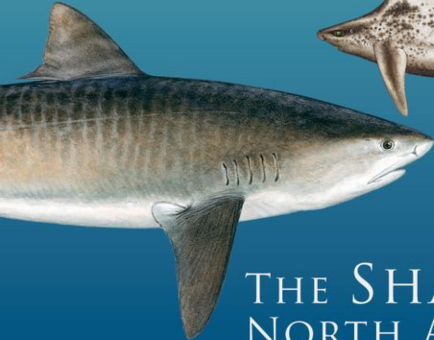


THE SHARKS OF NORTH AMERICA

JOSÉ I. CASTRO

COLOR ILLUSTRATIONS BY
DIANE ROME PEEBLES

THE SHARKS OF NORTH AMERICA

This page intentionally left blank

THE SHARKS OF NORTH AMERICA

JOSÉ I. CASTRO

COLOR ILLUSTRATIONS BY
DIANE ROME PEEBLES

MOTE MARINE LABORATORY

OXFORD
UNIVERSITY PRESS

OXFORD
UNIVERSITY PRESS

Oxford University Press, Inc., publishes works that further
Oxford University's objective of excellence
in research, scholarship, and education.

Oxford New York
Auckland Cape Town Dar es Salaam Hong Kong Karachi
Kuala Lumpur Madrid Melbourne Mexico City Nairobi
New Delhi Shanghai Taipei Toronto

With offices in
Argentina Austria Brazil Chile Czech Republic France Greece
Guatemala Hungary Italy Japan Poland Portugal Singapore
South Korea Switzerland Thailand Turkey Ukraine Vietnam

Published by Oxford University Press, Inc.
198 Madison Avenue, New York, New York 10016

www.oup.com

Library of Congress Cataloging-in-Publication Data
Castro, José I. (José Ignacio), 1948–
The sharks of North America / Jose I. Castro.
p. cm.
Includes bibliographical references and index.
ISBN 978-0-19-539294-4 (leather : alk. paper)
1. Sharks—North America. I. Title.
QL638.9.C346 2011
597.3097—dc22 2009032858

1 3 5 7 9 8 6 4 2

Printed in the United States of America
on acid-free paper

FOREWORD

In 1980 I met a young man who was visiting second-hand bookstores in Bethesda, Maryland, where I lived. He came to see me and told me he was writing a book on sharks. He had not published any papers on sharks but was writing a book on all the known sharks of North American waters! I was skeptical at first, but as we spoke I realized there was an awesome amount of knowledge about sharks, butterflies, rare books, Persian carpets, airplanes, and hunting guns in the cranial cavity behind his long, black, curly eyelashes.

When his first book came out in 1983, it was amazingly good and well received. *The Sharks of North American Waters* became a must-have item on the bookshelves of every student and specialist in sharks, including shark fishermen. José Castro even correctly predicted that the then new "Hawaiian megamouth" shark and the goblin shark would be caught in North American waters and so had included them in his book. Because most North American sharks are found in both hemispheres, this handy volume, 180 pages, 6 × 9 inches, could be taken anywhere in one's briefcase. It was crammed with information on more than 100 sharks. It was readable and accurate and had black-and-white drawings of each species.

Since then José and I have examined and dissected many rare and large sharks together, including the first female megamouth (we even shared a taste of its muscle: raw, fried, and baked by a Japanese gourmet cook). We dissected a huge basking shark in the pouring, freezing rain near Hatteras Inlet, North Carolina. We viewed live sixgill sharks from submersibles in the Cayman Islands and Bermuda. Here at Mote Marine Laboratory, I watched him elegantly dissect specimens of rare, great sharks and then take his gorgeous, colorful photographs of the whole shark, especially the reproductive system—all truly works of art. His photograph of the reproductive tract of a bigeye thresher shark—with two oophagous embryos and the eggs they were in the process of eating—is framed and hanging on my living room wall. Happily, his photo artwork is presented in more than 20 color plates in this new big book on North American sharks. These photographs are equal in beauty and accuracy to the 160+ color paintings by Diane Rome Peebles. These remarkable color plates of each shark, its teeth, and ventral views of the head were meticulously reviewed by José. It is my hope that, after a century passes, this first edition will not be taken apart by art connoisseurs as has been done with the color plates in Bleeker's *Atlas Ichthyologique*, and the text and plates, including the gorgeous, gutsy dissections, will remain intact.

At the banquet sessions of our American Elasmobranch Society meetings, the members love to affectionately kid José. We've had contests to see who could give the best imitation of José's charmingly accented voice dismissing his own artwork after he had wowed us with his color renditions of embryos *in situ* in a female shark. At our most recent meeting in Tampa in 2005, they raffled off, for a tidy sum in support of student travel, a José Castro doll in hunting clothes, carrying a camera and an address booklet. This fun doll now resides in my office.

José has expanded and updated the tremendous and pertinent information we now have on sharks, but you will need an extra suitcase to take this encyclopedic, 600-page, 10-pound treasure when you travel! I predict that there will never be another book on sharks as informative and beautiful as this one.

Genie Clark

This page intentionally left blank

PREFACE

This book is a comprehensive guide to North American sharks, summarizing the knowledge of these species through 2008. This book contains descriptions and life histories of all the species of sharks reported within 500 nautical miles of North American shores, as well as selected species from adjacent areas. The area covered includes the Arctic Ocean, the eastern Pacific from Alaska to southern Mexico, and the western Atlantic from Greenland to the Gulf of Mexico and the northern Caribbean Sea. There are 135 species accounts, each beginning with the etymology of the common and scientific names and a reference to the original description of each species. The accounts provide summaries of the biology, range, length and weight, size at maturity, mode of reproduction, brood size, size at birth, nurseries, age and growth, and relation to humans. Each species is illustrated by one or more color drawings, snout and tooth outlines, and an scanning microphotograph of the skin denticles.

This book started as a revision to my field guide, *The Sharks of North American Waters*, shortly after its publication in 1983 and was a long-term project carried out in spare time over many years. In the years after publication of the field guide, I often received two requests from users of the book. Many students and biologists requested references to source publications, so that they could obtain additional details while researching and writing papers; others simply requested that I give more details about given species. The present book is an effort to satisfy those requests. My attempt to produce a more comprehensive book, and the large body of knowledge accumulated in the last two decades, has resulted in a much larger book than I envisioned.

I started by asking, "What species of sharks inhabit North America, and what do we *really* know about them?" My goal was to publish a comprehensive and accurate book that would answer those questions. Early in the development of the book, I realized that it was not possible to rely on the literature to determine the species found in North America. Many specimens taken in our fisheries were not identified or were misidentified, and there were both unreported and undescribed species. I concluded that it would be necessary to examine the sharks actually collected in many of our fisheries and research operations throughout the continent, although the lack of deep-water fisheries in North America would greatly complicate the task. The literature would have to be examined critically, and the facts would have to be verified. I also decided that I would not copy existing illustrations, to avoid replicating errors, and found it necessary to create original illustrations based on actual specimens. Of course, this required obtaining fresh specimens of all the species covered, or at least preserved specimens in excellent condition.

Although I work for the National Oceanic and Atmospheric Administration, one of the great scientific organizations, I purposely did not seek institutional or financial support for this project. My reason for this decision was that I simply did not know how long the project would take. In all institutions, large and small, all projects must be supervised and must adhere to some schedule. I knew that if this project was subject to managerial or bureaucratic control, time limits would be imposed, and I simply did not have any idea of how long it was going to take. My concern was that a schedule, which may seem reasonable at the onset of a project, is often demonstrated by hindsight to have been overly optimistic. In this case there were too many questions that could be solved only by looking at shark specimens, and I could not predict how long it would take to obtain them. Making the illustrations alone would take years. There were myriad questions and logistical problems to be solved before the book could be finished. I did not want to be forced to publish an incomplete or rushed work just to satisfy someone else's schedule. Similarly, I decided to do the project alone, to avoid the problems of imposing my ideas on others and to avoid the dissentions of multiauthor projects. Thus, it was best to do the project by myself and on my own schedule. As it turned out, the project took well over a decade.

Along the way, the Mote Scientific Foundation offered to underwrite the color plates, and I gratefully accepted their generous offer. In the end, they covered the cost of most of the color illustrations and provided great assistance. In the long process of creating the book and illustrations, there were moments of despair, when I thought that obtaining and examining fresh specimens of all the species involved was an impossible task, or when financial considerations threatened the project. Amazingly, we obtained nearly all the needed specimens (how some rare specimens were obtained probably deserves to be told someday). The project was possible through the assistance of dozens of friends: biologists, commercial fishermen, aquarists, and sportsmen who helped me to collect specimens and data or who sent me much-needed specimens often at great trouble or financial loss. If there was ever a book that required the direct help of many people, this is it!

Since the publication of my 1983 field guide, a terrible onslaught has been unleashed upon sharks. The high price of shark fins destined for Asian markets and the depletion of bony fish stocks have combined to make sharks a highly profitable product, resulting in the rapid proliferation of shark fisheries throughout the world. These generally unrestrained fisheries have greatly reduced the populations of sharks and threaten the survival of many species. It is my hope that education, enlightenment, and appreciation of these interesting predators will induce the public to demand an end to the destruction of these great fishes. I hope that this book will contribute to that endeavor.

José I. Castro

ACKNOWLEDGMENTS

Diane Rome Peebles did the color illustrations. Diane and I had talked about the possibility of her illustrating this book in the early 1990s. Having admired her elegant work for many years, I was delighted when she agreed to undertake this project with me. Working with Diane, a consummate professional, was both an honor and a pleasure. Taryn Baacke Estell and Faith B. Keller drew most of the snout and teeth illustrations. Bryan Stone and Paul Vecsi also contributed some snout and teeth illustrations. The illustrations were prepared under my guidance, and I am responsible for any inaccuracies that may have escaped me.

Most of the illustrations were funded through a generous grant from the Mote Scientific Foundation to Mote Marine Laboratory, and for that I am grateful to Kumar Mahadevan and the late Perry W. Gilbert. It was Perry's idea that the foundation should sponsor this work, and Kumar did the rest, solving many financial problems and allowing me to proceed with the color illustrations. At Mote Marine Laboratory, Genie Clark allowed me the free use of her extensive field notes on Florida sharks and Cape Haze Marine Laboratory records. She generously shared her knowledge and friendship and encouraged me throughout the project. Bob Hueter provided two valuable assistants who helped me at different times; he also provided useful comments on the illustration of the whale shark. Peter Hull helped by securing many specimens.

In making this book I received help from many people. The late Perry Gilbert's help was significant. He was aware that I had lost my library (among other greater losses) in Miami during hurricane Andrew in 1992. Perry's generous gift of a wonderful reprint collection and numerous ichthyological books from his library allowed me to continue the work. Over the years, other friends helped me to replace my library or gave much needed references: Jim Atz, Eugene Balon, Eugenie Clark, Howard Evans, Bob Hueter, Glen Loates, Larry Page, and Bill Richards. Their help with books and reprints was invaluable and saved me considerable time. Maria Elena Ibarra, Consuelo "Coqui" Aguilar, and Gaspar Gonzales kindly provided me with a set of Felipe Poey's complete works that was most useful and enlightened me greatly.

I am also most grateful to all the friends and colleagues who helped me collect specimens and data, often at a great deal of trouble to them, and who encouraged me throughout the project: Hugo Aguirre, Alberto Amorim, the late Shelton Applegate, Jim Atz, Scott Bachman, Eugene Balon, Christine Balon, Henry "Hank" Bart, Larry Beerkircher, Maria Bello, Sally Boynton, David Brindle, Cheryl Brown, Michelle Bruni, George Burgess and the staff of the Florida Museum of Natural History, Bob Burhans, Greg Cailliet, Steve Campana, John Carlson, Jeff Carrier, Nicole Castagna, Leonardo Castillo, José Luis Castro Aguirre, Eugenie Clark, Graeme Charter, all my Chiapaneco fishermen friends, Geremy Cliff, Tristram Colkett IV, April Cook, Joao Correia, Chip Cotton, Clark and Diana Crabbe, Jerry Crow, Tobey Curtis, Dean Dougherty, Bob Davis, Cyndi Dawson, the late René de Dios, William "Trey" Driggers, Sheldon Dudley, Héctor Espinosa, Howard Evans, Manny Ezcurra, Brooke Flammang, Sarah Fretzer, John Galbraith, Jeffrey Gallant, Felipe Galván-Magaña, Jimmy Gelsleichter, R. Grant Gilmore, Ken Goldman, Dean Grubbs, Sonny Gruber, Peter Hall, Karsten Hartel, Chris Harvey-Clark, Michael and Linda Heithaus, Eric Hoffmeyer, Mauricio Hoyos, Gordon Hubbell, Hua-Hsun Hsu, Steve Kajiura, Glenda Kelly, Duncan and Carol Kniseley, Nancy Kohler, Hera Konstantinou, Jay Lamee, Jeff Landesman, Christine Light, Henry Luciano, Carl Luer, Dennis Lee, Anabela Maia, Meredith Marchioni, Jennifer Martin, Fernando Márquez, Yosuke Matsumoto, Matthew Miller, Masaki Miya, John Morrissey, Ken "Curly" Moran, John A. Moore, Jeff Morris, John A. "Jack" Musick, David McGowan, Matt McLeod, Kazuhiro Nakaya, Lisa Natanson, Cheryl Nicholson, Neil Overstrom, Ted Otis, José Luis Oviedo, Reinaldo "Ray" Pérez, Gus Pérez-Abreu, Juan Carlos Pérez-Jiménez, Andrew Piercy, Dan Pondella, Steve Poston, Gregg Poulakis, Harold "Wes" Pratt, Manny Puig, Mark Quartiano, Christopher Rackley, Mark Rackley, Sandra Raredon, Nelson E. Rios, Claudia Lorena Ruiz, Mark Sampson, Jorge Sánchez, Eric Sander, Keiichi Sato, Mike Schaadt, Ron Schatman, Ivan Schultz, Jason Seitz, Katie Shade, Robert Siders, Candance Silva, Guylaine Simard, Buck Snelson, Sandra R. Soriano, Oscar Sosa Nishizaki, Charlott Stenberg, Rick Stringer, Adam Summers, Chris Tanaka, Hisao Teshima, Taketeru Tomita, Antonio Sandes Torres, John Tyminski, Rick Waites, H. J. Walker, Tom Watts-FitzGerald, Nick Whitney, Tonya Renee Wiley, Jeff Williams, Makio Yanagisawa, Kara Yopak, and Forrest Young. I thank the Florida Institute of Oceanography, Dean Milliken, Randy Maxon, Rob Walker, and the captain and crew of RV *Suncoaster* for their support and use of their vessel, which allowed me to obtain many deep-water specimens. I thank Larry Page, George Burgess, Robert H. Robins, and the staff at the Florida Museum of Natural History for their splendid assistance with all the specimen loans, and their great camaraderie. I thank Henry "Hank" L. Bart for his assistance with specimens at the Tulane University Museum of Natural History and for being a gracious and splendid host. I thank Jorge and Lázaro Sánchez for their many courtesies at their facility, Casablanca Seafood, where we processed some very large specimens. Seven of my friends contributed a great number of specimens: George Burgess, Chip Cotton, William B. "Trey" Driggers III, John Galbraith, Rey Pérez, Juan Carlos Pérez-Jiménez, and Ron Schatman. They were the "knights in shining armor" who came to my rescue many times with the "impossible-to-get" specimens. John Galbraith, ichthyologist and naturalist extraordinaire, and Professor Kazuhiro Nakaya helped me to discriminate among the species of *Apristurus* catsharks in North America, which would have been impossible without their combined help. Given the nature of the project and the need for fresh specimens, I would have never been able to accomplish this book without the generous help of all these folks.

The use of the excellent scanning electron microscope at the Okinawa Churaumi Aquarium, through the courtesy of Senzo Uchida and Keiichi Sato, allowed me to obtain many of the images of the dermal denticles. I thank Tom Beasley and Barbara Maloney for their guidance in using the electron microscope at Florida International University. Their help was invaluable in obtaining many of the images presented here.

Beverly McMillan, Michael Heithaus, Stephen Spotte, Gregg Poulakis, Juan Carlos Pérez-Jiménez, and William B. "Trey" Driggers, III critically read the manuscript and made many valuable suggestions. Cheryl Nicholson, Katherine Shade, and Meredith Marchioni proofread the manuscript, pointing out many errors that I had missed. April Cook performed many tasks in the preparation of specimens during part of the project, and her help was invaluable. Elizabeth Simonson assisted (as a volunteer) with specimen preparation and many other organizational tasks. She was the catalyst that made many tasks possible at the end of the project. She alone was not intimidated by the prospect of going into the shark freezers looking for a long-lost specimen. The onerous and tedious task of preparing the initial bibliography fell to Sally Boynton, Esq., a long-time volunteer, who would come into my office chortling with mirth after finding some small transgression in the manuscript. Her help, support, and friendship meant a lot to me. Juan Carlos Pérez-Jiménez helped me immensely with the sharks of the Gulf of California and proofread the final bibliography. Meredith Marchioni took time from writing her dissertation to locate and organize the pen-and-ink drawings, coming to my help at various times. I also received splendid help from Mote Marine Laboratory librarian Susan Stover and the IAMSLIC[1] librarians who provided me with so many requested references. To all these great folks I express my sincere gratitude, while retaining all responsibility for all errors of fact or omission.

I thank my Japanese friends Senzo Uchida, Keiichi Sato, and Masaki Miya, who made it possible for me examine fresh goblin and frill sharks, as well as many other deep-water sharks in Japan. Senzo Uchida made it possible for me to visit Japan several times, and I learned a great deal from him and his staff at the splendid facilities of the Okinawa Churaumi Aquarium. My good friend Keiichi Sato shared his great knowledge of deep-water sharks and was always a splendid host.

I thank my friends Bob and Ida Fowler for their wonderful hospitality at their home, my favorite hideaway in Albany, Georgia, where I accomplished parts of the work. I thank Clark and Diana Crabbe for their friendship, hospitality, and splendid support at their home in Rancho El Barril, Baja California, where I had the opportunity to observe many species of sharks of the Sea of Cortez under most pleasant conditions. My friend Gerald (Gerry) Dratch was a pleasant cheerleader who always encouraged me by reminding me that we were both mortals and that I had to finish the book before one of us died. Jim Bohnsack encouraged me and did much to facilitate the project. Divina Grossman encouraged me throughout the project. Her advice and moral support meant a great deal to me.

Finally, I thank those who gave me the tools to undertake this project—first, my parents and family, who, in just a few years, planted the seed of education, which was to survive many years of separation and adversity, to germinate and bear fruit many years later. A series of gifted science and biology teachers influenced and helped me greatly from primary school (when there was no one else to help) to postgraduate training: Mr. Tabor at Citrus Grove Junior High, Mary Ellen Chestnut at Miami Senior High, E. Morton Miller and Taylor R. Alexander at the University of Miami, and, much later in graduate school, Christopher C. Koenig. John P. Wourms, and A. "Budd" Bodine were both mentors and friends at Clemson University during my doctorate there. I owe so much to all of them.

1. The International Association of Aquatic and Marine Science Libraries and Information Centers (see http://www.iamslic.org/).

CONTENTS

This page intentionally left blank

THE SHARKS OF NORTH AMERICA

This page intentionally left blank

INTRODUCTION

HOW TO USE THIS BOOK

This book uses standard dichotomous keys to help readers identify families and species of sharks. These keys are aids in shark identification that use easily observable anatomical features (e.g., fin position and shape of the teeth) or geographic range to identify families or species of sharks. Each key consists of a series of alternatives presented in numbered couplets. Starting with the first couplet, the reader should select the alternative that best matches the specimen being identified, and then follow it to the next indicated couplet, continuing the process until the family or species is identified. Once a species is reached, additional characteristics of the species may be added in parentheses to confirm the identification. These keys are not based on phylogenetic or taxonomic relationships; their design follows diagnostic convenience.

To identify and learn about a shark, first turn to the Key to the Families of North American Sharks (p. 11) to determine which family a given shark belongs to; the identification can be assisted using the figure on the right margin. Then use the key to that family to determine the species of shark. Finally, go to the indicated pages to confirm the identification and read about the species.

