BIOLOGY OF SHARKS AND THEIR RELATIVES

THIRD EDITION

Edited by

Jeffrey C. Carrier

Colin A. Simpfendorfer

Michael R. Heithaus

Kara E. Yopak

CRC Press
Taylor & Francis Group

Praise for the Book

With this third edition of the information-packed series *Biology of Sharks and Their Relatives*, editors Carrier *et al.* have again recruited leading researchers in the field to provide the latest technical information in elasmobranch science. Once characterized as perhaps the least understood group of vertebrates, sharks and their relatives have come under intense study over the past five decades, culminating in the extensive knowledge presented in this volume. From more traditional topics in elasmobranch biology to the timely issues of conservation and climate change, this book shows we can no longer say that sharks are poorly understood. Clearly, our field has come a long way, and it's all here in this comprehensive reference.

Dr. Robert E. Hueter
Mote Marine Laboratory Senior Scientist Emeritus
and OCEARCH Chief Scientist

One could not hope for a more comprehensive presentation of current research in traditional and contemporary areas of study pertaining to sharks and their relatives. I anticipate that every student of this fascinating group of animals, no matter the stage of their career, will want to own this book.

Dr. Sheldon Dudley
Department of Forestry, Fisheries and the Environment
Cape Town, South Africa

This is the premier book on the biology of sharks and their relatives. The editors have gathered the world's top experts on each topic to provide comprehensive insights into the diversity, lives, and conservation of this fascinating group. The book covers the sharks living in habitats from the Amazon River, to coral reefs, down to the abyssal plains, while also reviewing, updating, and setting future research directions across many fields of study, from paleontology to neurobiology. The chapters are clearly presented to provide an entry point for students, naturalists, or other people who are interested in these amazing species, and it will be the go-to resource for shark researchers for years to come.

Dr. Simon J. Pierce
Co-founder and Principal Scientist
Marine Megafauna Foundation

Whether you are a scientist, policymaker, or advocate, *Biology of Sharks and Their Relatives*, is essential reading. Beginning with a review of the evolutionary history of Chondrichthyans, followed by an examination of their biology, physiology, ecology, and conservation policies and ending with a review of the impacts of climate change, this book should be the first stop in the search for answers to the threats facing these critically important animals.

Lee Crockett
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Dedication

We respectfully dedicate this edition of Biology of Sharks and Their Relatives *to our friend and colleague, Jack Musick, who passed away February 2021. Jack was a co-editor on the first two editions and the second volume of the series. He did not wish to be credited on this edition but instead wanted to see each of the manuscripts so that he could stay current with the wide range of disciplines that we feature in the books. He made no secret of his quest to perfect his fly-fishing exploits for every salmonid of North America, and we knew that his passion for the rivers and streams rivaled his passion for the sharks and rays he studied during his decades of research. We were honored that he would still consider carrying the drafts of the manuscripts to the riverbanks to read between casts!*

Jack's greatest legacy will not be his hundreds of publications or his lifetime devoted to the conservation and management of elasmobranchs and sea turtles, although his contributions to these fields are enormous. Rather, he leaves to science an incredible group of former students who studied with Jack and developed into leading scientists themselves and who continue to carry forward his curiosity and scientific rigor, a fitting tribute to one of our foremost elasmobranch scholars with whom we were honored to collaborate. We will miss him dearly.

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Front cover: This image of a group of Silky Sharks (*Carcharhinus falciformis*) was taken at sunset in Gardens of the Queen, Cuba, an archipelago 60 miles off the southeast coast of Cuba that has been a protected marine park since 1996. Photograph courtesy of Tanya Houppermans.

Back cover: (Left) *Chimaera monstrosa*, also known as a ghost shark, chimaera, rabbitfish, or ratfish, is a deepwater holocephalan from the Northeast Atlantic Ocean and Mediterranean Sea. This image was taken in Trondheim Fjord in Norway, where a turbid surface layer creates especially dark conditions that allows light-sensitive deepwater species to enter relatively shallow water. Photograph courtesy of Andy Murch. (Right) A Southern Stingray (*Hypanus americanus*) cruises over the sand flats off the coast of Gun Cay, The Bahamas. This tiny cay is just south of Bimini and is approximately 50 miles from the United States. This shallow area at the edge of seagrass meadows allows for the rays to easily forage for food. Photograph courtesy of Duncan Brake.

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Contents

Preface

Biology of Sharks and Their Relatives had its origin in the backcountry of the Florida Keys in 2001 when Mike Heithaus and I spent time between longline sets for small sharks lamenting the lack of a general text on shark biology. We agreed that a truly wide-ranging text had not been produced since Perry Gilbert's *Sharks, Skates, and Rays* of the late 1960s. Although some books had been written since his book made its appearance, few were really of the same scope.

We spent several days developing what we thought we would like to see in a comprehensive examination of the state of shark research and proceeded to create a hypothetical Table of Contents. When we had worked ourselves into a feeding frenzy of sorts, I contacted CRC Press, based mostly on a recommendation from Dr. David Evans, my former graduate advisor at the University of Miami, who had written *The Physiology of Fishes* for CRC, to inquire whether they might be interested in such a text on sharks. We were told that the idea sounded promising and that Jack Musick, who had written several books on sea turtle biology for CRC Press, had also mentioned the need for such a collection of papers. We contacted Jack to gather his thoughts and gauge his interest in participating in such a project. He agreed with the concept and expressed his interest in co-editing such a text. We developed the concept and prospectus, submitted it to CRC, and a week later we were given the go-ahead. Now, 20 years later, we are presenting the third edition, which accompanies a second volume, *Sharks and Their Relatives II: Biodiversity, Adaptive Physiology, and Conservation*, published a decade ago, as well.

This third edition sees some changes to the editorial team. Jack, who had worked on the first two editions, retired in 2008 and chose not to be an editor on this edition, but he retained a strong interest in the content. It took two new editors to replace Jack's encyclopedic knowledge. The new editors, Kara Yopak and Colin Simpfendorfer, have a wealth of experience regarding the biology of sharks and their relatives. Kara is an associate professor at the University of North Carolina Wilmington and specializes in shark neuroanatomy, brain evolution, and bioimaging. Colin is an adjunct professor at James Cook University in Australia and works on shark life history, ecology, management, and conservation. The new editors bring an incredible breadth and depth of knowledge to the editorial group and have unquestionably added to the quality of the work.

In this edition, we have strived to present both current research and traditional models in order to prepare future researchers by providing them with solid historical foundations in shark research, in addition to presenting current trends from which to develop new frontiers in their own work. It has always been our goal to feature the most prominent scientists in every discipline and to intentionally include promising young scholars who will provide the future directions for studies of these intriguing animals. Our chapters are well founded in the most current research, and the reference sections of every chapter serve as incomparable resources for young investigators seeking a sound background for their own studies.

This edition continues that trend. We have updated traditional areas of study such as age and growth, reproduction, taxonomy and systematics, sensory biology, and ecology with contemporary research that incorporates emerging techniques including contributions from molecular genetics, exploratory techniques in artificial insemination, and the rapidly expanding fields of satellite tracking, remote sensing, accelerometry, and imaging. We have also included extensive studies of health, stress, disease and pathology, and social structure, all areas of coverage new to the series, and we continue to explore elasmobranch ecological roles and interactions with their habitats.

We conclude this edition with the most comprehensive review of conservation policies, management, and strategies that we have ever featured to examine approaches to better protect dwindling elasmobranch resources. Finally, we feature a consideration of the potential effects of impending climate change, a fitting conclusion that provides new demands for studies of adaptability and offers cautions for future conflicts faced by aquatic and terrestrial organisms alike.

As we present this compendium to our readers, we are left to ponder what new technologies and disciplines will inform the contents of the next edition and what unseen challenges await shark research in the coming decades.

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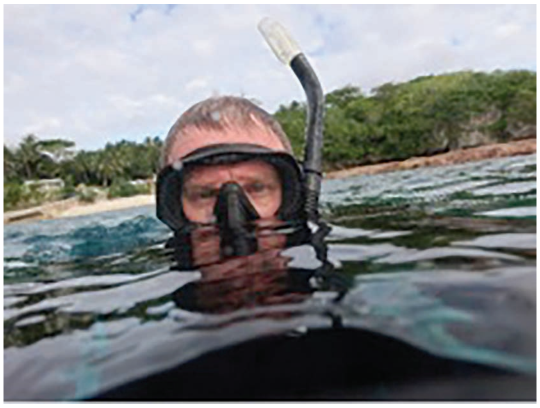
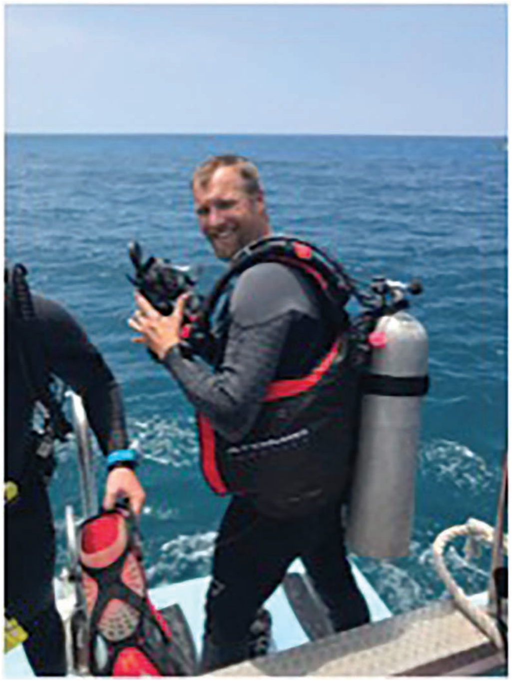
Editors

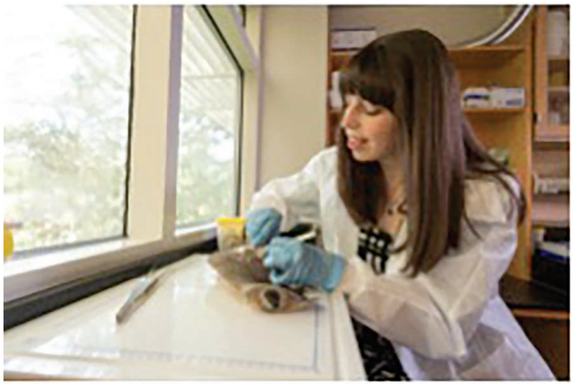


Jeffrey C. Carrier, PhD, is professor emeritus of biology at Albion College, Michigan, where he was a faculty member from 1979 to 2010. He earned a bachelor of science degree in 1970 from the University of Miami and completed a doctorate in biology from the University of Miami in 1974. While at Albion College, Dr. Carrier received multiple awards for teaching and scholarship and held endowed professorships in biology. His primary research interests center on various aspects of the physiology and ecology of nurse sharks in the Florida Keys. His most recent work has investigated the reproductive biology and mating behaviors of this species in a long-term study from an isolated region of the Florida Keys. Dr. Carrier has been a long-time member of the American Elasmobranch Society, the American Society of Ichthyologists and Herpetologists, Sigma Xi, the Society for Animal Behavior, and the Council on Undergraduate Research. He served multiple terms as president of the American Elasmobranch Society and received several distinguished service awards from the society. He holds an appointment as an adjunct research scientist with Mote Marine Laboratory's Center for Shark Research. In addition to his publications in the scientific literature, he has written and edited six previously published books on sharks and their biology, as well as numerous articles in the popular press.

Colin Simpfendorfer, PhD, is an adjunct professor in the College of Science and Engineering at James Cook University and Institute of Marine and Antarctic Science at the University of Tasmania. He has also worked at in the Center for Shark Research at Mote Marine Laboratory in Sarasota, Florida, and the Shark Fisheries Section of the Western Australian Department of Fisheries, Perth, Australia. He received his bachelor of science degree in marine biology and zoology in 1986 and doctorate in fisheries science in 1993, both from James Cook University. He has spent his career studying the life history, ecology, status, and conservation of sharks and rays with the principle aim of providing scientific information for improving their management. He regularly provides scientific advice to governments, nongovernmental organizations, and industry. Dr. Simpfendorfer is an author of over 250 peer-reviewed scientific papers on sharks and rays and has trained more than 30 master of science and doctoral students (some of which have authored or co-authored chapters in this book). He was a co-chair of the IUCN Species Survival Commission Shark Specialist Group from 2012 to 2020, working to improve the conservation status of this important group of ocean predators by assessing their status, developing conservation plans, and delivering quality scientific information to decision makers. He also serves on many national and international committees, including Australia's national Threatened Species Scientific Committee.



Michael R. Heithaus, PhD, is a professor in the Department of Biological Sciences and dean of the College of Arts, Sciences and Education at Florida International University (FIU) in Miami, Florida, where he has been a faculty member since 2003. He received his bachelor of arts degree in biology in 1995 from Oberlin College, Ohio, and his doctorate in 2001 from Simon Fraser University, Burnaby, British Columbia, Canada. He was a postdoctoral scientist and staff scientist at the Center for Shark Research at Mote Marine Laboratory and also served as a research fellow at the National Geographic Society's Remote Imaging Department. At FIU, Dr. Heithaus served as the director of the Marine Sciences Program before becoming the director of the School of Environment, Arts, and Society. Dr. Heithaus is a behavioral and community ecologist. His main research interests are in understanding the ecological roles and importance of large predators, especially their potential to impact community structure through non-consumptive effects. His work also explores the factors influencing behavioral decisions, especially of large marine taxa, including marine mammals, sharks and rays, and sea turtles, and the importance of individual variation in behavior in shaping ecological interactions. Dr. Heithaus is the co-lead of the Global FinPrint project, a worldwide survey of elasmobranchs on coral reefs. His lab is engaged in marine conservation and research projects around the world and has ongoing long-term projects in Shark Bay, Australia, and the coastal Everglades of southwest Florida. Dr. Heithaus is an author of over 200 peer-reviewed scientific papers and book chapters. He is a member of the Inaugural Board of the Academy of Science, Engineering and Medicine of Florida.



Kara E. Yopak, PhD, is an associate professor in the Department of Biology and Marine Biology at the University of North Carolina Wilmington (UNCW). Dr. Yopak received her bachelor of arts degree (biology with a specialization in marine science) in 2002 from Boston University and completed her doctorate in sensory neuroethology in 2007 at the University of Auckland, New Zealand. She was a postdoctoral scientist at the University of California–San Diego and later a research assistant professor at the University of Western Australia in Perth. She is currently director of the UNCW ZoMBiE Lab (Zootomical Morphology of the Brain and its Evolution; http://yopaklab.com/), whose research focuses on the evolution of the brain within and across cartilaginous fishes, particularly the ways in which variation in brain size, structure, and cellular composition underly complex behaviors and sensory specialization. Dr. Yopak and her students use novel techniques, such as magnetic resonance imaging, computed tomography, and flow cytometry, in conjunction with traditional neuroanatomical methods, to explore the processes driving brain evolution in this unique group of fishes. Her current collection of fish nervous system tissue includes over 1000 specimens (and counting!). Dr. Yopak is a longtime member of the American Elasmobranch Society (for which she serves a number of administrative roles, including several terms on the board of directors), as well as the Society for Integrative and Comparative Biology and the J.B. Johnston Club for Evolutionary Neuroscience. She is currently co-editor of the journal *Brain, Behavior and Evolution* and is a proud mentor for the Gills Club, a signature action by the Atlantic White Shark Conservancy that encourages young girls with a passion for shark biology. Dr. Yopak has contributed to chapters in previous editions of this book as an author and was honored to be invited to serve as a co-editor of this exciting new edition. (Photograph courtesy of Jeff Janowski, University of North Carolina Wilmington.)

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1 Bridging the Gap Between Chondrichthyan Paleobiology and Biology

Lisa B. Whitenack, Sora L. Kim, and Elizabeth C. Sibert

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ABSTRACT

Chondrichthyans have a long evolutionary history, reaching back over 450 million years. Despite the longevity of the chondrichthyan fossil record, it is remarkably incomplete. This chapter focuses on chondrichthyan paleobiology, which, as the name suggests, applies techniques from both biology and geology to understand the biological processes and ecology of the once-living organism. Paleobiology is highly interdisciplinary, employing tools from mathematics, computer science, physics, chemistry, and engineering. The chapter begins with an overview of chondrichthyan evolutionary history, from the relationships of early chondrichthyans through the implications of fossil chondrichthyan diversity patterns on today's chondrichthyans. The chapter then discusses what scientists know about fossil chondrichthyan biology in areas such as macroevolutionary trends, functional diversity, ecology, and biomechanics. Finally, the chapter discusses how the fossil record can be leveraged for conservation efforts. Knowledge of how organisms responded to and recovered from times of environmental disturbance or higher extinction rates can help us understand how contemporary organisms are responding to the current mass extinction crisis and how negative impacts might be mitigated. Integration across biology and paleobiology will further our collective knowledge of chondrichthyan ecology and evolutionary history to inform our conservation and management policies, as well as to mitigate anthropogenic impacts.

1.1 INTRODUCTION

Scientific studies of living (extant) chondrichthyans cover almost every imaginable subfield of biology, whether they are the particular subject of interest or are being used as a model organism. The table of contents of this book reflects the former, covering everything from molecular (e.g., biochemistry and genetics) to broad ecosystem studies and considering the past, present, and future of chondrichthyans on Earth. Here,

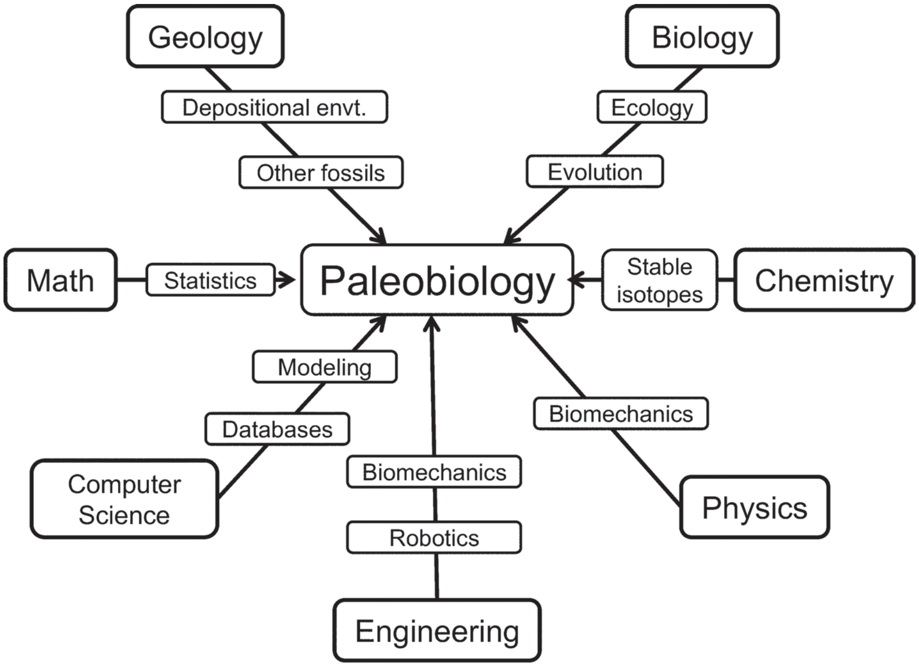

FIGURE 1.1 Disciplines and subdisciplines that are used in the field of paleobiology.

we focus on chondrichthyan paleobiology, which, as a discipline, is different from paleontology. Paleontology focuses on taxonomy; it treats chondrichthyan fossils as sediments in an effort to better understand depositional environments. Paleobiology, as the name suggests, applies techniques from both biology and geology to understand the biological processes and ecology of the once-living organism.

Chondrichthyans have a long evolutionary history, reaching back over 450 million years (Ma) (Andreev *et al.* 2015; Burrow *et al.* 2019; Ginter 2004; Sansom *et al.* 2012; Turner 2004). Throughout their time on the planet, these charismatic vertebrates have repeatedly filled a wide variety of ecological niches, ranging far beyond the pelagic predators of today's best known shark communities. Despite the longevity of the chondrichthyan fossil record, it is remarkably incomplete. This is not a phenomenon that is unique to chondrichthyans; most paleontologists have heard some variant of the statement "less than 1% of all organisms that have lived on Earth have been preserved in the fossil record."

A recent study by Shiffman *et al.* (2020) examined the over 30-year history of abstracts submitted to the American Elasmobranch Society (AES) and found that the most common research areas for members of this society, such as reproductive biology, movement/telemetry, age and growth, and population genetics, are linked to conservation and fisheries management. If we take a broader view beyond AES and search Google Scholar for "Chondrichthyes," limiting our search to "2019 through 2021," we come up with about 3400 results. A similar search for "shark" yields about 17,000 results. In addition to many of the themes identified by Shiffman *et al.* (2020), we also see studies on micro- to macroevolutionary processes (e.g., Fonseca *et al.* 2019; Jambura *et al.* 2020), genomics (e.g., Weber *et al.* 2020), developmental biology (e.g., Pears *et al.* 2020; Smith *et al.* 2020), parasitology (e.g., Schaeffner and Smit 2019), and even the production of biodiesel from shark liver oil (Al Hatrooshi *et al.* 2020). This is also where we see the studies that fall under the category of paleontology. Most of those papers describe new species or genera from various times during the last 450 Ma (e.g., Brito *et al.* 2019; Sokolskyi and Guinot 2021; Stumpf and Kriwet 2019; Villalobos-Segura *et al.* 2019).

Like many other fields of biology, paleobiology is highly interdisciplinary and employs tools from mathematics, computer science, physics, chemistry, and engineering (Figure 1.1). In fact, if we compare the description of the journal *Paleobiology* to the sections of this book, we find many of the same themes: evolution, morphology, molecular biology, ecology, adaptation, and extinction. There are numerous similarities in what these two groups of scientists are studying; however, the language and scope, both temporal and spatial, can be barriers to collaboration (Table 1.1). For example, marine conservationists and conservation paleobiologists agree on conservation goals, such as establishing baselines, and that long-term data should be used for these goals. However, the definition of "long-term" differs, with conservation paleobiologists operating on the geological time scale, considering thousands or millions of years at a time, and marine conservation scientists operating on the order of decades (Smith *et al.* 2018).

The overlap in research themes suggests an opportunity to bring two groups of researchers together. With this in mind, we have written this chapter to serve as a resource for those who are new to the chondrichthyan fossil record, those who are interested in how to apply techniques from neontology (biology of living organisms) to extinct chondrichthyans, and

TABLE 1.1
Concepts and Areas of Study Common to Neontology and Paleobiology and Data Used in Each Field

	Data Type	
Concept	**Neontology**	**Paleobiology**
Taxonomy and systematics	Molecular data and morphology	Morphology (mostly tooth shape)
Evolution and phylogeny	Molecular data and morphology	Morphology (mostly tooth shape)
Reproductive biology	Physiology	Morphology of reproductive anatomy when preserved, fossilized egg cases, fossilized fetal material
Age and growth, life history	Embryology, vertebral rings	Vertebral rings, tooth size
Biomechanics and functional morphology	Anatomy, morphology, performance testing, models	Anatomy, morphology, performance testing, models
Diet and feeding ecology	Behavioral data, stomach contents, stable isotopes, food web mapping and dynamics	Stable isotopes (geochemistry), trace fossils, concurrent fossils as potential prey (assemblage descriptions), tooth morphology
Community ecology	Biodiversity indices	Assemblage description, community structure, biodiversity indices
Population biology	Population dynamics	Body size distribution, latitudinal gradients
Biogeography and distribution	Movement and telemetry data, population genetics, latitudinal gradients	Body size distribution, latitudinal gradients, data from the Paleobiology Database
Conservation and management	Population assessments, movement and telemetry data, ecological data	Extinction and speciation rates

Note: This concept list is based on the contents of this volume and Shiffman *et al.* (2020).

those who are interested in how to leverage the extensive chondrichthyan evolutionary history (over 450 Ma, which includes surviving several mass extinction events) for their research on extant chondrichthyans. We begin with a synopsis of the chondrichthyan fossil record, followed by an overview of chondrichthyan paleobiology. We end by examining the ways in which the chondrichthyan fossil record can be leveraged to provide new insights into chondrichthyan conservation biology.

1.2 THE NATURE OF THE CHONDRICHTHYAN FOSSIL RECORD

A number of factors determine an organism's likelihood of fossilization, including the supply and durability of remains, nature of the pre-burial environment, rate and permanence of burial, diagenetic (fossilization) conditions, and the fate of the larger sedimentary body that remains are buried in (Behrensmeyer *et al.* 2000). The factors determining fossilization outside of supply are largely determined by the physical, chemical, and biological components of the environment in which the organism dies (or where teeth are shed, in the case of sharks) (Behrensmeyer *et al.* 2000). Burial is the first hurdle to overcome. Without rapid burial, remains are exposed to environmental conditions that may cause too much damage, and tissues are not subject to the chemical processes necessary for fossilization. Biological agents largely determine whether remains are buried or remain buried before they are destroyed by exposure to destructive forces; the actions of bioturbators, bioeroders, and scavengers tend to decrease the likelihood of fossilization, whereas organisms that form dens or burrows may increase the likelihood of fossilization if they bury remains as part of the burrow-building process (Behrensmeyer *et al.* 2000; Feichtinger *et al.* 2020a; Maisch *et al.* 2019; Underwood *et al.* 1999). Physical reworking from storm events or wave action can also prevent remains from staying buried. Provided that remains stay buried, chemical alteration is the next step. This process can occur through physical means, such as seawater infiltration, or can be aided by microbes (Carpenter 2005; Hedges 2002; Nemliher *et al.* 2004; Wang and Cerling 1994). In the ideal scenario, the remains are made more stable or durable through the replacement of materials with harder minerals, although replacement is not required for preservation in the fossil record, and some chondrichthyan remains retain their original bioapatite. Finally, the rocks and sediments that encase these altered remains must remain intact. Geologic processes, such as structural deformation and erosion from glaciers, water, or wind, can remove rock strata and their fossils from the geographic record entirely.

