apparently the most productive sawfish species. Now rare, but formerly common inshore, in shallow water down to at least 40 m (possibly ~100 m), also in brackish water in some river deltas, estuaries and shallow bays; appears to penetrate some rivers (in India, Myanmar and Thailand), but freshwater occurrences need verification. Relatively active (as compared with more benthic *Pristis* species) as evidenced by its more streamlined shark-like form, smaller pectoral fins, stouter tail with secondary keel on peduncle, and semi-lunate caudal fin. Feeds on fishes, cuttlefish (Sepiidae) and prawns. Highly vulnerable to bottom-trawl and gillnet fisheries. IUCN Red List conservation status Endangered (previously Critically Endangered).



Anoxypristis cuspidata, ~80 cm TL (W India). Composite

GENUS *Pristis* Linck 1790

Rostral teeth in 14–34 pairs (usually 20–28), and extend to base of rostrum, triangular in cross-section and with double posterior edges. Rostrum robust, widest at its base, ~5–7 times longer (*Pristis pristis*) or 7–10 times longer (*Pristis pectinata* group) than its greatest width. Nostrils short, broad, transverse, and with large anterior nasal flaps. Underside of snout without broad incurrent grooves connecting lateral edges of head and incurrent apertures of nostrils. Pectoral fins somewhat low, relatively long, with broad base. First dorsal fin anteriorly situated, its origin anterior to, over or posterior to pelvic-fin origins. Peduncle without secondary keel. Caudal fin without subterminal notch.

Two groups of species in the genus: *Pristis pristis*, with proportionally larger and heavier rostrum, usually fewer rostral teeth, and distinct caudal-fin lower lobe (formerly including other species such as *P. microdon*, now a single widespread species recognised); and *Pristis pectinata* group, with proportionally smaller and less heavy rostrum, usually more rostral teeth, and caudal-fin lower lobe not well-defined. *Pristis pristis* with definitive freshwater records. Four valid species, at least 2 in WIO.

KEY TO SPECIES

1a First dorsal-fin origin in front of pelvic-fin origins .... ***P. pristis***
1b First dorsal-fin origin above or behind pelvic-fin origins .... ***P. zijsron***

Pristis pristis (Linnaeus 1758)

Largetooth sawfish

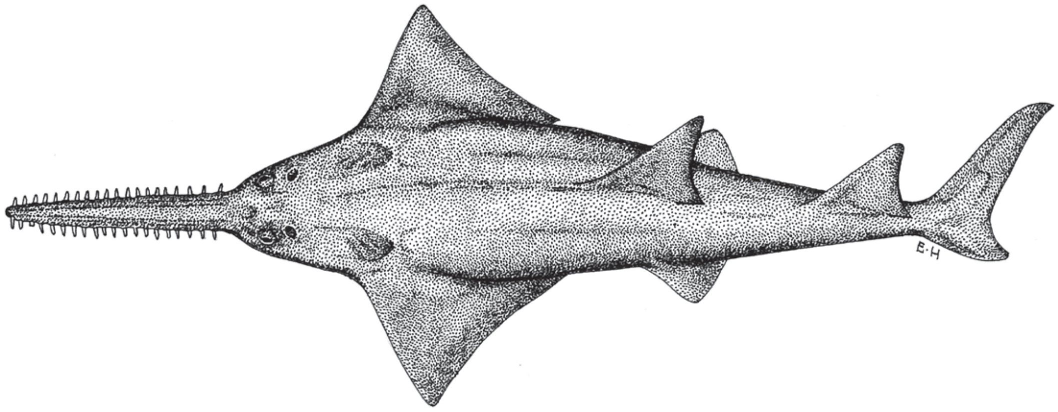
PLATE 51

Squalus pristis Linnaeus 1758: 235 ('Europa' [Mediterranean Sea; western Atlantic; Indian Ocean]).
Pristis microdon Latham 1794: 280, Pl. 26, Fig. 4 [no locality given]; SFSA No. 58; Munro 1955*; Wallace 1967*; Qureshi 1972*; Van der Elst 1988*; Compagno *et al.* 1989*; SSF No. 22.1* [1995]; Compagno & Last 1999*; Heemstra & Heemstra 2004*; White *et al.* 2006*; Last & Stevens 2009*.
Pristis pectinatus: Barnard 1925*; SFSA No. 59*.
Pristis annandalei Chaudhuri 1908: 391, Fig. (Elephant Point, Myanmar).
Pristis perotteti: Annandale 1909*; Barnard 1925 [as *perrotteti*].
Pristis pectinata: Compagno *et al.* 1989*.
Pristis pristis: Faria *et al.* 2013; Last *et al.* 2016.

Rostrum broad and stout, not significantly tapering anteriorly; rostrum length ~5–6 times its width at posteriormost lateral teeth. Pairs of rostral teeth 14–23 (with known variation between individuals, and males frequently with higher tooth count than females), moderately flattened, with double posterior edges, and a groove on posterior edge of lateral teeth at all stages. First dorsal-fin origin well ahead of pelvic-fin origins, and its insertion close behind pelvic-fin origins.

Body yellowish brown to greyish dorsally, white ventrally; fin webs yellowish. Attains 6.5 m TL, possibly 7 m TL.

DISTRIBUTION Circumglobal, with numerous suspected local extinctions. WIO: South Africa (Eastern Cape and KwaZulu-Natal), Mozambique, Madagascar, Réunion, Tanzania, Somalia, Oman, Pakistan and India.



Pristis pristis, 357 cm TL, mature male (South Africa). Source: SSF 1995

REMARKS Species identity for 'largetooth sawfishes' is confined to a single wide-ranging species with distinct subpopulations, which are considered ecologically (rather than genetically) different. *Pristis microdon* is a former name most commonly applied to records from the Indo-Pacific, from South Africa to northern Australia. Many local records of this species are of juveniles from freshwater and upper estuaries, as large individuals are now rarely seen. Viviparous with yolk sac; litters up to 13; size at birth 70–90 cm TL; gestation period ~5 months. Slow-growing; matures at 2.5–3 m TL, at ~8–9 years. Inshore, intertidal to commonly <10 m deep, and spending part of its lifecycle in freshwater systems. Feeds on small fishes and benthic invertebrates. Formerly common, its global abundance has declined sharply due to intense human pressure and vulnerability to entanglement in all types of fishing gear. IUCN Red List conservation status Critically Endangered globally.

Pristis zijsron Bleeker 1851

Green sawfish PLATE 52

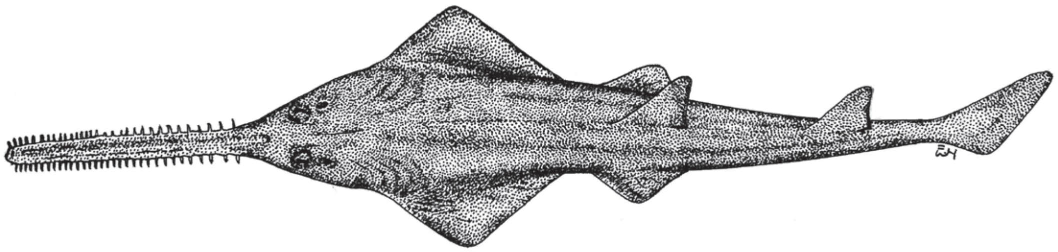
Pristis zijsron Bleeker 1851: 417, 442 (Bandjarmasin, Borneo, Indonesia); Munro 1955*; Qureshi 1972*; Compagno *et al.* 1989*; Randall 1995*; SSF No. 22.3* [1995]; Compagno & Last 1999*; Bonfil & Abdallah 2004*; Last & Stevens 2009*; Faria *et al.* 2013; Everett *et al.* 2015.
Pristis zysron: Annandale 1909; Blegvad & Løppenthin 1944*.
Pristis pectinatus: Annandale 1909*; Barnard 1925*; Smith 1949*.
Pristis pectinata: Compagno *et al.* 1989*; Debelius 1993*; SSF No. 22.2* [1995]; Compagno & Last 1999*; Last & Stevens 2009*.

Rostrum relatively slender, with sides nearly parallel near base; rostrum width at base 1/10–1/7 its length. Pairs of rostral teeth 23–34; lateral teeth moderately flattened, elongated, with double posterior edges and groove on posterior edges in adults. First dorsal-fin origin somewhat posterior to pelvic-fin origins but ahead of pelvic-fin insertions. Peduncle with no secondary keel below main keel.

Body greenish or greyish brown to olive dorsally, pale or white ventrally. Attains at least 5.4 m TL, possibly 7.3 m TL.

DISTRIBUTION Indo-Pacific, with localised extinctions probable. WIO: extant in southwestern Red Sea to Gulf of Aden, Persian/Arabian Gulf to Gulf of Oman, and off Pakistan, India and Sri Lanka; also East Africa off Kenya, Mozambique and Madagascar; presumed extinct from South Africa (KwaZulu-Natal) and Mascarenes (Everett *et al.* 2015).

REMARKS Probably the largest sawfish species, but large individuals have become rare. Life history poorly known; presumably more tolerant of cooler waters than other *Pristis* species. Lecithotrophic viviparity, with litters of ~12; size at birth ~80 cm TL. Matures at 3–4.3 m TL, at ~9 years. Inhabits inshore coastal waters, estuaries and freshwater river systems, most common in shallow waters, but to ~70 m deep. Feeds on small schooling fishes, crustaceans and other benthic invertebrates. Presumed extirpated from many areas of its native range due to intensive inshore gillnet and trawl fisheries and habitat loss. IUCN Red List conservation status Critically Endangered.



Pristis zijsron, 109 cm TL, immature male (South Africa). Source: SSF 1995

FAMILY RHINIDAE

Shark ray and wedgefishes

David A Ebert, Neil C Aschliman and Brett A Human

Medium to large shark-like rays (up to ~3.1 m TL), with depressed robust body, head either thick and broadly rounded, or flattened and wedge-shaped; and long tail, robust or flattened. No stinging spine on tail and no electric organs. Thorns variably developed above eyes, on each shoulder, and along dorsal midline; dermal denticles on dorsal surface otherwise granular, minute. Spiracles large, with or without skin folds at rear margins. Five paired gill slits on underside. Nostrils large, oblique; nostril length more than one-half mouth width. Large triangular pectoral fins, separate, not joined to body to form disc. Two large, upright to falcate, spineless dorsal fins; 1st dorsal fin larger than 2nd, its origin over or slightly before pelvic-fin mid-bases or origins. Caudal fin large, posterior margin concave; upper lobe longer than lower lobe.

Reproductive mode yolk-sac viviparity where known; at least one with supplementary uterine fluid. Wedgefishes and shark rays have been observed perched on their pectoral-fin tips with the anterior part of their body off the bottom. A common bycatch in artisanal and commercial fisheries and recognised as strong gamefish. Their high-quality flesh, highly-valued large fins, and susceptibility to a range of fishing gear, combined with an inshore habitat (from intertidal zone to ~90 m deep), raises conservation concerns.

Found in tropical to warm-temperate waters of eastern Atlantic, western Pacific and Indian oceans. Three genera and 10 species; 2 genera and at least 4 species in WIO. Although there are substantial morphological and anatomical character differences between the 2 genera such that they formerly comprised separate families, a recent molecular analysis indicated that they are sister groups and combined them into family Rhinidae (Last, Séret & Naylor 2016).

KEY TO GENERA

1a Head thickened, broadly rounded, and clearly separate from pectoral fins; spiracular folds absent........................... ***Rhina***

1b Head flattened, wedge-shaped, and separated from pectoral fins by shallow indentation at fin origins; spiracles with 2 skin folds on rear margin..................................... ***Rhynchobatus***

GENUS *Rhina* Bloch & Schneider 1801

Unmistakable bulky, shark-like ray with domed head and robust tail. Heavy ridges of spiky thorns above eyes, on central dorsal midline, and on shoulder. Spiracles without skin folds. Mouth broadly arched; lower jaw trilobed; numerous small blunt teeth in undulating rows and visible when mouth closed; tooth count 47/50. One species.

Rhina ancylostomus Bloch & Schneider 1801

Shark ray

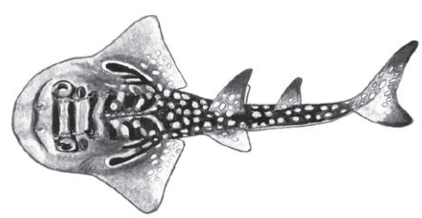
PLATE 57

Rhina ancylostomus Bloch & Schneider 1801: 352, Pl. 72 (Coromandel, India).

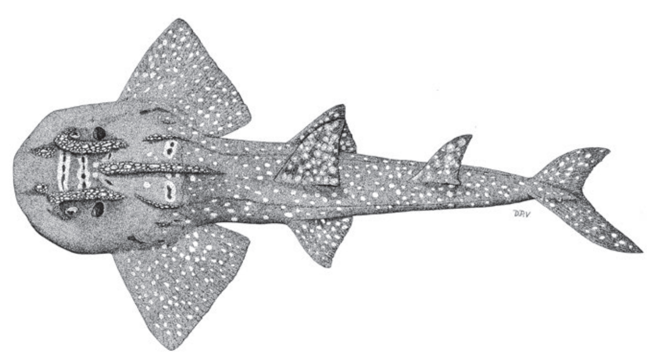
Rhina ancylostoma: SFSA No. 59a*; Wallace 1967*; SSF No. 27.1*; Compagno, Ebert & Smale 1989*; Manilo & Bogorodsky 2003; Heemstra & Heemstra 2004*; Last & Stevens 2009*; Last *et al*. 2016.

Diagnosis as for genus.

Body bluish grey to brownish dorsally, with numerous pale spots scattered over body, fins and tail (markings most pronounced in juveniles); mostly white ventrally. Attains 270 cm TL.



Rhina ancylostomus, 54 cm TL, juvenile (Oman).



Rhina ancylostomus, 130 cm TL, female (South Africa). Source: SSF

DISTRIBUTION Indo-Pacific (widespread). WIO: South Africa (KwaZulu-Natal) to Arabian Sea, Red Sea, Persian/Arabian Gulf, Pakistan, India, Sri Lanka, Seychelles, Madagascar, Réunion and Mauritius; elsewhere to east coast of India, Philippines, Taiwan, southern Japan, Australia and New Caledonia.

REMARKS Viviparous with yolk sac and supplementary uterine fluid; litters of 2–11; size at birth 46–48 cm TL. Males mature at 150–175 cm TL, females mature at ~180 cm. Uncommon but widely scattered; coastal, demersal, found close inshore on sandy and muddy bottoms and around coral reefs, possibly to ~90 m deep. Diet includes crustaceans (crabs) and other shellfish. A target species and bycatch in multiple artisanal and commercial fisheries throughout its range; traded in Asia for its fins. Harmless to people and a popular exhibit animal in public aquariums. IUCN Red List conservation status Critically Endangered globally; Near Threatened in Australian waters.

GENUS ***Rhynchobatus*** Müller & Henle 1837

Head depressed and not elevated above disc, anterior margins not indented; snout acutely pointed, triangular and depressed, and rostrum not forming a 'saw.' Mouth opening weakly undulating to nearly straight; circumoral grooves and lip folds present. Tail with well-developed lateral ridges. Pectoral fins rather small, originating posterior to nostrils and confluent with head and body, apices angular, and forming short narrow wedge-shaped disc; free rear tips ending well before pelvic-fin origins. Spiracles with 2 skin folds on rear margin. Supraorbital and scapular thorns inconspicuous, and males without alar or malar thorn patches; thorns in dorsal midline in front of 1st dorsal fin usually small, blunt; interdorsal thorns inconspicuous, and no thorns between 2nd dorsal fin and caudal fin. Tooth counts 31–52/37–48; vertebrae 144–211.

This genus is in need of revision to improve our understanding of the number of species and their distribution. Until recently, *Rhynchobatus djiddensis* (commonly known as the giant wedgefish) was thought to be the only representative in the Indian Ocean, ranging to the western Pacific. However, there may be at least 3 similar-looking species in the Indian Ocean, and *R. djiddensis* may not occur beyond WIO. Thus, the synonymies and distributions provided here are highly provisional. Eight species, plus an unknown number of undescribed species; 3 species, plus at least 1 undescribed species in WIO.

As a taxonomically problematic group, a key to species cannot be presented due to the lack of critical species descriptions. Characters and colouration listed for the species below are highly provisional for WIO representatives, as detailed redescriptions of all putative species are needed.

Rhynchobatus australiae Whitley 1939

Bottlenose wedgefish PLATE 57

Rhynchobatus djiddensis australiae Whitley 1939: 245, Fig. 14 (off Manning River mouth, New South Wales, Australia).
Rhynchobatus australiae: Compagno & Last 1999*, 2008; White & Dharmadi 2007; Last & Stevens 2009*; Bineesh *et al.* 2014.

Disc margin beside eyes concave; thorns not set on raised ridges; 1st dorsal-fin origin slightly behind pelvic-fin origins. Vertebrae 144–164.

Body pale grey to yellowish brown dorsally and ventrally; dorsal surface with few large white spots loosely arranged in 2 rows on each side of trunk, and well-defined dark spot surrounded by 4 white spots at base of each pectoral fin. Attains 3 m TL.

DISTRIBUTION WIO records: Mozambique to Arabian Sea, Red Sea, Persian/Arabian Gulf, Pakistan, India, Sri Lanka, Madagascar, and Seychelles. Indo-Pacific: tropical eastern Indian Ocean and western Pacific Ocean.

REMARKS Probably a species complex of 3 or 4 difficult-to-distinguish species; smaller individuals are easily misidentified with *R. laevis*. Very little known about its behaviour and biology. Litters of 7–19; size at birth 46–50 cm TL. In the Pacific, males mature at 110–130 cm TL, and females at ~150 cm TL. IUCN Red List conservation status Critically Endangered.

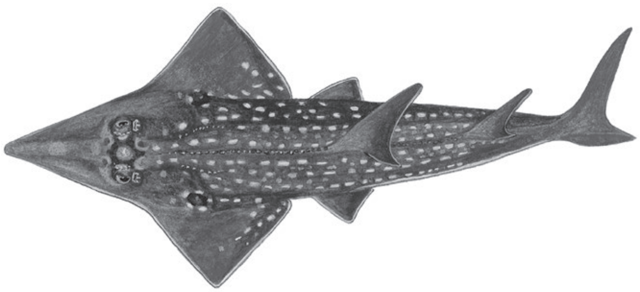
Rhynchobatus djiddensis (Forsskål 1775)

Whitespotted wedgefish PLATE 57

Raja djiddensis Forsskål *in* Niebuhr 1775: 18, viii (Red Sea).
Rhynchobatus djeddensis: Sauvage 1891; Barnard 1925*, 1927*; Smith 1959*; SFSA No. 60*; Wallace 1967*.
?*Rhinobates rueppelli*: Swainson 1838.
Rhynchobatus djiddensis: Morrow 1954; Compagno & Smale 1986; SSF No. 27.7*; Compagno & Randall 1987; Compagno *et al.* 1989*; Randall & Anderson 1993; Cliff & Wilson 1994*; ?Al-Abdessalaam 1995*; ?Randall 1995*; ?Branch *et al.* 1999; Compagno & Last 1999, 2008; Bonfil & Abdallah 2004*; Heemstra & Heemstra 2004*; Letourneur *et al.* 2004; Last & Stevens 2009.

Disc margin slightly concave in front of eyes; 1st dorsal-fin origin above or before pelvic-fin origins. Tooth count 31–42/37–48; vertebrae 204–211.

Body dark olive-green or yellowish brown dorsally and ventrally; dorsal surface with 3 or more rows of loosely arranged large white spots on each side of trunk, and well-defined dark spot surrounded by 4 or 5 white spots at each pectoral fin base; sometimes with dark polygonal mark between eyes. Attains 3.1 m TL.



Rhynchobatus djiddensis, 146 cm TL (South Africa). Source: CFSA

DISTRIBUTION Extent of global distribution difficult to ascertain due to taxonomic confusion; records from western Pacific and eastern Indian oceans probably represent a species complex. WIO: South Africa (Eastern Cape and KwaZulu-Natal) to Red Sea, Gulf of Aden, and to Persian/Arabian Gulf, Madagascar, Mauritius, Réunion, Seychelles and Maldives.

REMARKS The most commonly cited species of *Rhynchobatus*, yet poorly described. Previously considered wide-ranging in tropical to warm-temperate waters of Indo-Pacific, recent literature restricts it to the coast of East Africa and the Red Sea, being replaced by a similar-looking species from approximately Pakistan (Arabian Sea) and eastwards, and probably sympatric with at least one other possibly undescribed species in WIO (photographs of *Rhynchobatus* from Oman have a similar colour pattern to *R. djiddensis* from East Africa). Colouration reported to change with undisturbed and disturbed states, resulting in more prominent patterning in the latter, and probably adding to taxonomic confusion. Viviparous with yolk sac; litters of probably 4–7; size at birth 55–67 cm TL. Seasonal occurrence in South Africa during the summer is associated with pupping. Inshore over mud and sand bottoms, from surf line to ~30 m deep, and also caught in estuaries. Diet includes crabs, bivalve molluscs, squid and fishes. Common bycatch in nearshore artisanal and commercial fisheries where it occurs, and valued as a gamefish; highly valued for its fins and palatability of its meat. IUCN Red List conservation status Critically Endangered.

Rhynchobatus laevis (Bloch & Schneider 1801)

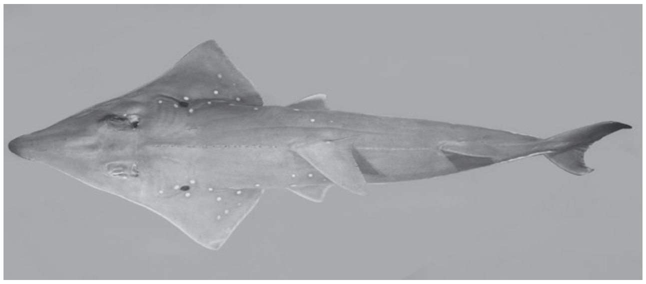
Smoothnose wedgefish

PLATE 57

Rhinobatus laevis Bloch & Schneider 1801: 354, Pl. 71 (Japan).
Rhinobatos laevis: Bloch & Schneider 1801*.
Rhynchobatus djeddensis: Day 1878*; Bianchi 1985*; Morón *et al.* 1998.
Rhinobatis djeddensis: Annandale 1909.
Rhynchobatus djiddensis: Carpenter *et al.* 1997*.
Rhynchobatus cf. *laevis*: Compagno & Last 1999*.
Rhynchobatus laevis: Compagno & Last 2008; Last & Stevens 2009*.

Diagnosis as for family. Disc margin slightly concave beside spiracles; 1st dorsal-fin origin over or slightly behind pelvic-fin origins. Vertebrae 144–149.

Body dark greyish brown to almost black dorsally, with few large white spots loosely arranged in 2 rows on each side of trunk; sometimes with a poorly defined dark spot and 3 white spots near it (not surrounding it) at each pectoral-fin base; paler ventrally. Attains possibly 200 cm TL.



Rhynchobatus laevis, 71 cm TL (Thailand). © JE Randall, Bishop Museum

DISTRIBUTION Indo-Pacific. WIO: Mozambique, Madagascar, Oman, possibly Persian/Arabian Gulf, Pakistan, India and Sri Lanka; possibly more wide-ranging, but unconfirmed; elsewhere to Thailand, Indonesia, Japan and Australia.

REMARKS Occurs in tropical waters of northern Indian Ocean, perhaps along with *R. australiae* or a similar-looking possibly undescribed species, and generally mistaken for *R. djiddensis* although probably allopatric to that species. Behaviour and biology poorly known, especially in WIO; litters of 7–26 (average 15) are reported elsewhere. Feeds mostly on benthic invertebrates. Taken heavily in gillnet fisheries in India, as well as in other fisheries where it occurs. Valued for its meat and fins, and a prized gamefish in Australia. IUCN Red List conservation status Critically Endangered.

FAMILY RHINOBATIDAE

Guitarfishes and shovelnose rays

Bernard Séret and Marcelo R de Carvalho

Small- to medium-sized rays (up to ~3 m TL) with wedge-shaped disc, depressed shark-like trunk, and thick tail. Head flattened and pectoral fins fused with head and trunk; snout more or less elongated, acutely to obtusely angular, and supported by stout rostral cartilage. Spiracles close to eyes, usually large, and with 1 or 2 skin folds along rear edge. Five pairs of gill slits on ventral side. Nostrils rather short (subequal to or slightly longer than internasal space), very oblique, without nasal curtain; anterior nasal flaps more or less well-developed, with medial extension of the inner margins onto internasal space defining genera. Two large, nearly equal-sized dorsal fins; 1st dorsal fin well behind pelvic fins. Pelvic fins large, not forming separate lobes, and origins under posterior margins of pectoral fins. Caudal fin strongly asymmetrical with well-developed upper lobe and small or absent lower lobe; no electric organs. Skin covered with granulations, and often with small thorny tubercles around eyes and spiracles and/or blunt tubercles in median dorsal row. Teeth in jaws numerous, small and blunt. Colour variable, either plain dorsally or with distinctive pattern of more or less symmetrically arranged spots, blotches, ocelli or bands; usually white ventrally, sometimes with dark blotch on underside of snout.

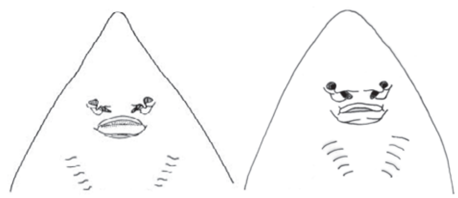
Reproductive mode of all species yolk-sac viviparity. Circumglobal and widely distributed, in warm-temperate to tropical waters, mostly inshore over continental shelf, although some occur in deeper water, to ~400 m. Some also enter estuaries and closed bays. Mainly bottom-dwelling, often resting on soft mud or sandy bottom, with shallow sandy habitat important as nursery areas. Feed mainly on benthic invertebrates and small bony fishes. Taken mostly as a bycatch of artisanal and commercial benthic trawl, gillnet, and beach-seine fisheries; appreciated in many countries for their meat, but fins usually too small for the shark-fin trade. IUCN Red List conservation status of the species varies from Endangered to Near Threatened.

The large genus *Rhinobatos* has been typically understood to comprise three subgenera: *Rhinobatos* Linck 1790, *Glaucostegus* Bonaparte 1846, and *Acroteriobatus* Giltay 1928 (cf. Last *et al.* 2004). The subgenus *Glaucostegus* was elevated to generic level by Compagno *et al.* (2005), and has now been placed in its own family, Glaucostegidae (Last *et al.* 2016). The other two groups left as subgenera of *Rhinobatos*, *Acroteriobatus* and *Rhinobatos*, are now elevated to full genera. Three genera and 33 species; 2 genera and 16 species in WIO, plus at least 2 other undescribed species.

KEY TO GENERA

1a Inner margins of anterior nasal flaps extending only slightly onto internasal space (as far as inner corners of nostrils); ridges of rostral cartilage well separated and nearly parallel to each other .... ***Rhinobatos***

1b Inner margins of anterior nasal flaps extending well onto internasal space, with both flaps almost joining at snout midline; ridges of rostral cartilage widely separated but with a weak constriction midway .... ***Acroteriobatus***



GENUS *Acroteriobatus* Giltay 1928

Distinguished from other rhinobatid genera in the region by well-developed anterior nasal flaps, inner edge of nostrils extending medially well onto internasal space and almost joining at snout midline; snout tip broadly acute; and rostral cartilage ridges widely separated but with slight constriction midway. Ten species, all in WIO, with 2 recently described species, *Acroteriobatus andysabini* and *A. stehmanni* Weigmann, Ebert & Séret 2021 in the key.

KEY TO SPECIES

1a Snout broadly pointed; disc wider, anterolateral margins conspicuously convex **2**

1b Snout more or less acutely pointed; disc narrower, anterolateral margins straight to slightly convex or slightly concave **3**

2a Dorsal surface plain brown (but with some small whitish spots in young) .... ***A. blochii***

2b Dorsal surface pale brown and with dark-edged pale blue blotches on pectoral fins and pelvic fins........ ***A. salalah***

3a Dorsal surface plain coloured; medium-sized, to ~200 cm TL .... ***A. zanzibarensis***

3b Dorsal surface with spots, blotches or bands **4**

4a Snout with 2 or 3 brown bands on each side; pectoral fins and pelvic fins with blue variegated markings .... ***A. variegatus***

4b No dark bands on snout **5**

Continued ...

KEY TO SPECIES

5a Blotches on dorsal surface not dark-edged, but sometimes edged by rings formed of dots; large bluish grey blotches on snout, greyish brown blotches on pectoral fins and pelvic fins, and symmetrically paired faint brown blotches on back of trunk .... ***A. leucospilus***

5b Blotches on dorsal surface usually dark-edged, and rings continuous and not formed of dots **6**

6a Numerous blotches on dorsal surface **7**

6b Fewer blotches on dorsal surface **9**

7a Dorsal surface with numerous large blue-grey ocellus-like blotches with narrow dark brown edges, sometimes incomplete .... ***A. ocellatus***

7b Dorsal surface with numerous relatively small brown blotches or dark-edged ocelli **8**

8a Centre of ocelli consisting of a small dark spot, or dorsal surface with brown blotches .... ***A. annulatus***

8b Centre of ocelli consisting of a small white spots .. ***A. omanensis***

9a Body brownish with orange tinge, blue-grey spots more numerous, ventral snout with V-shaped dark mark........ ***A. andysabini*** [Madagascar; Plate 58]

9b Body brownish with greenish tinge, blue-grey spots fewer, ventral snout without dark marking .... ***A. stehmanni*** [Socotra; Plate 59]

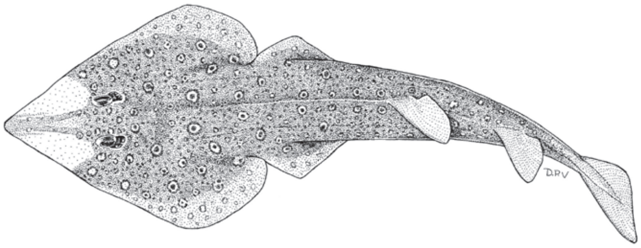
Acroteriobatus annulatus (Smith 1841)

Lesser guitarfish PLATE 58

Rhinobatus (*Syrrhina*) *annulatus* Smith (ex Müller & Henle) 1841: 116 (Cape of Good Hope, South Africa); Wallace 1967*.
Rhinobatos annulatus: SSF No. 27.2*; Compagno *et al*. 1989*; Heemstra & Heemstra 2004*.
Acroteriobatus annulatus: Last *et al.* 2016.

Disc moderately broad, anterolateral margins slightly convex; disc length ~39% TL, disc width ~1.15 in disc length. Snout triangular, bluntly pointed and short, preorbital length ~14% TL. Eyes slightly larger than spiracles; 2 prominent folds at rear edge of spiracles. Small tubercles around eyes and spiracles, and ~35 tubercles in median dorsal row.

Body pale brown background dorsally, with distinctive pattern of numerous dark-edged ocelli, with central dark spot surrounded by pale ring or else centre simply brownish; white ventrally. Attains 140 cm TL.



Acroteriobatus annulatus, 53 cm TL, male (South Africa). Source: SSF

DISTRIBUTION Southern Africa: Angola in southeastern Atlantic, to South Africa and southern Mozambique in WIO.

REMARKS Recent genetic analyses show no differences between the Atlantic Ocean and WIO (KwaZulu-Natal) forms. Litters of 2–10. Matures relatively quickly, males at ~59 cm TL and females at 68–89 cm TL; maximum age ~7 years. Most abundant rhinobatid in southern Africa; occurs from surfline to ~100 m deep, and in estuaries and enclosed bays, with shallow sandy areas serving as important nursery habitat. Feeds on small benthic invertebrates (mainly crustaceans) and small bony fishes. Caught by recreational shore anglers and in commercial gillnet, beach-seine and benthic trawl fisheries.

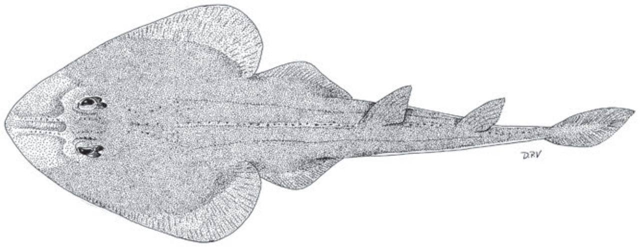
Acroteriobatus blochii (Müller & Henle 1841)

Bluntnose guitarfish PLATE 58

Rhinobatus (*Syrrhina*) *blochii* Müller & Henle 1841: 115, Pl. 37 (Cape of Good Hope, South Africa).
Rhinobatos blochii: SSF No. 27.3*; Compagno *et al*. 1989*.
Acroteriobatus blochii: Last *et al.* 2016.

Disc moderately broad and moderately long; anterolateral margins slightly convex, posterior margins entirely rounded; disc length ~42% TL, disc width ~1.1 in disc length. Snout acutely rounded and very short, preorbital length ~11% TL. Eyes slightly larger than spiracles; only 1 prominent fold at rear edge of spiracles. Minute tubercles around eyes, and small tubercles in median dorsal row (reducing with growth).

Body plain brown dorsally, but young with few white spots; white ventrally. Attains 96 cm TL.



Acroteriobatus blochii. Source: SSF, composite

DISTRIBUTION Southern Africa: Namibia (Walvis Bay) in southeastern Atlantic, to Cape of Good Hope (South Africa) in WIO.

REMARKS Often misidentified with *A. annulatus* where they overlap in distribution. Rare, biology unknown; occurs close inshore, in shallow bays and off sandy beaches. Occasionally taken in recreational shore fisheries.

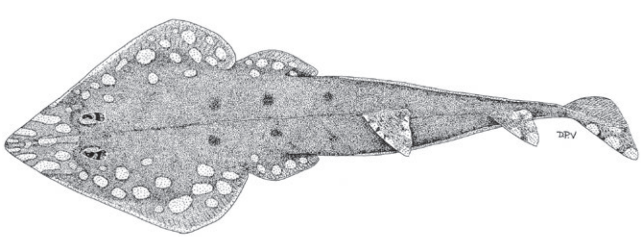
Acroteriobatus leucospilus (Norman 1926)

Greyspotted guitarfish PLATE 58

Rhinobatus leucospilus Norman 1926: 966, Fig. 18 (Durban, KwaZulu-Natal, South Africa); Wallace 1967*.
Rhinobatos leucospilus: SSF No. 27.5*; Compagno *et al*. 1989*; Heemstra & Heemstra 2004.
Acroteriobatus leucospilus: Last *et al.* 2016.

Disc moderately broad, anterolateral margins almost straight to slightly convex; disc length ~38% TL, disc width ~1.2 in disc length. Snout bluntly triangular and short, preorbital length ~12% TL. Eyes slightly larger than spiracles; 2 folds at rear edge of spiracles, outer fold more prominent. Very small tubercles around eyes and spiracles and on shoulders, and up to 50 tubercles in median dorsal row.

Body sandy brown background dorsally, with symmetrically arranged faint brown blotches across disc and trunk, and bluish spots on snout and pectoral- and pelvic-fin margins; dorsal fins and caudal fin with fainter grey-brown blotches and bluish spots; margins of pectoral fins and pelvic fins with bluish grey edges; white ventrally. Attains 120 cm TL.



Acroteriobatus leucospilus, 68 cm TL, female (South Africa). Source: SSF

DISTRIBUTION WIO: South Africa (Transkei region and KwaZulu-Natal) to Mozambique.

REMARKS Litters of 2–4; matures at ~56 cm TL. Apparently rare and poorly known; occurs from surfline to ~100 m deep. Feeds on benthic invertebrates (bivalves, gastropods, crabs, shrimp) and small bony fishes. Possibly taken by recreational shore anglers and in gillnet fisheries.

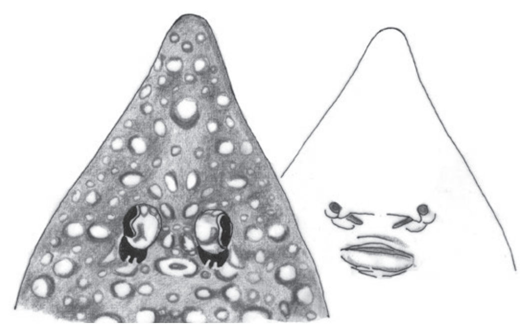
Acroteriobatus ocellatus (Norman 1926)

Maculate guitarfish PLATE 58

Rhinobatus ocellatus Norman 1926: 967, Fig. 20 (Bird Island, Algoa Bay, South Africa); Wallace 1967*.
Rhinobatos ocellatus: SSF No. 27.6 (not illustration); Compagno *et al.* 1989*; Heemstra & Heemstra 2004.
Acroteriobatus ocellatus: Last *et al.* 2016.

Disc moderately narrow, anterolateral margins straight to slightly concave; disc length ~36% TL, disc width ~1.2 in disc length. Snout bluntly triangular and relatively short, preorbital length 12–13% TL; 2 prominent folds at rear edge of spiracles. Small tubercles around eyes and spiracles and on shoulders and dorsal midline in young (becoming lost with growth and maturity).

Body brownish background dorsally, with numerous large ocellus-like blotches, with blue-grey centre and narrow dark brown edges, dark rims sometimes incomplete; blotch size decreases towards margins. Attains 81 cm TL.



Acroteriobatus ocellatus (South Africa). Composite

DISTRIBUTION WIO: South Africa (south coast) to southern Mozambique.

REMARKS Often misidentified with *A. annulatus* and *A. zanzibarensis*. Rare and little known from few specimens. Found along sandy coastal areas, usually close inshore, at 60–185 m. Likely taken as a bycatch in trawl and net fisheries.

Acroteriobatus omanensis

Last, Henderson & Naylor 2016

Oman guitarfish

Acroteriobatus sp.: Henderson *et al.* 2016.
Acroteriobatus omanensis Last, Henderson & Naylor 2016: 277, Figs. 1–7 (off Muscat, Gulf of Oman).

Disc broadly wedge-shaped, anterolateral margins slightly undulated; disc length 41.4–43.3% TL, disc width 1.3–1.4 in disc length. Snout bluntly angular and short, preorbital length 12.9–15.3% TL. Eye length 1.3–1.6 times spiracle length; 2 well-developed spiracular folds. Denticles minute (skin smooth to touch); some enlarged denticles on snout over orbits, on shoulders, on dorsal midline from nape to first dorsal origin, and between dorsal fins.

Dorsal surface medium greenish brown, paler along pectoral and pelvic posterior margins, with symmetrically arranged faint dark brown blotches and numerous small ocelli consisting of white central spot surrounded by a dark, diffuse-edged brownish rim; dorsal fins with small white spots, caudal fin with two large dark blotches, one each side, and a pair of dark saddles on caudal peduncle. Ventral surface whitish, with diffuse dark marking on snout tip; margins of nasal flaps vivid red or orange. Attains at least 60 cm TL.

DISTRIBUTION WIO: Gulf of Oman.

REMARKS Biology unknown. Described from three adult females and a male collected from Muscat fish market.

Acroteriobatus salalah (Randall & Compagno 1995)

Salalah guitarfish PLATE 59

Rhinobatos salalah Randall & Compagno 1995: 293, Fig. 4 (Salalah fish market, Oman, Arabian Sea); Randall 1995*; Manilo & Bogorodsky 2003; Bonfil & Abdallah 2004*.
Acroteriobatus salalah: Last *et al.* 2016.

Disc heart-shaped, somewhat roundish; anterolateral margins usually convex, posterior margins strongly convex; disc length ~37% TL, disc width ~1.1 in disc length. Snout tip bluntly pointed, snout broad and short; preorbital length ~11% TL; 2 prominent folds at rear edge of spiracles. Small tubercles around eyes and spiracles, and up to 55 blunt tubercles in median dorsal row.

Body tan dorsally, with dark-edged pale bluish spots on snout, pectoral fins and pelvic fins; white ventrally. Attains 78 cm TL.

DISTRIBUTION WIO: Arabian Sea (Oman and Pakistan).

REMARKS Known only from a few specimens collected from a fish market in Salalah, Oman, and a harbour in Karachi, Pakistan. Presumably occurs along sandy inshore areas. Likely taken in local fisheries.

Acroteriobatus variegatus (Nair & Lal Mohan 1973)

Stripenose guitarfish PLATE 59

Rhinobatos variegatus Nair & Lal Mohan 1973: 77, Fig. 4 (Gulf of Mannar, India); Manilo & Bogorodsky 2003.
Acroteriobatus variegatus: Last *et al.* 2016.

Disc relatively narrow, anterolateral margins almost straight; disc length ~37% TL, disc width ~1.3 in disc length. Snout triangular, pointed, and moderately long, preorbital length ~13% TL; 2 developed folds at rear edge of spiracles. Minute tubercles in front of eyes, and ~36 small tubercles in median dorsal row.

Body brownish grey dorsally; pectoral fins and pelvic fins with blue variegated markings; snout with 2 or 3 brown longitudinal stripes on each side of rostral cartilage, and snout tip slightly darker; white ventrally. Attains at least 65 cm TL.

Acroteriobatus variegatus, 28 cm TL (SW India). KV Akhilesh © CMFRI

DISTRIBUTION WIO: Gulf of Mannar (India).

REMARKS Known from few specimens in 10–40 m. Deep records (to 366 m) are probably erroneous.

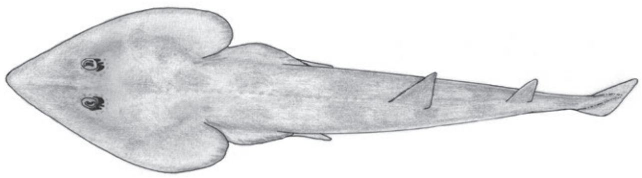
Acroteriobatus zanzibarensis (Norman 1926)

Zanzibar guitarfish

Rhinobatus zanzibarensis Norman 1926: 966, Fig. 19 (Zanzibar, Tanzania).
Acroteriobatus zanzibarensis: Last *et al.* 2016.

Disc rather narrow; anterolateral margins almost straight to slightly concave. Snout bluntly triangular and moderately long, preorbital length ~12% TL; 2 well-developed folds at rear edge of spiracles. Small tubercles around eyes and spiracles, and in two groups on shoulders; small blunt tubercles in median dorsal row.

Body plain coloured dorsally, white ventrally. Attains at least 75 cm TL.



Acroteriobatus zanzibarensis, male holotype (Zanzibar).
Drawn from photograph

DISTRIBUTION WIO: Tanzania (Zanzibar).

REMARKS Known only from two specimens (75 cm TL male and 20.5 cm TL female; depth of capture unknown); very similar if not identical to *A. ocellatus*, except for its plain colour and slightly concave anterolateral margins. IUCN Red List conservation status Near Threatened.

GENUS *Rhinobatos* Linck 1790

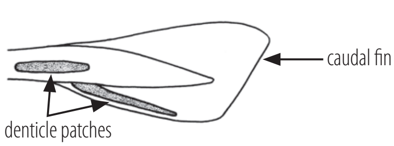
Distinguished from other rhinobatid genera in WIO by weakly developed anterior nasal flaps, inner margins extending to level of inner corner of nostrils; snout triangular and relatively acute; and rostral ridges well separated and more or less parallel to each other. Nineteen species, 6 in WIO, plus probably 2 undescribed species from Oman.

KEY TO SPECIES

1a Dorsal surface with pattern of prominent white spots or brown blotches 2
1b Dorsal surface plain or with faint blotches 3

2a Dorsal surface with widely scattered white spots .... ***R. punctifer***
2b Dorsal surface with symmetrically arranged brown blotches .... ***R. austini***

3a Skin mostly smooth, with no thorns on dorsal disc, and tail and unpaired fins generally naked, except for small patch of denticles across peduncle and caudal-fin lower lobe .... ***R. nudidorsalis***



Continued …

KEY TO SPECIES

3b Skin covered with minute denticles (but smooth to touch) and with more or less conspicuous tubercles around eyes and spiracles, on shoulders, and on dorsal midline **4**

4a No black marking on underside of snout; tubercles in median dorsal row minute .... ***R. lionotus***

4b Underside of snout with prominent or faint black blotch; tubercles in median dorsal row conspicuous **5**

5a Dorsal surface plain olive-brown .... ***R. holcorhynchus***
5b Dorsal surface tan with faint brownish blotches .... ***R. schlegelii***

Rhinobatos austini Ebert & Gon 2017

Austin's guitarfish PLATE 59

Rhinobatos austini Ebert & Gon 2017: 205 (near Port Shepstone, KwaZulu-Natal, South Africa).

Disc broadly wedge-shaped, anterolateral margins almost straight to slightly concave; disc length 42.0–43.8% TL, disc width ~1.3 in disc length. Snout bluntly angular and moderately long, preorbital length 13.6–14.6% TL. Eye length 1.33–1.58 times spiracle length; 2 distinct folds at rear edge of spiracles. Denticles minute (skin smooth to touch), slightly coarser on dorsal midline from nape to first dorsal origin, between dorsal fins and on caudal peduncle.

Dorsal surface light to medium brown, with a pattern of symmetrical dark brown blotches and spots, some aligned on saddle-like darker bands. Ventral surface mostly white, with a prominent tear-shaped blackish blotch on snout tip. Attains at least 115 cm TL.

Rhinobatos austini, 103 cm TL (S Mozambique). O Alvheim © IMR

DISTRIBUTION WIO: South Africa (KwaZulu-Natal) to Mozambique.