Description of Species Accounts This book covers 135 species of sharks, with species accounts that summarize our present knowledge of North American species. I have also included some species from adjacent areas. These are clearly marked as "extralimital species" and are included because they have been reported as occurring in North American waters due to identification errors, or are included to complete families of sharks and extend the area where this book can be useful for identifying sharks. Some accounts are brief because of our limited knowledge of the species. Statements or observations that are not the author's are followed by a bibliographic citation in parentheses. All accounts are written in the same format to facilitate comparisons, and contain the following sections:

Common name: The species accounts begin with the common English names of the species and the etymology of the name. The common names used are those designated by the American Fisheries Society (A.F.S.) in Special Publication No. 29, Common and Scientific Names of Fishes from the United States, Canada, and Mexico, sixth edition (Nelson et al. 2004). When a common name has not been designated, but a vernacular name exists, the latter is used. When no common names are in use, the name given to the species by the Food and Agriculture Organization of the United Nations (F.A.O.) is used.

Spanish name: The Spanish names given are the native names I have encountered in usage or in the literature of the Spanish Caribbean and Mexico. Some useful references for Spanish names are "*Guía para los tiburones de aguas cubanas,*" by Guitart Manday (1968); *Lista de nombres científicos y comunes de peces marinos cubanos (Nomenclator),* by Rodríguez et al. (1984); *Guía de campo para la identificación de especies de tiburones y cazones en la Sonda de Campeche,* by Uribe Martínez (1990); *Guía para la identificación de las especies de tiburones de importancia comercial del Golfo de México* by this author (Castro 2001a); and *Guía para la identificación de las especies de tiburones de importancia comercial del Océano Pacífico* (Castro 2001b). I also provide the Spanish names given by the American Fisheries Society (Nelson et al. 2004), although these names often differ widely from the names actually used in the Spanish Americas.

To placate editors who thought this work was already too long, I have explained only a few of the Spanish etymologies, primarily when a colorful name may have been misunderstood by nonnative Spanish speakers, or when I just could not resist explaining it.

Scientific name: The scientific name given is that currently used in the scientific literature. Each scientific name consists of two words in Latin or in latinized form. The first word is the genus to which the species belongs, or generic name; the second word is the species or specific name. A scientific name includes the last name of the author or authors that formally described the species, and the year that the scientific name was published. Some authors' names are enclosed in parentheses, indicating that the author originally placed the species in a different genus than the one to which it is presently assigned. The scientific name is followed by a reference to the publication where it was first published. The etymology of each scientific name is given in an attempt to explain the name. Many different sources were used in deciphering scientific names; the most useful of these is Jaeger's *A Source-Book of Biological Names and Terms,* third edition (1962).

Synonyms: Most sharks have several obsolete scientific names, published after the original, accepted description of the shark. These names, known as synonyms, are invalid as scientific names. Synonyms are often encountered in older literature, and a complete list would cover many pages. These synonyms are of interest to specialists and students and are already available in publications by Bigelow and Schroeder (1948) and Compagno (1984 a, b). Thus, I have not attempted to repeat the extensive synonymies found in those works. I have merely listed the more common synonyms that may be encountered by the reader.

Identification: The identification section includes the most important, diagnostic, anatomical characteristics used to recognize the species, with the key identifying marks in italics. The shape and number of teeth are given because these are often diagnostic. The shape of the teeth is also useful in elucidating the feeding habits of a species. The number of teeth in each side of the upper jaw is written before the number of teeth in each side of the lower jaw. For example, U: 12–1–12, L: 15 to 17–2–15 to 17 indicates 12 teeth on the animal's left side of the upper jaw, 1 tooth in the center of the jaw (symphysis), and 12 teeth on the right side of the upper jaw; 15 to 17 teeth on the left side of the lower jaw, 2 teeth in the center, and 15 to 17 on the right side. In cases where the center of the jaw cannot be distinguished readily, the total number of teeth in that jaw is indicated. For example, U: 24 to 30, L: 28 to 32 indicates that there are 24 to 30 teeth in the upper jaw and 28 to 32 in the lower jaw. The shape of the dermal denticles is given because it is often useful to distinguish among species. The dermal denticles pictured are from the flanks just below the first dorsal fin. The shape of the denticles varies all over the body. The denticles protect the shark with a tough skin and have other important properties. Their primary function appears to be, in many cases, to provide laminar flow of the water over the body, minimizing drag and allowing the shark to move effortlessly and quietly through the water. The shape of the denticles can be species specific and in some cases can be a great aid to identification. In some cases sharks of a given genus can have similar denticles. The denticles are covered by a thin layer of skin and mucus, but that layer is sometimes lost upon preservation. The denticles of neonates and juveniles are often different from those of adults. The denticles shown here are from the illustrated specimens.

The color of the illustrations is that of live or freshly caught specimens, since the coloration of most sharks will fade or dull shortly after death. I have attempted to illustrate sharks in their fresh coloration, often going to great lengths to verify these colors. However, the coloration of most sharks is variable, often changing with light conditions and angle of view, and often varying from one specimen to another. In the cases of some deep-water sharks, it is possible, or even likely, that we may have illustrated sharks that I considered fresh but were actually faded specimens.

The colors of sharks (or other animals) can be caused by either structural colors or pigments. Structural colors result from the interaction of light and thin surface tissues, and are responsible for the iridescence[1] of some sharks when fresh out of the water. These colors change with the angle of view or light and can be easily destroyed by simply scratching the skin or by a jet of water. Different colors may be reflected in different directions by surface structures.[2] As tissues dry or shrivel up, iridescence disappears. By contrast, colors due to pigments do not change with the direction of viewing and fade only slowly as the pigment decays. Pigments are organic compounds found in or among the animal's cells and can serve many different purposes, such as camouflage, protection against ultraviolet rays, or adding strength to structures. Pigments can be endogenous (produced by the animal) or exogenous (acquired, usually through the diet). The golden hammerhead is an example of a species with both structural and pigmentary colors. When the shark is fresh out of the water, it has an overall iridescence that changes with the viewing angle. This is due to interference or diffraction of light in the thin outer skin. The golden hammerhead also has yellow and orange pigments in and among its skin cells. These pigments are acquired through the diet (see p. 526) and cause its bright yellow or orange colors. These pigmentary colors look the same regardless of angle of view and cannot be scratched or washed off. Some pigmentary colors endure for a long time and can even survive freezing for many days.

1. Iridescence (from the Greek *iris,* the rainbow) "is the phenomenon of glittering with different colors that change according to the angle from which the object is seen" (Fox and Vevers 1960: 5).

2. A discussion of this phenomenon is beyond the scope of this book; the reader may refer to texts such as *The Nature of Animal Colours* by H. Munro Fox and G. Vevers (1960) or to *Animal Biochromes and Structural Colors* by D. L. Fox (1976).

Similar species: Similar species occurring in the same area are listed with their distinguishing characteristics. The most similar species is listed first, and the least similar is listed last.

Range: The range given for a species is its worldwide distribution, the known or approximate limits of its North American distribution, and areas where the species may be locally common. A species can be referred to as polar, subpolar, temperate, subtropical, or tropical, depending on the waters it inhabits. Polar waters are those where the surface temperature is usually below 5°C. In polar areas, or in seas influenced by polar currents, bottom temperatures as low as –1°C can occur, due to the presence of salt in seawater, which depresses the freezing point. Subpolar waters range from 5 to 10°C. Temperate waters include a wide zone, ranging from 10°C on the polar side to 20°C on the side toward the equator. Those waters in the warmer part of the temperate zone are called warm-temperate; those on the polar side are referred to as cold-temperate. Subtropical waters range from 15 to 30°C. Tropical waters form two wide zones, one on each side of the Equator, where the surface temperature is 25°C or higher.

The range of a species is a three-dimensional space determined by its tolerance limits to physical factors. Temperature is one of the most important factors affecting the distribution of sharks; it usually decreases rapidly with depth, from maxima of 25–30°C at the surface to 2°C at depths greater than 2,000 m. The average temperatures at different depths for the oceans as a whole, according to Murray and Hjort (1912), are as follows:

Meters	Degrees Centigrade
183	15.95
366	10.05
549	7.05
732	5.44
1,097	3.89
2,012	2.28
2,743	1.83
4,023	1.78

Whereas the temperature of deep waters is generally uniform and stable regardless of latitude or season, the temperature of surface waters is highly variable, changing with latitude and season. Thus, species inhabiting surface waters are often migratory and move about seasonally seeking favorable conditions, while species inhabiting deep waters live under stable conditions with few barriers to their distribution and thus are often widely distributed. In temperate latitudes of the Northern Hemisphere, the warmest temperatures are found close to shore during summer. In winter, coastal waters can cool off rapidly, while offshore waters remain warmer and more stable. It follows that a species adapted to warm waters may be found close to shore in the northern parts of its range during the summer; when the temperature begins to fall in autumn, it may seek warmer offshore waters or migrate southward. A cool-water-adapted species may be found close to the surface in the northern parts of its range, while in the southern parts it may inhabit much deeper waters where correspondingly cooler temperatures are found.

Size and weight: This section gives representative sizes and weights for the species and its maximum known size. The length given is total length, which is measured in a straight line between perpendiculars, from the tip of the snout to the tip of the tail at its maximum extension (see figure X). Length measurements are in centimeters (cm), or in millimeters (mm) for very small structures or small embryos. Occasionally, I have used meters as measurement units for the largest sharks. Weights are usually given in kilograms (kg). In a few cases, I have given the fork length or the precaudal length of specimens when quoting works using those measurements, and when the measurement could not be accurately converted to total length.

Biology: The general section on biology gives a summary of habitat, including depth and temperature preferences, habits, diet, and migrations.

Size at maturity: This section summarizes the size at which males and females become sexually mature, giving the methods used to determine maturity.

Reproduction: The section on reproduction gives mode of reproduction, mating and birth seasons, length of the gestation period, duration of the reproductive cycle, size of the young at birth, and brood[3] size. When the size of the young at birth is unknown, the size of the smallest free-swimming specimen known is given. See Appendix 1 for more on shark reproduction.

3. Throughout this book, I use the terms "young" and "brood," purposely avoiding the terms "pups" and "litter" that prevail throughout the elasmobranch literature. Pups are the young of certain mammals, such as canines and pinnipeds, and litter refers to the offspring produced at one birth by a multiparous mammal. Brood is the traditional term for the progeny of fishes and birds. Those who insist on using definitions other than those provided by dictionaries can claim that the terms "pup" and "litter" are well entrenched in the elasmobranch literature or can advocate the Humpy Dumpy rule: "'When *I* use a word,' Humpty Dumpy said, in a rather scornful tone, 'it means just what I choose it to mean—neither more nor less'" (Carroll 1936, p. 214).

Nurseries: Nursery areas, or simply nurseries, are geographically discrete parts of the species range where the gravid females deliver their young or deposit their eggs and where the young spend their first weeks, months, or years (Castro 1993b). Nursery areas are often in shallow coastal areas of high productivity, such as *Spartina* marshes and mangroves, where prey is abundant and where large predators are scarce.

The use of nursery areas by elasmobranchs has been known since ancient times. Aristotle first recorded, in his *Historia Animalium* (probably written around 343 B.C.) that "The Selachia come in from the high seas and out of deep water towards land and produce their young there; this is for the sake of the warmth and because they are concerned for the safety of their young" (Aristotle 1970: 265). Little else was said about the subject for the next 2,000 years.

Age and growth: The life span of sharks can be determined by keeping them in captivity, by tagging, or, more commonly, by counting growth rings in their vertebrae or spines and estimating the age. Only a few species of sharks have been kept in captivity for long periods of time. When sharks have been captured young and have lived in captivity for prolonged periods, a rough idea of their potential life span can be obtained. Although keeping sharks in captivity for many years is a difficult feat, some sharks have lived for decades in captivity, indicating that they have long life spans. Unfortunately, most aquaria do not keep accurate records of the life span of their captive sharks, and valuable data on the longevity of sharks is lost. Tagging sharks with long-lasting tags that are not easily shed or rejected by the shark has produced estimates of longevity for some species. When a shark is tagged, if the tag is not shed, and if the shark is recaptured many years later, a rough estimate of its life span can be obtained. When a large number of tagged sharks of a given species are recaptured, one begins to get an idea of the possible life span, assuming that the tag does not decrease the life span. For example, more than 60,000 blue sharks have been tagged by the National Marine Fisheries Service's Cooperative Shark Tagging Program over the last few decades (Kohler et al. 1998). The longest period between tagging and recovery is 8.5 years. Thus, if the sharks were tagged when only a few years of age, it is likely that the maximum life span of the blue shark is about 15–20 years.

The most commonly used method for aging sharks is to count the number of growth bands that sharks periodically deposit in their vertebrae or spines. These rings can be visually counted, usually after the rings have been enhanced with dyes, or viewed under X-rays. If the rate at which the shark produces the growth rings is determined, one can then estimate the age. When a shark is tagged and at the same time injected with the antibiotic oxytetracycline, a fluorescent ring is deposited on the vertebrae. If the shark is recaptured at a later time and its vertebrae are recovered, the number of rings formed after the deposition of the tetracycline ring can be used to confirm the rate of ring deposition and the age of the shark. When the rate of ring deposition is confirmed by injection with tetracycline or any other method, the age estimate is said to be "validated." Although there are many age estimates for many species of sharks, few estimates have been validated. To further complicate the situation, it is possible, and even likely, that some sharks may deposit growth rings regularly during their juvenile stage and then stop depositing such rings after maturation, or deposit them at irregular periods. Age determination and validation of age estimates are dynamic areas of shark research, and much remains to be learned.

Relation to humans: This section summarizes the interactions of humans with the species, such as commercial exploitation, uses of the species, and protected status.

Illustrations Each shark species is illustrated by one or more profile figures and outlines of the snout, upper and lower teeth, and dermal denticles. The left side of the shark is illustrated, as is customary in the ichthyological literature, with the pectoral and pelvic fins depressed to show their shape and relationship to the other fins. Diane Rome Peebles prepared all of the color illustrations. The illustrations were generally prepared from fresh specimens. It was our goal to show the colors of live or fresh specimens. Whenever possible, each specimen was photographed soon after capture. In the early part of the project, I used Kodachrome 64 film to ensure color fidelity. As this film became difficult to obtain, I switched to Fujichrome Velvia and eventually to digital Nikon cameras. Each specimen was photographed in profile and in anatomical detail. Some 60 standard measurements were taken on each specimen, and proportions were calculated. The specimen was then forwarded to the illustrator for her examination. She then prepared a profile outline based on the specimen, the photographs, and the proportional measurements. The outline was then sent to me for checking against the photographs and proportional measurements. The proportions in the outline had to be within 1% of the proportions previously calculated for the specimen. After the profile outline was accepted, we agreed on a color scheme, and then the illustration could be prepared.

Some sharks become severely distorted when taken out of the supporting water. When taking profile photographs, with the shark on its right side, every attempt was made to support the shark being photographed to avoid a lateral flattening. This flattening was more pronounced in large or heavy sharks and in deep-water species. Although we attempted to avoid the resulting distortion, some illustrations may show a shark as having a deeper body than would be observed when alive in the water. All the illustrations were prepared under my direction or supervision, and I am responsible for any errors or inaccuracies.

The outline drawings of snouts, teeth, and denticles were prepared from the actual snouts and teeth. Tooth sets were prepared from the jaws of the specimens illustrated. The teeth were separated and placed on a cardboard backing. Their outlines were then traced or drawn free-hand. The dermal denticles illustrated were taken from an area just below the first dorsal fin and were photographed using scanning electron microscopes.

Glossary A glossary at the end of the book explains selected words that may not be familiar to the casual reader.

Bibliography The references cited in the text are listed in the back of the book. Entries are listed alphabetically under the first author's last name(s). Please note that, for Spanish authors, it is customary to use two last names, the first last name being the patronymic. For example, in Juan Carlos Perez Delgado, Perez is the patronymic. In English literature, this person's name would often be indexed as Delgado, omitting the patronymic, thus corrupting the name. To preserve the correct names, I have treated such Spanish last names as if they were hyphenated last names.

THE KNOWLEDGE AND STUDY OF SHARKS

The knowledge of sharks has lagged considerably behind that of bony fishes. There are several reasons for this. First, fishes were studied because of their commercial value as food or sport, and it was desirable to know their life histories to know when and where to find them. The impetus of commercial value ensured that funds were allocated to scientific studies on commercially important species. Sharks usually lacked commercial value because they were considered unappetizing due to their often unpleasant smell, caused by the presence of urea and trimethylamine in their blood. Consequently, most ichthyologists studied commercially important bony fishes and generally ignored elasmobranch fishes. Classical books on fishes devoted only a few pages to the study of sharks. For example, the great book *Fishes* by David Starr Jordan (1907), used to train ichthyologists for decades, covers all the elasmobranchs in only 37 of its 789 pages. Thus, the study of sharks was often left to the self-trained.

Numerous logistical problems make the study of sharks difficult. The large size attained by many species of sharks often makes it very difficult for biologists to study them. Large sharks are usually difficult for fishermen to bring back to port, and many rare or unusual specimens are not boated or are discarded overboard. Even when specimens are obtained by scientists, their large size often prevents them from being preserved, even in museum collections. In commercial fisheries, it is difficult for scientists to examine sharks because they are typically gutted, finned, or discarded quickly after capture. Thus, biologists wishing to study sharks must often examine them at sea, because the gutted carcasses brought back to port yield little biological data. Today, a multitude of fishing regulations prevent or discourage fishermen from bringing back rare or unusual sharks found dead on their lines. Thus, these specimens are discarded back into the sea and the opportunity to learn about them is lost.

Sharks are often fast-moving and wide-ranging fishes that cannot easily be studied in their environment. The status of our underwater technologies prevents us from observing and studying sharks in their environments, as we do with land animals or even some marine bony fishes. In most cases we are able to obtain only brief glances of these fishes or at best a few minutes of observation. Observations in captivity are also difficult because only a relatively few species of sharks can be maintained for long periods of time in present-day aquaria. Although much has been learned about the behavior of small bony fishes in captivity, attempting to study the behavior of most sharks in aquaria is akin to trying to study gorilla behavior by watching gorillas confined to small cages. Because of the problems outlined above, much of what is learned about sharks today is still inferred from dissection of dead specimens. Although some small sharks could be studied in aquaria, little has been published on sharks based on captive studies. The interesting behavioral study of captive bonnetheads by Myrberg and Gruber (1974) seems to be the only one of its kind.

In the late 1970s and early 1980s, shark fishing tournaments became very popular along the eastern United States, probably influenced by Peter Benchley's 1974 popular book and movies about a man-eating shark. At about the same time, commercial shark fisheries started to develop in the southeastern United States and throughout the world, engendered by the rising price of shark fins and declining stocks of other fishes. Since 1990 the commercial value of sharks has increased dramatically because of the reduction in catches of bony fishes and the increasing demand for shark fins in Asia. (The fins are,an essential ingredient in the traditional Chinese shark fin soup, and their value exceeds the value of the flesh of a shark). With the impetus of commercial shark fisheries and the popular interest in sharks, the desire and need for information on sharks grew. As shark fisheries grew unrestrained, the need for regulation became evident, which in turn demanded more knowledge of sharks. These factors engendered a new interest in sharks, and more biologists started to study sharks. At present there is great commercial and scientific interest in sharks.

THE SHARK LITERATURE

I have reviewed the relevant scientific literature to the best of my ability, making every effort to review all the articles on each North American species. The overall quality of the shark literature is poor. Confusion about species or specific names was common until the middle of the twentieth century. The publication of Bigelow and Schroeder's (1948) monumental work on sharks of the western North Atlantic solved many of the existing identification problems. However, considerable confusion remained about the identity and species names of hammerheads, requiem sharks, and squaloid sharks until relatively recent times. The taxonomy of the hammerheads fluctuated until the publication of Gilbert's (1967) revision of the family, although questions about the identity of some hammerheads still remain. The taxonomy of the requiem sharks of the genus *Carcharhinus* was not settled until the publication of Garrick's (1982, 1985) excellent reviews. Thus, the older literature must be used with caution unless the species identity can be verified. Considerable confusion still exists today about the species in many genera, such as *Centrophorus, Mustelus,* and *Apristurus.*

The shark literature up to the 1980s suffered from a perennial lack of qualified "reviewers."[4] Because there were few biologists who had studied sharks, manuscripts were often reviewed by ichthyologists who knew little about sharks. Consequently, many flawed articles have been published, containing much misinformation and misleading concepts that became established lore. The reader should also be aware that, because of the small number of scientists involved and the logistical difficulties in working with sharks, there is little verification of published works, so erroneous information, once published, tends to survive for a long time.