Many chondrichthyans fare well in terms of their input into the potential fossil record, although some parts of the skeleton are far less likely to fossilize than others (Figures 1.2 and 1.3). Whole-body fossils of chondrichthyans are quite rare (but see Ehret *et al.* 2009; Grogan *et al.* 2012; Marramà *et al.* 2018; Williams 2001), because most skeletal cartilage is poorly mineralized. Teeth, on the other hand, are the most common chondrichthyan fossil (Cappetta 1987; Cappetta and Schultze 2012; Ginter *et al.* 2010). Teeth in elasmobranchs and other extinct groups are constantly shed throughout their lifetimes and at a fairly high rate (Moss 1967; Luer *et al.* 1990; Reif *et al.* 1978; Wass 1973). Teeth are extremely durable, thanks to the mineral-heavy composition of enameloid and dentine (Enax *et al.* 2012, 2014; van Vuuren *et al.* 2015; Whitenack *et*

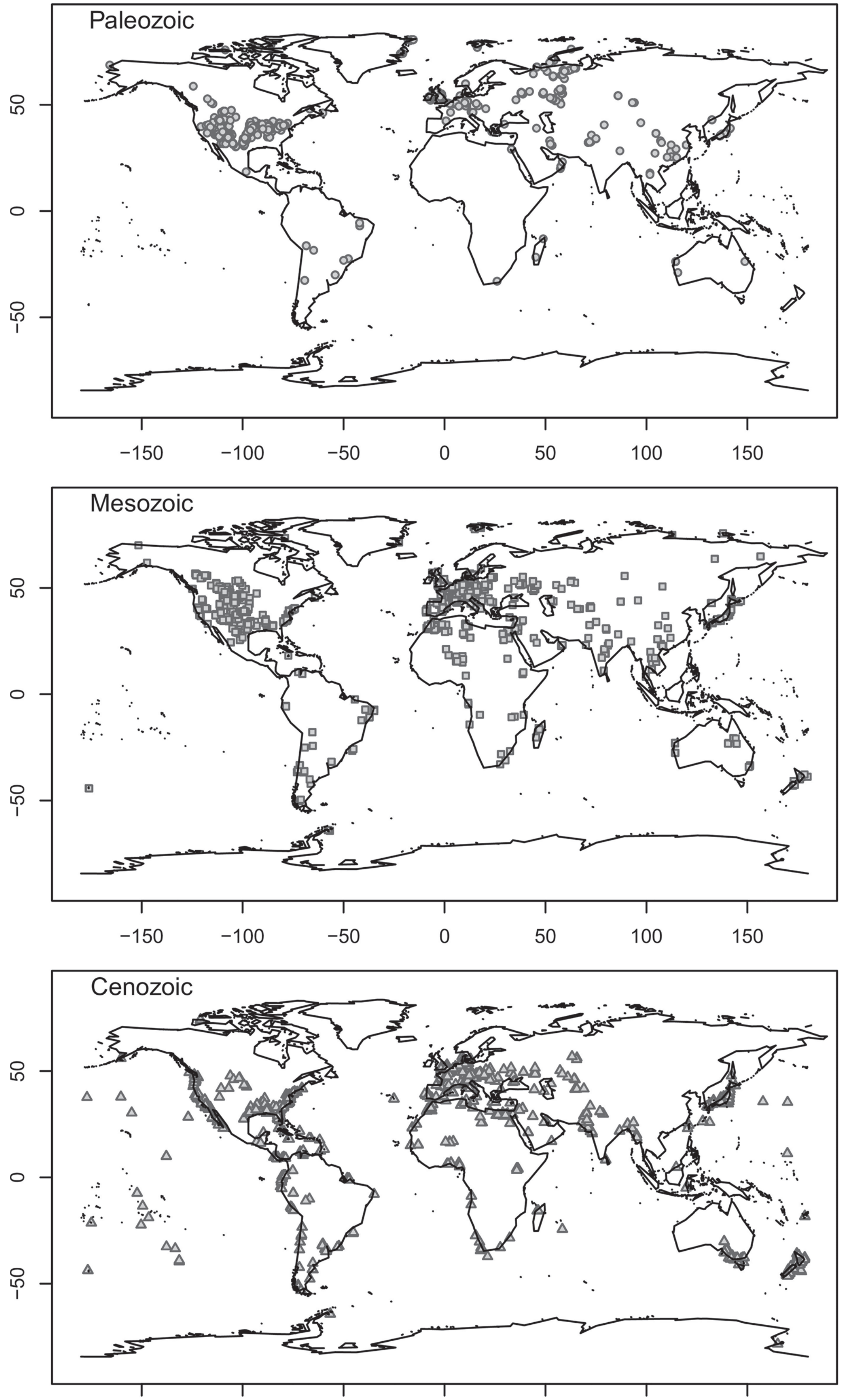

FIGURE 1.2 Maps showing the localities of chondrichthyan fossils from the Paleozoic (circle), Mesozoic (square), and Cenozoic (triangle) eras. (Data from the Paleobiology Database; Uhen *et al.* 2021.)

FIGURE 1.3 Diversity of preservation for extinct chondrichthyans. (A) *Cladoselache* cartilage and teeth (CMNH9207, Cleveland Museum of Natural History). (B) Assorted dermal denticles from an ocean core. (C) *Ptychodus mortoni* (UC1343, Field Museum of Natural History). (D) *Damocles serratus* (CM35473, Carnegie Museum of Natural History). (E) Typical drawer of fossil shark teeth from museum collections. (F) *Helicoprion* tooth whorl (AMNH 8247, American Museum of Natural History).

al. 2010). Chondrichthyan enameloid is mostly composed of fluorapatite and contains less than 5% organic material (Chen *et al.* 2014; Cuny *et al.* 2018; Francillon-Vieillot *et al.* 1990). Dentine is less mineralized and contains approximately 20% organic material (LeGeros 1981). Dermal denticles, the scales that cover the bodies of nearly all sharks, also are extremely durable due to their calcium phosphate composition and shed throughout the lifetime of the shark, providing a rich fossil record, particularly in deep-sea sediments (Dillon *et al.* 2017; Doyle and Riedel 1985; Sibert and Norris 2015; Sibert and Rubin, 2021; Sibert *et al.* 2017; Turner 2004). Other skeletal elements that are heavily mineralized with enameloid and/or dentine, such as dorsal fin spines and stingray tail spines, are found less frequently than teeth and denticles but more often than the rest of the skeleton (Cappetta 1987; Zangerl 1981). The remaining parts of the skeleton are rarely found, as cartilage is usually not durable enough to survive the fossilization process. Even skeletal parts that are mineralized with apatite, such as vertebral centra and jaws, rarely fossilize because the organic material linking tesserae together tends to break down during decomposition; tesserae then disarticulate, leaving the underlying cartilage unprotected (Underwood *et al.* 2015). Despite these challenges, the rich dental record, combined with well-preserved but rare body fossils, provides an excellent window into the diversity and evolution of chondrichthyans throughout their over 450 Ma on Earth.

1.3 EVOLUTIONARY HISTORY

The class Chondrichthyes is thought to be monophyletic, from both morphological and molecular analyses (Coates *et al.* 2018; Grogan *et al.* 2012; Heinicke *et al.* 2009; Naylor *et al.* 2012; Sorenson *et al.* 2014; Stein *et al.* 2018). Modern chondrichthyans are generally split into two groups, the Elasmobranchii and the Holocephali (= Euchondrocephali) (Nelson *et al.* 2016). The sharks, skates, and rays of the Elasmobranchii dominate today's extant chondrichthyan diversity, with approximately 1416 species across 70 families, whereas the Holocephali are represented only by the chimaeras, which include approximately 56 species across three families (Fricke *et al.* 2021), mostly living in the deep sea (Didier 2004). Here we provide a broad overview of the chondrichthyan fossil record, highlight some particularly important groups of fossil chondrichthyans, and discuss their evolutionary trends through the Phanerozoic Eon. We encourage interested readers to seek out the *Handbook of Paleoichthyology*, particularly the volumes concerned with elasmobranch teeth (Cappetta and Schultze 2012; Ginter *et al.* 2010), for further information on the detailed fossil record of chondrichthyans and their taxonomy. Additionally, *Fishes of the World* (Nelson *et al.* 2016) lays out a comprehensive description of ancient chondrichthyan taxonomy, as well as morphological descriptions and information about some fossil occurrences.

1.3.1 Relationships of Early Chondrichthyans

The fossil record of vertebrates extends back well over 500 Ma (Janvier 2015); the evolutionary innovation of jaws, which allowed jawed vertebrates (the Gnathostomes) to become more effective predators, occurred shortly thereafter. The chondrichthyan clade likely originated in the Silurian Period (443.8–419 Ma); however, an Ordovician Period origination (485–443.8 Ma) is possible. The oldest hypothesized chondrichthyan fossils are isolated denticles found in sediments that are between 440 and 450 million years old (Andreev *et al.* 2015; Burrow *et al.* 2019; Ginter 2004; Sansom *et al.* 2012; Turner 2004). The taxonomic affinity of these isolated early denticles is unclear, due in part to the paucity of taxonomically diagnostic body fossils from these time periods. However, their strong resemblance to later chondrichthyan denticles has led to their placement within the chondrichthyan lineage. Further complicating matters, acanthodians (also known as "spiny sharks") have recently been classified by some as stem chondrichthyans (Brazeau and de Winter 2015; Coates *et al.* 2018; Long *et al* 2019; Qiao *et al.* 2016). Acanthodians have cartilage mineralization patterns ("prismatic cartilage") similar to those of fishes we classically think of as chondrichthyans. Further supporting this relationship are fossils such as *Doliodus problematicus*, a fossil chondrichthyan from the Early Devonian possessing a mix of acanthodian and chondrichthyan characteristics (Maisey *et al.* 2009, 2014).

The oldest chondrichthyan teeth are from the Lower Devonian period, ~420 to 410 Ma, and are enumerated in Ginter *et al.* (2010). The oldest body fossils of definitive chondrichthyans are from the Devonian Period, as well (Miller *et al.* 2003; Ginter 2004). Most early chondrichthyan body fossils are represented by skulls and brain cases rather than full skeletons (Coates and Sequeira 1998; Coates *et al.* 2018)—unsurprising in a sense, as having a more solidified brain case would be to the advantage of the early chondrichthyans, both to strengthen their jaws and to protect their brain, and additional mineralization improves fossilization potential.

Given their outstanding fossilization record when compared with the rest of the body, teeth have been the primary tool used to study extinct chondrichthyan evolutionary history. Fossil chondrichthyan teeth were historically classified into cladodont, hybodont, and modern type groups based on their morphology (e.g., number and type of cusps, degree of flattening). These groups were considered to be evolutionarily sequential, with the primitive cladodonts giving rise to the hybodonts giving rise to modern sharks (Cappetta 1987). However, this classification scheme is no longer used, because it does not accurately reflect our current understanding of the evolutionary history of the Chondrichthyes nor the morphological diversity within each grouping (Ginter *et al.* 2010; Sequiera and Coates 2000), although the hybodonts are generally considered monophyletic and sister taxa to modern selachians. Long *et al.* (2019) reviewed early chondrichthyans in the context of broader gnathostome evolution, and Grogan *et al.* (2012) provided a review of early chondrichthyan fossils, noting that a wide diversity of early chondrichthyans have been found from the Devonian (419–358.9 Ma) and Carboniferous (358.9–298.9 Ma) periods. These fossils are found in a wide variety of habitats, including from freshwater riverine, lacustrine, estuarine, coastal, and open ocean settings—significantly more diverse than the range of habitats occupied by extant chondrichthyans. These early chondrichthyans rapidly diversified repeatedly across multiple habitat types throughout the Paleozoic and Mesozoic (e.g., Grogan *et al.* 2012; Long *et al.* 2019; Young 1982; and references therein). Indeed, although most stem vertebrate radiations likely occurred in nearshore habitats, chondrichthyans appear to have diversified across a wide range of habitats in the early part of the Paleozoic Era (Sallan *et al.* 2018).

1.3.2 Paleozoic Chondrichthyans (Reign of the Holocephali)

The Devonian Period (419–358 Ma) is commonly known as the "Age of Fishes" for the rapid diversification of most groups of fishes that have existed on the planet and their dominance in marine ecosystems (Agassiz 1833–1845; Friedman and Sallan

2012). Although the Age of Fishes is best known for the evolution of such groups as the Placoderms (large armored jawed fishes) and other stem jawed and jawless fishes, most stem chondrichthyan lineages also originated during the Devonian Period (Friedman and Sallan 2012). However, the majority of rapid diversification of these lineages of stem chondrichthyans took place during the Carboniferous (358–299 Ma) and Permian (299–252 Ma) periods, during the second half of the Paleozoic Era. It is during this time that chondrichthyans flourished, expanding into nearly all aquatic habitats and filling an incredibly diverse array of ecological niches (Ginter *et al.* 2010; Grogan *et al.* 2012; Long *et al.* 2019) (Figures 1.4 and 1.5).

The earliest elasmobranchs originated in the Devonian Period and were diversifying alongside a wide variety of stem chondrichthyans, holocephalans, as well as primitive osteichthyans, in Paleozoic waterways (Burrow *et al.* 2008; Friedman and Sallan 2012; Ivanov *et al.* 2011; Maisey 2001; Maisey 2012; Swinehart *et al.* 2020). Early chondrichthyans were highly ecologically diverse, representing a range of sizes and modes of life. Indeed, ancient vertebrates formed diverse and complex food webs similar to those of the modern ocean, with multiple trophic levels and complex predator–prey interactions (Kriwet *et al.* 2008). Most early chondrichthyans represented a range of sizes and modes of life. *Stethacanthus*, with its dorsal brush complex (Figure 1.4b), and *Damocles* (Figure 1.3d), with its large dorsal fin spine extending over its head, are wonderful examples of early elasmobranchs with unusual morphologies that do not exist in extant sharks. The teeth of Paleozoic elasmobranchs were quite different from those of extant chondrichthyans (Figure 1.4).

Many early elasmobranchs possessed teeth that featured a large flat base with a large lingual extension. These teeth were multicusped, with a large medial cusp surrounded by lateral cusps (Ginter *et al.* 2010) (Figures 1.4e and 1.4f). The xenacanthids were a group of stem elasmobranchs that diversified and lived in freshwater ecosystems in the Carboniferous and Permian periods and could reach lengths of up to 5 meters (Beck *et al.* 2016) (Figure 1.4c). A typical xenacanthid tooth looks nothing like a modern shark tooth; it consists of two large separate cusps arranged in a V-shape, with a tiny cusplet in between and button-like base (Figure 1.4h). Although the xenacanthids, along with most other early chondrichthyans, were mostly extinct by the end of the Permian (252 Ma), a few lineages persisted into the early Mesozoic Era. The Cladodontomorphi, another lineage of stem elasmobranchs, which include taxa such as *Symmoria*, *Cladoselache* (Figures 1.3a and 1.4a), and *Ctenacanthus*, similarly dominated in diversity throughout the Paleozoic. Although it was initially thought that cladodonts had gone extinct at the end of the Permian Period, a recent discovery suggests that they were able to persist until the Cretaceous Period, possibly using the deep-sea habitat as a refugium (Guinot *et al.* 2013).

The holocephalans, represented today by only a few mostly deep-sea species, were incredibly ecologically diverse in the Paleozoic (Didier 2004; Ginter *et al.* 2010; Lund and Grogan 1997). Their body form ranged from the recognizable fusiform shape of modern sharks to flattened body forms reminiscent of today's batoids to highly modified organizations. A spectacular example is the Iniopterygia, a late Paleozoic order of stem holocephalans with modified pectoral fins coming out of their heads (Zangerl and Case 1973) (Figure 1.5). The teeth of Paleozoic holocephalans are as diverse as their bodies, including broad tooth plates, bulbous tooth plates, and teeth with both serrated and unserrated cutting edges (Zangerl 1981) (Figure 1.5). Most famous are *Edestus* and *Helicoprion*, which are known from their ever-growing tooth whorls (Tapanila *et al.* 2013). The highly diverse holocephalans likely filled a variety of ecological niches that are filled by ray-finned fishes today, ranging from small, highly maneuverable primary and secondary consumers that fed on algae and benthic invertebrates to large, voracious predators.

There is considerable focus among paleontologists to find the oldest specimen of any particular clade, which can provide a framework for understanding the evolutionary timeline of a group. However, fossils of any age and the rocks they are preserved within can provide important insights into not just the timing of an evolutionary event but also the environmental and ecological conditions that these organisms evolved within. Although there are Paleozoic chondrichthyans preserved around the world, certain localities can provide insights not only into the evolutionary history of the groups preserved but also into the ecology of an ancient community. One such locality is the Bear Gulch Bay, an Upper Mississippian (~318 Ma) limestone outcrop in Montana. Bear Gulch preserves an extensive diversity and abundance of Carboniferous-aged chondrichthyans, as well as other early vertebrates living in a near-shore tropical reef habitat. This provides the opportunity to study community composition, ecological roles, and even ontogeny for an ancient marine vertebrate community (Grogan *et al.* 2012).

At Bear Gulch, chondrichthyans accounted for nearly 59% of all vertebrate diversity but comprised only 20% of the fossil specimens, compared with osteichthyans (bony fishes), which represented only 38% of species but 79% of specimens. This suggests that, at least in this environment, chondrichthyans were highly diverse, but osteichthyans were more abundant, perhaps already setting up a vertebrate food web where chondrichthyan predators fed on osteichthyan prey. Assessments of alpha and beta diversity of chondrichthyans across habitat gradients in the outcrop revealed significant differences in the relative abundances of chondrichthyan clades among near-shore, bay mouth/basin, and reef habitats, indicating habitat specialization. Although these habitats have similar numbers of genera, several individual genera tend to be specific to a particular habitat. The bay mouth and upper basin assemblages shared the most genera, with the nearshore assemblages being less similar to other habitats. Further ecological assessment of the taxa, based on body size, mouth gape, maneuverability, and other morphological features, indicated significant ecological partitioning, both across the environmental gradients and within taxonomic lineages (see Grogan *et al.* 2012 and references therein for a more complete discussion of the ecological assessments done using the Bear Gulch fauna, including

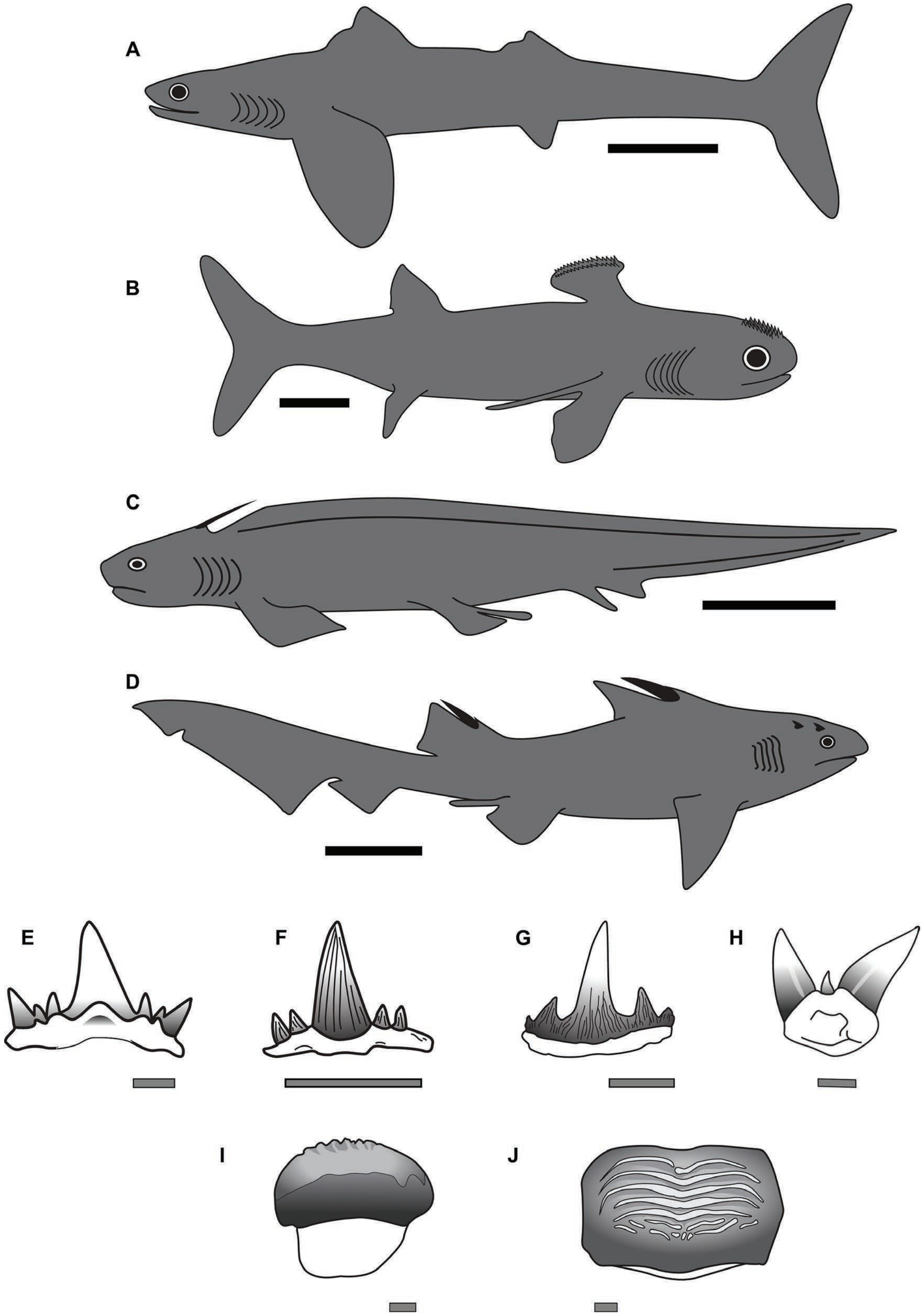

FIGURE 1.4 Representative extinct elasmobranchs. (A) *Cladoselache fyleri* (based on Zangerl 1981). (B) *Stethacanthus altonensis* (based on Zangerl 1981). (C) *Triodus sessilis* (based on Zangerl 1981). (D) *Hybodus* sp. (based on Maisey 1982). (E) *Cladodus elegans* (based on British Geological Society specimen 56574B as pictured in Ginter *et al.* 2010). (F) *Stethacanthus* sp. (based on Ginter *et al.* 2010). (G) *Egertonodus basanus* (based on Cappetta and Schultze 2012). (H) *Xenacanthus compressus* (based on specimen PF8499, Field Museum of Natural History). (I) *Ptychodus polygyrus* lateral view (based on specimen PF127, Field Museum of Natural History). (J) *P. polygyrus* occlusal view (based on specimen PF127, Field Museum of Natural History). Black scale bar = 10 cm; gray scale bar = 0.5 cm.