REMARKS This species was previously considered a variant of *Rhinobatos holcorhynchus*. Described from four female specimens only. Biology unknown. Coastal, from shore to about 100 m depth. Likely to be caught in local fisheries.

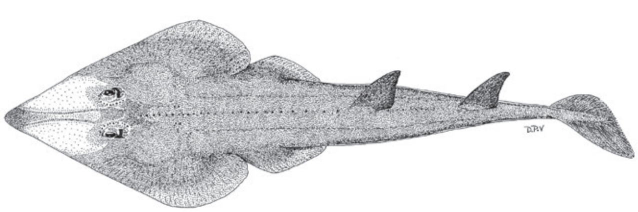
Rhinobatos holcorhynchus Norman 1922

Slender guitarfish PLATE 59

Rhinobatus holcorhynchus Norman 1922: 318 (KwaZulu-Natal, South Africa); Wallace 1967*.
Rhinobatos holcorhynchus: SSF No. 27.4*; Compagno *et al*. 1989*; Heemstra & Heemstra 2004.

Disc rather narrow and moderately long, anterolateral margins almost straight to slightly concave; disc length 41–42% TL, disc width ~1.3 in disc length. Snout triangular, sharply pointed and long, preorbital length 15–16% TL. Eyes about twice size of spiracles; 2 distinct folds at rear edge of spiracles. Denticles minute (skin smooth to touch), but with small tubercles on rostrum, around eyes and spiracles, and 1 or 2 on each shoulder; larger, irregular tubercles in median dorsal row.

Body plain dark olive-brown; margins of pectoral fins and pelvic fins somewhat dusky; snout noticeably translucent on each side of rostral cartilage; white ventrally, but with conspicuous dark blotch on underside of snout. Attains at least 127 cm TL.



Rhinobatos holcorhynchus, 45 cm TL, male (South Africa). Source: SSF

DISTRIBUTION WIO: South Africa (KwaZulu-Natal) to Kenya.

REMARKS Biology unknown. Rare; occurs offshore, at 75–253 m. Likely taken in local fisheries.

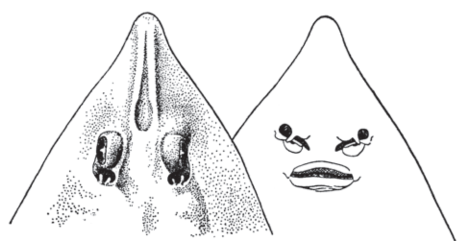
Rhinobatos lionotus Norman 1926

Smoothback guitarfish

Rhinobatus lionotus Norman 1926: 961, Fig. 14 (East Channel, mouth of Hooghly River, India).
Rhinobatos lionotus: Compagno & Randall 1987; Talwar & Jhingran 1991.

Disc broad, anterolateral margins slightly concave. Snout bluntly triangular and moderately long, preorbital length 12% TL; 2 strongly developed folds at rear edge of spiracles. Denticles minute (skin smooth to touch), except small tubercles around eyes and spiracles, 1 on each shoulder, and in median dorsal row.

Body plain brownish grey to olive-green dorsally; white ventrally. Attains at least 53 cm TL.



Rhinobatos lionotus (India). Source: Norman 1926

DISTRIBUTION Indian Ocean: known only from the holotype, collected from estuary of Hooghly River, West Bengal, but possibly also in the Arabian Sea and Sri Lanka.

REMARKS Taken at ~73 m deep. The status of this species is doubtful and should be re-examined. Biology unknown; apparently inhabits brackish water of river mouths.

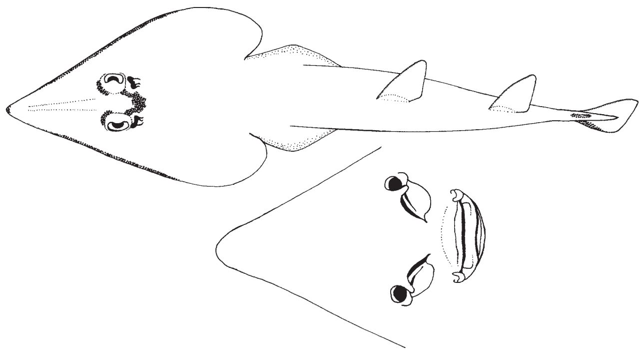
Rhinobatos nudidorsalis Last, Compagno & Nakaya 2004

Bareback shovelnose ray PLATE 59

Rhinobatos nudidorsalis Last, Compagno & Nakaya 2004: 154, Figs. 2–6 (Saya de Malha Bank, Mascarene Ridge).

Disc narrow and moderately long, anterolateral margins almost straight to slightly concave; disc length ~41% TL, disc width ~1.4 in disc length. Snout bluntly triangular and moderately long, preorbital length ~15% TL. Spiracles smaller than eyes; 2 strongly compressed folds at rear edge of spiracles, outer fold larger. No thorns on dorsal surface of disc; tail and unpaired fins almost entirely naked, except small patch of denticles across peduncle and caudal-fin lower lobe.

Body plain brownish pink dorsally; short dark streak on each side of snout near tip; pinkish white ventrally. Attains 50 cm TL.



Rhinobatos nudidorsalis, 50 cm TL, mature male, denticle patches on dorsal body shown by stippled areas (Mascarene Ridge).
Drawn from Last *et al.* 2004

DISTRIBUTION Known only from the holotype, a mature male, collected from Saya de Malha Bank.

REMARKS Taken from relatively deep water (~125 m). IUCN Red List conservation status Near Threatened.

Rhinobatos punctifer Compagno & Randall 1987

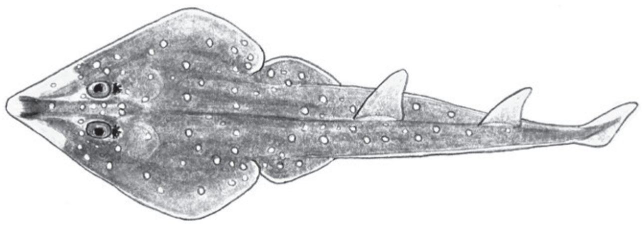
Spotted guitarfish

PLATE 60

Rhinobatos punctifer Compagno & Randall 1987: 336, Fig. 1 (Gulf of Aqaba, Red Sea); Randall 1995*; Randall & Compagno 1995*; Bonfil & Abdallah 2004*.

Disc moderately broad and relatively long, anterolateral margins almost straight to slightly concave; disc length ~44% TL, disc width ~1.1 in disc length. Snout bluntly triangular and moderately long, preorbital length ~13% TL; 2 prominent folds at rear edge of spiracles. No tubercles around eyes and spiracles or on shoulders; small blunt tubercles in median dorsal row.

Body brownish grey dorsally, with conspicuous small white spots (widely scattered or more or less arranged in rows); creamy white ventrally, but with dusky blotch on underside of snout. Attains at least 88 cm TL.



Rhinobatos punctifer, 71 cm TL (Gulf of Aqaba).

DISTRIBUTION WIO: Red Sea (including Gulf of Aqaba and Gulf of Suez) and off Oman (Muscat).

REMARKS Litters of up to 7; size at birth ~25 cm; matures at ~62 cm TL. Not rare; occurs inshore on continental shelf, at 10–70 m. Feeds mainly on small crustaceans. Regularly taken in local fisheries. Variants of *R. punctifer* are very similar to *R. annandalei* Norman 1926, from India, and are difficult to distinguish from their colour pattern and morphology; however, molecular analysis suggest divergences that need further investigation.

Rhinobatos schlegelii Müller & Henle 1841

Brown guitarfish

Rhinobatus (*Rhinobatus*) *schlegelii* Müller & Henle 1841: 123, Pl. 42 (Japan).
Rhinobatos schlegelii: Compagno & Last 1999*; Bonfil & Abdallah 2004*.

Disc narrow and moderately long, anterolateral margins almost straight to slightly concave; disc length ~41% TL, disc width ~1.3 in disc length. Snout triangular, broadly pointed, and moderately long, preorbital length ~12% TL; 2 weak folds on rear edge of spiracles. Minute tubercles around eyes and spiracles, and on shoulders; small blunt tubercles in median dorsal row.

Body tan background dorsally, with symmetrical pattern of faint brown botches over entire disc and trunk; white ventrally, but with black longitudinal bar on snout tip. Attains 100 cm TL.

DISTRIBUTION Indo-Pacific, though a known species-complex; records from Oman and India in WIO most likely represent a species within this complex, but records from South Africa are misidentifications.

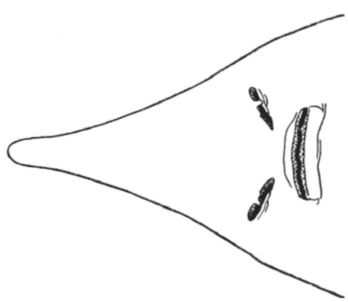
REMARKS Taxonomy uncertain: critical examination of the forms of this species is needed. Occurs inshore on continental shelf, to ~200 m deep, on sand and mud bottom. Feeds mainly on invertebrates (shrimp, cephalopods) and bony fishes.

FAMILY GLAUCOSTEGIDAE

Giant guitarfishes

Bernard Séret and Marcelo R de Carvalho

Large to very large rays (2–3 m TL) with wedge-shaped to spade-like disc, depressed shark-like trunk, and thick tail. Head flattened and pectoral fins fused with head and trunk; snout relatively elongated and acutely triangular, with tip acutely to bluntly rounded, or knob-like, and supported by stout rostral cartilage. Small spiracles close to small eyes, and with 1 or 2 skin folds along rear edge. Five pairs of gill slits on ventral side. Nostrils long (subequal to or noticeably longer than internasal space), oblique to transverse, without nasal curtain; anterior nasal flaps weakly developed, forming small triangular lobe inserted on front margin of nostril.



Glaucostegus head ventral view.

Two large, nearly equal-sized dorsal fins; 1st dorsal fin well behind pelvic fins. Pelvic fins large, not forming separate lobes, and origins under posterior margins of pectoral fins. Caudal fin strongly asymmetrical with well-developed upper lobe and small or absent lower lobe; no electric organs. Skin covered with fine granulations, often with small thorny tubercles near eyes, on shoulders and snout, and/or blunt tubercles in median dorsal row. Teeth in jaws numerous, small and blunt. Colour plain dorsally with pale translucent snout sharply demarcated by rostral cartilage and anterior skull; usually white ventrally, with snout faintly translucent, sometimes with dark blotch on underside of snout.

Reproductive mode of all species yolk-sac viviparity. Circumglobal and widely distributed, in warm-temperate to tropical waters, mostly inshore over continental shelf, although some occur in deeper water, to ~400 m. Some also enter estuaries and closed bays, and one species has been recorded in freshwater. Mainly benthic, often resting on soft mud or sandy bottom, with shallow sandy habitat important as nursery areas. Feed mainly on benthic invertebrates and small bony fishes. Taken mostly as a bycatch of artisanal and commercial benthic trawl, gillnet, and beach-seine fisheries; appreciated in many countries for their meat, and the large fins have high value in the shark-fin trade. IUCN Red List conservation status of WIO species is Vulnerable.

The subgenus *Glaucostegus* (formerly in *Rhinobatos*) was elevated to generic level by Compagno *et al.* (2005), but is now a recently erected family (Last *et al.* 2016), with one genus and 6 species; at least 5 species in WIO (*Glaucostegus cemiculus* appears unlikely in WIO).

GENUS *Glaucostegus* Bonaparte 1846

See family account.

KEY TO SPECIES

1a Snout tip expanded into club-like knob .... ***G. thouin***
1b Snout tip not expanded into club-like knob **2**

2a Snout longer and pointed, preorbital length <5 in TL **3**
2b Snout shorter or moderately long, preorbital length >5 in TL **4**

3a Internarial space wide, subequal to nostril length .. ***G. granulatus***
3b Internarial space narrow, ~½ nostril length .... ***G. typus***

4a Snout moderately long, preorbital length 5–7 in TL .... ***G. cemiculus***
4b Snout short, preorbital length >7 in TL **5**

5a Anterolateral margins of disc almost straight; 2 folds on rear edge of spiracles; distinct median dorsal row of thorns .... ***G. halavi***
5b Anterolateral margins of disc convex; 1 weak fold on rear edge of spiracles; no distinct median dorsal row of thorns .... ***G. obtusus***

Glaucostegus cemiculus (Geoffroy Saint-Hilaire 1817)

Blackchin guitarfish PLATE 60

Rhinobatus cemiculus Geoffroy Saint-Hilaire 1817: Pl. 27, Fig. 3 (Lake Menzilah, Alexandria, Egypt, Mediterranean Sea).
Rhinobatos cemiculus: Whitehead *et al.* 1984*.
Glaucostegus cemiculus: Compagno *et al.* 2005.

Disc moderately broad, anterolateral margins almost straight and slightly undulating; disc length ~39% TL, disc width ~1.1 in disc length. Snout triangular and moderately long, preorbital length ~14% TL; 2 folds at rear edge of spiracles, outer fold more prominent. Small orbital and interspiracular thorns, 1–3 scapular, and in median dorsal row.

Body plain beige to pale brown dorsally; outer margins of disc and fins sometimes reddish brown; white ventrally, but with conspicuous black blotch on underside of snout tip (mainly in juveniles). Attains 265 cm TL.

Glaucostegus cemiculus, 2.1 m TL (Ghana). O Alvheim © IMR

DISTRIBUTION Recorded from Madagascar as *Rhinobatos petiti*; elsewhere known from Mediterranean Sea and eastern Atlantic.

REMARKS *Glaucostegus cemiculus* probably does not occur in WIO. However, the nominal species *Rhinobatos petiti* Chabanaud 1929 (known only from holotype) from Madagascar was synonymised with it in Séret & McEachran (1986): pending the collection of further specimens, the synonymy with *G. cemiculus* is maintained. Litters of up to 20 (usually 4–6); size at birth ~34 cm TL. Males mature at 138–154 cm TL, and females at 153–164 cm TL. Coastal, mainly in shallow water but to ~100 m deep, and also enters estuaries and coastal lagoons; rests partly buried on sandy or muddy bottom. An active hunter, feeds on small benthic invertebrates and small fishes. Targeted for its fins in artisanal fisheries in West Africa. IUCN Red List conservation status Endangered.

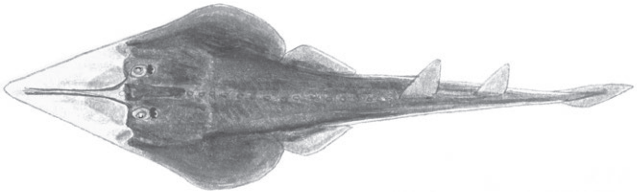
Glaucostegus granulatus (Cuvier 1829)

Sharpnose guitarfish PLATE 60

Rhinobatus granulatus Cuvier 1829: 396 (Puducherry, India).
Rhinobatos granulatus: Randall 1995*; Randall & Compagno 1995*; Compagno & Last 1999*; Bonfil & Abdallah 2004*.
Glaucostegus granulatus: Compagno *et al.* 2005.

Disc relatively narrow and long; anterolateral margins concave at level of snout tip, then almost straight; disc length almost half of TL, disc width ~1.4 in disc length. Snout triangular, acutely pointed and long, preorbital length ~22% TL. Eyes smaller than spiracles; 2 weakly developed folds at rear edge of spiracles, inner fold rudimentary. Conspicuous tubercles on rostral ridges, around eyes and spiracles, and on shoulders; strong and compressed tubercles in median dorsal row.

Body greyish brown dorsally, and margins usually reddish; each side of snout noticeably translucent; white ventrally. Attains 280 cm TL.



Glaucostegus granulatus, 39 cm TL (Persian/Arabian Gulf).

DISTRIBUTION Indo-Pacific (range poorly defined). WIO: Persian/Arabian Gulf to India and Sri Lanka; records from Red Sea and Oman need confirmation; elsewhere possibly to Indonesia, Philippines, China, New Guinea and Australia.

REMARKS Often misidentified with *G. typus*, which is common in the Indo-Pacific. Coastal, inshore and offshore, to ~119 m deep, but mainly in shallow water and also enters estuaries and coastal lagoons. Biology little known, other than litters of 6–10. Directly and indirectly fished throughout its range; once moderately abundant, now irregularly caught.

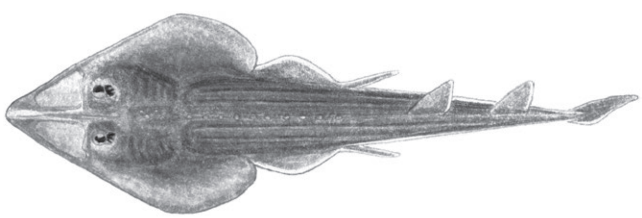
Glaucostegus halavi (Fabricius 1775)

Halavi guitarfish PLATE 60

Raja halavi Fabricius *in* Niebuhr (ex Forsskål) 1775: 19, viii (Jeddah, Saudi Arabia, Red Sea).
Rhinobatos halavi: Randall 1995*; Randall & Compagno 1995*; Compagno & Last 1999*; Bonfil & Abdallah 2004*.
Glaucostegus halavi: Compagno *et al.* 2005.

Disc narrow and moderately long, anterolateral margins slightly convex to almost straight; disc length ~40% TL, disc width ~1.4 in disc length. Snout bluntly triangular and somewhat short, preorbital length ~13% TL; 2 folds at rear edge of spiracles, inner fold rudimentary. Small tubercles on rostral ridges, and around eyes and spiracles; large blunt tubercles in median dorsal row.

Body plain tan dorsally, and margins slightly paler; large translucent area on each side of snout; white ventrally. Attains 171 cm TL.



Glaucostegus halavi, ~1 m TL, mature male (Red Sea).

DISTRIBUTION WIO: Red Sea, Gulf of Oman, and probably Gulf of Aden and other areas of northeastern Arabian Sea; reports from Mediterranean Sea and elsewhere in Indo-Pacific need confirmation.

REMARKS Litters of up to 10; size at birth ~29 cm TL; males mature at ~83 cm TL. Coastal, in shallow inshore waters and sheltered bays, to ~40 m deep; young observed in very shallow water washing onto beach with breakers and then sliding back into water. Aggregates during spawning. Feeds mostly on small crustaceans. A target species and utilised bycatch mainly in artisanal fisheries.

Glaucostegus obtusus (Müller & Henle 1841)

Widenose guitarfish PLATE 60

Rhinobatus (*Rhinobatus*) *obtusus* Müller & Henle 1841: 122, Pl. 37 (Puducherry, India).
Rhinobatos obtusus: Compagno & Last 1999*; Sujatha 2002*; Manilo & Bogorodsky 2003.
Glaucostegus obtusus: Compagno *et al.* 2005.

Disc moderately broad and moderately long, anterolateral margins slightly convex; disc length ~41% TL, disc width ~1.1 in disc length. Snout triangular, obtusely angular and short, preorbital length ~14% TL; 1 weak fold at rear edge of spiracles. Small tubercles on rostral ridges, around eyes, on shoulders, and in median dorsal row; tubercles stronger in young and reduced or absent in adults (often limited to series of few small ones on midback).

Body plain brown to greenish brown dorsally, and margins reddish brown; white ventrally. Attains 93 cm TL.

DISTRIBUTION Indo-Pacific. WIO: Pakistan to India and Sri Lanka; reports from South Africa (KwaZulu-Natal) are probably misidentifications; elsewhere to Indonesia.

REMARKS Biology unknown, other than litters of 2–16. Coastal, inshore and offshore over continental shelf. Previously moderately abundant, now irregularly taken in local fisheries.

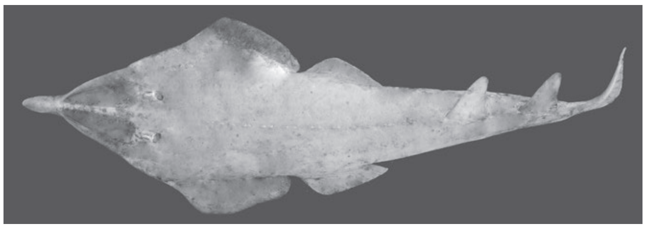
Glaucostegus thouin (Anonymous [Lacepède] 1798)

Clubnose guitarfish PLATE 60

Raja thouin Anonymous [Lacepède] 1798: 287, 677, 685, Pl. 1, Figs. 2–4 [probably Indonesia].
Rhinobatos thouin: Compagno & Last 1999*; Bonfil & Abdallah 2004*; Yano *et al.* 2005*; White *et al.* 2006*.
Glaucostegus thouin: Compagno *et al.* 2005; Last *et al.* 2010*.

Disc rather narrow and moderately long, anterolateral margins almost straight; disc length ~42% TL, disc width ~1.3 in disc length. Snout acutely triangular and long, tip distinctly extended as club-like knob; preorbital length (including knob) ~18% TL; 2 weak folds at rear edge of spiracles. Small tubercles around eyes and spiracles, 2 on each shoulder, and larger irregular tubercles in median dorsal row.

Body plain greyish brown to olive-brown dorsally, and pectoral- and pelvic-fin margins paler; entire snout translucent on each side of rostral cartilage, but snout tip sometimes greyish; white ventrally. Attains 3 m TL.



Glaucostegus thouin (SW India). KK Bineesh © CMFRI

DISTRIBUTION Indo-Pacific. WIO: Red Sea and southwestern India; elsewhere, Thailand, Vietnam, Indonesia and New Guinea.

REMARKS Biology unknown. Coastal, inshore, mainly in shallow water <60 m deep; juveniles inhabit sand flats and mangrove estuaries. Feeds primarily on shellfishes. Previously moderately abundant, now irregularly taken in artisanal and commercial fisheries.

Glaucostegus typus (Anonymous [Bennett] 1830)

Giant shovelnose ray

PLATE 61

Rhinobatus typus Anonymous [Bennett] 1830: 694 (Sumatra, Indonesia; India).
Rhinobatos typus: Compagno & Last 1999*; Bonfil & Abdallah 2004*; White *et al.* 2006*.
Glaucostegus typus: Compagno *et al.* 2005; Last & Stevens 2009*; Last *et al.* 2010*; Kottelat 2013.

Disc rather narrow and moderately long, anterolateral margins almost straight to slightly concave; disc length ~41% TL, disc width ~1.3 in disc length. Snout bluntly triangular and moderately long, preorbital length ~17% TL; 2 weak folds at rear edge of spiracles. Small tubercles around eyes and spiracles, and larger irregular tubercles in median dorsal row.

Body plain greyish brown to olive-brown dorsally, and pectoral- and pelvic-fin margins paler; snout tip sometimes darker grey; white ventrally. Attains at least 270 cm TL, probably more.

DISTRIBUTION Indo-Pacific (widespread). WIO: southern India and Sri Lanka; elsewhere to Thailand, Indonesia, Philippines and northern Australia.

REMARKS Size at birth 30–40 cm TL; matures at 150–180 cm TL. Juveniles often found in mangroves, estuaries and coastal lagoons; adults occur inshore, over continental shelf, to ~100 m deep, and also the only rhinobatid reportedly able to live and breed in freshwater. Feeds primarily on crustaceans (crab, prawns) and also small bony fishes. Previously moderately abundant, now irregularly taken in local fisheries.

ORDER RAJIFORMES

FAMILY RAJIDAE

Hardnose skates

Neil C Aschliman and David A Ebert

Small- to large-sized skates (up to ~250 cm TL). Head and body depressed, with wing-like pectoral fins forming flattened rhomboidal disc; snout pointed, short and rounded to long and angular. Five pairs of gill slits on underside of head. Mouth small, with numerous small teeth in powerful jaws. Pelvic fins deeply notched, divided into anterior and posterior lobes. Tail rather slender but not whip-like, with usually 2 small dorsal fins near tail tip (rarely 1 or none), and reduced caudal fin; most species with one or more rows of enlarged denticles or thorns from mid-dorsal disc to tail, but no stinging spine. Trunk vertebrae 22–44, predorsal caudal vertebrae 29–81.

Speciose and morphologically diverse but poorly defined with no unambiguous characters uniting current members of the family. However, the snout is typically rigid (unlike softnose skates, family Arhynchobatidae) and supported by stiff cartilage, and in several genera the rostral bar is attenuated and extended. The distribution and size of spinules, enlarged denticles or thorns on the dorsal surface of the disc and tail, are important characters for distinguishing species (see thorn patterning diagram in the chapter on **Anatomy of sharks, rays and chimaeras**). While external morphology is difficult to use in distinguishing hardnose skates from softnose skates, anatomical characters defining (but not exclusive to) Rajidae include: scapulocoracoid lacking anterior bridge, clasper expanded distally (3–9 terminal cartilages), and clasper glans with component rhipidion.

Reproductive mode oviparity; females may deposit an estimated 50–300 or more dark brown, keratinous egg cases annually. Adult males typically have small hooked malar spines or thorns, used to clasp females. Found in estuaries and inshore habitats on continental shelf as well as on continental slope to >4 000 m deep. Mostly feed on bottom-living invertebrates and fishes. Skates have been the subject of target and non-targeted fisheries worldwide; mostly taken as bycatch in WIO. Some species are of commercial interest as skate 'wings' are considered good eating.

Worldwide in all seas. Currently the largest family of batoids, with 16 genera and at least 158 valid species; 8 genera and at least 23 species in WIO, of which 5 are from deep water.

KEY TO GENERA

1a Tip of snout firm and not flexible; anteriormost extension of pectoral fins distinctly separated from snout by semi-translucent area **2**

1b Tip of snout rather flexible; anteriormost extension of pectoral fins (abutting or nearly abutting tip of snout) not separated from snout by semi-translucent area .... ***Neoraja***

2a Snout moderately to distinctly elongated; anterolateral margins of disc concave (except in *Okamejei heemstrai*, but colour pattern distinguishes this species from *Dipturus* and *Rostroraja*); internarial width usually <70% of distance from tip of snout to front edge of nostrils **3**

2b Snout generally not elongated; anterolateral margins of disc straight to moderately convex; internarial width usually >70% of distance from tip of snout to front edge of nostrils **4**

3a Pores on ventral surface of disc darkly pigmented .... ***Dipturus***

3b Pores on ventral surface of disc not darkly pigmented .... ***Rostroraja***

4a Triangular thorn patch over nuchal and scapular areas **5**

4b No distinct triangular thorn patch over nuchal and scapular areas (except some species of *Raja* with several nuchal thorns and 1 or 2 scapular thorns) **6**

5a Thorns similarly sized in 1 to several rows along mid-dorsal disc and tail in juveniles and adults .... ***Rajella***

5b Thorns in several rows along mid-dorsal disc and tail, and median row either smaller than lateral row(s) or absent in large juveniles and adults .... ***Leucoraja***

6a Pores on ventral surface of disc darkly pigmented .... ***Okamejei***

6b Pores on ventral surface of disc not darkly pigmented **7**

7a Snout very short and broad; tooth rows in upper jaw <61 .... ***Raja***

7b Snout moderately elongate and angular; tooth rows in upper jaw 61–76 .... ***Orbiraja***

GENUS *Dipturus* Linnaeus 1758

This genus is in need of revision as most characters currently used to distinguish *Dipturus* from *Okamejei* are not useful. Disc quadrangular, moderately broad to broad; pectoral-fin apex angular to slightly rounded. Snout acutely triangular and long to very long (generally >60% HL). Eyes relatively small, eye diameter less than interorbital space. Pelvic-fin anterior lobes moderately long to long and approaching length of posterior lobes. Tail relatively short to moderately long, moderately stout and often slightly broader at midlength. Disc with patterns of few small to moderately small thorns, otherwise smooth. Thorns (when present): 1 preorbital and ~9 orbital, 1 to several scapular and/or nuchal, and 1 median row in males and 3–5 median and lateral rows in females. Trunk vertebrae 30–35, predorsal caudal vertebrae 42–72. Egg cases >6.5 cm long excluding horns. Disc generally brown to almost black dorsally, and plain or vaguely patterned; pale grey to greyish brown ventrally, with darkly pigmented pores. Size up to ~200 cm TL. Worldwide, except for northeastern and tropical western Pacific, and most diverse in southeastern Atlantic (off southern Africa) and in South Pacific (off Australia). Depth range mostly ~40–1 000 m. About 50 species, 8 in WIO (2 of the species are from deep water and have no species accounts).

KEY TO SPECIES

1a Tail relatively long and slender, width at 1st dorsal-fin origin <½ width at base **2**
1b Tail not long and slender, width at 1st dorsal-fin origin >½ width at base **3**

2a Pelvic-fin anterior lobes not extending to rear edge of posterior lobes; tail length from 2nd dorsal-fin insertion to tail tip <5% TL ..... ***D. lanceorostrata*** [deep water, from 430–439 m]
2b Pelvic-fin anterior lobes extending to or beyond rear edge of posterior lobes; tail length from 2nd dorsal-fin insertion to tail tip >5% TL ..... ***D. johannisdavisi***

3a Ventral surface of disc broadly covered with denticles ..... ***D. springeri***
3b Ventral surface of disc not broadly covered with denticles, although enlarged denticles may occur on snout and along anterior margins **4**

4a Tail relatively short; distance from snout tip to rear edge of cloaca equal to or greater than sum of distances from rear edge of cloaca to tail tip, and from snout tip to front edge of upper jaw ..... ***D. doutrei***
4b Tail relatively long; distance from snout tip to rear edge of cloaca less than sum of distances from rear edge of cloaca to tail tip, and from snout tip to front edge of upper jaw **5**

5a Snout very long and greatly extended; distance from snout tip to front edge of eyes ~5.5 times interorbital width; preoral snout ~3 times internarial space ..... ***D. stenorhynchus***
5b Snout moderately long and moderately extended; distance from snout tip to front edge of eyes 3–4.5 times interorbital width; preoral snout <2.5 times internarial space **6**

6a Dorsal surface medium brown to greyish brown and without small dark spots; no median row of thorns on rear half of disc and tail ..... ***D. crosnieri*** [deep water, from 300–850 m]
6b Dorsal surface pale brown and scattered with small dark spots; median row of thorns on rear half of disc and tail **7**

7a Nuchal thorns 2, poorly developed; disc width (DW) at level of eyes 1.7–1.9 times preorbital length ..... ***D. campbelli***
7b Nuchal thorn 1, well-developed; disc width (DW) at level of eyes 2.3–2.5 times preorbital length ..... ***D. pullopunctatus***

Dipturus campbelli (Wallace 1967)

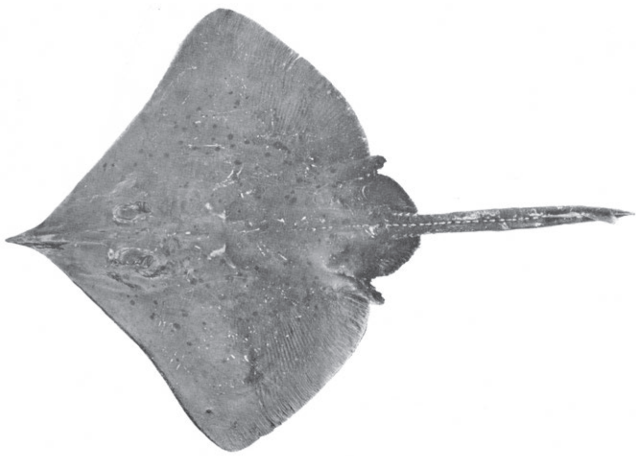
Blackspot skate

PLATE 61

Raja campbelli Wallace 1967: 24, Fig. 12 (KwaZulu-Natal, South Africa).
Raia pullopunctata Smith 1964: 285, Pl. 25a [in part].
Raja pullopunctata: SSF No. 25.15*.
Raja (*Dipturus*) *campbelli*: Séret 1989.
Dipturus campbelli: McEachran & Dunn 1998; Compagno 1999, 2005; Heemstra & Heemstra 2004; Compagno & Ebert 2007*; Ebert *et al*. 2008; Last 2008.

Disc rather narrow, DW <60% TL; pectoral-fin apex weakly angular. Snout acutely triangular and moderately extended; length 17–20% TL. Teeth in upper jaw 45. Pelvic-fin anterior lobes moderately long, not reaching rear edge of posterior lobes. Tail relatively short, slightly shorter than distance from snout tip to rear edge of cloaca, and moderately wide over its length or slightly broader at midlength than at its base. Ventral surface with enlarged denticles on anterior margins of disc and snout tip. Dorsal surface with ~7 orbital thorns, 1 or 2 nuchal, in median row on mid-dorsal disc to 1st dorsal fin, 1 interdorsal, and short lateral row on tail.

Disc brown to medium grey dorsally, with scattered small dark spots; grey ventrally, with conspicuous black pores. Attains 66 cm TL.



Dipturus campbelli, 66 cm TL, female holotype (South Africa).
Source: Wallace 1967

DISTRIBUTION WIO: possibly endemic to South Africa (KwaZulu-Natal) and southern Mozambique.

REMARKS Size at hatching <18 cm TL. Males mature by 56 cm TL, and females by 63 cm TL. Poorly known with patchy, limited distribution; found over outer continental shelf to upper slope, at 137–403 m. Probably caught incidentally by trawlers. IUCN Red List conservation status Near Threatened.

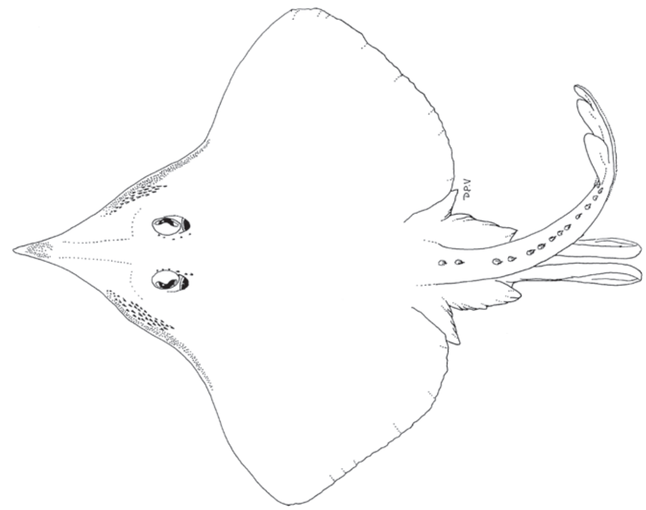
Dipturus doutrei (Cadenat 1960)

Javelin skate PLATE 61

Raja doutrei Cadenat 1960: 294, Figs. 1–11, 13, 15 (Senegal); Hulley 1970*.
Raja (*Dipturus*) *doutrei*: Hulley 1972*; Lloris 1982; SSF No. 25.11*; Séret 1989; Stehmann 1990, 1995; Compagno *et al.* 1991; Bianchi *et al.* 1993.
Dipturus doutrei: McEachran & Dunn 1998; Compagno 1999, 2005; Compagno & Ebert 2007*; Ebert *et al.* 2008; Last 2008.

Disc angular and broad, DW 72–75% TL; pectoral-fin apex narrowly rounded. Snout distinctly extended, acutely triangular and long, ~20% TL. Teeth in upper jaw 27–35. Pelvic-fin anterior lobes moderately long, not extending to rear edge of posterior lobes. Tail relatively short, shorter than distance from snout tip to rear edge of cloaca, and relatively broad at base and slightly broader at midlength. Ventral surface with enlarged denticles along anterior margins of disc and on snout. Dorsal surface with 6 or 7 small orbital thorns, 13–26 in median row on tail to 1st dorsal fin, and 1 or 2 interdorsal; females with lateral row of thorns on tail. Predorsal caudal vertebrae 43–49.

Disc dark brown dorsally, with scattered irregular darker blotches, and blackish towards tail tip; brown ventrally, with black pores and scattered paler patches. Attains ~115 cm TL; males mature at ~101 cm TL (Last *et al.* 2016).



Dipturus doutrei, 62 cm DW (Namibia). Source: SSF

DISTRIBUTION Eastern Atlantic (Mauritania to South Africa), and just rounding Cape of Good Hope (South Africa) into WIO.

REMARKS Little known; found over outer continental shelf to deep slope, at 163–1 200 m (usually 450–600 m). Some records may be misidentifications of *D. springeri*. A bycatch of deepwater trawl fisheries for bony fishes. Diet includes benthic bony fishes, shrimp and crabs.

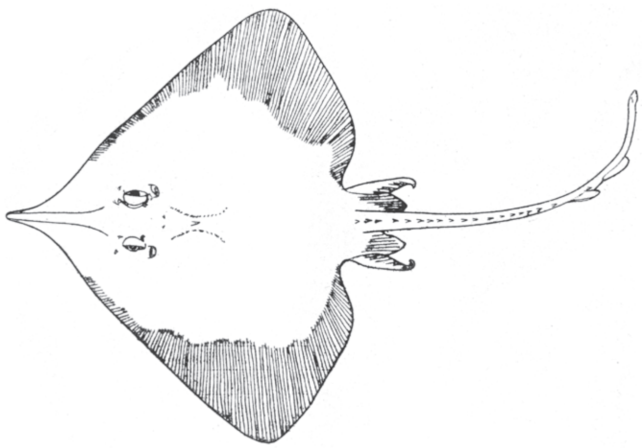
Dipturus johannisdavisi (Alcock 1899)

Travancore skate PLATE 62

Raja johannisdavisi Alcock 1899: 21 (Laccadive Sea, off India); Alcock 1900 [Fig.].
Raja (*Dipturus*) *johannisdavisi*: Stehmann 1976; Séret 1986, 1989.
Dipturus johannisdavisi: McEachran & Dunn 1998; Compagno 1999, 2005; Manilo & Bogorodsky 2003; Last 2008.

Small-sized with moderately broad disc, DW 55–66% TL; pectoral-fin apex slightly angular. Snout distinctly extended and moderately long, length 18–19% TL. Teeth in upper jaw 36–42. Pelvic-fin anterior lobes long and extending beyond rear edges of posterior lobes. Tail relatively long, equal to or greater than distance from snout tip to rear edge of cloaca, and narrow at base and slightly attenuated distally. Ventral surface with enlarged denticles along anterior margins of disc and on snout. Dorsal surface with 2 or 3 preorbital and 1 or 2 post-orbital thorns, in median row on tail, and 1 interdorsal.

Disc uniformly dark brownish black dorsally and ventrally. Attains at least 54 cm TL (Last *et al.* 2016).



Dipturus johannisdavisi (India). Source: Alcock 1900

DISTRIBUTION WIO: Gulf of Aden (Yemen), Lakshadweep and India (Travancore coast); a record from Tanzania (Zanzibar) is questionable.

REMARKS Found over continental slope; known from 220–660 m (Last *et al.* 2016).

Dipturus pullopunctatus (Smith 1964)

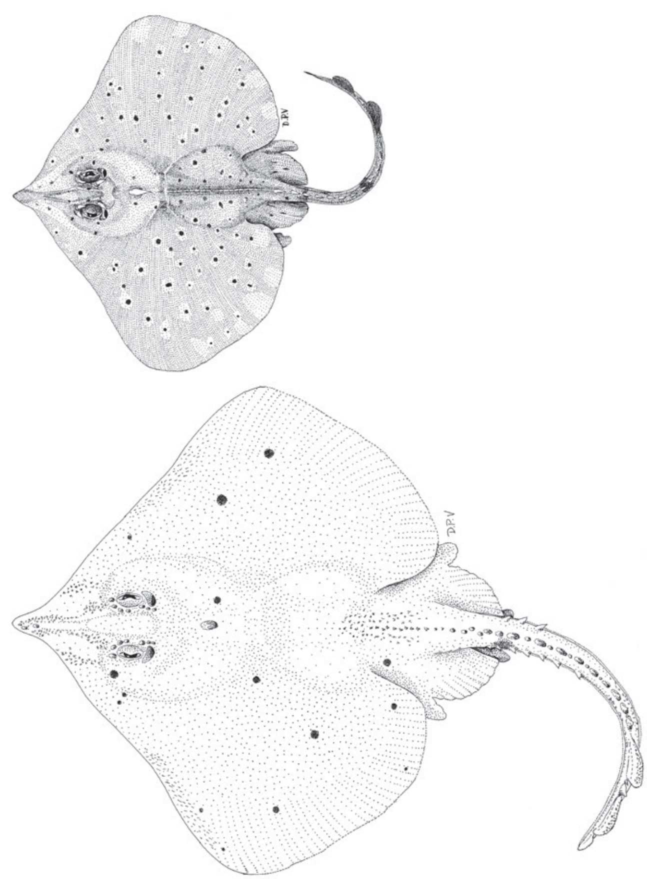
Slime skate

PLATE 62

Raia pullopunctata Smith 1964: 285, Pl. 25a (Algoa Bay, Eastern Cape, South Africa).
Raja pullopunctata: Hulley 1966*, 1970*; Wallace 1967*.
Raja (*Dipturus*) *pullopunctata*: Hulley 1972*; SSF No. 25.15*; Séret 1989; Compagno *et al*. 1991; Ebert *et al*. 1991; Bianchi *et al*. 1993; Stehmann 1995; Walmsley-Hart *et al*. 1999.
Dipturus pullopunctatus: McEachran & Dunn 1998; Compagno 1999, 2005.
Dipturus pullopunctata: Heemstra & Heemstra 2004; Compagno & Ebert 2007*; Ebert *et al*. 2008*; Last 2008.

Disc angular, DW 1.2–1.4 times disc length and 76–78% TL; pectoral-fin apex broadly rounded. Snout moderately extended, acutely triangular and long, length 15–17% TL and 3.4–4 times interorbital space; angle anterior to spiracles 92°–108°. Jaws moderately large and strong. Teeth in upper jaw 53–58; teeth sharp and pointed in males, rounded in females. Pelvic-fin anterior lobes moderately long, not extending to rear edge of posterior lobes. Tail moderately long, about equal to distance from snout tip to rear edge of cloaca, and narrow at base and slightly attenuated distally. Thorns in juveniles: 2 preorbital and 1 post-orbital, 1 enormous nuchal, 8–12 in median row on mid-dorsal disc to 1st dorsal fin, and 1 interdorsal. Thorns in adults: 3–8 small orbital, 1 or 2 typically extremely large nuchal, 8–12 in median row on mid-dorsal disc to 1st dorsal fin, and 1 or 2 interdorsal; ventral surface with spinules on snout tip, internasal area and anterior margins of disc. Egg cases very large, ~13 cm long excluding horns; surface striated and covered with dense fibres; broad lateral keels; horns tapering, with anterior horns hook-like and slightly longer than inward-curving posterior horns. Predorsal caudal vertebrae 50–58.

Disc tan or pale brown dorsally, with widely spaced small dark spots (especially in juveniles, maybe lost in adults), and sometimes surrounded by paler ring or small white spots (especially in adults); usually with very large dark blotch at each pectoral-fin base; greyish ventrally, with black pores. Attains 125 cm TL (females reach larger sizes than males).



Dipturus pullopunctatus, 14 cm DW, juvenile holotype (top); 52 cm DW, mature male (bottom; both South Africa). Source: SSF

DISTRIBUTION Southern Africa: Namibia (Lüderitz) in southeastern Atlantic, to Eastern Cape, Agulhas Bank (off South Africa) and possibly to Mozambique (Bazaruto) in WIO.

REMARKS Size at hatching <19 cm TL. Males mature at 88–96 cm TL; females' maturation and maximum size vary widely between populations: off the west coast of South Africa, females mature at 100–111 cm TL and attain 125 cm, and off the south coast, females mature at 78–82 cm TL and attain only 103 cm. Occurs over shallow continental shelf to upper slope, at 15–457 m (usually 100–300 m). Becomes extremely slippery when handled. Feeds mostly on benthic fishes, crabs, mysids, mantis shrimp, krill, bivalves and cuttlefish. Commonly taken in hake-directed longline and trawl fisheries but not in large quantities.

Dipturus springeri (Wallace 1967)

Roughbelly skate

PLATES 62 & 63

Raja springeri Wallace 1967: 18, Figs. 9–10 (KwaZulu-Natal, South Africa).
Raja (*Dipturus*) *springeri*: Hulley 1972*; SSF No. 25.20*; Séret 1989; Compagno *et al.* 1991; Ebert *et al.* 1991; Bianchi *et al.* 1993; Stehmann 1995.
Dipturus springeri: McEachran & Dunn 1998; Compagno 1999, 2005; Compagno & Ebert 2007*; Ebert *et al.* 2008; Last 2008.

Large-sized with very broad disc, DW ~1.4 times disc length and 80–85% TL; pectoral-fin apex acutely angled. Snout triangular and long, length 19–23% TL and 4.8–5.1 times interorbital space; angle anterior to spiracles ~85°. Teeth sharp, cuspidate; 35–40 in upper jaw. Pelvic-fin anterior lobes long, extending to or beyond rear edge of posterior lobes. Tail relatively short, shorter than distance from snout tip to rear edge of cloaca, and narrow at base and not attenuated distally or else slightly broader at midlength. Ventral surface densely covered with small denticles. Dorsal surface with 2–7 small orbital thorns, no nuchal thorns, ~15 in median row on tail to 1st dorsal fin, and 2 interdorsal. Predorsal caudal vertebrae 53–56.

Disc dark grey dorsally and ventrally; pores on ventral surface black. Attains 190 cm TL (females reach larger sizes than males).

Dipturus springeri, 27 cm DW, 34 cm TL (Kenya). Source: SSF

DISTRIBUTION Southern Africa: Namibia (Lüderitz) in southeastern Atlantic, to South Africa, Mozambique, Kenya and off Madagascar in WIO.

REMARKS Size at hatching <27 cm TL; slow-growing. Males mature at 125–134 cm TL, and females at 171–190 cm TL. Uncommon, in scattered localities; occurs on outer continental shelf to slope, at 50–970 m. Diet includes fishes (rattails, round herring), crustaceans and squid.