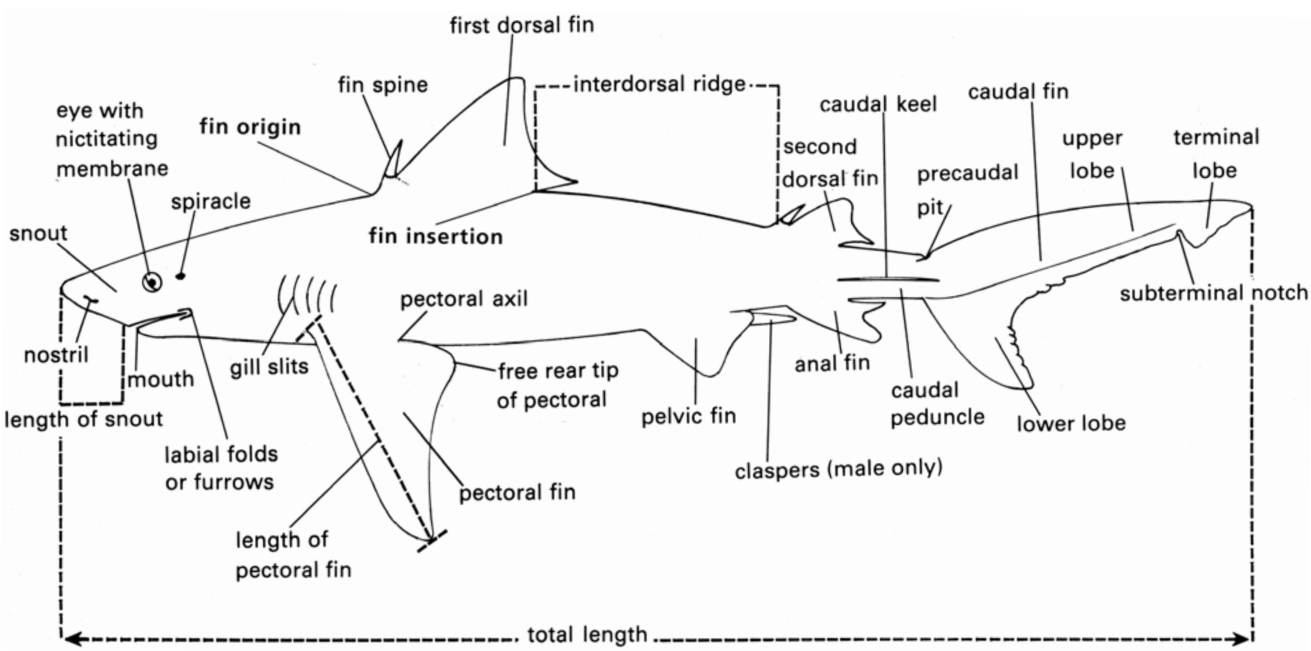
Even today, the lack of reviewers qualified to critically read articles on sharks continues to bedevil journal editors. Even the modern literature must be read with caution, as I have seen numerous recent articles and theses where common species have been misidentified, judging by the accompanying illustrations. The problems of the current literature are not limited to the usual identification problems or lack of qualified reviewers. Today there is steep competition for manuscripts among the numerous journals, and some editors are compelled to fill a journal issue with many flawed articles. I know of several recently published articles that had been rejected by various independent reviewers but were published nevertheless, probably due to the editorial need to fill a journal issue. Another unfortunate trend of the current shark literature is the publication of much "armchair" research. The current interest in sharks, combined with the increasing logistical and legal difficulties in obtaining the necessary study specimens, has engendered numerous "armchair" studies by authors lacking firsthand knowledge of sharks, who did not examine any specimens, or who used questionable data collected by others in the distant past. Thus, even the current literature must be examined critically by the reader before it is accepted. I have attempted to rectify the numerous errors I found in the literature, providing the necessary evidence to justify my emendations. I do not claim to have corrected all the misinformation in the shark literature.

In this book I have cited references and justified, qualified, or explained nearly every statement in the species accounts. I have attempted to give evidence for most of my statements, writing in such a way that the reader can follow the logic behind the facts or conclusions stated. This may cause the writing to sometimes appear verbose and long-winded, and has resulted in a book much larger than I had envisioned.

4. When articles are submitted to a scientific journal, it is customary to send them for review to two or more qualified "reviewers" or "referees," who check it for scientific merit and accuracy. The reviewers recommend to the editor to accept the article for publication as it is, to accept it conditionally pending a revision, or to reject it entirely, based on their evaluations of its merit. Journals that publish articles so reviewed are said to be "peer reviewed," and this is the standard of most scientific disciplines. This system works well only when the editors make an effort to find qualified, unbiased, and knowledgeable reviewers, and when the reviewers take the time to carefully evaluate a manuscript. Lazy editors, who ignore reviewer's recommendations just to fill the journal issue, or ignorant and biased reviewers often cause the system to fail and cause bad science and misinformation to be published or may keep worthy articles from being published. The peer-review system often works poorly with articles that challenge accepted dogmas (which history sometimes demonstrates to be wrong!), causing articles that push the frontiers of knowledge to be rejected. Nevertheless, this system is necessary and valuable in the dissemination of knowledge.

Articles that are not "peer reviewed," such as project reports, "working documents," or articles published in newsletters and magazines, are often referred to as the "gray literature." I have generally avoided using these.

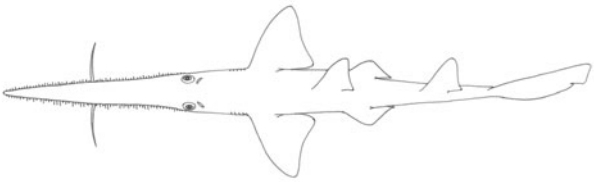
This page intentionally left blank



Parts and measurements of a shark

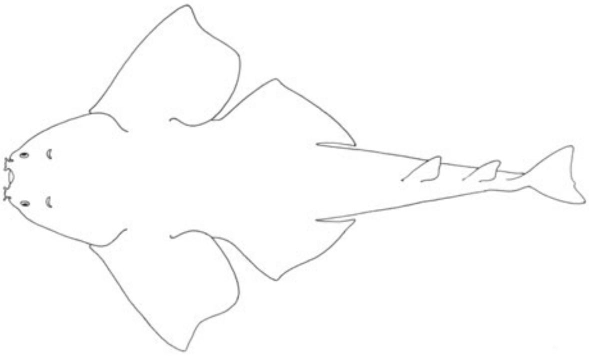
A KEY TO THE FAMILIES OF NORTH AMERICAN SHARKS

1a. Snout elongated into a flat, sawlike blade with teeth and two long barbels on the ventral surface...**PRISTIOPHORIDAE**[1] Sawsharks (p. 159)



1b. Snout without a flat, sawlike blade 2

2a. Body flattened and skatelike, eyes on top of the head and two large spiracles behind the eyes .... **SQUATINIDAE,** Angel sharks (p. 162)



2b. Body not flattened, eyes on the side of the head 3

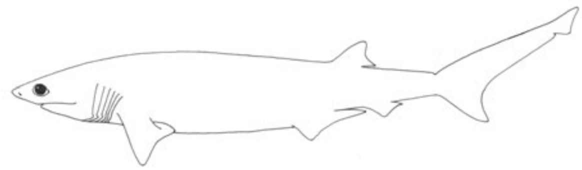
3a. Gill slits 6 or 7, only one dorsal fin 4

3b. Gill slits 5, two dorsal fins 5

1. The sawsharks are small deep-water sharks and should not be confused with the shallow-water sawfishes. The sawfishes are sharklike rays and are among the largest elasmobranchs. The sawfishes have ventral gill slits and pectoral fins that arise from the head far anterior to the dorsal fins. They also lack the nasal barbels on the underside of the snout. Sawfishes are endangered species and may not be taken.

4a. Mouth terminal, first gill slit continuous under throat................**CHLAMYDOSELACHIDAE,** Frill shark (p. 21)

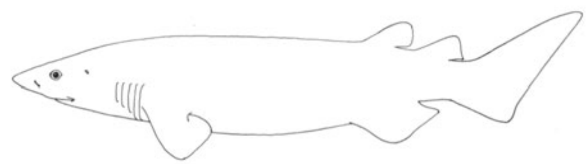
4b. Snout projecting ahead of mouth, first pair of gill slits not continuous under throat..**HEXANCHIDAE,** Cowsharks (p. 26)



5a. Anal fin absent.. 6

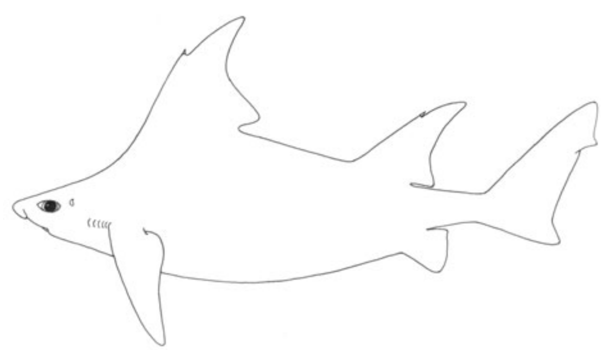
5b. Anal fin present 13

6a. First dorsal fin originating well behind the origin of the pelvic fins, skin covered with large, thornlike denticles (dorsal fins without spines) ....**ECHINORHINIDAE,** Bramble sharks (p. 42)



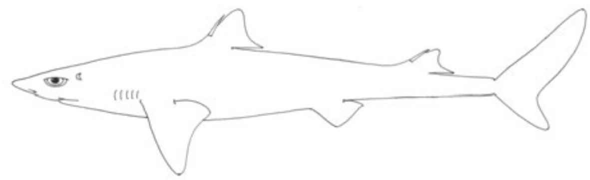
6b. First dorsal fin originating ahead of origin of pelvic fins; skin lacking large, thornlike denticles 7

7a. Trunk triangular in cross section; first dorsal fin originating over pectoral anterior base, first dorsal fin larger and longer than pectoral fin, with strongly falcate rear margins (large dorsal spines embedded in the skin, with only the tips showing)... **OXYNOTIDAE,** Rough sharks (p. 137)



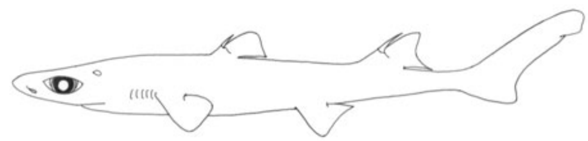
7b. Trunk rounded or oval in cross section, first dorsal fin originating behind pectoral fin axil, first dorsal fin smaller than pectoral fin, with straight, rounded, or weakly falcate margins... 8

8a. Teeth similar in both jaws, but may be larger in lower jaw, with a single, bladelike, oblique cusp .... **SQUALIDAE,** Dogfishes (p. 50)



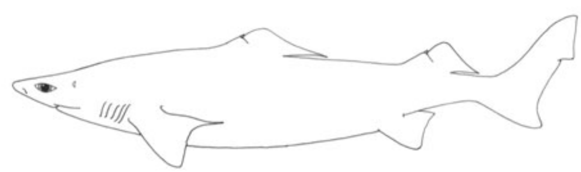
8b. Teeth dissimilar in both jaws or with several cusps (a large central cusp with lateral cusplets)....................................... 9

9a. Upper teeth with several cusps (a large central cusp with lateral cusplets), small shark less than 1 m, coloration uniformly black or with black undersides.. **ETMOPTERIDAE,** Black dogfishes and Lanternsharks (p. 91)



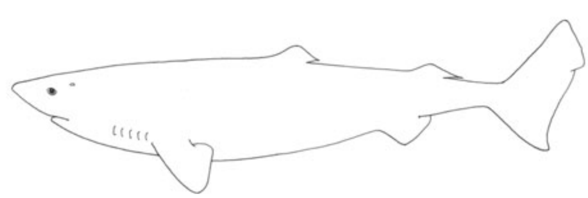
9b. Upper teeth with a single cusp.. 10

10a. Pectoral fin free, rear tip pointed (often drawn in to a long pointed lobe); a series of grooves on throat behind mouth; OR snout very long, its length greater than distance from mouth to pectoral fin origin.. **CENTROPHORIDAE,** Gulpers and birdbeak dogfishes (p. 67)



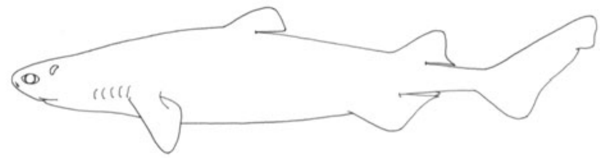
10b. Pectoral fin free, rear tip rounded; throat area smooth, lacking grooves behind mouth; snout short, its length shorter than distance from mouth to pectoral fin origin 11

11a. Second dorsal fin with a spine............... **SOMNIOSIDAE** (in part), Genera *Scymnodon* and *Centroscymnus* (p. 115)

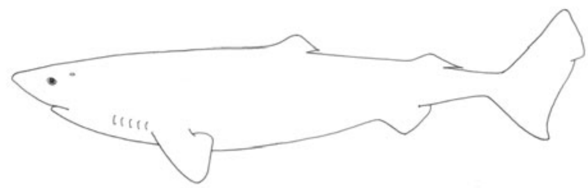


11b. Second dorsal fin spineless.. 12

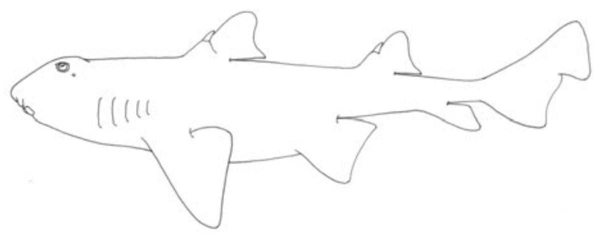
12a. Snout-to-eye distance equal to 1–2 eye diameters or less, length of first dorsal fin base smaller than second dorsal fin base (usually very small sharks except for *Dalatias*)................**DALATIIDAE,** kitefin, cookiecutter, and pygmy sharks (p. 140)



12b. Snout-to-eye distance at least 3 eye diameters, length of dorsal fin bases about equal or first dorsal fin base greater than second dorsal fin base (often giant sharks, with one exception) ....**SOMNIOSIDAE** (in part), Genus *Somniosus,* sleeper sharks (p. 115)



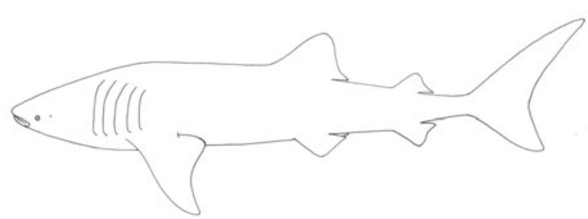
13a. Both dorsal fins with a spine..**HETERODONTIDAE,** Bullhead sharks (p. 174)



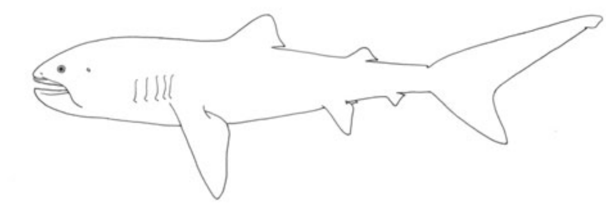
13b. Dorsal fins without spines.. 14

14a. Mouth terminal, nearly even with tip of snout.. 15
14b. Mouth ventral, snout projecting well ahead of mouth... 16

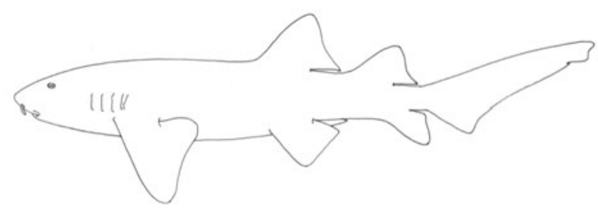
15a. Body covered with white spots..**RHINCODONTIDAE,** Whale shark (p. 193)



15b. Body not covered with white spots (white band above upper lip, minute teeth) .... **MEGACHASMIDAE,** Megamouth shark (p. 225)



16a Nasal barbels present (first dorsal fin over pelvic fin) .... **GINGLYMOSTOMATIDAE,** Nurse sharks (p. 183)

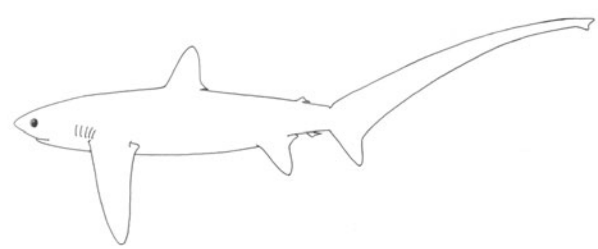


16b. Nasal barbels absent.. 17

17a. Snout elongated into long, flat blade; anal fin much larger than first dorsal fin .... **MITSUKURINIDAE,** Goblin shark (p. 201)

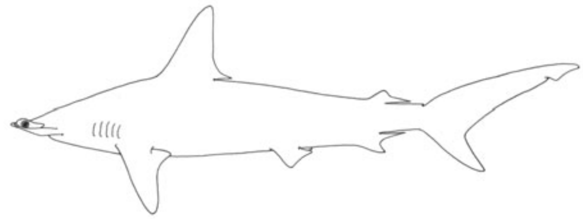
17b. Snout not flattened into a flat blade, anal fin smaller than first dorsal fin 18

18a. Caudal fin as long as the rest of the body .... **ALOPIIDAE,** Thresher sharks (p. 231)



18b. Caudal fin shorter than half the body length 19

19a. Head flattened, shovel or hammer shaped (eyes at ends of lobes) ......**SPHYRNIDAE,** Hammerhead sharks (p. 504)

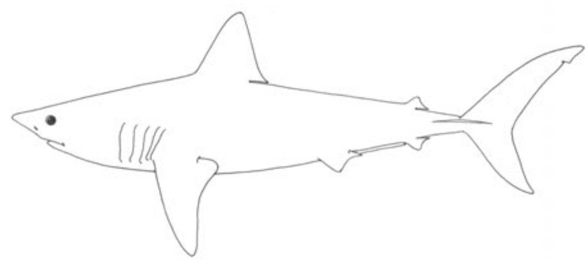


19b. Head not flattened, not hammer or shovel shaped 20

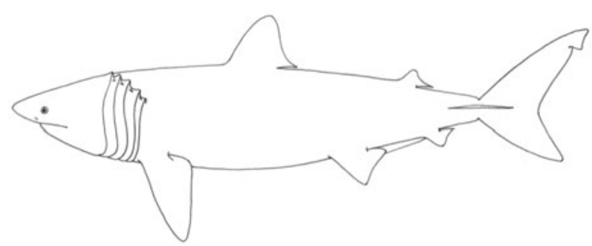
20a. Caudal peduncle with pronounced lateral keels, lunate tail with nearly equal lobes.. 21

20b. Caudal peduncle without lateral keels, heterocercal tail with one lobe much larger than the other........................... 22

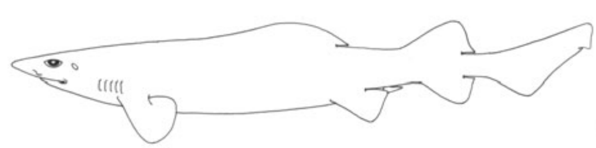
21a. Teeth large and few in number, gill slits not extending to the upper surface of head, no gill rakers on the internal gill arches ....**LAMNIDAE,** Mackerel sharks (p. 256)



21b. Teeth minute and numerous, gill slits extending on to the upper surface of head (black gill rakers usually present on the internal gill arches) ....**CETORHINIDAE,** Basking shark (p. 248)



22a. First dorsal fin much longer (six or seven times) than high.............**PSEUDOTRIAKIDAE,** False catshark (p. 352)

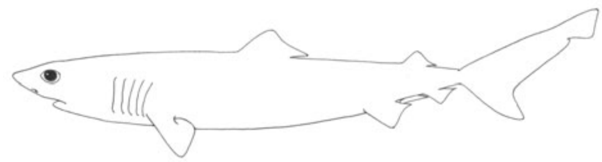


22b. First dorsal fin not longer than high.. 23

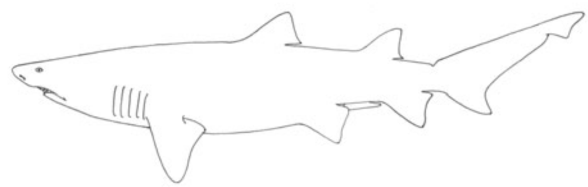
23a. Fifth gill slit anterior to pectoral fin base, eyes without a nictitating eyelid 24

23b. Fifth gill slit over or posterior to pectoral fin base, eye with a nictitating eyelid 25

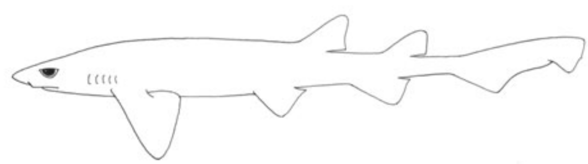
24a. Eyes very large (horizontal diameter about half the length of the first gill slit), lower precaudal pit present ....
.... **PSEUDOCARCHARIIDAE,** Crocodile shark (p. 221)



24b. Eyes small (horizontal diameter of eye less than one half the length of the first gill slit), lower precaudal pit absent ......
.... **ODONTASPIDIDAE,** Sand tiger and ragged tooth sharks (p. 206)

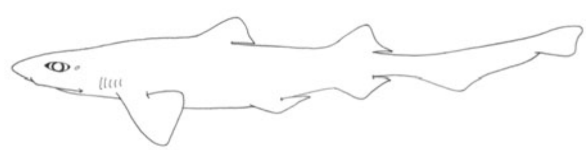


25a. First dorsal fin origin over or behind pelvic fin base .... **SCYLIORHINIDAE,** Catsharks (p. 290)



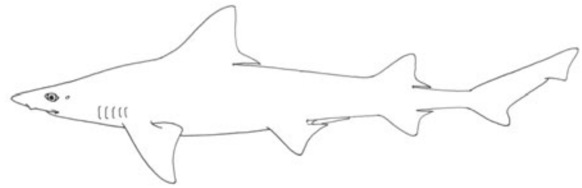
25b. First dorsal fin origin anterior to pelvic fin base 26

26a. First dorsal fin height less than second dorsal fin height, the midpoint of first dorsal fin base closer to pelvic fins origin than to pectoral fin axil (a small shark less than 50 cm) .... **PROSCYLLIDAE,** Ribbontail catsharks (p. 349)

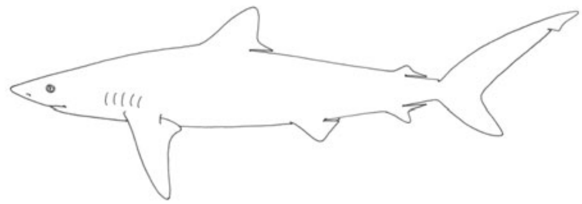


26b First dorsal fin height greater than second dorsal fin height.. 27

27a. Precaudal pit absent.. **TRIAKIDAE,** Hound sharks (p. 357)



27b. Precaudal pit present ....**CARCHARHINIDAE,** Requiem sharks (p. 388)



SPECIES ACCOUNTS

FAMILY CHLAMYDOSELACHIDAE

The Frill Shark

The family Chlamydoselachidae includes a single species, the frill shark, the most primitive living shark. It is an eel-like shark with a large terminal mouth, a very flexible, uncalcified skeleton, and a single dorsal fin set far back on the body. The frill shark is one of the deepest dwelling sharks and, although widely distributed, is a rare catch. The existence of a second species of frill shark inhabiting South African waters has been suggested (Compagno et al. 2005) but has not been described.