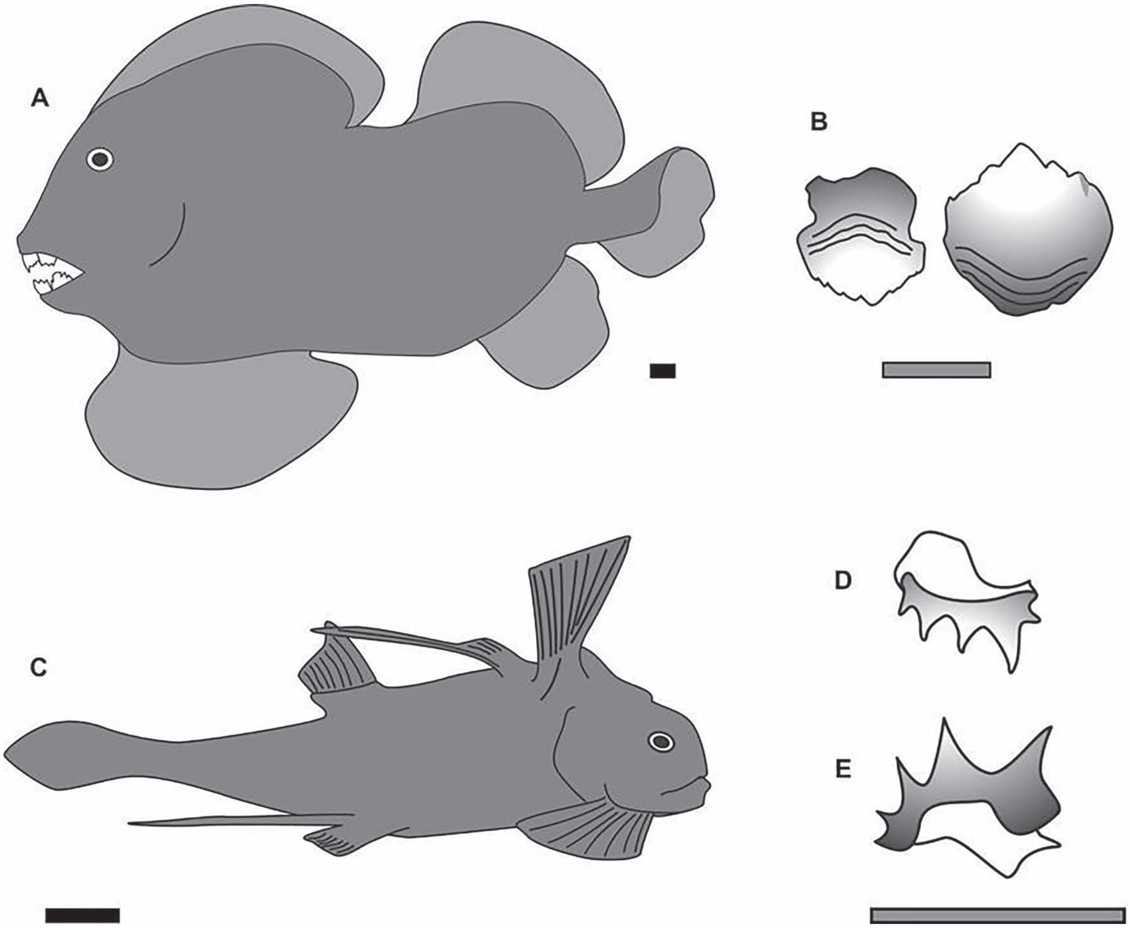

FIGURE 1.5 Representative extinct holocephalans. (A) *Belantsea montana* (based on Lund 1989). (B) Teeth from *Belantsea montana* (based on Lund 1989). (C) *Rainerichthyes zangerli* (based on Grogan and Lund 2009). (D, E) Tooth whorls from *Rainerichthyes zangerli* (based on Grogan and Lund 2009). Black scale bar = 1 cm; gray scale bar = 0.5 cm.

community size structure, ontogenetic and sexual dimorphism analyses, and even reconstructions of reproduction strategies). Bear Gulch is just one example of a single locality in time and space. It provides an example, however, of how, by combining an evolutionary and taxonomic framework and a set of ecologically minded questions, fossil data can provide insights into myriad aspects of chondrichthyan biology throughout their evolutionary history. We do note that chondrichthyan assemblages like those at Bear Gulch are extraordinarily rare. Other lagerstätten with significant chondrichthyan material include the Cleveland Shale (Devonian), lithographic limestones of southern Germany (Jurassic), Green River Formation (Eocene), and Bolca Lagerstätte (Eocene).

1.3.3 Mesozoic and Cenozoic Chondrichthyans (Reign of the Elasmobranchii)

Whereas the Paleozoic Era featured a wide range of chondrichthyan ecologies aned body plans, the vast majority of early chondrichthyans were extinct by the end of the Permian Period, and only a few lineages entered the Mesozoic Era, although evidence for major extinction at the Permo–Triassic is limited (Friedman and Sallan 2012). The most conspicuous of the Mesozoic chondrichthyan groups is the Elasmobranchii, which were relatively rare and of low diversity throughout the Paleozoic but diversified rapidly in the Mesozoic to become the dominant chondrichthyan lineage today (Cuny and Benton 1999; Maisey *et al.* 2004; Underwood 2006). Other Mesozoic chondrichthyans include the holocephalans and the hybodonts, and there were a few lineages of stem chondrichthyans that persisted into the Triassic Period (252–201 Ma), although they did not diversify further and disappeared from the fossil record by the Cretaceous Period (145–66 Ma) (see Figure 1 in Cappetta and Schultze 2012 and references therein).

Although holocephalans were dominant and highly diverse during the Paleozoic Era, they were relatively rare in the Mesozoic and Cenozoic fossil record (Didier 2004; Grogan *et al.* 2012; Long *et al.* 2019; Stahl 1999). Today's extant holocephalans live mostly in the deep sea (Didier 2004), which is poorly represented in the vertebrate fossil record, as deep-sea vertebrates are rarely preserved in the easily accessible part of the fossil record. Thus, the relative paucity of holocephalans from the Mesozoic and Cenozoic geologic record may be indicative of a shift in habitat that occurred near the end of the Paleozoic Era. Indeed, this hypothesis of the deep sea as a refuge for Paleozoic-aged lineages is common among marine invertebrates (e.g., brachiopods and crinoids, which dominated shallow marine environments in the Paleozoic Era and are found almost exclusively in the deep sea today) (Ramirez-Llodra *et al.* 2010). It has been suggested that gaps in the chondrichthyan record may be best explained by lineages moving into the deep sea, where fossil preservation potential is extremely low (Guinot *et al.* 2013). Although there are holocephalan fossil occurrences from the Mesozoic and Cenozoic, they are significantly rarer than those in the Paleozoic and are often found in extreme habitats, such as around Antarctica (Kriwet *et al.* 2016; Stahl and Chatterjee 1999, 2003).

The hybodonts were another group of important Paleozoic and Mesozoic chondrichthyans and are primarily distinguished by their tooth shape; they are multicusped, with a tall central cusp and subsequent medial and distal cups decreasing in size, and they have a lingolabially compressed tooth base with a labial peg (Ginter *et al.* 2010) (Figure 1.4). As they have no living relatives, their taxonomic position within the chondrichthyan tree is poorly understood; however, they are generally considered to be euselachians or, more broadly, elasmobranchs, and they have many of the same characteristics that define Elasmobranchii today (Maisey 2012). The hybodonts originated in the Paleozoic Era, diversifying alongside the holocephalans and other stem chondrichthyans; however, unlike the majority of Paleozoic chondrichthyans, the hybodonts did not see a dramatic or sustained reduction in diversity at the end of the Permian Period but rather continued to diversify and thrive throughout the early part of the Mesozoic Era (Rees 2008; Rees and Underwood 2008). Hybodont diversity began to decline in the middle Jurassic (Rees and Underwood 2008), and they were mostly limited to freshwater environments throughout the Cretaceous (Cuny *et al.* 2007). Hybodonts were extinct by the end of the Cretaceous Period (Maisey *et al.* 2004), although the cause of the hybodont extinction is unclear. They appear to have experienced a protracted decline throughout the Cretaceous rather than a single extinction event at the end of the Maastrichtian (Kriwet and Benton 2004).

The elasmobranch lineage dates back to the Devonian Period (Maisey 2001; Burrow *et al.* 2008; Ivanov *et al.* 2011; Swinehart *et al.* 2020), but elasmobranchs were relatively rare and had low diversity throughout the Paleozoic Era. The first definitive Neoselachii fossil, representing the group that contains all modern sharks, skates, and rays, is from the early Triassic Period (Cuny and Benton 1999). The Neoselachii diversified throughout the Mesozoic, with considerable diversification in the Jurassic and Cretaceous periods (Maisey *et al.* 2004; Underwood 2006). This period coincides with the Mesozoic Marine Revolution, a nearly 100-million-year interval of increased diversification across invertebrate and vertebrate lineages, largely driven by increased predation pressure in marine ecosystems (Vermeij 1977; Harper 2003). Because the majority of Mesozoic neoselachians were predators, it has been hypothesized that the Mesozoic radiations in Neoselachii may be related to shifts in available prey, most notably radiations in ray-finned fishes (e.g., Thies and Reif 1985). However, changes in habitat availability, reproductive mode, and environmental conditions may have provided unique opportunities for neoselachians to diversify throughout the Jurassic and Cretaceous (Maisey *et al.* 2004; Underwood 2006; Kriwet *et al.* 2009). Further, while ray-finned fishes did diversify throughout the Mesozoic, the majority of their radiation occurred in the Cenozoic (Near *et al.* 2012; Alfaro *et al.* 2018; Rabosky *et al.* 2018). In contrast, the majority of neoselachian order- and family-level diversity was established during the Jurassic and Cretaceous Periods of the Mesozoic Era (see Section 1.3.4), and there have been no new lineages in the group since that time, indicating that neoselachian family-level diversity was not tied to ray-finned fish diversification in the Cenozoic Era. It is possible that species-level diversification may have different patterns; however, the nature of the chondrichthyan fossil record (mostly teeth and incomplete body fossils) leads to doubt in species designation and therefore subsequent analyses of species-level diversity. For example, for the extinct genus *Cladodus*, which is largely based on isolated teeth, paleontologists have designated anywhere from five to 48 different species (Duffin and Ginter 2006), obscuring species-level co-evolutionary analyses.

1.3.4 Chondrichthyan Diversity Patterns in the Phanerozoic

The temporal diversification patterns of chondrichthyans, like most of the other animal life on Earth, have been shaped by major events in Earth's history, particularly mass extinction events (Raup 1972; Sepkoski 2002; Friedman and Sallan 2012), such as those at the Permo–Triassic boundary (P–T; 252 Ma), the Triassic–Jurassic boundary (T–J; 201 Ma), and the Cretaceous–Paleogene boundary (K–Pg; 66 Ma). Using a database of chondrichthyan fossil occurrences through the past 430 Ma (Uhen *et al.* 2021), we compiled a record of chondrichthyan genus-level diversity (Figure 1.6). We assessed the timing, magnitude, and rate of turnover in chondrichthyan fossil diversity (Foote 2000) (Figure 1.7), and we present the results of that analysis here.

From their Devonian and Silurian origins, chondrichthyans diversified rapidly throughout the second part of the Paleozoic Era, reaching a peak in order-level diversity at the end of the Carboniferous Period. There was a mass extinction at the end of the Devonian Period, with some turnover across assemblages in early chondrichthyans (Friedman and Sallan 2012); however, it is characterized by a decrease in size among vertebrate clades (Sallan and Galimberti 2015) rather than a major extinction in chondrichthyans. These Paleozoic chondrichthyans were incredibly diverse morphologically and ecologically, with stem chondrichthyans and holocephalans dominating the Paleozoic chondrichthyan assemblages.

The P–T mass extinction 251 million years ago marked a turning point for chondrichthyans in terms of their ecological role in marine ecosystems. Although chondrichthyans did not suffer the >95% genus-level losses that many other animal groups did at the P–T extinction (Koot 2013; Raup and Sepkoski 1982), their evolutionary trajectory was considerably impacted by the event. The P–T extinction was the largest extinction event observed in the Phanerozoic chondrichthyan record, and it is observed across all taxonomic levels (Figure 1.7).

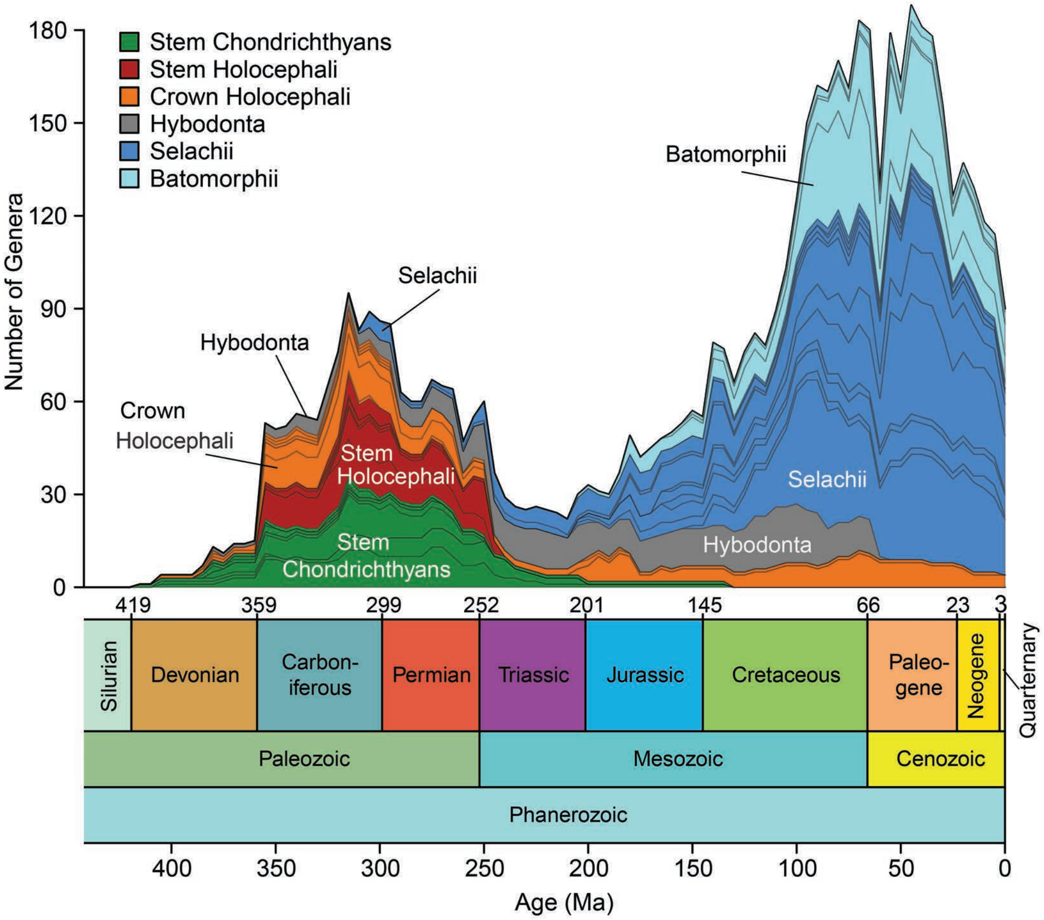

FIGURE 1.6 Genus-level richness of chondrichthyans through the Phanerozoic Eon, compiled from the Paleobiology Database (Uhen *et al.* 2021), split into stem chondrichthyans, stem Holocephali, crown Holocephali, Hybodonta, Selachii, and Batomorphii. Light gray lines indicate the taxonomic orders within the larger groups. The Hybodonta are represented by a single order. A geologic time scale is provided at the bottom of the figure for reference, and numbers above the geologic time scale indicate the age in millions of years (Ma) of transitions between the geologic periods.

Indeed, the P–T extinction is the only extinction during the Phanerozoic that significantly impacted the number of chondrichthyan orders, and this reduction in order-level diversity coincided with a significant reduction in ecological diversity, as well. Although some stem chondrichthyans and holocephalans survived the extinction event (Guinot *et al.* 2013), they did not thrive in the new Mesozoic Era, and most were extinct by the end of the Triassic Period. There were members of some groups that survived the extinction; however, their relative abundance and diversity decreased dramatically, indicating a significant ecological shift at the event. Hybodonts passed through the extinction event, maintaining their diversity through the Mesozoic. Following the P–T extinction event, there was an interval of nearly 50 Ma of low standing diversity in chondrichthyans. The Triassic–Jurassic boundary, 201 Ma, is marked by a mass extinction in marine invertebrates (Sepkoski 2002); however, some chondrichthyans thrived in the aftermath of the T–J extinction. Elasmobranchs rapidly diversified through the Jurassic and early Cretaceous, returning the chondrichthyans to Paleozoic-like levels of taxonomic, if not ecological, diversity (Maisey *et al.* 2004; Underwood 2006). The rapid elasmobranch diversification in the Jurassic and Early Cretaceous Periods established the lineages of extant chondrichthyan diversity observed today.

In contrast to the P–T extinction, the Cretaceous–Paleogene mass extinction 66 million years ago (Schulte *et al.* 2010) did not initiate a regime change in the trajectory of chondrichthyan evolution. Kriwet and Benton (2004) reported an ~30% extinction in the elasmobranchs; however, unlike the P–T extinction, which is characterized by a dramatic reduction in order- and family-level diversity, the K–Pg extinction was not as severe; there was no extinction of taxonomic orders, and only a small percentage of families were lost. The K–Pg extinction did drive a decline in total genus-level diversity, but this rebounded quickly following the extinction, returning to Cretaceous-levels of diversity within 10 million years of the extinction event (Figure 1.6). However, raw counts of taxonomic diversity (richness) do not always give an indication of changes in paleoecology or community structure. For example, the K–Pg extinction caused a permanent ecological change in marine vertebrate communities, marked by a dramatic decrease in the relative abundance of chondrichthyans as compared with

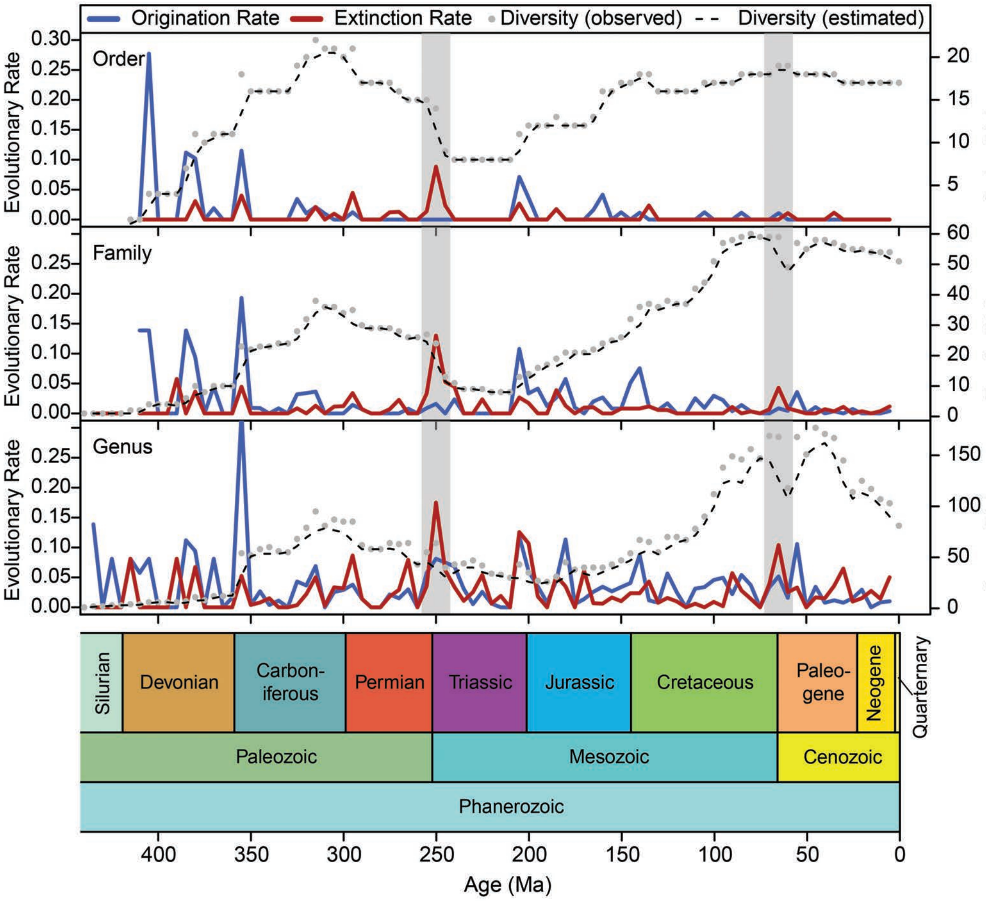

FIGURE 1.7 Diversity patterns of chondrichthyans through the Phanerozoic Eon, based on the Paleobiology Database (Uhen *et al.* 2021). Per-capita origination and extinction rates calculated after Foote (2000) are shown in solid light and dark lines, respectively. Observed richness is shown as solid gray circles, and estimated richness (Foote 2000) is shown with the dotted black line. The top panel shows order-level richness and dynamics, the middle panel shows family-level richness and dynamics, and the bottom panel shows genus-level richness and dynamics. A geologic time scale is provided for reference.

ray-finned fishes in the open ocean (Sibert and Norris 2015). This shift was driven largely by a rapid increase and radiation in ray-finned fishes, rather than a reduction in chondrichthyans. However, the change in the marine vertebrate community was permanent. Although chondrichthyans rapidly returned to pre-extinction levels of diversity after the K–Pg, they remained a much-reduced part of the open ocean vertebrate community compared with the rapidly diversifying teleost fishes throughout the Cenozoic (Sibert *et al.* 2016).

Fossil-inferred genus-level richness in chondrichthyans appears to have reached a maximum between 50 and 30 Ma, but family- and order-level chondrichthyan diversity remained relatively constant throughout the Late Mesozoic and Cenozoic Eras, with only minor reductions (Friedman and Sallan 2012) (Figure 1.6), though recent work with fossil denticles from the open ocean suggests there may have been a major extinction in pelagic sharks around 19 million years ago in the early Miocene (Sibert and Rubin 2021). Further work using open ocean–preserved denticles will continue to refine our understanding of shark evolutionary history, augmenting and expanding the near-shore dominated chondrichthyan fossil record. Chondrichthyans have persisted through extreme climate change throughout the past 100 Ma, including whole-ocean oceanic anoxic events throughout the Cretaceous (Jenkyns 1980), the K–Pg mass extinction (Alvarez *et al.* 1980; Hull *et al.* 2020; Kriwet and Benton 2004; Schulte *et al.* 2010), the rapid warming of the Paleocene–Eocene Thermal Maximum (PETM) and Eocene hyperthermals (Speijer *et al.* 2012; Zachos *et al.* 2010), the permanent glaciation of Antarctica (Berger 2007; Salamy and Zachos 1999; Zachos *et al.* 1996), and the broad-scale Cenozoic cooling of the past 50 million years (Westerhold *et al.* 2020; Zachos *et al.* 2001, 2008). Persistence of chondrichthyans through these intervals of significant global climate and oceanographic changes suggests that this evolutionarily long-lived clade is resilient to global change and able to adapt to shifting environmental conditions. However, although chondrichthyans have survived through these intervals of global change with no major decreases in diversity over the past 100 Ma, there is a paucity of diversification in the clade throughout that interval, and when diversity is lost it is not replaced. There are several possibilities as to why chondrichthyan diversity was not replaced throughout the Cenozoic. It is possible that, as ray-finned fishes radiated rapidly throughout the Late Cretaceous and Cenozoic, they were more rapidly able to evolve and fill vacated niche space, effectively out-competing chondrichthyans (Alfaro *et al.* 2018; Near *et al.* 2012; Rabosky *et al.* 2018). Modern chondrichthyans fill only a small subset of ecological niches that they occupied in the Paleozoic, indicating increased ecological specialization and reduced niche occupation in chondrichthyans throughout the past 200 Ma. In other words, chondrichthyans may have been slowly excluded from vacated niches while teleosts rapidly diversified in aquatic habitats, perhaps displacing chondrichthyans throughout the Cenozoic.

1.3.5 Implications of Fossil Chondrichthyan Diversity Patterns for Today's Chondrichthyans

Throughout their 450+ Ma on Earth, chondrichthyans have thrived in aquatic ecosystems, filling ecological roles from primary consumer to top predator and everything in between. They are in many ways the ultimate survivors, persisting throughout mass extinctions and major environmental fluctuations of the Phanerozoic Eon. However, they have become increasingly ecologically specialized through time, and modern chondrichthyans no longer fill most ecological niches that they dominated in the Paleozoic. Further, most chondrichthyan extinctions over the past 100 Ma have not been refilled by diversification within the clade but rather have been superseded by radiations in teleost fishes, effectively pruning their phylogenetic tree. In today's rapidly changing world, anthropogenic stressors, such as overfishing (Pacoureau *et al.* 2021; Queiroz *et al.* 2019), are dramatically reducing shark populations, and the rates of extinction are rapidly reaching those of the major extinctions of the Phanerozoic (Barnosky *et al.* 2011). Although it is unlikely that chondrichthyans will survive the Anthropocene extinction completely unscathed, they have a long evolutionary history of resilience to extinctions and global change, and it is likely that at least some surviving lineages will continue to persist in the oceans of the future.

1.4 FOSSIL CHONDRICHTHYAN BIOLOGY

To elucidate the processes and mechanisms driving shark evolution through geologic time, we need a deeper understanding of ancient shark ecology. Ecology is the study of relationships between organisms and their physical environment and, in its inception, Ernst Haekel (1866) acknowledged that "biotic and abiotic" forces shape existence and adaptation (translated by Stauffer 1957). Extant sharks only represent a sliver of chondrichthyan evolution; our modern understanding of habitat preference, diet variation, physiological processes, and biomechanical functions can help build a framework for interpretations from the fossil record. However, geologic time offers various climate and evolutionary "experiments" that give the necessary spatial and temporal context required to understand evolutionary history. Further, the rich chondrichthyan fossil record contains key ecological data encoded in its presence, morphology, and geochemistry to answer questions related to macroecology, ecological dynamics, and functional ecology.

1.4.1 Macroecology Trends

Macroecology is the study of ecological patterns and processes over large time and spatial scales (Brown 1995). Initially, macroecology as an area of study identified patterns of species diversity, body size, or geographical range with statistical approaches. However, more recent studies are delving into processes and mechanisms with theoretical modeling approaches. Many suggest there are biotic and abiotic factors to consider, although these factors have different implications for ectothermic versus endothermic, terrestrial versus marine, and invertebrate versus vertebrate taxa (Sunday *et al.* 2011; Tomašových *et al.* 2015). Modern shark ecology embodies the knowledge necessary to build the theoretical evaluation of macroecological processes for shark communities and taxa. However, to understand ecological resilience, especially for conservation and management in relation to future climate change, the fossil record offers insights into variations on decadal, millennial, and geological time scales (Kidwell 2015). To our knowledge, the only macroecological study to date leveraging the fossil shark and paleoclimate record in tandem is Condamine *et al.* (2019), which attributed declining Lamniformes diversity to cooling climate and increasing competition. The resolution is not at the organismal, population, and community scale of neontology (i.e., modern ecology), but the fossil record offers historical contingencies and ecological legacy, which are crucial in predicting ecological response to future climate change (Jackson *et al.* 2009; Kidwell 2015). Further, the fossil record includes "results" from past climate states that are not in existence, such as the ice-free Arctic (Kim *et al.* 2014) and Southern oceans (Kim *et al.* 2020), that indicate multiple stability domains and adaptive capacity of an ecosystem and taxa (Gunderson 2000).