Dipturus stenorhynchus (Wallace 1967)

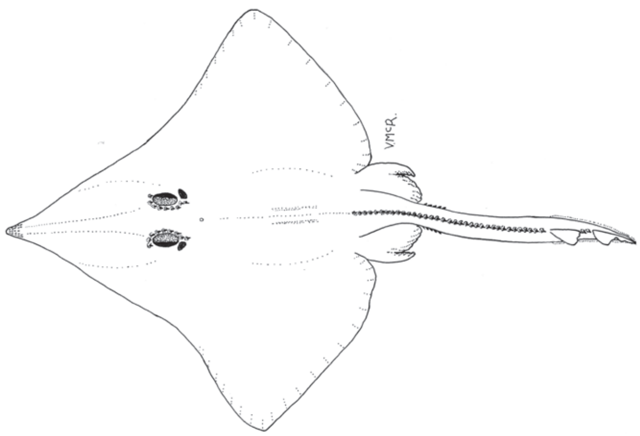
Prownose skate

PLATE 63

Raja stenorhynchus Wallace 1967: 23, Fig. 11 (east of False Bay, South Africa).
Raja (*Dipturus*) *stenorhynchus*: Hulley 1972*; SSF No. 25.21*; Séret 1989.
Dipturus stenorhynchus: McEachran & Dunn 1998; Compagno 1999, 2005; Compagno & Ebert 2007*; Ebert *et al.* 2008; Last 2008.

Disc broad, DW ~1.1 times disc length and 60–66% TL; pectoral-fin apex angular. Snout acutely triangular and greatly elongated, length 21–24% TL and ~5.5 times interorbital width; angle anterior to spiracles ~64°. Teeth in upper jaw 38. Pelvic-fin anterior lobes moderately long, almost reaching rear edge of posterior lobes. Tail moderately short, shorter than distance from snout tip to rear edge of cloaca, and moderately narrow at base, often slightly broader at midlength, and triangular in cross-section. Ventral surface with enlarged denticles along anterior margins of disc and near front of snout. Dorsal surface with cluster of small denticles on snout tip, 9–11 small orbital thorns, 1 nuchal thorn, ~35 thorns in median row on tail, 4 or 5 laterally thorns near base of tail, and 1 interdorsal thorn. Predorsal caudal vertebrae 49.

Disc dark grey dorsally and ventrally; pores on ventral surface black. Attains 60+ cm DW, 105 cm TL.



Dipturus stenorhynchus, 60 cm DW, female holotype (S Mozambique). Source: SSF

DISTRIBUTION WIO: South Africa (False Bay to KwaZulu-Natal) and central Mozambique.

REMARKS Poorly known from few specimens. Size at hatching <24 cm TL. Males mature at 83–98 cm TL, and females at >50 cm TL. Occurs over edge of continental shelf and slope, at 253–761 m; may be more widespread in deeper water.

GENUS *Leucoraja* Malm 1877

Disc heart-shaped and moderately broad to broad, DW usually >52% TL; pectoral-fin apex narrowly to broadly rounded. Snout moderately short and broad, with tip slightly produced as small oblique process. Eyes moderately sized, eye diameter slightly less to slightly more than interorbital space. Pelvic-fin anterior lobes usually much shorter than (rarely about as long as) posterior lobes. Tail relatively short, length generally <60% TL, and relatively broad at base and attenuated distally. Dorsal fins rather large, and not separated at bases or separated by distance <½ length of 1st dorsal-fin base. Dorsal surface sparsely to densely covered with coarse denticles, generally denser in juveniles than in adults; moderate-sized thorns on snout tip, along orbital rim, medial to spiracles, in triangular patch on nuchal and scapular area, and along mid-dorsal disc to tail in several fairly regular rows, with median row reduced or absent in large juveniles and adults. Body tan to dark grey or brown dorsally, and either plain or patterned with spots, bars or ocelli; pale ventrally, and plain or with dark blotches. Predorsal caudal vertebrae 64–81. Size up to ~150 cm TL. Primarily limited to North Atlantic, tropical and eastern South Atlantic and Indian oceans. Found on continental shelf and upper slope, from shoreline to ~600 m deep. Thirteen species, 2 in WIO, and 1 undescribed species known from Madagascar Ridge in 750–1 050 m (S Weigmann, pers. comm.).

KEY TO SPECIES

1a Pelvic-fin anterior lobes about as long as posterior lobes; dorsal-fin bases not separated; teeth in upper jaw 38 .... ***L. compagnoi***

1b Pelvic-fin anterior lobes much shorter than posterior lobes; dorsal fins separated by small interspace; teeth in upper jaw 59–69 .... ***L. wallacei***

Leucoraja compagnoi (Stehmann 1995)

Tigertail skate

PLATE 63

Raja (*Leucoraja*) *compagnoi* Stehmann 1995: 43, Fig. 10 (Strandfontein, Western Cape, South Africa).
Leucoraja compagnoi: McEachran & Dunn 1998; Compagno 1999, 2005; Compagno & Ebert 2007*; Ebert *et al.* 2008; Last *et al.* 2008.

Disc moderately narrow, DW ~56% TL; pectoral-fin apex broadly rounded. Snout obtuse and moderately long, length ~11% TL. Teeth in upper jaw 38. Pelvic-fin anterior lobes long, approximately reaching rear edge of posterior lobes. Tail moderately long, length ~57% TL, and moderately broad at base and attenuated distally. No interdorsal space. Thorns numerous and small along orbital rim, in triangular patch over nuchal and scapular area, and in several rows from shoulder to 1st dorsal fin, with thorns in parallel rows larger than those along midline.

Disc tan to medium brown dorsally; white ventrally. Maximum size unknown.

DISTRIBUTION South Africa: Western Cape in southeastern Atlantic, to Eastern Cape and KwaZulu-Natal in WIO.

REMARKS Likely confused with the abundant *L. wallacei,* and thus overlooked by fisheries biologists; known only from a few juvenile and subadult specimens. Size at hatching <14 cm TL. Size at maturity unknown, but the largest recorded male was an adolescent measuring ~52 cm TL, and the largest female was immature at ~29 cm TL. Found on upper continental slope, at 383–1 300 m (Weigmann 2016); adults possibly occur deeper.

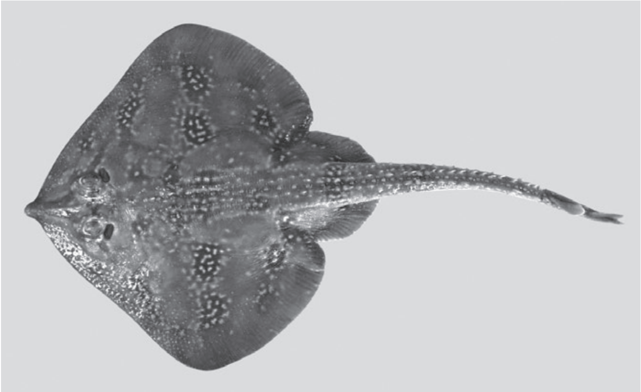
Leucoraja wallacei (Hulley 1970)

Yellowspotted skate PLATE 64

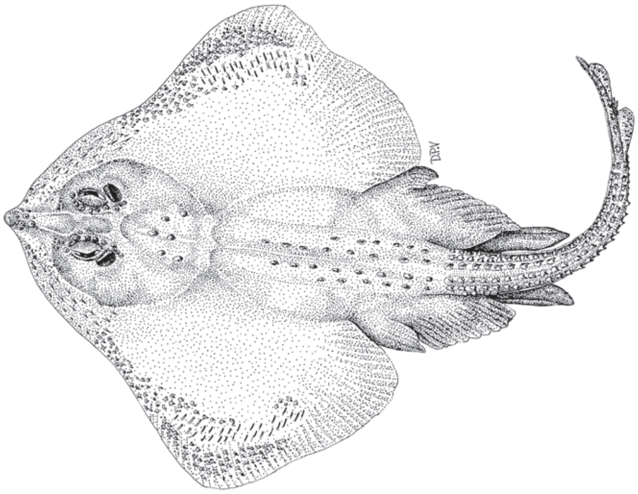
Raja wallacei Hulley 1970: 210, Pl. 12, Fig. 19 (off Cape Town, South Africa).
Raja (*Leucoraja*) *wallacei*: Hulley 1972*; SSF No. 25.23*; Compagno *et al*. 1991; Ebert *et al*. 1991.
Leucoraja wallacei: McEachran & Dunn 1998; Compagno 1999, 2005; Compagno & Ebert 2007*; Ebert *et al*. 2008*; Last *et al*. 2008.

Disc moderately broad and slightly wider than long, DW 56–62% TL; pectoral-fin apex broadly rounded. Snout short, broad and blunt, with rounded terminal process, length 9.6–11% TL and 2.3–3.1 times interorbital space; angle anterior to spiracles ~110°. Jaws fairly strong; teeth in upper jaw 59–67, cusps sharper in males than in females. Pelvic-fin anterior lobes much shorter than posterior lobes. Tail relatively long, length 53–55% TL, and moderately broad at base and attenuated distally. Interdorsal space small; 1st dorsal fin slightly larger than 2nd. Ventral surface with spinules on snout tip and anterior margins of disc. Dorsal surface with spines on snout tip, anterior margins of disc and tail; 7–10 small orbital thorns, 2 or 3 supraspiracular, on nuchal and scapular areas, ~34 large thorns in median row on disc and tail, plus lateral rows on tail; no interdorsal thorns; mid-dorsal thorns smaller, partially absent or totally absent in large juveniles and adults. Egg cases medium-sized, ~8 cm long excluding horns; surface smooth, with fine striations and no fibres; no lateral keels; posterior apron ~50% wider than anterior apron; horns taper to filamentous tips, and posterior horns about twice as long as anterior horns. Predorsal caudal vertebrae 70.

Disc yellowish brown dorsally, scattered with bright yellow spots mostly in rosettes or whorls (some specimens greyish brown with whitish spots); whitish ventrally. Attains 100 cm TL (females reach larger sizes than males).



Leucoraja wallacei, 51 cm TL (South Africa). O Alvheim © IMR



Leucoraja wallacei, 52 cm DW, 84 cm TL, male (South Africa). Source: SSF

DISTRIBUTION Southern Africa: Namibia (Lüderitz) in southeastern Atlantic, to Agulhas Bank (South Africa) and Mozambique in WIO.

REMARKS Size at hatching <16 cm TL. Males mature at 64–78 cm TL, and females at 65–81 cm TL, both sexes at ~9 years. Common; found on continental shelf to upper slope, at 70–517 m (usually 150–300 m). Feeds mostly on prawns, but also bony fishes, including dragonets (Callionymidae) and ophichthid eels. Caught incidentally in hake trawl fisheries and discarded. IUCN Red List conservation status Vulnerable.

GENUS *Neoraja* McEachran & Compagno 1982

Disc heart-shaped and relatively narrow, DW usually 50–60% TL; pectoral-fin apex broadly rounded; anterior margins of disc strongly concave to straight. Snout moderately short, length usually 8–10% TL; broadly rounded or angular, and tip slightly produced as small triangular process; anteriormost extension of pectoral fins (nearly abutting snout tip) not separated from snout by semi-translucent area. Eyes relatively large, eye diameter equal to or greater than interorbital space. Pelvic-fin anterior lobes relatively long, but not reaching rear edge of posterior lobes. Tail moderately long, length 55–60% TL, and moderately slender at base and tapering distally. Dorsal surface densely covered with fine denticles; small thorns on orbital margin, on nuchal and scapular areas (but not forming triangular patch), and on mid-dorsal disc, becoming median row and 1–3 irregular lateral rows on tail. Predorsal caudal vertebrae 65–74. Brown to greyish brown dorsally; pale with wide margin of brown to greyish brown ventrally. Dwarf skates, adults attain up to ~35 cm TL. Found on outer continental shelf and slope, at 295–1 640 m. Occurs in western central and eastern Atlantic Ocean, extending to South Africa (Eastern Cape) in WIO. Five species, 1 in WIO.

Neoraja stehmanni (Hulley 1972)

South African pygmy skate PLATES 64 & 65

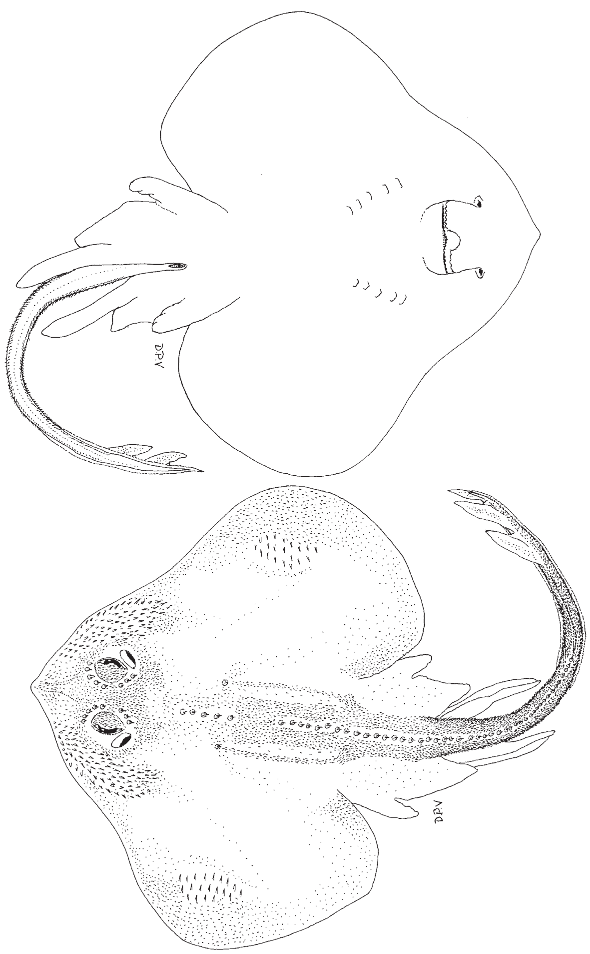
Breviraja stehmanni Hulley 1972: 254, Figs. 1–5 (Cape Basin, Atlantic Ocean).
Neoraja stehmanni: McEachran & Stehmann 1984; SSF No. 25.5*; McEachran & Dunn 1998; Compagno 1999, 2005; Compagno & Ebert 2007*; Ebert *et al*. 2008*.

Very small-sized, DW 54–58% TL; pectoral-fin apex broadly rounded. Snout obtuse and moderately short, length 8.9–11.5% TL and 2.9–3.8 times interorbital space; angle anterior to spiracles 115°–130°. Eyes large and close-set, eye diameter slightly greater than interorbital space. Pelvic-fin anterior lobes relatively long, nearly reaching rear edge of posterior lobes. Tail relatively long, length 58–60% TL, and moderately slender at base and attenuated distally. No interdorsal space; dorsal fins similar in size and shape. Jaws small; teeth in upper jaw 38–44, teeth blunt and flat in females and juveniles, and with single long, acute cusp in males. Ventral surface smooth. Dorsal surface of disc covered with denticles, also 2–10 large orbital thorns, 1–4 nuchal, and 11–38 in interrupted median row from shoulder to 1st dorsal fin. Egg cases very small; surface smooth and lacking fibres; broad lateral keels; posterior horns taper to acute inwardly pointing tips. Predorsal caudal vertebrae 65–74.

Disc greyish brown dorsally; pale ventrally, but darker on front and rear margins, on snout tip and underside of tail; 6 or 7 dark crossbars on tail. Attains 21 cm DW, 37 cm TL.

DISTRIBUTION South Africa: from Orange River mouth in southeastern Atlantic to Agulhas Bank in WIO.

REMARKS Size at hatching <15 cm TL. Matures at ~30 cm TL. Occurs on outer continental shelf, on upper to deep slope, at 102–1 025 m (usually >600 m). Its known distribution is unusually localised compared with other offshore southern African skates, but this may change with further deep-slope exploration. Diet includes shrimp. Probably taken incidentally in hake bottom-trawl fisheries.



Neoraja stehmanni, 20 cm DW, 33 cm TL (South Africa). Source: SSF

GENUS *Okamejei* Ishiyama 1958

This genus is in need of revision as most characters currently used to distinguish *Okamejei* from *Dipturus* are not useful. Disc quadrangular and moderately broad, DW usually 55–65% TL; pectoral-fin apex weakly angular. Snout acutely angled, slightly to moderately extended and moderately long, length usually 13–17% TL. Eyes moderately small, eye diameter roughly equivalent to interorbital space. Pelvic-fin anterior lobes much shorter than posterior lobes. Tail moderately long, length 44–56% TL, and moderately narrow at base and slightly tapering distally. Dorsal surface largely free of denticles; several moderate-sized thorns on orbital margin, 1 to several nuchal thorns, rarely in median row between nuchal area and base of tail, but in one to several regular or irregular rows on tail; ventral surface smooth. Predorsal caudal vertebrae 35–55. Dark brown dorsally, plain or patterned with yellowish or dark spots, rings, ocelli or reticulations; whitish ventrally, with dark margins and darkly pigmented pores. Small-sized, usually <55 cm TL. Occurs over shallow continental shelf to slope, throughout tropical to warm-temperate waters of Indo-Pacific. Twelve species, 2 in WIO.

KEY TO SPECIES

1a Dorsal surface of disc with numerous brown spots and streaks but no ocelli; complete median row of thorns from nuchal area to 1st dorsal fin, and 1 interdorsal thorn; prenasal length <10% TL; interspiracular distance >7% TL; distance between 5th gill slits >9% TL .... ***O. pita***

1b Dorsal surface of disc with or without spots and streaks, and with 2 or more ocelli; no median row of thorns between nuchal area and 1st dorsal fin, 2 interdorsal thorns; prenasal length >12% TL; interspiracular distance <6% TL; distance between 5th gill slits <8.8% TL .... ***O. heemstrai***

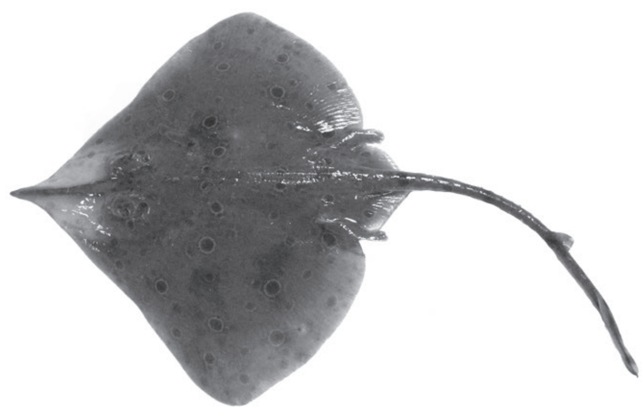
Okamejei heemstrai (McEachran & Fechhelm 1982)

East African skate PLATE 64

Raja (*Okamejei*) *heemstrai* McEachran & Fechhelm 1982: 441, Figs. 1–5 (Kenya); Séret 1989; Fricke & Al-Hassan 1995.
Okamejei heemstrai: McEachran & Dunn 1998; Compagno 1999, 2005; Jeong *et al*. 2007; Compagno & Ebert 2007*; Ebert *et al*. 2008.

Disc moderately narrow, DW 56–63% TL; anterior margins not convex. Snout very acute and relatively long, length 15–17% TL. Teeth in upper jaw 31–35. Eye diameter greater than interorbital space. Pelvic-fin anterior lobes relatively long, not reaching rear edge of posterior lobes. Tail moderately long, length 52–56% TL, and slender at base and attenuated distally. Interdorsal distance greater than length of 1st dorsal-fin base; 1st dorsal fin anteriorly set. Dorsal surface with 1–4 small orbital thorns, 1 interspiracular, 1 or 2 nuchal, in 3–5 irregular rows on tail between base and 1st dorsal fin, and 2 interdorsal. Predorsal caudal vertebrae 47–53.

Disc dark brown dorsally, with symmetrically arranged, small, bicoloured ocelli and sooty blotches on disc, pelvic fins and tail; pale grey ventrally. Attains at least 61 cm TL.



Okamejei heemstrai (Mozambique). © P Bouchet, MNHN

DISTRIBUTION WIO: Mozambique to Kenya.

REMARKS Known from few specimens; 2 mature females measured 60 and 61 cm TL. Occurs on outer continental shelf and uppermost slope, at ~200–500 m.

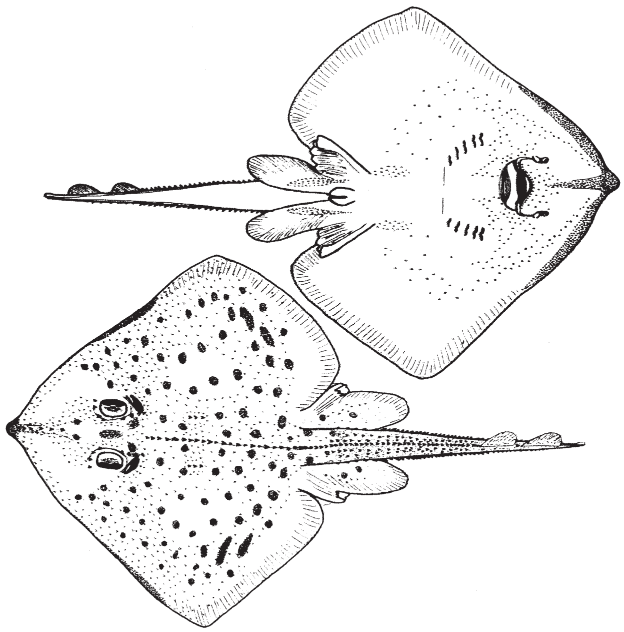
Okamejei pita (Fricke & Al-Hassan 1995)

Pita skate

Raja (*Okamejei*) *pita* Fricke & Al-Hassan 1995: 3, Figs. 1–2 (Fao, Iraq, Persian/Arabian Gulf).
Okamejei pita: McEachran & Dunn 1998; Compagno 1999, 2005; Jeong *et al*. 2007; Last & Gledhill 2008.

Holotype: disc moderately broad, DW ~64% TL; anterolateral margins slightly convex. Snout moderately acute and not extended, and moderately long, length ~15% TL. Teeth in upper jaw 46. Eye diameter less than interorbital space. Pelvic-fin anterior lobes ~¼ length of posterior lobes. Tail length ~50% TL, and relatively broad at base and attenuated distally. Interdorsal space narrow, <½ length of 1st dorsal-fin base. Dorsal surface covered with denticles except for area on centre of pectoral fins; 5 small orbital thorns, 3 medial to spiracle, ~9 nuchal, 2 scapular, ~30 in median row on mid-dorsal disc to tail, and 1 interdorsal. Predorsal caudal vertebrae 58.

Disc pale brown dorsally, with small dark brown blotches on disc and pelvic fins; pale brownish ventrally. Attains at least 46 cm TL.



Okamejei pita, 46 cm TL, female holotype (Iraq).
Source: Fricke & Al-Hassan 1995

DISTRIBUTION Known only from the holotype (female) in the Persian/Arabian Gulf.

REMARKS Collected over mud bottom in shallow water (<15 m deep). The genus for this species is uncertain, and its likely it will eventually be placed in the genus *Leucoraja* or *Rajella*. IUCN Red List conservation status Critically Endangered.

GENUS ***Orbiraja*** Last, Weigmann & Dumale 2016

Similar to and until recently included in the genus *Okamejei*. Tail with 3 well-developed rows of thorns along the midline, closely spaced and distant from lateral thorn rows. Tooth rows in upper jaw 61–76. Disc brown dorsally; pectoral fins with a pair of moderately large, ring-like ocelli. Ventral head without dark-edged pores. Small-sized, <55 cm TL. Occurs over continental shelf to slope, typically below 100 m depth, in WIO (Gulf of Aden, India) and Philippines. Three nominal species, 1 in WIO but additional undescribed species are suspected.

Orbiraja powelli (Alcock 1898)

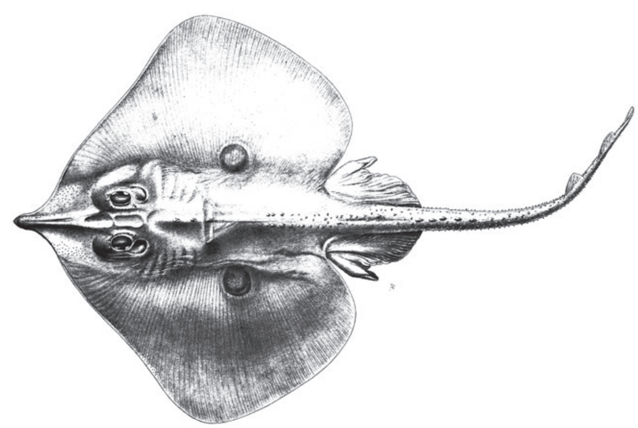
Indian ring skate

PLATE 65

Raja powelli Alcock 1898: 145 (Gulf of Martaban, Myanmar); Alcock 1899 [Fig.].
Raja (*Okamejei*) *powelli*: Stehmann 1976; McEachran & Fechhelm 1982; Séret 1989; Fricke & Al-Hassan 1995.
Okamejei powelli: McEachran & Dunn 1998; Compagno 1999, 2005; Manilo & Bogorodsky 2003; Jeong *et al.* 2007; Last & Gledhill 2008.
Orbiraja powelli: Last *et al.* 2016*.

Small-sized with moderately broad disc, DW 61–63% TL; anterolateral margins slightly convex. Snout very acute, extended and relatively long, length 15–16% TL. Teeth in upper jaw 72–75. Eye diameter less than interorbital space. Pelvic-fin anterior lobes ~¾ length of posterior lobes. Tail moderately long, length ~52% TL, and slender at base and attenuated distally. Interdorsal space greater than length of 1st dorsal-fin base; 1st dorsal fin anteriorly set. Dorsal surface with 3–5 small orbital thorns, 3 nuchal, 24–33 in irregular row on tail, and 5 or 6 interdorsal. Predorsal caudal vertebrae 49–55.

Disc orange-brown to dark brown dorsally, with scattered paler spots overall, and large circular target-like eyespot at each pectoral-fin base. Attains 53 cm TL (Last *et al.* 2016).



Orbiraja powelli (India). Source: Alcock 1899

DISTRIBUTION Indian Ocean: Gulf of Aden (Yemen) and India (Travancore coast).

REMARKS Possibly the same species as *Orbiraja philipi* (Lloyd 1906) from the Gulf of Aden (collected from ~250 m). Poorly known; occurs on continental shelf and upper slope, at 15–460 m. Caught rarely in demersal longlines and used for its meat. IUCN Red List conservation status Near Threatened.

GENUS *Raja* Linnaeus 1758

Disc quadrangular, moderately broad to broad, DW generally 63–75% TL; pectoral-fin apex weakly angular to angular. Snout obtusely angled to rounded, slightly extended and moderately long. Eyes relatively small, eye diameter slightly less than interorbital space. Pelvic-fin anterior lobes considerably shorter than posterior lobes. Tail moderately short, and moderately broad at base and attenuated distally. Dorsal surface largely free of denticles; 2–6 orbital thorns (usually separated into anterior and posterior groups), 1–4 nuchal, 0–1 scapular, in median row on mid-dorsal disc to tail (row on disc may be interrupted or absent), and generally 1 or 2 interdorsal. Predorsal caudal vertebrae 45–69. Disc generally brown to dark brown dorsally, and patterned with pale or dark spots, dark bars or ocelli; white to dusky ventrally, with or without darker disc margins. Size range ~50–120 cm TL. This genus is in need of revision. *Raja* proper occurs in the eastern Atlantic and southwestern Indian oceans, and Mediterranean Sea; another assemblage occurs in the North Pacific, and another amphi-American group in the eastern Pacific and western Atlantic oceans. Currently 27–30 species recognised, 2 in WIO.

KEY TO SPECIES

1a	Dorsal surface of disc scattered with faint brown spots, particularly along fin margins; circular or nearly circular, blue-black eyespot, with 3 distinct rings of colour, at each pectoral-fin base .... ***R. ocellifera***
1b	Dorsal surface of disc scattered with black spots; sometimes with transversely oblong, gold and black eyespot at each pectoral fin-base .... ***R. straeleni***

Raja ocellifera Regan 1906

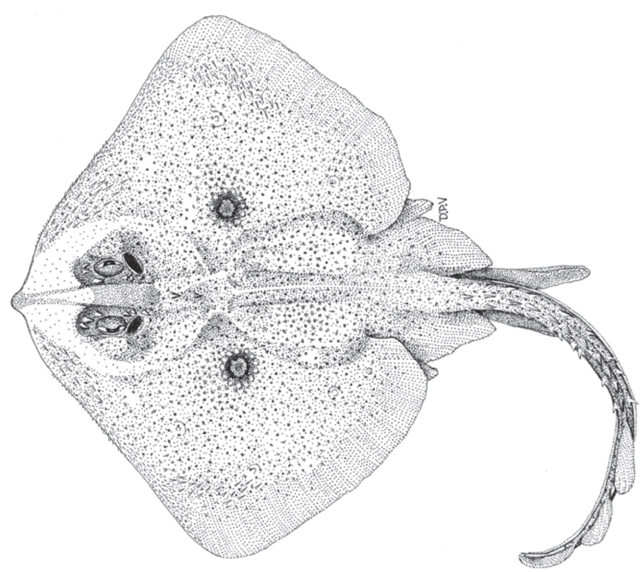
Twineye skate

PLATE 65

Raja miraletus (*non* Linnaeus 1758): Wallace 1967*; Hulley 1969*; McEachran & Dunn 1998; Compagno 1999, 2005; Heemstra & Heemstra 2004; Compagno & Ebert 2007*; Ebert *et al*. 2008*.
Raja (*Raja*) *miraletus* (*non* Linnaeus 1758): Hulley 1972*; Lloris 1982; SSF No. 25.14*.
Raia ocellifera Regan 1906: 2, Pl. 2 (Algoa Bay, South Africa); SFSA No. 69*; Smith 1964.
Raja ocellifera: Last *et al*. 2016*.

Small-sized with angular disc; DW ~1.3 times disc length. Snout short, with rounded terminal process, length 2.2–2.5 times interorbital space; angle anterior to spiracles 110°–116°. Teeth in upper jaw 36–46. Eyes close-set. Distance from mid-vent to 1st dorsal-fin origin 1.1–1.4 times distance from snout tip to mid-vent. Juveniles with some scapular thorns (diminishing with growth), but largely without spines or denticles on dorsal and ventral surfaces. Thorns in adults: 2 or 3 preorbital and 2 post-orbital, 2 or 3 nuchal, 20–23 in median row on tail (from pelvic-fin area to 1st dorsal fin), and 0–2 interdorsal; adults with spinules on ventral surface of snout, otherwise dorsal and ventral disc surfaces smooth. Females with 2 lateral rows of large thorns, one on either side of tail. Egg cases oblong and very small, <5 cm long excluding horns; surface smooth but densely covered in fibres with fine striations beneath; no lateral keels; posterior apron ~1.3 times length of anterior apron; horns stout and equal in length; posterior horns taper to filamentous tips, anterior horns hook-like and taper to acute tips. Predorsal caudal vertebrae 46–48.

Disc reddish brown dorsally, with scattered faint brown spots, particularly along fin margins; large blue-black eyespot with 3 distinct rings of colour at each pectoral-fin base; whitish ventrally, sometimes with small dark spot on snout tip. Attains ~50 cm TL.



Raja ocellifera, 28 cm DW, 42 cm TL, male (South Africa). Source: SSF

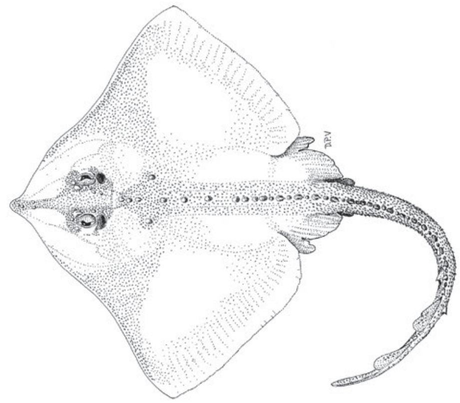
DISTRIBUTION WIO: South Africa (Cape Point, Western Cape, to Thukela Bank, KwaZulu-Natal, and abundant on Agulhas Bank).

REMARKS Smallest free-swimming specimen ~27 cm TL; hatchling size unknown. Males mature at 38–43 cm TL, and females at 40–45 cm TL, both sexes at ~2–3 years. Occurs on continental shelf to upper slope, over a range of soft bottom (sand-mud and seagrass beds), from 10–106 m. Feeds on various benthic animals and fish offal. Abundant and exploited throughout much of its range; caught by ski-boat anglers and likely a bycatch of deepwater fisheries. IUCN Red List conservation status Endangered.

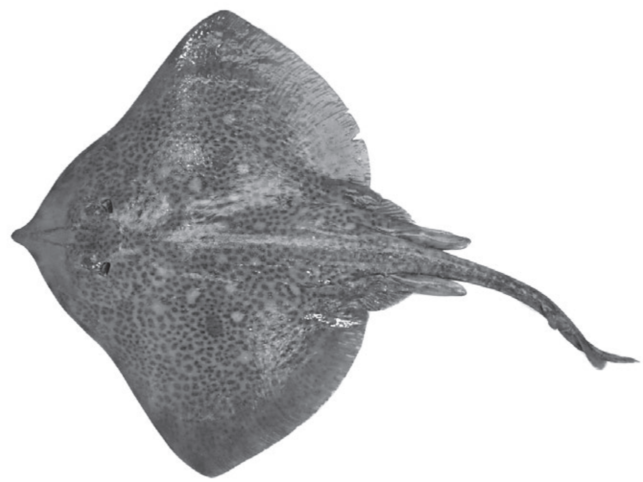
Raja straeleni Poll 1951

Biscuit skate PLATE 65

Raja straeleni Poll 1951: 118, Fig. 54, Pls. 8, 13 (West Africa); Hulley 1970*; McEachran & Dunn 1998; Compagno 1999, 2005; Heemstra & Heemstra 2004*; Compagno & Ebert 2007*; Ebert *et al*. 2008*.
Raja (*Raja*) *straeleni*: Hulley 1972*; Lloris 1982; SSF No. 25.22*.
Raja clavata (*non* Linnaeus 1758): SSF No. 25.8*.



Raja straeleni, 36 cm DW, female (South Africa). Source: SSF



Raja straeleni, 60 cm TL (South Africa). O Alvheim © IMR

Disc broad and angular; DW 1.2–1.5 times disc length. Snout moderately long, length 2.8–3.2 times interorbital space; tip triangular and broad-based, angle anterior to spiracles 95°–100°. Teeth in upper jaw 35–45. Distance from mid-vent to 1st dorsal-fin origin 1.2–1.5 times distance from snout tip to mid-vent. Ventral surface with spines on snout tip and anterior margins of disc. Dorsal surface largely free of denticles, but with strong thorns at all stages: 1 or 2 preorbital and 1–3 post-orbital, 0–1 supraspiracular, 0–2 scapular, 4 or 5 nuchal, 20–52 in median row from mid-dorsal disc to 1st dorsal fin, and 0–6 interdorsal; also, a few lateral thorns on front portion of tail, with more hook-like thorns towards tip. Males entirely covered with spinules dorsally; females with spinules only on snout tip, anterior margins of disc, mid-dorsal disc and tail. Egg cases medium-sized, ~7.5 cm long excluding horns; surface smooth but densely covered in fibres; broad lateral keel; length of posterior apron ~1.3 times anterior apron; horns taper to filamentous tips, and length of posterior horns ~1.2 times anterior horns. Predorsal caudal vertebrae 48–52.

Disc pale brown to grey dorsally; adults with scattered small to large black spots, sometimes forming rosettes or whorls (no dark spots in juveniles); often with transversely oblong gold and black eyespot at each pectoral-fin base; white or mottled grey ventrally, and pores not pigmented. Attains ~91 cm TL (Last *et al.* 2016); females reach larger sizes than males.

DISTRIBUTION Eastern Atlantic (Mauritania to South Africa), and to South Africa (Eastern Cape) in WIO, and possibly also Mozambique, southern Madagascar and Mauritius.

REMARKS Has been confused with *R. clavata* from Northern Hemisphere, which needs further taxonomic study. Size at hatching <16 cm TL. Males mature at 56–68 cm TL, and females at 55–71 cm TL. Very common in southern Africa; found in shallow bays and near shore to continental slope, to ~820 m deep (usually above 200 m). Migrates inshore during the warm season and towards deeper offshore waters in winter. Feeds on bony fishes, benthic invertebrates and fish offal. Caught by shore and ski-boat anglers and hake trawlers for their edible pectoral fins.

GENUS *Rajella* Stehmann 1970

Disc heart-shaped to rhomboidal, narrow to moderately narrow, DW generally 49–61% TL; pectoral-fin apex obtusely angled to broadly rounded. Snout slightly to moderately extended, acutely angled to broadly rounded, and moderately short to moderately long. Eyes moderately sized, eye diameter slightly less than to greater than interorbital space. Pelvic-fin anterior lobes short to moderately long but considerably shorter than posterior lobes. Tail moderately long to long, length generally 51–60% TL, and moderately broad at base and attenuated distally. Dorsal surface largely covered with denticles and relatively densely covered with medium to large thorns; generally with complete row of orbital thorns, triangular patch on nuchal and scapular area, in 1 to several rows from shoulder area to 1st dorsal fin, and 1 to several interdorsal thorns; size of thorns in median row equal to or larger than those in lateral rows. Predorsal caudal vertebrae 55–73. Disc pale grey, brown or brownish black dorsally; whitish to nearly black ventrally. Small-sized, adults attain ~70–90 cm TL. Occurs on outer continental shelf and slope to deep slope. Distributed throughout the Atlantic and southwestern Indian oceans, but also one member each from off Indonesia, the Galápagos, and Australia in the Pacific Ocean. Fifteen species, 5 in WIO, two of which are from deep water.

KEY TO SPECIES

1a Mid-dorsal disc to tail with 3 or more (median plus parallel) rows of thorns, rows either continuous or interrupted **2**

1b Mid-dorsal disc to tail with 2 parallel rows of thorns and no median row; no rostral thorns .... ***R. ravidula***
[deep water, from 496–1 056 m; Plate 66]

2a Median row of thorns on disc and tail continuous **3**

2b Median row of thorns on disc interrupted or thorns reduced in size; tail grey ventrally, with white dorsal tip .... ***R. dissimilis***
[deep water, from 420–1 640 m; Plate 66]

3a Tail length from cloaca to tip about equal to, or slightly shorter than precaudal length from snout tip to cloaca **4**

3b Tail length from cloaca to tip much longer than precaudal length from snout tip to cloaca .... ***R. caudaspinosa***

4a Dorsal surface pale grey without blackish spots; thorns very large and conspicuously pale to white .... ***R. barnardi***

4b Dorsal surface medium grey to brownish, often with blackish spots; thorns small and inconspicuous .... ***R. leopardus***

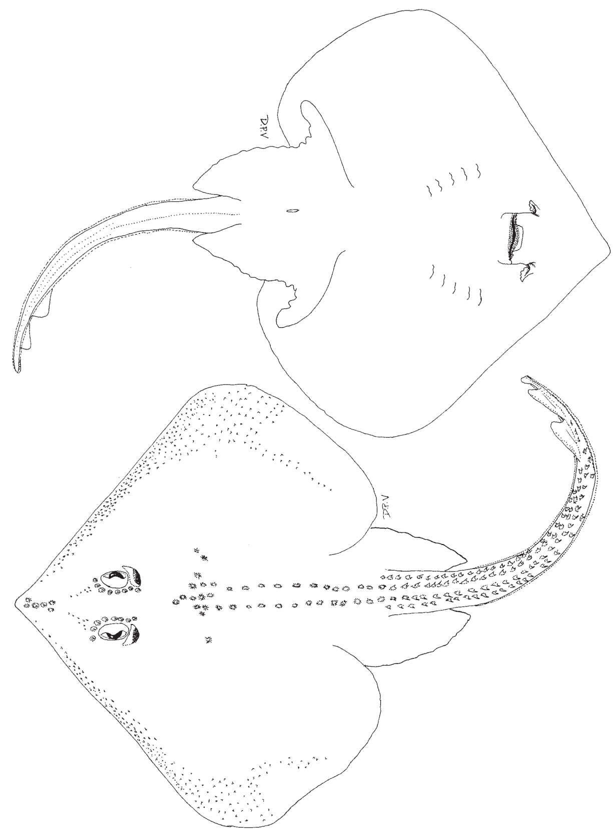
Rajella barnardi (Norman 1935)

Bigthorn skate PLATE 66

Raja barnardi Norman 1935: 43, Fig. 14 (off Cape Town, South Africa).
Raja confundens Hulley 1970: 203, Pl. 11, Fig. 17 (off Cape Columbine, South Africa).
Raja (*Rajella*) *confundens*: Hulley 1972*; SSF No. 25.9*; Ebert *et al.* 1991.
Raja (*Rajella*) *barnardi*: Stehmann 1995.
Rajella barnardi: McEachran & Dunn 1998; Compagno 1999, 2005; Long & McCosker 1999; Compagno & Ebert 2007*; Ebert *et al.* 2008*; Last & Stehmann 2008.

Disc angular, DW 1.2–1.3 times disc length; pectoral-fin apex rounded. Snout moderately long, length 2.5–3.3 times interorbital space; tip not attenuating but continuous with anterior margins of disc, and with short rounded terminal process; angle anterior to spiracles 99°–120°. Mouth small and jaws weak, with blunt teeth; teeth in upper jaw 39–45. No interdorsal space. Ventral surface smooth. Dorsal surface with 5–10 circumorbital thorns, 1 or 2 supraspiracular and 1 or 2 interspiracular, 2–8 lateral nuchal and 2–9 medial nuchal, 2 or 3 scapular, and 17–24 in median row from nuchal area to 1st dorsal fin, flanked by 2 lateral rows on tail; thorns with stellate bases over rostral cartilage and anterior margins of disc. Egg cases rather small, ~5.5 cm long excluding horns; surface smooth with fine striations; lateral keels broad and feathery, extending length of case (including horns); posterior apron ~1.5 times width of anterior apron; horns robust and tapered; posterior horns ~1.7 times length of anterior horns, anterior horns with attachment fibres near tips. Predorsal caudal vertebrae 55–63.

Body grey dorsally and ventrally, with darker patches along posterior margins of disc and pelvic fins, around vent, and along tail. Attains 75 cm TL.



Rajella barnardi, 44 cm DW (South Africa). Source: SSF

DISTRIBUTION Primarily eastern Atlantic (Mauritania to South Africa), and fewer records to South Africa (Eastern Cape) in WIO.

REMARKS Size at hatching <11 cm TL. Males mature at 60–62 cm TL, and females at 59–65 cm TL. Common, with wide depth range and concentrations in some areas; occurs on outer continental shelf to deep slope, at 128–1 809 m (usually >200 m). Feeds mainly on small crustaceans (mysids), also polychaetes, bony fishes and squid. Caught incidentally in deep-trawl fisheries.

Rajella caudaspinosa (Von Bonde & Swart 1923)

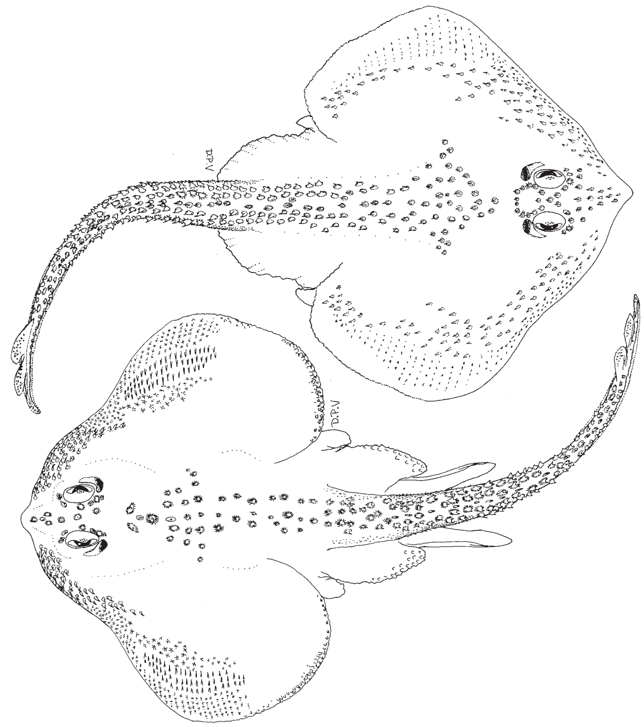
Munchkin skate PLATE 66

Raia caudaspinosa Von Bonde & Swart 1923: 8, Pl. 21, Fig. 1 (KwaZulu-Natal, South Africa); Hulley 1970*.
Raia albalinea Von Bonde & Swart 1923: 6, Pl. 20, Fig. 1 (KwaZulu-Natal, South Africa).
Raja (*Rajella*) *caudaspinosa*: Hulley 1972*; SSF No. 25.7*.
Rajella caudaspinosa: McEachran & Dunn 1998; Compagno 1999, 2005; Long & McCosker 1999; Compagno & Ebert 2007*; Ebert *et al*. 2008*; Last & Stehmann 2008.