FRILL SHARK

Chlamydoselachus anguineus Garman, 1884

Fig. 1a. *Chlamydoselachus anguineus*, frill shark, female, 179 cm, from southern New England (39°57′ N, 71°00′ W; Walter Tate, collector; MCZ # 153745, courtesy of Karsten Hartel).

Common name Frill shark, an allusion to the appearance of the head and its large gill slits, which encircle the head, forming a frill.

Spanish name The species lacks a vernacular name in the Spanish Caribbean. The A.F.S. name is *tiburón anguila.*

Scientific name *Chlamydoselachus anguineus* Garman, 1884, in *Bulletin of the Essex Institute* 16: 47–55, fig. 10. The original description is brief but was soon followed by a more comprehensive version (Garman 1885). According to Garman, *Chlamydoselachus* means "the snake-like frilled shark," from the Greek *chlamydos,* cloak or mantle, an allusion to the gill covers that fit like a cloak or frill around the animal's throat, and the Greek *selachus,* shark; *anguineus:* snakelike, from the Latin *anguis,* a snake.

Synonyms None.

Identification The *eel-like* frill shark has a *terminal mouth* with long jaws, six large gill slits with large gill covers, and a single dorsal fin set far back, posterior to the pelvic fins. The lower jaw extends almost to the tip of the snout, creating an enormous gape, and *the first pair of gills is continuous across the throat.* The teeth have *three large, fanglike, inwardly directed cusps,* with an additional minute cusp on each side of the central cusp. The teeth form interlocking, longitudinal rows and are alike in both jaws. Tooth number varies, averaging U: 13–13 and L: 13–1–13. The first six or seven rows of teeth on each side are much larger than those in the corners of the mouth. The dermal denticles are the most primitive of any shark. They are flattened, arrowhead-shaped with a central grooved ridge, and sparse. Frill sharks are dark to light brown with darker fin edges. Some specimens have paler undersides.

Similar species The sixgill shark and the bigeye sixgill shark also have six gill slits and a single dorsal fin, but none of their gill covers is continuous across the throat, and the lower jaws extend only to beneath the eye.

Range The frill shark is probably cosmopolitan in deep waters, although its distribution appears to be patchy. Whether this reflects a narrow niche, the difficulty of capturing such a deep-dwelling fish, or the lack of deep-water fisheries in some areas is uncertain. Trunov (1968) noted that all four captures by AtlantNIRO[1] vessels in 1965 were at depths of 260–363 m in the area of the southwestern African shelf between 18°53′ and 21°22′ S latitude, and he mentioned that the distribution of frill sharks was highly localized.

In the Atlantic Ocean, the frill shark has been reported mainly in the eastern Atlantic off Arctic Norway (Varanger Fjord, Barents Sea; Collett 1897), the British Isles (four records; Wheeler 1962), the Iberian Peninsula (Roule 1912; Bolívar 1907; Gudger and Smith 1933), Madeira (seven records: one from Roule 1912; six from Cadenat and Blache 1981), and the North African coast (off Cap Blanc; Domanevskiy 1975). There are three reports from the western North Atlantic: two from the eastern United States (see below) and the other from Suriname and French Guiana, where three specimens were caught at 754–810 m (Uyeno et al. 1983). In the South Atlantic, the species has been reported from Namibia (Smith, J. L. B. 1967; Bass et al. 1975a).

In the western Pacific, the frill shark is recorded from Japan (Nishikawa 1898; Gudger 1940; Tanaka et al. 1990), Australia (Last and Stevens 1994), and New Zealand (Nakaya and Bass 1978). Most records, however, are from Japanese waters (mainly Suruga and Sagami bays), where several hundred specimens have been recorded since 1888. In the eastern Pacific the species has been reported from California (see below) and the western coast of South America.

1. Atlantic Research Institute of Marine Fisheries and Oceanography of the State Fisheries Committee of the Russian Federation.

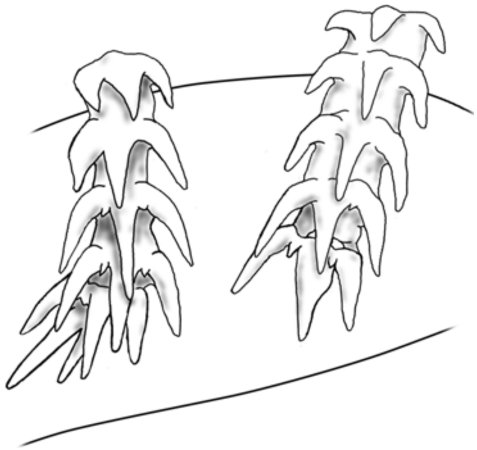


Fig. 1b. Teeth.

Records also exist for the Northwestern and Hawaiian submarine ranges (Borets 1986).

The frill shark has also been reported from the Indian Ocean. According to Tumokhin (1980), 10 frill sharks—seven females and three males—were caught in August 1976 and April 1977 by bottom trawls in open waters of the southwestern Indian Ocean at 1,200–1,440 m.

There are three North American records of frill sharks as of February 2007. In June 1948, a 172-cm female was captured by drift net at 17–18 m, 33 km southwest of Point Arguello, Santa Barbara County, California (Noble 1948). In 2003, a 186-cm female was caught on the continental slope off Martha's Vineyard, Massachusetts, between Block and Alvin canyons (39°57′ N, 71°00′ W) at 400 m (Moore et al. 2003). In 2004, a frill shark was observed and photographed at 874 m on the outer Blake Plateau east of Georgia (Sedberry et al. 2007).

Size and weight Most specimens captured measured 130–150 cm, adult females being slightly larger. The largest specimen on record is a 196-cm female obtained by Bashford Dean in Japan in the early 1900s (Gudger and Smith 1933). A 191-cm female captured in 1896 at 180–275 m in Varanger Fjord, on the Arctic coast of Norway, is apparently the second largest specimen on record (Collett 1897). A 147-cm adult male I examined weighed 5.4 kg, whereas a 182-cm, ovigerous female weighed 15.4 kg.

Biology The frill shark is the most primitive living shark, a relict surviving in the deep oceans since the time when sharks had eel-like bodies, terminal mouths, multicuspid teeth, incompletely segmented vertebral columns, and poorly calcified vertebrae. Based on catch records, the frill shark usually inhabits deep cold waters (240–1,500 m). It is rarely caught near the surface, and little is known of its biology.

Despite the highly localized distribution of the frill shark and its relative scarcity, its anatomy and reproductive processes are better known than those of many common species. Its discovery in 1888 caught the attention of ichthyologist Bashford Dean at the American Museum of Natural History in New York City. In the early 1900s, Dean traveled to Japan and secured 39 specimens (Gudger and Smith 1933). Dean, a scholar with diverse interests ranging from archaic fishes to medieval body armor, studied the frill shark for many years, making exquisite drawings of developing embryos. He also provided other scholars with anatomical

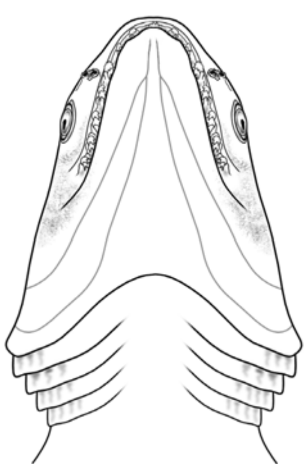


Fig. 1c. Snout.

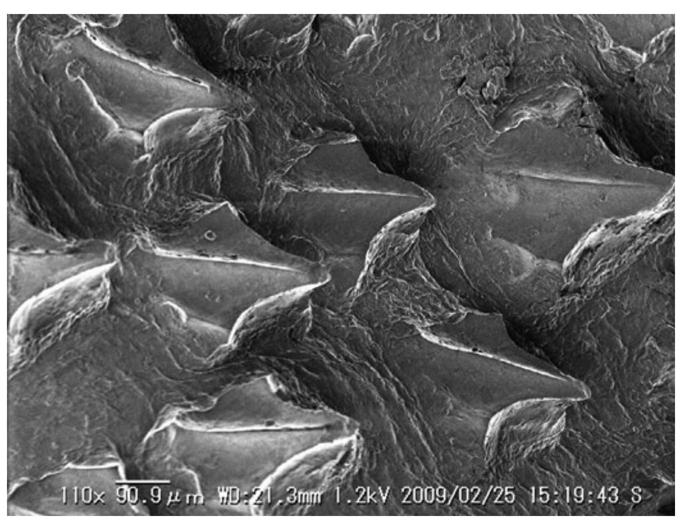


Fig. 1d. Dermal denticles.

material that resulted in several published works. Unfortunately, Dean died in 1928 before finishing his studies of the frill shark. Later, Eugene W. Gudger, also of the American Museum of Natural History, and Bertram G. Smith, professor of anatomy at New York University, used Dean's materials and notes to prepare a series of monographs on the frill shark and the Japanese horn shark. The resulting monographs are splendid, comprehensive works seldom equaled in the study of sharks. Those dedicated to the frill shark are *The Cranial Anatomy of Chlamydoselachus anguineus* (Allis 1923), *The natural history of the frilled shark Chlamydoselachus anguineus* (Gudger and Smith 1933), *The anatomy of the frilled shark Chlamydoselachus anguineus* (Smith, B. G. 1937), and *The breeding habits, reproductive organs and external embryonic development of Chlamydoselachus, based on notes and drawings by Bashford Dean* (Gudger 1940). Little has since been learned about the frill shark, and all that we know about it is derived from Japanese-caught fishes in Suruga and Sagami bays; its ecology and behavior remain mysteries.

Frill sharks have been taken over a wide depth range. Tanaka et al. (1990) collected 264 specimens with midwater and bottom trawl nets set at depths of 60–240 m in the inner part of Suruga Bay from 1981 to 1988. According to those authors, few frill sharks were caught between August and November, when the temperature of the 100 m layer rises above 15°C. This increase in temperature apparently prevents the sharks from moving upward, and they might actually migrate to deeper waters or colder latitudes. In the African shelf, specimens have been taken at 260–500 m (Trunov 1968; Domanevskiy 1975). The greatest known depth at which this shark has been caught is 1,340–1,570 m (Golovan 1976). The specimen observed off Georgia by Sedberry et al. (2007) was in 874 m and 4.3°C temperature.

Diet: The diet of the frill shark was unknown for many years because nearly all captured specimens had empty stomachs (Wheeler 1962; Tumokhin 1980). Its small, slender teeth evolved for seizing thin-skinned prey such as squids. Its distensible jaws, enormous gape, and inward-directed teeth suggest that it feeds on relatively large prey. Frill sharks have an interesting longitudinal fold along the ventral midline. It appears to serve as an expansion fold, allowing the stomach and body wall to expand after a large meal.

The only recent report on the frill shark diet is that of Kubota et al. (1991), who analyzed stomach contents of 139 specimens caught in Suruga Bay in the 1980s. Squid was the most common food item, present in 23 stomachs. Bony fishes were found in four stomachs, and unidentifiable remains in 11 stomachs. The squids included two intact specimens of *Todarodes pacificus* measuring 16–20 cm mantle length. The fishes were not identified because only vertebrae remained.

The empty stomachs of such a large percentage of captured sharks led to the speculation that a gorged frill shark might lie quiescent until its large meal has been digested, indifferent to prey and baited hooks (Smith, J. L. B. 1967). The reasons for the high percentage of empty stomachs remain unknown.

According to Gudger (1935), this shark has a fold of tissue in the mouth believed to act as a breathing valve. The structure would allow it to breathe while motionless or resting on the bottom (Gudger 1935). However, I have not been able to discern such structure in the mouth of the fresh frill sharks I have examined.

Size at maturity

Males: Tanaka et al. (1990) reported that males mature at about 110 cm, based on males of 117.8–154.8 cm having elongated, hard claspers and appreciable amounts of sperm in the seminal vesicles and sperm sacs.

Females: Females apparently mature at about 135 cm. B. G. Smith (1937) refers to a 155-cm female as "nearly mature," although the methods he used to determine maturity are unclear. Given that Smith also mentioned two fully mature females of 135 cm and 148.5 cm, it is likely that the specimen was a mature female in the resting stage of the ovarian cycle. Tanaka et al. (1990) used the size of ovarian eggs (oocytes) and "condition of the uterus" to assess the maturity of females. Those having small oocytes, threadlike uteri, and oviducal (shell) glands of less than 15 mm were classified as immature; other females were deemed mature. The oviducal gland criterion was not explained. Tanaka et al. reported that their largest immature female measured 155.9 cm and the smallest gravid female was 137.7 cm, concluding that females mature at 140–150 cm.

Reproduction Despite the restricted availability of gravid frill sharks, their reproductive processes have been well described by Gudger (1940), based on specimens obtained and studied by Bashford Dean. The frill shark is an aplacental viviparous species. Like most primitive sharks, it has two functional ovaries of equal size. The ripe oocytes and fertilized eggs are huge, measuring 90 × 96 mm (Gudger 1940). As many as 12 large, ripe oocytes have been reported in one shark (Nishikawa 1898). Interestingly, only the right uterus is typically functional, the left one remaining rudimentary. Presumably, there is no space in the abdominal cavity of this long, slender shark for two gravid uteri, given the large size of the eggs and embryos.

Development: The ovulated egg passes through the shell gland, acquiring a thin, pale brown, transparent capsule. The encapsulated egg is ellipsoidal, measuring 65–75 mm × 102–124 mm. The eggs were illustrated by Nishikawa (1898) and Garman (1913). Later, Gudger and Smith (1933) and Gudger (1940) reproduced their illustrations. The blastodisc is yellowish-red, as in other sharks, and is circular, 1.3 mm in diameter. The embryos have been described by Ziegler (1908) and Gudger (1940).

Gestation: The duration of gestation in frill sharks is unknown. Two estimates have been proposed, both speculative. Gudger and Smith (1933: 302) speculated that gestation would last "for a year or more" because of the huge size of the eggs, the great size of the embryos, and the low temperature at depths of 450–760 m where these sharks live. They concluded that "taking into consideration the large size of the yolk-sac in the second year, it seems possible that hatching may not take place until at least the second summer following impregnation, and indeed that it may not take place till after the little shark is quite two years old" (Gudger and Smith 1933: 303). Tanaka et al. (1990) suggested an even longer gestation period of "at least three and a half years." This conclusion was derived from the growth rate of early encapsulated embryos, which ranged from 10.2 to 16.6 mm per month (average 14 mm per month). Tanaka et al. estimated that if the growth rate remained continuous, gestation would last more than 39 months. As they admitted, their estimate is based on several assumptions, the most critical (and, to me, unlikely) is that the rate of embryonic growth of 14 mm per month is continuous throughout development.

Size at birth: The largest reported embryo is 54.9 cm long (Tanaka et al. 1990); the smallest free-swimming specimen, captured in Suruga Bay, measured 53.5 cm in length (Yasuhara et al. 1983). These data suggest that birth occurs at 53–55 cm. Neonate specimens are seldom captured. The only other reference to a neonate is that of Collett (1890), who reported a 61-cm free-swimming female obtained at Funchal, Madeira.

Brood size: Tanaka et al. (1990) reported that frill shark females from Suruga Bay, Japan, carried 2–10 embryos still inside the egg capsules, whereas females with "free embryos" (hatched from the egg capsules) carried two to eight embryos per female.

Nurseries Unknown.

Age and growth Frill shark specimens have not been aged because of their uncalcified skeletons.

Relation to humans Although numerous specimens have appeared in Japanese fish markets over the years, the frill shark is too difficult to capture to be of much economic importance. It is a rare catch outside Japan.

FAMILY HEXANCHIDAE

The Cowsharks

The family Hexanchidae, or cowsharks, includes the sixgill and sevengill sharks, a small group of widely distributed deep-water sharks. The family is easily recognized by the six or seven gill slits, subterminal mouth, and single dorsal fin set posterior to the pelvic fins. The only other sharks with six gill slits are the frill shark and one species of sawshark; all others have five gill slits. Cowsharks have dissimilar teeth in the upper and lower jaws: the upper teeth are fanglike, and the lower teeth sawlike and rectangular. Cowsharks are aplacental viviparous. Their skeletons are poorly calcified, which is considered a primitive characteristic. Four species are presently recognized: three are deep-water, bottom-dwelling species found over the outer continental shelves, and one is a shallow-water, coastal species. These species are classified in three different genera: *Heptranchias, Hexanchus,* and *Notorynchus.* Sometimes these genera are elevated to families. Sharks of the genus *Hexanchus* have six gill slits, while those in *Heptranchias* and *Notorynchus* have seven gills slits.

KEY TO THE HEXANCHIDAE

1a. Six pairs of gill slits 2

1b. Seven pairs of gill slits 3

2a. Five large, broad sawlike teeth on each side of lower jaw (maximum size about 180 cm) .... **Bigeye sixgill,** *Hexanchus nakamurai* (p. 36).

2b. Six large, broad sawlike teeth on each side of lower jaw .... **Sixgill shark,** *Hexanchus griseus* (p. 31).

3a. Snout broadly rounded, dorsal surface with numerous dark spots (a shark of the North Pacific) .... **Broadnose sevengill shark,** *Notorynchus cepedianus* (p. 38).

3b. Snout narrowly tapering, dorsal surfaces uniformly light brown or gray, spots .... **Sharpnose sevengill shark,** *Heptranchias perlo* (p. 28).