Body size is an important ecological trait, as it indicates energy balance and integrates aspects of resource availability, temperature, and physiology. It is well established within shark neontology that body size (both length and mass) relates to the age of an individual. Further, there are also robust relationships that relate tooth crown height with total length for extant sharks (Shimada 2004; Shimada *et al.* 2020). There is growing interest in examining shark body size to explore facets of paleobiology with respect to nursery habitats and onset of gigantism for the largest species—White Sharks (*Carcharodon carcharias*) and "Megalodon" (*Otodus megalodon*) (Pimiento and Balk 2015; Pimiento *et al.* 2010, 2019; Shimada *et al.* 2020; Villafaña *et al.* 2020)—but body size studies for other chondrichthyan lineages remain scarce. To date, broader perspectives of chondrichthyan body size are focused on extinction in deep time (419–323 Ma) (Sallan and Galimberti 2015) or selection pressure with respect to extinction (Payne and Heim 2020; Payne *et al.* 2016). The vast fossil record for sharks provides the opportunity for statistically robust body size distributions that rival those for invertebrates, the focus of many macroevolutionary and macroecology studies. Many evolutionary theories and observed processes are based on size, diversity, and morphometrics of fossil invertebrate taxa (e.g., brachiopods, ostracods, bivalves, mollusks) through geological time (e.g., Berke *et al.* 2014; Jablonski *et al.* 2017; Tomašových *et al.* 2015). In addition, many macroecology studies feature mammals in relation to body size or climate interaction that often have a substantially sparser fossil record (although more preserved elements) (Balisi and Van Valkenburgh 2020; Cardillo *et al.* 2005; Clauset and Erwin 2008; Millien *et al.* 2006; Saarinen *et al.* 2014). An examination of Chondrichthyes and comparison to invertebrates or mammals would likely demonstrate unifying and diverging patterns among lower and higher trophic level taxa.

1.4.2 Functional Diversity

The fossil record offers a longer temporal framework to evaluate ecological and evolutionary processes and mechanisms. This context is particularly important for conservation and management practices in the current era, as aspects of modern functional diversity (e.g., habitat preference, trophic level, body size, mobility range) are vestiges of past environmental change or anthropogenic impacts (Gusmao *et al.* 2016; Krug *et al.* 2010; Patzkowsky 2017; Pimiento *et al.* 2020; Tomašových and Kidwell 2017; Tomašových *et al.* 2016). However, many ecological traits for extant sharks, especially mesopredators, remain elusive. For example, cookiecutter sharks were thought to feed primary on large, pelagic prey, but biochemical evidence suggests a reliance on micronektonic and forage species (e.g., organisms that connect plankton to higher trophic level predators) (Carlisle *et al.* 2021). Discerning the nuanced ecological differences among sharks is necessary for effective conservation and management strategies, as increased functional diversity improves resilience (Dulvy *et al.* 2017; Micheli and Halpern 2005; Pimiento *et al.* 2020). The fossil record can offer examples of how functional diversity changes and ecological structure change through time, including after mass extinction events (e.g., Permian–Triassic mass extinction) (Dineen *et al.* 2014).

An effective example of how to use the fossil record to study functional diversity comes from the Bivalvia. Modern bivalves demonstrate a decrease in functional richness and increase in functional evenness (i.e., even distribution of genera throughout a trait space) with increased latitude (Berke *et al.* 2014). To understand the processes and mechanisms underlying this pattern, Berke *et al.* (2014) drew from the rich bivalve fossil record, which gives the spatial and temporal resolution necessary to evaluate origination rates and range expansion. Some of this work has also begun for fishes. A global assessment of the functional diversity of fishes (i.e., ray-finned and cartilaginous) revealed profound changes in the past 65 years, as fishing pressure increasingly targets species with greater functional richness; hence, fishing plays greater or larger roles within an ecosystem (Trindade-Santos *et al.* 2020). However, to fully evaluate the functional evenness and richness of a taxon, its evolutionary history with respect to ecological plasticity and environmental change is an important consideration (Berke *et al.* 2014; Huang *et al.* 2015; Jablonski *et al.* 2017).

How do changes in functional diversity change ecological structure? This question is the heart of conservation and management policies, but the best case studies are likely encoded within the fossil record. For example, the Late Triassic mass extinction event has many characteristics we are observing with modern climate change—high biodiversity loss, increased carbon dioxide concentrations, global warming, and ocean acidification—and had a disproportionate impact on calcified marine organisms (Dunhill *et al.* 2018). An analysis of marine animal occurrences from the Paleobiology Database demonstrated that there was no functional diversity loss but there were regional differences (Dunhill *et al.* 2018). The spatial and temporal span of the shark fossil record would allow similar types of comparisons, but modern analogs are needed to discern functional diversity, including richness and evenness, from extant taxa.

1.4.3 Where Did Sharks Live?

In addition to the biological information encoded in tooth form, the chemistry of shark teeth also offers important clues to their diet and environment (e.g., Kim *et al.* 2014, 2020; Zacke *et al.* 2009). The enameloid on shark's teeth is thin but highly resistant to alteration due to its mineralogical composition of fluorapatite (Thomas *et al.* 2011; Enax *et al.* 2014). The chemical signal in fossil teeth can indicate conditions during the organism's lifetime or shortly after death during the fossilization process (Koch 2007). To date, the most common chemical techniques use isotopes, which are different forms of the same element based on the number of neutrons within the nucleus. Stable isotope ratios (e.g., $^{2}H/^{1}H$, $^{13}C/^{12}C$, $^{15}N/^{14}N$, $^{18}O/^{16}O$) vary throughout an ecosystem based on biological, physical, and chemical processes that cause mass-dependent differentiation between the heavy and light isotopes. In contrast, most radioactive isotopes have a heavier atomic mass (^{14}C is the exception), and their nuclei emit radioactivity during the decay process. The comparison of isotopes, where one is the product of radioactive decay, serves as a temporal tracer for events on the geological time scale. Three isotope systems commonly used for environmental reconstruction are oxygen for water temperature and salinity (e.g., $\delta^{18}O$), strontium to discern geologic age (e.g., $^{87}Sr/^{86}Sr$), and neodymium for ocean currents (ε_{Nd}).

The oxygen isotope composition recorded in shark enameloid reflects the water temperature and salinity when the tooth was formed during the individual's life. The advantage of shark teeth for water temperature and salinity reconstructions lies in their recording of regional variability integrated through time and space for comparison to much finer resolution datasets, such as foraminifera and bivalves. The differentiation in lifestyle (e.g., migratory, ontogeny) and habitat preferences (e.g., neritic, oceanic, bathyal) allows for environmental reconstruction of an oceanic region's cross-section, which may change through time (Zacke *et al.* 2009). However, the migratory nature of some shark species and the conveyor belt system of tooth replacement means that a shark tooth may record the oxygen isotope composition of a different locality (Zeichner *et al.* 2017). Further, shark teeth may be transported from their original depositional environment and be concentrated in nearshore environments during fossilization, potentially resulting in misleading temperature and salinity estimates. Insight into the likely habitat preference and migration pattern based on a modern analog, as well as stratigraphic context and taphonomic process from sedimentology, will help elucidate if the sharks are autochthonous species to the locality. In addition, analysis of fossil species may reveal ecological plasticity, with a larger fundamental niche than what is expressed in the modern realized niche. There are numerous examples of fossil shark taxa thriving in reduced salinity conditions (Vennemann and Hegner, 1998; Kocsis *et al.*, 2009; Fischer *et al.*, 2013; Kim *et al.*, 2014), whereas today only a few species are known to inhabit brackish to freshwaters for extensive periods of time (i.e., Bull Shark, *Carcharhinus leucas*; river sharks of the genus *Glyphis*; Largetooth Sawfish, *Pristis pristis*; and freshwater stingrays in the Myliobatiformes order). Linking paleoceanography and climate change to biological patterns offers insights into the evolutionary history and ecological plasticity of Chondrichthyes taxa.

Strontium and neodymium are two radiogenic isotopes that are indicative of large-scale marine and climate processes. The mixing time for the global ocean is ~1500 years, but these two elements have different residence times, which means their isotope compositions record processes at different scales. Strontium is a conservative tracer, due to its long residence time of 2.5×10^6 years, and is often used to discern absolute time, as seawater composition fluctuates through time based on continental rock weathering rates. Global seawater strontium composition (i.e., $^{87}Sr/^{86}Sr$ or $\delta^{88/86}Sr$) is relatively stable, but values fluctuate depending on river inputs. The source of strontium in freshwater is minerals in soil or bedrock, which varies depending on its age, as ^{87}Sr is a product of radioactive decay. Hence, the delivery of water from rivers incising older versus younger bedrock influences the global strontium seawater composition. In contrast, the residence time for neodymium is relatively short (500–1000 years) (Tachikawa *et al.* 2003), and oceans have different values depending on the age of rocks within the basin. Therefore, ε_{Nd} indicates changes in ocean circulation patterns (Kim *et al.* 2020; Scher and Martin 2006; Scher *et al.* 2015). Both strontium and neodymium isotope compositions are recorded in bioapatite from early diagenetic fluids, which imprints the environmental conditions at post-burial rather than the biologic signal (Martin and Scher 2004). The resolution of oceanographic and climate processes from geochemical tracers in shark teeth is coarse and often lacks precise age control, but the resistance of enameloid to diagenesis and preservation of nearshore, shallow marine systems is a key advantage.

1.4.4 WHAT DID SHARKS EAT?

Many modern shark diet and trophic studies rely on stable isotope analysis of nitrogen. The heavier nitrogen isotope (^{15}N) biomagnifies as biochemical processes during metabolism differentiates (i.e., fractionates) and concentrates ^{14}N in waste products. Traditional, or bulk, nitrogen isotope analysis requires protein within the soft tissue (e.g., blood, muscle) or collagen within mineralized tissue (e.g., dentin, cartilage). Most chondrichthyan ecology studies focus exclusively on soft tissues, but there are a few exceptions using teeth and vertebrae (Carlisle *et al.* 2015; Kim *et al.* 2012; Polo-Silva *et al.* 2021; Zeichner *et al.* 2017). However, protein does not preserve well during fossilization, and only in rare instances are $\delta^{15}N$ values from collagen preserved past 10^5 years (Iacumen *et al.* 1997; Fuller *et al.* 2014). Recent studies have explored the possibility of other geochemical indicators of diet and trophic level in mineralized tissues preserved in the fossil record. Although the interpretative framework for mineral-bound nitrogen, calcium isotopes, and zinc isotopes is still in development, early data from modern and fossil shark specimens are promising.

The mineralization of enamel(oid) initiates with a protein matrix during amelogenesis; therefore, small amounts (5%–8%) of organic nitrogen can be bound within the structure (Enax *et al.* 2012). Recent methodological and analytical advances allow for the isolation of mineral-bound nitrogen (Ren *et al.* 2009) and isotopic analysis with the denitrifier method (Sigman *et al.* 2001; Casciotti *et al.* 2002). Most published studies to date feature mineral-bound nitrogen in invertebrates (e.g., $CaCO_3$) and discern changes in nutrient dynamics within marine ecosystems over geological timescales (e.g., Ren *et al.* 2009; Straub *et al.* 2013). There are also modern ground-truthing studies and one captive experiment that indicate a correspondence of mineral-bound nitrogen isotope composition with soft-tissue $\delta^{15}N$ values and particulate organic matter (the diet for invertebrates) (Ren *et al.* 2009; Gillikin *et al.* 2017; Smart *et al.* 2018; Leichliter *et al.* 2021). Enameloid-bound nitrogen isotope analyses for fossil shark taxa within a comparative framework of predators (Kast 2020) or lower trophic taxa will elucidate the trophic level of ancient sharks, which can be compared with modern systems.

Two additional isotope systems that hold promise for determining trophic level from fossil material are calcium and zinc. Much of the initial application of these isotopic systems has been in mammals and indicates decreasing $\delta^{44/42}Ca$ and $\delta^{66}Zn$ values with trophic level (Clementz *et al.* 2003; Jaouen *et al.* 2013; Tacail *et al.* 2020). Both of these elements play critical roles in biochemical processes; calcium is integral in the mineralogy of bioapatite, whereas zinc is crucial for protein–ligand binding. In addition, both elements have relatively long residence times in the ocean, so that there are only small variations on a global scale.

Calcium isotope analysis ($\delta^{44/42}Ca$ values) of modern elasmobranchs indicates close correspondence with trophic level, and trophic offsets are observed within a Pliocene marine food web (Martin *et al.* 2015). One challenge in calcium isotope analysis for trophic studies is that seawater calcium isotope composition is linked to the global carbon cycle, as the balance of marine carbonate precipitation and burial fluctuates over geologic time, which affects the baseline $\delta^{44/42}Ca$ values through geologic time. However, Akhtar *et al.* (2020) constructed a $\delta^{44/42}Ca$ record for the past 100 million years from fossil shark teeth and proposed a partitioning coefficient to discern biological versus environmental factors. Calcium isotope analysis is a well-established technique and robust against diagenetic alteration, but further modern and paleontological studies are needed to advance it as a trophic indicator for ancient sharks.

The application of zinc isotopes to discern trophic levels for sharks is in the early stages, but foundational work with mammals shows promise for shark paleobiology (McCormack *et al.* 2021). Zinc is well preserved in mineralized tissues and thought to be robust against diagenesis, but investigations of trophic level have not yet ventured past the Late Pleistocene (Bourgon *et al.* 2020). An examination of archeological Arctic marine mammals revealed that bone δ^{66}Zn values decrease among consumers and demonstrate patterns complementary to those of bone collagen δ^{13}C and δ^{15}N values, two more traditional diet isotope systems (Jaouen *et al.* 2016). However, there is scatter with mobile, benthic feeding species compared with taxa foraging from the pelagic food web (i.e., walrus vs. polar bears and seals) (Jaouen *et al.* 2016). Studies with modern terrestrial mammals indicate variable δ^{66}Zn values within tissues (Balter *et al.* 2010) and different fractionation patterns for terrestrial herbivores versus carnivores (Jaouen *et al.* 2013, 2016). Additional studies to examine the patterns of zinc isotope distribution among shark mineralized tissue, associations with trophic level, and correspondence to prey are needed for the application of δ^{66}Zn values to shark paleobiology.

1.4.5 How Do Sharks Work?

Given the paucity of whole-body fossils, it is not surprising that biomechanical and functional morphological studies of extinct chondrichthyans are few and far between. Many tend to focus on feeding, given that the majority of the fossil record is composed of teeth (e.g., Abler 1992; Ramsay *et al.* 2015; Whitenack and Motta 2010). Most studies concerning the form and function of extinct chondrichthyans use morphology to predict function, using analogy to modern forms. Extant shark teeth tend to be categorized by putative function and morphology together (Cappetta 1987); these functional morphotypes are then applied to extinct elasmobranch species (e.g., Cappetta 1987; Cicimurri 2004). Computer modeling of White Shark jaws has been used to extrapolate bite force in the megatoothed extinct shark Megalodon (Wroe *et al.* 2008).

The increasing availability of new technologies, such as computed tomography (CT) scanning, three-dimensional (3D) printing, computer numerical control machining, robotics, and sophisticated modeling programs, has the potential to lead to new functional and biomechanical studies of extinct chondrichthyans, as they have with extant fishes of all types (e.g., Roberts *et al.* 2014; Herbert and Motta 2018). CT scanning of chondrichthyan fossils allows for the non-destructive capture of 3D morphology, and, when the data from the scans have been segmented (processed), paleobiologists can work with the data as they are or modify the data. They can create computer models that remove the effects of distortion from the fossilization process, create composite models from multiple individual fossils, or even modify morphology to explore unfilled areas of morphospace (see Lautenschlager 2016 and references therein). Although many of these possibilities have not yet been applied to fossil chondrichthyans, CT scanning (including micro-CT scanning and absorption-based synchrotron microtomography) has been a mainstay of shark paleontology for the purposes of resolving fine anatomical details, such as neurocranium and brain structure (e.g., Coates *et al.* 2017; Jambura *et al.* 2019; Lane 2010; Maisey and Anderson 2001; Pradel *et al.* 2009; Tapanilla *et al.* 2013). CT scanning and other methods of capturing 3D morphology have been the starting point for finite-element modeling of the structural stability of extinct chondrichthyan teeth (Whitenack *et al.* 2011; Ballel and Ferrón 2021), computer modeling of *Helicoprion* bite mechanics (Ramsay *et al.* 2015), and 3D-printed physical models of jaw and hyoid movement in the symmoriiform shark *Ferromirum oukherbouchi* (Late Devonian) (Frey *et al.* 2020). Buser *et al.* (2020) have written an excellent how-to guide on using open-source software for those who wish to incorporate CT scanning into their research.

Chapter 3 in this book serves as an accessible primer for those interested in the biomechanics of extant sharks and rays. Because the laws of physics have not changed over time, those same principles apply to the biomechanics of extinct chondrichthyans. We refer readers to that chapter for details and here we outline potential applications of those techniques to extinct chondrichthyans. However, fossils can present a unique challenge for biomechanists; soft tissues such as joint cartilage and ligaments are missing, and fossils are sometimes tectonically deformed compared with their original state.

Despite their overwhelming prevalence in the chondrichthyan fossil record, teeth are understudied with respect to biomechanics and function, especially when one considers the diversity of tooth morphologies across the more than 400-million-year history (Cappetta 1987; Ginter *et al.* 2010; Whitenack *et al.* unpublished data). There are several morphologies for which we have no functional data nor any extant analog. Holocephalans in particular have been left out of these types of analyses, even when we look at extant chondrichthyans. The rarity of body fossils, including stomach contents, usually leads to ecological reconstructions that are based solely on assigning teeth to functional morphotypes (e.g., Cappetta 1987; Cicimurri 2000, 2004; Peyer 1968; Stahl and Parris 2004), finding potential feeding traces in co-occurring fossils (e.g., Hill *et al.* 2015; Mapes and Hansen 1984), or simply guessing based on what other fossils co-occur in the same strata. Direct evidence of predation is rare (but see Ehret *et al.* 2009; Kriwet *et al.* 2008; Vullo 2011). Biomechanical testing on extant shark teeth has revealed that functional morphotypes do not often hold for a given tooth morphology (Corn *et al.* 2016; Whitenack and Motta 2010), which suggests that quantitative testing of tooth performance in both extant and extinct taxa is needed.

Denticles are another commonly preserved, but largely overlooked, group of chondrichthyan fossils. There is a robust literature about how extant elasmobranch denticles function in flow and drag reduction (e.g., Dean and Bhushan 2010; Motta *et al.* 2012; Oeffner and Lauder 2012; Raschi and Tabit 1992;

Reif and Dinkelacker 1982; Chapter 3 in this book), which has led to the establishment of functional morphotypes, such as drag reduction type, abrasion strength type, and defense type (Raschi and Tabit 1992; Reif 1978). There have been limited attempts to apply these functional morphotypes derived from extant taxa to denticles of extinct taxa (Feichtinger *et al.* 2020b) and no performance testing of denticles from extinct chondrichthyans. Studies using 3D-printed extant shark skins (Wen *et al.* 2014, 2015) or other means of fabrication (Bechert *et al.* 2000; Lang *et al.* 2008) may serve as a template for future studies on extinct chondrichthyan denticles to determine whether functional morphotypes hold for extinct taxa. Given that dermal denticles of extant elasmobranchs suffer from many of the same complications we see in teeth, including variation between sexes and ontogenetic stages (Reif 1985; Crooks *et al.* 2013) and having multiple functions (Feichtinger *et al.* 2020b), performance testing could shed light on the function of denticles from extinct chondrichthyans. This could be especially useful for extinct chondrichthyans with denticle morphologies that are not found in extant chondrichthyans and for sharks such as symmoriiforms, where denticles are not found in the integument and are thought to be present only on the brush complex or near sensory canals (Ginter *et al.* 2010; Maisey 2005, 2007).

Swimming performance and hydrodynamics can also be examined on a macroscale, even in the absence of well-preserved fins, tails, and bodies. Vertebrae are an integral part of swimming mechanics, as the bending of the vertebral column functions as a spring loaded by energy from the surrounding musculature (Porter *et al.* 2016). How this spring bends is determined by the stiffness of the vertebral column, which is a result of the degree of calcification in each individual centrum, as well as the shape of the spring itself and its individual elements (Porter *et al.* 2009, 2016; Chapter 3 in this book). The shape of individual vertebral centra is a strong predictor of body curvature during turning maneuvers in extant sharks (Kajiura *et al.* 2003; Porter *et al.* 2009).

Finally, biomechanics has the potential to be a powerful tool to examine those wonderfully enigmatic chondrichthyans who have features that look nothing like modern sharks and their relatives. Although *Helicoprion* is perhaps the poster child of this group, other Paleozoic chondrichthyans have an assortment of ornamentation and body shapes that have no modern analog. Reconstructing and hydrodynamic testing of the brush complex of *Stethacanthus* or the dorsal spines of *Falcatus* and *Damocles*, for example, could be the key to understanding some of the consequences of such unusual headgear (Figures 1.3 and 1.4).

1.5 LEVERAGING THE FOSSIL RECORD FOR CONSERVATION

Approximately 30% of extant chondrichthyans are estimated or assessed as threatened with extinction (Dulvy *et al.* 2014, 2021; International Union for Conservation of Nature 2021; Stein *et al.* 2018), primarily due to overfishing (e.g., MacNeil *et al.* 2020; Pacoureau *et al.* 2021; Chapters 21 through 25 in this book). Climate change is not a significant current extinction threat for most species, although some rare and specialized species are exceptions (Chin *et al.* 2010). One area of paleobiology that has significant potential for interfacing with chondrichthyan neontology is conservation paleobiology. The goal of this area of research is to leverage geohistorical tools, such as those from paleontology and geology, to understand, mitigate, and restore our current biodiversity and environmental crises (e.g., Dillon *et al.* 2017; Savarese 2018; Tyler and Schneider 2018b). The Earth has previously experienced five mass extinction events of varying magnitudes (Raup and Sepkoski 1982; Stanley 2016). Knowledge of how organisms responded to and recovered from times of environmental disturbance or higher extinction rates can help us understand how contemporary organisms are responding to the current mass extinction crisis and how we might be able to mitigate negative impacts (Barnosky *et al.* 2011; Payne *et al.* 2016; Penn *et al.* 2018). We also can use data from more recent fossil assemblages to understand biodiversity and environmental baselines prior to human documentation of such information and prior to human existence (Jackson *et al.* 2001; Kidwell 2015). Finally, past extinction, origination, and immigration events have played a significant role in determining modern biodiversity patterns outside of anthropogenic influences (Huang *et al.* 2015). Having a firm handle on these nuances will be helpful for understanding which human activities affect the current status of a particular organism. For example, 10 out of the 15 extant lamniform sharks are threatened with extinction; longline fisheries targeting pelagic fishes, such as billfishes and tuna, have been blamed (Stein *et al.* 2018). However, when the 140-Ma evolutionary history of Lamniformes is considered, it becomes clear that the clade has been in decline at least since the Eocene due to competition with the Carcharhiniformes and global cooling (Codamine *et al.* 2019). This is not to say that humans have not contributed to the current crisis, but rather that these sharks were already particularly vulnerable, and the temperature changes from our current global climate change may exacerbate rates of decline due to other anthropogenic factors such as fisheries. A broader look at the fossil record of extant genera, which reaches back approximately 190 Ma, reveals that species that are currently threatened have a significantly older fossil record and are more evolutionary distinct than non-threatened elasmobranchs (Stein *et al.* 2018; Palliard *et al.* 2020).

Conservation paleobiologists tend to divide sources of data by time frame: "near time" encompasses the Pleistocene and Holocene epochs (~2.6 million years ago to present day) and "deep time" is anything older than 2.6 million years. This division reflects the different information that we can get from older versus younger fossils. Although younger fossils tend to have less exposure to destructive diagenetic processes and are evolutionarily closer to their extant descendants, older fossils provide a broader range of evolutionary and ecological possibilities and perspectives (Kidwell and Flessa 1995; Rick and Longwood 2013; Tyler and Schneider 2018b).

Near-time skeletal remains include taxa that are still extant or very close relatives of extant taxa. Conservation biologists have used data from skeletal remains that are contemporaneous with human existence to construct historical baselines and understand anthropogenic influence on sharks and their relatives prior to the last several decades. This is the realm of time covered by historical ecology and zooarchaeology. For example, records of White Shark sightings (McPherson and Myers 2009); historical landing data and naturalists' descriptions of sharks in the Adriatic Sea (Fortibuoni *et al.* 2010) and North Sea (Bom *et al.* 2020); collections of weapons bearing shark teeth and stingray spines (Drew *et al.* 2013); and combining fisheries data and data on shark remains in middens in Jamaica (Hardt 2009) have been used to gain insight into elasmobranch populations of the recent past. Data from middens have also been used to inform goals for marine protected areas off the coast of Kenya (McClanahan and Omukoto 2011).