Small-sized with rough tail and thick disc, DW 1.2–1.4 times disc length; pectoral-fin apex broadly rounded. Snout obtusely pointed and with rounded terminal process, and short, length 2–2.6 times interorbital space; angle anterior to spiracles 125°–130°. Eyes large, bulging and close-set. Mouth small and jaws weak, with blunt teeth; teeth in upper jaw 32–36. Tail thick and longer than disc; no interdorsal space. Ventral surface smooth. Dorsal surface very rough: 5–9 circumorbital thorns, 0–1 interorbital, 1 or 2 interspiracular, 3 or 4 scapular, 4 or 5 median nuchal, 22–23 in mid-dorsal row from nuchal area to 1st dorsal fin, thorns decreasing in size towards tail, and flanked on each side by 1 row of thorns on back and 2 rows on tail; large thorns with stellate bases in 4–6 staggered rows on anterior margins of disc. Egg cases poorly known, but half-developed specimen was small, ~3 cm long excluding horns; surface finely striated and smooth beneath fibrous covering, with narrow lateral keels, and posterior horns tapering to acute tips. Predorsal caudal vertebrae 66–73.

Disc pale grey to brownish dorsally, with or without scattered darker spots, and juveniles with distinctive white bars; whitish ventrally. Attains 32+ cm DW, 65 cm TL.

Rajella caudaspinosa, 17 cm DW, 35 cm TL, juvenile holotype of *Raia albalinea* (South Africa). Source: Von Bonde & Swart 1923



Rajella caudaspinosa, 26 cm DW, female (top); 29 cm DW, male (bottom) (South Africa). Source: SSF

DISTRIBUTION Southern Africa: most common from Namibia to South Africa (Cape Agulhas) in southeastern Atlantic; rare off south Cape coast of South Africa in WIO.

REMARKS Size at hatching <10 cm TL. Males mature at 53–59 cm TL, and females at 50–57 cm TL. Similar in appearance to other members of the genus. Probably uncommon; occurs on outer continental shelf and upper slope, at 102–1 098 m deep (usually >200 m). Feeds mainly on small crustaceans (mysids), also lightfishes and polychaetes. Taken incidentally in hake trawl fisheries.

Rajella leopardus (Von Bonde & Swart 1923)

Leopard skate PLATE 66

Raia leopardus Von Bonde & Swart 1923: 7, Pl. 20, Fig. 2 (KwaZulu-Natal, South Africa).
Raja (*Rajella*) *leopardus*: Hulley 1972*; SSF No. 25.13*; Stehmann 1990, 1995; Compagno *et al*. 1991.
Rajella leopardus: McEachran & Dunn 1998; Compagno 1999; 2005; Long & McCosker 1999; Compagno & Ebert 2007*; Ebert *et al*. 2008*; Last & Stehmann 2008.

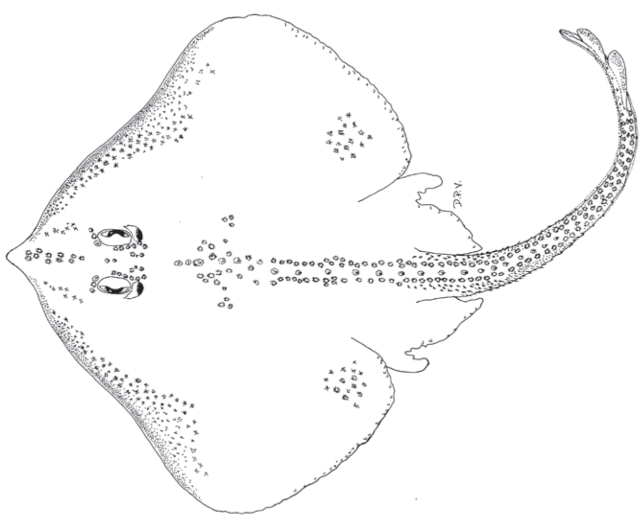
Disc angular, barely wider than long; pectoral-fin apex rounded. Snout obtusely pointed with triangular terminal process and moderately long, length 2.8–4.4 times interorbital space; angle anterior to spiracles 100°–110°. Tail about as long as disc, with thick base. Jaws large, teeth blunt; teeth in upper jaw 52–70. Dorsal surface in juveniles and adults with spinules on snout, anterior margins of disc and sides of tail. Thorns in juveniles: 4 or 5 circumorbital, none or 1 supraspiracular, 1 interspiracular, 1 or 2 scapular, 3–5 median nuchal, 25–30 mid-dorsal thorns from nuchal area to 1st dorsal fin, and 3–6 small thorns on each side of tail at pelvic fins. Thorns in adults: 5–13 circumorbital and supraspiracular, 1 or 2 interspiracular, 2 or 3 scapular, 4–9 median nuchal thorns forming triangular patch of 1 or 2 rows, and 19–29 in mid-dorsal row from mid-disc to 1st dorsal fin, flanked on each side by 1 row along back and 2 or 3 rows on tail. Ventral surface in adults with spines on snout tip and anterior margins of disc. Egg cases small, ~5.5 cm long excluding horns; surface smooth; lateral keels broad and feathery in appearance, extending full length, including horns; posterior horns ~1.2 times as long as anterior horns, anterior horns with fibrous tendril. Predorsal caudal vertebrae 55–58.

Disc grey to brown dorsally, with numerous dark spots (more common in juveniles); pale ventrally, sometimes mottled with dusky blotches and patches. Attains 93 cm TL.

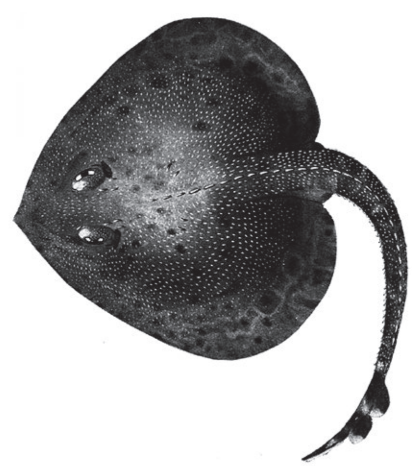
DISTRIBUTION Southern Africa: Namibia to Cape of Good Hope in southeastern Atlantic, to South Africa (Eastern Cape) in WIO.

REMARKS Size at hatching <15 cm TL; matures at 61–73 cm TL. Poorly known, yet the most common skate off southern Africa, along with *R. barnardi*. Occurs on upper continental slope, at 73–1 026 m (usually 300–500 m). Feeds mostly on decapod crustaceans and bony fishes (including dragonets, rattails, hake and lanternfish), also sea pens, cuttlefish and polychaetes. Caught incidentally in hake trawl fisheries.

EDITORS' NOTE In the original description it was not specified if *leopardus* was used as a noun or an adjective. We follow *Eschmeyer's Catalog of Fishes* in assuming it is a noun. Other publications have used the adjectival form, *Rajella leoparda*.



Rajella leopardus, 38 cm DW (South Africa).
Redrawn from Hulley 1970



Rajella leopardus, 15 cm DW, 25 cm TL, type (South Africa).
Source: Von Bonde & Swart 1923

GENUS ***Rostroraja*** Hulley 1972

One species.

Rostroraja alba (Lacepède 1803)

White skate PLATE 67

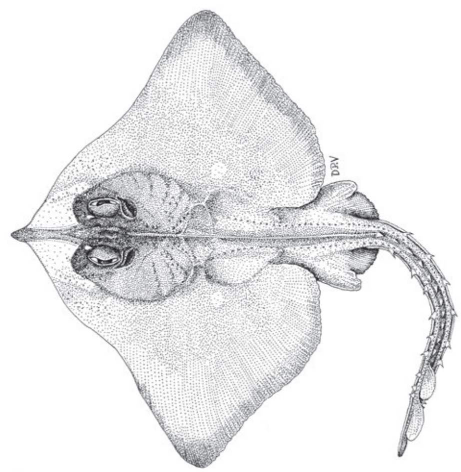
Raja alba Lacepède 1803: 661, 663, Pl. 20, Fig. 1 (France, English Channel); Hulley 1966*, 1970*; Wallace 1967*.
Raja (*Rostroraja*) *alba*: Hulley 1972*; SSF No. 25.6*.
Rostroraja alba: McEachran & Dunn 1998; Heemstra & Heemstra 2004; Compagno 2005; Compagno & Ebert 2007*; Ebert *et al*. 2008*.

Large-sized with broad disc, DW 1.4–1.5 times disc length; pectoral-fin apex angular. Snout broad-based and attenuating to long point covered with small thorns; snout length 2.5–3.2 times interorbital space; angle anterior to spiracles ~105°. Jaws powerful, with sharp teeth; teeth in upper jaw 40–45. Ventral surface in juveniles with spinules on snout, internasal area, and anterior margins of disc; ventral surface in adults with spinules on snout, internasal area, anterior margins of disc, gill slits, abdomen and tail. Dorsal surface in juveniles with 1 preorbital and 0–1 post-orbital thorns, 10–16 from pelvic fins to 1st dorsal fin, 7–17 in lateral row on tail, and 0–2 interdorsal. Dorsal surface in adults with ~6 circumorbital thorns, 16–30 in median row from pelvic fins to 1st dorsal fin, 17–29 in lateral row on tail, and 0–2 interdorsal; no nuchal or scapular thorns. Egg cases oblong and very large, >12 cm long excluding horns; surface coarsely striated and rough; broad lateral keels; posterior horns very long, ~3 times length of anterior horns, and tapering and flattening towards tips; anterior horns short, tapered, and with attachment fibres. Predorsal caudal vertebrae 62–67.

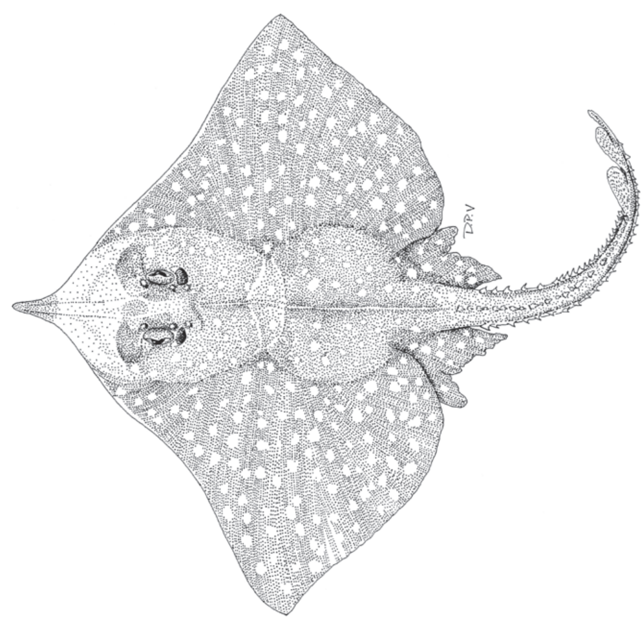
Adults grey to brown dorsally, usually with many small white spots (no dark spots); white ventrally. Juveniles brown dorsally, with darker margins on disc and fins; white ventrally, with grey margins on disc. Hatchlings reddish brown dorsally, often with blue spots. Attains 160 cm DW, 240 cm TL (females reach larger sizes than males).

DISTRIBUTION Mediterranean Sea, eastern Atlantic (British Isles to South Africa), and rounding Cape of Good Hope (South Africa) to central Mozambique in WIO.

REMARKS Size at hatching <40 cm TL. Males mature at ~120 cm TL, and females at ~130 cm TL (Last *et al.* 2016). Bottom predator, feeds mainly on bony fishes but also other elasmobranchs, fish offal, crustaceans and cephalopods. Found on continental shelf and upper slope, over sandy and rock-sand bottom, at 10–750 m (usually 50–500 m); once frequently captured but now rare in many parts of its range. Common in trawls off South Africa and occasionally taken by anglers off sandy beaches. IUCN Red List conservation status Endangered.



Rostroraja alba, 30 cm DW, 30 cm TL, juvenile (South Africa). Source: SSF



Rostroraja alba, 66 cm DW (South Africa). Source: SSF

FAMILY **ARHYNCHOBATIDAE**

Softnose skates

Neil C Aschliman and David A Ebert

Large group of morphologically diverse skates, yet distinguished by basihyal cartilage supporting the floor of mouth with lateral projections, and external clasper glans components relatively few and similar in most species.

(External morphology is otherwise difficult to use in distinguishing softnose skates from hardnose skates of family Rajidae.) Disc quadrangular to rhomboidal. Snout tip typically flexible due to supporting rostral cartilage being very slender, uncalcified, segmented, and/or separated from the neurocranium (pattern of these features varying between genera). Mouth transverse to arched; teeth numerous. Tail slender, with lateral skin folds, weak electric organs, usually 2 posteriorly set small dorsal fins, and reduced caudal fin. Skin often prickly, particularly along dorsal midline.

Reproductive mode oviparity; females lay horny egg cases with long tips. Benthic in shallow tropical waters. Rare, although some species are of commercial interest as skate 'wings' are considered good eating. Distributed mostly in the Pacific, southwestern Atlantic, and southern Indo-Pacific; uncommon in WIO, being largely replaced by hardnose skates.

About 14 genera and at least 111 species; 2 genera with 3 species in WIO, 2 of which are deepwater species, *Notoraja hesperindica* Weigmann, Séret & Stehmann 2021 and *Bathyraja tunae* Stehmann 2005, both found off Mozambique and Madagascar.

GENUS *Bathyraja* Ishiyama 1958

Softnose skates with sub-rhomboidal disc and uncalcified flexible snout. Small-sized to giant, size range ~50–175 cm TL. Distributed mostly throughout northern and southeastern Pacific, southwestern Atlantic, and Southern Ocean, with few species occurring in the Atlantic or WIO. Some species occur at tremendous depths, over 3 000 m. At least 50 species; 2 species in WIO, but *Bathyraja tunae* from the Mozambique Channel is known only from a deepwater slope, at >1 700 m.

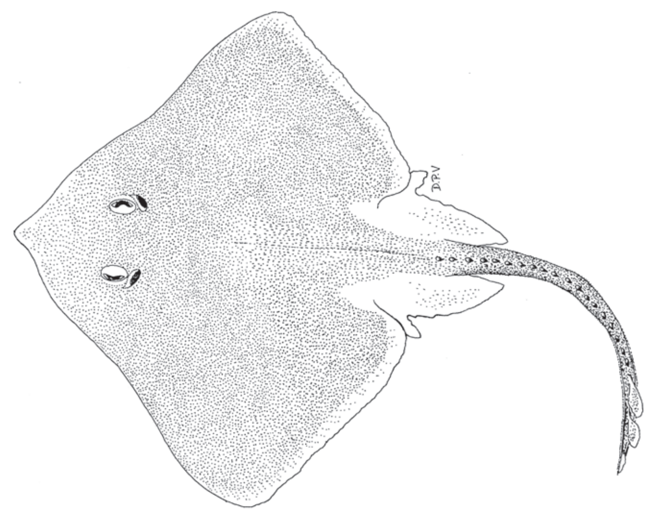
Bathyraja smithii (Müller & Henle 1841)

Softnose skate PLATE 67

Raja smithii Müller & Henle 1841: 150, Pl. 49 (South Africa).
Raia smithii: Von Bonde & Swart 1923.
Raia smithi: Barnard 1925*.
Breviraja smithii: Hulley 1970*, 1972*.
Bathyraja smithii: SSF No. 25.1*; Stehmann 1986; Compagno *et al.* 1989*, 1991; Ebert *et al.* 1991, 2008; Compagno 2005; Compagno & Ebert 2007*.

Mouth broad, with strong jaws and sharp teeth. Dorsal-fin bases separated. Disc width 1.3–1.4 disc length (Last *et al.* 2016); tail shorter than disc length. Preorbital snout length 2–2.6 interorbital width; angle of snout anterior to spiracles 90°–100°. Tooth count 23–28 in upper jaw. Skin spinulose dorsally and smooth ventrally at all life stages; thorns on dorsal disc lost in adults, except for single median row of 14–19 large thorns on tail, sometimes 1 interdorsal thorn, but no lateral thorns on tail; thorns on dorsal surface of disc in juveniles: 1 preorbital, 1 or 2 post-orbital, 3 or 4 scapular, 2 nuchal, ~30 median from nuchal region to 1st dorsal fin, and 1 interdorsal. Predorsal vertebrae 68–71.

Body greyish dorsally, sometimes with white spots; mostly white ventrally, with dark grey or black blotches around gill slits and vent, along disc margins, and underside of tail. Attains 120 cm TL.



Bathyraja smithii, 62 cm DW (South Africa). Source: SSF

DISTRIBUTION Southern Africa: Namibia in southeastern Atlantic, to South Africa (Agulhas Plateau and Eastern Cape) in WIO.

REMARKS Size at hatching <13 cm TL. Males mature at 95–97 cm TL, and females at ~80–90 cm TL (Last *et al.* 2016). Egg cases probably very large: an incomplete specimen, only one-third developed, was ~8 cm long excluding horns, with striated surface covered with dense fibres, broad lateral keels, and very long and thin horns tapering to filamentous tips. Moderately abundant on deep slopes, known from 250–1 020 m (one report from 40 m requires validation, but mostly >600 m, and most records of juveniles). Feeds on bony fishes (particularly hake, jacopever, barracudina and dragonet) and crustaceans, including shrimp and crabs, and sometimes squid and octopus in deeper waters. Incidentally caught in deepwater hake trawl fisheries, but considered of no commercial value.

FAMILY **ANACANTHOBATIDAE**

Legskates

Neil C Aschliman and David A Ebert

Small to medium-sized skates (to ~70 cm TL) with subcircular disc; snout long, often with small terminal fleshy filament; pelvic fins with a unique deep incision completely separating the lobes, anterior lobes slender and limb-like (enabling them to 'walk' across the benthos); tail short, uniformly slender, dorsal fins absent, and caudal fin rudimentary. Eyes small to large; spiracles small, subcircular. Mouth narrow. Skin usually smooth (except median denticle row on tail of small juveniles of *Sinobatis melanosoma*), or with patches of thorns confined to alar region in adult males.

Reproductive mode oviparity. Restricted distributions in deep water, over outer continental shelf and slope of western Atlantic, western Pacific and southwestern Indian oceans, with known depth range 150–1 725 m. Some species known only from a few specimens (some of which have been subsequently lost). Five genera and 14 species recognised; 3 genera and 3 species in WIO (of which 2 genera and 2 species known from deep water).

KEY TO GENERA

1a Tail short, 35–36% TL, ~½ body length; dorsal disc pale grey-brown, paler ventrally .... ***Sinobatis***
[one deepwater species, *Sinobatis brevicauda* Weigmann & Stehmann 2016, from 960–1 130 m, Saya de Malha Bank, in WIO]

1b Tail long, more than ½ body length to greater than body length; dorsal disc dark grey-brown or reddish brown with ocelli and pale spots **2**

2a Tooth rows 29–35 in upper jaw; internasal flap overhangs corners of mouth; dorsal disc light reddish brown with scattered spots and ocelli, ventral disc whitish .... ***Anacanthobatis***

2b Tooth rows 18–26 in upper jaw; internasal flap does not overhang corners of mouth; disc dark grey-brown, colour darker ventrally .... ***Indobatis***
[one deepwater species, *Indobatis ori* (Wallace 1967), from 1 000–1 725 m, in WIO]

GENUS ***Anacanthobatis***

Von Bonde & Swart 1923

Legskates with terminal filament extending from small rounded projection at tip of snout. Tail slender, and shorter or longer than disc; no dorsal fins; caudal fin weakly developed, but with lower lobe which is smaller than upper lobe; pelvic-fin posterior lobes fused to base of tail along length. Skin smooth. Occurs on continental shelf and slope, in tropical and subtropical waters of western central Atlantic, western Pacific and WIO. Ten species, 1 in WIO.

Anacanthobatis marmorata

Von Bonde & Swart 1923

Spotted legskate

PLATE 68

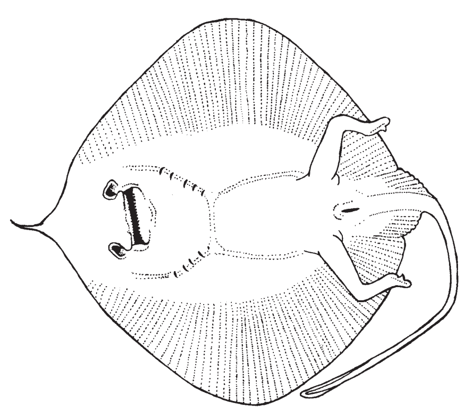
Leiobatis marmoratus Von Bonde & Swart 1923: 18, Pl. 23 (KwaZulu-Natal, South Africa); Wallace 1967*; Hulley 1973*.
Anacanthobatis marmoratus: SSF No. 26.1*; Compagno *et al.* 1989*; Compagno 2005; Compagno & Ebert 2007*; Ebert 2014*.
Anacanthobatis marmorata: Last *et al.* 2016*.

Diagnosis as for genus. Disc width ~1.2 times disc length. Tail shorter than disc length, with narrow lateral skin folds. Snout angle anterior to spiracles ~102°. Internasal flap fringed and overlapping corners of mouth. Tooth count 28–35 in upper jaw. Dorsal surface with dermal papillae; dorsal and ventral surfaces otherwise smooth, without dermal denticles, but adult males with alar thorn patch.

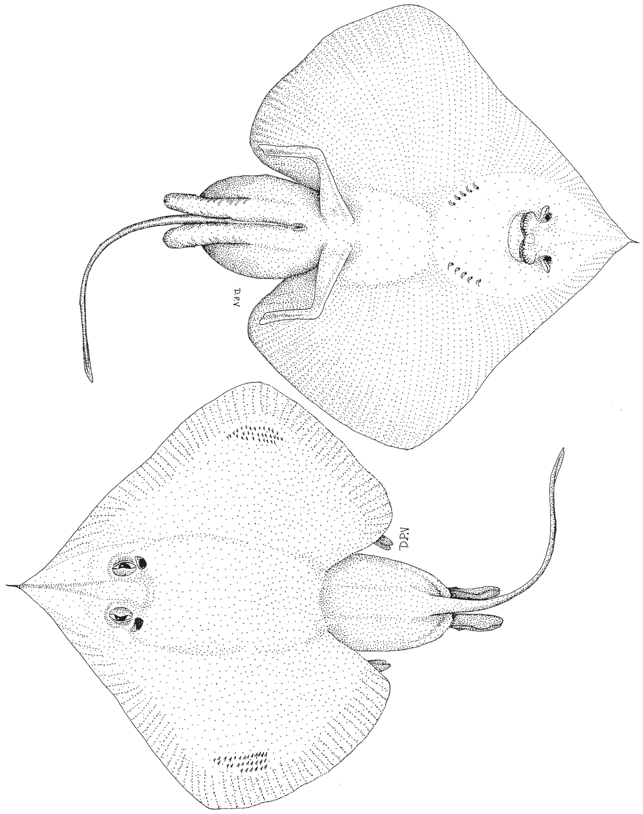
Body mottled pale brown and white dorsally, with scattered ocelli; terminal filament and dermal papillae dark brown; pale ventrally. Attains at least 29 cm TL (Last *et al.* 2016).

DISTRIBUTION WIO: South Africa (KwaZulu-Natal) to southern Mozambique.

REMARKS Possibly the smallest southern African skate, although known from few records. Occurs on edge of outer continental shelf and upper slope, with reliable depth records of 162–433 m.



Anacanthobatis marmorata, 11 cm DW, ventral view of juvenile (S Mozambique).



Anacanthobatis marmorata, 17 cm DW, male (S Mozambique).
Source: SSF

FAMILY GURGESIELLIDAE

Pygmy skates

Neil C Aschliman and David A Ebert

Small-sized skates (to ~60 cm TL) with subcircular to rhomboidal disc; snout short to moderately long, rigid to semi-rigid, with or without small process at tip; pelvic fins deeply notched, anterior lobes slender and limb-like (lobes fused in *Gurgesiella* species) enabling a 'walking' motion across the benthos; tail slender and long, usually with 2 posteriorly set small dorsal fins, or 1 fin, or dorsal fins absent, and caudal fin small. Eyes large; spiracles small, subcircular. Mouth narrow. Skin with sparse small denticles, and thorn patterns variable between genera and species, but adult males of all genera with alar and malar thorns.

Reproductive mode oviparity. Restricted distributions over outer continental shelf and slope of western Atlantic, western Pacific and southern Indian oceans, known to 1 095 m (Last *et al.* 2016), and inshore to 39 m, off South Africa. Some species are well recorded and others are known only from one or several specimens (some of which have been subsequently lost). Three genera and 19 species recognised worldwide with 2 genera and 5 species in WIO. One deepwater WIO genus, with 2 species, *Fenestraja maceachrani* (Séret 1989) from off Madagascar in 600–765 m, and *F. mamillidens* (Alcock 1889) from Gulf of Mannar and western Sri Lanka known from ~1 090 m.

GENUS *Cruriraja* Bigelow & Schroeder 1948

Legskates without terminal filament on snout. Tail stout at base, and with lateral skin folds; 2 dorsal fins; caudal fin weakly developed, lower lobe very weakly developed or absent. Dorsal surface of disc with sparse thorns and sometimes with rows of thorns on midback or tail; ventral surface of disc and tail smooth. Occurs on continental slope, in tropical and subtropical waters of western central to southwestern and southeastern Atlantic and WIO, at ~150 to >1 000 m deep. Eight species, 3 in WIO.

KEY TO SPECIES

1a	Snout with ~15 rostral thorns	***C. andamanica***
1b	Snout with 3–7 rostral thorns	**2**
2a	No thorns on midback; tips of pelvic-fin anterior lobes pointed	***C. parcomaculata***
2b	Thorns in continuous rows on midback; tips of pelvic-fin anterior lobes spatulate	***C. hulleyi***

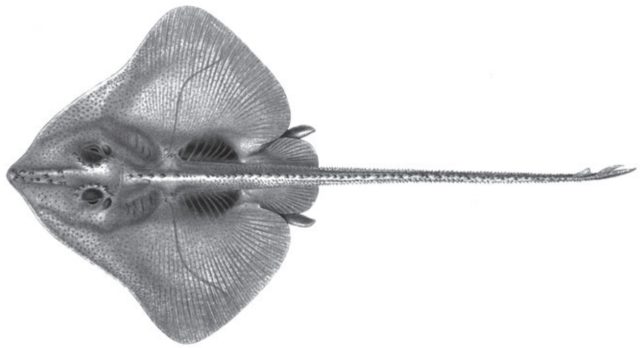
Cruriraja andamanica (Lloyd 1909)

Andaman pygmy skate

Raia andamanica Lloyd 1909: 140, Pl. 46, Fig. 2 (Andaman Sea).
Cruriraja andamanica: Stehmann 1976*; McEachran & Fechhelm 1982; Fischer *et al.* 1990; Compagno 2005; Ebert 2014*.

Diagnosis as for genus. Snout with ~15 rostral thorns; scapular thorns present; thorns in single row from nuchal to mid-disc region, and in irregular row on tail.

Body uniformly slate grey dorsally and ventrally. Attains at least 50 cm TL (Last *et al.* 2016).



Cruriraja andamanica, 21 cm TL, male holotype (Andaman Sea).
Source: Lloyd 1909

DISTRIBUTION WIO: Known from few specimens, collected off Tanzania, and also from Andaman Sea and possibly off Indonesia (Last *et al.* 2016).

REMARKS Taken in tropical water over continental slope, at 274 m (Tanzania) and 511 m (Andaman Sea).

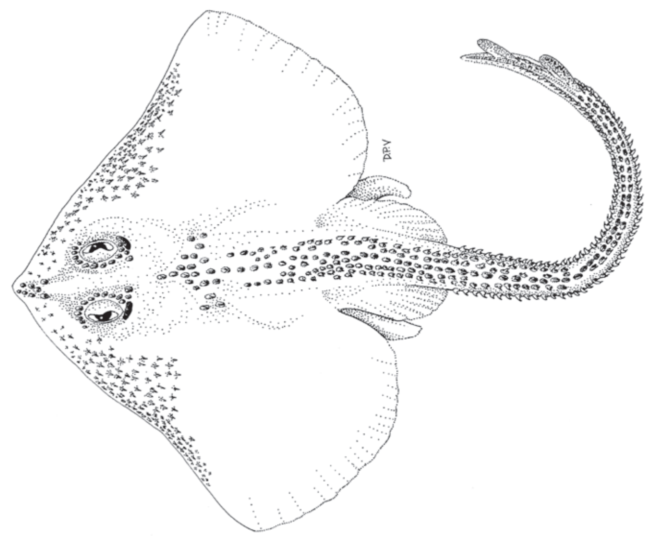
Cruriraja hulleyi Aschliman, Ebert & Compagno 2010

Roughnose legskate PLATE 68

Cruriraja hulleyi Aschliman, Ebert & Compagno 2010: 364, Figs. 1–3 (south coast of South Africa); Ebert 2014*.
Cruriraja parcomaculata: Smith 1964*; Wallace 1967*; Hulley 1970*, 1972*; Compagno *et al.* 1989*; Compagno 2005; Compagno & Ebert 2007*.

Disc quadrangular, ~1.2 times wider than long (DW ~57% TL). Snout short, tip pointed, without terminal filament; snout angle anterior to spiracles 80°–90°. Teeth blunt and flat in females and juveniles, and acute with single cusp in adult males; tooth count 37–47/38 or 39. Pelvic-fin anterior lobe tips spatulate. Tail longer than disc, broad, depressed and tapering to 1st dorsal fin; lateral skin folds long, extending to tail tip, and broadest at level of dorsal fins. Interdorsal distance greater than half (but not exceeding) length of dorsal-fin bases. Dorsal fins moderate and equally sized; 1st dorsal-fin tip rounded, 2nd dorsal-fin tip angular; interdorsal distance greater than half (but not exceeding) length of dorsal-fin bases. Dorsal surface generally smooth other than areas of thorns: rostral thorns 4 or 5; orbital thorns 9, in regularly spaced medial semicircle from preorbital area to spiracle; post-orbital thorns 2; scapular thorns in tight irregular patches of 4–9 thorns each; nuchal thorns 1–3; thorns in 1–5 continuous rows on midback, followed by 1 or more rows of well-developed and strongly recurved tail thorns; interdorsal thorns 6. Ventral surface entirely smooth. Precaudal vertebrae 66–69.

Body yellowish brown dorsally, with large darker brown blotches spanning eyes and along rows of thorns on midback; dorsal surface of claspers and tail duskier and darker brown; uniformly pale ventrally. Juvenile specimen densely mottled dorsally, with circular brown spots on pale field, and tail with brown banding interspersed with smaller brown spots. Attains 60 cm TL.



Cruriraja hulleyi, 33 cm DW (South Africa). Source: SSF

DISTRIBUTION Southern Africa: Namibia (Lüderitz) to South Africa (East London, Eastern Cape).

REMARKS Individuals tend to be larger on west coast of southern Africa than on south coast. Size at hatching ~10 cm TL; matures at ~47 cm TL. Egg cases small, vase-like, <5 cm long excluding horns, with coarsely striated surface and very narrow lateral keels; posterior horns longer than anterior horns, tapering to thin tips, curving inwards and with fine attachment fibres; anterior horns hook-shaped, with acute tips. Moderately common on outer continental shelf and upper slope, at 39–545 m (most commonly 200–500 m). Feeds mostly on mysid shrimp, but also small bony fishes and various invertebrates, including crustaceans, squid, polychaetes and flatworms. Caught incidentally by hake bottom trawlers.

Cruriraja parcomaculata (Von Bonde & Swart 1923)

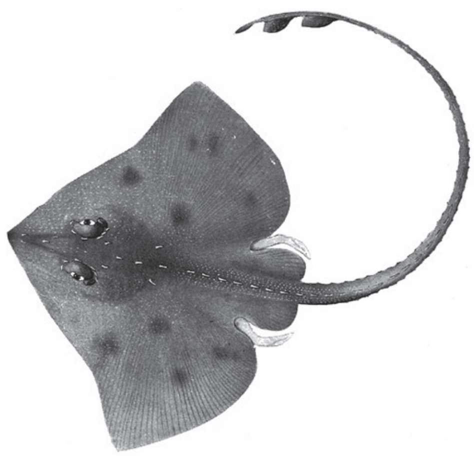
Triangular legskate

PLATE 68

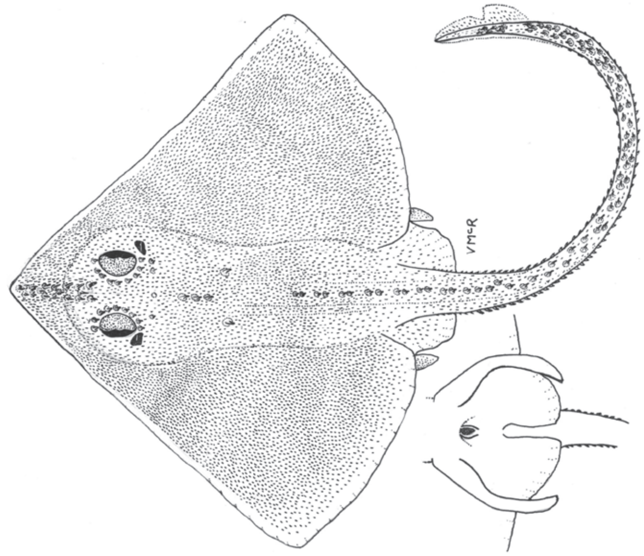
Raia parcomaculata Von Bonde & Swart 1923: 9, Pl. 21, Fig. 2 (KwaZulu-Natal, South Africa).
Cruriraja triangularis: Smith 1964*; Wallace 1967*; Hulley 1970, 1972; Compagno *et al.* 1989*; Compagno 2005; Compagno & Ebert 2007*.
Cruriraja parcomaculata: Aschliman *et al.* 2010; Ebert 2014*.

Disc ~1.3 times wider than long (DW up to 62% TL). Snout short, tip pointed, without terminal filament; snout angle anterior to spiracles 60°–70°. Tooth count 39–42/34–42. Pelvic-fin anterior lobe tips pointed. Interdorsal distance less than half length of dorsal-fin bases. Dorsal surface generally smooth other than areas of thorns: rostral thorns 3–7; post-orbital thorn 1; at most 1 scapular thorn (lacks patches of scapular thorns); nuchal thorn 1; no median row of thorns; interdorsal thorns 4. Ventral surface smooth, except for denticles on underside of claspers.

Body grey-brown dorsally, with darker patches alongside midline; pale ventrally; no bands on tail. Attains 43 cm TL.



Cruriraja parcomaculata, ~10 cm DW, 18 cm TL, juvenile type (South Africa). Source: Von Bonde & Swart 1923



Cruriraja parcomaculata, 16 cm DW, female holotype of *C. triangularis*, dorsal view; 12 cm DW, paratype, ventral view of pelvic fins (South Africa). Source: SSF

DISTRIBUTION WIO: South Africa (KwaZulu-Natal) to Mozambique.

REMARKS Smaller than *C. hulleyi* but of similar proportions; however, the snout is longer and has more acute angle. Males mature at 35–37 cm TL and attain >39 cm TL; females mature at 32–37 cm TL and attain ~43 cm TL. Size at hatching ~9 cm TL. Egg cases small, boxy, not vase-like, <5 cm long excluding horns, with coarsely striated surface, prominent longitudinal ridges and covered by thin fibrous layer, and without lateral keels; posterior horns very long, tapering towards tips and curved inwards, their length greater than egg case proper. Found on outer continental shelf and upper slope, on mud bottom, at 65–680 m (most records from >200 m).

ORDER MYLIOBATIFORMES

FAMILY HEXATRYGONIDAE

Sixgill stingray

David A Ebert and Neil C Aschliman

Unusual ray with 6 pairs of gill slits on underside, flabby body, and long triangular fleshy snout with pointed flexible tip (which changes shape with growth). Disc widest just behind snout; disc length greater than disc width. Eyes small; spiracles far back from eyes and about twice eye diameter. Nostrils far apart; no oronasal grooves; internasal flaps very short, broad, fleshy, and not joined as flap reaching mouth. Mouth broad and nearly transverse. Teeth small, bluntly rounded, and exposed when mouth closed. Pelvic fins small, fleshy and broadly rounded. Tail shorter than disc length, with 1 or 2 long serrated stinging spines, no dorsal fins, and low caudal fin. Skin smooth, without dermal denticles or thorns.

Monotypic.

GENUS *Hexatrygon* Heemstra & Smith 1980

Diagnosis as for family. Although at least 5 species have been described, the genus is considered monotypic as all specimens appear referable to one species, widely distributed in Indo-West to central Pacific.

Hexatrygon bickelli Heemstra & Smith 1980

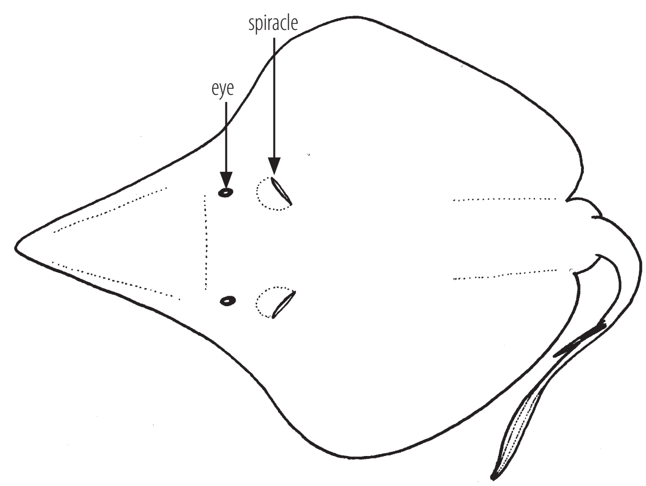
Sixgill stingray PLATE 69

Hexatrygon bickelli Heemstra & Smith 1980: 6, Figs. 1–13, 15 (beach at Port Elizabeth, Eastern Cape, South Africa); Compagno *et al.* 1989*; SSF No. 31.1* [1995]; Last & Stevens 2009*; Babu *et al.* 2011; Ebert 2014*.

Diagnosis as for family. Tooth count 44–102 in both jaws (varies with growth); vertebrae 101; spiral valve turns 13 or 14.

Body brownish to dark violet-blue or pinkish dorsally, and snout uniformly paler; paler or white ventrally, except darker along disc margins; caudal fin dark brown to black. Attains 168 cm TL.

Hexatrygon bickelli, 23 cm DW, prenatal pup. The skin over the cranial cavity has been removed to show the size of the brain which does not increase with growth (South Africa). Source: SSF 1995



Hexatrygon bickelli, 50 cm DW, female holotype (South Africa). Source: Heemstra & Smith 1980

DISTRIBUTION Indo-Pacific. WIO: South Africa (south coast), Mozambique, India and Sri Lanka.

REMARKS Viviparous; litters of 3–5; size at birth ~50 cm TL. Matures at 105–113 cm TL. Rarely seen, deepsea ray of continental slope, at 300–1 120 m, found close to bottom but may venture into midwater; a few records are of strandings on beaches in South Africa, and once observed and photographed by divers in relatively shallow water (~30 m) off Japan.

FAMILY PLESIOBATIDAE

Deepwater stingray

David A Ebert and Neil C Aschliman

Giant stingray with oval disc (slightly longer than wide), broadly pointed snout, and small eyes. Head not elevated above pectoral fins. Mouth large, with numerous small teeth, and no oral papillae. Nostrils almost circular; internasal flap broad, rectangular, and posterior edge with well-developed fringe. Tail slightly shorter than disc length, not whip-like, without lateral skin folds, and with 1–3 long serrated stinging spines near midpoint of tail; no dorsal fins; caudal fin slender, long and well developed. Dorsal surface of disc and tail covered with small close-set acutely pointed denticles; ventral surface similar, except smooth on disc edges, pelvic-fin margins, internasal flap and small area immediately behind mouth.

Monotypic.

GENUS *Plesiobatis* Wallace 1967

Diagnosis as for family. One species, previously placed in family Urolophidae (round stingrays), patchily distributed in Indo-West and central Pacific.

Plesiobatis daviesi (Wallace 1967)

Deepwater stingray PLATE 69

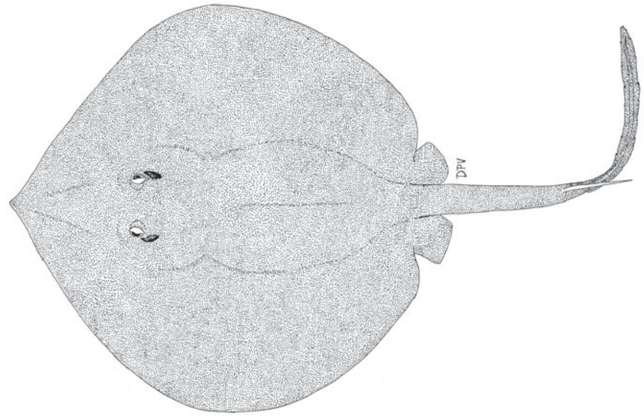
Urotrygon daviesi Wallace 1967: 8, Figs. 3–4 (Mozambique Channel, off Limpopo River mouth); SSF No. 30.16*; Compagno *et al.* 1989*.
Plesiobatis daviesi: Ebert *et al.* 2002; Last & Stevens 2009*; Ebert 2014*.

Diagnosis as for family. Tooth count 30–62 in both jaws; spiral-valve turns 14 or 15.

Body grey-black to brownish or purplish brown dorsally, and on pelvic fins, caudal fin and ventral margins of disc; white ventrally. Attains 270 cm TL, 151 cm DW.

DISTRIBUTION Indo-Pacific. WIO: South Africa (KwaZulu-Natal) to southern Mozambique, and southern India to Sri Lanka; elsewhere to Philippines, Taiwan, Kyushu-Palau Ridge (Philippine Sea), Ryukyu Is., Australia and Hawaii.

REMARKS Biology poorly known; research is needed on the different populations. Presumed viviparous with yolk sac; size at birth ~50 cm TL. Males mature at 130–172 cm TL, and females at >200 cm TL. Possibly rare; demersal on soft bottom of outer continental shelf and upper slope, from 44–700 m, mostly >275 m. May migrate to midwater to feed. Diet includes bony fishes, cephalopods and crustaceans. Specimens observed with wounds from bites of cookiecutter shark *Isistius brasiliensis*.



Plesiobatis daviesi, 90 cm DW (S Mozambique). Source: SSF

FAMILY DASYATIDAE

Stingrays

B Mabel Manjaji-Matsumoto, Marcelo R de Carvalho, Hugo RS Santos, Ulisses L Gomes and Peter R Last

Small- to very large-sized (~30 cm to 3 m DW) with head, trunk and broadly expanded pectoral fins forming flattened trapezoidal, rhomboidal or oval disc (disc width at most 1.3 times disc length). Snout variably obtuse, rounded, more or less pointed or acute; eyes and spiracles dorsally situated. Mouth transverse and ventral, and mouth floor usually with fleshy oral papillae; teeth small and numerous, in rows forming bands in both jaws. Five pairs of gill slits on underside. Internasal flap well-developed, posterior edge fringed. Tail slender to whip-like, sometimes significantly longer than disc, usually with skin folds (no skin folds in *Urogymnus* and *Himantura*); usually 1 or 2 long, serrated, venomous spines posteriorly set on tail (no stinging spine in *Urogymnus*) (stinging spines are often dropped, leaving a scar, and subsequently replaced); no dorsal fin; no caudal fin. Dorsal surface smooth or covered with small denticles, and variably with patches or rows of enlarged denticles, thorns, tubercles or other dermal derivatives (their size, density and distribution varying with growth and sex). Body uniformly coloured or with markings dorsally, some species ornately patterned; generally pale to whitish ventrally, and disc margins sometimes darker.

Reproductive mode viviparity with yolk-sac placenta and histotroph, wherein uterine secretions nourish the embryos;

litters of few young (<8). Worldwide, primarily in tropical to warm-temperate waters; usually found in shallow coastal marine waters, brackish lagoons and estuaries, and occasionally in freshwater, but a few species occur deeper than 100 m. Several species of *Dasyatis* and *Himantura* are restricted to freshwater in tropical regions of Africa, Southeast Asia and Australia. Most species are benthic or demersal, sometimes remaining partially buried in soft substrates for prolonged periods, and a few are semipelagic or pelagic. Abundant in certain localities and sold locally in markets as the thickest part of the disc is esteemed as meat in some regions. The venomous stinging spine can inflict a painful or fatal injury, although these rays are not naturally aggressive towards people. A few species are popular with aquarists because of their grace and beauty.

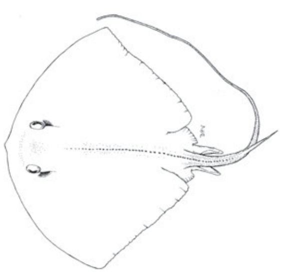
Nineteen genera and ~90 species; 14 genera and at least 27 species in WIO.

KEY TO GENERA

1a Dark transverse mask-like bar across eye region .... ***Neotrygon***

1b No dark transverse bar across eye region **2**

2a Dorsal surface uniformly dark purple to blackish; brownish black to dark grey or purplish ventrally; anterior margin of disc convex, pectoral-fin posterior margins nearly straight and oblique to body axis; teeth cuspidate in both sexes .... ***Pteroplatytrygon***



2b Dorsal surface colouration usually variable, not plain purplish black; mostly whitish to yellowish ventrally; disc oval, rhomboidal or quadrangular; cuspidate teeth only in males **3**

3a Tail base moderately to greatly depressed in cross-section; tail relatively short, usually less than 2.2 times disc width **4**

3b Tail base slightly depressed to almost rounded in cross-section; tail whip-like, more than 2.2 times disc width (when undamaged) **11**

Continued ...