SHARPNOSE SEVENGILL, OR PERLON SHARK

Heptranchias perlo (Bonnaterre, 1788)

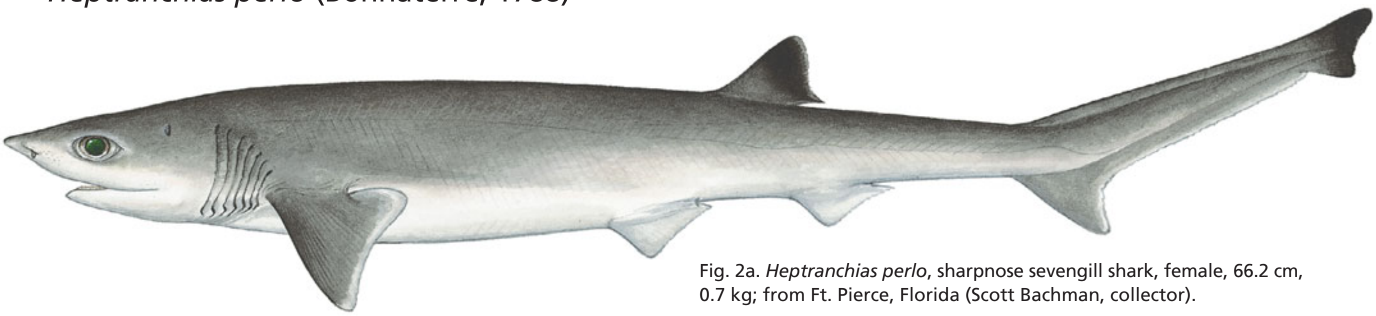


Fig. 2a. *Heptranchias perlo*, sharpnose sevengill shark, female, 66.2 cm, 0.7 kg; from Ft. Pierce, Florida (Scott Bachman, collector).

Common name Sharpnose sevengill, sevengill, seven-gilled, or perlon shark. The name sharpnose sevengill has been used to distinguish this species from the broadnose sevengill shark; perlon shark is derived from the Old French name (see below).

Spanish name *Tiburón de siete branquias* (Cuba, A.F.S.).

Scientific name *Heptranchias perlo* (Bonnaterre, 1788), originally described as *Squalus perlo* in *Tableau Encyclopédique et Méthodique des Trois Règnes de la Nature, Ichthyologie:*10. *Heptranchias:* from the Greek *hept,* seven, and *branchos,* gill; *perlo:* from *le perlon,* an old French name for the species, first described by Broussonet (1780), from *perle,* pearl. The allusion is not clear; it probably refers to the skin, which Broussonet calls smooth and grayish ("*lisse & grisâtre*").

Synonyms *Squalus cinereus* Gmelin, 1788; *Heptranchias cinereus* Rafinesque, 1810; *Heptranchias angio* Costa, 1837; *Heptanchus cinereus* Müller and Henle, 1839; *Heptranchias deani* Jordan and Starks, 1901; *Heptranchias dakini* Whitley, 1931 [a].

Identification The sharpnose sevengill shark is recognized by a *single dorsal fin* with its origin behind the pelvic fins, *seven gill slits,* and *a narrow tapering snout.* The upper teeth are fanglike with long tapering cusps, and the side teeth have small lateral cusplets. The lower teeth are broad and sawlike, with one larger cusp followed by four or five smaller ones, except for the small symmetrical central tooth. Teeth number U: 9 to 11–9 to 11, L: 5–1–5. The dermal denticles have three points, with the central point the largest, and are closely overlapping. Coloration is brownish gray above with paler undersides. The tips of the dorsal and caudal fins are black.

Similar species The broadnose sevengill shark also has seven gill slits, but its snout is broadly rounded (see illustration), and it has *dark dorsal spots.* The broadnose sevengill shark, abundant off western North America, has not been reported from eastern North America, although it inhabits the South Atlantic off Brazil (Sadowsky 1970).

Range The sharpnose sevengill shark is cosmopolitan in deep subtropical and warm-temperate waters. It has long been known in the Mediterranean (Risso 1810; Garman 1913). It has also been reported from Japan (Garman 1913), Australia (as *Heptranchias dakini* by Whitley 1931a), and New Zealand (as *H. perlo* by Garrick and Paul 1971). Garrick and Paul (1971) have shown that the Australian *H. dakini* is a synonym of *H. perlo.* The species has also been found in the eastern Atlantic from southern Ireland to southern England and in the Gulf of Gascogne (Cappetta 1985), the Great Meteor Seamount in the central eastern Atlantic (Frentzel-Beyme and Köster 2002), equatorial Africa (Poll 1951), and Natal and southern Mozambique (Bass et al. 1975a).

Although the species is common in moderately deep water (100–200 m) along southeastern North America, there are few records of it in the literature. The North American specimens examined by Bigelow and Schroeder (1948) were limited to two animals from Cuba, and they knew of no other material from the western North Atlantic. Nevertheless, the sharpnose sevengill is found from Cape Cod (where it is rare) to Florida and the Gulf of Mexico. I have seen dozens of specimens caught by tilefish fishermen off South Carolina, as well as some from the Gulf of Mexico.

Size and weight The sharpnose sevengill is a small shark; most specimens caught measure less than 100 cm. The largest specimen that I have examined was a 114.1-cm female weighing 2.5 kg, obtained off Georgetown, South Carolina, in 1984. Forster et al. (1970) reported that their largest specimen from the Indian Ocean was a male measuring 101 cm. Garrick and Paul (1971) wrote that the largest female from New Zealand measured 137 cm. Capapé (1980) gives 118 cm for the largest male and 139 cm for the largest

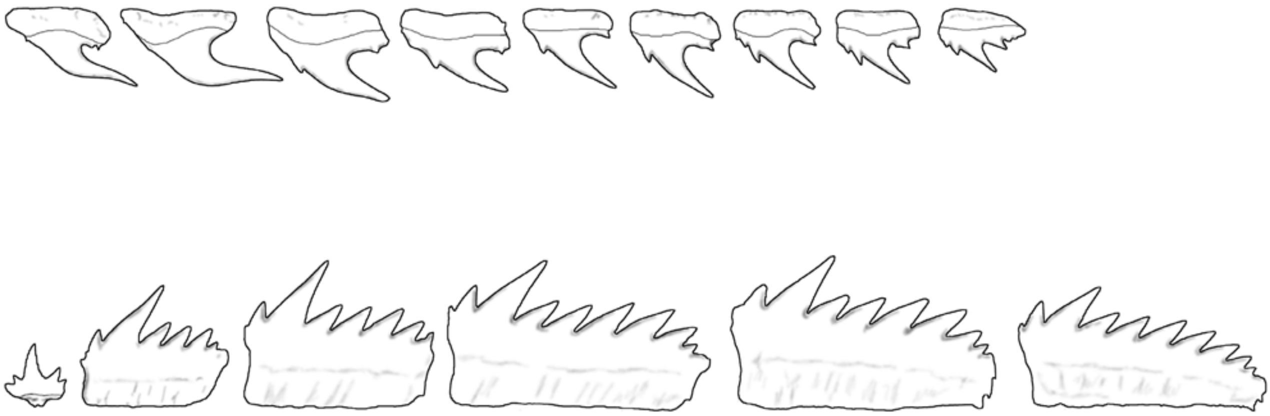


Fig. 2b. Teeth.

female from Tunisia. These last two are the largest specimens I have been able to document.

Larger sizes published for this species are likely caused by confusion with the broadnose sevengill shark or the sixgill shark. Bigelow and Schroeder (1948) quoted a maximum size of 2.1 m based on Günther (1870). According to Tortonese (1956) it is said to reach 3 m. Bini (1967) wrote that the largest sevengill shark reliably measured was slightly less than 2 m and that a specimen captured off Israel measured 2.5 m. There is, however, no evidence to validate these sizes.

I have recorded the following lengths and weights for specimens caught off the southeastern United States:

Male: 56 cm, 0.54 kg; 62 cm, 0.68 kg.

Female: 66 cm, 0.74 kg; 87.5 cm, 1.45 kg; 98.2 cm, 2.7 kg.

Biology This is a warm-water species common along the edges of the continental shelves, where it appears to be most abundant at depths of 180–450 m (Castro 1983). Despite its abundance from the Carolinas to the Gulf of Mexico, its life history is poorly known. There are no American publications on this species, and it is necessary to turn to works published in other areas to complement our meager knowledge of American specimens. Capapé (1980) examined a total of 154 individuals taken off the northern coast of Tunisia, concluding that they showed no differences from Mediterranean specimens or those from both sides of the Atlantic. Garrick and Paul (1971) found no differences between the Australian form (described as *H. dakini*) and the

Fig. 2c. Snout.

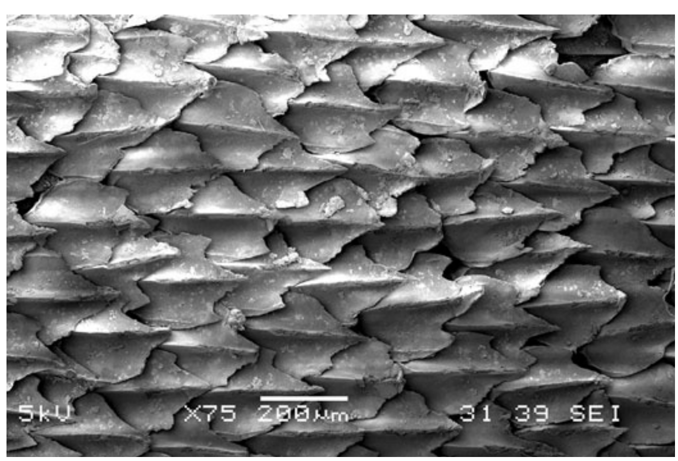


Fig. 2d. Dermal denticles.

worldwide *H. perlo*. The differences between the American population and those of other areas appear to be minor.

The sharpnose sevengill shark is occasionally caught on longlines set for tilefish along the southeastern coast of the United States (North Carolina to Georgia) and in the Gulf of Mexico, usually at depths of 180–450 m. Captures elsewhere indicate a similar depth range. In the central eastern Atlantic, the species has been caught in traps at 297–435 m (Frentzel-Beyme and Köster 2002). Australian captures indicate a depth range of 100–400 m, with some captures in shallower waters. Captures off New Zealand usually occur at 235–275 m, with some at 50 m (Garrick and Paul 1971). In Japan the species has been reported in 150–250 m (Tanaka et al. 1975). This shark feeds on squids and small fishes, but little else is known about its habits.

Size at maturity

Males: Most published information on size of males at maturity is too imprecise to accurately determine this characteristic. Bigelow and Schroeder (1948) wrote that males "may mature" at 60–75 cm, without stating the basis for their claim. Capapé (1980) used the relative clasper length to determine maturity, but he did not associate the length of the clasper with calcification or spermatogenesis. He recognized three growth phases or groups of individuals: juvenile phase, or individuals less than 80 cm; maturation phase, or individuals 81–92 cm; and an adult phase comprising individuals longer than 92 cm. From his graphs it can be determined that the male adult phase must begin at about 95 cm. Tanaka et al. (1975) examined 191 specimens from the Japanese coast off Kyushu. They used relative clasper length and relative testis weight to determine maturity, but they, too, failed to correlate the clasper and testis growth with clasper calcification, spermatogenesis, or any other functional indicator of maturity. These authors concluded that males reach maturity at 70–85 cm.

Females: Capapé (1980) found that vitellogenesis (formation of yolk) begins when females reach 85 cm. The largest oocytes (45 mm in diameter and weighing more than 37 g) are not found in females of less than 100 cm. The smallest gravid females were larger than 105 cm. Capapé concluded that females mature when they attain a total length of 85–100 cm and are invariably mature at lengths greater than 100 cm.

Reproduction The sharpnose sevengill shark is aplacental viviparous. Little else is known of its reproductive processes.

Size at birth: Parturition probably occurs when the embryos reach about 25 cm. Bigelow and Schroeder (1948) reported that a 26-cm specimen from Japan had a faint yolk-sac scar, indicating its recent birth. Bass et al. (1975a) mentioned that the smallest sharpnose sevengill shark caught in the Indian Ocean was a 27-cm female. Capapé (1980) gives the birth size at around 30 cm.

Brood size: Bigelow and Schroeder (1948) reported a brood of nine young from a 93-cm female (Museum of Comparative Zoology no. 36897); they also cited an unverified report of a brood of 18, but the report is questionable.

Nurseries Unknown.

Age and growth Unknown.

Relation to humans In North American waters the sharpnose sevengill shark is too small and scarce to be of economic importance. The flesh is said to be mildly poisonous (Halstead et al. 1990), but I have not found firsthand evidence of this effect.

SIXGILL SHARK

Hexanchus griseus (Bonnaterre, 1788)

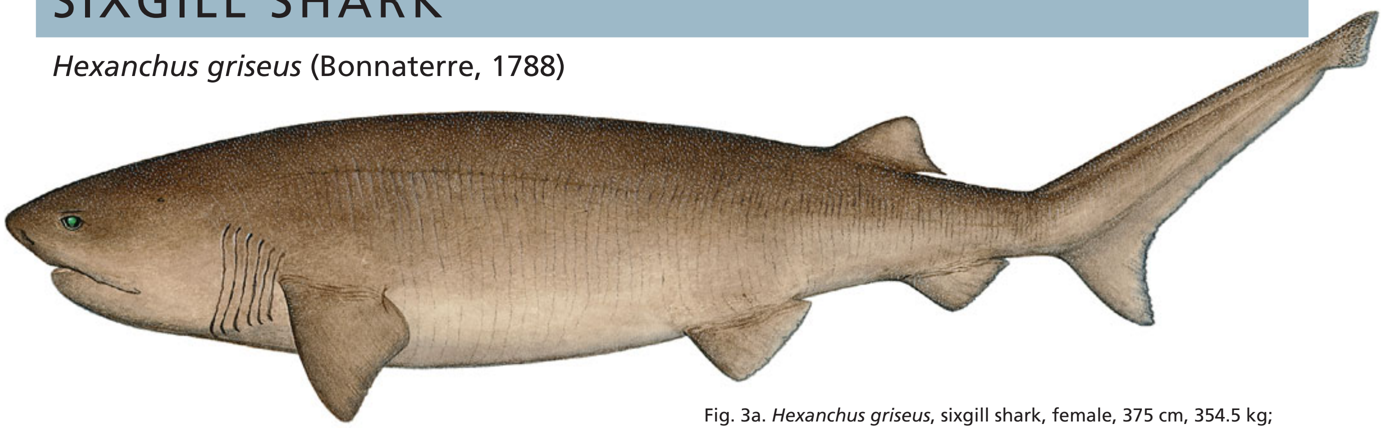


Fig. 3a. *Hexanchus griseus*, sixgill shark, female, 375 cm, 354.5 kg; from Key West, Florida (Jay Lamee, collector).

Common name Sixgill shark, reflecting its distinctive number of gill slits.

Spanish name *Cañabota, marrajo* (Cuba). The A.F.S. name is *tiburón de seis branquias.*

Scientific name *Hexanchus griseus* (Bonaterre, 1788), originally described as *Squalus griseus* in *Tableau Encyclopédique et Méthodique des Trois Règnes de la Nature, Ichthyologie:* 9. *Hexanchus:* one of Rafinesque's words, apparently a mistake for *Hexancus,* from the Greek *hex,* six, and *ankos,* a bend or hollow; *griseus:* Latin, gray.

Synonyms *Squalus griseus* Gmelin, 1788; *Squalus vacca* Bloch and Schneider, 1801; *Notidanus griseus* Günther, 1870; *Hexanchus corinus* Jordan and Gilbert, 1880.

The sixgill shark of the Pacific coast of North America was described as *Hexanchus corinus* by Jordan and Gilbert, in 1880. Supposedly, *H. corinus* differs from *H. griseus* primarily in that its lower teeth (other than the median tooth) have fine serrations along their inner edges. Bigelow and Schroeder (1948) noted that differences in dentition and other characteristics were not significant and referred the Pacific form to *H. griseus.* To my knowledge, there are no recent comprehensive comparisons of the two forms, probably because comparative material is lacking. The large size of these sharks usually prevents the preservation of entire specimens, which are necessary for such comparative work.

Identification The sixgill shark can be recognized by its *single dorsal fin, six gill slits,* and *six large, broad, sawlike teeth on each side of the lower jaw.* The frontal upper teeth have one large curved cusp; other upper teeth have oblique cusps with an increasing number of additional side cusplets. The lower teeth are much broader and more sawlike than the upper teeth. There is one small, broad, and symmetrical tooth at the symphysis. Teeth number U: 9 or 10–9 or 10, L: 6–1–6, disregarding the minute, budlike teeth at the corners of the jaws. Compared to females, males have lower teeth with a much larger first cusp, a feature that presumably helps them to grasp females securely during copulation. The dermal denticles have three points with a prominent central ridge terminating in the central point. There are two color morphs (forms) of the sixgill shark. One is chocolate brown with little, if any, countershading. The other has distinct countershading, being pale brown above and lighter below. I have seen both forms together in Bermuda, where Eugenie Clark and National Geographic photographer Emory Kristof photographed them together (Clark and Kristof 1990). These color morphs appear to be variations of the same species, although the possibility that they might be separate species cannot be discounted.

Similar species The bigeye sixgill shark has five large teeth on each side of the lower jaw. The frill shark has a terminal mouth and fanglike teeth.

Range The sixgill shark is cosmopolitan in deep temperate, subtropical, and tropical waters. In North America, it has been reported from Nova Scotia to Florida and the Gulf of Mexico and from British Columbia to California; the species is common in deep water along the southeastern coast of the United States and in shallow waters of the Pacific Northwest. Records of sixgill sharks from the Atlantic coast of North America are few because of its deep-water habitat. The first record for North America was a 310-cm specimen caught in March 1886 in North Carolina, at the Currituck Inlet lifesaving station. This specimen was forwarded to the U.S. National Museum, where a plaster cast was made and exhibited for several years (Smith, H. M. 1907). In 1963 a "13-foot, one-ton" sixgill shark was reported from 400 m, 72 km off the Mississippi River delta (Sport Fishing Institute 1963), with the comment that the species had not been taken in North American waters since

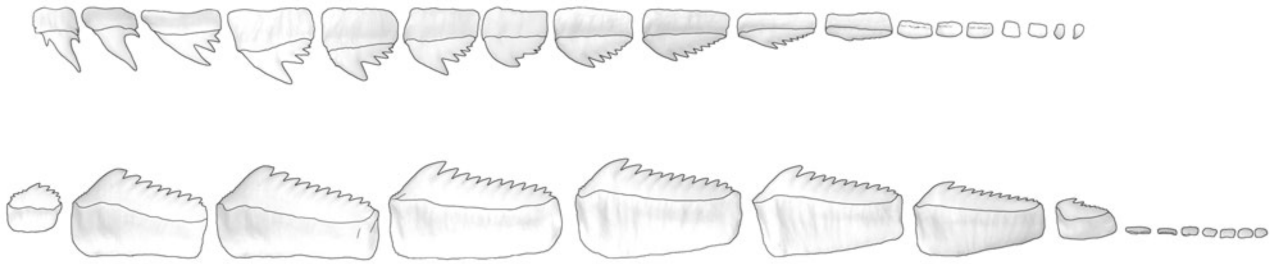


Fig. 3b. Teeth.

1886. Sixgill sharks are seldom seen north of Cape Hatteras, although the northernmost records are two small juveniles caught at 155–183 m off Nova Scotia (Gilhen 1989), and I have examined a 195-cm juvenile was taken off New England by John Galbraith in 2005. All other current records for eastern North America are from North Carolina southward. Branstetter and McEachran (1986a) reported a 325-cm male caught 108 km off Port Isabel, Texas. I examined specimens from Bermuda and Florida. Sixgill sharks have been seen from submersibles on many occasions off the southeastern coast of the United States, but most of these observations have not been published because they are considered commonplace.

Sixgill sharks appear in shallower water (40 m) off Vancouver Island, British Columbia, from June to September (Dunbrack and Zielinski 2003). Small juveniles have been reported from shallower water in San Francisco Bay (Herald and Ripley 1951) and Puget Sound (my observation).