Studies that reach past human existence are much rarer. In very recent remains (<100,000 years old), ancient DNA (aDNA) has been recovered from a variety of organisms, but it is a rare occurrence (Alter *et al.* 2007; Hadly and Barosky 2017). The half-life of DNA is estimated to be 521 years (Allentoft *et al.* 2012), indicating that the use of aDNA is constrained to the last million years old or so. aDNA has been recovered from 700,000-year-old frozen horse remains (Orlando *et al.* 2013) and a 1.2-million-year-old mammoth tooth (van der Valk *et al.* 2021). However, reliable and accurate sequences beyond that time period have not been published. Recovery of elasmobranch DNA from recent remains has occurred, but most of the remains used in these studies are not fossilized and are less than two centuries old (Ahonen and Stow 2008; Fioravanti *et al.* 2020; Gubili *et al.* 2015; Nielsen *et al.* 2017). DNA has also been recovered from and used to identify elasmobranch skeletal remains from middens in New Zealand that range from 400 to 750 years ago (Seersholm *et al.* 2018; Shepherd and Campbell 2021). Chondrichthyan aDNA recovery from older remains either has not been attempted or has not been successful, based on its absence from the literature.

However, other, more accessible data can be gathered from near-time remains that can be used to establish a pre-human baseline, such as taxonomic identity and ecological characteristics, including richness, relative abundance of species, and population dynamics information (Kowalewski 2017; Lyons and Wagner 2017). To date, shark dermal denticles have been the only skeletal remains used for this purpose (Dillon *et al.* 2017, 2020). Denticles from mid-Holocene reefs in Panama were used to reconstruct ancient shark communities compared with the current shark community, including making inferences about shark ecology based on the link between extant shark denticle morphology and ecology (Dillon *et al.* 2017). Importantly, these techniques were ground-truthed by finding a positive correlation between denticle accumulation rates in current sediments and extant shark abundance measured by visual assessments, hook and line surveys, and remote video (Dillon *et al.* 2020). A similar technique using elasmobranch teeth could also prove to be a powerful tool.

Studies using fossils from deep time (>2.6 million years ago) have the potential to examine issues of extinction, invasion, and ecosystem recovery on a macroscale. Our current biodiversity crisis is the first large-scale global loss of species since the K–Pg mass extinction 66 Ma (Barnosky *et al.* 2011; Payne *et al.* 2016). On the other hand, chondrichthyans as a whole have been through several mass extinction events during their evolutionary history (Kriwet and Benton 2004; Friedman and Sallan 2012; Koot 2013). We cannot make one-to-one comparisons from past mass extinction events to our current one; some putative causes of past extinction, such as flood basalts or asteroid impacts, are not part of our current mass extinction. Rapid ocean temperature change, such as the rapid warming (5°C–6°C over a few thousand years) associated with the Paleocene–Eocene Thermal Maximum (PETM) 56 Ma, has been associated with extinction in some marine groups in the Cenozoic (e.g., Arcila and Tyler 2017; Thomas 2007; Thomas and Shackleton 1996); however, the extinctions at the PETM do not approach the levels associated with other mass extinctions, nor are there any notable impacts of the PETM on chondrichthyan diversity (Figure 1.7). Past mass extinctions have been characterized as bottom–up, starting at the base of the food web with primary producers, whereas our current crisis has been top–down, with the removal of apex predators and other consumers (Ferretti *et al.* 2010; Vermeij 2004, 2017). However, the larger picture is similar. Interaction of species, whether it is to eat or to avoid being eaten, drives a significant amount of evolutionary change (Van Valen 1973; Benton 2009). Even when an extinction event is bottom–up, cascades of secondary extinction still impact consumers (Roopnarine 2016). Past mass extinctions often have causes that create multiple environmental stressors, such as global climate change, anoxic events, sea-level change, and ocean acidification (Bond and Grasby 2017; Hönisch *et al.* 2012; Hull and Darroch 2013; Lowery *et al.* 2020). We see many of these same things in our current crisis.

We can look across multiple extinction events to make inferences about patterns of extinction and post-extinction recovery among the chondrichthyans and the influence of evolutionary processes on whether species can survive. Understanding the conditions that limit or promote adaptive responses to change are important for predicting how organisms will respond to our current crisis. In what situation or at what threshold can we expect adaptation to either rescue organisms or seal their demise? The fossil record is potentially full of natural experiments that can give us these answers.

The effect of global climate change on extant chondrichthyan species is an excellent example. Although the root cause of current global climate change differs from periods of climate change in the past, we can look at previous warming events and see how organisms responded: Did they shift their distribution with environmental changes, did they go extinct, or did they adapt to the new conditions (Aronson *et al.* 2007; Currano *et al.* 2008; Jaramillo *et al.* 2010; Speijer *et al.* 2012)? Historically, periods of global warming coincided with times of organismal diversification and adaptation, albeit those periods occurred on a longer time scale and rates of environmental change were slower compared with what we are currently seeing (Cornette *et al.* 2002). As outlined above, chondrichthyans have experienced numerous warming and cooling events in their history, yet have persisted relatively unscathed. Understanding the patterns regarding which chondrichthyans survived and which did not and the "whys" behind these patterns is key to understanding the current extinction crisis.

One way that organisms have survived past extinction events has been via refugia—areas sheltered from the conditions that caused the mass extinction events (Guinot *et al.* 2013). This area can be a contracted part of a species' range, an area outside of its range, or a new habitat altogether, such as a move to deep water (Keppel *et al.* 2012; Schneider 2018). Species occupy refugia anywhere from several generations to millions of years, depending on the nature of the crisis. As environmental recovery occurs, species then expand out of the refugium (Schneider 2018). The time spent in refugia affects the speciation, evolution, and distribution of species after they leave the refugium (e.g., Harries *et al.* 1996; Pitcher 2001; Allock and Strugnell 2012; Pellisier *et al.* 2014). For example, refugia from the last glacial maximum (26.5–20 thousand years ago), as well as phylogeographic effects of the refugia, have been identified via genetic tools for the Thornback Ray (*Raja clavata*) (Chevolot *et al.* 2006); Blacknose Shark (*Carcharhinus acronotus*) (Portnoy *et al.* 2014); and Pigeye Shark (*C. amboinensis*) (Tillett *et al.* 2012).

Conservation biologists make use of refugia concepts when establishing marine protected areas (MPAs), marine reserves, and no-take zones. Reserves for fishes typically function as isolated geographic refugia (taxa are restricted to smaller and fewer locations) and harvest refugia (no-take zones) and may successfully reduce the effects of environmental stressors from the current crisis and therefore function as long-term refugia (Baskett and Barnett 2016; Schneider 2018). Numerous studies are dedicated to understanding the environmental drivers behind extant elasmobranch distributions to aid in establishing MPAs and guidelines for management (e.g., Dwyer *et al.* 2020; Espinoza *et al.* 2014; Osgood and Baum 2015, and references therein). We also need to understand what might happen to the organisms within the refugia beyond the decadal time scale, so that we can plan further ahead (Schneider 2018). Data from the geohistorical record can help, as we can see what caused organisms to spend time in refugia, how refugia and the organisms living in them changed over time, and which organisms recovered and why (Pitcher 2001). When available, fossils can also be used to confirm the locality of refugia (Ludt and Rocha 2014).

1.6 CONCLUSION: BRIDGING THE GAP BETWEEN PALEOBIOLOGY AND BIOLOGY

The study of modern shark ecology and evolution could benefit from the temporal and spatial scope of paleobiology, and, similarly, paleobiology could benefit from the approach and themes of modern biology. We are not suggesting that every chondrichthyan study requires a paleobiological component, just as every biological study does not need to incorporate genetic sequencing. Not all questions require a paleontological perspective or *can* use data from the fossil record. However, we demonstrate in this chapter that certain areas of study would benefit from a paleobiological approach, and vice versa. The key is to choose the fossils, techniques, and time frames appropriate for the question.

Stephen Jay Gould provided a useful framework for our concluding remarks in his 1985 paper on paleobiology. In it, he wrote about evolutionary time and processes working at three different tiers: evolutionary events of ecological moments, trends within lineages and clades that operate over millions of years, and mass extinctions (Gould 1985). Ecological moments capture an instant in time, effectively encompassing most of the study of modern shark biology and ecology and today's moment in time. Paleobiologists tend to work in the other two tiers, as we outlined in this chapter. One of Gould's central arguments was that the tiers interact with each other, with higher tiers (e.g., mass extinction) undoing the progress at the lower tiers (e.g., ecological moments and evolutionary trends). Although we can ignore the "undoing" part of Gould's work for our purposes, he made a good point about the interaction among these seemingly distinct tiers. The evolutionary and phylogenetic history of chondrichthyans impacts their ecological moments, and paleobiologists can leverage modern data and neontological techniques to better understand extinct chondrichthyans, just as biologists can leverage paleobiological concepts to enhance our understanding of extant fauna.

Our understanding of chondrichthyan evolution and ecology would greatly benefit from collaborative, interdisciplinary groups with complementary knowledge. In working on this chapter, we as a paleobiology team, consisting of a biomechanist (LBW), a geochemist (SLK), and a paleoceanographer (ECS), found synergy in combining our perspectives. Often, in shark biology and paleontology, there are territories drawn with respect to methods, regions, and taxa. Historically, biology and paleontology were linked under the umbrella of "natural history," and much of the grounding of our understanding of ecology and evolution came from the broad perspectives of the natural historians of the 18th and 19th centuries, such as Charles Darwin, Alexander von Humboldt, and others. However, throughout the 20th century, the field fractured into increasingly specialized subdisciplines of evolutionary biology, ecology, molecular biology, and geosciences. Recently, the approach of incorporating geological, historical, and modern records has gained momentum (Jablonski and Shubin 2015), but mostly for the purposes of conservation paleobiology (Tyler and Schneider 2018a) and focus on terrestrial systems. To our knowledge, most marine studies to date focus on invertebrate taxa or in relatively near time (see chapters in Tyler and Schneider 2018a and papers outlined in Jablonski and Shubin 2015). Chondrichthyans have a long and rich fossil record and offer abundant opportunities to better understand the past, present, and future of aquatic vertebrates and their roles in ecosystems in a changing world. The study of chondrichthyan ecology is greatly enhanced by drawing on the temporal and spatial scope of deep-time evolutionary approaches, just as the study of evolution benefits greatly from a thorough grounding in modern ecological principles. Moving forward into the 21st century, we encourage integration across these diverse disciplines to further our collective knowledge of chondrichthyan ecology and evolutionary history to inform our conservation and management policies, as well as to mitigate anthropogenic impacts.

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2 Taxonomy and Diversity of Extant Elasmobranchs

William T. White, Helen L. O'Neill, and Gavin J.P. Naylor

CONTENTS

ABSTRACT

This chapter discusses the importance of taxonomy and provides readers with insights into the taxonomic process, from naming to allocating type specimens to publishing new names. Life sciences rely heavily on a strong taxonomic foundation. There are 1202 extant species of elasmobranchs, representing 658 skates and rays and 544 sharks. The most diverse groups are the skate families Rajidae and Arhynchobatidae, with 156 and 107 species, respectively, as well as the catshark family Pentanchidae and the whaler shark family Carcharhinidae with 113 and 57 species, respectively. Sharks and rays display a range of ecomorphotypes based on their morphology, habitat, and behavior. A total of 18 ecomorphotypes are recognized, highlighting the diversity of the elasmobranchs. This chapter also examines the broad zoogeographic patterns of elasmobranchs around the world. The Indo-West Pacific contains the highest number of elasmobranch species, with 64% of all extant elasmobranchs occurring in this region. In contrast, the polar regions have an extremely depauperate elasmobranch fauna, with only 18 species. This chapter finishes by paying homage to the important pioneering work of Dr. Leonard Compagno.

2.1 INTRODUCTION

In 1758, Carl Linnaeus established a binomial system for classifying biological organisms in the 10th edition of his *Systema Naturae*. This is now referred to as the Linnaean system of naming organisms. Although 1758 is the date at which the current naming system begins, it should be noted that names have been applied to various species centuries before that date. A good example is the Greek philosopher Aristotle (384–322 BC), who, in his pioneering *History of Animals*, made numerous references to a ray as "narce," which, given the probable locality around Greece, likely refers to a torpedo ray. Included in his writings on this species, he states, rather humorously, that "the narce also has plainly caused stupefaction in men" in reference to its "peculiar force which it has in its body" (Cresswell 1902), obviously in relation to the electric discharge it can deliver. Another noteworthy scientist was Georg Rumphius (1627–1702), a German-born botanist who worked in eastern Indonesia for the Dutch East India Company. His publication *Herbarium Amboinense* included 1200 plant species; of these, he gave species names to 930. The material collected, described, and illustrated by Rumphius was later used by Carl Linnaeus to develop the binomial nomenclatural system. Prior to 1758, species were allocated Latin names in various formats, including a single Latin name (uninomial), two Latin names (binomial), three Latin names (trinomial), or even a whole sentence describing the species in Latin. The binomial system established by Linnaeus became a universally accepted convention for naming species, and the 1758 date became the starting point for the consistent binomial nomenclature still used to this day. Linnaeus also established the system of classification of organisms using a nested hierarchical system: kingdom > class > order > genus > species. In modern taxonomy, phylum is also included after kingdom and family after order.

Starting with the 22 species of elasmobranchs named by Linnaeus in 1758, the number of new valid species named remained relatively low until the 1830s. After the 1830s, the number of new species almost doubled and remained at a moderate to low level until the end of the 20th century (Figure 2.1a). The first two decades of the 21st century saw a renaissance of elasmobranch taxonomy, with 161 new species being named in the 2000s and 138 new species in the 2010s. This rapid increase can be attributed to several key factors: the likely important apical role that elasmobranchs play in the marine and freshwater ecosystems; the recognition that they are among the most threatened group of marine organisms; and the rapid expansion of molecular discrimination tools that can highlight cryptic species and species complexes. The cumulative number of new elasmobranchs rapidly increased after 2006 (Figure 2.1a), showing a remarkably similar trend to the cumulative number of new species of reptiles (Figure 2.1b). In contrast, the cumulative number of new species of birds began to asymptote around the 1890s, with only a slight increase after this time. The cumulative number of new mammals began to level off in the early 20th century but has begun to increase more rapidly after 2000. This suggests that there are still many species of elasmobranchs that are unresolved or new to science.

In the field of elasmobranch taxonomy, a small group of scientists have made noteworthy contributions and left a legacy for the future. By far the most important contribution has been from Dr. Peter Last (retired, CSIRO Australian National Fish Collection), who has authored 167 new elasmobranch descriptions (Table 2.1). The fact that four of the five most productive taxonomists are still alive is testament to the renaissance that has occurred over the last two decades. It is also noteworthy that, out of the eight top-20 most productive taxonomists that are still alive, only three were still active and not retired at the beginning of 2021. Several younger taxonomists are now making significant impacts in elasmobranch taxonomy, including Simon Weigmann (Germany), Sarah Viana (Brazil), and Fahmi (Indonesia).

This chapter takes readers on a journey through the taxonomic process for naming species and the rules that must be followed and explores our current understanding of the biodiversity of elasmobranch species.

2.2 TAXONOMY OF EXTANT ELASMOBRANCHS

2.2.1 What Is Taxonomy and Why Is It Important?

Taxonomy, in a biological sense, is the branch of science concerned with the classification of organisms. It encompasses the nomenclature (naming), classification (hierarchical organization), description, and identification of taxa. Basic and applied subdisciplines across the life sciences, ranging from physiology to ecology and from fisheries management to conservation biology, rely on a strong taxonomic foundation. In a perfect world, the taxonomy of a group (e.g., elasmobranchs) would be completely resolved to ensure that all other life sciences had a solid foundation to work from. But, taxonomy is dynamic, with new information continually coming to hand that challenges previous views and can result in taxonomic changes. For example, most stingrays (Dasyatidae) were previously thought to belong to one of nine genera, with most species belonging to the genera *Dasyatis* and *Himantura*. However, a recent reclassification of this family has revealed that they belong to one of 18 genera, with *Dasyatis* and *Himantura* being two of the least species-rich genera (Last *et al.* 2016a).

Nomenclatural changes generally do not have much effect on other disciplines. Changing the genus name of a stingray, for example, does not change how the population structure of a species in that genus is assessed or how the species is managed based on its conservation status. But, taxonomic name changes can have implications for some research areas (e.g., biogeography, paleontology). For example, the genus *Dasyatis* was previously considered to be a globally distributed genus, but new information has allowed scientists to learn that this genus is restricted to the Atlantic Ocean (Last *et al.* 2016a). Reclassification of the genera can allow for more clarity when considering the evolutionary pathways for dispersal of species through time. In a paleontological sense, the relationship of extinct species to extant species must be reevaluated when major taxonomic changes occur on extant species or groups. Conservation management also relies heavily on a strong taxonomic foundation. In Australia, two species recently assessed as Critically Endangered by the International Union

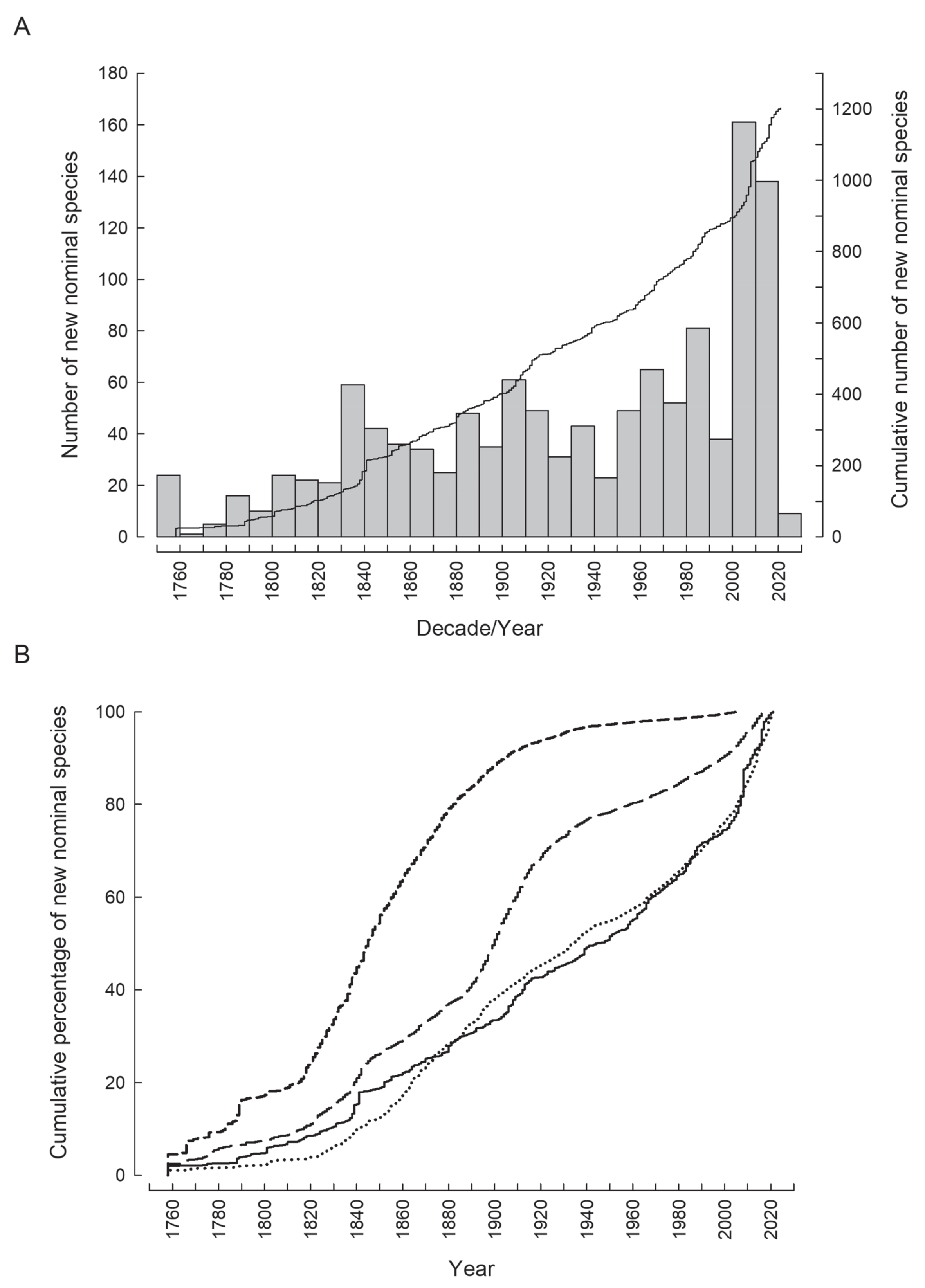

FIGURE 2.1 (A) Number of currently recognized nominal species of elasmobranchs described in each decade since 1758 (bars) and cumulative number of nominal species (line). (B) Cumulative number of nominal species of elasmobranchs (solid line), birds (short-dashed line), mammals (long-dashed line), and reptiles (dotted line), scaled to 100%. Data for the number of species described per decade for birds, mammals, and reptiles were taken from Burgin *et al.* (2018), Pimm *et al.* (2006), and Uetz *et al.* (2021), respectively.

TABLE 2.1
Top 20 Most Productive Alpha-Taxonomists and Number of Elasmobranchs They Have Described

Name	Years Lived	Active	Species Described, *n*
Last, Peter R.	Alive	Y[a]	167
White, William T.	Alive	Y	69
Séret, Bernard	Alive	Y[a]	51
Müller, Johannes P.	1801–1858	—	42
de Carvalho, Marcelo, R.	Alive	Y	42
Henle, Friedrich G.J.	1809–1885	—	41
Schroeder, William C.	1894–1977	—	36
Bigelow, Henry B.	1879–1967	—	35
Compagno, Leonard J.V.	Alive	N	35
Springer, Stewart	1906–1991	—	32
Garman, Samuel	1843–1927	—	30
Stehmann, Matthias F.V.	Alive	Y[a]	30
McEachran, John D.	Alive	Y[a]	28
Ebert, David A.	Alive	Y	26
Jordan, David S.	1851–1931	—	26
Bleeker, Pieter	1819–1878	—	23
Günther, Albert	1830–1914	—	22
Linnaeus, Carl	1707–1778	—	22
Whitley, Gilbert P.	1903–1975	—	22
Gilbert, Charles H.	1859–1928	—	19

Note: Many species have multiple authors in the authority; in these cases, equal weighting was given to all authors and each was included in the counts.

[a] Retired.

for Conservation of Nature's Red List of Threatened Species are the Whitefin Swellshark (*Cephaloscyllium albipinnum*) and the Longnose Skate (*Dentiraja confusa*). These two species were described as new in 2008, and the taxonomic evaluation of these species provided the foundation for their Red List assessments to be produced. If this taxonomic investigation had not occurred, these discrete and distinct species would remain unrecognized and undocumented. As such, there would be no incentive to look out for their long-term survival and/or conservation.

In the modern world, extinction risk due to anthropogenic effects is an increasing concern (Dulvy *et al.* 2014). Current rates of extinction increase the likelihood that species will be lost before we even knew they existed. In 2019, the Lost Shark (*Carcharhinus obsoletus*) was formally named and described based on three preserved specimens in museum collections (Figure 2.2). Despite comprehensive surveys of fish landing sites and markets in the areas where these specimens were collected (i.e., Vietnam, Sarawak, and Gulf of Thailand), no records of this species are known since 1934 (White *et al.* 2019). The inferred population decline due to overfishing and the suspected population size of fewer than 50 individuals led to this species being assessed as Critically Endangered (Possibly Extinct) (Dulvy *et al.* 2020). This is the first example of an elasmobranch species possibly going extinct before it has been described in modern times, but it is sadly unlikely to be the last!

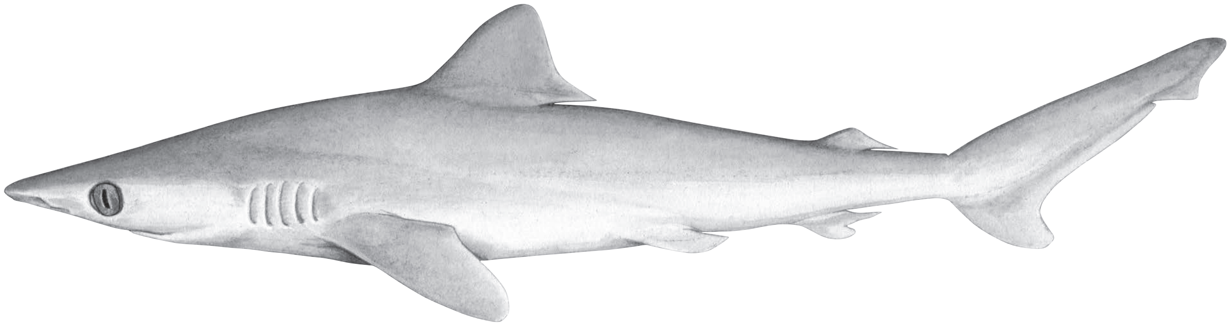

FIGURE 2.2 The Lost Shark (*Carcharhinus obsoletus*) has not been collected since 1934 and has been assessed as Critically Endangered (Possibly Extinct). (Illustration by Lindsay Marshall, www.stickfigurefish.com.au.)