KEY TO GENERA

4a Trunk thin, thickness less than 2 times snout length; small rays, birth size 5–10 cm disc width **5**

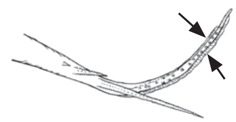
4b Trunk relatively thicker, robust, thickness more than 2 times snout length; medium to large rays, birth size typically at 15–20 cm disc width, some species born at more than 30 cm disc width **6**

5a Snout rather long and pointed, length exceeding 3 times combined orbit and spiracle length .... ***Telatrygon***

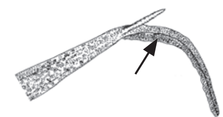
5b Snout shorter, length less than 3 times combined orbit and spiracle .... ***Brevitrygon***

6a Tail with dorsal and ventral skin folds, folds rudimentary to low; dorsal disc surface smooth, except for large adults with sparse denticles **7**

6b Tail with ventral skin fold, fold distinct; dorsal disc surface granular or with 1 or 2 median rows of thornlets **8**



6a



6b

7a Tail beyond sting very thorny; dorsal disc colour uniform plain (row of pores on anterior disc white in one species) .... ***Bathytoshia***

7b Tail only sparsely covered with denticles, usually as prickles confined to before sting and in large adults; dorsal disc colour uniform plain to blue marbling centrally .... ***Dasyatis***

8a Disc circular to oval; ventral skin fold reaching tip of tail; dorsal disc with dark speckling, spotting or mottling **9**

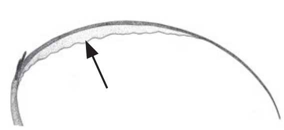
8b Disc rhomboidal; ventral skin fold not reaching tip of tail (when tail undamaged) **10**

9a Disc oval; dorsal disc with dark specks, or blue spots ... ***Taeniura***

9b Disc circular; dorsal disc with black and white mottling (may appear uniform grey due to sediment covering disc) .... ***Taeniurops***

10a Ventral skin fold on tail deep and prominent, its height 2–3 times tail height above fold; dorsal surface with a distinct denticle band .... ***Pastinachus***

10b Ventral skin fold on tail low, its height less than tail height above fold; dorsal surface without a distinct denticle band .... ***Megatrygon***



Continued ...

KEY TO GENERA

11a Disc subcircular to oval; dorsal disc uniform brown to grey, without any spotting or colour pattern; tail not banded **12**

11b Disc suboval to rhomboidal; dorsal disc plain, with speckles, spots, rings (large adults with reticulations); tail usually banded in young, becoming weakly banded to plain in adults........ **13**

12a Dorsal surface sparsely to densely covered with denticles, without a distinct denticle band .... ***Urogymnus***

12b Dorsal surface densely covered with denticles within a distinct denticle band .... ***Pateobatis***

13a Dorsal disc plain or with dark speckles, white or black spots .... ***Maculabatis***

13b Dorsal disc with black spots, rings (spots and/or rings may coalesce in large adults to form reticulations) .... ***Himantura***

GENUS *Bathytoshia* Whitley 1933

Enormous stingrays (adults to 3 m DW) with disc rhomboidal, dorsal surface smooth or rough; tail usually with 1 stinging spine, dorsal skin fold low or absent, ventral fold long or short; median thorns absent, or in row along disc onto tail; tail spiny, adults with bucklers and tubercles on dorsal midline; body white ventrally and sometimes with dark margins, plain dorsally. Three species, 2 in WIO.

KEY TO SPECIES

1a Dorsal surface of disc with median row of enlarged denticles, without obvious row of whitish spots; tail longer than disc length .... ***B. lata***

1b Dorsal surface of disc without median row of enlarged denticles, with pair of diagonal rows of whitish spots on pectoral-fin bases; tail shorter than disc length.. ***B. brevicaudata***

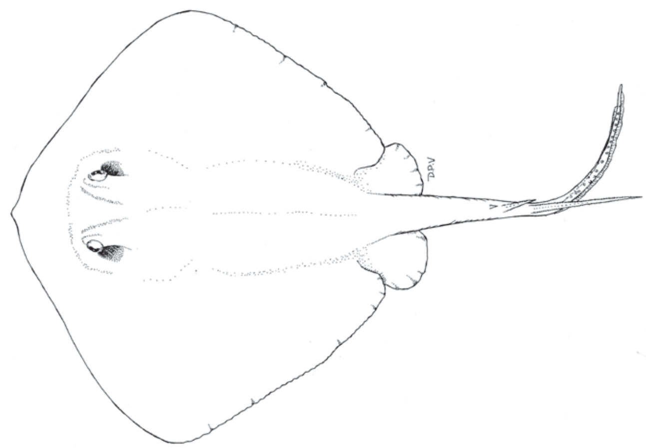
Bathytoshia brevicaudata (Hutton 1875)

Short-tail stingray PLATE 69

Trygon brevicaudata Hutton 1875, Vol. 16: 317 (Otago Harbour, Dunedin, New Zealand).
Trygon brevicaudatus: Russell 1996; Fricke 1999.
Trygon schreineri Gilchrist 1913: 33, Fig. (False Bay, South Africa).
Dasyatis brevicaudata: Wallace 1967*; SSF No. 30.1*.
Bathytoshia brevicaudata: Last *et al.* 2016*.

Disc slightly wider than long; snout broadly triangular; trunk thick. Internasal flap broad, short; posterior edge fringed. Tail shorter than disc length, dorsal skin fold rudimentary, ventral skin fold long, low. Dorsal surface of disc smooth; tail with scattered small denticles, densest towards tip, and median row of large thorns before stinging spine (juveniles sometimes with only 1 stout, oval-shaped thorn immediately before spine). Tooth count 26–45/27–50; oral papillae 5–7.

Body greyish brown dorsally, but blackish above eyes, and with paired row of white pores directed anterolaterally on pectoral-fin bases; whitish ventrally, with greyish margins; tail blackish towards tip. Attains 3 m DW, 4.3+ m TL.



Bathytoshia brevicaudata, 77 cm DW (South Africa). Source: SSF

DISTRIBUTION Southeastern Atlantic and southern Indo-Pacific. WIO: South Africa (False Bay) to Mozambique and Mauritius.

REMARKS Possibly the largest stingray; common to abundant but not well known. Size at birth ~36 cm DW. Occurs in temperate waters, primarily offshore, on outer shelves, uppermost slopes and around offshore islands, but also inshore, near rocky reefs, on open sandy bottoms and in bays and estuaries. Midwater aggregations observed near New Zealand. Feeds on benthic invertebrates (crabs, bivalves) and small bony fishes; preyed on by orca whales and large sharks. Taken as a bycatch but usually discarded.

Bathytoshia lata (Garman 1880)

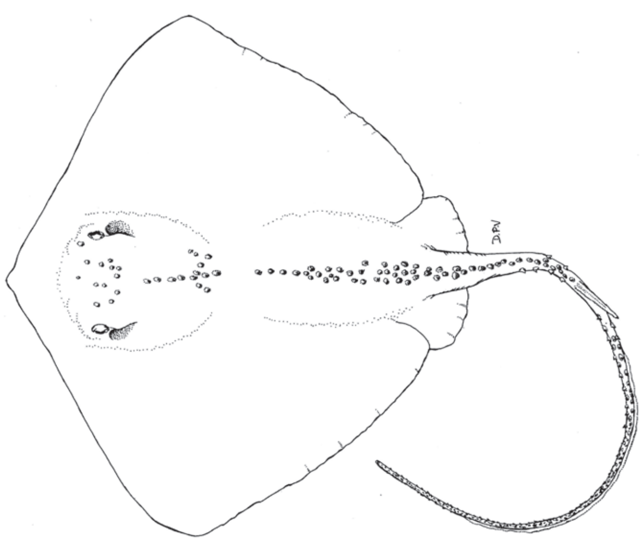
Thorntail stingray PLATE 69

Trygon lata Garman 1880: 170 (Hawaiian Is.).
Dasyatis thetidis Ogilby *in* Waite 1899: 46 (New South Wales, Australia); Wallace 1967*; SSF No. 30.4*; Compagno *et al.* 1989*; Fricke 1999; Fricke *et al.* 2009.

Dasybatis agulhensis Barnard 1925: 78 (Agulhas Bank, South Africa).
Dasyatis lubricus Smith 1957: 429, Pl. 15 (Algoa Bay, South Africa).
Bathytoshia lata: Last *et al.* 2016*.

Disc slightly wider than long; anterior margins nearly straight to weakly undulate, lateral apices narrowly rounded, and posterior margins nearly straight to weakly convex. Snout broadly triangular, tip slightly protruding. Eyes small. Internasal flap broad, short, and posterior edge fringed. Tail longer than disc length, broad-based and tapering; dorsal skin fold minute, and ventral skin fold long, low; usually 1 stinging spine. Pelvic fins small, broadly rounded. Dorsal surface of disc granular, with sparse enlarged pointed denticles centrally, from nape to stinging spine; tail uniformly very thorny beyond stinging spine in adults. Juveniles mostly smooth, with few thorns along midline from snout to base of tail. Tooth count 25–43/29–48; oral papillae 3–5.

Body dark grey to olive-brown dorsally; whitish ventrally. Attains 2 m DW, at least 4 m TL.



Bathytoshia lata, 133 cm DW (South Africa). Source: SSF

DISTRIBUTION Indo-Pacific. WIO: South Africa (Eastern Cape) to Mozambique and Réunion.

REMARKS Poorly known. Most common inshore, demersal, on soft bottoms, around reefs, and in estuaries and lagoons, but also well offshore, to ~440 m deep. Feeds on invertebrates (crabs, mantis shrimp, bivalves, polychaetes) and fishes (conger eels). Occasionally caught as commercial bycatch and by recreational anglers.

GENUS *Brevitrygon*

Last, Naylor & Manjaji-Matsumoto 2016

Disc small, oval to suboval. Tail short with stinging spine close to tail base, dorsal and ventral skin folds usually absent or with rudimentary ventral skin fold; median disc thorns weak, larger if present on tail, scapular thorns absent. Body white ventrally with dark margin, dorsal surface plain; posterior tail with or without pale lateral stripe. Four species, 2 in WIO.

KEY TO SPECIES

1a Mid-scapular denticle present but small, narrow and heart-shaped; denticle band narrow, constricted at nape in juveniles and adults; interspiracular distance 17–18%; tail 1.3–1.5 times disc width .... ***B. walga***

1b Mid-scapular denticle inconspicuous; denticle band wide, constricted beside spiracles in adults; interspiracular distance 18–19%; tail longer, 1.5–1.7 times disc width ....***B. imbricata***

Brevitrygon imbricata (Bloch & Schneider 1801)

Bengal whipray

PLATE 70

Raja imbricata Bloch & Schneider 1801: 366, 553 (Tharangambadi, India).
Raja obtusa Ehrenberg *in* Klunzinger 1871: 680 (Red Sea).
Dasyatis imbricata: Dor 1984.
Himantura imbricata: Compagno & Roberts 1982; Randall 1995*; Manilo & Bogorodsky 2003.
Brevitrygon imbricata: Last *et al.* 2016*.

Disc oval, about as wide as long; pectoral-fin anterior margins deeply concave, lateral apices evenly rounded, and posterior margins weakly convex. Snout with broad apical lobe; distance from preorbital snout to maximum disc width 42–50% DW. Eyes smaller than spiracles. Tail stout, shorter than disc, with rudimentary ventral skin fold. Dorsal disc with band of denticles, largest denticles medially and decreasing in size laterally; row of enlarged but low to flattened spear-shaped thorns, confined to midline above head region and on tail from base to stinging spine. Oral papillae 2.

Disc uniformly dark brownish dorsally, with paler margins; whitish ventrally, with darker margins. Attains 30 cm DW, 65 cm TL.

DISTRIBUTION Indian Ocean (patchy, poorly defined). WIO: Red Sea, Pakistan, India, Sri Lanka and Mauritius.

REMARKS Small-sized; poorly known. Often confused with *H. walga*. Size at birth ~10 cm DW. Found inshore; demersal. Feeds on benthic invertebrates. Caught in large numbers by demersal trawlers; used for human consumption.

Brevitrygon walga (Müller & Henle 1841)

Scaly whipray PLATE 70

Trygon walga Müller & Henle 1841: 159 (Red Sea).
Trygon nuda Günther 1870: 476 (Indian Seas).
Dasybatis uylenburgi Giltay 1933: 13 (East Indies).
Brevitrygon walga: Last *et al.* 2016*.

Disc oval, about as wide as long; pectoral-fin anterior margins broadly concave, lateral apices evenly rounded, and posterior margins weakly convex. Snout with broad apical lobe; distance from preorbital snout to maximum disc width 40–43% DW. Eyes smaller than spiracles. Tail stout, shorter than disc, with rudimentary ventral skin fold. Dorsal disc with band of denticles, mid-scapular denticle small but largest, narrow heart-shaped, largest denticles medially and decreasing in size laterally; row of enlarged but low to flattened spear-shaped thorns, confined to midline above head region and on tail from base to stinging spine. Oral papillae 2.

Disc uniformly dark brownish dorsally, with paler margins; whitish ventrally, with darker margins. Attains 30 cm DW, 70 cm TL.

DISTRIBUTION WIO: Red Sea, Persian/Arabian Gulf, Pakistan, India.

REMARKS Small-sized; poorly known. Often confused with *Brevitrygon imbricata*. Size at birth ~7–10 cm DW. Found inshore; demersal. Feeds on benthic invertebrates. IUCN Red List conservation status Near Threatened.

GENUS *Dasyatis* Rafinesque 1810

Anterior margin of disc more or less angular, never convex or broadly rounded; dorsal surface of disc and tail relatively smooth, or with numerous small or large denticles. Tail usually with 1 stinging spine; tail base somewhat broad, tail not whip-like beyond stinging spine; ventral skin fold low (never close to twice height of tail at its deepest section) and not normally extending to tail tip. Teeth rhomboidal, thin-crowned. Body pale to whitish ventrally. Five species, 1 in WIO.

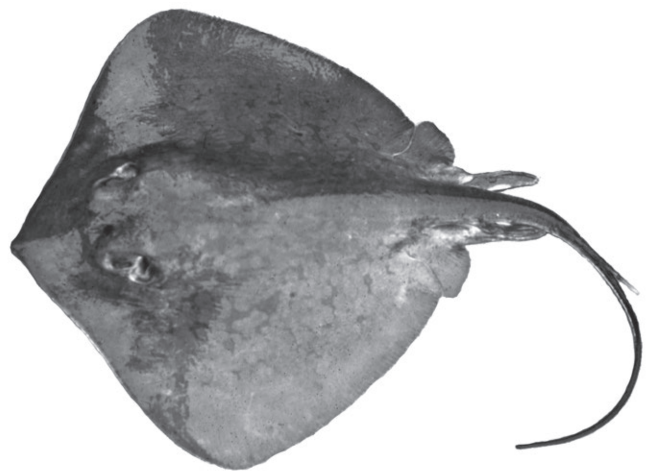
Dasyatis chrysonota (Smith 1828)

Blue marbled stingray PLATE 70

Trygon chrysonota Smith 1828: 2 (off Gamtoos River, Eastern Cape, South Africa).
Dasyatis pastinaca: Wallace 1967*; Van der Elst 1981*; SSF No. 30.3*; Cowley & Compagno 1993*.
Dasyatis chrysonota: Heemstra & Heemstra 2004*; Last *et al.* 2016*.

Disc rhomboidal, slightly longer than wide; snout triangular. Tail subequal to disc length; dorsal skin fold indistinct, and ventral skin fold long, low. Dorsal surface of disc smooth, without thorns, but sometimes with small, flattened, conical denticles near front margin. Oral papillae 5.

Disc with unique pattern of conspicuous bright blue finger-like reticulations on golden brown or greenish golden background dorsally; whitish ventrally, but with grey margins in juveniles; tail without banding. Attains 75 cm DW, ~160 cm TL.



Dasyatis chrysonota, 46 cm DW, male (South Africa).
PC Heemstra © NRF-SAIAB

DISTRIBUTION Southern Africa: Angola and Namibia in southeastern Atlantic, to South Africa (KwaZulu-Natal) and possibly Mozambique in WIO.

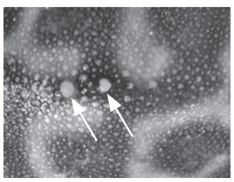
REMARKS Cowley & Compagno (1993) re-evaluated the taxonomic status of the blue stingray, usually misleadingly referred to as *Dasyatis pastinaca* (Linnaeus 1758), identifying the African forms as separate from the northeastern Atlantic and Mediterranean form; they tentatively ranked it as subspecies *D. chrysonota marmorata* (Steindachner 1892) (from Senegal), itself separate from *D. chrysonota chrysonota* (from South Africa, Namibia and Angola). Here, both subspecies are recognised as valid species. Occurs from surf zone to ~110 m deep, usually close inshore, along sandy beaches, near river mouths and sometimes on rocky reefs, and deeper offshore during winter. Litters of 1–7, females produce up to 20 young during their lifetime; size at birth 15–20 cm DW; gestation period ~9 months. Males mature at ~39 cm DW, at ~4 years; females mature at ~51 cm DW, at ~7 years. Feeds mostly on benthic invertebrates; smaller individuals (<30 cm DW) prefer polychaetes and amphipods, and larger individuals consume mostly crabs and mantis shrimp. A bycatch of trawl fisheries and an important sport fish.

GENUS *Himantura* Müller & Henle 1837

Disc rounded to oval, rhomboidal or quadrangular. Snout broad or broadly angular to blunt; snout tip with or without small protrusion (apical lobe). Tail tapering and whip-like, without skin folds. Dorsal surface of disc and tail smooth or granular, often with areas of thorns or tubercles in adults. Oral papillae on floor of mouth 0–7. Four species, 3 in WIO, plus 1 other undescribed.

KEY TO SPECIES

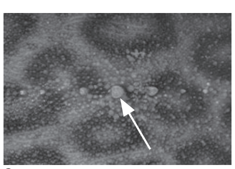
1a Disc weakly quadrangular, pectoral-fin apices broadly rounded; central disc with 1 dominant pearl-shaped suprascapular thorn followed by 2 or 3 slightly smaller thorns .... ***H. undulata***



1b Disc somewhat quadrangular; primarily with heart-shaped suprascapular thorns 2

2a Central disc with row of up to 15 heart-shaped thorns; dorsal disc with leopard-like markings in adults, and large dark spots in juveniles .... ***H. leoparda***

2b Central disc with 1 or 2 heart-shaped thorns; dorsal disc with fine dark spots and reticulations in adults, and small dark spots in juveniles .... ***H. uarnak***



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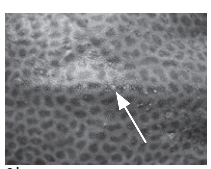


2b

Himantura leoparda Manjaji-Matsumoto & Last 2008

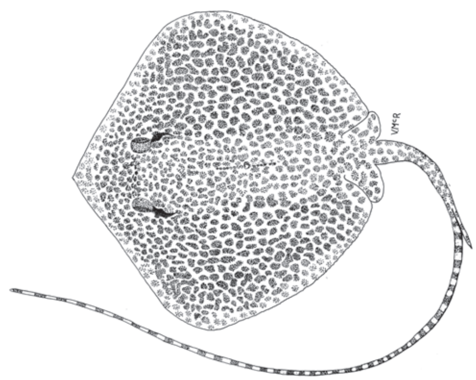
Leopard whipray

PLATE 70

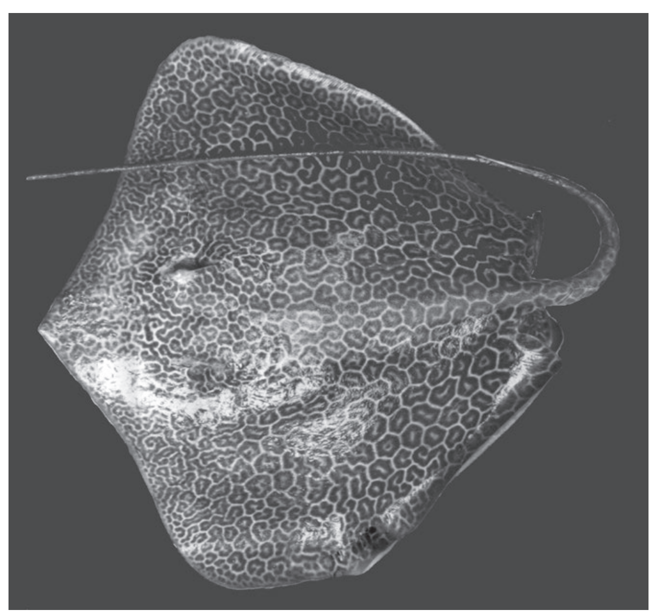
Himantura leoparda Manjaji-Matsumoto & Last 2008: 293, Figs. 1–5 (Gulf of Carpentaria, Queensland, Australia); Last *et al*. 2016*.
Dasyatis uarnak (*non* Gmelin 1789): Wallace 1967*.
Himantura fava (*non* Annandale 1909): Compagno & Roberts 1982.
Himantura uarnak (*non* Gmelin 1789): Van der Elst 1981*; SSF No. 30.10*; Compagno *et al.* 1989*.
Himantura sp. 1: Gloerfelt-Tarp & Kailola 1984.
Himantura undulata (*non* Bleeker 1852): Last & Stevens 1994.

Disc quadrangular or rhomboidal, slightly wider than long; pectoral-fin anterior margins concave, lateral apices moderately angular to narrowly rounded, and posterior margins convex. Snout broadly triangular, tip acutely pointed; distance from preorbital snout to maximum disc width ~38% DW. Tail long, 2.5–3.7 times DW, usually with 1 stinging spine. By ~33 cm DW, denticles form sub-rectangular band on disc, tapering from interorbital area to base of tail; row of up to 15 prominent heart-shaped thorns on midback (usually 2 of these enlarged); no thorns on midline of tail. Tooth count ~59 in upper jaw; oral papillae 4.

Disc sandy brown background dorsally, covered with leopard-like spots: thick dark brown irregular rings, each ring yellowish inside; juveniles greyish brown with moderately large dark brown polygonal spots; white ventrally; tail of young with dorsolateral spots to stinging spine, and banded dark and pale beyond. Attains 110 cm DW, ~4.7 m TL.



Himantura leoparda, 34 cm DW, immature male (South Africa). Source: SSF



Himantura leoparda (South Africa). © AR Thorpe

DISTRIBUTION Indo-Pacific (widespread). WIO: South Africa (KwaZulu-Natal) to Oman, and probably to Sri Lanka.

REMARKS Biology not well known due to confusion with other species; often confused with *H. uarnak* and *H. undulata*. Demersal on soft substrates; prefers shallow coastal waters, but found to at least 70 m deep. Probably heavily caught in coastal fisheries. IUCN Red List conservation status Vulnerable.

Himantura uarnak (Gmelin 1789)

Reticulate whipray PLATE 70

Raja sephen var. *uarnak* Forsskål *in* Niebuhr 1775: 18, viii (Red Sea) [name not available].
Raja uarnak Gmelin 1789: 1509 [Red Sea].
Pastinachus uarnak: Rüppell 1835*.
Trygon uarnack: Richardson 1846.
Leiobatis (*Himantura*) *uarnak*: Bleeker 1877*.
Trygon narnak: Tillier 1902.
Dasyatis uarnak: SFSA No. 79b*; Wallace 1967*.
Himantura uarnak: Day 1865; Van der Elst 1981*; Compagno & Heemstra 1984*; SSF No. 30.10*; Randall 1995*; Heemstra & Heemstra 2004*; Last & Stevens 2009*; Last *et al*. 2016*.

Disc rhomboidal, about as long as wide; pectoral-fin anterior margins weakly concave, lateral apices narrowly rounded to angular, and posterior margins broadly convex. Snout broadly triangular, with small apical lobe; distance from snout tip to maximum disc width 33–43% DW. Tail extremely long, 2.9–3.5 times DW, usually with 1 stinging spine. Disc mostly smooth, with band of small flat denticles extending from head onto tail; central disc with 1 or 2 enlarged heart-shaped thorns. Tooth count 26–40/27–44; oral papillae 4 or 5 in two transverse rows.

Disc pale brown dorsally, with intricate pattern changing with growth: close-set, fine dark brown polygonal spots in juveniles, and broad dark brown reticulations and/or short narrow irregular bars in adults; spots distributed over brown background, and bars or reticulations separated by narrow yellowish brown lines; pale ventrally, with moderately wide brownish margins; tail banded dark (brown to blackish) and pale (white to yellow) in juveniles, and with reticulations and blackish towards tip in adults. Attains ~200 cm DW, ~6 m TL or more.

DISTRIBUTION Indo-Pacific (widespread). WIO: South Africa (Eastern Cape) to Red Sea, eastern Mediterranean Sea, Persian/Arabian Gulf, Pakistan, India, Sri Lanka, Madagascar, Seychelles and Mauritius.

REMARKS Often confused with *H. undulata* and other reticulate-patterned rays of the '*uarnak*' species-complex. Found inshore to ~50 m deep; common off sandy beaches and in shallow estuaries and lagoons, also over coral reefs. Litters of up to 5; size at birth 21–28 cm DW. Feeds on invertebrates (crabs, shrimp, mantis shrimp, bivalves, gastropods, worms, jellyfish) and bony fishes. Caught as a utilised bycatch of commercial fisheries, and also in artisanal fisheries and by shore anglers. IUCN Red List conservation status Vulnerable globally.

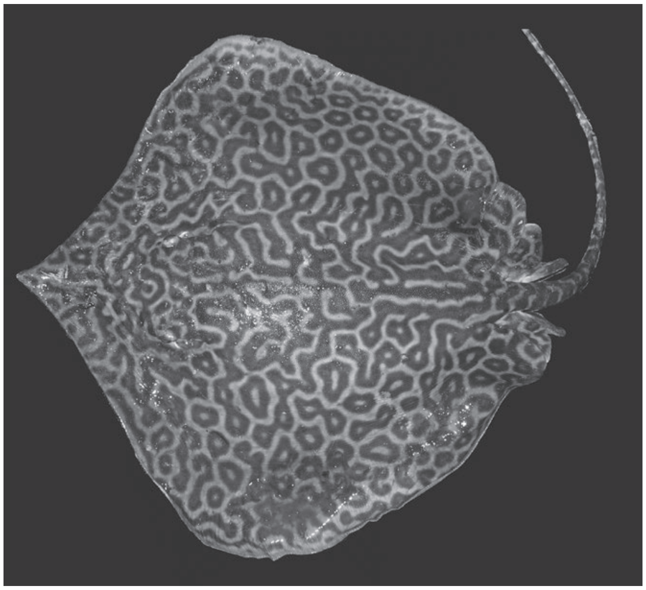
Himantura undulata (Bleeker 1852)

Honeycomb whipray PLATE 71

Trygon undulata Bleeker 1852: 70 (Jakarta and Semarang, Java, Indonesia).
Trygon russellii (*non* Gray 1834): Blyth 1860.
Leiobatis (*Himantura*) *undulatus*: Bleeker 1877.
Trygon favus Annandale 1909: 25, Pls. 1, 3 (off Odisha, India).
Himantura undulata: Compagno 1999; Last *et al*. 2016*.

Disc weakly quadrangular, about as long as wide, and thick; anterior margins of disc strongly concave, lateral apices broadly rounded, and posterior margins broadly convex. Preorbital snout moderately long, with distinct apical lobe; distance from snout tip to maximum disc width 45–46% DW. Tail length ~3 times DW. Teeth subequal in upper and lower jaws, cone-shaped with blunt peak and prominent horizontal groove; oral papillae 2–4, broad-based, distally pointed, the middle two connected by low serrated ridge. Disc with well-defined band of denticles extending from head onto tail; dominant pearl-shaped suprascapular denticle, followed by 2 or 3 slightly smaller denticles, and small stellate-based denticles present outside of band (less obvious in adults).

Dorsal surface of disc with large dark brown polygonal spots in young, and broad yellowish brownish undulations and elongated loops or large and hollow polygonal spots in larger specimens and adults; spots or loops separated by slightly narrower or equally wide paler lines; disc white ventrally, often with dusky margin; tail in young laterally banded posterior to stinging spine, dark bands about 3 times wider than pale bands, and tail uniformly pale ventrally; tail in larger specimens and adults with fine dark brown reticulations on pale background. (Dorsal disc colouration appears sexually dimorphic based on the few specimens examined.) Attains 200 cm DW.



Himantura undulata, ~ 1 m DW (Malaysia).
M Manjaji-Matsumoto © BMRI-UMS

DISTRIBUTION Indo-Pacific (possibly widespread but range not well defined). WIO: southern Africa to Red Sea and Lessepsian migrant to eastern Mediterranean Sea.

REMARKS Often confused with other species in the '*uarnak*' species-complex. Litters of up to 5; size at birth 21–28 cm DW. Found inshore, to ~50 m deep; common along sandy beaches and in shallow estuaries and lagoons; also found on coral reefs and may enter freshwater. A commercially valuable bycatch in a range of artisanal and commercial fisheries. Feeds on invertebrates (crabs, shrimps, mantis shrimps, bivalves, gastropods, worms, jellyfish) and small bony fishes. IUCN Red List conservation status Endangered.

GENUS ***Maculabatis*** Müller & Henle 1837

Disc suboval to rhomboidal; tail long and whip-like with stinging spine near tail base, dorsal and ventral fin folds absent; 1–3 mid-scapular thorns, or thorns in row on nape; well-developed denticle band, rest of disc naked or with patchy denticles; body white ventrally, plain or with spots dorsally, disc may have yellow or dark margins; juveniles usually with distal tail half or fully banded. Six species and 3 undescribed, 5 species in WIO.

KEY TO SPECIES

1a Dorsal disc with white spots in young and adults ..... ***M. gerrardi***
1b Dorsal disc plain in young, sometimes with faded dark speckles in adults **2**

2a Base of tail forward of caudal sting with white spots ..... ***M. bineeshi***
2b Base of tail forward of caudal sting plain **3**

3a Enlarged mid-scapular denticle preceded by a row of distinct denticles; internasal space 8.4–9.6% disc width ..... ***M. arabica***
3b Enlarged mid-scapular denticle not preceded by a row of distinct denticles; internasal space narrower, 7.1–8.1% disc width **4**

4a 1 or 2 mid-scapular denticles, small, oval to heart-shaped; tail dark or with weak saddles on dorsal half in young and adults; banded in neonates ..... ***M. randalli***
4b 5 mid-scapular denticles, large, longer than wide; tail uniform greyish or brownish in adults; banded on dorsal half in young, dark band broadest ..... ***M. ambigua***

Maculabatis ambigua

Last, Bogorodsky & Alpermann 2016

Baraka's whipray — PLATE 71

Himantura gerrardi (*non* Gray 1851): Bogorodsky *et al.* 2014.
Himantura sp. 1: Last *et al.* 2016*.
Maculabatis sp. 1: Last *et al.* 2016*.
Maculabatis ambigua Last, Bogorodsky & Alpermann 2016: 67, Figs. 1–6 (Red Sea); Last *et al.* 2016*.

Disc rhomboidal, slightly wider than long; pectoral-fin anterior margins weakly concave, lateral apices moderately angular, and posterior margins broadly convex. Snout moderately long, tip acutely pointed; preoral snout length 19–21% DW; distance from snout tip to maximum disc width 33–35% DW. Tail very long, 2.3–2.5 times DW. Dermal denticles in distinct band on disc, small, flat, somewhat rounded, extending onto tail; 5 scapular thorns on midback. Tooth count 36 (upper jaw); oral papillae 4.

Disc greyish or brownish dorsally, sometimes dark margin in young; disc white ventrally; tail uniform greyish in adults, weak band on tail posterior to stinging spine in young (but bands fading with size). Attains 90 cm DW, ~290 cm TL.

DISTRIBUTION WIO: South Africa (Eastern Cape) to Red Sea, Tanzania (Zanzibar), Pakistan, India and Sri Lanka.

REMARKS Resembles *M. randalli*, also found in the WIO. Biology unknown.

Maculabatis arabica Manjaji-Matsumoto & Last 2016

Pakistan whipray PLATE 71

Himantura sp. C: Manjaji 2004.
Himantura sp.: Henderson *et al*. 2016.
Himantura sp. 2: Last *et al*. 2016.
Maculabatis sp. 2: Last *et al*. 2016.
Maculabatis arabica Manjaji-Matsumoto & Last 2016: 337, Figs. 1–6 (west of Turshian Creek, Pakistan); Last *et al*. 2016*.

Disc rhomboidal, slightly wider than long; pectoral-fin anterior margins weakly concave, lateral apices moderately angular, and posterior margins broadly convex. Snout moderately long, tip acutely pointed; preoral snout length 21% DW; distance from snout tip to maximum disc width 35% DW. Tail very long, 2.2–2.6 times DW. Dermal denticles in distinct band on disc, small, flat, somewhat rounded, extending onto tail; 1–3 scapular thorns on midback, preceded by row of up to 10 smaller enlarged denticles. Oral papillae 2–4.

Disc pale brown to greenish dorsally, paler disc margin and denticle band; disc white ventrally; tail uniform pale brownish in adults, band on dorsal half of tail posterior to stinging spine in young (dark bands broader). Attains 61 cm DW, >200 cm TL.

DISTRIBUTION Northwestern Indian Ocean: Arabian Sea (off Pakistan and western India).

REMARKS Attains similar size as *M. randalli*, also found in the WIO, but has a narrower internasal space. Probably feeds on small invertebrates.

Maculabatis bineeshi Manjaji-Matsumoto & Last 2016

Short-tail whipray PLATE 71

Dasyatis uarnak (*non* Gmelin 1789): Jones & Kumaran 1970, Fig. 16, two specimens 425 and 480 mm DW (compiled distribution partly in error).
?*Himantura gerrardi* (*non* Gray 1851): Ishihara *et al*. 1998, 44, Pl. 3, brief description of two specimens, MTUF 30005.
Himantura sp. D: Manjaji 2004.
Himantura sp. 3: Last *et al*. 2016.
Maculabatis sp. 3: Last *et al*. 2016.
Maculabatis bineeshi Manjaji-Matsumoto & Last 2016: 344, Figs. 7–13 (west of Turshian Creek, Pakistan).
Maculabatis bineeshi: Last *et al*. 2016*.

Disc rhomboidal, slightly wider than long; pectoral-fin anterior margins weakly concave, lateral apices moderately angular, and posterior margins broadly convex. Snout moderately long, tip acutely pointed; preoral snout length 21% DW; distance from snout tip to maximum disc width 26% DW. Tail long, 2.3–2.6 times DW. Dermal denticles in distinct band on disc, small, flat, somewhat rounded, extending onto tail; 1–3 scapular thorns on midback. Oral papillae 4.

Disc pale brown; white ventrally, disc and pelvic fins with broad yellowish margins; tail dark, weak band on dorsal half of tail posterior to stinging spine. Attains 42 cm DW.

DISTRIBUTION Northern Indian Ocean: Persian/Arabian Gulf, Arabian Sea (off Pakistan) and Bay of Bengal (Odisha, India).

REMARKS The secondary denticle band is well developed by 24 cm DW. Probably feeds on small invertebrates.

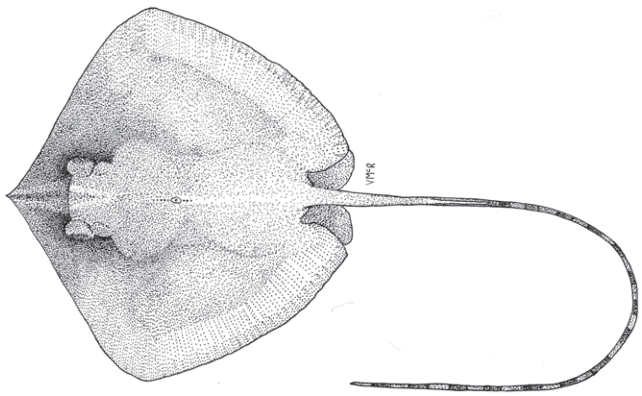
Maculabatis gerrardi (Gray 1851)

Whitespotted whipray PLATE 72

Trygon gerrardi Gray 1851: 116 (India).
Leiobatis (*Himantura*) *gerrardi* Bleeker 1877: Fig. 1, Pl. 559.
Trygon alcockii Annandale 1909: 27, Fig. 3 (Puri, Odisha, India).
Trygon uarnak (*non* Gmelin 1789): Anonymous 1955*.
Himantura gerrardi: Compagno & Heemstra 1984; SSF No. 30.9*; Randall 1995*; Manilo & Bogorodsky 2003; Bonfil & Abdallah 2004; Heemstra & Heemstra 2004; Bogorodsky *et al.* 2014.
Maculabatis gerrardi: Last *et al*. 2016*.

Disc rhomboidal, slightly wider than long; pectoral-fin anterior margins weakly concave, lateral apices moderately angular, and posterior margins broadly convex. Snout moderately long, tip acutely pointed; preoral snout length 19–23% DW; distance from snout tip to maximum disc width 33–43% DW. Tail very long, 2.7–3.4 times DW. Dermal denticles in distinct band on disc, small, flat, somewhat rounded, extending onto tail; a few small scapular thorns on midback. Tooth count 22–26/25–30; oral papillae 2–5.

Disc greyish brown to pale olive-brown dorsally, sparsely spotted or with white spots or blotches scattered over entire surface or confined to rear half of disc; spots extending along sides of tail to stinging spine; disc whitish ventrally, sometimes with narrow brown margins posteriorly; tail with pale and dark brown bands beyond stinging spine in both young and adults (but bands fading with size). Attains 100 cm DW, >200 cm TL.



Maculabatis gerrardi, 19 cm DW, 60 cm TL (South Africa). Source: SSF

DISTRIBUTION Indo-Pacific (widespread). WIO: South Africa (Eastern Cape) to Red Sea, Tanzania (Zanzibar), Pakistan, India and Sri Lanka.

REMARKS Often confused with *H. uarnak*. Size at birth 18–21 cm DW. Males mature at 46–48 cm DW; females mature by ~64 cm DW. Common, demersal, in coastal regions including estuaries, to at least 60 m deep. Feeds on invertebrates (bivalves, crustaceans) and small fishes. Often hooked by shore anglers. IUCN Red List conservation status Endangered.

Maculabatis randalli

(Last, Manjaji-Matsumoto & Moore 2012)

Arabian banded whipray PLATE 72

Himantura randalli Last, Manjaji-Matsumoto & Moore 2012: 21, Figs. 1–6 (Kuwait City fish market, Persian/Arabian Gulf).
Trygon gerrardi (*non* Gray 1851): Blegvad & Løppenthin 1944.
Himantura gerrardi (*non* Gray 1851): Randall 1995*.
Himantura sp. B: Manjaji 2004.
Maculabatis randalli: Last *et al.* 2016*.

Disc rhomboidal, slightly broader than long; anterior margins almost straight to weakly concave, lateral apices rounded, and posterior margins broadly convex. Snout moderately long, preoral length 1.5–1.6 times interorbital width; apical lobe weak. Tail 2.2–2.4 times disc width, slender and tapering gently towards stinging spine and less so beyond to tail tip; tail behind stinging spine subcircular with deep longitudinal ventral groove and prominent midlateral ridge in juveniles, and weakly depressed in adults. Denticle band covering entire dorsal surface of tail in adults; small, broadly heart-shaped to seed-shaped denticles on midback. Tooth rows ~34/40; oral papillae 2.

Body uniformly pale brown dorsally, occasionally with dark flecks (specimens <25 cm DW), and disc margins sometimes paler; disc whitish ventrally; tail dark dorsally and sharply demarcated from paler surface ventrally (in adults), or with conspicuous white saddles and almost uniformly dark distally (in neonates and juveniles). Attains 54 cm DW (males) to 62 cm DW (females).

DISTRIBUTION WIO: Persian/Arabian Gulf.

REMARKS So far recorded only from the Persian/Arabian Gulf, where it is possibly endemic. Found on soft substrates, to ~60 m deep. Presumably feeds on invertebrates (particularly sergestid shrimp *Acetes*).

GENUS *Megatrygon*

Last, Naylor & Manjaji-Matsumoto 2016

Disc rhomboidal. Tail short, broad at base, tapering abruptly, and whip-like beyond stinging spine; dorsal skin fold indistinct, and ventral skin fold long, low. Denticle band absent. One species.

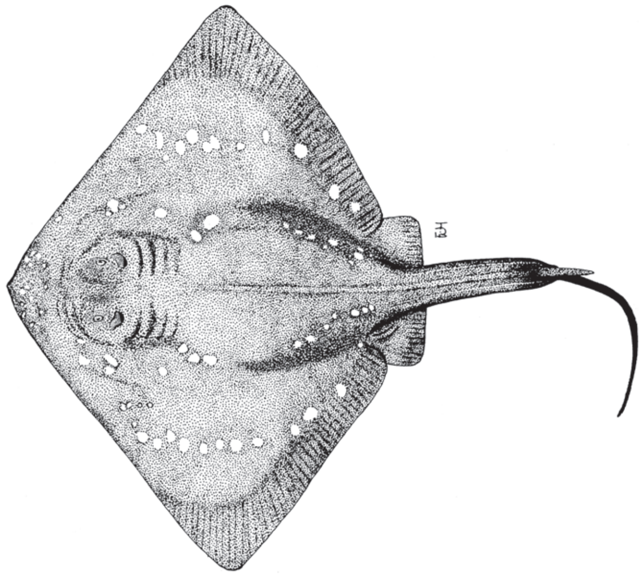
Megatrygon microps (Annandale 1908)

Small-eye stingray PLATE 72

Trygon microps Annandale 1908: 393, Pl. 27 (off Chittagong coast, India, Bay of Bengal).
Dasyatis microps: Pierce *et al.* 2008*; Last & Stevens 2009*; Bineesh *et al.* 2014.
Megatrygon microps: Last *et al.* 2016*.

Disc broad and angular; pectoral-fin anterior margins almost straight, tips angular; snout weakly rounded. Eyes small; spiracles large. Tail slightly shorter than disc width; usually 1 stout stinging spine. Pelvic fins relatively large. Dorsal surface covered with minute stellate denticles, larger denticles on snout tip and between eyes and spiracles, and slightly larger denticles covering base and sides of tail to stinging spine. Oral papillae 5.

Body brown to reddish or pinkish brown dorsally, darkening towards tail tip; row of white pores on either side of snout near anterior margin; large pale spots near eyes and spiracles, and in loose rows surrounding centre of disc, and distinctive paired row on outer pectoral fins; row of small white spots laterally at base of tail; tail blackish beyond stinging spine; disc whitish ventrally, but margins and tail dusky. Attains 220 cm DW, 320 cm TL.



Megatrygon microps, ~2 m DW (S Mozambique).

DISTRIBUTION Indo-Pacific (patchy). WIO: Mozambique, southern India and Maldives.

REMARKS Large-sized stingray. Litters of 1; size at birth 31–33 cm DW. Depth range and habitat poorly known; inhabits shallow coastal areas, reefs, estuaries and river mouths, and probably deeper waters; assumed to be predominantly demersal, but also semipelagic. Probably an occasional bycatch throughout its range.

GENUS ***Neotrygon*** Castelnau 1873

Orbital region with dark mask-shaped pattern. Thorn-like denticles confined to single variable-length row on midline of disc. Tail short, with generally 2 stinging spines, relatively broad-based and slender beyond stinging spines, and with short dorsal skin fold and long low ventral skin fold. Ten species, 1 in WIO. *Neotrygon indica* Pavan-Kumar *et al*. 2018, from the Gulf of Mannar (species based on DNA and spot colour pattern), has not been examined or included.

Neotrygon caeruleopunctata

Last, White & Séret 2016

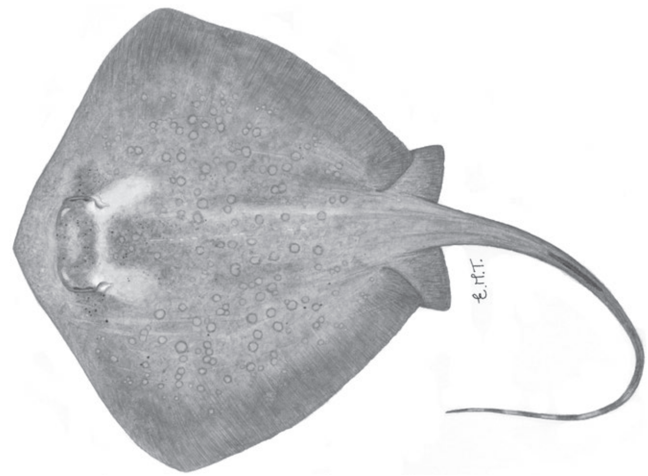
Blue-spotted maskray PLATE 72

Dasyatis kuhlii (non Müller & Henle 1841): Compagno & Heemstra 1984*; SSF No. 30.2*; Last & Stevens 2009*.

Neotrygon caeruleopunctata Last, White & Séret 2016: 546, Figs. 5c, 6c, 7c, 10 (Kedonganan fish market, Bali, Indonesia); Last *et al.* 2016*.

Disc rhomboidal, wider than long, and trunk thick; pectoral-fin apices angular. Snout blunt, preoral length 13–15% DW. Pelvic fins moderately large. Tail subequal to or slightly longer than disc, broad-based, with usually 2 stinging spines, and short dorsal skin fold and long low ventral skin fold. Short row of posteriorly directed, flattened thorns in scapular region (juveniles often lacking thorns); tail smooth. Tooth count 25–32 in each jaw; oral papillae 2.

Disc greyish to reddish brown dorsally, with prominent blue ocelli with brighter blue centres, and scattered fine black spots; prominent dark transverse bar across orbital region; whitish ventrally, with dusky margins; tail banded black and white beyond stinging spines; skin folds on tail pale with darker outer margins. Attains at least 47 cm DW, 76 cm TL.



Neotrygon caeruleopunctata, 36 cm DW, adult (South Africa).
Source: SSF

DISTRIBUTION Indo-Pacific, but probably a species-complex. WIO: South Africa, Mozambique, Madagascar, Mauritius, Red Sea, India and Sri Lanka.