Size and weight Few measurements exist of the large sixgill sharks. The largest specimen that appears to have been measured reliably and illustrated is a 482-cm female caught off La Coruña, Spain, on 26 October 1906 (Bolívar 1907). Some incredible sizes have been stated for this species, both in the literature and anecdotally. There are reports in the older literature of a sixgill shark "26 feet 5 inches" (8.05 m) long, based on an account by Day (1880–1884). Bigelow and Schroeder (1948: 83) called this fish "a giant of its kind if its size was stated correctly." Years later, Lineweaver and Backus (1970) traced the error with an explanation that shows how such mistakes are often created and perpetuated. In *The Zoologist,* Jonathan Couch stated that "On the 19th of February of the present year [1846] there was caught by a fisherman of Polperro, and immediately brought to me, a specimen of a fish, which I recognized as the Six-branchial, or Gray Shark: a species new to the Fauna of Cornwall. . . . The length of the specimen was 2 feet, 2 1/2 inches" (Couch 1846: 1337–1338). Later, Day (1880–1884: 308) in his *Fishes of Great Britain and Ireland,* in the account of *Hexanchus griseus,* reported that "February 19th, 1846, one 26 feet 5 inches in length [was] captured at Polperro, in Cornwall. . . . It is said to grow to a large size." Couch, in his major work *A History of the Fishes of the British Islands* (1868: 21), makes no mention of the gigantic specimen mentioned by Day, referring again to his small 1846 specimen: "The example from which the description is taken, measured in length no more than two feet two inches and a half; but it has been caught at a length of eleven or twelve feet." Polperro fishermen commonly brought specimens to Couch, so it is unlikely that a giant sixgill shark captured the same day as the specimen 2 feet 2 1/2 inches in length would have escaped his notice. As Lineweaver and Backus (1970) suggested, Day probably converted 2 feet 2 1/2 inches into 26.5 inches. This figure was subsequently misinterpreted by the printer or editor and printed as "26 feet 5 inches," thus engendering an error that would live long in the shark literature.

Convincing anecdotal evidence suggests that sixgill sharks do perhaps exceed 550 cm. I occasionally hear reports of huge sixgill sharks from fishermen and scientists alike, but so far no one has actually measured one of those elusive giants.

Few accurate weight records exist for sixgill sharks from the Atlantic coast of North America. Branstetter and McEachran (1986a) reported a 325-cm, 211-kg male from the Gulf of Mexico. A 195-cm female taken off New England weighed 45.9 kg. The large female illustrated here was caught off Key West, Florida; it measured 381 cm and weighed 354 kg, while a 452-cm female taken off Bimini, Bahamas, in 1993 weighed 558 kg (Ron Schatman, pers. comm., December 2002). Ebert (1986a) gave the following sizes for Pacific specimens: 150 cm, 18.2 kg; 168 cm, 27.3 kg; 208 cm, 60.0 kg; 210–242 cm, 54.1 kg; 273 cm, 107.3 kg.

Biology The sixgill shark is a common, bottom-dwelling, deep-water species, usually reported from depths of 300–1,000 m. Most specimens caught or observed at these depths are juveniles measuring less than 400 cm. Carey and Clark

(1995) tracked two female sixgill sharks off northwestern Bermuda in 1987. One shark, estimated to be 310–350 cm, was captured and outfitted with a transmitter. After release it moved offshore and descended to 1,000 m. That evening it moved farther offshore, making an excursion to 1,500 m, the maximum depth recorded. At dawn, it rose from 1,000 m and spent the day between 700 and 900 m. Tracking was discontinued that evening and resumed 24 hours later. The shark continued swimming at 600–1,000 m for the following 36 hours, ordinarily following the bottom contour at 914 m. A second female, estimated to be 380 cm, swam at 700–1,000 m, rising a few times to 600 m. At 800 m the temperature was 9.5°C, and at 600 m it was 14–16°C.

Adult sixgill sharks exceed 450 cm in length. They seldom are captured or seen, presumably because few people fish or dive in the deep water they inhabit or because their large size allows them to break away from most fishing gear. Perhaps their poorly calcified jaws tear easily and hooked animals are freed. Although records are scant, adult sixgill sharks apparently live at depths exceeding 1,200 m. According to Bigelow and Schroeder (1948), sixgill sharks have been caught in Portuguese waters at 800–1,875 m. In the Indian Ocean, Forster et al. (1970) collected sixgill sharks at 200–950 m. Most of Forster et al.'s specimens were caught at night at 200–499 m. The two specimens captured during daylight came from the deeper part of the range, at 455 and 950 m. All specimens examined were juvenile females. Their only large specimen, estimated at 450 cm, was caught at about 950 m, but, unfortunately, it was not examined.

If adult sixgill sharks dwell at depths greater than 1,000 m, what is their source of food? Such large animals must require large prey and great amounts of energy, even if they are slow moving and inhabit cold water. The large, flat, saw-like teeth of the lower jaw form a continuous cutting edge. The fact that the cutting teeth are on the lower jaws, and the thinness of the teeth suggest a diet of relatively soft prey. I suspect that sixgill sharks scavenge dead whales as sleeper sharks do at higher latitudes. Sunken whale carcasses can persist for many months (Smith and Baco 2003) at depths few sharks are thought to inhabit. Perhaps they also feed on giant squid, as sleeper sharks do in the Antarctic (Cherel and Duhamel 2004), but just how these sharks catch giant squid is an interesting mystery.

Despite living most of their lives in darkness, sixgill sharks have the largest pineal window that I have seen. The pineal window is a light-colored spot on top of the head between the eyes, and is common in many deep-water sharks. When compared to the surrounding tissue, this structure allows up to seven times more light to enter the brain cavity and impinge on the pineal organ (Gruber et al. 1975). The pineal organ (*epiphysis cerebri*) is an area of the brain (diencephalon) known to be as photosensitive as the retina, and its threshold of light reception is below that of moonlight (Hamasaki and Streck 1971). However, we can only speculate on its function in deep-water sharks.

The differences between Atlantic and Pacific forms of the sixgill shark are not well studied, and the possibility that they could be separate species cannot be ruled out. I treat the two forms separately here.

Atlantic form: I have observed several Atlantic sixgill sharks from submersibles off the Bahamas and Grand Cayman at depths of 300–850 m. This slow-moving shark gives the impression of gliding effortlessly a meter or two above the bottom. Its movements are slow when searching for food or even while scavenging. This is probably an energy-saving

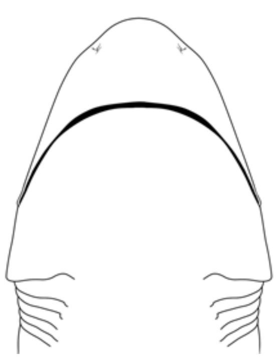


Fig. 3c. Snout.

Fig 3d. Snout (neonate)

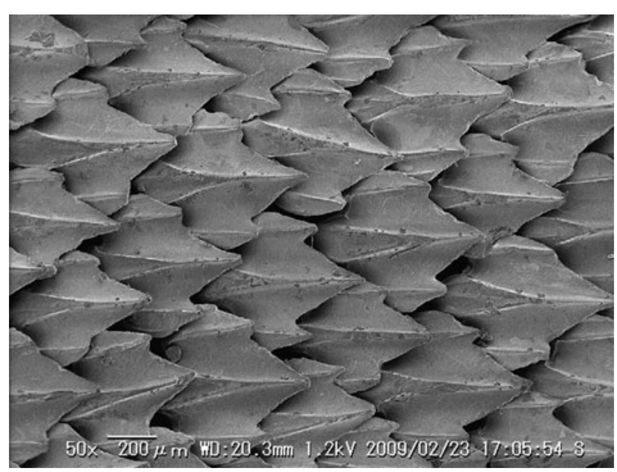


Fig. 3e. Dermal denticles.

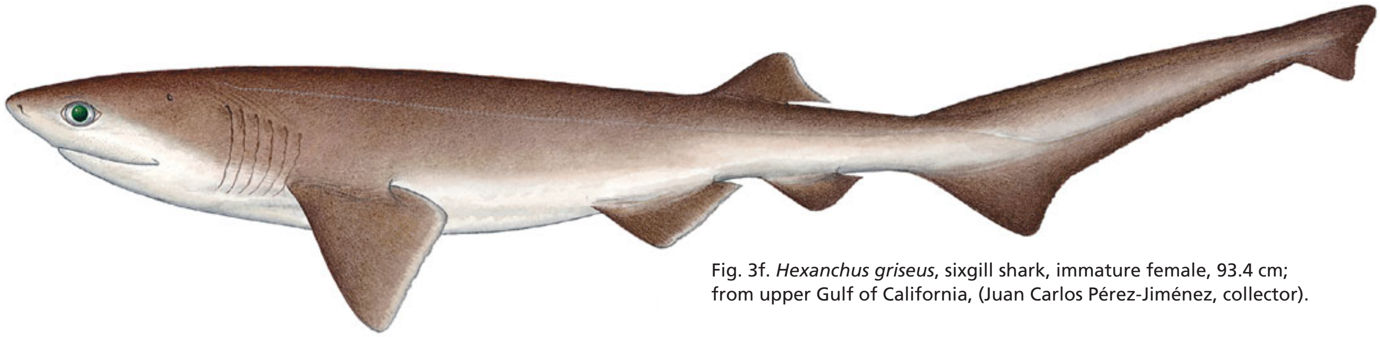


Fig. 3f. *Hexanchus griseus*, sixgill shark, immature female, 93.4 cm; from upper Gulf of California, (Juan Carlos Pérez-Jiménez, collector).

adaptation for an animal that must search vast areas for a meal, whether by predation or scavenging. Obviously, it is capable of rapid movement when attacking prey or otherwise stimulated. I saw a large specimen (~360 cm) veer off quickly with powerful tail strokes when encountering the cone of illumination in front of the submersible. The sixgill shark also has the remarkable ability to stand vertically on its head with little horizontal movement, remaining over a given spot in this position while feeding. I watched a 330-cm female use suction feeding to pick up bait we had scattered over the bottom. There are few reports of the diet of Atlantic sixgill sharks. One 300-cm specimen I examined in Bermuda contained the remains of a small whale or a dolphin (vertebrae and blubber). Glenn Ulrich (South Carolina Marine Resources Division) observed and filmed a sixgill shark from a submersible while it made several unsuccessful attempts to capture a very nimble crab (*Gerion* sp.).

Pacific form: Unlike the Atlantic form, the Pacific sixgill shark is often found in shallow water along the colder northwestern coast of North America. Herald and Ripley (1951) reported three sixgill sharks taken inside San Francisco Bay, California. One was a female (129 cm, 9 kg) caught on hook and line at a depth of 11 m between Hunter Point and Coyote Point. The other was a 67-cm male caught on 19 March 1945 "at the intake of the Pacific Gas and Electric plant." The third was a 335-cm, 210-kg female captured in July 1928, about 1 km inside the Golden Gate Bridge near Sausalito. Miller and Greenfield (1965) reported a 75-cm juvenile sixgill shark caught in October 1964 at 27 m in East Sound, Orcas Island, Washington, where the bottom temperature was 9.5°C. This shark bore a yolk-sac scar between the two pectoral fins. Knaggs et al. (1975) reported the capture of an 85-cm specimen in a midwater trawl fished at 14–38 m in Todos Santos Bay, Mexico, on 6 October 1970. Ebert (1986a) recorded six specimens (150–242 cm) from 30 m inside San Francisco Bay, California. Dunbrack and Zielinski (2003) wrote that sixgill sharks occur regularly at 20–40 m on a shallow reef in the Strait of Georgia, British Columbia, between June and September.

Diet: Ebert (1986a) examined the stomach contents of 19 sixgill sharks from California, finding prey items in nine of them. All prey items occurred only once, except for spiny dogfish (*Squalus acanthias*), which were found in three stomachs. Other items included whale blubber, pinniped remains, prickly sharks (*Echinorhinus cookei*), ratfish (*Hydrolagus collei*), hake (*Merluccius productus*), Pacific lamprey (*Lampetra tridentata*), Pacific hagfish (*Eptatretus stoutii*), and unidentified bony fishes.

Size at maturity

Atlantic form: Size of *males* at maturity is not known because of previous confusion with the bigeye sixgill shark. Eugenie Clark and I examined a 282-cm immature male caught 7 July 1986 off Bermuda. Branstetter and McEachran (1986a) reported that a 325-cm male from the Gulf of Mexico had calcified claspers. These observations suggest that Atlantic males mature at about 300 cm.

Females appear to reach maturity at about 450 cm. A 432-cm female that I examined, caught off Marathon Key, Florida, in February 1992, was immature. Its two ovaries were immature, measuring 56 × 5 cm, and contained whitish oocytes 5–10 mm in diameter, most measuring 5–7 mm. Desbrosses (1938) reported that the female sixgill sharks from coastal France were immature to lengths of 350 cm and that gravid females had been reported with lengths of 452, 482, 450, and 465 cm. Vaillant (1901) related the capture of a 452-cm gravid female off Arcachon, France, in November 1900.

Pacific form: Males of the Pacific form appear to reach maturity at about 310 cm. Crow et al. (1996) reported that males captured off Hawaii measuring 273–308 cm had uncalcified claspers, and those 309–331 cm had calcified claspers.

The size at maturity of Pacific *females* is not precisely known. Springer and Waller (1969) stated that no mature sixgill shark had ever been reported from the eastern Pacific. Ebert (1986a) reported a 421-cm gravid female caught at 160 m in May 1975 off Church Rock, San Luis Obispo

County, California. According to Ebert this is apparently the only mature sixgill shark reported from the eastern North Pacific.

Reproduction The sixgill shark is an aplacental viviparous species like other members of the family. Few gravid females have been examined by biologists, and little is known about the reproductive processes of the species.

Size at birth: Few data exist on size of the young at birth. Based on the female reported by Vaillant (1901), which carried embryos of 65–68 cm, and the specimen reported by Ebert (1986a) that carried embryos measuring 68–74 cm, it appears that sixgill sharks are born at 65–74 cm. However, this needs verification.

Brood size: There is little information on the brood size of the sixgill shark because pregnant specimens are seldom caught, probably because of their large size and deep-water habitat. The few available reports indicate very large broods. Vaillant (1901) reported the capture of a 452-cm female off Arcachon, France, in November 1900 that, according to the fishermen, contained 108 young. Bolívar (1907) mentioned that a 482-m female caught off La Coruña, Spain, carried 42 young and was observed to abort five others during capture. The female reported by Ebert (1986a) carried 51 young.

Nurseries There is no information on the location of the nurseries of the sixgill shark along the eastern coast of North America. Small juveniles (80–120 cm) are common all along the Pacific coast from Puget Sound to the Gulf of California, but reports of neonates are rare. One such report is of a 67-cm specimen from San Francisco Bay (Herald and Ripley 1951). I have examined a few small sixgill sharks (79–83 cm) collected at 200–220 m in the northern Gulf of California in March by Oscar Sosa and J. C. Pérez Jiménez (one of these neonates is illustrated on page 34). These observations suggest that the nurseries along western North America are distributed over a large area.

Three gravid females have been taken in the eastern Atlantic, off the French and Spanish coasts. In addition to the two females mentioned above, a gravid female said to be about 400 cm and weighing some 400 kg, taken near St. Raphaël (near Cannes), France, at 850 m in August 2003. Nine "near-term" embryos averaging 61 cm in length were obtained from this shark (Michèle Bruni, curator of the Musée Océanographique de Monaco, pers. comm., January 2006).

Age and growth The sixgill shark has not been aged because of its uncalcified vertebrae.

Relation to humans The sixgill shark is too rarely caught in North American waters to be of economic importance. A few specimens are caught seasonally in deep-water grouper and snapper fisheries off Florida. The sixgill shark has been on the list of federally protected species on the eastern coast of the United States since 1992. Given that there are no fisheries for it in this region, and that sixgill sharks are seldom encountered in pelagic fisheries because their deep-water habitat, the reasons for protecting the species are precautionary, the intention evidently to prevent future fisheries from developing.

In the late 1970s, divers in coastal British Columbia, Canada, began seeing sixgill sharks with regularity during the summer at Tyler Rock in Barkley Sound, on the west coast of Vancouver Island and off Flora Island in the Strait of Georgia. By 1993 shark ecotourism had developed in the area, with several companies regularly taking scuba divers to see sixgill sharks (Harvey-Clark 1995).

BIGEYE SIXGILL SHARK

Hexanchus nakamurai Teng, 1962

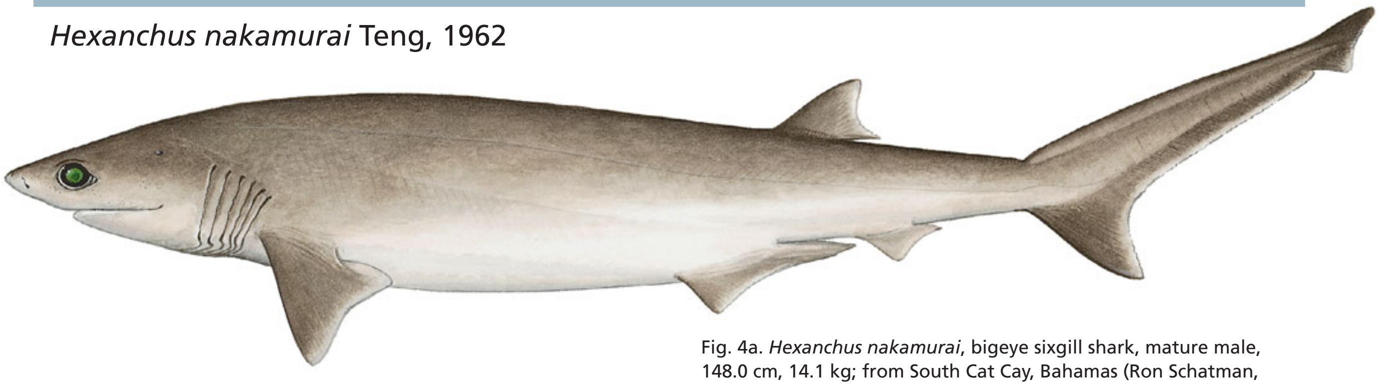


Fig. 4a. *Hexanchus nakamurai*, bigeye sixgill shark, mature male, 148.0 cm, 14.1 kg; from South Cat Cay, Bahamas (Ron Schatman, collector).

Common name Bigeye sixgill shark or small sixgill shark. The name alludes to having six gills and eyes proportionally larger than those of the much bigger sixgill shark (*Hexanchus griseus*).

Spanish name *Cazón de fondo* (Cuba). The A.F.S. name is *cazón de seis branquias.*

Scientific name *Hexanchus nakamurai* Teng, 1962, in *Clasification and Distribution of the Chondrichthyes of Taiwan:* 30–33, fig. 5. *Hexanchus:* one of Rafinesque's words, apparently a mistake for *Hexancus,* from the Greek *hex,* six, and *ankos,* a bend or hollow; *nakamurai:* named after H. Nakamura (1936), who first illustrated the species.

Synonyms *Hexanchus vitulus* Springer and Waller, 1969. The bigeye sixgill shark was known by this scientific name until recently. Teng (1962) described this species as *Hexanchus griseus nakamurai,* a subspecies of the sixgill shark, in his unpublished Ph.D. dissertation. According to Compagno (1984a), doubts as to whether Teng's unpublished dissertation constituted a formal "publication" led to the wide use of the name *vitulus.* The name *H. nakamurai* has been adopted by the A.F.S. (Nelson et al. 2004).

Identification The bigeye sixgill shark is recognized by its *single dorsal fin, six gill slits,* and *five large, broad, sawlike teeth on each side of the lower jaw.* The upper teeth are long and pointed; the lower teeth are broad and sawlike, with a small central tooth at the symphysis. The teeth number U: 9–9, L: 5–1–5, disregarding the minute, budlike teeth at the sides of the mouth. The dermal denticles have three ridges that end in three points, the central one being the largest. Coloration is pale grayish brown above with lighter undersides.

Similar species The sixgill shark has *six* large, broad teeth at each side of the lower jaw. The frill shark has a terminal mouth and fanglike teeth.

Range The distribution of the bigeye sixgill shark is patchy and poorly understood. The species has been reported from the Gulf of Mexico, Florida, and West Indies region (Springer and Waller 1969), the southwest Indian Ocean (Forster et al. 1970; Bass et al. 1975a), and Taiwan (Nakamura 1935;

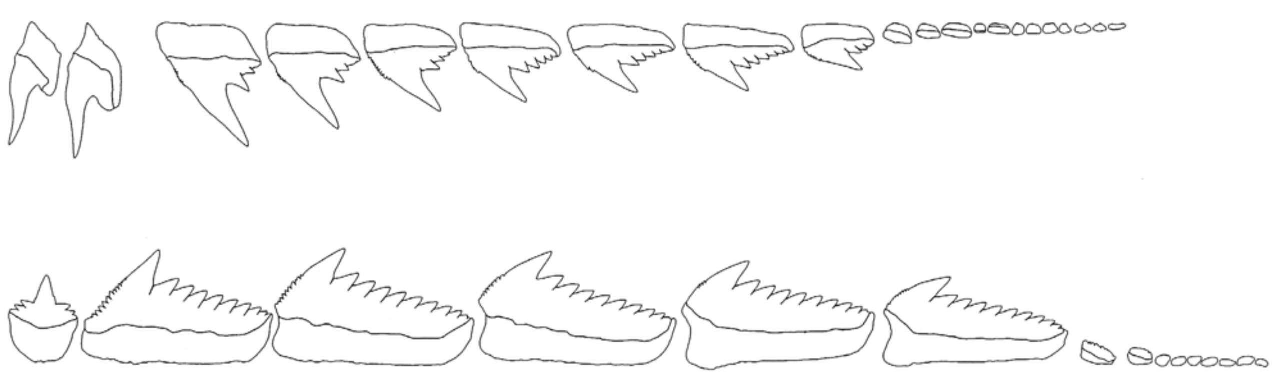


Fig. 4b. Teeth.