2.2.2 What Is a Species?

The question even many an experienced taxonomist would like to avoid is simply, "What is a species?" It sounds simple to provide a conclusive statement on what the principal taxonomic unit is, but let us introduce the species concept. The species concept attempts to describe the criteria that an animal, or group of animals, must have to qualify as a separate species from others. In a perfect world, one species concept would exist, and everyone would agree on it. Unfortunately, that world does not exist, and there are multiple species concepts being applied to taxonomic works with little agreement. The three major species concepts in biology are as follows:

- *Biological species concept*—This is the most widely applied and most frequently used concept. It defines a species taxon as a group of organisms that can interbreed and produce reproductively viable offspring; that is, they themselves can reproduce successfully. In this concept, the integrity of the species is maintained by interbreeding together with reproductive barriers between species (i.e., reproductive isolation) (Ereshefsky 2007). One problem with this concept for sexually reproducing species, though, is that most taxonomists work on preserved specimens, and reproductive isolation cannot be tested (Gordh and Beardsley 1999).
- *Ecological species concept*—This concept defines a species taxon as a set of individuals that are adapted to a particular set of resources or niche in the environment. In this concept, a stabilizing selection will maintain species integrity, whereas disruptive selection can lead to speciation (Ereshefsky 2007). Stabilizing selection occurs where a particular phenotype is favored and rapidly becomes the most abundant, whereas the other phenotypes are selected against. In contrast, disruptive selection occurs where phenotypes at the extremes of a phenotypic distribution are favored, and intermediate phenotypes are selected against.
- *Phylogenetic species concept*—This concept defines a species taxon as a monophyletic lineage that contains all of the descendants of a common ancestor (Ereshefsky 2007).

These three species concepts can result in different classifications for the same group of organisms. There are two different philosophical views on classification: pluralist and monist. Monists maintain that a single species concept needs to be agreed on and adopted. In contrast, pluralists hold the view that different species concepts produce different classifications, all of which are valid. One argument for pluralism is that there are different evolutionary forces at play, as described by Ereshefsky (2007): "Interbreeding species are the result of interbreeding; ecological species are caused by natural selection; and phylogenetic species are the result of genealogy." The take-home message is that there is no single, agreed-upon concept that universally captures what it is to be a "species." Philosophers and biologists to this day disagree on the definitions, and, given the complex evolutionary forces at play across diverse organisms, it is unlikely to be resolved in our lifetime or ever. In conclusion, when asking taxonomists "what is a species?" don't be alarmed if they struggle to provide a clear answer.

2.2.3 Molecular Tools

2.2.3.1 Species Discrimination

In the last three decades, the proportion of molecular studies has greatly increased, and the field has evolved more than any other life sciences discipline (Dudgeon *et al.* 2012; Durmaz *et al.* 2015). As technology has advanced, new genetic techniques are coming to hand that can open new doors into our understanding of species and ecosystems. The use of molecular techniques to help distinguish among closely related species has become a widely adopted method for biodiversity and fisheries assessments. They are particularly useful when dealing with parts or damaged specimens (e.g., shark fins, jaws, trunks). A molecular technique was first used in elasmobranchs in the 1990s, when Heist and Gold (1999) used a 395-base pair (bp) region of mitochondrial DNA (mtDNA) to discriminate among 11 species in the U.S. Atlantic coastal shark fishery. It was later shown that a 1400-bp mtDNA region could distinguish among 35 species of western North Atlantic sharks based on the observation of low intraspecific sequence variation in relation to interspecific variability (Greig *et al.* 2005). They concluded that mtDNA could be used as a method for species identification.

Hebert *et al.* (2003) proposed that a single gene sequence could be used to differentiate most, if not all, animal species. They proposed the use of the mtDNA gene cytochrome oxidase subunit 1 (*CO1*) as a global identification system, which was likened to an individual "barcode" for each species (i.e., DNA barcoding). This proposal spawned the Barcode of Life Database (www.boldsystems.org). The first large-scale demonstration of the use of *CO1* for sharks and rays was the study conducted by Ward *et al.* (2008) on Australasian samples. This study showed that 99% of the 210 chondrichthyan species that were recognized as distinct species based on morphological criteria could be discriminated using the *CO1* gene. One of the limitations of the *CO1* gene, at least for sharks and rays, is that it is a small gene (655 bp) and has a relatively slow rate of evolution. Naylor *et al.* (2012) selected a larger and faster evolving gene, NADH dehydrogenase subunit 2 (*ND2*, 1044 bp), to investigate its utility as a more suitable species-discriminating gene for elasmobranchs. In this study, 4283 specimens representing 574 species of elasmobranchs were sequenced. These samples included representatives from all known families and almost three-quarters of known genera. The *ND2* sequencing results were typically consistent with the *CO1* results, but it was able to distinguish among some groups that *CO1* failed to separate. For example, some smoothhound sharks (*Mustelus* spp.) that could not be distinguished based on *CO1* sequences were discriminated from each other using the *ND2* sequences (e.g., Gummy Shark, *Mustelus antarcticus*; Rig, *Mustelus lenticulatus*; Western Spotted Gummy Shark, *Mustelus stevensi*) (Naylor *et al.* 2012).

2.2.3.2 Problems with and Misuse of Molecular Species Identification

Despite the effectiveness of molecular tools, they must be applied with caution, because several complications have been encountered that produce confounding results. Mitochondrial DNA is inherited maternally (i.e., from the mother). So, in situations where two species hybridize, the progeny will have an mtDNA sequence that is identical to that of the mother. If this is overlooked, it can lead to taxonomic uncertainty. For example, Morgan *et al.* (2011) detected hybridization between the Australian Blacktip Shark (*Carcharhinus tilstoni*) and the Common Blacktip Shark (*Carcharhinus limbatus*) in northern Australia. If the hybrid progeny were DNA barcoded, they would be interpreted as either one of those species, depending on the identity of the mother. This becomes further complicated when hybrid offspring have mitochondrial DNA sequences that match the mother but morphology match the other species, the father. This discordance can lead to over-splitting of taxa if the hybridization goes unnoticed. Naylor *et al.* (2012) suggested that it was likely that some of the taxonomic groupings in their study, and in other molecular species discrimination studies, may have been affected by hybridization.

Introgression is a form of hybridization, with repeated backcrossing of interspecific hybrids with one of the parent species. This can result, over the course of multiple generations, in movement of genes from one species to another. It can yield complex mixtures of parental genes that are difficult to interpret. Introgressive hybridization in sharks and rays is poorly documented. Corrigan *et al.* (2017) found historical introgression between the Dusky Shark (*Carcharhinus obscurus*) and the Galapagos Shark (*Carcharhinus galapagensis*), likely following a range expansion. Pazmiño *et al.* (2019) also found introgression between these species and suggested that a combination of nuclear and mtDNA markers should be used to properly assess species identification, particularly when species are closely related.

Ancestral polymorphisms can also confound taxonomic interpretation of sequence data (Charlesworth 2010). Ancestral polymorphisms are variants that have arisen in populations prior to the speciation that generated the species or subspecies. This can lead to paraphyletically distributed alleles, where different populations of the same species do not appear to be their own closest relatives (Naylor *et al.* 2012). Ancestral polymorphisms are most prevalent when populations are large, with high levels of polymorphism, and the time between vicariant events is short (Naylor *et al.* 2012). Using a series of independent nuclear markers is the best method for identifying this. Walter *et al.* (2017) explored ancestral polymorphisms as a possible explanation for the mixed genetic signatures among individuals of the Greenland Shark (*Somniosus microcephalus*).

When looking at the mtDNA marker *ND2*, Naylor *et al.* (2012) found that, in most cases, the greater the overall sequence divergence between forms, the more likely they are to be different species. However, sequence variation differs among lineages and, as a result, a sequence divergence threshold to define clear species separation cannot be set. This has been an issue with some conventional DNA barcoding studies. Ward *et al.* (2008) found that ~96% of within-species sequences showed less than 2% divergence. Unfortunately, many subsequent studies have used information such as this to suggest that over 2% divergence likely indicates a separate species. In sharks and rays, *CO1* sequences can show highly variable divergence rates between and within species. For example, Ward *et al.* (2008) found that some species of *Mustelus* showed no interspecific divergence when the *CO1* gene was used, but Finucci *et al.* (2018) found that *CO1* sequences of Ogilby's Chimaera (*Chimaera ogilbyi*) demonstrated intraspecific divergences of up to ~7%.

Missing data within sequences can also be an issue. Naylor *et al.* (2012), concerned about the potential impact of missing data on their phylogenetic inferences, restricted their analyses of the *ND2* sequences to those where at least 1000 bp (of the entire 1044-bp complement) were generated. Even with this restriction in place, the authors cautioned that variation observed among some closely related species may be the result of minor differences in pairwise differences due to missing data. Failing to consider the effect of missing data in analyses of barcode sequences can induce the appearance of variation where it does not exist. This problem is generally more severe with distance-based approaches and can often be avoided by using maximum-likelihood–based approaches (Swofford *et al.* 1996).

Experimental error is also important to consider, as it can affect the accuracy of species identification. Errors can occur during the polymerase chain reaction amplification phase when low-fidelity Taq polymerases are used or during the sequencing reaction phase. Interpretation of the resulting chromatograms can be ambiguous, resulting in assignment errors. Errors can also occur at the alignment stage, but are less of a concern when using a protein-coding gene (e.g., *CO1*, *ND2*), because they can be aligned at both the nucleotide and amino acid levels. Another basic error that can occur prior to sequencing is the mislabeling of samples or mix-up issues as they are subsampled. Such basic problems can lead to misinterpretation of data in species identification studies. Thus, careful interpretation of the results is needed to ensure that no problems have occurred.

2.2.3.3 Integration or Conflict

As with many new tools, DNA barcoding has suffered from the "shiny object syndrome," where a new approach is touted as a solution to long-standing problems but, with the passage of time, is found not to be the "silver bullet" it was initially claimed to be. There have been several thoughtful critiques of the application of DNA barcoding to documenting species diversity (e.g., Moritz and Cicero 2004; Will *et al.* 2005). In the early years of DNA barcoding, it was even claimed by some that "barcoding" negated the need for classical taxonomic approaches. For example, in what we view as a particularly misguided publication, Cook *et al.* (2010) suggested that DNA sequencing alone could form the basis of species descriptions without any need for morphology to be used at all. We strongly discourage this approach, because, without morphology, end users have no visual means for discriminating among species. The Whitespotted Eagle Ray complex is a good example of this problem. Richards *et al.* (2009) used molecular species discrimination tools to first highlight this group as a possible complex of species, but the sequence data alone could not successfully resolve the taxonomic issues. The nomenclatural complexity of this group required careful assessment, which was subsequently undertaken by White *et al.* (2010), based on the findings from Richards *et al.* (2009). Thus, integration of different techniques was essential to successfully resolve the taxonomy of the group.

As with all tools, molecular techniques are constantly being improved to deliver better outcomes. Molecular taxonomic research over the last two decades now indicates that, although single mtDNA markers can provide adequate data in most cases, inclusion of additional nuclear markers can be important. Only then can the level of hybridization and introgression be investigated, which is crucial for improving our understanding of species discrimination in sharks and rays. Integrating molecular data with morphological data is also important. The case of Ogilby's Chimaera by Finucci *et al.* (2018) is a good example of integrating morphological data with mtDNA and nuclear data to resolve a species complex. If only mtDNA data had been used, this complex would likely have been incorrectly split into four species instead of the single species recovered from the integrative dataset. The stability of taxonomic names of sharks and rays in the future will rely on more integrative approaches to resolve taxonomic issues.

2.2.4 How a Species Is Formally Named

2.2.4.1 Nomenclature

Nomenclature is defined as "the devising or choosing of names for things, especially in a science or other discipline" (Lexico 2021). In terms of life sciences, nomenclature is the branch of taxonomy concerned with applying a scientific name to a taxon based on a particular classification scheme in accordance with international rules and conventions. The classification scheme follows the binomial system credited to Linnaeus, with the start of zoological nomenclature being taken as the tenth edition of his *Systema naturae* in 1758. For zoology, the international rules and conventions that govern the binomial classification scheme are set out in the International Code of Zoological Nomenclature (ICZN) (International Commission on Zoological Nomenclature 2021). The binomial naming system gives each species a scientific name composed of two parts: the first is the generic name and the second the specific name; for example, the Chain Catshark has the genus name *Scyliorhinus* and the specific name of *retifer*. The generic and specific names mostly follow Latin grammar rules. Within a kingdom (e.g., Animalia), no two genera can be the same. If two generic names are the same, they are termed homonyms. In such cases, the newest generic name is deemed invalid, and a new generic name must be established for that taxa/taxon. The older generic name remains unchanged, and homonymy is prevented. In contrast, specific names can be repeated within a kingdom, or any other level other than genera. Thus, if the combination of generic and specific names is different, a specific name can be used multiple times. For example, the specific name *australis* (Latin for south or southern) is used for six elasmobranch species (*Apristurus australis*, *Cirrhigaleus australis*, *Dentiraja australis*, *Gymnura australis*, *Himantura australis*, and *Squatina australis*), and all are valid.

The combination of a generic and species name must not be repeated to prevent homonymy. An example of a homonym in an elasmobranch is the species name *Raja africana*. Bloch and Schneider (1801) described *Raja africana* based on a specimen from Guinea which is now considered a junior synonym (see next section on synonyms) of the Porcupine Ray (*Urogymnus asperrimus*). Then, 176 years later, Capapé (1977) described a new species of skate from off Mauritania also as *Raja africana*. Thus, the skate species required a new name, regardless of the Bloch and Schneider name being considered a synonym and in a different family. White and Fricke (2021) allocated a replacement name of *Raja mauritaniensis* to this skate, preventing the homonymy (Figure 2.3).

A basic understanding of Latin grammar is beneficial for forming new species names, although not a prerequisite. Scientific names can be sourced from other languages (e.g., Greek), but the combination of generic and specific name must be treated as if it was a Latin phrase. Generally, the specific name must be the same gender (feminine, masculine, or neuter) as the generic name. For example, most Latin nouns ending in *-a* are feminine, most ending in *-us* are masculine, and those ending in *-um* are neuter (of neither sex). In Greek, nouns ending in *-is* or *-ys* are feminine, *-os* is masculine, and *-on* is neuter. Why is this important to understand? One confusing aspect of taxonomy, which can often frustrate non-taxonomic researchers, is when species names change. Even more confusing is when the specific name changes just because the genus has changed. For example, in the revised classification of stingrays provided by Last *et al.* (2016a), the Mangrove Whipray was reclassified from the genus *Himantura* to the genus *Urogymnus*. This resulted in a change from a feminine generic name to a masculine generic name, meaning the specific name also needed to change gender. Thus, the scientific name changed from *Himantura granulata* to *Urogymnus granulatus*. Similarly, the Atlantic Stingray (*Dasyatis sabina*) changed to *Hypanus sabinus*, as the terminations *-is* and *-a* are feminine and *-us* is masculine. Thus, when a specific name is being applied, one must consider the gender of the genus name to enable allocation of a correct specific name. It should be noted that, if the original author of a species description made an error in the gender allocated to the species name (e.g., *fasciata* instead of *fasciatus*), then the stem name (i.e., *fasciat-*) would still be valid, and the suffix would simply be changed to the correct gender

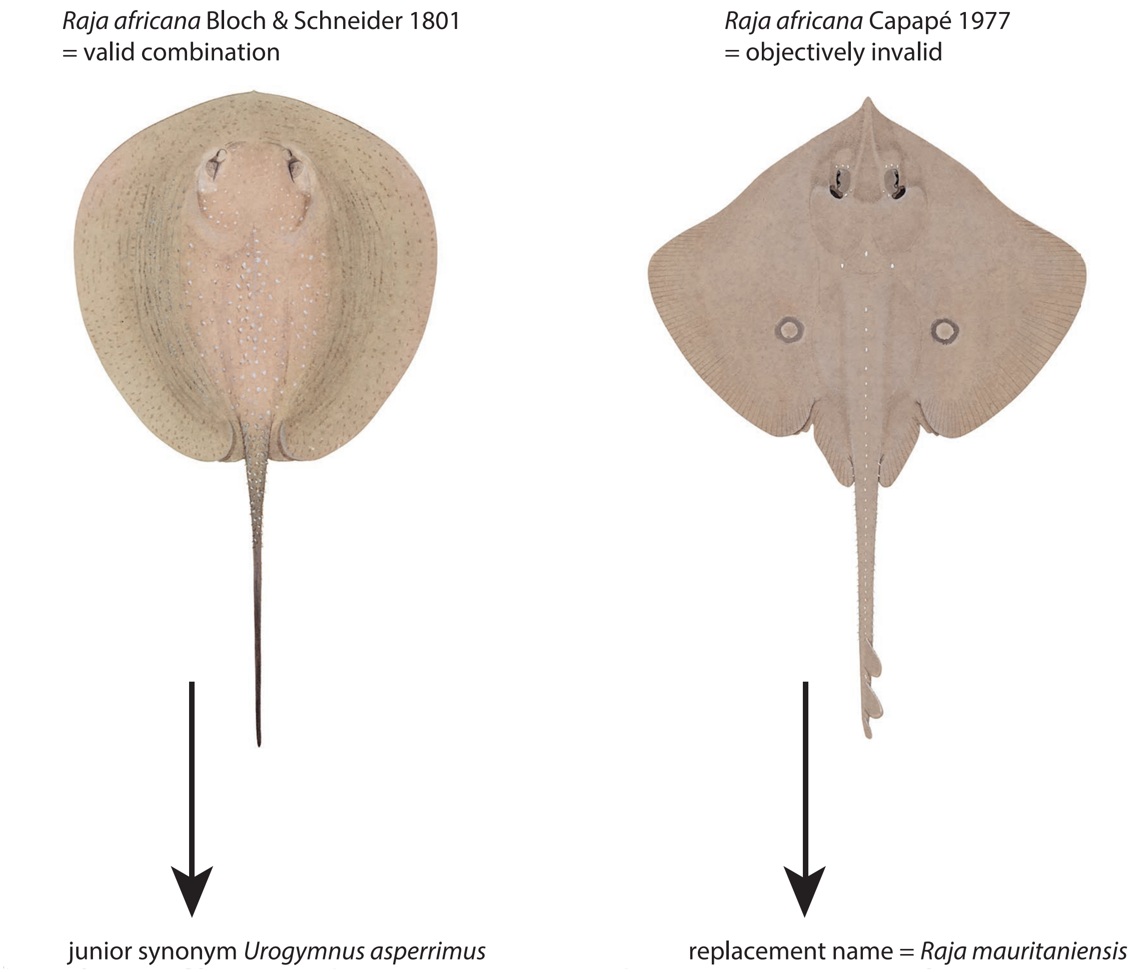

FIGURE 2.3 The *Raja africana* homonym problem: one name, two species, and a replacement name. (Illustrations by Lindsay Marshall, www.stickfigurefish.com.au.)

in subsequent publications (i.e., *fasciatus*). The specific name can also be assigned as a noun in apposition, in which case it does not have to agree in gender with the generic name. For example, the specific name of David's Angel Shark (*Squatina david*) is stated by the authors as being a noun in apposition (Acero *et al*. 2016). In this case, the specific name does not have to agree with the gender of the genus *Squatina* and cannot be altered. In modern taxonomy, a specific name intended as a noun in apposition needs to be clearly designated as such by the original authors.

The specific names applied to new species can be based on a variety of sources at the authors discretion; however, in modern taxonomy, the etymology or origin of the name must be presented. The most common, and many would consider the most ideal, source of a species name is a Latin adjective based on of a key feature of the new species. For example, for a shark with distinct white fin tips, the Latin *album* (white) and *pinnulas* (fins) could be combined to form the specific name *albipinnus* or *albipinna*. A specific name may also reflect the geographic location of a species. In these cases, the most common suffix used is -*ensis*, but -*icus* or -*anus* are also accepted. Examples in elasmobranchs include the Southern Sleeper Shark (*Somniosus antarcticus*), the Australian Weasel Shark (*Hemigaleus australiensis*), and the Mexican Hornshark (*Heterodontus mexicanus*). It should be noted that it is preferred that only the stem component of the geographic region be used, not the entire name. For example, *mexicanus* is preferable to *mexicoanus*, and *australiensis* preferred over *australiaensis*.

Patronyms are another common form of specific name where they honor a person of note. The current rules allow a name honoring a male to be formed by adding -*i* at the end; for a female, -*ae* is used. Reasons to assign a patronym include a person's direct assistance to that study, acknowledgment of that person's lifelong work in a relevant field, their discovery of the species, their collection of the type specimens, or honoring that person's memory, among other reasons. For example, Edmunds' Spurdog (*Squalus edmundsi*) was named after Matt Edmunds, who contributed directly to the study of Australian spurdog species (White *et al*. 2007). The Brown Lanternshark (*Etmopterus compagnoi*) was named after Leonard Compagno by Fricke and Koch

(1990) to acknowledge his extensive taxonomic study on elasmobranchs. The Spotted-Belly Catshark (*Atelomycterus erdmanni*) was named after Mark Erdmann, who discovered the species and collected the type specimens of this catshark from Indonesia (Fahmi and White 2005). Genie's Dogfish (*Squalus clarkae*) was named in memory of the late Eugenie Clark by Pfleger *et al.* (2018).

The authority of a scientific name is another source of confusion at times. The authority of a scientific name is the author(s) who described it and the year in which the name was first published. The use of parentheses around the authority of a species denotes that the genus name is different from that designated by the original authors. When the genus name has remained the same from the original publication, no parentheses are used. For example, the authority for the Indonesian Angel Shark (*Squatina legnota*) is "Last and White 2008," because the genus name has remained unchanged. In contrast, the authority for the Angel Shark (*Squatina squatina*) is "(Linnaeus 1758)," because it was originally allocated to the genus *Squalus*.

2.2.4.2 Synonymies

The creation of a new scientific name represents a new available name for a species. Many species have been assigned multiple available names, which are termed synonyms. Synonyms can be the result of detailed taxonomic revisions of groups or unknowingly assigning a new name to an already named species. When there is more than one available name for a species, the earliest published name is typically considered the valid name for that species. This is termed the "Principle of Priority," whereby the oldest available name takes precedence over others applied to a taxon. The remaining available names become junior synonyms. For example, the Basking Shark has a total of 20 available names, of which *Cetorhinus maximus* (Gunnerus 1765) is the oldest available name and takes priority as the valid name and senior synonym. The remaining 19 names are considered junior synonyms. Although this seems straightforward, several caveats exist, which a taxonomist needs to consider. According to the code, reversal of precedence can be applied when both of the following criteria have been met:

- The senior synonym (oldest name) has not been used as a valid name after 1899.
- The junior synonym in question has been used for that taxon as its presumed valid name in at least 25 published works by at least 10 authors in the immediately preceding 50 years, over a span of not less than 10 years.

This can be a complicated issue to resolve, and, in some cases, a submission to the ICZN is required to request a ruling. For example, *Squalus conductus* Osbeck 1765 is considered a synonym of the Common Blacktip Shark (*Carcharhinus limbatus*) and, given it was named more than 70 years prior to *C. limbatus*, is the oldest available name. However, because that name had not been used as valid after 1899, it is considered *nomen oblitum*, and reversal of precedence is invoked (ICZN Article 23.9.1.1). Luckily, this is a rare occurrence in the taxonomy of sharks and rays. The key consideration with synonyms is that all available names must be considered for a taxon before a new name is applied. An excellent source for researching available names of any fish is the online Catalog of Fishes (Fricke *et al.* 2021).

A good example of the need to research available names is highlighted in the revision of the *Carcharhinus dussumieri–sealei* complex by White (2012). In this paper, the author found that this complex consisted of four species and not two as previously thought. Investigation of the available names found that the additional species in the complex already have available names, including the Indonesian Whaler Shark (*Carcharhinus tjutjot*) and the Australian Blackspot Shark (*Carcharhinus coatesi*). If the available names were not investigated and new names proposed, these would have subsequently been considered junior synonyms of the valid senior synonyms. This "resurrection" of junior synonyms to valid species names is as important as describing a new species, although it often gets overlooked and receives less attention.