REMARKS The taxonomic status of this species requires investigation, as multiple colour morphs exist which may represent different species. Litters of 1 or 2; size at birth ~16 cm DW. Males mature at ~25 cm DW. Common inshore, typically in deep water, to ~90 m deep, but moves into shallow lagoons or onto reef flats at high tide; demersal, over sandy bottoms near rocky or coral reefs, and sometimes lies buried in sand with only its eyes and tail showing. Feeds on invertebrates (crabs, shrimp) and small fishes. A utilised bycatch in many parts of its range.

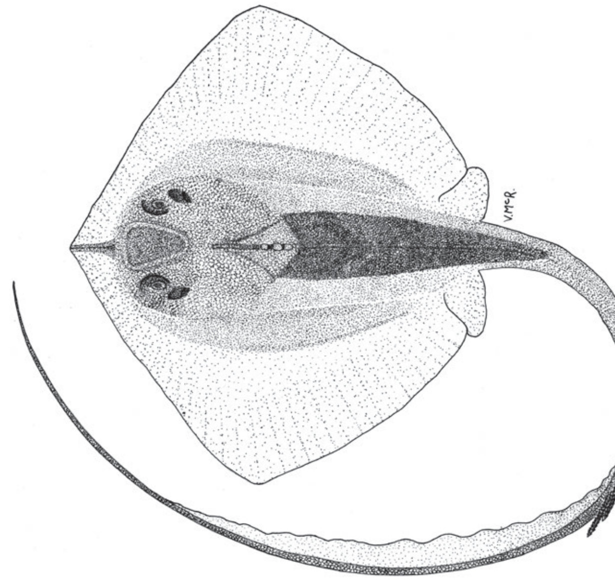
GENUS ***Pastinachus*** Rüppell 1829

Disc robust and strongly rhomboidal; distance from cloaca to stinging spine >½ DW. Tail broad-based; ventral skin fold long and prominent, its depth up to 2–6 times tail height over fold; no dorsal skin fold. Nuchal thorns 1–3; no enlarged thorns elsewhere on disc or tail. Five species, 2 in WIO.

KEY TO SPECIES

1a Denticles on disc flat; 4 small mid-scapular thorns; disc uniform dark greyish brown; tail fold and tail tip black .... ***P. ater***

1b Denticles on disc starry-based; 2 small mid-scapular thorns; disc uniform yellowish brown; tail fold bluish .... ***P. sephen***



Pastinachus ater, 45 cm DW, female (South Africa). Source: SSF

Pastinachus ater (Macleay 1883)

Broad cowtail ray PLATE 72

Taeniura atra Macleay 1883: 598 (New Guinea).
Pastinachus ater: Last *et al*. 2016*.

Disc rhomboidal, 1.2–1.3 times wider than long; pectoral-fin anterior margins nearly straight or weakly convex, lateral apices rounded to angular, and posterior margins weakly convex. Snout broadly rounded and blunt, often with slightly produced tip. Tail long, up to twice disc length, with deep ventral skin fold not reaching tail tip; usually 1 stinging spine, posteriorly set. Dorsal surface with broad band of fine denticles from near snout tip to tail, excluding disc margins; disc entirely smooth in neonates, and juveniles develop up to 4 circular tubercles at centre, which may become indistinct in adults. Tooth count ~20 in each jaw; oral papillae 5.

Disc dark greyish brown dorsally; whitish ventrally; tail and ventral skin fold black. Attains 200 cm DW, 3 m TL or more.

DISTRIBUTION Indo-Pacific (widespread but scattered). WIO: Persian/Arabian Gulf, Oman, Red Sea to South Africa (KwaZulu-Natal), Seychelles and Maldives.

REMARKS Biology and range poorly known. Demersal on continental and insular shelves. Ventures into estuaries and freshwater. Feeds on invertebrates (crustaceans, polychaetes, sipunculids, molluscs) and bony fishes. Caught in various fisheries and used for its skin and meat.

Pastinachus sephen (Fabricius 1775)

Cowtail stingray PLATE 73

Raja sephen Fabricius *in* Niebuhr (ex Forsskål) 1775: 17, viii (Red Sea).
Trigon forskalii Rüppell 1829: 53, Pl. 13 (Red Sea).
Dasyatis sephen: Smith 1957*, 1961; Wallace 1967*.
Hypolophus sephen: SSF No. 30.12*.
Dasybatus (*Pastinachus*) *gruveli* Chabanaud 1923: 45 (Gulf of Thailand).
Pastinachus sephen: Bonfil & Abdallah 2004*; Last *et al*. 2016*.

Disc rhomboidal, up to ~1.3 times wider than long; pectoral-fin anterior margins nearly straight or weakly convex, lateral apices rounded to angular, and posterior margins weakly convex. Snout broadly rounded and blunt, often with slightly produced tip. Tail long, up to twice disc length, with deep ventral skin fold not reaching tail tip; usually 1 stinging spine, posteriorly set. Dorsal surface with broad band of fine denticles from near snout tip to tail, excluding disc margins; disc entirely smooth in neonates, and juveniles develop up to 4 circular tubercles at centre, which may become indistinct in adults. Tooth count ~20 in each jaw; oral papillae 5.

Disc greyish brown to almost black dorsally; whitish ventrally, but with dark margins on disc and pelvic fins in young; tail and ventral skin fold dark brown or black. Attains 180 cm DW, 3 m TL or more.

DISTRIBUTION Northwestern Indian Ocean. WIO: Persian/Arabian Gulf, Red Sea to Pakistan.

REMARKS Biology and range poorly known; two distinct species (thick-fold and thin-fold tail forms) have been confused. Size at birth ~18 cm DW. Prefers shallower water, but found to ~60 m deep, on reef flats, in estuaries and intertidal lagoons, and far up rivers in freshwater. Feeds on invertebrates (crustaceans, polychaetes, sipunculids, molluscs) and bony fishes. Caught in various fisheries and used for its skin and meat. IUCN Red List conservation status Near Threatened.

GENUS *Pateobatis*

Last, Naylor & Manjaji-Matsumoto 2016

Disc suboval to rhomboidal. Tail short, to very long and whip-like, with 1–3 stinging spines close to tail base, dorsal and ventral skin folds absent; 1–3 heart- or pearl-shaped mid-scapular thorns, or thorns in row on nape. Dorsal body plain, white ventrally, often with dark margin; tail plain. Five species, 3 in WIO.

KEY TO SPECIES

1a	Disc subcircular; snout produced and narrowly triangular	***P. bleekeri***
1b	Disc rhomboidal; snout broadly triangular or convex	**2**
2a	Snout broadly convex; tail very long, 2–2.6 times disc width; dorsal surface of disc with small denticles but no enlarged thorns along midline of disc and tail base	***P. fai***
2b	Snout broadly triangular; tail slightly longer than disc width; 1 or 3 rows of enlarged upright thorns along midline of disc and tail base, to stinging spine	***P. jenkinsii***

Pateobatis bleekeri (Blyth 1860)

Bleeker's whipray PLATE 73

Trygon bleekeri Blyth 1860: 41 (Calcutta fish market, India).
Pateobatis bleekeri: Last *et al.* 2016*.

Disc subcircular, slightly wider than long; pectoral-fin anterior margins straight, lateral apices broadly rounded, and posterior margins broadly convex. Snout produced, preoral snout length ~⅓ disc length, or twice interorbital width. Tail whip-like, ~3 times disc length. Adults with sharply defined band of denticles extending from snout to base of tail, and 1 or 2 larger pearl-like thorns on midback. Oral papillae 2.

Body usually uniformly greyish or brownish; young often with small dark blotches on dorsal disc, more conspicuous on central disc and head, fading towards pectoral-fin margins; creamy white ventrally. Attains 105 cm DW, ~4 m TL.

DISTRIBUTION Indo-Pacific. WIO: Pakistan, India and Sri Lanka.

REMARKS The Indian record is based on a colour photograph of a juvenile specimen from "India" identified as *H. bleekeri* in FishBase (Froese & Pauly 2014). Found inshore, to at least 30 m deep, over soft bottoms, and also enters estuaries. Feeds on invertebrates (crustaceans, molluscs, polychaetes) and small fishes. Probably taken in moderate quantities in demersal fisheries. IUCN Red List conservation status Endangered.

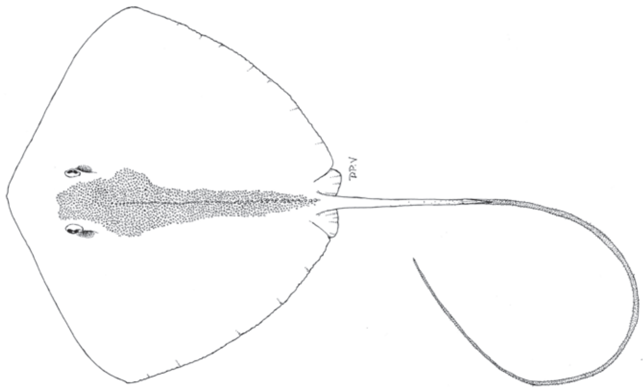
Pateobatis fai (Jordan & Seale 1906)

Pink whipray PLATE 73

Himantura fai Jordan & Seale 1906: 184, Fig. 2 (Apia, Upolu I., Samoa); Last & Compagno 1999; Bonfil & Abdallah 2004*; Last & Stevens 2009*.
Trygon purpurea Smith (ex Müller & Henle) 1841: 160, Pl. 52 [South Africa].
Trygon liocephalus Klunzinger 1871: 678 (Al-Qusayr, Egypt, Red Sea).
Dasyatis purpureus: Wallace 1967*.
Himantura sp.: SSF No. 30.11*.
Pateobatis fai: Last *et al.* 2016*.

Disc rhomboidal, trunk thick; pectoral-fin anterior margins broadly convex, lateral apices moderately angular, and posterior margins broadly convex. Snout broadly convex with feeble tip; preoral snout length 2.3–3 in mouth width; distance from snout tip to maximum disc width 32–39% DW. Tail narrow, very long (2–2.6 times DW), whip-like beyond stinging spine; usually 1 serrated stinging spine. Dorsal surface, from centre of disc to entire tail, covered with small rounded denticles; few small sharp thorns along midline, becoming densest on tail; juveniles mostly smooth or with sparse covering of small, flat, heart-shaped denticles from interorbital area to tail. Tooth count 20–22/28–31; oral papillae 4.

Disc uniformly pale brown to greyish dorsally, with pinkish margins and darker pelvic fins; sometimes with small white blotch in front of eyes and spiracles; pale ventrally; tail dark grey to black beyond stinging spine. Attains 184 cm DW, ~5 m TL (possibly more).



Pateobatis fai, 77 cm DW, female (South Africa). Source: SSF

DISTRIBUTION Indo-Pacific (range poorly defined). WIO: South Africa, Egypt (Suez Canal), Pakistan, India and Maldives.

REMARKS Often confused with *P. jenkinsii*. Current WIO records of *P. fai* are based on photographs alone. Occurs in intertidal zone to ~200 m deep (but usually above 70 m); prefers soft sandy bottoms. Aggregations (of sometimes stacked individuals) have been observed. Feeds on small benthic invertebrates. A bycatch of commercial fisheries, and sold as food.

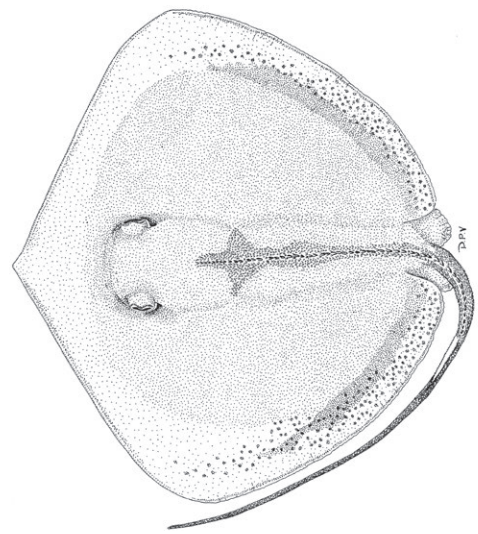
Pateobatis jenkinsii (Annandale 1909)

Jenkins whipray PLATE 73

Trygon jenkinsii Annandale 1909: 28, Fig. 4 (Ganjam coast, Odisha, India).
Dasyatus jenkinsii: Morrow 1954.
Himantura draco Compagno & Heemstra 1984: 6, Figs. 1–8 (off Durban, KwaZulu-Natal, South Africa); SSF No. 30.8*.
Himantura jenkinsii: Randall 1995*; Heemstra & Heemstra 2004; Last & Stevens 2009*.
Pateobatis jenkinsii: Last *et al.* 2016*.

Disc rhomboidal, slightly wider than long, trunk thick; pectoral-fin anterior margins straight, lateral apices broadly rounded, and posterior margins convex. Snout broadly triangular, tip feebly pointed; distance from preorbital snout to maximum disc width 31–37% DW. Pelvic fins small. Tail slightly longer than disc width, with up to 3 stinging spines. Conspicuous band of imbricated, flat, narrow, heart-shaped denticles on head and scapular region, and 1 or 3 irregular rows of enlarged wedge-shaped thorns on midline from centre of disc to stinging spine; flat and spinulose denticles interspersed on all surfaces of tail posterior to stinging spine; small granulations elsewhere on disc. Tooth count 28/31; oral papillae 2–4.

Dorsal surface of disc uniformly yellowish brown, but some specimens with small black spots along posterior margins; disc and margins white ventrally; tail greyish beyond stinging spine. Attains at least 104 cm DW, ~200 cm TL.



Pateobatis jenkinsii, 56 cm DW, immature male holotype of *Himantura draco* (South Africa). Source: SSF

DISTRIBUTION Indo-Pacific (patchy). WIO: South Africa (KwaZulu-Natal), Mozambique, northwestern Madagascar, Socotra I., Oman, India and Sri Lanka.

REMARKS Likely misidentified as *H. fai* in some literature. Size at birth 20–27 cm DW; males mature at ~70 cm DW. Found inshore to ~50 m deep, typically demersal on sandy substrates. Feeds on crustaceans and small fishes. Caught in various inshore fisheries; sold as food and valued for its skin.

GENUS *Pteroplatytrygon* Fowler 1910

Disc trapezoidal, ~⅓ wider than long; pectoral-fin anterior margins convex, posterior margins weakly convex to straight. Snout short, with small rounded tip. Eyes almost lateral, not protruding above disc. Internasal flap laterally expanded, exceeding edges of nostrils. Teeth with 1 or 2 pointed cusps. Tail with well-developed ventral skin fold. Dorsal and ventral surfaces of disc both dark. One species.

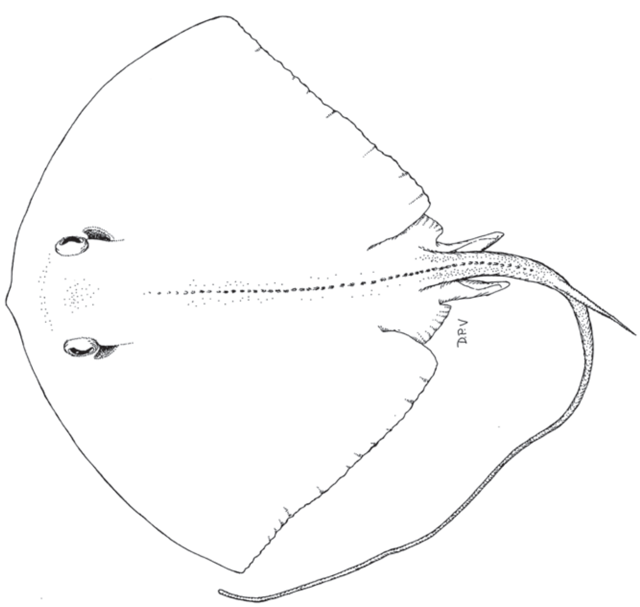
Pteroplatytrygon violacea (Bonaparte 1832)

Pelagic stingray PLATE 73

Trygon violacea Bonaparte 1832, fasc. 1, punt. 6, Pl. 155 (Italy, Mediterranean Sea).
Trygon purpurea: Müller & Henle 1841*.
Dasyabatus purpureus: Barnard 1925*.
Pteroplatytrygon violacea: McEachran & Fechhelm 1998; Compagno 1999; Fricke *et al.* 2009; Last *et al.* 2016*.

Anterior margins of disc evenly rounded. Snout broad, preorbital snout length 11–17% DW. Eyes small, not protruding above disc. Tail broad-based and long, can exceed twice disc length when undamaged; 1 or 2 stinging spines; ventral skin fold long and low. Denticles on dorsal surface randomly and widely spaced; interorbital area with minute denticles; short thorns along midline of disc and tail; males sometimes with denticles on ventral surface of disc. Tooth count 25–39/25–38; oral papillae 5–15.

Disc dark purplish to bluish black or sometimes dark blue-green dorsally; slightly paler brownish black to dark grey ventrally; tail and ventral skin fold black. Attains 80 cm DW (usually <60 cm DW), 160 cm TL.



Pteroplatytrygon violacea, 35 cm DW (Cook Is.). Source: SSF

DISTRIBUTION Almost circumglobal in tropical to warm-temperate seas, including Mediterranean Sea. WIO (scattered records): Kenya, Mozambique, South Africa, Madagascar and Réunion.

REMARKS Males mature at 35–40 cm DW, and females at 40–50 cm DW. Litters of 4–9; size at birth 15–25 cm DW. Perhaps the only truly pelagic stingray, as it occurs in the epipelagic zone of open ocean as well as in deep bays near land; usually hooked above 100 m over deeper water, but recorded to 238 m deep. Feeds on invertebrates (krill, amphipods, shrimp, jellyfish, squid, octopus) and pelagic fishes. A common bycatch of pelagic longliners and mostly discarded.

GENUS *Taeniura* Müller & Henle 1837

Disc oval; snout short; tail broad and compressed, with 1 or 2 posteriorly located stinging spines, and low ventral skin fold tapering and reaching tail tip. Skin mostly smooth. One or 2 species, 1 in WIO.

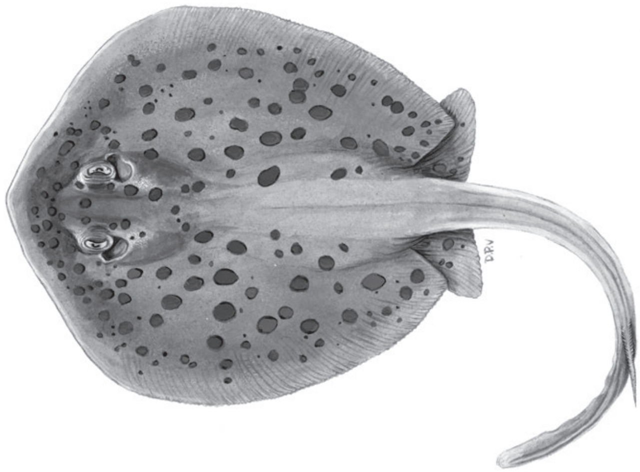
Taeniura lymma (Fabricius 1775)

Blue-spotted ribbontail ray PLATE 74

Raja lymma Fabricius *in* Niebuhr (ex Forsskål) 1775: 17, viii (Yemen, Red Sea).
Raia lymnia: Bonnaterre 1788*.
Raja lymna: Bloch & Schneider 1801.
Taeniura lymma: Wallace 1967*; SSF No. 30.13*; Heemstra & Heemstra 2004*; Last & Stevens 2009*; Last *et al.* 2016*.

Disc oval and elongated; anterior margins weakly convex, lateral apices and posterior margins broadly rounded. Snout angular and bluntly rounded, tip not pointed; dorsal midline with low fleshy ridge. Internasal flap narrow, posterior edge fringed. Eyes moderately large, protruding; interorbital space narrow. Tail stout, relatively short (<½ TL); 1 or 2 stinging spines set beyond midlength of tail; deep ventral skin fold extending to tail tip. Skin mostly smooth, but a few rows of widely spaced thorns in nuchal area, and short row of small flat denticles on midback in adults. Tooth count 15–24 in each jaw; oral papillae 2.

Body yellowish brown or greyish brown dorsally, with large bright blue spots on most of disc (excluding margins) and pelvic fins; mostly white ventrally, sometimes with brown disc margins; tail usually with pair of blue lateral stripes (no stripes in southern African specimens) and bluish towards tip. Attains at least 35 cm DW, at least 75 cm TL.



Taeniura lymma, 17 cm DW (South Africa). Source: SSF

DISTRIBUTION Indo-Pacific (widespread). WIO: South Africa (KwaZulu-Natal) to Red Sea, Madagascar, Mauritius, Seychelles, Tanzania (Zanzibar), Arabian Sea, Gulf of Oman, Persian/Arabian Gulf, Pakistan, India, Sri Lanka and Maldives.

REMARKS Poorly known although abundant in some areas. Litters of up to 7. Males mature by ~21 cm; females still immature at 24 cm DW. Benthic on shallow coral reefs and nearby sandy areas, to ~30 m deep; moves in large groups onto sandy flats during rising tide to feed on benthic invertebrates (molluscs, worms, shrimps, crabs) and small bony fishes. Commonly taken by artisanal and small commercial fisheries near coral-reef habitats.

GENUS ***Taeniurops*** Garman 1913

Disc circular; tail compressed, with 1 posteriorly positioned stinging spine, and deep ventral skin fold not tapering but reaching tail tip. Two species, 1 in WIO.

Taeniurops meyeni (Müller & Henle 1841)

Blotched fantail ray PLATE 74

Taeniura meyeni Müller & Henle 1841: 172, Pl. 75 (Mauritius, Mascarenes); Heemstra & Heemstra 2004.
Taeniura melanospilos: Wallace 1967*; SSF No. 30.14*.
Taeniurops meyeni: Last & Stevens 2009*; Last *et al.* 2016*.

Disc nearly circular, slightly wider than long, all outer margins evenly rounded. Internasal flap short, very broad, posterior edge with short fringe. Tail relatively short, less than disc width; usually 1 stinging spine; ventral skin fold long and broad, extending to tail tip. Pelvic fins small. Dorsal surface of disc and tail uniformly covered with small stellate denticles in adults, and smooth in young; no true thorns, but a few rows of enlarged denticles along midline of disc and tail. Tooth count 37–46/39–45; oral papillae 5–7.

Body usually dark purplish, bluish or brownish grey dorsally, or pale with scattered irregular dark spots or mottling and dusky specks or streaks; disc whitish ventrally, with darker margins; tail black beyond stinging spine. Attains 180 cm DW, 330 cm TL.

Taeniurops meyeni, 144 cm DW, female (South Africa).
Source: Smith & Smith 1963

DISTRIBUTION Indo-Pacific (widespread). WIO: South Africa (KwaZulu-Natal) to Red Sea, Madagascar, Mauritius, Seychelles, Arabian Sea, Persian/Arabian Gulf, Gulf of Oman, Pakistan, India, Sri Lanka and Maldives.

REMARKS Size at birth ~35 cm DW; males mature at 100–110 cm DW. Bottom-dwelling in lagoons, estuaries and on reefs; common close to shore, but recorded to 439 m deep. Feeds on invertebrates (bivalves, crabs, shrimp) and small benthic fishes. Caught throughout its range by line gear and trawls, as a targeted or bycatch species, and also by recreational anglers in southern Africa. IUCN Red List conservation status Vulnerable globally; Least Concern in Maldives.

GENUS *Telatrygon*

Last, Naylor & Manjaji-Matsumoto 2016

Disc sub-rhomboidal to rhomboidal; dorsal surface of disc smooth, with row of median thorns on nape; snout elongate, acutely angular. Tail long, and filamentous distally; caudal sting close to tail base; tail with thorns absent, and denticles rarely present. Body white ventrally, disc usually with dark edge; dorsal disc and tail plain. Three species and one undescribed; 1 species in WIO.

Telatrygon crozieri (Blyth 1860)

Indian sharpnose ray PLATE 74

Trygon crozieri Blyth 1860: 45 (Arakan coast, India)
Telatrygon crozieri: Last *et al*. 2016*.

Disc rhomboidal, slightly longer than wide; anterior margins concave, posterior margins convex. Snout triangular, elongated; head more than half disc length. Eyes small. Tail slightly longer than disc width; dorsal skin fold indistinct/rudimentary, and ventral skin fold long, very low. Dorsal surface with median row of up to 12 variably enlarged thorns before stinging spine in adults, but smooth in juveniles. Tooth count 40–55 in each jaw; no oral papillae.

Disc brown dorsally; whitish ventrally, with brown margins and dark brown ventral skin fold on tail. Attains 29 cm DW, 75 cm TL.

DISTRIBUTION Indo-Pacific: southern India in WIO, and eastwards.

REMARKS Resembles *T. zugei* from western Pacific. Small-sized. Litters of 1–3; size at birth 7–10 cm DW. Males mature at ~18 cm DW, and females at ~19 cm DW. Occurs on continental and insular shelves; benthic, typically in shallow waters <100 m deep, over flat sandy areas and in estuaries. Feeds on small crustaceans (prawns) and fishes. A sizeable component of the elasmobranch bycatch in parts of its range. IUCN Red List conservation status Near Threatened.

GENUS *Urogymnus* Müller & Henle 1837

Disc suboval to circular; snout rounded to angular; dorsal surface often covered with large prickly denticles; 1–3 mid-scapular thorns, or thorns absent. Tail short to long, stinging spine on tail absent, or in normal position, or set well back; dorsal and ventral skin folds absent. Ventral body white, plain dorsally, disc often dark edged, tail plain, not banded. Five species, 3 in WIO.

KEY TO SPECIES

1a	Snout evenly rounded; tail subequal to disc length, stinging spine on tail absent	***U. asperrimus***
1b	Snout pointed; tail longer than disc length, 1 or 2 stinging spines on tail	**2**
2a	Tail 1.5–2 times disc length; disc with scattered small white spots dorsally, tail white beyond stinging spine	***U. granulatus***
2b	Tail 1.9–2.4 times disc length; disc plain dorsally, tail blackish beyond stinging spine	***U. polylepis***

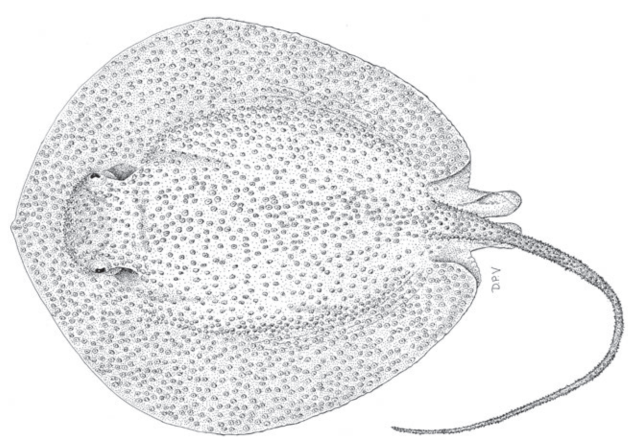
Urogymnus asperrimus (Bloch & Schneider 1801)

Porcupine ray PLATE 75

Raja asperrima Bloch & Schneider 1801: 367 (off Mumbai, India).
Raja africana Bloch & Schneider 1801: 367 (Guinea, West Africa [?]).
Urogymnus asperrimus: SSF No. 30.15*; Bonfil & Abdallah 2004*; Last & Stevens 2009*; Last *et al*. 2016*.

Disc oval, almost as wide as long, and greatly elevated at centre (convex appearance in lateral view). Snout tip evenly rounded, barely protruding. Pelvic fins small, slender. Tail about equal to disc length; no stinging spine. Dorsal surface of central disc and tail covered with plate-like denticles and very sharp enlarged thorns (especially in adults). Tooth count 48 in each jaw; oral papillae 3–5.

Disc pale to dark grey-brown dorsally, without markings; whitish ventrally; tail tip blackish. Attains 147 cm DW, ~330 cm TL.



Urogymnus asperrimus, 94 cm DW (Kenya). Source: SSF

DISTRIBUTION Eastern Mediterranean Sea and Indo-Pacific (scattered); records from eastern Atlantic are of the closely related *U. ukpam*. WIO: South Africa to Red Sea, Madagascar, Seychelles, Arabian Sea, Persian/Arabian Gulf, Gulf of Oman, Pakistan, India, Sri Lanka, Maldives and Chagos.

REMARKS Unusual and poorly known; relatively uncommon compared to other sympatric stingrays. Benthic, usually close to shore, over sand, coral gravel, seagrass beds and near reefs, to ~30 m deep. Matures at 90–100 cm DW. Observed aggregating when feeding on benthic invertebrates (sipunculids, polychaetes, crustaceans) and small fishes by ploughing the bottom and expelling sand through its spiracles. Presumably a bycatch of some coastal fisheries. IUCN Red List conservation status Vulnerable.

Urogymnus granulatus (Macleay 1883)

Mangrove whipray

PLATE 75

Trygon granulata Macleay 1883: 598 (Port Moresby, Papua New Guinea).
Trygon ponapensis Günther 1910: 493, Pl. 180 (Kabary, Pohnpei, CarolineIs.).
Himantura marginatus (*non* Blyth 1860): James 1980.
Himantura granulata: Last & Stevens 1994*; Bineesh *et al.* 2014; Bogorodsky *et al.* 2014*; Last *et al.* 2016*.

Disc oval, slightly longer than wide, and trunk thick; pectoral-fin anterior margins straight to weakly concave, lateral apices evenly rounded, and posterior margins broadly convex. Snout tip narrowly pointed; distance from preorbital snout to maximum disc width 42–51% DW. Eyes moderately large, protruding above disc; interorbital area broad. Internasal flap broad, short; posterior edge with fine fringe. Pelvic fins small, slender. Tail moderately long, 1.5–2 times disc length, and with 1 or 2 stinging spines. Dorsal surface of disc smooth in juveniles (<23 cm DW), and main band of denticles in adults with small and large denticles, largest over branchial area and along midline of back and tail as far as stinging spine; ventral surface entirely smooth. Tooth count 40–50/38–50; oral papillae 2–7.

Body brownish or greyish dorsally (often covered in black mucus), with darkened outer margins; small white spots speckled over disc, pelvic fins, and tail before stinging spine; adults pale ventrally, with dark blotches on disc margins, and juveniles uniformly pale or with greyish yellow margins; tail entirely white beyond stinging spine. Attains 141 cm DW, 3.5 m TL.

DISTRIBUTION Indo-Pacific (patchy, poorly defined). WIO: Gulf of Aqaba and central Red Sea (Al Lith, Saudi Arabia), Gulf of Aden and Maldives; also Gulf of Mannar (India and Sri Lanka).

REMARKS Large-sized; locally rare. Size at birth ~14 cm DW. Prefers shallow inshore habitats, but adults found to at least 85 m deep; demersal, over hard bottoms, rocky areas and corals, broken rocky-sandy substrate, sand flats, and in estuaries and mangroves. Feeds on crustaceans and small fishes. Caught by inshore artisanal and subsistence fisheries and some coastal commercial fisheries. IUCN Red List conservation status Vulnerable.

Urogymnus polylepis (Bleeker 1852)

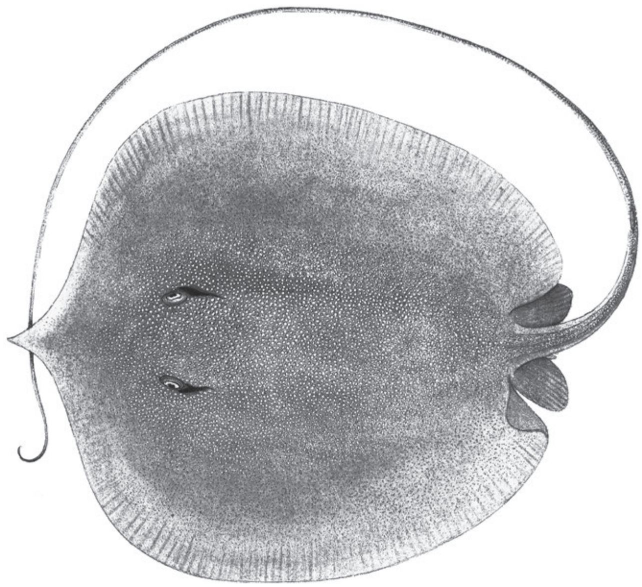
Giant freshwater whipray

PLATE 75

Trygon polylepis Bleeker 1852: 73 (Jakarta, Java, Indonesia).
Leiobatis (*Himantura*) *polylepis*: Bleeker 1877*.
Urogymnus laevior Annandale 1909: 37 (Malabar coast, India).
Trygon fluviatilis (*non* Hamilton 1822): Annandale 1910*.
Himantura chaophraya Monkolprasit & Roberts 1990: 204, Fig. 1 (Chao Phraya River, upriver from Ayutthaya, Thailand).
Himantura polylepis: Last & Manjaji-Matsumoto 2008.
Urogymnus polylepis: Last *et al.* 2016*.

Disc subcircular, longer than wide; pectoral-fin anterior margins truncate, lateral apices broadly rounded, and posterior margins broadly convex. Snout long, 41–50% DW, tip with large triangular apical lobe. Tail long, slender, 1.9–2.4 times DW. Band of denticles along midtrunk moderately sparse, without well-defined margin; mid-scapular denticles small or inconspicuous; tail only sparsely covered with denticles, but denser in large adults. Tooth count 22–23/19–23; oral papillae 4–7.

Disc uniformly pale brown or greyish dorsally; white ventrally, with broad dark brown marginal band, inner part of band with dark brown blotches; tail darker brown to blackish dorsally, and tail base white ventrally, becoming blackish beyond stinging spine. Attains 200 cm DW, at least 4 m TL.



Urogymnus polylepis. Source: Bleeker 1877

DISTRIBUTION Widespread in large rivers of Southeast Asia (India to eastern Indonesia) and also Malabar coast, India, in WIO.

REMARKS The description of *Himantura chaophraya* from Thailand failed to take into account the description of *H. polylepis* (Bleeker 1852). Last & Manjaji-Matsumoto (2008) compared the holotype of *H. polylepis* (from Java, Indonesia) with material from the Chao Phraya River (Thailand), Sabah (Malaysia) and India, and confirmed *polylepis* as the senior name. Even so, the taxonomic status of subpopulations in different drainages requires further research. Litters of up to 4; size at birth ~30 cm DW. Males mature at 90–130 cm DW, and females at ~80 cm DW. Found mostly in freshwaters of large rivers with muddy or sandy bottom, and less often in estuarine waters. Feeds mostly on freshwater and estuarine crustaceans and fishes. Caught incidentally in artisanal fisheries. IUCN Red List conservation status Endangered; subpopulation in Thailand assessed Critically Endangered.

FAMILY GYMNURIDAE

Butterfly rays

Brett A Human, Leandro Yokota and Marcelo R de Carvalho

Small- to large-sized (to ~260 cm DW) with extremely flattened body; head depressed and not elevated above disc, anterior margin not indented; snout short and obtuse, sometimes with small knob at tip. Pectoral-fin origins anterior to nostrils and confluent with head and body, forming greatly laterally expanded rhomboidal or diamond-shaped disc (disc width 1.5–2.2 disc length); pectoral-fin tips narrowly rounded, rear margins straight or convex. Dorsal surface smooth, without thorns. Five pairs of short gill slits on underside; no electric organs. Eyes small, widely separated; spiracles with or without posteriorly projecting dermal tentacle on inner rear margin. Internasal flap broad, short and reaching mouth; posterior edge smooth or weakly fringed. Mouth transverse or slightly arched, with numerous small teeth. Pelvic fins small, angular, not bilobed; claspers short and stout. Tail usually banded, filamentous and flexible, cylindrical or slightly depressed, shorter than disc, and with low dorsal or ventral skin folds variably present or absent; dorsal fin absent or small, low, rounded or angular, its origin just behind pelvic-fin insertions or beyond; 0–2 stinging spines; no caudal fin. Tooth rows 52–130/52–130; spiral valve turns 6–12.

Historically, the family Gymnuridae was separated into two genera based on the presence (*Aetoplatea*) or absence (*Gymnura*) of 1 small dorsal fin. However, recent studies have shown that this character varies even within species (Jacobsen & Bennett 2009; Nunes & Piorski 2009; Yokota & Carvalho 2017), hence it cannot be used as a generic character. *Aetoplatea* is thus a junior synonym of *Gymnura*. Furthermore, the development of dorsal and ventral skin folds on the tail has been shown to be a sexually dimorphic trait in *G. marmorata* and *G. crebripunctata*. Similarly, the presence or absence of stinging spines is inconsistent in some of the species. Although some regional revisions of gymnurids have been conducted recently, a review of all species globally is needed to develop characters that separate them as well as to better understand their distributions and biology. Possibly vary their colour pattern to match the sea bottom. Reproductive mode is viviparity with histotroph, wherein uterine secretions nourish the embryos (by being absorbed through the spiracles and delivered into the pharynx of the young). A common bycatch in commercial fisheries, although the flesh is not highly regarded.

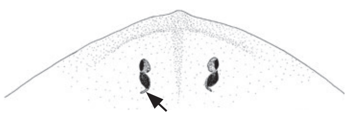
One genus and 12 species recognised pending a revision; 3 or 4 described species and possibly 1 undescribed species in WIO.

GENUS *Gymnura* Van Hasselt 1823

Diagnosis as for family. Found in tropical and warm-temperate seas; 12 species, 3 or 4 in WIO (as *Gymnura zonura* is recorded in the Bay of Bengal, the possibility of it occurring in the WIO was considered). In addition, frequent reference in the literature to a ray similar to *G. micrura* in the WIO may be an undescribed species or misidentifications (and likewise for records of *G. micrura* elsewhere in Indo-Pacific).

KEY TO SPECIES

1a Spiracles with dermal tentacle on inner rear margin 2



1b Spiracles without dermal tentacle on inner rear margin 3

2a Tail with pale and dark bands; no dorsal fin .... ***G. natalensis***
2b Tail without banding; 1 small, low dorsal fin .... ***G. tentaculata***

3a No dorsal fin; tail relatively long, post-cloacal length 50–100% disc length .... ***G. poecilura***
3b Dorsal fin usually present; tail (post-cloacal length) 40–65% disc length .... ***G. zonura***

Gymnura natalensis (Gilchrist & Thompson 1911)

Diamond ray

PLATE 76

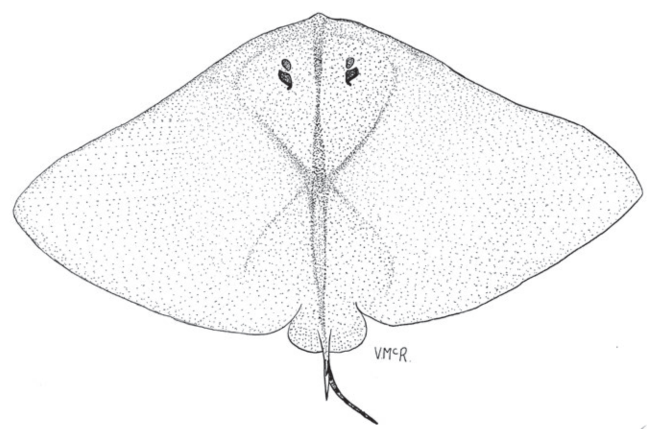
Pteroplatea natalensis Gilchrist & Thompson 1911: 56 (KwaZulu-Natal, South Africa); Gilchrist & Thompson 1916; Von Bonde & Swart 1923; Barnard 1925.
Pteroplatea micrura: Barnard 1925.
Gymnura natalensis: Smith 1949*; Wallace 1967*; SSF No. 30.7*; Compagno *et al.* 1989*; Cliff & Wilson 1994*; Heemstra & Heemstra 2004*; Jacobsen & Bennett 2009.

Spiracles with rudimentary dermal tentacle on inner rear margin. No dorsal fin; tail with dorsal and ventral skin folds, and 1 or 2 stinging spines; tail short, post-cloacal length 35–50% disc length (tail usually longer in embryos and small juveniles: post-cloacal length 50–60% disc length). Tooth count 68–93/70–93.

Disc grey to olive-green, often with large dark blotches and smaller yellowish green spots; pale ventrally; tail with pale and dark bands (most prominent in juveniles); has limited ability to change colouration to match substrate. Attains 250 cm DW.

DISTRIBUTION Southern Africa: Namibia in southeastern Atlantic, to South Africa and southern Mozambique in WIO.

REMARKS Displays marked ontogenetic differences in morphology: disc almost triangular in juveniles, and rhomboidal in adults. Specimens from South Africa identified as *G. japonica* are misidentified specimens of *G. natalensis*. Occurs in temperate to warm-temperate waters, inshore, commonly off sandy beaches, to ~75 m deep; usually solitary on seabed, although observed swimming in shoals in midwater. Females enter inshore areas and estuaries in summer to give birth; litters of 2–9; size at birth ~35 cm DW; gestation period 12 months. Males mature at 100–110 cm DW, and females at 145–150 cm DW; females attain larger sizes than males. Diet includes bony fishes, crabs and worms. A common bycatch of prawn trawl fisheries and in anti-shark nets, and regularly taken by shore anglers. Although the spine at the base of the tail normally poses little threat, the authors can attest to the potency of the venom.



Gymnura natalensis, 67 cm DW, female (South Africa). Source: SSF

Gymnura natalensis, 185 cm DW (South Africa). Source: SSF

Gymnura poecilura (Shaw 1804)

Longtail butterfly ray PLATE 76

Raja poecilura Shaw 1804: 291 (Visakhapatnam, India) [based on Russell 1803, Pl. 6].
Pteroplatea micrura: Day 1865, 1889*; Wood-Mason & Alcock 1891*; Alcock 1892*.
Gymnura poecilura: James 1966*; Bianchi 1985*; Compagno & Randall 1987; Al-Abdessalaam 1995*; Randall 1995*; Carpenter *et al*. 1997*; Morón *et al*. 1998; Compagno & Last 1999*; Sujatha 2002; Bonfil & Abdallah 2004*; White & Dharmadi 2007; Jacobsen & Bennett 2009.
Gymnura hormosensis Vossoughi & Vosoughi 1999: 304 [validity uncertain].
Gymnura japonica: Sujatha 2002.

Spiracles without dermal tentacle on inner rear margin. No dorsal fin; tail with dorsal and ventral skin folds (dorsal fold more prominent), and no or 1 stinging spine (rarely 2 spines); tail long, post-cloacal length 50–100% disc length, with larger individuals presenting proportionately longer tail.

Disc uniformly olive-green to greyish brown dorsally or peppered with minute darker spots or pale spots; pale ventrally (whitish to brownish or coppery); tail usually with prominent pale and dark bands in repeating pattern of long dark (almost black) band, short white band, short dark band, short white band, and long dark band (total 8–12 dark bands). Attains 100 cm DW.

Gymnura poecilura, 89 cm DW, 75 cm TL, female (Red Sea).
© SV Bogorodsky

DISTRIBUTION Indo-Pacific (widespread but disjunct). WIO: Somalia, Red Sea (common), Oman, Gulf of Oman, Persian/Arabian Gulf, Pakistan, India and Sri Lanka.

REMARKS Embryos and juveniles have almost triangular disc as compared with rhomboidal disc of adults. A new species (*G. hormosensis*) from the Strait of Hormuz (Persian/Arabian Gulf) was proposed with uncertainty based on minor colouration differences; the illustration provided closely agrees with *G. poecilura*, particularly the banding pattern on tail, and the few characters provided for it are identical to those for *G. poecilura* (including no tentacle on spiracles). Therefore, this work follows Yoshigou *et al.* (2004) in placing *G. hormosensis* as a junior synonym of *G. poecilura*. However, it is possible that the specimens from the WIO are of a species similar to *G. poecilura* (i.e. *G.* cf. *poecilura*). Biology poorly known. Litters of up to 7; size at birth 18–21 cm DW; females mature at ~41 cm DW. Occurs inshore, mostly over sandy and muddy bottoms, with narrow depth range to just ~30 m deep. Diet includes bony fishes, crustaceans and molluscs. A bycatch of commercial trawls and gillnets, and targeted by artisanal and commercial fisheries as the fins are retained for consumption. IUCN Red List conservation status Near Threatened.

Gymnura tentaculata (Valenciennes 1841)

Tentacled butterfly ray PLATE 76

Aetoplatea tentaculata Valenciennes *in* Müller & Henle 1841: 175 (Red Sea? [possibly Malabar coast of India]); Bianchi 1985; Compagno & Randall 1987; Kailola 1987*; Yoshigou *et al*. 2004.
Pteroplatea tentaculata: Annandale 1909*.
Gymnura tentaculata: Wallace 1967; Jacobsen & Bennett 2009.

Spiracles with dermal tentacle on inner rear margin. Tail with low dorsal fin; dorsal and ventral skin folds variably present or absent; stinging spine minute or absent; tail (post-cloacal length) 45–60% disc length.

Disc dark olive dorsally, frequently with yellowish green blotches (disc green dorsally, with dark brown spots and reticulations in young); white or marbled ventrally; tail without banding. Attains at least 76 cm DW.

DISTRIBUTION Indian Ocean: Red Sea to southern India and to Bay of Bengal; records from elsewhere in northern WIO require confirmation.

REMARKS Apparently rare, known from very few specimens. Morphologically very similar *G. australis* which otherwise has distinct tail banding; records from New Guinea in western Pacific are misidentifications of *G. australis*. Biology virtually unknown. Presumably a bycatch of inshore fisheries throughout its range. IUCN Red List conservation status Data Deficient.