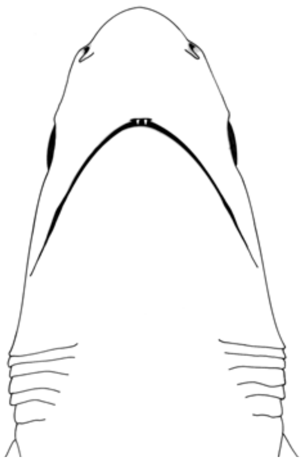


Fig. 4c. Snout.

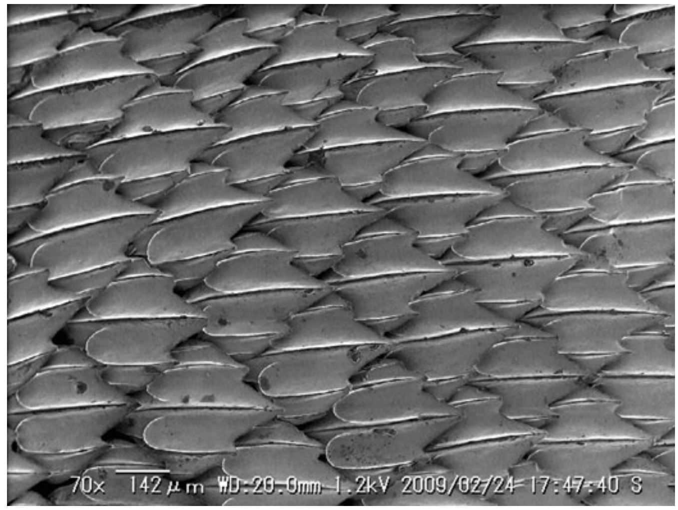


Fig. 4d. Dermal denticles.

Teng 1962). I have found it to be abundant in deep waters of the northern Gulf of Mexico, off the Bahamas, and off Grand Cayman, suggesting that the bigeye sixgill is common throughout the region. Like many other deep-water sharks, it is probably widely distributed in deep tropical, subtropical, and warm-temperate waters, there being few barriers to its movements.

Size and weight The bigeye sixgill shark probably grows to about 180 cm. Representative sizes and weights of specimens that I have examined are as follows:

Male: 144 cm, 12.2 kg; 157 cm, 15 kg.

Female: 155 cm, 16.4 kg; 164 cm, 18.4 kg; 165 cm, 20.6 kg; 169 cm, 23.6 kg.

Biology The bigeye sixgill is a shark of the deep continental slopes. This species was not generally recognized as distinct from the sixgill shark until 1969, and thus is poorly known. Although locally common at depths of 200–500 m in warm waters of the Florida–Caribbean region, there have been no published works on the species since 1969.

I have observed bigeye sixgill sharks from submersibles off the Bahamas at 465 m and off Grand Cayman at 305 m. The shark moves slowly with gentle tail beats, appearing to glide effortlessly. Its flexible body allows it to turn quickly and, like its larger congener, the sixgill shark, the bigeye sixgill has the ability to feed while positioned head down and almost motionless. On one occasion off the Bahamas, during a dive to 465 m in the *Johnson-Sea-Link II* submersible, I watched as a bigeye sixgill, swimming just above the submersible's sphere, suddenly attacked a lane snapper (*Lutjanus synagris*) on the bottom barely three meters away. The shark dashed in front of the sphere so quickly that I was not fully aware of what had just crossed my field of view. In a few seconds I saw the shark practically standing on its head, seizing the snapper.

Size at maturity There are no published data on size at maturity for the bigeye sixgill shark. I examined a mature 144-cm male and a 155-cm female that carried 40–50 mm oocytes.

Reproduction Development is aplacental viviparous, but little else is known about its reproductive processes.

Size at birth: Young are born at about 40–43 cm. Forster et al. (1970) reported embryos 39–42 cm from females in the Indian Ocean. Bigelow and Schroeder (1948) recorded a 43-cm newborn female from Cuba, indicating that the young measure about 40 cm at birth.

Brood size: A brood of 13 was reported from the Indian Ocean (Forster et al. 1970). Females that I examined, taken off Bimini, Bahamas, from May to July, carried from 7 to 20 ripe oocytes in each ovary, providing evidence of large broods. The largest oocytes measured 50 mm in diameter.

Nurseries I have examined a few small juveniles of 68–82 cm from deep water off Panama City, Florida, which indicates that some of the bigeye sixgill nurseries are in the northern Gulf of Mexico.

Age and growth The bigeye sixgill has not been aged.

Relation to humans None.

BROADNOSE SEVENGILL SHARK

Notorynchus cepedianus Péron, 1807

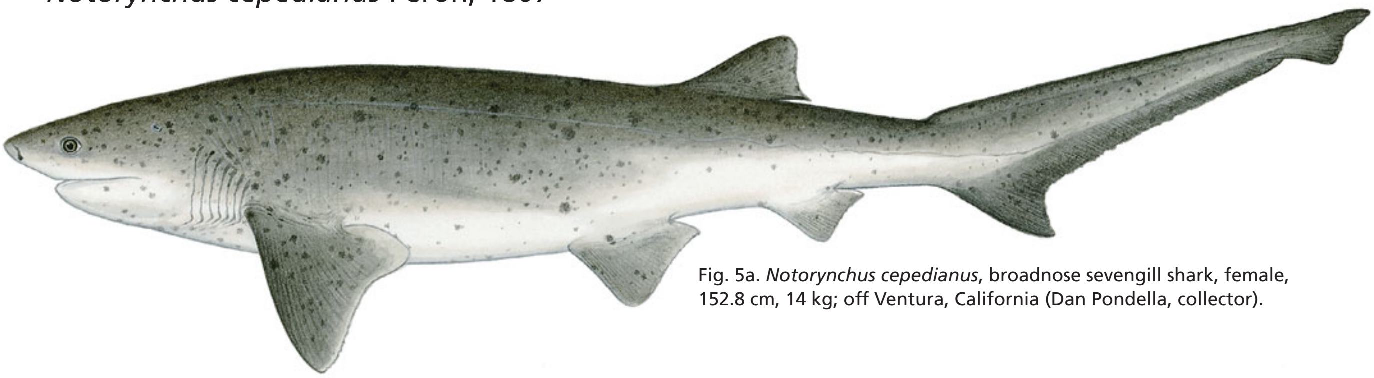


Fig. 5a. *Notorynchus cepedianus*, broadnose sevengill shark, female, 152.8 cm, 14 kg; off Ventura, California (Dan Pondella, collector).

Common name Broadnose sevengill shark, a recent name intended to distinguish it from the sharpnose sevengill, or perlon shark. The species is usually called the sevengill shark or simply "sevengill." In the past it was also called cow shark and mud shark (Walford 1935).

Spanish name *Tiburón manchado* (Mexico). The A.F.S. name is *tiburón pinto.*

Scientific name *Notorynchus cepedianus* Péron, 1807, in *Voyages Australes* 1: 337. *Notorynchus:* from the Greek *notos,* back, and *rhynchus,* from the Greek *rhynchos,* snout (the etymology or allusion is not clear); *cepedianus* honors the French naturalist B. G. E. de la Ville, Comte de Lacépède (1756–1825).

Synonyms *Heptanchus indicus* Müller and Henle, 1839; *Notidanus indicus* Agassiz, 1835; *Notorynchus maculatus* Ayres, 1855; *Notorhynchus borealis* Gill, 1864 [a]; *Heptranchias pectorosus* Garman, 1884; *Notorynchus macdonaldi* Whitley, 1931 [b]; *Notorynchus platycephalus* Fowler, 1925; among others. This species has been described under numerous names from diverse localities throughout the world. Bass et al. (1975a) considered it a single species with worldwide distribution, a view generally accepted today. In the recent past the name *Notorhynchus maculatus* Ayres, 1855 was widely used.

Identification The broadnose sevengill shark is recognized by its *seven gill slits, a flattened head with a broadly rounded snout* (see illustration), *a single dorsal fin,* and *numerous dark spots on the dorsal surface.* The upper teeth are long and pointed; the lower teeth are broad and sawlike. Counting the large teeth only, teeth number U: 7–1–7, L: 6–1–6. The dermal denticles have three points and a prominent central ridge that terminates in a long point. Sevengills are sandy gray to reddish brown above with dark spots, and whitish below. Albinos and partial albinos have been reported. Herald (1953) described a partial albino sevengill caught in the 1952 Coyote Point Derby, California. This specimen (now at the California Academy of Sciences, cataloged as CAS no. 20623) was white with numerous dark specks on its dorsal surface. The eye had an unpigmented iris and a dark blue pupil. Ebert (1985) described a "piebald" specimen caught in San Francisco Bay. It had a white background dorsally with unusually large spots 3–18 mm in diameter that covered the dorsal surface and extended onto the sides and upper surfaces of the fins. Its lower side was the normal olive brown. Ebert described the shark's eye color as "black consistent with normal eye coloration."

Similar species The sharpnose sevengill shark also has seven gill slits, but it has a pointed snout and lacks spots on its dorsal surface.

Range The broadnose sevengill shark is widely distributed in temperate waters. It has been reported from both sides of the Pacific Ocean, the South Atlantic, and the Indian Ocean. In the eastern Pacific, it has been reported from British Columbia to southern California (Walford 1935; Hart 1973), Colombia (Franke and Acero 1991), and Chile (Pequeño 1979). The report from Colombia of two specimens caught off the beach at Playa Blanca (Franke and Acero 1991) is interesting because the distribution of this species has been considered antitropical. In the western Pacific, it has been reported from southern Japan (Lindberg and Legeza 1967), Australia (Whitley 1940), and New Zealand (Phillipps 1935). In the South Atlantic, the sevengill has been reported from the Strait of Magellan (Guzman and Campodonico 1976), Argentina (Lahille 1928), Brazil (Sadowsky 1970), and Namibia (Bass et al. 1975a). In the Indian Ocean, it has been reported from South Africa (Bass et al. 1975a).

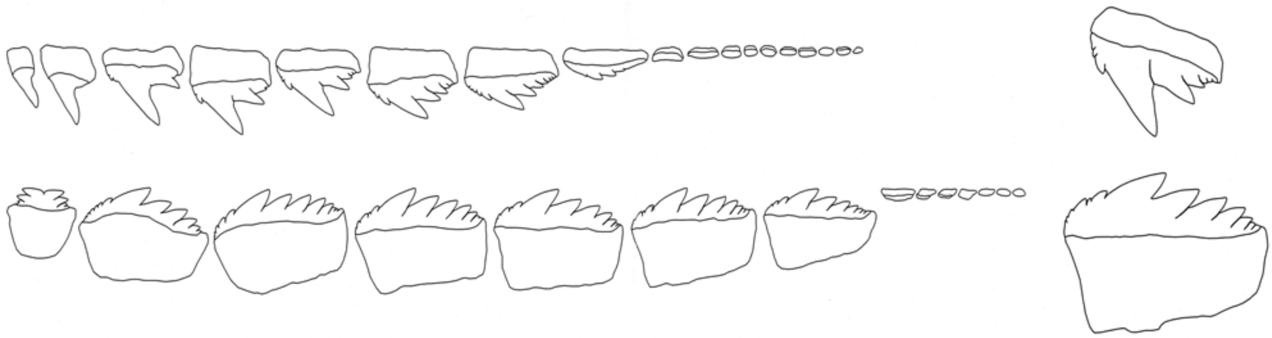


Fig. 5b. Teeth.

In North America the broadnose sevengill shark ranges from northern British Columbia (off Butedale and Bonilla Island; Hart 1973) to southern California (San Diego; Walford 1935). Bonham (1942) reported a 260-cm female found on the beach at Grayland, Grays Harbor County, Washington, and mentioned that the species is not commonly recorded from the state. Barnhart (1936) noted that it was only occasionally taken off San Diego, but rather commonly from Monterey to Washington. Roedel (1953) stated that the sevengill shark was common in San Francisco, Tomales, and Monterey bays.

Size and weight Sevengill sharks reach about 300 cm. Most sevengills caught are juveniles of 70–125 cm and 2–9 kg. A 197-cm adult male weighed 35 kg. Herald (1968) recorded the capture of a 264-cm female weighing 107 kg in San Francisco Bay in March 1966. Van Dykhuizen et al. (1998) stated that a female caught in Humboldt Bay, California, measured 295 cm and weighed 125 kg. Ebert (1989) noted that the heaviest female sevengill shark recorded was 291 cm and 182 kg.

Biology The sevengill is a common, large shark of the shallow coastal bays of central California. It is the only member of the family Hexanchidae that lives in shallow coastal waters; all other sixgill and sevengill sharks generally inhabit deep waters. Herald (1953) relates that, at the Sixth Coyote Point Shark Derby, held 14 September 1952, with the fishing limited to South San Francisco Bay between 7 A.M. and 3 P.M., the 1,484 registered fishermen caught 1,871 sharks, of which 301 (16%) were sevengills. Despite its abundance, the biology of the sevengill shark is poorly understood, and

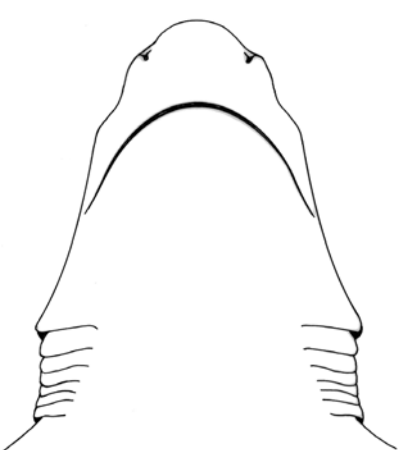


Fig. 5c. Snout.

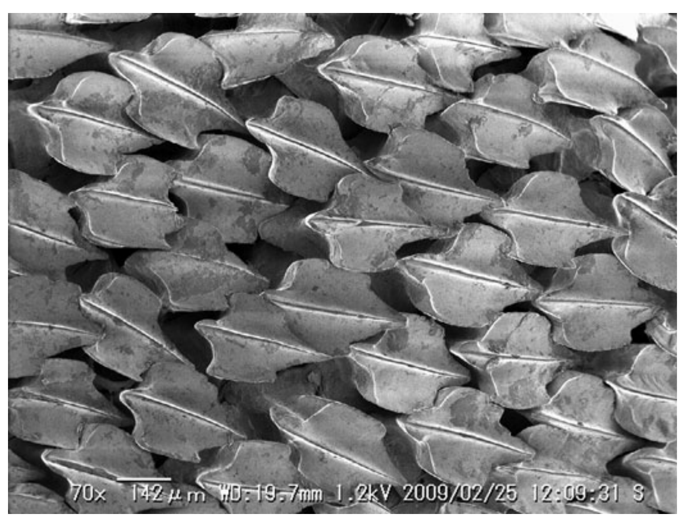


Fig. 5d. Dermal denticles.

much of what has been written about it is anecdotal or based on questionable old data. However, its anatomy is well known thanks to the extensive work of J. Frank Daniel in the early 1900s in California. Much of Daniel's work was later published in his book *The Elasmobranch Fishes* (Daniel 1934), which remains a useful anatomical reference.

Nearly all sevengills caught in the shallow bays of California are immature. Herald and Ripley (1951) examined 37 of 59 specimens caught in a 1950 shark derby in San Francisco Bay, and all were juveniles. According to these authors, sevengill sharks apparently leave the bay by the time they reach about 170 cm and 23 kg, which might account for the rarity of gravid females in the literature.

Ebert (1991a) observed sevengill sharks foraging in the shallow mudflats of Humboldt Bay, California, in the predawn hours during spring tides. They usually moved into the deeper channels after sunrise.

Diet: According to Ebert (1989), the sevengill shark is an apex predator in the ecosystem of the northern California bays, preying on numerous other elasmobranchs, bony fishes, and marine mammals. The species preys on at least five species of sharks and rays, with the brown smoothhound (*Mustelus henlei*) being the most important. Other prey species reported by Ebert (1989, 1991a) include the Pacific lamprey (*Lampetra tridentata*), leopard shark (*Triakis semifasciata*), bat ray (*Myliobatis californica*), big skate (*Raja binoculata*), jack smelt (*Atherinopsis californiensis*), salmon (*Oncorhynchus* sp.), white surf perch (*Phanerodon furcatus*), and California sea lion (*Zalophus californianus*). Ebert (1991b) also found that South African sevengill sharks fed on numerous species of sharks and rays.

Two authors have described the homing ability of the sevengill. Ebert (1996) stated that a large specimen estimated at 300 cm was recaptured at the tagging site 730 days later. Van Dykhuizen et al. (1998) discussed a female sevengill collected in Humboldt Bay on 23 July 1990. It measured about 298 cm and was estimated at 112–135 kg. The shark was displayed at Monterey Bay Aquarium until 16 June 1994, when it was released in Monterey Bay because of abrasions caused by collisions with the aquarium windows. Tagged prior to release, the shark was recaptured 845 days later in Humboldt Bay, 503 km north of the release location.

Size at maturity

Males: Size at maturity is not precisely known because most authors have used poor or confusing criteria to define maturity. Herald (1968) stated that a specimen 197.4 cm and 34.5 kg was the youngest mature sevengill on record and gave the size of the testes as 179 mm with a diameter of 39 mm, but did not elaborate further on the criteria used to determine maturity. Compagno (1984a) reported that males mature at 150–180 cm, but the source of this information was unclear. Ebert (1989) stated that all male sevengill sharks larger than 150 cm that he had examined were mature. However, he judged maturity based on the abrupt increase in clasper length that occurs at that body length and on development of the "clasper sac mechanism" but did not demonstrate the correlation of clasper size with calcification or maturity. Although clasper elongation provides an indication of approaching maturity, it is not a definitive indicator. This is because the claspers usually elongate well before the animal reaches maturity (Castro 1996). Likewise, the presence of sperm alone is not a good criterion for maturity, because in many species sperm production precedes clasper calcification (Castro 1996), and sperm production is also dependent on the stage of the reproductive cycle. Ebert later (1996) adopted the criterion of calcification of the "terminal cartilage elements" of the clasper, revising the size at maturity to 155 cm.

Females: Size at maturity is not known precisely because gravid females have seldom been encountered or reported. Bass et al. (1975a) mentioned having traced records of two mature females of 209 and about 192 cm, the condition of maturity being perhaps anecdotal. Compagno (1984a) wrote that females mature at 192–208 cm, probably based on the literature. However, Ebert (1986a) stated that the smallest mature female was 268 cm and weighed 127.3 kg, based on oocyte diameter. Later, Ebert (1989) stated that females mature at about 250 cm and weigh in excess of 91 kg, predicted on seeing a female with 75-mm oocytes and uterine eggs (D. Ebert, pers. comm., July 2003).

Reproduction The sevengill shark is an aplacental viviparous species. As in most primitive sharks, females have two functional ovaries of equal size (Daniel 1934). Beyond this, there is little information on its reproductive processes, despite the abundance of sevengills in coastal California waters. Bass et al. (1975a) were unable to find any records of embryos, and more than a quarter-century later, I have found only one vague report. Ebert (1989) mentioned that a female examined in May contained 82 near-term young and had no developed oocytes in the ovaries. From this observation he speculated that female sevengill sharks give birth every 18–24 months. This conjecture was based on "Herald and Ripley's (1951) speculation that sevengills enter San Francisco Bay for breeding is correct, then the time from parturition to fertilization may be from 6 to 12 months. Additionally, based on Holden's (1974) calculations for *Hexanchus griseus,* the time from fertilization to parturition (gestation) would extend another year. Therefore, after first parturition adult female sevengill sharks would give birth every 18 to 24 months."(Ebert 1989:107) This is all highly speculative. All that can really be said about the reproductive cycle of the sevengill is that the ovarian cycle and gestation are not concurrent, and that the cycle is possibly biennial, considering that many other species have biennial cycles. The gestation period must be determined empirically; it cannot be extrapolated from Holden's (1974) calculations of the length of gestation for the sixgill shark (*H. griseus*), a different species living in a different environment.