Determining the oldest available name for a species can be a complicated and difficult task. Some historical publications list only new scientific names, with little or no written description, with no illustrations provided or types allocated. In the instance, because such names are the oldest available name for a taxon, resurrecting them to species level can be risky. For example, in a revision of the Indo-Pacific pelagic eagle rays (Aetobatidae), White *et al.* (2010) considered the name *Aetobatus ocellatus* as the valid name for the Indo-Pacific Whitespotted Eagle Ray (*Aetobatus narinari* complex). But, subsequently, Kottelat (2013) stated that this was an incorrect assignment and used the name *Aetobatus mula* (Forskål) named in 1775, stating that it was the oldest available name. Two names were made available in 1775 by Forskål—*Raja mula* and *Raja tajara*—and both names were previously considered synonyms of *Aetobatus narinari* (Euphrasen 1790). These names were not used by White *et al.* (2010) as the senior synonym of this species, because the identity of the taxon to which these names refer cannot be accurately determined. No types or illustrations exist, and the description only enables readers to determine it was an eagle ray. In this region, another eagle ray of the family Myliobatidae also occurs, the Ocellate Eagle Ray (*Aetomylaeus milvus*). The coloration of this eagle ray includes some white spots and ocelli, which can also be present in the Whitespotted Eagle Rays. Examination of the syntypes (see Section 2.2.4.3) of the Ocellate Eagle Ray by the first author revealed that it consists of two species, *Aetomylaeus milvus* and *Aetobatus ocellatus*. This supports the idea that older Forskål names could represent either of these species and thus cannot be used as the valid name. This confusion could have been avoided if White *et al.* (2010) had not included the two Forskål names in the synonymy of *A. ocellatus* but instead referred to them as *nomen dubium* (i.e., a scientific name that is of doubtful or unknown application). Resurrecting senior synonym names where the identity of the exact taxon is uncertain

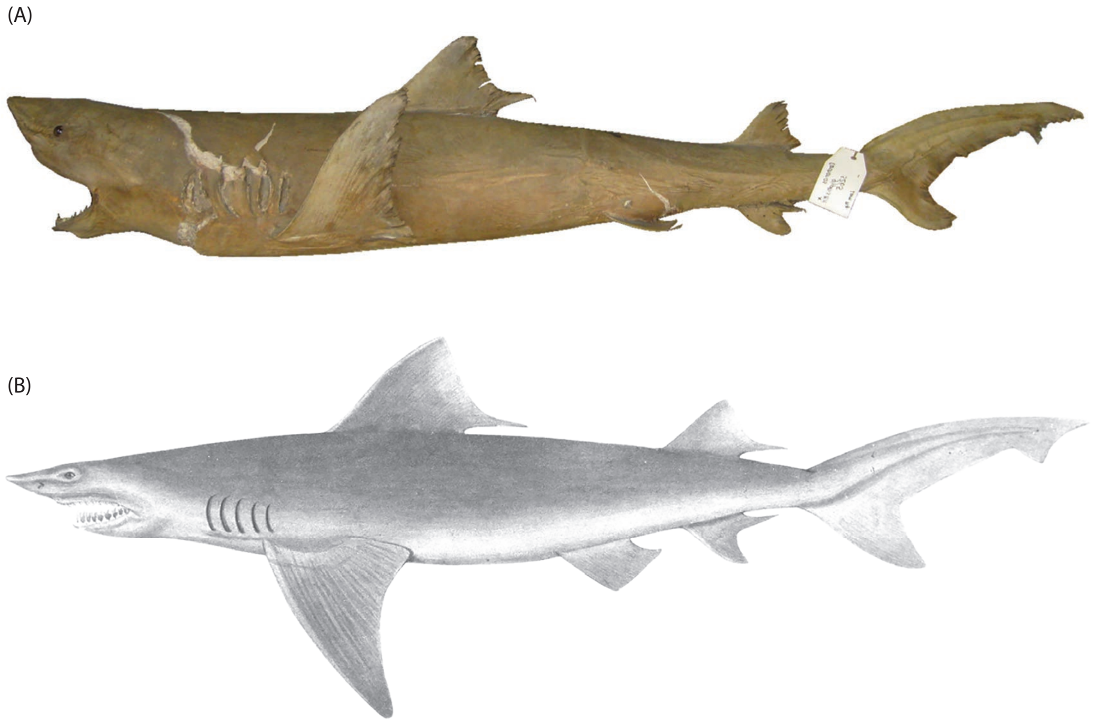

FIGURE 2.4 Holotype of the Speartooth Shark (*Glyphis glyphis*). (A) Dried and stuffed specimen in the Museum für Naturkunde in Berlin (ZMB 5265). (B) Original illustration of the holotype in Müller and Henle (1839).

creates confusion in the literature and should be avoided. Nomenclatural issues can be time consuming but are a necessary part of taxonomy to provide stable names.

2.2.4.3 Allocation of Types

Species are described based on type specimens, which act as a "blueprint" on which the description is based and are published in a scientifically recognized publication. The allocation of type specimens to a new scientific name and formal description is permanent. Even if a species is subsequently found not to be a valid taxon, the type specimens will always be linked to the scientific name that was published. Type specimens are ideally deposited in biological collections maintained by museums and universities, making them accessible to other scientists for future study. In some cases, type specimens can belong to private collections, but this is not ideal, because accessibility is often more difficult or impossible.

There are multiple categories of type specimens, some of which are seldom used in modern times. A **holotype** is a single specimen designated as the name-bearing type specimen by the original author of a species. When a holotype is designated, if any additional specimens are used to help describe the species by the original authors, they are termed **paratypes**. In modern times, new species descriptions must include a holotype at a minimum, with or without paratypes. Some older publications do not specifically designate a holotype, but if only a single specimen is referred to, it is recognized as the unique holotype for that species. For example, the original description of the Speartooth Shark (*Glyphis glyphis*) by Müller and Henle (1839) states, "Ein Exemplar trocken, im zoolog. Museum in Berlin durch Lamare Piquot" (which translates as "one copy dry, in the zoolog. Museum in Berlin by Lamare Piquot"). This single specimen thus represents the holotype of the Speartooth Shark (Figure 2.4) which was collected by the French traveler Christophe-Augustine Lamare-Piquot (1785–1873).

In older studies, formal descriptions sometimes listed several specimens on which the authors based their descriptions but without allocation of a primary, name-bearing type. These specimens are termed **syntypes** and have equal rank with each other in relation to the species description. For example, the original description of the Bull Shark (*Carcharhinus leucas*) by Valenciennes in Müller and Henle (1839) was based on four dry specimens from the Antilles deposited in Paris (Muséum national d'Histoire naturelle). These four specimens, two of which are lost (Fricke *et al.* 2021), are syntypes for the Bull Shark. Within a series of syntypes, no single specimen is the name-bearing type. Instead, all specimens are of equal rank.

When taxonomic research is undertaken on a type series consisting of syntypes, a single syntype can be designated as the name-bearing type. This specimen is referred to as a **lectotype**, and the remaining representative syntypes become **paralectotypes**. For example, the Whitecheek Shark (*Carcharhinus dussumieri*) was described by Valenciennes in Müller & Henle (1839) based on four specimens (syntypes). In his revision of the genus *Carcharhinus*, Garrick (1982) subsequently designated one of these specimens as the lectotype, with the remaining three specimens becoming paralectotypes. The designation of a syntype to a lectotype in a formal scientific publication is permanent and cannot be changed. The decision of which syntype to allocate as the lectotype is influenced by several factors. In some cases, it is possible to discern which syntype was used for the description or illustration of the species in the original description (e.g., based on size, sex, or unique feature). In such cases, it is ideal to select that specimen as the lectotype. However, a more important factor in lectotype selection is the current condition of the preserved syntypes. The best condition syntype will be easier to obtain morphological data from and thus will be a better specimen to use as the name-bearing type (lectotype).

If the original author did not cite any specimens in a species description, or if a holotype has been either lost or destroyed, a **neotype** can be designated as a substitute specimen. The allocation of a neotype should occur only if it provides taxonomic stability to a genus or species complex. For example, the Blackspot Shark (*Carcharhinus sealei*) was described based on a single specimen (holotype), which was subsequently destroyed during World War II. During a revision of the *dussumieri–sealei* species complex by White (2012), a neotype was designated for the Blackspot Shark, removing any doubt over its identity. However, if the Blackspot Shark was readily distinguishable from other members of its genus and not part of a complex, there would have been no valid reason for neotype designation. In another scenario, White *et al.* (2010) designated a neotype for the Whitespotted Eagle Ray (*Aetobatus ocellatus*), for which no types previously existed. The difficulty in distinguishing among the various species of the Whitespotted Eagle Ray complex warranted the designation of a neotype. When neotype designation is justified, it is beneficial to select a specimen from as close to the type locality as possible. For example, the neotype selected by White (2012) for the Blackspot Shark was collected from the Sandakan fish market in Sabah, Malaysian Borneo, the same location where the holotype was collected, albeit ~140 years earlier!

A less common category of types is an **allotype**. An allotype is selected from the paratypes and is of opposite sex to the holotype. Although rarely used for elasmobranchs, one group where designation of an allotype would be beneficial is skates. In some skates, adult male and female body shapes can vary substantially, and males have patches of thorns on their discs (alar and malar patches). In recognition of the differences in morphology between adult males and females, Last (2008) designated a primary female paratype for several new species of skates to highlight the differences from the adult male holotype (e.g., Endeavour Skate, *Dentiraja endeavouri*). Although these were not designated as allotypes by the original author, the designated primary female paratype for each species can be considered as an allotype.

2.2.4.4 Physical Description of a Species

Physical descriptions are a crucial component of any taxonomic paper. The main criticism of the use of genetics only to define new taxa is the lack of a physical description of the species for use by end-users. The description of a shark or ray species can be broadly divided into three categories: external morphology, internal morphology, and meristics. External morphology includes the physical layout of the animal (e.g., body broad and compressed) and measurements of the various physical features. Although various Food and Agriculture Organization (FAO) species guides highlight the main standard measurements for sharks and rays (e.g., Compagno 2001), different genera or families often differ slightly in their methodology and measurements. This is due to varying features of the animal, such as dorsal-fin spines in dogfish sharks or divided pelvic fins in skates. Some taxonomic revisions of shark and ray groups include a revised standard methodology for future users to follow. These include, for example, skates (Last *et al.* 2008b), the deepwater catshark genus *Apristurus* (Nakaya *et al.* 2008), spurdogs (*Squalus*) (Last *et al.* 2007b), angel sharks (*Squatina*) (Last and White 2008), and whaler sharks (*Carcharhinus*) (Garrick 1982). An important consideration when taking measurements is whether the measurement is direct (or point-to-point) or a horizontal measurement. In some cases, both measurements types are taken for some characters to allow for comparison with previous studies. This important standardization of morphometric measurements in relation to collecting adequate basic size data from fishery catches was highlighted by Francis (2006). Squamation (denticle and thorn characteristics) is another important external character for sharks and rays. In stingrays, the morphology of the overall denticle band and the morphology of individual enlarged denticles or thorns are particularly important characters. In most sharks, denticle morphology is also an important taxonomic character, although it too must be standardized, as denticle morphology can vary depending on the part of the body examined and the ontogenetic stage of the animal examined.

Internal morphology often used in taxonomic studies includes skeletal morphology, tooth and jaw morphology, cranial foramina, musculature, liver morphology, and length of the intestine. Skeletal morphology can be observed through dissection of specimens, radiographs (x-rays), or computed tomography (CT) scan imagery (Figure 2.5). The morphology of the rostral node on skates is a useful taxonomic character and can be obtained from x-rays (Last *et al.* 2008b).

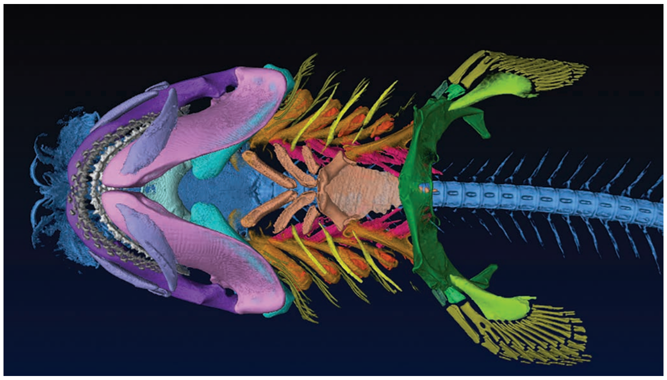

FIGURE 2.5 Micro-CT scan of the anterior region of the Blackspotted Catshark (*Aulohalaelurus labiosus*) in dorsoventral view, highlighting the skeletal characteristics in fine detail. (From the 2021 Acfas La preuve par l'image competition, "Portrait haut en couleur" ["Colorful portrait"], by Margot Angibaud, Université du Québec à Rimouski.)

In the smoothhound genus *Mustelus*, the morphology of the palatoquadrate is an important character and can be readily observed using x-rays. In some species, the palatoquadrate is subdivided near the symphysis, whereas in other species it is not subdivided (White *et al.* 2021). CT scanning imagery has become far more accessible in recent years, and its use for describing internal morphology, particularly skeletal, is particularly useful. Cranial morphology was typically examined through dissection of specimens; however, these meticulous dissections are time consuming and result in irreversible damage to valuable specimens. CT scans and x-rays do not damage valuable specimens and allow for more detailed examination of the various foramina and ridges on the crania. Internal organ morphology is less commonly examined in detail, but it can be a useful character in some groups. For example, the morphology of the liver and length of the duodenum relative to the intestine are important characters, both between species and subgroups, in the deepwater catshark genus *Apristurus* (e.g., Iglésias 2013).

Tooth morphology is a particularly useful taxonomic character for sharks and rays and can be examined through dissection, CT scans, or *in situ*. Dentition is a key diagnostic character for whaler sharks, Carcharhinidae (Garrick 1982)—for example, the shape and angle of the cusps, presence of cusplets, and degree of serrations on the edges. Detailed descriptions and images of the dentition should be included in taxonomic descriptions of sharks and rays. Teeth of sharks are extremely well represented in the fossil record for two main reasons. First, they fossilize well and secondly, as they are continually replaced, there are often large quantities of teeth present at fossil sites. A good understanding of the dentition of extant sharks and rays is crucial for understanding the taxonomy of extinct species. The morphology of the jaws themselves is also important although rarely examined in detail.

Meristics relate to the counting of quantitative features of fishes, such as the number of vertebral centra, number of pectoral- and pelvic-fin radials, number of tooth files, and number of turns on the intestinal spiral valve. Vertebral centra in sharks and rays are divided into monospondylous (single centrum per vertebrae) and diplospondylous (two centra per vertebrae). In an x-ray, the monospondylous centra appear wider than the diplospondylous centra and, in most cases, the transition between the two is relatively easy to determine. The vertebral centra counts most commonly taken are monospondylous, diplospondylous trunk (up to upper caudal-fin origin), and diplospondylous caudal (posterior to upper caudal-fin origin). Different taxonomic groups sometimes require different methodologies for counting, so it is important to check taxonomic methodology in the literature for the group being studied. For example, in skates, predorsal centra counts are used instead of the precaudal counts of sharks and shark-like rays (Last *et al.* 2008b). In batoids, the number of pectoral- and pelvic-fin radials is an important taxonomic character, particularly in skates (Last *et al.* 2008b).

The number of tooth files (often incorrectly referred to as "rows" in the literature) is a key diagnostic character in sharks. For example, different species within the genus *Carcharhinus* can often be distinguished by their tooth file counts. The number of intestinal spiral valve turns (when present) is becoming more widely used in some groups as a useful diagnostic count. Spiral valve counts can be important for distinguishing among species of the deepwater catshark genus *Apristurus* (e.g., Iglésias 2013); however, not all groups possess a spiral-valve intestine. Other counts that can be important for sharks and rays include the number of thorns, such as in skates (Last *et al.* 2008a), and the number of enlarged hyomandibular pores, such as in sharpnose sharks (*Rhizoprionodon*) (Springer 1964).

2.2.4.5 Inter- and Intraspecific Variation

Comparisons among similar forms is important when describing new species. Ideally, morphological and meristic data should be collected from the most closely related species and used to make detailed comparisons with the new species. This has two main aims: (1) to provide key characters for distinguishing closely related taxa from one another (e.g., in the field), and (2) to justify the designation of the new taxa as a distinct species. A dichotomous key is a useful inclusion when formally describing a new taxon. This may include all congeners (species in the same genus) or may be limited to a geographical region for a large and widespread genus. A key provides an important identification aid for future researchers and can remain valid in the literature for many years. The use of images and illustrations for highlighting key differences between closely related taxa is also important. An image can quickly, and often more accurately, show how to distinguish between two taxa.

Understanding morphological intraspecific variation is an important part of taxonomic research; however, the number of specimens examined during a study is often too low for a detailed investigation of intraspecific variation. This regularly does not occur due to difficulty obtaining specimens and storing them, particularly for larger specimens. Moving forward, taxonomic research should better document the level of intraspecific variation for the species being examined. In scenarios where limited samples are available for a species, attempts should be made to document the variation within a more abundant species within the same genus or species complex. Although the level of variation within species in a particular genus likely varies, it will at least provide some indication as to where variation may occur in species with lower samples sizes.

One of the most striking examples of the importance of adequately documenting intraspecific variation is in the Gulper Shark (*Centrophorus granulosus*). This large species (reaching ~1.6 m in length) was previously known by various names, which were subsequently relegated to junior synonyms including, most commonly, the names *Centrophorus acus* and *Centrophorus niaukang*. Last and Stevens (2009) distinguished these two species primarily by their lateral trunk denticle morphology: *Centrophorus acus* has denticles on narrow stalks and leaf-like crowns with three or more cusps, whereas *Centrophorus niaukang* has denticles on broad bases and flat crowns with a single or no cusp. Denticle differences at this level in other shark groups could easily represent different genera or even families. During the taxonomic investigation of this "species complex" by White *et al.* (2013), more than 50 specimens were examined from a wide size range (308 to 1623 mm total length [TL]). Examination of the lateral trunk denticles across the entire size range of this species revealed a significant ontogenetic shift in denticle morphology. Large differences were also found in the morphological characters between individuals less than 700 mm TL and those above 870 mm TL, with smaller specimens having longer heads, larger eyes, and paired fins closer together (White *et al.* 2013). This example highlights that poorly understood variation in the Gulper Shark through ontogeny hindered the taxonomic resolution of this species.

2.2.4.6 Publishing

The publication of a new scientific name or nomenclatural change to an existing name must meet certain criteria before it can be considered valid by the ICZN. First, "it must be issued for the purpose of providing a public and permanent scientific record" (ICZN Article 8.1.1). Second, "it must be obtainable, when first issued, free of charge or by purchase" (ICZN Article 8.1.2). Finally, "it must have been produced in an edition containing simultaneously obtainable copies by a method that assures" (ICZN Article 8.1.3) … "numerous identical and durable copies" (ICZN Article 8.1.3.1) or "widely accessible electronic copies with fixed content and layout" (ICZN Article 8.1.3.2). Previously, electronic publications were not valid unless some printed copies were also distributed to meet the criteria for new scientific names. This was finally amended in 2011 to follow the rapidly increasing number of online-only publications (ICZN Article 8.5). To be considered published, online-only work must have been published after 2011 (ICZN Article 8.5.1), state the date of publication within the work (ICZN Article 8.5.2), and be registered in the Official Register of Zoological Nomenclature (ZooBank) and contain evidence in the work that this has occurred (ICZN Article 8.5.3) by including ZooBank registration numbers for both the publication and any new nomenclatural acts.

All new species names published after 1999 must have a name-bearing type (i.e., holotype or syntypes) included in the original publication. Although syntypes are allowed, it is recommended that a holotype be designated (ICZN Recommendation 16E). A statement of intent that the types are or will be deposited in a collection, including the name and location of that collection, also must be included. Ideally, name-bearing types should be deposited in an institution that maintains a research collection with facilities for preserving them and making them accessible for study (ICZN Recommendation 16C).

It must be emphasized that the above criteria for publishing new scientific names relate only to what is set out by the ICZN. These criteria only cover the type of publication, ZooBank registration, and allocation of name-bearing types. However, taxonomic publications, including revisions and new species descriptions, should include most of the following sections: synonymy, diagnoses, description (including color), distribution, size, and etymology. They should also have a detailed section on comparisons with similar species. The requirements for publishing taxonomic research essentially come down to the guidelines for the journal in question. There are examples of species descriptions being published in reports rather than in recognized journals. Most notably, a series of four such reports published by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) between 2007 and 2010 included 63 papers describing 76 new species of sharks, rays, and chimaeras (Last *et al.* 2007a, 2008a, 2008b, 2010). This rapid taxonomic approach aimed to speed up the naming and describing of the large number of sharks and rays known to be undescribed mostly in the Australasian region. In this case, each paper was reviewed externally, and the reports were part of a numbered series. Because these were published prior to 2011, printed copies were produced and sent to libraries of major museum collections around the world to meet ICZN standards.

2.2.5 THE IMPORTANCE OF TAXONOMIC ACCURACY

2.2.5.1 Nomenclatural Stability

Following the ICZN guidelines for selecting available names can, at times, lead to undesirable nomenclatural changes. In such cases, there may be a need to protect the stability of the names that are in wide usage or to avoid name changes to other taxa. Reversal of precedence (ICZN Article 23.9.1) aims to prevent unused senior synonyms from taking precedence over widely accepted names. For example, the name *Mustelus felis* Ayres 1854 predates the widely accepted and commonly used species *Triakis semifasciata* Girard 1855, for which it is a synonym. Reversal of precedence allows the unused senior synonym, *Mustelus felis*, to be disregarded as the valid name for this species. In some cases, the decision of which name to use is not straightforward, and a submission to the ICZN may be required to request a ruling. When a ruling has been made by the ICZN, that decision cannot be overturned. For example, the genus name of the Whale Shark was spelled two ways within the original publication: *Rhincodon* and *Rhiniodon*. In this case, the ICZN ruled that *Rhincodon* was to be preserved over *Rhiniodon* (Opinion 1278). This ensures that all subsequent publications will only use the now accepted genus *Rhincodon*.

Nomenclatural decisions can lead to flow on changes to other related or unrelated taxa. For example, the Onefin Catshark (*Pentanchus profundicolus*) is the only catshark species to possess a single dorsal fin; however, it has been suggested that it is an *Apristurus* that happened to develop only one of its two dorsal fins. This form of abnormality, a single fin where two are typical, has been recorded in other sharks, including the Tawny Nurse Shark (*Nebrius ferrugineus*) (Yanagisawa 1983; Taniuchi and Yanagisawa 1987). If it is confirmed that *Apristurus* and *Pentanchus* are synonyms, *Pentanchus* Smith and Radcliffe 1912 has precedence over *Apristurus* Garman 1913, because it was published earlier. In this case, the genus name of 39 *Apristurus* species would have to be changed to the genus *Pentanchus*. In this scenario, this

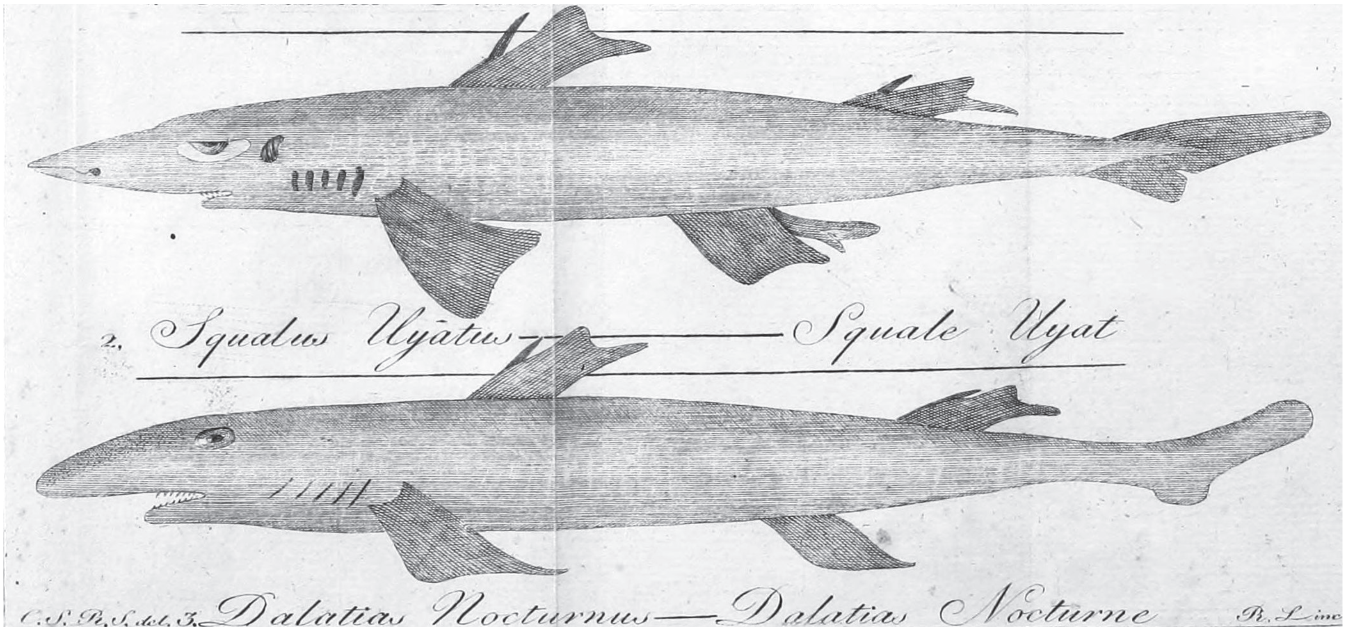

FIGURE 2.6 Original illustrations of *Squalus uyatus* (top) and *Dalatias nocturnus* (bottom) from Rafinesque (1810).

change would have to occur if the genera are confirmed to be synonyms. A compounding issue is that the genus *Apristurus*, as it currently stands, is paraphyletic (i.e., should be two or three genera). To ensure nomenclatural stability, the genus must be revised to ensure that names do not change multiple times in a short period of time.

The Little Gulper Shark (*Centrophorus uyato*) presents one of the most complicated and still unresolved nomenclatural problems in elasmobranchs. It is well reported that the specific name *uyato* is problematic. It was described by Rafinesque (1810) as *Squalus uyatus* from off Italy, but the original illustration (Figure 2.6, top) and description do not conform with what we know as *Centrophorus* but rather to a species of spurdog (*Squalus*). This then leads to a new available name to be sourced for this species. Another species described and illustrated by Rafinesque in the same publication, *Dalatias nocturnus* (Figure 2.6, bottom), appears to fit the genus *Centrophorus*. Given that there is only a single gulper shark species in the Mediterranean, the use of this name appears justified. But therein lies the problem. The Rafinesque publication is also the first use of the genus *Dalatias*, which he uses for two species, *D. nocturnus* and *D. sparophagus*. The latter species is considered to be the type species of the genus *Dalatias*. However, the description of that species by Rafinesque includes mention of gray coloration above and pale below, which does not match with the uniformly dark coloration of the Seal Shark (*Dalatias licha*), the sole member of this genus. If *D. sparophagus* cannot be resolved (i.e., becomes *nomen nudum*) and *Dalatias nocturnus* is considered the next available name for *C. uyato*, then a significant nomenclatural issue arises. Because *Dalatias* predates *Centrophorus* by 27 years, it would become the senior synonym of *Centrophorus*, leading to all gulper shark species being placed into the genus *Dalatias* and *Dalatias licha* requiring a different genus name. Such a change would have a negative influence on nomenclatural stability, and a way to avoid such change is required to clarify this issue.