Gymnura zonura (Bleeker 1852)

Zonetail butterfly ray

PLATE 77

Aetoplatea zonurus Bleeker 1852: 79 (Jakarta, Java, Indonesia).
?*Pteroplatea micrura*: Annandale 1909.
Pteroplatea zonura: Annandale 1909*.
Aetoplatea zonura: Compagno & Last 1999*.
Gymnura zonurus: Sujatha 2002.
Gymnura japonica: White & Dharmadi 2007.
Gymnura zonura: White & Dharmadi 2007; Jacobsen & Bennett 2009.

Spiracles without dermal tentacle on inner rear margin. Tail usually with low dorsal fin (fin may be absent); ventral skin folds variably present; usually 1 stinging spine (absent in some specimens); tail (post-cloacal length) 40–65% disc length.

Disc medium to dark olive-green dorsally, often presenting speckled with minute darker spots and larger whitish spots; pale ventrally; tail with prominent pale and dark bands in repeating pattern of long dark (almost black) bands and shorter white bands (total 6–10 dark bands). Attains 108 cm DW.

DISTRIBUTION Tropical waters of eastern Indian Ocean and western Pacific, and possibly west coast of India in WIO.

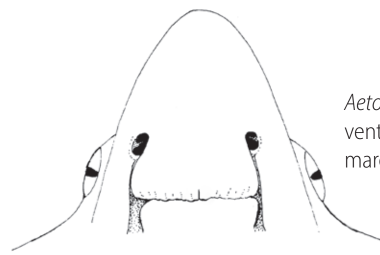
REMARKS Biology unknown in WIO; elsewhere males mature at 46–50 cm DW, and females are immature at 51 cm DW, but mature by 78 cm DW. Litters of 2–5; size at birth probably 14–28 cm DW. Narrow depth range, to ~40 m deep, over soft substrates. Heavily caught in demersal gillnet fisheries in Indonesia and probably throughout its range. IUCN Red List conservation status Vulnerable.

FAMILY MYLIOBATIDAE

Eagle rays

Marcelo R de Carvalho and Mateus C Soares

Moderate- to large-sized rays (to 9 m TL, 3.3 m DW; most species attain <200 cm DW) with rhomboidal or lozenge-shaped disc much wider than long; head projecting beyond disc, snout rounded; pectoral fins meet head below eyes, angular with concave posterior margins. Fleshy lateral ridge supporting snout, either continuous with pectoral-fin origins (*Myliobatis*) or not continuous and situated well below pectoral-fin origins at level of eyes (*Aetomylaeus*). Head relatively narrow to somewhat broad (*Myliobatis*), thick, and elevated from disc. Snout varying from short (*Myliobatis*) to relatively elongate (*Aetomylaeus*), with additional fleshy rostral lobe (resembling duck's bill) or small knob. Eyes lateral, medium to moderately large, anteromedial to spiracles; spiracles elongated, lateral, margins smooth and without papillae, rims not elevated. Mouth narrow to relatively broad, transverse, straight, and without prominent knobs, depressions or lip folds. Nostrils relatively small, usually slightly elongate, only slightly anterior to mouth, connected to mouth by broad oronasal grooves; internasal flap broad, overlapping mouth, straight or slightly undulate, but not notched. Teeth large and blunt, greatly flattened, laterally expanded, plate-like, roughly hexagonal; 6–10 tooth rows in each jaw (sometimes more; lateral teeth may be lacking in adults of *Aetomylaeus vespertilio*). Five pairs of small gill slits on underside of front half of disc. No electric organs.



Aetomylaeus bovinus, 68 cm DW, ventral head with internasal flap margin straight (South Africa).

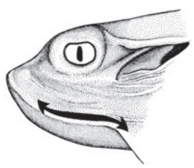
Pelvic fins slightly longer than wide, not bilobed, projecting past disc, and posterior margins rounded or straight. Tail long (~1.5–3 times disc length), filamentous and whip-like, cylindrical and without lateral skin folds; 1 small dorsal fin, relatively high, angular or rounded-angular, set over or just behind pelvic-fin insertions, and rear tip joined to tail surface; prominent stinging spine close behind dorsal fin in most species (stinging spines in only 1 species of *Aetomylaeus*); no caudal fin. Dorsal surface with minute dermal denticles, or smooth above and below with only a few reduced thorns or tiny denticles on disc midline or around eyes. Body uniformly brown, greenish, grey or yellowish to blackish dorsally, or with spots, small ocelli, faint banding, or mildly reticulated; generally pale to whitish ventrally.

Circumglobal in temperate and tropical waters, inhabiting relatively shallow waters of continental and insular shelves; semipelagic, in schools of a few to hundreds of individuals (*Myliobatis*). The expanded, wing-like pectoral fins of eagle rays permit great propulsion, allowing them to reach high speeds and leap from the water; also found resting on the bottom, raising their body with their pectoral fins. Reproductive mode is viviparity with histotroph (uterine secretions that nourish embryos), with litters of 2–10. Females enter shallow water or estuaries to give birth, observed leaping to facilitate parturition; copulation has been recorded in captivity. Feed on hard-shelled prey items (molluscs and crustaceans), which they crush with pavement-like tooth plates, and also on bony fishes, worms and squid; often use their fleshy rostral lobe to expose buried prey. Species with a stinging spine are usually harmless to people due to its anterior position at base of tail, but larger species have powerful jaws. A few species are common in public aquariums.

Two genera and 18 species; both genera and 6 species in WIO.

KEY TO GENERA

1a Fleshy lateral ridge around snout continuous with pectoral-fin origins; dorsal-fin origin behind pelvic-fin rear tips .... ***Myliobatis***



1b Fleshy lateral ridge around snout well beneath pectoral-fin origins, not continuous, and fins joining head at level of eyes; dorsal-fin origin over pelvic fins .... ***Aetomylaeus***

GENUS *Aetomylaeus* Garman 1908

Fleshy lateral ridge around snout well beneath pectoral-fin origins, not continuous, at level of eyes; rostral lobe fleshy, long, duck-bill-shaped. Posterior edge of internasal flap relatively straight. Both jaws with 7 rows of plate-like teeth, centre row widest, and 3 rows of diamond-shaped teeth at each side. Stinging spine lacking except in 1 species in WIO. Currently 6 species recognised, 5 in WIO; in addition, a probable undescribed species has been photographed in the Maldives (referred to as *Aetomylaeus vespertilio* in Debelius 1999, and *Aetomylaeus* sp. in Hennemann 2001).

KEY TO SPECIES

1a Stinging spines present .... ***A. bovinus***

1b No stinging spines 2

2a Dorsal-fin origin just behind (rarely over) pelvic-fin insertions 3

2b Dorsal-fin origin just before or over pelvic-fin insertions 4

Continued ...

KEY TO SPECIES

3a Dorsal surface of disc with pattern of broken, transverse, darker stripes anteriorly and darker reticulate pattern posteriorly .... ***A. vespertilio***

3b Rear half of dorsal surface of disc with more or less evenly scattered whitish spots and incomplete ocelli .... ***A. maculatus***

4a Dorsal surface of mid-disc with darker stripes, and rear half of disc with numerous ocelli of varying size .... ***A. milvus***

4b Dorsal surface, from head to rear of disc, with pale, evenly spaced crossbars (faded in larger individuals) .... ***A. nichofii***

Aetomylaeus bovinus (Geoffroy Saint-Hilaire 1817)

Bull ray

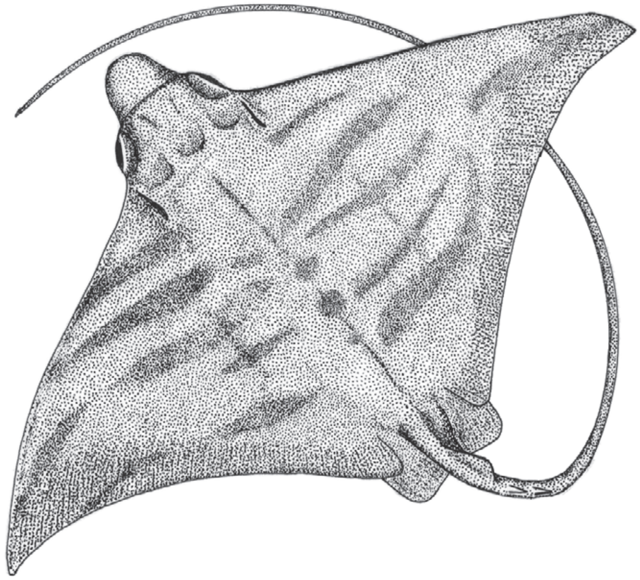
PLATE 78

Myliobatis bovina Geoffroy Saint-Hilaire 1817: no page number, Pl. 26, Fig. 1 (off Alexandria, Egypt, Mediterranean Sea).
?*Aetomylus huletti* Smith 1953: 513, Fig. 77a (KwaZulu-Natal, South Africa).
Pteromylaeus bovinus: Barnard 1925; Smith 1949*; Wallace 1967*; Van der Elst 1988*; Compagno *et al.* 1989*; SSF No. 28.3* [1995]; Heemstra & Heemstra 2004*.
Aetomylaeus bovinus: Weigmann 2016; White & Last 2016.

Pectoral-fin anterior margins strongly convex. Snout elongate, relatively slender, and rostral lobe fleshy, duck-bill shaped. Posterior edge of internasal flap straight or shallowly notched; 7 rows of plate-like teeth in both jaws: central row widest, and 3 rows of small diamond-shaped teeth at each side. Pelvic fins narrow. Dorsal-fin origin over pelvic fins. Tail 1.6–1.8 times disc length; 1–4 small serrated stinging spines just behind dorsal fin. Skin rough to touch on head, tail and along midback, but smooth on snout, outer angles and posterior margins of disc, and pelvic fins. Males with short conical horn above each eye.

Body brown dorsally, with 7 or 8 irregular transverse pale blue-grey crossbars over disc and head (faded in adults and darker in juveniles, stripes reportedly become more intense upon capture due to stress); uniformly white ventrally. Attains 180 cm DW.

DISTRIBUTION Mediterranean Sea and southern Africa to East Africa: Namibia in southeastern Atlantic, to South Africa, Mozambique and Tanzania (Zanzibar) in WIO.



Aetomylaeus bovinus. (South Africa).

REMARKS Until recently this species was placed in the genus *Pteromylaeus*, now considered a synonym of *Aetomylaeus* (White 2014). Litters of 4–6; size at birth ~48 cm DW. Males mature at ~95 cm DW, and females at ~110 cm DW. Found over sandy and muddy bottoms, from shoreline to ~150 m deep; also enters estuaries and lagoons. Feeds on bony fishes, crustaceans (crabs), squid and molluscs. A bycatch in various artisanal and commercial fisheries, and often caught by shore anglers; powerful swimmer able to leap from water.

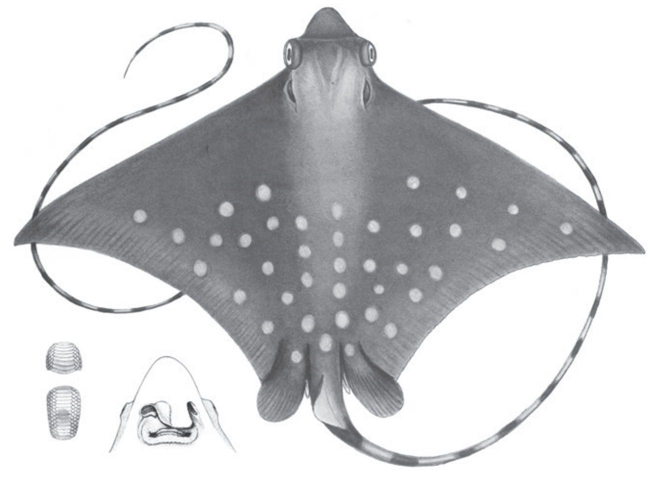
Aetomylaeus maculatus (Gray 1834)

Mottled eagle ray PLATE 77

Myliobatus maculatus Gray 1834: no page number, Pl. 101 (Penang, Malaysia).
Myliobatis maculatus: Annandale 1909; Blegvad & Løppenthin 1944.
Aetomylaeus maculatus: ?Munro 1955* [probably *A. milvus*]; Compagno & Last 1999*; White *et al*. 2006*.

Pectoral fins falcate, with posterior margins concave and anterior margins slightly convex. Rostral lobe triangular, relatively short. Eyes slightly bulging, slightly smaller than spiracles. Pelvic fins slender, protruding beyond posterior margin of disc. Dorsal-fin origin just behind (rarely over) pelvic-fin insertions. Tail whip-like, very long.

Body brown dorsally, with whitish spots and irregular ocelli on rear half of disc and pelvic fins; uniformly white ventrally; tail with alternating pale and dark bands. Attains at least 78 cm DW.



Aetomylaeus maculatus. Source: Bleeker 1852

DISTRIBUTION Indo-Pacific. WIO: Arabian Sea, Persian/Arabian Gulf (Iran), India and possibly Sri Lanka.

REMARKS Little known. Males mature at 54–72 cm DW. Occurs predominantly inshore; once commonly found near reefs and in estuaries and mangroves, but has become uncommon in parts of its range. Incidental catch in inshore demersal fisheries; sold in fish markets in Southeast Asia. IUCN Red List conservation status Endangered.

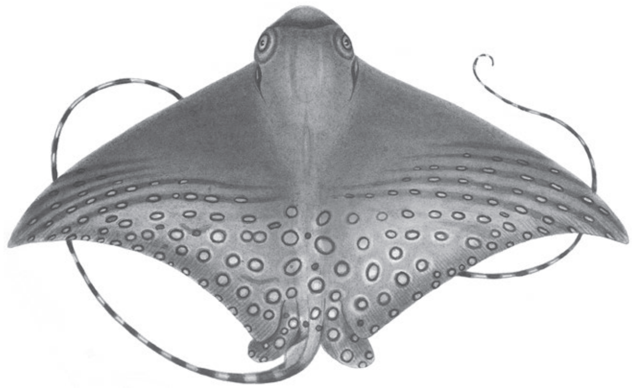
Aetomylaeus milvus (Valenciennes 1841)

Ocellate eagle ray PLATE 77

Myliobatis milvus Müller & Henle (ex Valenciennes) 1841: 178 (Red Sea); Klunzinger 1871.
Aetomylaeus maculatus: ?Munro 1955*.
Aetomylaeus milvus: Compagno & Last 1999*; Bonfil & Abdallah 2004*; White & Last 2016.

Disc width about twice disc length, with concave posterior margins and broadly convex anterior margins. Head relatively wide, but rostral lobe blunt, subtriangular, not greatly protruding. Eyes proportionally large. Pelvic fins slightly protruding beyond posterior margin of disc. Dorsal-fin origin just before or over pelvic-fin insertions.

Body brownish dorsally, with transverse darker bands at mid-disc, extending from centre to outer margins of pectoral fins, and with numerous greenish irregular ocelli posteriorly; uniformly white ventrally; tail strongly banded. Attains at least 37 cm DW.



Aetomylaeus milvus. Source: Bleeker 1852

DISTRIBUTION Indo-Pacific. WIO: Red Sea, Persian/Arabian Gulf, Pakistan, India and possibly Sri Lanka.

REMARKS Small-sized, sparsely recorded and poorly known. Found inshore. Of questionable taxonomic validity, as it may represent the juvenile stage of *A. vespertilio* or *A. maculatus*.

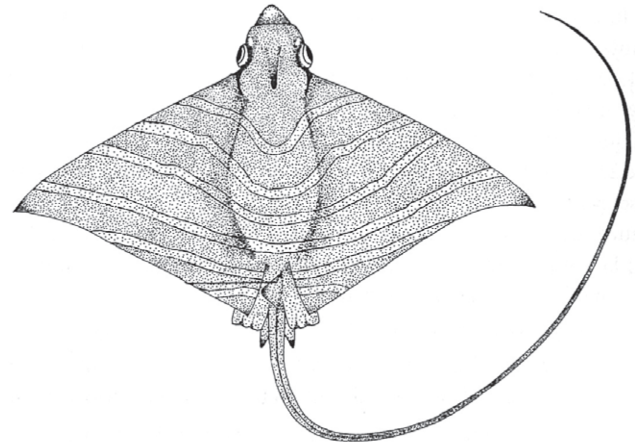
Aetomylaeus nichofii (Bloch & Schneider 1801)

Banded eagle ray PLATES 77 & 78

Raja niehofii Bloch & Schneider 1801: 364 ('East Indies') [spelled *nichofii* in text but corrected in corrigenda, p. 579].
?*Raja fasciata* Shaw 1804: 286, Pl. 143 [no locality given].
Myliobatis nieuhofii: Annandale 1909.
Myliobatis nieuhofii cornifera Annandale 1909: 52, Pl. 2, Fig. 4a (India).
Myliobatis nichofii: Blegvad & Løppenthin 1944*.
?*Aetomylus huletti* Smith 1953: 513, Fig. 77a (KwaZulu-Natal, South Africa).
Aetomylaeus nichofii: Munro 1955*; Qureshi 1972*; Randall 1995*; Compagno & Last 1999*; White *et al.* 2006*; Last & Stevens 2009*; White & Last 2016.

Disc width almost twice disc length. Internasal flap skirt-shaped with fine fringe. Dorsal-fin origin just before or over pelvic-fin insertions. Tail long, whip-like, 1.5–2 times disc length. Skin normally smooth, without thorns; large adults may have minute, widely spaced denticles on disc.

Body bronze or greyish brown background dorsally, with transverse bands of pale colour on disc (usually 5 bands) and head (usually 2 bands) in adults (bands not evident in preserved specimens), and juveniles with darker, broader, more irregular bands; white ventrally; tail grey at base, darker towards tip. Attains 72 cm DW, 100 cm TL.



Aetomylaeus nichofii, 51 cm DW, 95 cm TL, adult male (Pakistan). Source: Capapé & Desoutter 1979

DISTRIBUTION Indo-Pacific. WIO: Mozambique, Persian/Arabian Gulf (Iran and Oman), Pakistan, India, Sri Lanka and Maldives.

REMARKS Litters of 4 or more; size at birth ~17 cm DW. Males mature at 39–42 cm DW. Wide-ranging but increasingly uncommon; occurs inshore and offshore, to at least 70 m deep, and sometimes in brackish waters. Feeds on worms, crustaceans, snails and bony fishes. Marketed throughout most of its range. IUCN Red List conservation status Vulnerable.

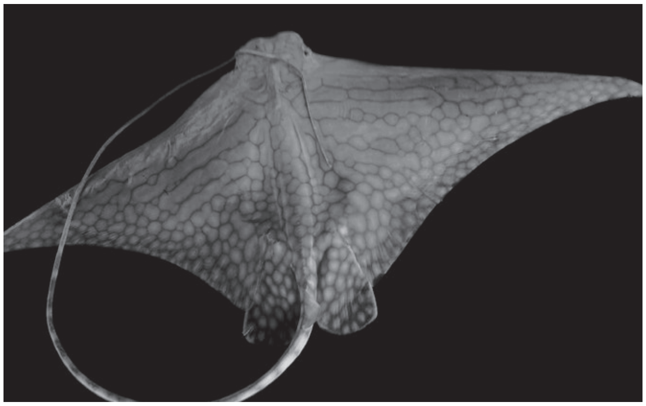
Aetomylaeus vespertilio (Bleeker 1852)

Ornate eagle ray PLATE 77

Myliobatis vespertilio Bleeker 1852: 85 (Jakarta, Java, Indonesia).
Aetomylaeus vespertilio: SSF No. 28 [1995]; Compagno 1999; Compagno & Last 1999*; Hennemann 2001*; Bonfil & Abdallah 2004*; White *et al.* 2006*; Last & Stevens 2009*; Bineesh *et al.* 2014; White & Last 2016.

Disc width about twice disc length. Pectoral-fin posterior margins deeply concave. Internasal flap skirt-shaped with indistinct fringe. Pelvic fins narrowly rounded. Dorsal-fin origin just behind or over pelvic-fin insertions. Tail extremely long, whip-like, up to 3 times disc length. Skin smooth, except adults with narrow band of tiny flat denticles along midline.

Body pale to dark brown dorsally, with irregular darker brown to black transverse lines on front half of disc and dark reticulate pattern on rear half of disc, head with few black spots and stripes, and white spots on pelvic fins and base of tail; white ventrally; tail mainly blackish. Attains 240 cm DW, at least 3.5 m TL.



Aetomylaeus vespertilio (SW India). KK Bineesh © CMFRI

DISTRIBUTION Indo-Pacific (widespread but scattered). WIO: Maldives, South Africa (KwaZulu-Natal) to Arabian Sea and Red Sea.

REMARKS Large-sized; naturally uncommon and rarely observed, hence poorly known. Males mature at ~170 cm DW. Occurs inshore on continental shelf, over sandy bottoms, in muddy bays and on coral reefs, to ~110 m deep. Caught in low numbers in demersal fisheries and marketed. IUCN Red List conservation status Endangered.

GENUS *Myliobatis* Cuvier 1816

Fleshy lateral ridge supporting snout continuous with pectoral-fin origins; pectoral-fin tips blunt. Posterior edge of internasal flap relatively straight or slightly concave, not deeply notched; 7 rows of plate-like teeth in each jaw: central row widest, and 3 rows of diamond-shaped teeth at each side. Dorsal-fin origin behind pelvic-fin tips; prominent stinging spine just behind dorsal fin. About 11 species, 1 in WIO.

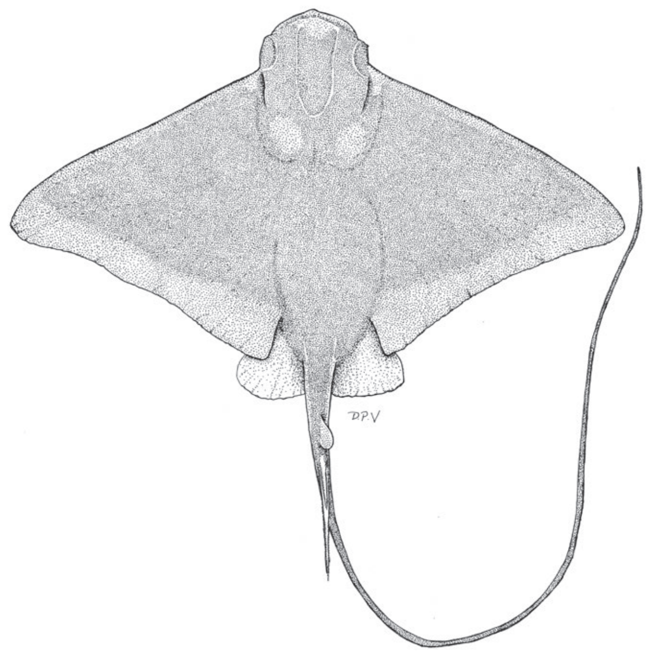
Myliobatis aquila (Linnaeus 1758)

Common eagle ray PLATE 78

Raja aquila Linnaeus 1758: 232 (Mediterranean Sea and northeastern Atlantic).
Myliobatis cervus Smith 1935: 169, Fig. 1 (Knysna, Western Cape, South Africa).
Myliobatis aquila: Barnard 1925*; Smith 1949; Wallace 1967*; SSF No. 28.2*; Van der Elst 1988*; Compagno *et al.* 1989*; Heemstra & Heemstra 2004*; White & Last 2016.

Disc width about twice disc length, with mostly straight anterior margins and slightly concave posterior margins; pectoral-fin apices slightly rounded. Snout short, very broad, rounded, and with small anterior protuberance. Pelvic fins large, truncate. Dorsal fin entirely behind pelvic fins, rounded at apex. Tail whip-like, about twice disc length; stinging spine slender and long. Males with small conical horn above each eye.

Body dark brown, olive-green or blackish dorsally, occasionally with irregular dusky black spots; white ventrally. Attains 150 cm DW.



Myliobatis aquila, 36 cm DW (South Africa). Source: SSF

DISTRIBUTION Mediterranean Sea, eastern Atlantic and Indian Ocean. WIO: South Africa (Western Cape) to southern Mozambique (Bazaruto), and possibly western Mascarenes.

REMARKS Common, but poorly known; a systematic review of populations is needed. Litters of 3–7, born in shallow water; size at birth 20–23 cm DW; gestation period 6–8 months. Males probably mature by ~55 cm DW, and females by ~60 cm DW. Found inshore and offshore, but normally in shallow waters of bays and estuaries and on rocky reefs, but recorded to 537 m deep off southern Africa; semipelagic, observed swimming in small groups near bottom. Feeds on crustaceans (crabs), molluscs, worms and bony fishes. A bycatch of various fisheries and a good sport fish; excellent for eating.

FAMILY AETOBATIDAE

Pelagic eagle rays

Marcelo R de Carvalho and Mateus C Soares

Moderate-sized to very large rays (to ~9 m TL, 3 m DW; most species attain <200 cm DW) with lozenge-shaped disc much wider than long; head robust, projecting beyond disc; pectoral fins meet head at level of eyes, angular, with concave posterior margins and broadly rounded free rear tips. Fleshy lateral ridge supporting snout not continuous and situated well below pectoral-fin origins at level of eyes. Head relatively narrow, thick and elevated from disc. Snout elongate and oval, with fleshy rostral lobe. Eyes lateral, moderately large and anteromedial to spiracles; spiracles dorsolateral and elongated, visible in dorsal view, margins smooth without papillae or elevated rims. Mouth narrow, transverse, straight, and without prominent knobs, depressions or lip folds. Nostrils relatively small and slightly elongate, just anterior to mouth, and connected to mouth by rather large oronasal grooves; internasal flap broad, overlapping mouth, posterior edge deeply notched with inverted V-shape. Teeth large and blunt, greatly flattened, laterally expanded, plate-like, and chevron-shaped; both jaws with a single tooth row in postnatal specimens, lacking lateral teeth.

Aetobatus narinari, 60 cm DW, ventral head with V-shaped notch on internasal flap (Mozambique).

Five pairs of small gill slits on underside of front half of disc. No electric organs. Pelvic fins slightly longer than wide, not bilobed, projecting past disc, and posterior margins rounded. Tail long (~1.5–3 times disc length), filamentous and whip-like, cylindrical and without lateral skin folds; 1 small dorsal fin, raked and with rounded-angular apex, positioned just behind pelvic-fin insertions, with short free rear tip. Stinging spine(s) close behind dorsal fin, relatively long. No caudal fin. Dorsal surface almost entirely smooth above and below. Body uniformly brown to greenish, or grey dorsally with white spots or ocelli; generally pale to whitish ventrally.

Circumglobal in most tropical and subtropical seas, inhabiting relatively shallow waters of continental and insular shelves; pelagic, solitary, in small groups, or schools of up to~200 individuals. The powerful expanded, wing-like pectoral fins of these active rays allows the acceleration required to reach high speeds and leap from the water; also found resting on the bottom, raising their body with their pectoral fins.

Viviparous with histotroph (uterine secretions that nourish embryos), with litters of usually up to 4. In general biology, feeding and reproduction, this family is very similar to Myliobatidae (see Myliobatidae for details). Species of the *Aetobatus narinari* complex are common in public aquariums.

One genus with 5 species; 3 species in WIO.

GENUS *Aetobatus* Blainville 1816

See family account.

KEY TO SPECIES

1a	Dorsal surface uniformly coloured, without conspicuous markings; snout elongate, tapering and acute	***A. flagellum***
1b	Dorsal surface with spots or ocelli; snout less elongate, less acute	**2**
2a	Dorsal background colour yellowish brown; entire surface of disc covered with spots or ocelli	***A. narinari***
2b	Dorsal background colour greenish brown or greenish grey; sometimes with spots or ocelli only on rear margins of disc	***A. ocellatus***

Aetobatus flagellum (Bloch & Schneider 1801)

Longheaded eagle ray

PLATE 79

Raja flagellum Bloch & Schneider 1801: 361, Pl. 73 (Coromandel coast, India).
Aetobatis flagellum: Annandale 1909*.
Aetobatus flagellum: Compagno & Last 1999*; Bonfil & Abdallah 2004*; White *et al*. 2006*; White & Last 2016.

Disc diamond-shaped, with angular pectoral fins, much broader than long, and with concave posterior margins. Snout conspicuously elongate and pointed, narrowly tapering ahead of eyes. Eyes small, slightly oval, ventrolateral; spiracles large, elliptical. Internarial flap long, with pronounced median notch posteriorly. Teeth in up to 6/13 rows; lower tooth plate very broad, ~⅔ mouth width. Pelvic fins protrude beyond posterior margin of disc. Dorsal fin small, its origin behind pelvic-fin insertions. Tail very long and slender, whip-like; stinging spine elongate, slender.

Body uniformly dark greenish brown to brown dorsally, unspotted, without conspicuous markings; uniformly white ventrally. Attains at least 57 cm DW, 126 cm TL.

DISTRIBUTION Indo-Pacific (disjunct); records from eastern Atlantic and Hawaii in central Pacific require verification. WIO: Red Sea, Persian/Arabian Gulf (Kuwait) and India.

REMARKS Naturally uncommon and little known, but biology probably similar to *A. narinari*. Found inshore on continental shelf and in brackish water. Likely caught in local demersal fisheries. IUCN Red List conservation status Endangered.

Aetobatus narinari (Euphrasen 1790)

Spotted eagle ray

PLATES 78 & 79

Raja narinari Euphrasen 1790: 217, Pl. 10 (St Barthélemy I., West Indies; Brazil).

Aetobatis narinari: Klunzinger 1871; Day 1878*; Annandale 1909; Gilchrist & Thompson 1911; Barnard 1925; Blegvad & Løppenthin 1944*; Randall 1995*.

Stoasodon narinari: Smith 1949*.

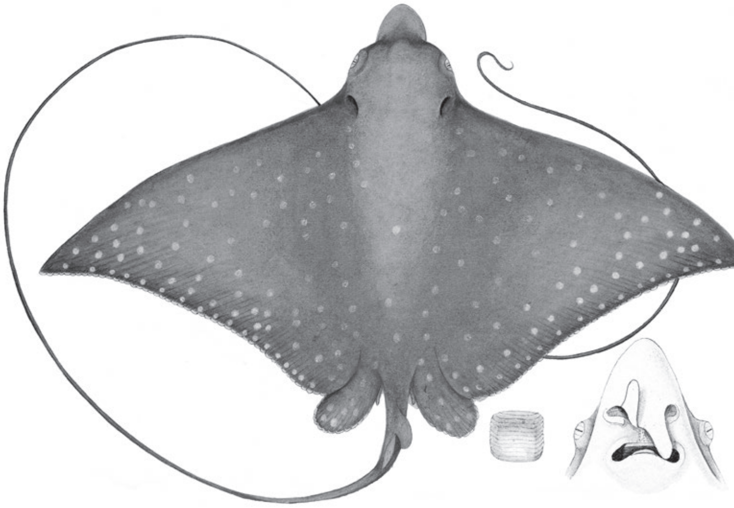
Aetobatus narinari: Munro 1955*; Wallace 1967*; Qureshi 1972*; SSF No. 28.1*; Van der Elst 1988*; Compagno *et al.* 1989*; Debelius 1993*; Randall 1995*; Compagno & Last 1999*; Debelius 1999*; Hennemann 2001*; Bonfil & Abdallah 2004*; Heemstra & Heemstra 2004; White *et al.* 2006*; Fricke *et al.* 2009; Last & Stevens 2009*; White 2014; White & Last 2016.

Head and body thick; snout and rostral lobe relatively long. Pectoral fins angular; anterior margins oblique to body axis, posterior margins slightly concave. Spiracles large, set over pectoral-fin origins. Posterior edge of internasal flap notched, inverted V-shape, and fringed; 1 row of plate-like teeth in each jaw, lower teeth protruding. Pelvic fins narrowly rounded. Dorsal fin over pelvic fins. Tail extremely long, up to 3 times disc length. Skin smooth.

Body blue to black dorsally (in WIO region), with many white spots or rings; uniformly white ventrally; tail black. Attains 3.3 m DW, possibly more; ~8.8 m TL (assuming undamaged tail).

DISTRIBUTION Circumglobal in most tropical and subtropical seas (likely a species-complex). WIO: South Africa to Red Sea, Gulf of Oman, Persian/Arabian Gulf, Pakistan, India, Sri Lanka, Maldives, Madagascar, Seychelles and Réunion.

REMARKS Recent molecular studies suggest *A. narinari* may represent two or more species, and colour differences can be noted between populations in Atlantic, Indian and Pacific oceans. The nominal species *Myliobatus ocellatus* Kuhl 1823 is now employed as a senior synonym of *A. narinari* in the Indo-Pacific, but it is not clear whether this should apply to the species in WIO. Biology poorly known. Females mate with up to 4 different males within 1 hour; litters of up to 4; size at birth 17–36 cm DW; gestation period 12 months or less. Males mature at ~100 cm DW, and females at ~214 cm DW, at age 4–6 years for both sexes. Occurs near reefs, beaches, estuaries and bays, to ~60 m deep, and occasionally found in open ocean or in estuaries and lagoons. Active and agile swimmer near surface and able to rapidly accelerate and leap from water; observed singly, in small groups, as well as in schools of over 200 individuals. Uses its rostral lobe and exposed tooth plate to hunt benthic invertebrates (shrimps, crabs, clams, snails, worms, oysters, octopus, squid and sea urchins). Preyed on by sharks which tend to follow pregnant eagle rays to feed on newborn pups. Caught in artisanal fisheries throughout its range. A powerful fighter for anglers, but its meat is not much appreciated. Common in public aquariums. IUCN Red List conservation status Near Threatened.



Aetobatus narinari. Source: Bleeker 1877

Aetobatus ocellatus (Kuhl 1823)

Ocellated eagle ray

PLATE 79

Myliobatus ocellatus Kuhl *in* Van Hasselt 1823: 316 (Jakarta, Java, Indonesia).
Aetobatis guttata: Annandale 1909.
Aetobatus flagellum: Misra 1962*.
Aetobatus guttatus: Compagno & Last 1999*.
Aetomylaeus ocellatus: Sujatha 2002.
Aetobatus ocellatus: White & Last 2016.

Disc much broader than long, acute at tips. Head broad, much broader than snout; snout moderately elongate and not very acute. Pectoral-fin anterior margins relatively straight, nearly perpendicular to body axis, or slightly convex; posterior margins slightly concave; fin bases rather narrow. Spiracles large. Lower tooth band ~½ mouth width. Pelvic fins protrude beyond posterior margin of disc. Dorsal fin behind pelvic-fin insertions. Tail long and whip-like; stinging spine slender, elongate.

Body greenish brown to grey dorsally, with white spots usually more numerous on rear half of disc, but pattern of spots highly variable; uniformly white ventrally. Attains at least 125 cm DW, 4 m TL.

DISTRIBUTION Indian Ocean and western central Pacific. WIO: Pakistan, India and Sri Lanka.

REMARKS The name *Aetobatus ocellatus* was recently resurrected to be used in place of *A. narinari* in the Indo-Pacific region. However, whether the WIO specimens are conspecific with *A. ocellatus* from the western central Pacific, from where it was described, needs to be determined. Poorly known, but biology probably similar to other myliobatids.

FAMILY **RHINOPTERIDAE**

Cownose rays

Brett A Human

Moderate- to large-sized (up to 210 cm DW), heavy-bodied rays with head depressed but elevated above disc, and forehead strongly indented with associated pair of lobe-like rostral flaps originating under spiracles and opposite mouth, continuing to front of head and uniting at front indentation. Disc rhomboidal, much wider than long (disc width 1.5–2 times disc length). Pectoral-fin origins posterior to nostrils and spiracles, fin tips acutely angular, and posterior margins concave. Eyes and spiracles lateral; 5 pairs of short gill slits on underside of head. Snout short, indented, and without rostral cartilage; internasal flap reaches mouth, with serrate posterior edge. Mouth ventral, transverse; teeth plate-like, arranged in 7 or more rows. Pelvic fins rounded or angular, and not bilobed; claspers short and stout. Dorsal fin small, prominent, its origin at base of tail, near pelvic-fin insertions. Tail filamentous, cylindrical, subequal to or much longer than disc, and without skin folds; no caudal fin. Dorsal surface smooth and without thorns, or with small denticles; 1 or more short stinging spines at base of tail and just behind dorsal-fin free rear tip (1 spine in WIO representatives). No electric organs.

Reproductive mode viviparity with histotroph, with uterine secretions nourishing few embryos. Highly social rays, schools of hundreds to even thousands of individuals have been observed, with such schools so far associated with breeding and dominated by females (when sex ratios have been reported). Some species are known to undertake long migrations. The gregarious nature of cownose rays makes them susceptible to various commercial net-gear fisheries (trawls, gillnets, seine nets), with accounts of thousands in a single catch; they are also caught by recreational anglers and exploited for the aquarium trade.

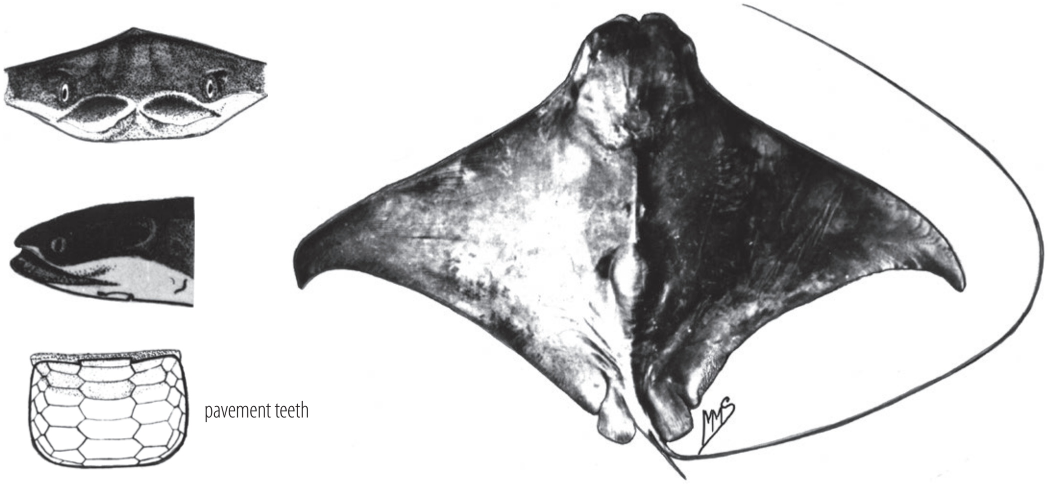
Poorly known group taxonomically, although easily recognisable by their blunt, anteriorly indented heads and odd-looking rostral flaps. A revision of this family would probably result in fewer valid species as some species currently recognised may be merely geographic variants of others. The primary character historically used to separate species (the number of tooth rows) has proven to be highly variable within a species; moreover, dentition is likely to be sexually dimorphic (as in *Rhinoptera javanica*), particularly in reference to tooth width versus length in the middle rows in both jaws, with females probably having wider teeth than males. However, head width and tail length may prove to be useful diagnostic characters. Circumglobal in tropical to warm-temperate seas. One genus with ~10 species; 2 species in WIO.

GENUS ***Rhinoptera*** Kuhl 1829

Diagnosis as for family. A taxonomically perplexing group, with ~10 species currently recognised, but probably fewer are valid. The following key is highly provisional pending the discovery of more reliable characters.

KEY TO SPECIES

1a Tail length less than disc length; tooth width ~8 times tooth length in middle row of upper jaw .... ***R. jayakari***
1b Tail length equal to or greater than disc length; tooth width <5.6 times tooth length in middle row of upper jaw .... ***R. javanica***



Rhinoptera javanica,
65 cm DW (S Mozambique).
Source: SSF

Rhinoptera javanica Müller & Henle 1841

Flapnose ray PLATE 79

Rhinoptera javanica Müller & Henle 1841: 182, Pl. 58 (Java, Indonesia [Malabar coast, India]); Day 1878*, 1889*; James 1962*, 1970*; Wallace 1967*; Srinivasarengan 1981; Bianchi 1985*; SSF No. 28.4*; Séret & McEachran 1986; Compagno *et al*. 1989*; Cliff & Wilson 1994*; Morón *et al*. 1998; Compagno & Last 1999*; Vossoughi & Vosoughi 1999*; Sujatha 2002; Bonfil & Abdallah 2004*; White *et al*. 2006*; White & Dharmadi 2007; Last & Stevens 2009*.
Rhinoptera adspersa Müller & Henle (ex Valenciennes) 1841: 183 (India); Day 1878, 1889; Compagno & Last 1999*.

Disc width 1.5–2 times disc length; tail 1–3 times disc length. Tooth width 2.5–5.6 times tooth length in middle row of upper jaw; tooth count 7–11/7–10.

Body uniformly dark brown to olive dorsally; white ventrally. Attains 150 cm DW.

DISTRIBUTION Indo-Pacific (widespread but range not well defined). WIO: South Africa, Mozambique, Seychelles, Arabian Sea, Gulf of Aden, Red Sea, Persian/Arabian Gulf, Pakistan, India and Sri Lanka.

REMARKS The diagnostic features provided here have been gathered from western and northern Indian Ocean references, as the morphometric values provided for this species from Australia are very different (e.g., tail 2.6–3.4 times disc length; tooth width 10–13 times tooth length in middle row of upper jaw). Apparently common throughout its range, but poorly known. Litters of up to 6 (generally 1 or 2); size at birth 31–61 cm DW, born in January and February in India. Pelagic; inshore to ~30 m deep, including in bays, estuaries, mangroves and near reefs. Migrates inshore daily to feed; diet includes bivalves (clams, oysters) and crustaceans; can occur in large schools. Taken in artisanal fisheries and as bycatch in commercial net-gear fisheries and anti-shark nets; widely utilised. IUCN Red List conservation status Vulnerable.

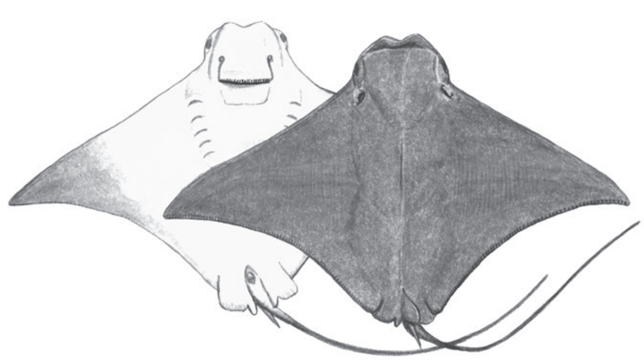
Rhinoptera jayakari Boulenger 1895

Short-tail cownose ray PLATE 79

Rhinoptera jayakari Boulenger 1895: 141 (off Muscat, Gulf of Oman); Randall 1995*; Manilo & Bogorodsky 2003; Bonfil & Abdallah 2004; Last *et al.* 2010*; Bogorodsky *et al.* 2014*.
Rhinoptera javanica: Schwartz 1990; Al-Abdessalaam 1995*.
Rhinoptera sp. 1: White *et al*. 2006*; White & Dharmadi 2007.

Disc width ~1.75 times disc length; tail ~⅔ times disc length. Tooth width ~8 times tooth length in middle row of upper jaw; tooth count 9/9.

Body uniformly pale grey to olive-green dorsally; pale ventrally; tail darker. Attains 80 cm DW.



Rhinoptera jayakari (Mozambique).

DISTRIBUTION Indo-Pacific. WIO: southern Red Sea (Jizan, Saudi Arabia), Gulf of Aden to Gulf of Oman, and southward to Mozambique and South Africa (KwaZulu-Natal); elsewhere to Indonesia, Japan and possibly Australia.

REMARKS The taxonomic validity of this species is questioned in Compagno's (1999) checklist of living elasmobranchs. Locally rare. Sometimes forms schools; observed in Arabian Sea off Oman apparently basking at surface, in groups of tens and amounting to several hundred individuals within a few nautical miles, presumably feeding on benthos in nearly anoxic waters created by Somali current, which may force the rays to the surface to recover. Extent of its range unknown due to confusion with *R. javanica*. Historically a locally discarded bycatch of artisanal and commercial fisheries, but the pectoral fins have become valuable in the shark-fin trade. Presumably feeds on molluscs and other benthic invertebrates.

FAMILY MOBULIDAE

Devilrays

Andrea D Marshall

Small-sized to enormous (1–8 m DW), with rhomboidal or chevron-shaped disc, broader than long; head trapezoidal, protruding, with prominent forward-projecting cephalic lobes (extensions of pectoral fins, which are curled while swimming and unfurled when feeding); pectoral-fin tips acute, posterior margins concave; pelvic fins small and barely projecting beyond disc; tail whip-like, and some species with very small serrated spine at base; dorsal fin small, angular, at base of tail and over pelvic fins; no skin folds or caudal fin. Eyes and spiracles lateral; 5 pairs of short to wide gill slits on underside, and internal gill openings with unique fringed filter plates. Mouth broad, terminal or subterminal; teeth small, peg-like, embedded in bands on both jaws or on lower jaw only. Skin on dorsal and ventral surfaces usually covered with small denticles.

Pelagic rays with modified branchial filter plates enabling them to feed on small planktonic crustaceans, gastropods, coral and fish spawn, as well as small fishes. Typically inhabit shallow inshore waters, around reefs, bays, atolls and island groups, but also offshore reefs and seamounts; graceful, powerful swimmers, observed singly or in small or large groups, often feeding or basking at surface or interacting around aggregation sites. Their movement patterns and migratory habits are not well understood. Reproductive mode viviparity with histotroph, wherein embryos are nourished by uterine secretions; very low fecundity, with litters of only 1 or 2; the reproductive season often coincides with summer when water temperatures are highest. Presumably, mobulids cannot sustain targeted fisheries for long due to low reproductive potential and relatively small population sizes, yet there are increasing catches in directed fisheries, as bycatch, and incidentally in trawl fisheries. Urgent conservation measures for most species are needed. The meat is used for food, the skin for leather, and the branchial filter plates have particularly high value as medicinal products in Asia. Increasingly, some species are the subject of dive tourism (although human interactions without codes of conduct may affect their natural behaviour).