Size at birth: According to Ebert (1989) the young are born at a length of about 45 cm.

Brood size: Broods appear to be large. Herald (1968) reported that a 264-cm gravid female of 107 kg contained 83 oocytes each about 51 mm in diameter. Another female of 295 cm and 125 kg carried about 100 oocytes about 10 mm in diameter (Van Dykhuizen et al. 1998). Ebert (1989) refers to a female that contained 82 near-term embryos in May.

Nurseries It is not known where females give birth to their young. Juveniles are found in the shallow bays of central California.

Age and growth The sevengill shark has not been aged because of its uncalcified skeleton.

Relation to humans The sevengill is considered one of the most palatable sharks, and small amounts of meat are found in California markets. Sevengills are often exhibited in marine aquariums, where they can live for several months, but often require force-feeding (Herald 1968). Several authors have described the aggressiveness of sevengill sharks. Roedel and Ripley (1950: 41) observed that a sevengill "is a pugnacious shark that will attempt to bite its captors," and Herald and Ripley (1951: 326) stated that "the belligerent disposition of this shark as well as its tendency to use its jaws and sharp teeth on anything in the vicinity makes it a dangerous liability." Herald (1968) described how a sevengill attacked a diver at San Francisco's Steinhart Aquarium after the diver attempted to capture the shark by hand. The shark slipped from his grasp and swam away, then circled back toward the diver, who threw up his arm in front of his face. The sevengill bit his arm, removing a section of flesh. Herald (1968) also related other cases of divers and fishermen who experienced the business end of sevengill sharks they had provoked.

FAMILY ECHINORHINIDAE

The Bramble Sharks

The family Echinorhinidae includes two widely distributed species, the bramble shark and the prickly shark. These large, heavy-bodied sharks have two small, spineless dorsal fins, the first originating behind the pelvic fin origins; thin, bladelike multicuspid teeth (except juveniles) that are alike on both jaws (they are diagnostic for the genus); and a caudal fin without a subterminal notch. In both species the skin is covered with characteristic dermal denticles that are large and spinelike. Both species dwell in deep waters but regularly enter shallow waters. They have often been included in the Squaloidae because they lack an anal fin; however, most authors now place them in a separate family because of their many unique characteristics, such as the shape of their teeth and their peculiar skin denticles. The family consists of a single genus, *Echinorhinus.*

KEY TO THE ECHINORHINIDAE

1a. Very large, sparse, and irregularly distributed spinelike dermal denticles, some measuring up to 1.5 cm in diameter at the base and larger when two or more are joined together; denticle bases with a scalloped edge, and the spines are finely ridged.... .... **Bramble shark,** *Echinorhinus brucus* (p. 44).

1b. Dermal denticles less than 4 mm in diameter and never joined together, with stellate bases and heavily ridged spines .... **Prickly shark,** *Echinorhinus cookei* (p. 47).

BRAMBLE SHARK

Echinorhinus brucus (Bonnaterre, 1788)

Fig. 6a. *Echinorhinus brucus,* bramble shark, female, 261.4 cm, 81.36 kg; from Gulf of Mexico, edge of Mississippi Canyon, 27 km south of Grand Isle, Louisiana (James E. Flanner, collector).

Common name Bramble shark, an allusion to the enlarged, spinelike dermal denticles that cover its body. In the older English literature (e.g., Yarrell 1841; Couch 1868), it was known as the spinous or spiny shark.

Spanish name There are no native common names for it in the Spanish Caribbean or Mexico because of its rarity.

Scientific name *Echinorhinus brucus* (Bonnaterre, 1788), originally described as *Squalus brucus* in *Tableau Encyclopédique et Méthodique des Trois Règnes de la Nature, Ichthyologie:* 11. *Echinorhinus: echino* means spiny or prickly, from the Greek *echinos* (Latin *echinus*), a sea urchin, and *rhinus* is from the Greek *rhine,* the name of a shark with rough skin (also a file or rasp), both allusions to its spiny skin; *brucus:* New Latin from the Greek *brux,* the depths of the sea, or *bruchios,* of the depths of the sea, referring to the bramble shark's deep habitat.

Synonyms *Squalus spinosus* Gmelin, 1788; *Echinorhinus obesus* Smith, 1849; *Echinorhinus* (*Rubusqualus*) *mccoyi* Whitley, 1931 [a].

Identification The bramble shark has two small dorsal fins located far back on the body, a *first dorsal fin located over or behind the pelvic fin origin;* it *lacks an anal fin,* and the caudal fin lacks a subterminal notch. The teeth have several smooth-edged cusps, with the largest cusp curved toward the corners of the mouth; the teeth number U: 10 to 13–10 to 13, L: 11 to 13–11 to 13 and are similar in both jaws. It has *conspicuous, large, spinelike dermal denticles that are sparsely and irregularly distributed.* The denticles measure up to 1.5 cm in diameter at the base and larger when two or more are joined together; their bases have a scalloped edge, and the spine bases are finely ridged. In adults, large denticles cover the underside of the snout. Color varies from brown to black above, with purplish metallic hues; the undersides are paler. A fisherman who caught a specimen off Louisiana reported that when fresh it had a greenish glow that disappeared sometime after death. Some specimens have been reported with dark blotches.

Similar species The more common prickly shark has smaller, uniformly distributed dermal denticles, less than 4 mm in diameter and never joined together; the bases of its denticles are stellate, and the spines are heavily ridged.

Range The bramble shark is widely distributed in deep temperate and tropical waters. It has been reported numerous times from the eastern Atlantic and the western Indian Ocean (Smith, J. L. B. 1949; Nair and Lal Mohan 1971), but it is rare in the western Atlantic, and there are no records of its presence in the eastern Pacific. It is also present in the South Atlantic, but there are few records. There is one report from Brazil (Soto et al. 1995), one from Patagonia (Caille and Olsen 2000), and an unpublished account of a large specimen caught off Tobago in 1986. Unfortunately, only the tail of the Tobago specimen was brought to me for identification after the specimen had been discarded. However, its characteristic skin denticles made the identification obvious.

The bramble shark is a rare catch in North American waters. Only a handful of specimens have been reported in the western North Atlantic in the last 100 years. The first known North American specimen washed ashore at Provincetown, Massachusetts, in December 1878 (Goode and Bean 1879). The second report is of a 216-cm, 78-kg female caught some 120 km northeast of Cape Hatteras, North Carolina, at a depth of 187 m, and a bottom temperature of 10.6°C (Musick and McEachran 1969). The third reported specimen was a female 280 cm and 200 kg, caught some 69 km northeast of Cape Hatteras at 111 m, in March

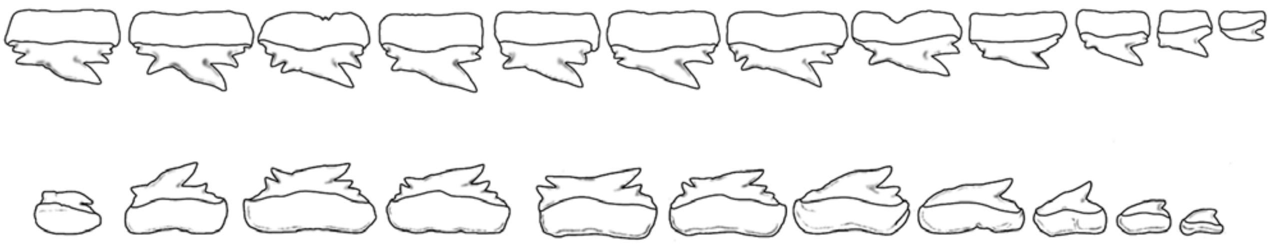


Fig. 6b. Teeth.

1992 (Schwartz 1993). Three recent unpublished records from the Gulf of Mexico (Louisiana) also exist. Two of these specimens are preserved at the Florida Museum of Natural History in Gainesville. The third was a 261-cm, 81-kg female captured at about 200 m, at the edge of Mississippi Canyon, 27 km south of Grand Isle, Louisiana, in December 1994. I examined this specimen while fresh, and it is illustrated in this work. It is preserved in the Tulane University Collections (cat. no. 172379).

Reports of bramble sharks from the western coast of North America are doubtful because of earlier confusion with the prickly shark, and early reports of bramble sharks there are about prickly sharks. There are no confirmed reports of bramble sharks in the eastern Pacific Ocean.

Size and weight The bramble shark is a heavy-bodied shark. The largest on record is a 280-cm female from North Carolina (Schwartz 1993), but the species is said to grow to 3.1 m (Compagno 1984a). Reported weights for females are 228 cm, 72 kg (gravid female, Ivory Coast); 261 cm, 78 kg; and 280 cm, 200 kg.

Biology The bramble shark is a widely distributed, but scarce, deep-water species that occasionally enters shallow coastal waters. The species has been known for centuries, but because of its scarcity, its life history is still poorly known. The first accurate depiction of the species, with a good accompanying anatomical description, is that of Turner (1875). Until the early 1960s, prickly sharks of the Pacific Ocean were mistaken for bramble sharks. Hence, pre-1960 publications referring to bramble sharks off the western coast of North America (e.g., Hubbs and Clark 1945; Collyer 1953) are actually about prickly sharks. Garrick, in 1960, published an excellent redescription of the prickly shark, clarifying distinctions between the two species (Garrick 1960a).

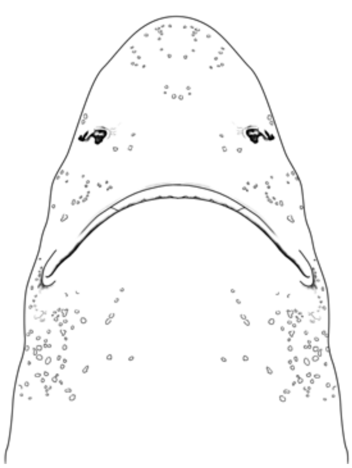


Fig. 6c. Snout.

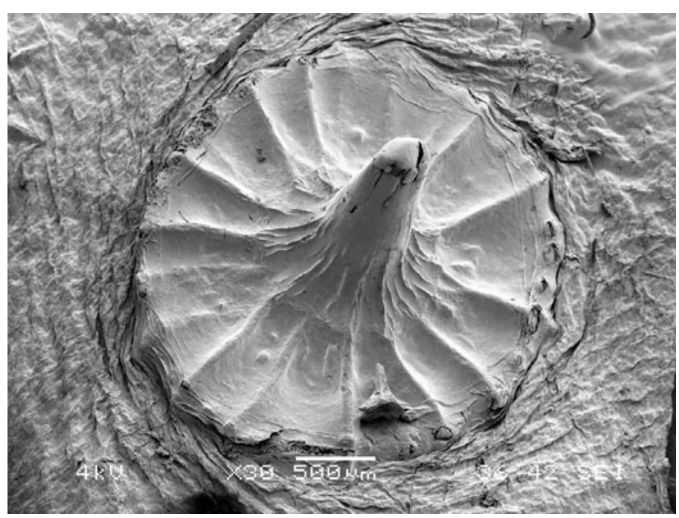


Fig. 6d. Dermal denticle.

Based on European catches, it is believed that bramble sharks usually dwell near the bottom at depths of 400–900 m, undertaking a summer migration to shallow waters of 20–200 m (Bauchot and Pras 1980). Little is known of the diet. The stomach of a Virginia specimen (Musick and McEachran 1969) contained one spiny dogfish about 54 cm long, a segment of the vertebral column of another spiny dogfish, and a hake (*Urophycis tenuis*) about 35 cm long.

There is evidence that the bramble shark was abundant in the eastern Atlantic in the eighteenth and nineteenth centuries, becoming scarcer afterward. Yarrell (1841) mentioned five captures on the English coast between 1830 and 1838, plus a dead specimen cast ashore in the Moray Firth, Scotland. Rappé (1984) listed 10 captures in the North Sea, all between 1830 and 1893, all during the summer. Rappé also mentioned that there were very few records of bramble sharks taken around the British Isles in the twentieth century and none in the North Sea, and that in the 1960s and 1970s, the species had been captured only once, near Cornwall in 1969. Wheeler (1969) in his work on fishes of the British Isles and northwestern Europe stated that, comparing the nineteenth-century records to those of the twentieth century, the bramble shark appeared to have become much rarer in northern waters. This scarcity has also been noted on the continental coasts. Quéro and Emonnet (1993) quoted references showing that that bramble sharks were regularly fished along the Arcachon coast of France during the eighteenth century and that they started to become rare there in the second half of the nineteenth century, although they were still common between Bidassoa and Adour. Quéro and Emonnet (1993) noted that in 25 years of observations, they had seen only one bramble shark in 1968, and knew of two others, one caught in 1981 and another landed at Santander, Spain. It is suspected that the decline in catches resulted from fishing mortality. It appears that the bramble shark is highly susceptible to overfishing, like many other sharks.

Size at maturity Unknown. The Ivory Coast female was pregnant at 228 cm.

Reproduction The bramble shark is an aplacental viviparous species. One female I examined had two active and well-developed ovaries. Silas and Selvaraj (1972) illustrated a 30-cm embryo but gave no details of the mother or its capture, other than that it was captured in April off India.

Size at birth: The young are probably born at about 40–50 cm.

Brood size: A female caught off southern Natal, South Africa, in April 1973 carried 24 embryos averaging 16.5 cm (Bass et al. 1976). A 228-cm female from Ivory Coast contained 15 young 62–68 mm, weighing about 250 g each (Cadenat and Blache 1981).

Nurseries Unknown.

Age and growth The species has not been aged because of its rarity. It is thought to be a long-lived species as a result of its deep-water habitat, large size, and apparent susceptibility to overfishing.

Relation to humans None. Given its rarity, catches should be preserved for scientific study.

PRICKLY SHARK

Echinorhinus cookei Pietschmann, 1928

Fig. 7a. *Echinorhinus cookei,* prickly shark, female, 235 cm, 103.4 kg; from Monterey Canyon, California (Cyndi Dawson, collector).

Common name Prickly shark, a reference to the thornlike dermal denticles that cover its body.

Spanish name *Tiburón espinoso* (Mexico). The A.F.S. name is *tiburón espinoso negro.* The color reference is without meaning.

Scientific name *Echinorhinus cookei* Pietschmann, 1928, in *Anzeiger der Akademie der Wissenschaften in Wien* (*Mathematisch-Naturwissenchaftliche Klasse*) 27: 36. Pietschmann actually wrote two accounts of the prickly shark, labeling both as new species descriptions. The original 1928 description in German is brief and lacks illustrations. It was followed in 1930 by a more extensive description in English of "*Echinorhinus cookei,* new species" in an article titled "Remarks on Pacific Fishes" (Pietschmann 1930) that includes illustrations of the teeth, dermal denticles, and the entire specimen. *Echinorhinus: echino* means spiny or prickly, from the Greek *echinos* (Latin *echinus*), a sea urchin, and *rhinus* is from the Greek *rhine,* the name of a shark with rough skin (also a file or rasp), both allusions to the spiny skin; *cookei:* latinized form of Cooke, after Dr. C. Montague Cooke Jr., a conchologist at the Bishop Museum.

Synonyms None.

Identification The prickly shark has two small dorsal fins located far back on the body, the *first dorsal fin located over or behind the pelvic fin origin.* It *lacks an anal fin,* and the tail lacks a subterminal notch. A conspicuous lateral line extends like an open furrow from just over the gills to the tail. The teeth have three to seven smooth-edged cusps, the longest cusp curved toward the corners of the mouth; they number U: 10 to 12–10 to 12, L: 11 to 14–11 to 14 and are similar in both jaws. The juveniles have single-cusped teeth. The body is *covered by very large dermal denticles,* with *stellate bases and strongly ridged spines.* These denticles measure up to 0.4 cm in diameter at the base; they are *uniformly distributed* over the body. In adults the underside of the snout has very small dermal denticles and is almost smooth. Color in life is brown to grayish brown, often with purplish hues above and paler below.

Similar species The bramble shark has larger, irregularly distributed denticles with rounded bases, scalloped edges, and finely ridged spinelike cusps.

Range The prickly shark inhabits tropical and temperate waters of the Pacific and Indian oceans. Numerous records indicate that it is distributed throughout the Pacific basin: New Zealand (Garrick 1960a), Australia (Last and Stevens 1994), Taiwan (Compagno 1984a), Japan (Taniuchi and Yanagisawa 1983), Hawaiian Islands (Pietschmann 1928, 1930; Borets 1986; Crow et al. 1996), California (Miller and Lea 1972), Mexico (Collyer 1953), Peru (Chirichigno 1963), and Chile (Flores and Rojas 1979).

In North America it has been reported from southern California to central Mexico (Hubbs and Clark 1945, as *E. brucus;* Miller and Lea 1972; Chávez-Ramos and Castro-Aguirre 1974; Aguirre et al. 2002). The prickly shark once was considered uncommon along the California coast. However, the exploration of Monterey Canyon has revealed that the species is at least locally abundant in summer and early fall (Crane and Heine 1992).

Size and weight The prickly shark attains a large size, possibly about 4 m. Garrick (1960a) mentioned a New Zealand (Moeraki) specimen believed to be about 4 m long. Later, Garrick and Moreland (1968) recorded a 298.5-cm specimen from Cook Strait, New Zealand. There are few available weights for prickly sharks: 267 cm, 192 kg; 295 cm, 222 kg; 305 cm, 266 kg. As Garrick (1960a) has pointed

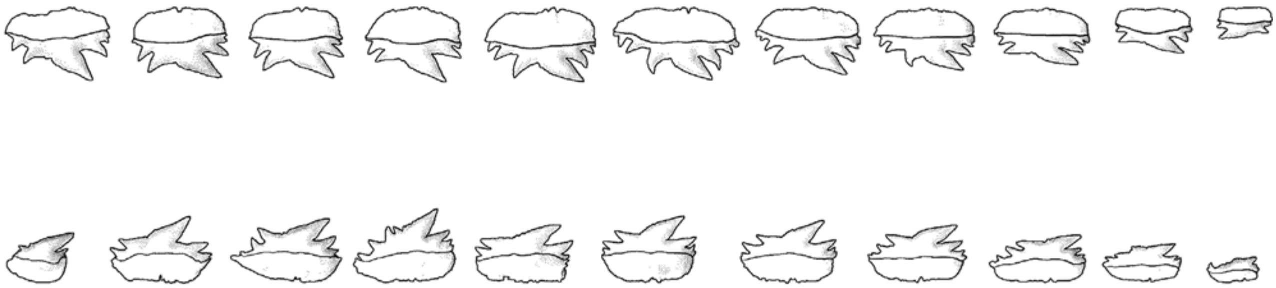


Fig. 7b. Teeth.

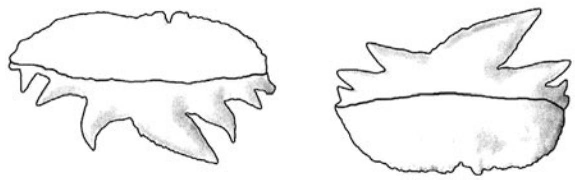


Fig. 7c. Teeth (detail).

out, the juveniles are quite slender when compared to the heavy-bodied adults.

Biology Although the prickly shark is fairly common off California, its habits are poorly known. Hubbs and Clark (1945: 67) first reported the species from California as a "bramble shark," presciently noting that "probably *Echinorhinus* will prove to be much less rare in California than the available data would seem to indicate." Prickly sharks continued to be mistaken for bramble sharks until the early 1960s. For this reason, publications prior to 1960 referring to bramble sharks off the western coast of North America (e.g., Hubbs and Clark 1945; Collyer 1953) are actually about the prickly shark. In 1960, Garrick published an excellent redescription of the prickly shark, clarifying the distinctions between the two species (Garrick 1960a).

Almost nothing is known of the habits of the prickly shark. It appears to be a deep-water species that frequently visits surface waters, perhaps seasonally. Prickly sharks have been observed by scuba divers in Monterey Canyon, Cali-

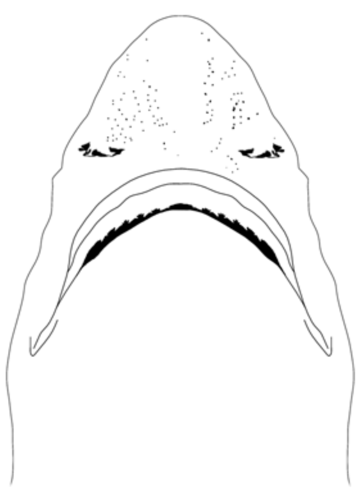


Fig. 7d. Snout.

Fig. 7e. Dermal denticles.