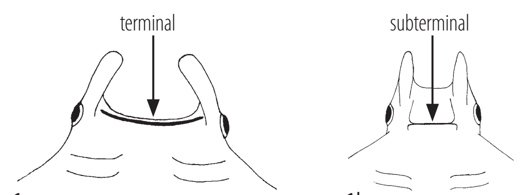
Mobulidae species occur worldwide in tropical and temperate seas. A complicated nomenclatural history, gaps in taxonomic and genomic sampling and poor representations of mobulids in museum collections has contributed to taxonomic confusion with species being regularly confused. Recent efforts to clarify long-standing taxonomic and phylogenetic uncertainties have resulted in significant changes to the taxonomic arrangement of the family and several species being synonymised. There are at least 10 distinct species in the currently recognised single genus *Mobula*, of which 7 occur in WIO. However, *Mobula* has been found to be paraphyletic, but additional research is still warranted to fully resolve the taxonomic uncertainty.

GENUS ***Mobula*** Rafinesque 1810

See family account.

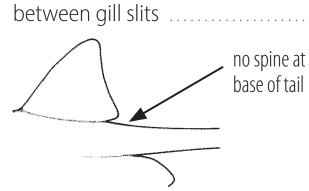
KEY TO SPECIES

1a Mouth terminal; teeth in lower jaw only 2
1b Mouth subterminal; teeth in both jaws 3



1a 1b

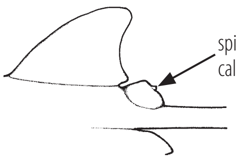
2a Large-sized to 5 m DW, calcified mass with embedded stinging spine at base of tail greatly reduced and in most cases absent; skin embedded with small non-overlapping, evenly spaced denticles, with stellate bases and laterally elongated knob-like protrusions; mouth typically white to pale grey; ventral surface mostly white, often with irregular dark spots or patches across rear half of disc and often medially between gill slits .... ***M. alfredi***



Continued …

KEY TO SPECIES

2b Large-sized to 7 m DW, calcified mass present at base of tail with embedded vestigial stinging spine and with tip protruding 1–2 mm; skin densely embedded with small overlapping denticles, with distinctly bifid cusps, which form distinct ridges and furrows; mouth typically dark grey to black; ventral surface white with posterior margins of pectoral fins typically charcoal grey for length of fin, often with irregular dark spots or patches centrally on abdomen, but without dark markings medially between gill slits .... ***M. birostris***



3a Spiracles ovoid, slit-like, set above plane of pectoral fins; large-sized, to >5 m DW 4

3b Spiracles small, nearly circular, set slightly below plane of pectoral fins; small- to medium-sized, to <2 m DW 5

4a Medium- to large-sized, disc width approximately twice disc length; pectoral-fin anterior margins nearly straight, becoming slightly convex distally; head and cephalic lobes short; rostral margin straight; branchial filter plates separate; tail as long as or longer than DW with prominent white denticles laterally, and a small stinging spine at base encased in a calcified mass; dorsal-fin tip white; skin rough, body densely covered with small denticles yet sparsely distributed on ventral side of pectoral fins .... ***M. mobular***

4b Large-sized, disc width ~1.6 times disc length; pectoral fins sinusoidal (leading margin of pectoral fins with distinct curving); head elongate, but cephalic lobes short and thick; rostral margin broadly concave; branchial filter plates fused; pelvic area narrow, elongated, with conspicuous abdominal pores near pelvic-fin insertions; tail short (<½ DW), base compressed, without stinging spine; dorsal fin uniformly dark; skin rough, covered with long, thick posteriorly pointing thorn-like denticles .... ***M. tarapacana***

5a Small-sized with short head and short cephalic lobes; pectoral-fin anterior margins straight; rostral margin straight; tail base quadrangular; dorsal fin usually white-tipped; skin distinctly smooth.. ***M. kuhlii***

5b Small-sized with elongated head and long cephalic lobes; pectoral-fin anterior margins straight to weakly convex; rostral margin deeply concave; tail base quadrangular; dorsal fin uniformly dark; skin mostly smooth, some denticles at dorsal-fin base .... ***M. eregoodoo***

5c Medium-sized with short head and short cephalic lobes; pectoral-fin anterior margins wavy, with prominent double curvature; rostral margin relatively straight; tail base depressed; dorsal fin white-tipped; skin sparsely covered with short blunt denticles.. ***M. thurstoni***

Mobula alfredi (Krefft 1868)

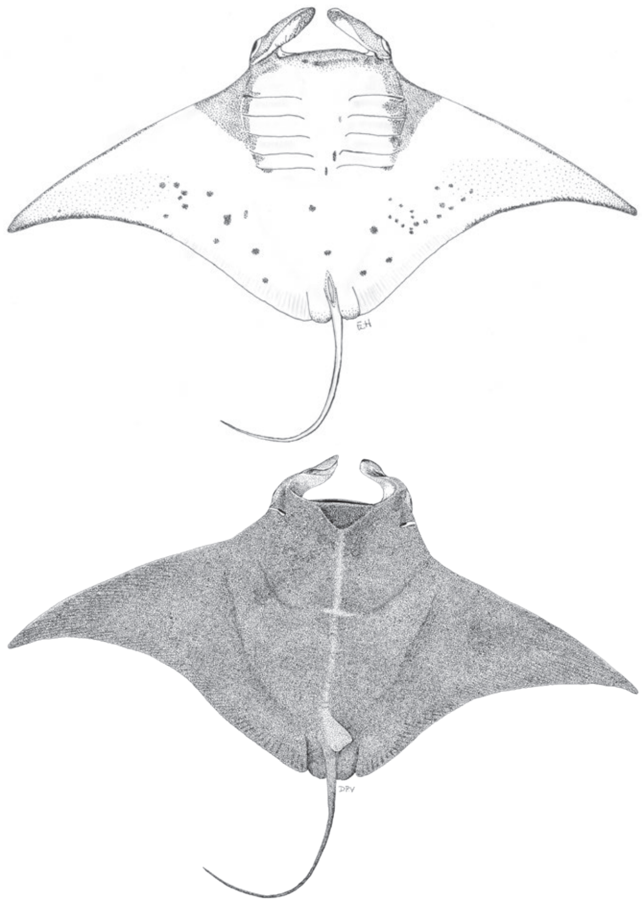
Reef manta ray

PLATE 80

Deratoptera alfredi Krefft 1868: 3, 9, Fig. (entrance to Sydney Harbour, Australia).
Manta fowleri Whitley 1936: 182 (Line Is., central Pacific).
Manta pakota Whitley 1936: 183 (Marquesas Is.) [based on '*Pakoka*' in Pinchot 1930*].
Manta alfredi: Marshall *et al.* 2009*.
Mobula alfredi: White *et al.* 2017.

Disc width more than twice disc length. Spiracles small and furrow-like; branchial filter plates fused. Head very short, broad; cephalic lobes long, large, and ventral margin overlapping dorsal margin when rolled; rostral margin straight. Mouth terminal; lower-jaw teeth small, cusped, not overlapping, with ~6–8 rows, 142–182 files across width of tooth band, and total tooth count 900–1 500; upper jaw without teeth or rows of tiny peg-like denticles. Tail whip-like, short (<½ DW). Calcified mass with embedded stinging spine at base of tail greatly reduced and in most cases absent. Dermal denticles small, knob-like, evenly distributed.

Body black dorsally, with variable pale to white shoulder patches (anterior distal edges emanate posteriorly from spiracles, generally forming anterior-facing hook shape); mouth white to pale grey; cream to white ventrally, with variable blue-grey to black spots and shading across posterior half of disc and often medially between gill slits. Melanistic colour morph entirely black dorsally and predominantly black ventrally, except for variably sized white blaze along ventral midline (reports from Maldives). Leucistic colour morph extremely pale dorsally and with greatly reduced markings and shading ventrally (reports from southern Mozambique and Maldives). Attains 5 m DW.



Mobula alfredi, ~2.4 m DW, ventral and dorsal view (South Africa).
Source: SSF (lower dorsal view)

DISTRIBUTION Fragmented populations occur in tropical to subtropical seas throughout the Indian Ocean and Pacific Ocean west of the Hawaiian Is. and French Polynesia. WIO: Red Sea to South Africa (Port St Johns, Eastern Cape), Madagascar, Oman to Persian/Arabian Gulf, India and Sri Lanka to Maldives and Chagos.

REMARKS Litters of 1, rarely 2; size at birth ~150 cm DW; gestation period ~1 year. Males mature at ~3 m DW, and females at ~3.5 m DW (maturity varies with region); reproductive periodicity commonly biennial or triennial; relatively long-lived, up to ~40 years. Found more commonly in shallow inshore waters, especially in association with areas of upwelling and high biological productivity, around coral and rocky reefs, bays, atolls and island groups, but also offshore reefs and seamounts. Sometimes seen in large groups; less migratory and with smaller home ranges than *M. birostris*, but can move seasonally in response to food abundance. IUCN Red List conservation status Vulnerable.

Mobula birostris (Walbaum 1792)

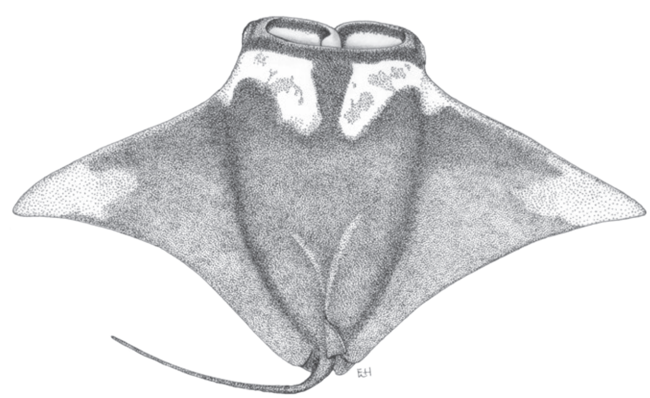
Giant manta ray

PLATES 80 & 81

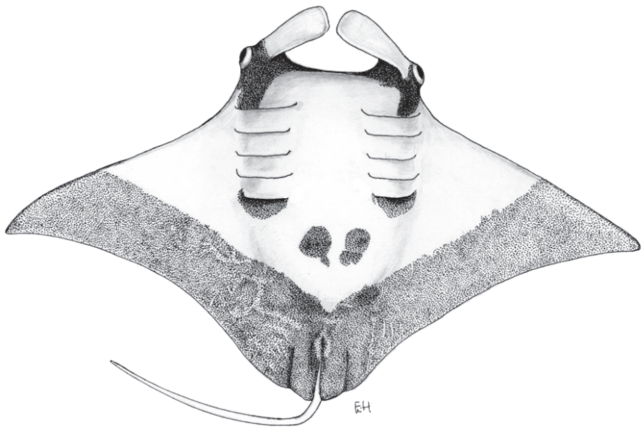
Raja birostris Walbaum 1792: 535 [no locality given].
Ceratoptera ehrenbergii Müller & Henle 1841: 187 (Red Sea).
Manta birostris: Bigelow & Schroeder 1953*; Wallace 1967*; SSF No. 29.1*; Compagno *et al.* 1989*; Randall 1995*; Ishihara *et al.* 2001*; Manilo & Bogorodsky 2003; Bonfil & Abdallah 2004*; Marshall *et al.* 2009*.
Mobula birostris: White *et al.* 2017.

Disc width more than twice disc length. Spiracles small and furrow-like; branchial filter plates fused. Head short, broad; cephalic lobes long, large, with ventral margin overlapping dorsal margin when rolled; rostral margin straight to slightly concave. Mouth terminal; teeth small, cusped, slightly overlapping, with ~12–16 rows, 220–250 files across width of tooth band, and total tooth count ~3 000–4 000; upper jaw without functional teeth but with at least 2 rows of tiny rough peg-like denticles. Tail whip-like, short (<½ DW). Calcified mass present at base of tail with embedded vestigial stinging spine with tip protruding 1–2 mm. Denticles small, dense, overlapping, forming long sagittally-oriented raised ridges and furrows on skin.

Body predominantly black or greyish blue dorsally, with angular shoulder patches with posterior-facing hook shapes; mouth dark grey to black; cream to white ventrally, with irregular dark spots or patches centrally on abdomen but without dark spots or patches medially between gill slits, and posterior margins of pectoral fins typically charcoal grey for length of fin. Melanistic colour morph entirely black dorsally and predominantly black ventrally, except for variably sized white blaze along ventral midline. Leucistic colour morph with white mouth, lighter colouration dorsally and little colouration ventrally (reports from southern Mozambique). Attains up to 7.1 m DW (anecdotal reports to ~9 m DW).



Mobula birostris, ~5 m DW, dorsal view (S Mozambique).



Mobula birostris, ~5 m DW, ventral view, different specimen from dorsal view (S Mozambique).

DISTRIBUTION Circumglobal and widespread in tropical to temperate seas. WIO: from South Africa (East London) and Madagascar to the Red Sea, Oman to India to the south of the Maldives.

REMARKS The largest living ray. Litters of 1; estimated size at birth ~150 cm DW. Males mature at ~3.8 m DW, and females at ~4 m DW. Most often sighted along productive coastlines with regular upwelling, near oceanic island groups, and around offshore pinnacles and seamounts. Telemetry studies indicate *M. birostris* spends considerable time in deeper offshore waters, between 50–200 m, and is capable of periodic dives below 1 000 m. Typically encountered in shallow inshore waters >30 m. Appears to be migratory but often revisits aggregation areas (sightings in specific locations may be common, seasonal or sporadic). Not often found in large groups, and encountered by divers less frequently than *M. alfredi*. Sympatric with *M. alfredi* in a few locations, such as Mozambique and South Africa, but the two species exhibit different movement patterns and habitat use. Has high value in directed and artisanal fisheries, and taken as bycatch; increasingly the subject of dive tourism. IUCN Red List conservation status Endangered.

Mobula eregoodoo Cantor 1949

Longhorned devilray PLATE 81

Dicerobatis eregoodoo Cantor 1849: 1420 (Penang, Malaysia; Coromandel, India).
Mobula eregoodootenkee (*non* Bleeker 1859): Bonfil & Abdallah 2004* [as *M. eregoodootenke*]; Last & Stevens 2009*.
Mobula eregoodootenkee (*non* Cuvier 1829): Notarbartolo di Sciara 1987*; SSF No. 29.3 [1995]; Manilo & Bogorodsky 2003 [as *M. eregoodootenke*].
Mobula kuhlii (*non* Valenciennes 1841): White *et al.* 2017* (in part).
Mobula eregoodoo: Notarbartolo di Sciara *et al.* 2019*.

Disc wider than long; pectoral-fin anterior margins straight to weakly convex, posterior margins concave; head elongated, cephalic lobes long; rostral margin deeply concave. Spiracles very small, nearly circular, set below level of pectoral fins. Branchial filter plates reduced, each with 4–6 short lateral lobes; terminal lobe elongated, leaf-shaped and without ridges. Teeth with 1–3 (mostly 2) small narrow-based cusps on buccal edge of crown. Tail shorter than disc length, and base quadrangular; no stinging spine. Skin smooth, except some denticles at dorsal-fin base.

Body dark greyish brown dorsally; dorsal fin uniformly dark; white ventrally, but pectoral-fin anterior margins with dark blotch midway. Attains 130 cm DW.

DISTRIBUTION Indo-Pacific (widespread). WIO: Madagascar, South Africa (KwaZulu-Natal), to Red Sea, Oman, Persian/Arabian Gulf, Pakistan, India and Sri Lanka; elsewhere to Malaysia, Indonesia, Taiwan and Australia.

REMARKS Previously misidentified as *M. diabolus* (*non* Shaw 1804). *Mobula eregoodoo* was then synonymised with *M. kuhlii*, but Notarbartolo di Sciaria *et al.* (2019) recognised it as a valid species. Usually litters of one. Locally common but little known; found in coastal continental waters, and not recorded from oceanic islands or epipelagic zone. Appears to mostly feed on small fishes. Likely a bycatch of several fisheries. IUCN Red List conservation status Endangered.

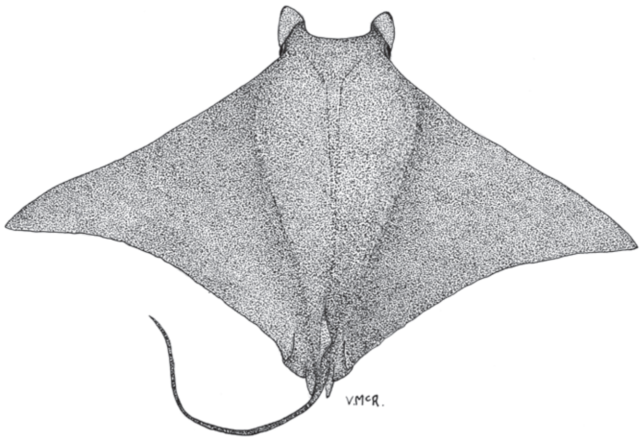
Mobula kuhlii (Valenciennes 1841)

Pygmy or lesser devilray PLATES 80 & 81

Cephaloptera kuhlii Valenciennes (ex Müller & Henle) 1841: 185, Pl. 59 (India); Duméril 1865*.
Mobula kuhlii: Notarbartolo di Sciara 1987*; Compagno *et al.* 1989*; Randall 1995*; Manilo & Bogorodsky 2003; White *et al.* 2006*; Notarbartolo di Sciara *et al.* 2017; White *et al.* 2017* (in part).

Disc width approximately twice length; pectoral-fin anterior margins straight, posterior margins concave; broad head with short cephalic lobes. Ventral margin of lobes not overlapping dorsal margin when rolled; rostral margin straight; mouth subterminal. Spiracles small, nearly circular, set below level of pectoral fins. Branchial filter plates with leaf-shaped terminal lobes. Tail can be longer than disc length when unbroken, and base quadrangular; no stinging spine. Skin distinctly smooth.

Body dark brown or grey dorsally often with a darker collar over posterior part of the head above spiracles (fades in dead specimens), white ventrally with or without pale brown to grey pectoral-fin tips; pectoral-fin anterior margins can be grey and sometimes with dark blotch mid-way; dorsal fin often white-tipped but can also be uniformly dark; tail counter-shaded dark dorsally and white ventrally. Attains 120 cm DW.



Mobula kuhlii, 111 cm DW, male (South Africa). Source: SSF

DISTRIBUTION Indo-Pacific (widespread but patchy). WIO: South Africa (KwaZulu-Natal) to Mozambique, Tanzania (Zanzibar), Somalia, Seychelles, Oman, India to Sri Lanka.

REMARKS Litters of 1; size at birth ~31 cm DW. Males mature at ~115 cm DW. Common; occurs inshore over continental shelf but not into epipelagic zone. Feeds on planktonic crustaceans, and possibly small fishes and cephalopods. Likely a targeted catch or utilised bycatch throughout its range. IUCN Red List conservation status Endangered.

Mobula mobular (Bonnaterre 1788)

Spinetail devilray

PLATE 81

Raia mobular Bonnaterre 1788:5 (Montredon, near Marseille, France).
Cephaloptera japanica Müller & Henle 1841: 185 ([Nagasaki] Japan).
Mobula japanica: Notarbartolo di Sciara 1987*, 1988; SSF No. 29.4 [1995]; Manilo & Bogorodsky 2003; Bonfil & Abdallah 2004*; White *et al.* 2006*; Last & Stevens 2009*.
Mobula mobular: White *et al.* 2017*.

Disc width twice length; pectoral-fin anterior margins straight to slightly convex, posterior margins concave; head and cephalic lobes short, and ventral margin of lobes not overlapping dorsal margin when rolled; rostral margin relatively straight; mouth subterminal. Spiracles ovoid, transverse slits, set above level of pectoral fins. Branchial filter plates separate from each other; 3rd arch with 85–95 plates on each face, each with 18–25 lateral lobes, and terminal lobe leaf-shaped with median longitudinal ridge. Pelvic fins distinctly wedged-shaped; conspicuous abdominal pores near pelvic-fin insertions. Dorsal fin high, relatively advanced on body. Tail very long (subequal to or longer than DW), with prominent white denticles entire length; serrated stinging spine exposed (~3–5 cm long) and base embedded in calcified mass. Dermal denticles dense, but sparser on ventral surface of pectoral fins.

Body bluish black dorsally, with pale crescent-shaped shoulder patches (distinct in juveniles, fading in adults); cephalic lobes grey with black tip, outer surface white; dorsal-fin tip white; white denticles laterally on tail; white ventrally, sometimes with dark patches in adults (but pectoral-fin anterior margins never dark). Attains 320 cm DW.

DISTRIBUTION Probably circumglobal in tropical to warm-temperate seas (distribution not completely defined). WIO: South Africa (KwaZulu-Natal), Gulf of Aden, Persian/Arabian Gulf, Oman to Pakistan, India and Sri Lanka.

REMARKS Biology poorly known. Litters of 1. Occurs inshore and offshore and is capable of exploiting deepwater habitats. Feeds largely on planktonic crustaceans and occasionally small fishes. A bycatch of other fisheries and increasingly targeted for human consumption. IUCN Red List conservation status for *Mobula mobular* in the Mediterranean is Endangered, and before *Mobula japonica* became a junior synonym of *M. mobular*, it was listed as Near Threatened globally and Vulnerable throughout Southeast Asia.

Mobula tarapacana (Philippi 1892)

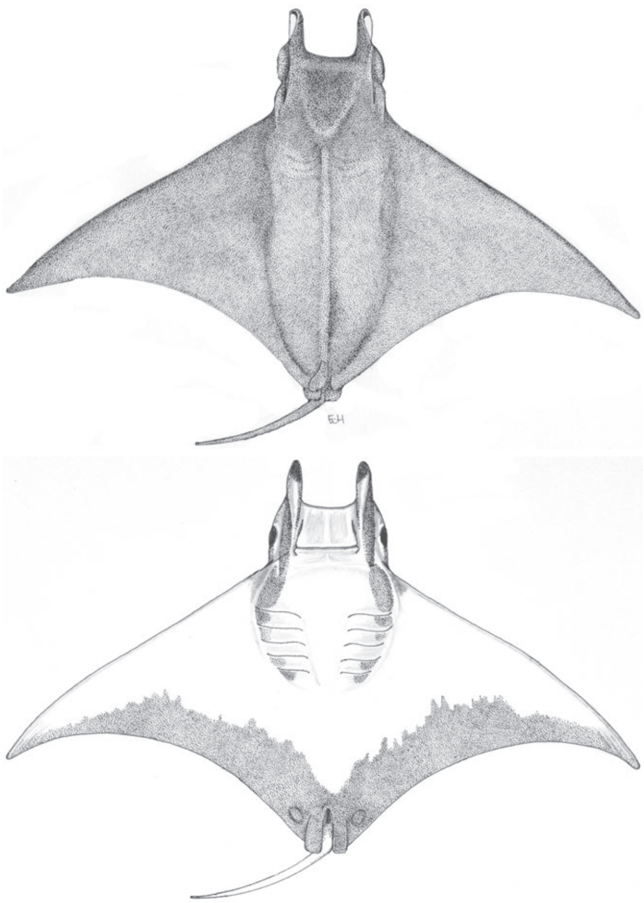
Sicklefin devilray

PLATE 81

Cephaloptera tarapacana Philippi 1892: 8, Pl. 3, Fig. 2 (Tarapacá Region, Chile).
Mobula tarapacana: Notarbartolo di Sciara 1987*, 1988; Compagno *et al.* 1989*; SSF No. 29.5 [1995]; Bonfil & Abdallah 2004*; White *et al.* 2006*; White *et al.* 2017.

Disc wider than long; pectoral-fin anterior margins weakly concave, becoming broadly convex towards slender apex, and posterior margins concave (fins sickle-shaped); head long; cephalic lobes short and thick, and ventral margin of lobes not overlapping dorsal margin when rolled; rostral margin broadly concave; mouth subterminal. Spiracles longitudinal slits, set above plane of pectoral fins, and inside surface corrugated by several transverse skin folds; crease from eye to origin of spiracle. Branchial filter plates fused; 3rd gill arch with 50–65 plates, each with 15–22 lateral lobes, and terminal lobe broadly rounded distally and concave proximally. Teeth relatively large and tessellated (not overlapping). Pelvic-fin area uniquely narrow, elongated, with conspicuous abdominal pores near pelvic-fin insertions. Tail short (<½ DW), compressed at base and distinctly rounded towards tip; no stinging spine. Skin rough, covered with long, thick, posteriorly pointing thorn-like denticles.

Body olive-green to bronze dorsally; dorsal fin uniformly dark; ventral surface white anteriorly and grey posteriorly (separated by irregular demarcation line), underside of rostrum to lower jaw silvery, inner cephalic lobes grey with black tip, dark eye-spots sometimes near pectoral-fin tips, and rarely with dark patches on gill slits.Attains 3.28 m DW (unconfirmed reports to 3.70 m DW).



Mobula tarapacana (WIO). Composite

DISTRIBUTION Probably circumglobal (but scattered) in tropical to warm-temperate seas. WIO: South Africa (Eastern Cape) to Red Sea, India, Sri Lanka and Maldives.

REMARKS Litters of 1; size at birth 105–132 cm DW. Males mature at 240–250 cm DW, and females at 270–280 cm DW. Undertakes long migrations and, like some other species of *Mobula,* can make deep dives >1 800 m. More oceanic pelagic occurrence that other mobulids, but occasionally coastal. Feeds on planktonic crustaceans and small fishes; larger mesh size of branchial filter plates suggests it is ichthyophagous or a more general feeder than other mobulids. A bycatch of pelagic gillnet, purse-seine and longline fisheries, and a minor component in the increasing mobulid catches elsewhere in its range. IUCN Red List conservation Endangered.

Mobula thurstoni (Lloyd 1908)

Bentfin devilray

PLATE 81

Dicerobatis thurstoni Lloyd 1908: 179, Fig. 3, Pl. 4 (India, northern Indian Ocean).

Mobula thurstoni: Notarbartolo di Sciara 1987*, 1988*; Compagno *et al.* 1989*; Randall 1995*; SSF No. 29.6 [1995]; Manilo & Bogorodsky 2003; White *et al.* 2006*; Last & Stevens 2009*; White *et al.* 2017.

Disc width approximately twice length; pectoral-fins sinusoidal (margins somewhat wavy), anterior margins convex and posterior margins notably concave (fin with prominent double curvature); head and cephalic lobes short, and ventral margin of lobes not overlapping dorsal margin when rolled; rostral margin relatively straight; mouth subterminal. Spiracles small, nearly circular, set below level of pectoral fins. Branchial filter plates 70–75, separate, each with 15–20 lateral lobes, and terminal lobe elliptical or leaf-shaped. Teeth small and wide-based, overlapping in adults. Tail ~60% disc length, flattened at base but overall ovoid in cross-section; no stinging spine. Dermal denticles sparse.

Body dark blue to black dorsally, and silvery grey around eyes; anterior margins of pectoral-fin sometimes with white stripe, and trailing edge of ventral surface of fin sometimes with dark metallic green patch (not in Indo-Pacific and Atlantic specimens); ventral surface of pectoral and pelvic fins often with dark posterior margins; often with 2 conspicuous abdominal pores at level of pelvic insertion; dorsal fin white-tipped; mostly white ventrally (of variable intensity), and often silvery near pectoral-fin tips; tail counter-shaded dark dorsally and white ventrally. Attains 180 cm DW.

DISTRIBUTION Probably circumglobal (scattered) in tropical to subtropical seas. WIO: South Africa (Eastern Cape and KwaZulu-Natal), Madagascar, Maldives to Red Sea, Oman to India and Sri Lanka.

REMARKS Litters of 1; size at birth 65–85 cm DW; gestation period probably 1 year. Matures at ~150 cm DW; reproductive periodicity reportedly every 2 or more years. Most commonly found in shallow neritic waters, to ~100 m deep, but sometimes seen several kilometres offshore over deeper waters; not schooling, observed singly or in small groups. Feeds on planktonic crustaceans (euphausiids, mysids). IUCN Red List conservation status Endangered globally but suspected to be Vulnerable in the Indian Ocean and throughout Southeast Asia.

ORDER CHIMAERIFORMES

FAMILY CALLORHINCHIDAE

Elephantfishes

Jenny M Kemper and David A Ebert

Highly distinctive cartilaginous fishes with relatively elongate, torpedo-like body (to 125 cm TL); prominent, fleshy, plough-shaped snout, terminal end transverse and leaf-shaped. Single pair of gill openings covered by soft flap; head with well-developed system of mucous canals and sensory pores; lateral-line canals enclosed, pored (not open grooves), readily visible and continuous from behind eyes to peduncle. Eyes small, set high on head; no spiracles. Mouth small, directed anteroventrally, with plate-like dentition; tooth plates large and robust, 2 pairs in upper jaw, 1 pair in lower jaw. Pectoral fins large, fan-like; bases of paired fins thick and fleshy, and outer fin webs thin and flexible. Two widely separated dorsal fins: 1st dorsal fin erectile, high and triangular, preceded by long, serrated, moveable and mildly venomous spine; 2nd dorsal fin short-based (relative to other Chimaeriformes), its length nearly equal to pectoral-fin to pelvic-fin space, anterior one-third of fin tall, sloping posteriorly to a low, evenly tall fin. Anal fin tall, narrow-based, separated from caudal fin only by deep notch. Caudal fin heterocercal, narrow and arched, about as long as pectoral fins; no caudal filament. Skin smooth.

Reproductive mode oviparity; females produce large, horny, spindle-shaped egg cases. Elephantfishes display relatively fast growth, early maturity and high fecundity. Occur close inshore to continental slope. Feeble swimmers; the distinctive snout is used to probe the bottom for feeding on invertebrates and small fishes. Caught commercially, as bycatch, and by shore anglers.

Common in temperate oceans of Southern Hemisphere. One genus, *Callorhinchus* Lacepède 1798, with 3 species, 1 in WIO.

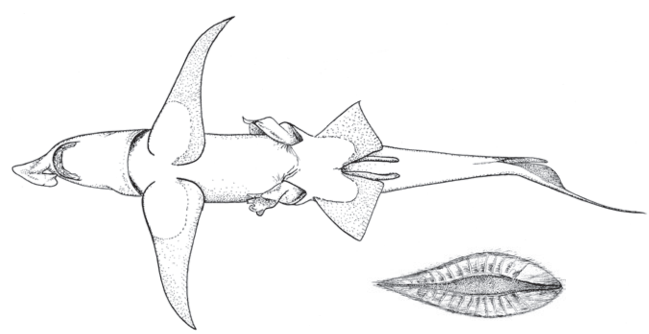
Callorhinchus capensis Duméril 1865

Cape elephantfish PLATE 82

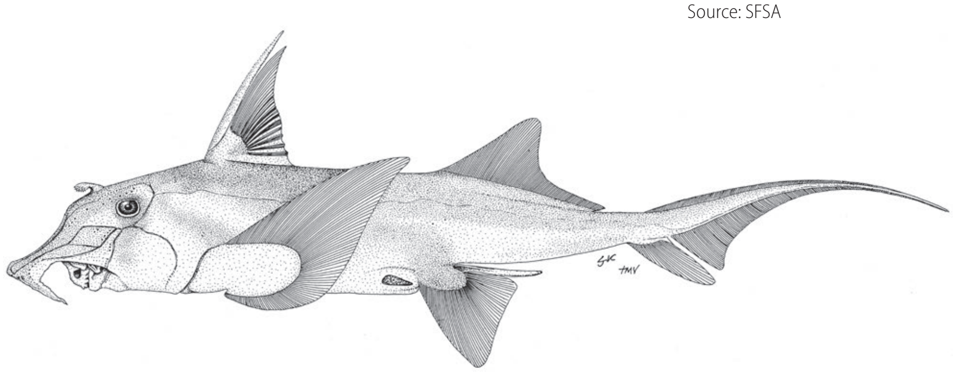
Callorhynchus capensis Duméril 1865: 695, Pl. 13, Fig. 5 (Cape of Good Hope, South Africa); SFSA No. 95*; Krefft 1990.
Callorhinchus capensis: SSF No. 34.1*; Compagno, Ebert & Smale 1989*; Compagno, Ebert & Cowley 1991; Bianchi & Carpenter *in* Bianchi *et al.* 1993*; Freer & Griffiths 1993; Heemstra & Heemstra 2004*.

Diagnosis as for family. Pelvic claspers simple, rod-like, without dilated tips or denticles; frontal tenaculum club-like, with small spines near apex; pre-pelvic tenacula relatively complex, spoon-shaped, with medial barbs on inner surface. Egg cases elongate, oval, with broad lateral flanges.

Body silvery, with dusky spots or blotches on head and trunk; fin webs brown. Attains 122 cm TL.



Callorhinchus capensis, 22 cm TL, male, ventral view, and egg case.
Source: SFSA



Callorhinchus capensis, 42 cm to rear of 2nd dorsal fin, male (South Africa).
Source: SSF

DISTRIBUTION Southern Africa: Namibia to Cape of Good Hope in southeastern Atlantic, to South Africa (abundant on south coast, rarely to KwaZulu-Natal) in WIO.

REMARKS Found from near shore and in shallow bays to continental slope, near bottom, usually over soft substrate, to 366 m deep (mostly <120 m). One egg per oviduct, up to 22 eggs per female per season; size at birth ~13 cm TL. Males mature at ~43 cm TL, and females at 46–50 cm TL; reproductive periodicity year-round, peaking in summer. Feeds on invertebrates (echinoderms [urchins], bivalves, gastropods, crustaceans [mantis shrimp], polychaetes) and small bony fishes. Caught in directed bottom-set gillnet fisheries, and a bycatch of demersal trawl fisheries; sold for human consumption. In South Africa, commonly known as St Joseph.

FAMILY RHINOCHIMAERIDAE

Longnose chimaeras

Jenny M Kemper and David A Ebert

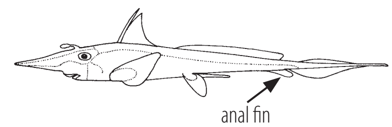
Medium- to large-sized cartilaginous fishes with somewhat compressed, elongate body (to ~130 cm TL), tapering to narrow diphycercal tail; snout elongated into cylindrical or flattened pointed projection, not plough-shaped. Mouth ventral, with beak-like tooth plates: two pairs in upper jaw, one pair in lower jaw; dentition smooth, either without hypermineralised tritors (grinding surfaces) or with ridged hypermineralised tritors. Pair of single gill openings covered by soft flap; lateral-line canals open grooves. Two dorsal fins: 1st dorsal fin erectile, triangular, and preceded by tall, smooth or serrated spine; 2nd dorsal fin long and low, with straight or slightly undulating distal margin. Anal fin high and narrow-based, or absent. Caudal fin lanceolate; terminal filament present or absent; upper caudal margin with or without series of tubercles (or denticles in males). Pelvic claspers slender and rod-like, with small, fleshy but denticulate tips; adult males also with single frontal tenaculum and paired pre-pelvic tenacula. Skin smooth and deciduous.

Reproductive mode oviparous; egg cases ovoid and large, with spindle-shaped capsule; fan-like lateral flanges, narrower than that of the callorhinchids, with a constricted central spindle. Rare to moderately common, benthopelagic, over continental slope and abyssal plains, generally inhabit deep water at ~100–2 000+ m; adults and juveniles may occupy different habitats. Minimal interest to fisheries, primarily as bycatch in bottom-trawl fisheries.

Worldwide but scattered, in tropical to temperate seas. Three genera and 8 species; all 3 genera and 5 species in WIO, but only 2 genera, with at least 2 and possibly 3 species in WIO at depths of <200 m.

KEY TO GENERA

1a Anal fin present .... ***Neoharriotta***



1b No anal fin .... ***Harriotta***

GLOSSARY

tenaculum (pl. tenacula) – an appendage on the forehead of male chimaeroid fishes, weakly differentiated to ridge-like in male juveniles (frontal tenaculum); additional small, retractable appendage on each side just in front of the pelvic fins with intromittent organs (claspers), of chimaeroid males, only partially differentiated in male juveniles, and hidden in a slit when retracted (pre-pelvic tenaculum).

GENUS *Harriotta* Goode & Bean 1895

Body elongate, tapering posteriorly to caudal filament; snout very long, relatively slender, with pointed and often upturned tip, and adult males often with rounded knobs on tip. Head convex in lateral profile; eyes small to moderately large. Mouth located below eyes; tooth plates thick, hypermineralised, with transverse ridges and tritors (except in small juveniles). Pectoral fins broad, tips sometimes reaching beyond pelvic-fin origins when depressed. First dorsal fin short-based, high, preceded by tall spine with serrations; spine as high as 1st dorsal fin and almost entirely free from its margin; 2nd dorsal fin low and long, either widely separated from or basally connected to 1st dorsal fin, and its distal margin convex to straight. No anal fin. Upper and lower margins of caudal fin either similar or lower margin longer and taller; upper edge without tubercles. Two species, 1 in WIO.

Harriotta raleighana Goode & Bean 1895

Narrownose chimaera PLATE 82

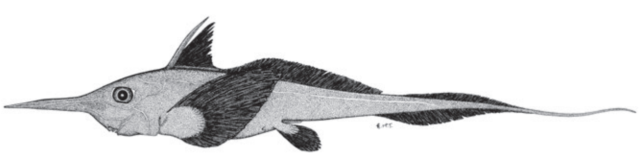
Harriotta raleighana Goode & Bean 1895: 472, Pl. 19 (northwestern Atlantic, Gulf Stream); Jordan & Evermann 1900*; Garrick 1971*; Garrick & Inada 1975; Stehmann & Bürkel *in* Whitehead *et al*. 1984*; SSF No. 33.1*; Compagno *et al*. 1989*; Krefft 1990; Compagno *et al*. 1991; Last & Stevens 1994*; Didier 1995; Gomon 2008*.

Relatively small-bodied; snout moderately long, slightly flattened with blunt tip, often bent upwards, its width greatest at midlength. Eyes moderately large, diameter about half distance between eye and dorsal spine. Mouth in front of or below eyes. Pectoral fins broad and short, apices rather angular and reaching beyond pelvic-fin origins when depressed. First dorsal fin tall, spine relatively straight and usually taller than 1st dorsal fin, and fin tip reaching at least to 2nd dorsal-fin origin when depressed; interdorsal space short; 2nd dorsal-fin mainly straight, base more than twice length of pelvic fins. Caudal-fin upper portion shorter than lower portion, but both distal margins similar in height; origin of lower margin approximately opposite 2nd dorsal-fin insertion; caudal filament long. Frontal tenaculum small; pre-pelvic tenacula with large spines along inner margin.

Body uniformly chocolate brown and skin deciduous; fin edges darker; pelvic fins brownish black. Attains 120 cm TL (including caudal filament).

DISTRIBUTION Atlantic and Pacific oceans (widespread), and Indian Ocean (not widely recorded). WIO: South Africa (off Cape Point) and Mozambique Seamount.

REMARKS Biology poorly known. Size at birth ~13 cm (body length without caudal filament); few juveniles ever collected. Primarily deep water, over upper continental slope, on or near bottom, at ~380–2 600 m, but with an unconfirmed report from 100 m deep; apparently fairly abundant where they occur. Feeds mostly on benthic invertebrates. Minor bycatch of deepwater bottom-trawl fisheries; used for its meat and as fishmeal.



Harriotta raleighana, male juvenile.
Source: SSF, drawn from Fischer in Bigelow & Schroeder 1952

GENUS ***Neoharriotta*** Bigelow & Schroeder 1950

Diagnosis as for family. Snout tip without knobs or tubercles; eyes large; tooth plates thick and ridged with hypermineralised tritors. Anal fin separated from lower caudal fin only by deep notch; upper caudal margin without denticles in males. Three species, 2 in WIO.

KEY TO SPECIES

1a	Head and body uniform chocolate brown; caudal-fin filament short, less than snout length	***N. pinnata***
1b	Body mottled grey-brown, snout and head darker; caudal-fin filament long, greater than snout length	***N. pumila***

Neoharriotta pinnata (Schnakenbeck 1931)

Sicklefin chimaera PLATE 82

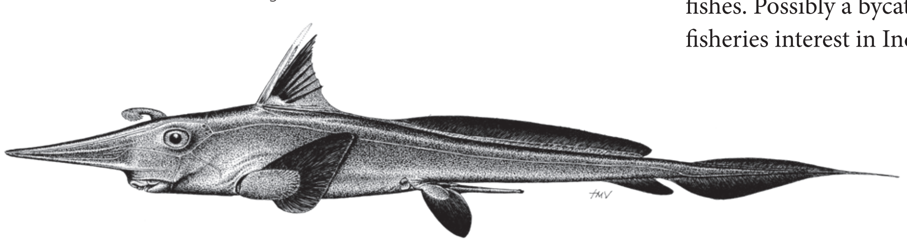
Harriotta pinnata Schnakenbeck 1931: 40, Figs. 6–9 (Walvis Bay, Namibia).
Neoharriotta pinnata: SSF No. 33.2*; Compagno *et al*. 1989*; Krefft 1990; Compagno *et al.* 1991; Didier 1995; Didier & Stehmann 1996*; Manilo & Bogorodsky 2003; Ali *et al.* 2009*; Akhilesh *et al.* 2011.

Diagnosis as for genus. Snout moderately slender, elongate, slightly flattened and blunt-tipped. Oral and preopercular lateral-line canals separated by large space. Pectoral fins short and broad. First dorsal-fin spine serrated; height of 2nd dorsal fin uniform. Pelvic fins rounded. Anal fin tall, curved. Caudal fin with short terminal filament. Frontal tenaculum of adult males very large.

Body uniformly chocolate brown. Attains 147 cm TL (including caudal filament).

DISTRIBUTION Eastern Atlantic (apparently widespread: Western Sahara to Namibia) and Indian Ocean. WIO: South Africa (off Cape Point), and Oman to India.

REMARKS Biology unknown and few adult voucher specimens have ever been collected. Probably matures at 50–55 cm (body length without caudal filament). Found in relatively shallower habitats, on continental shelf and upper slope, than other members of the family, on or near bottom, at 113–760 m. Likely feeds on small benthic invertebrates and fishes. Possibly a bycatch of deepwater fishery trawls; of some fisheries interest in India.



Neoharriotta pinnata, 76 cm (to rear of 2nd dorsal fin), male (Namibia).
Source: SSF

Neoharriotta pumila Didier & Stehmann 1996

Arabian sicklefin chimaera PLATE 82

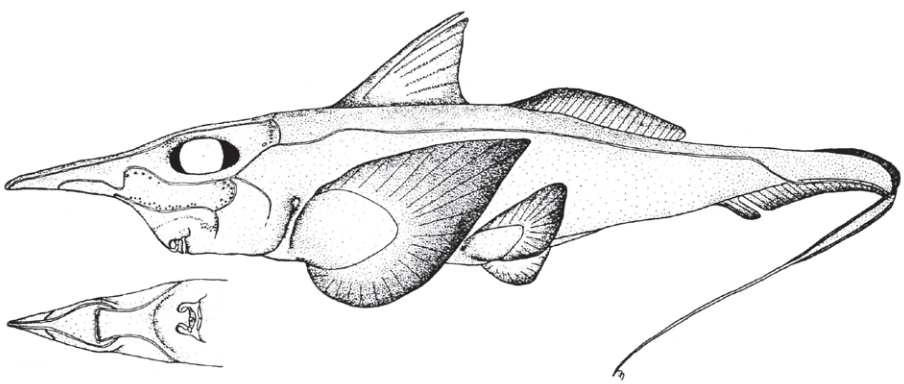
Neoharriotta pumila Didier & Stehmann 1996: 957, Figs. 2–3 (off Socotra I., Arabian Sea); Manilo & Bogorodsky 2003.

Diagnosis as for genus. Small-bodied and tapering to caudal fin with a long filament. Snout broad at base and tapering to blunt point. Eyes large and horizontally ovoid. Preopercular and horizontal lateral-line canals separated by narrow space. Pectoral fins large, rounded, broad-based. First dorsal-fin spine serrated, upper half of spine free from fin, and fin as tall as or taller than spine; 2nd dorsal fin much lower than 1st, sloping posteriorly; interdorsal space short. Dermal denticles in space between 2nd dorsal fin and upper caudal lobe in adults of both sexes. Pelvic fins more rectangular than rounded, with straight distal margin. Anal fin slender with blunt tip, fin origin behind 2nd dorsal-fin insertion. Caudal fin with long terminal filament; upper portion of fin uniform in height, and margin without denticles; lower portion taller anteriorly, its origin before 2nd dorsal-fin insertion. Pre-pelvic tenacula each with 5 small denticles on medial edge, and four rows of 4 or 5 small curved denticles on ventral surface.

Body mottled grey-brown, snout and head darker; fins dark grey to black; paler ventrally and at bases of paired fins. Attains 65 cm TL (including terminal filament).

DISTRIBUTION WIO: Somalia and Socotra (Gulf of Aden and Arabian Sea), and possibly southwestern India.

REMARKS Rare, known only from localised populations, but may have a wider distribution at greater depths; inhabits outer continental shelf and upper to middle slope, on or near bottom, at 100–1 120 m. Matures at ~16 cm (body length without caudal filament). Presumably feeds on benthic invertebrates (bivalves and polychaetes) and fishes.



Neoharriotta pumila, ~45 cm TL (including caudal filament), female paratype (Socotra).
Source: Didier & Stehmann 1996