2.2.5.2 Importance of Biological Collections

In taxonomy, access to the specimens used in a previous study is important so that results can be interrogated or added to a larger dataset with new material. Biological collections include those in museums or research centers but can also be private collections. Specimens that are preserved well will last centuries, with material dating back to the late 1700s available in some collections. A crucial aspect of collections is accessibility by researchers, both for specimens and data. We are at an interesting point in time, where biological collections and their staff are being increasingly used for their vast database of knowledge and skills, but resources to maintain collections is more difficult to secure. Specimens in collections represent a snapshot of biodiversity in time, whereby a specimen collected 50 years ago can provide insights into what we are seeing today. They also represent important sources of genetic information, especially as genetic capabilities improve and new techniques for harvesting DNA are developed. Over the last two decades, a number of collections have been closed or had serious resource reductions (e.g., Dalton 2003; Gropp 2003). The recent economic downturn from the 2020 coronavirus pandemic has also severely affected a number of collections, particularly in the United States; for example, both the American Natural History Museum in New York and the Field Museum of Natural History in Chicago underwent serious cuts and staff layoffs in 2020 (Pennisi 2020).

Ironically, some have considered the reductions in resourcing for biological collections to be a reflection of a bias toward molecular biology (Gropp 2003). The increasing need for access to genetic material in collections should strengthen the case for a biological collection. Specimens in collections represent millions of dollars of collection costs (e.g., shipping and labor costs), and their loss would be detrimental across the life sciences: from taxonomy, to ecology, to biogeography, to molecular studies, to fisheries, to climate change studies. The cost of maintaining preserved biological collections and their associated data is minimal compared to those searching for fresh material every time it is needed. Also, some research questions cannot be answered with only contemporary samples, as historic samples are required. Obtaining fresh material is becoming increasingly more complex, with new requirements and permitting making collecting less *ad hoc* than it was previously. It is our hope that the importance of biological collections is understood by future generations to ensure their survival.

2.3 BIODIVERSITY OF ELASMOBRANCHS

Elasmobranchs are a highly diverse and specialized vertebrate group, consisting of 1202 species that are currently considered valid. They range in size from the tiny Pygmy Ribbontail Catshark (*Eridacnis radcliffei*), which attains a maximum of only 19 cm in length, to the enormous Whale Shark (*Rhincodon typus*), which reaches at least 12 m in length. They are represented in all of the world's oceans and at all latitudes, from the Arctic to the Antarctic. Elasmobranchs are primarily found in marine waters but also occur in estuaries and in freshwater rivers and lakes; for example, some freshwater stingrays (Potamotrygonidae) occur more than 5000 km from the sea. They also occur across a wide depth gradient, from intertidal waters (e.g., epaulette sharks, *Hemiscyllium*) down to the abyssal plains of the deep ocean. The Great Lanternshark (*Etmopterus princeps*), for example, has been recorded down to depths of 4500 m in the North Atlantic, although few sharks exist in abyssal regions (Priede *et al.* 2006). Elasmobranchs have become specialized predators at all levels of the food chain, including planktivorous species such as the Basking Shark (*Cetorhinus maximus*), ectoparasitic species such as the Cookiecutter Shark (*Isistius brasiliensis*), and super predators that hunt cetaceans and pinnipeds, such as the White Shark (*Carcharodon carcharias*). Some species are nocturnal (e.g., epaulette sharks, *Hemiscyllium* spp.), but others are diurnal. Elasmobranchs are variable in their size and form, comprised of many different morphotypes. Some possess highly specialized features, including a saw-like rostra, bioluminescence, and organs capable of producing an electrical discharge.

2.3.1 Skates and Rays

A total of 658 extant species of skates and rays (Batoidei) are currently considered valid. These are comprised of four orders: Myliobatiformes (stingrays, eagle rays, cownose rays, and devil rays), Rhinopristiformes (guitarfishes, wedgefishes, and sawfishes), Rajiformes (skates), and Torpediniformes (electric rays). The Rajiformes are by far the most species-rich group, consisting of 296 species, followed by the Myliobatiformes, with 232 species (Figure 2.7). The Rajiformes order is comprised of four families, two of which

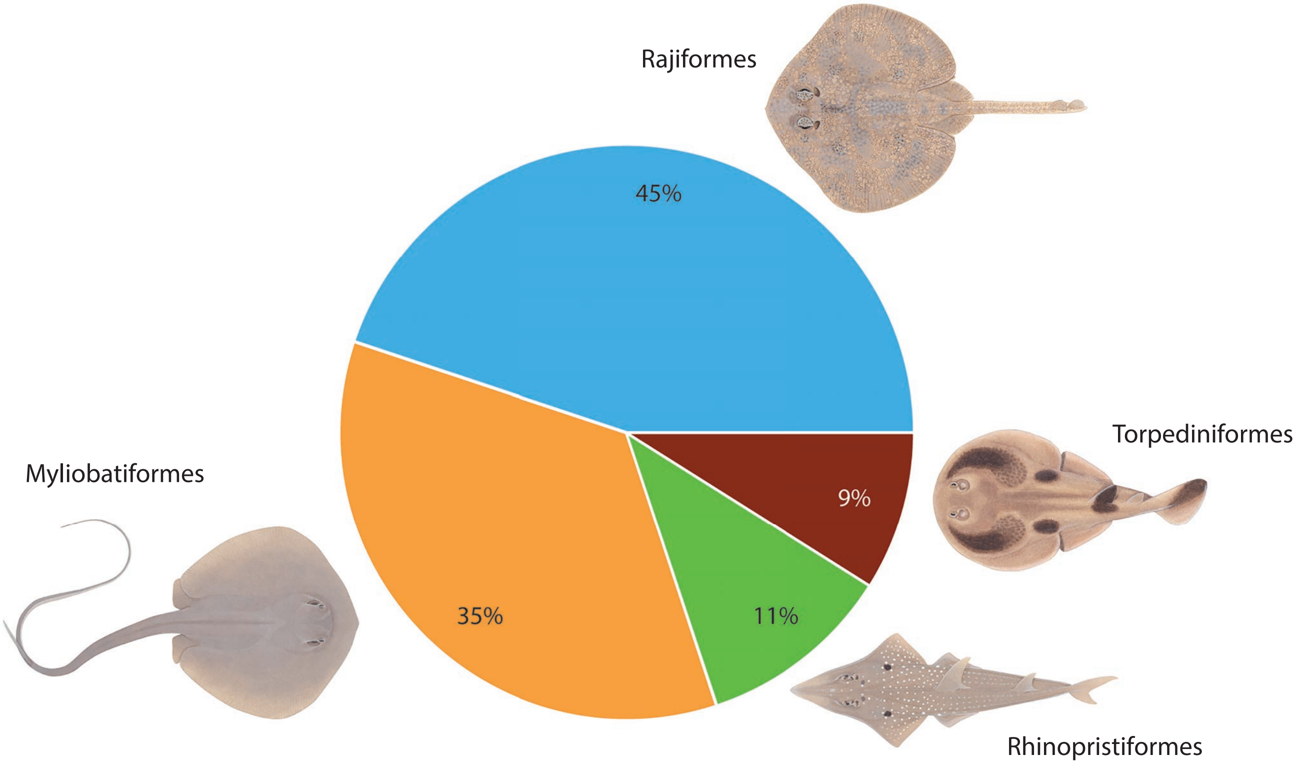

FIGURE 2.7 Composition of skate and ray species by orders. (Illustrations by Lindsay Marshall, www.stickfigurefish.com.au.)

contain 89% of all skate species: the Rajidae (hardnose skates) and the Arhynchobatidae (softnose skates), with 156 and 107 species, respectively. Two minor families, Anacanthobatidae (leg skates) and Gurgesiellidae (pygmy skates), contain only 14 and 19 species, respectively. The Gurgesiellidae was only recently resurrected as a valid family containing the genera *Cruriraja*, *Fenestraja*, and *Gurgesiella* (Last *et al.* 2016c). It is likely that many more species of skates will be discovered as surveys of deep waters in previously unexplored regions are undertaken. Recent deepwater surveys off Papua New Guinea found two new species of skates, despite the limited numbers of sharks and rays collected (White *et al.* 2018).

The Myliobatiformes order (232 species) is comprised of 11 families, but about 70% of the species occur in one of three families: Dasyatidae (stingrays), Potamotrygonidae (freshwater stingrays), and Urolophidae (stingarees), containing 95, 39, and 28 species, respectively. In contrast, the Hexatrygonidae (sixgill stingrays) and Plesiobatidae (deepwater stingarees) are monotypic (i.e., comprised of only a single species). The family Aetobatidae (pelagic eagle rays), a single genus with five species, was recently resurrected by White and Naylor (2016) based on morphological and molecular data.

The Rhinopristiformes order (72 species) is comprised of seven families; 64% of its species occur in two families: Rhinobatidae (guitarfishes) and Rhinidae (wedgefishes), with 35 and 11 species, respectively. This order was recently formally established, and the familial classification was revised by Last *et al.* (2016b). In this revision, two additional families were named: Glaucostegidae (giant guitarfishes) and Trygonorrhinidae (banjo rays). The family Pristidae (sawfishes) was also moved into this order from its previous placement in the separate order Pristiformes. The Pristidae genera *Anoxypristis* and *Pristis* were only slightly differentiated from the genus *Glaucostegus* based on *ND2* gene sequence analysis (Naylor *et al.* 2012). Improved taxon and gene sampling has constantly retrieved the same result (Last *et al.* 2016b). However, due to the extreme morphological differences between these genera, the Pristidae was retained as distinct from Glaucostegidae within the Rhinopristiformes.

The Torpediniformes order (58 species) is comprised of four well-established families, with most species belonging to the families Narcinidae (numbfishes, 30 species) and Torpedinidae (torpedo rays, 18 species). The taxonomy of this group requires urgent revision. Preliminary molecular analyses have revealed that some families are paraphyletic, and the generic and familial classification of this group requires revising.

2.3.2 SHARKS

A total of 544 extant species of sharks are currently considered valid, representing eight orders: Carcharhiniformes (ground sharks), Heterodontiformes (horn sharks), Hexanchiformes (frill, sixgill, and sevengill sharks), Lamniformes (mackerel sharks), Orectolobiformes (carpet sharks), Pristiophoriformes (sawsharks), Squaliformes (dogfishes), and Squatiniformes (angel sharks). The Carcharhiniformes (293 species) are the most species-rich group, containing 54% of all shark species, followed by the Squaliformes, with 26% of all shark species (Figure 2.8). The Carcharhiniformes order is comprised of ten families, with 90% of species belonging to one of four families: Pentanchidae (deepwater catsharks, 113 species), Carcharhinidae (whaler sharks, 57 species), Scyliorhinidae (catsharks, 47 species), and Triakidae (smoothhounds, 46 species). These families are relatively stable from a taxonomic standpoint, except for the catsharks that require urgent taxonomic revision; for example, the Pentanchidae and Scyliorhinidae were previously considered to be a single family, the Scyliorhinidae. Ongoing taxonomic revision of the catsharks could lead to more families being erected.

The Squaliformes order (143 species) is comprised of seven families, but 65% of the species belong to only two families: Etmopteridae (lanternsharks) and Squalidae (spurdogs), with 52 and 41 species, respectively. The smallest family is the Echinorhinidae (bramble sharks), with only two species. Echinorhinidae has previously been placed in its own order, Echinorhiniformes, but is currently included in the Squaliformes due to their close affinity to squaliform species. The family Centrophoridae (gulper sharks) is currently being revised, with several taxonomic changes likely to occur. New species of dogfish sharks, particularly lanternsharks, are likely to be discovered as deepwater surveys of areas previously not surveyed are undertaken.

The Heterodontiformes order (nine species) is comprised of a single family (Heterodontidae) and genus (*Heterodontus*). The Hexanchiformes order (seven species) is comprised of two families, the monogeneric Chlamydoselachidae (frill sharks) and the Hexanchidae (sixgill and sevengill sharks). The latter family is comprised of a single genus and three species of sixgill sharks (*Hexanchus*) and two monotypic genera of sevengill sharks (*Heptranchias* and *Notorynchus*).

Despite being a relatively small order, the Lamniformes (15 species) consists of eight morphologically distinctive families. They range from the small oceanic Pseudocarchariidae (Crocodile Shark) to the large planktivorous Cetorhinidae (Basking Shark). These two families, as well as Mitsukurinidae (Goblin Shark), Carchariidae (Sandtiger Shark), and Megachasmidae (Megamouth Shark), are all monotypic. The largest family is the Lamnidae (mackerel sharks), with five species belonging to one of three genera (i.e., *Carcharodon*, *Isurus*, and *Lamna*). The family Carchariidae (sandtigers) was only recently separated as distinct from Odontaspididae (deepwater sandtigers) (Stone and Shimada 2019).

The Orectolobiformes order (45 species) is comprised of seven families, two of which are monotypic: Rhincodontidae (whale sharks) and Stegostomatidae (zebra sharks). The most species-rich families are the Hemiscylliidae (longtailed carpetsharks) and Orectolobidae (wobbegongs), with 17 and 12 species, respectively. Most families have undergone few recent taxonomic changes, although some taxonomic investigations are underway on members of the Hemiscylliidae. The Pristiophoriformes order (10 species) contains a single family, Pristiophoridae, with two genera: *Pliotrema* (sixgill sawsharks) and *Pristiophorus* (sawsharks). The genus *Pliotrema*

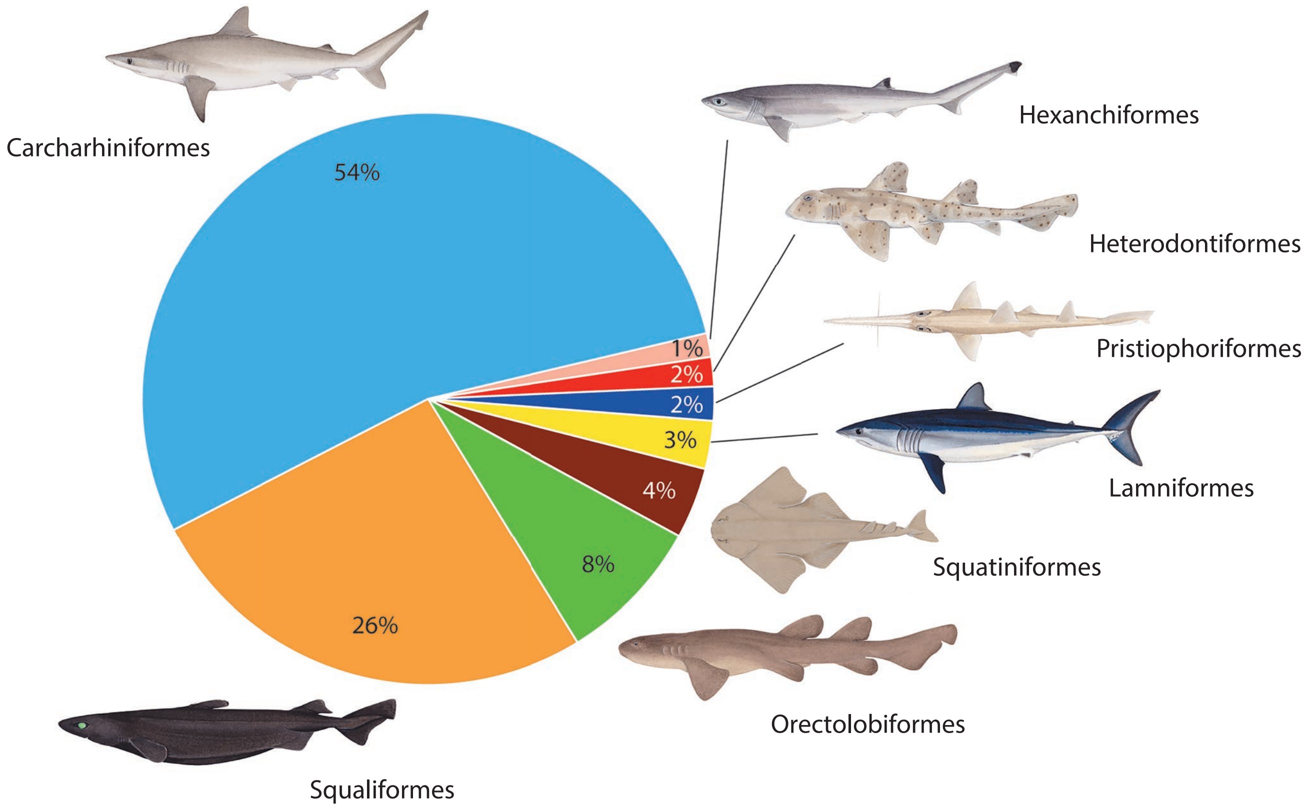

FIGURE 2.8 Composition of shark species by orders. (Illustrations by Lindsay Marshall, www.stickfigurefish.com.au.)

was previously considered to be monotypic, but a recent revision by Weigmann *et al.* (2020) included the description of two new species for the genus. The Squatiniformes order (22 species) is comprised of a single family (Squatinidae, angel sharks) and genus (*Squatina*).

2.3.3 Ecomorphotypes

Animals exhibit different body plans and ecomorphotypes based on morphological similarity, habitat, and behavior. Thomson and Simanek (1977) grouped sharks into four main body plans based primarily on caudal fin morphology and swimming behavior. Body type one constitutes the "macropelagic ecomorphotypes," which have caudal fins with a high aspect ratio (lunate or nearly lunate) and lateral keels and are obligate ram ventilators, meaning they must swim to respire. Body plan two is comprised of the "littoral ecomorphotypes," which have a lower aspect ratio caudal fin (i.e., upper lobe much longer than lower lobe) and flattened ventral head surface and are obligate ram and/or suction ventilators. Body plan three includes the "benthic ecomorphotypes," which have a small or no ventral caudal-fin lobe, more anteriorly located pelvic fins, and a ventilation system that primarily relies on suction. Body type four is comprised of the "bathic and micropelagic ecomorphotypes," which lack an anal fin, have a large upper caudal-fin lobe, and rely on suction ventilation. Although these groupings provide a general overview of body plans in sharks, they do not represent the diversity of morphological modifications that sharks have undergone during their long evolutionary journey. Compagno (1990), following on from his earlier work, including Compagno (1977, 1988), divided chondrichthyans into 18 major ecomorphotypes. The following arrangement for elasmobranch ecomorphotypes builds on Compagno's earlier work (Figure 2.9, Table 2.2).

The **littoral** ecomorphotype has a generalized, unspecialized body morphology and occurs mostly on insular and continental shelves. Although occurring over similar habitats, littoral species differ from benthic ecomorphotypes in being more active and mobile. This ecomorphotype is considered to be the most conservative form in extant elasmobranchs. Characters of these species include a slightly flattened head, small nostrils, small spiracles and gill openings, eyes that are mostly horizontally oval, usually small teeth, cylindrical body with firm muscle and tough skin, short body cavity, moderate-sized pectoral fins, and asymmetrical caudal fin with low ventral lobe (Compagno 1990). They are typically active swimmers, but are often capable of resting on the bottom. A total of 165 species (~14%) of elasmobranchs have a littoral ecomorphotype. These primarily belong to the Carcharhinidae (54 species), Triakidae (46 species), and Squalidae (41 species) but also include all members of the Carchariidae, Galeocerdidae, Hemigaleidae, Leptochariidae, Odontaspididae, and Sphyrnidae, and the two species of the triakid genus *Gollum*. Lucifora *et al.* (2011) assigned the *Gollum* species to the bathic ecomorphotype, but we consider

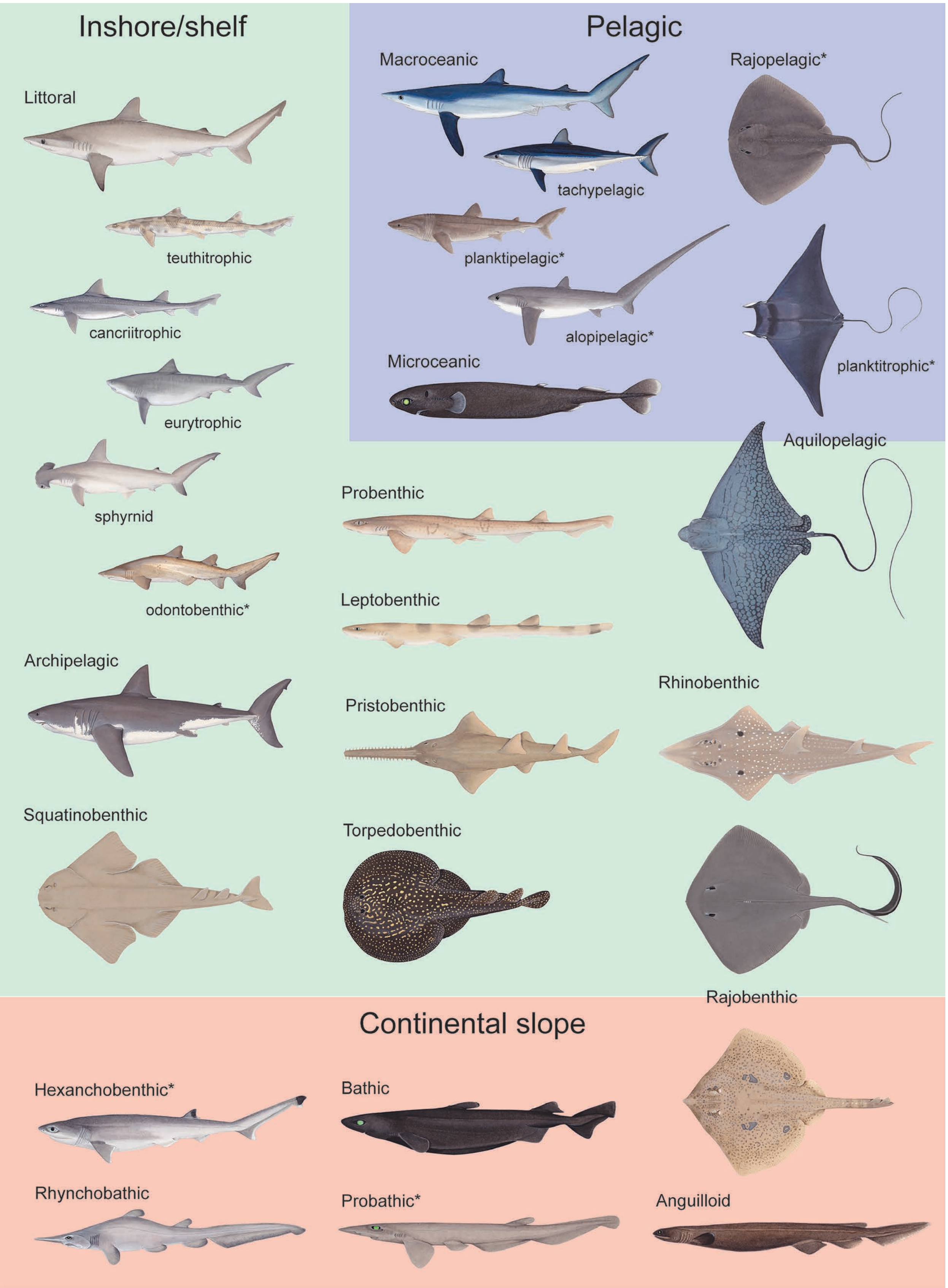

FIGURE 2.9 Ecomorphotypes and subtypes of elasmobranchs, grouped by the three main realms: inshore/shelf, pelagic, and continental slope. Asterisks (*) denote new ecomorphotypes/subtypes designated in this chapter. (Illustrations by Lindsay Marshall, www.stickfigurefish.com.au.)

TABLE 2.2
Number of Elasmobranch Species (by Order) in Each of the Ecomorphotypes

Ecomorphotype	Carcharhiniformes	Heterodontiformes	Hexanchiformes	Lamniformes	Myliobatiformes	Orectolobiformes	Pristiophoriformes	Rajiformes	Rhinopristiformes	Squaliformes	Squatiniformes	Torpediniformes	Total
Littoral	121	—	—	3	—	5	—	—	—	41	—	—	170
Teuthitrophic	4	—	—	—	—	–	—	—	—	—	—	—	4
Cancritrophic	28	—	—	—	—	–	—	—	—	—	—	—	28
Eurytrophic	2	—	—	—	—	–	—	—	—	—	—	—	2
Sphyrnid	9	—	—	—	—	–	—	—	—	—	—	—	9
Odontobenthic[a]	—	—	—	3	—	–	—	—	—	—	—	—	3
Probenthic	69	9	—	—	—	2	–	—	—	—	—	—	—
Leptobenthic	31	—	—	—	—	25	–	—	—	—	—	—	—
Squatinobenthic	—	—	—	—	—	12	—	—	—	—	22	—	34
Rhinobenthic	—	—	—	—	—	—	—	—	67	—	—	—	67
Pristobenthic	—	—	—	—	—	—	10	—	5	—	—	—	15
Torpedobenthic	—	—	—	—	—	—	—	—	—	—	—	58	58
Rajobenthic	—	—	—	—	191	—	—	296	—	—	—	—	487
Rajopelagic[a]	—	—	—	—	1	—	—	—	—	—	—	—	1
Bathic	—	—	—	—	—	—	—	—	—	93	—	—	93
Hexanchobenthic[a]	—	—	5	—	—	—	—	—	—	—	—	—	5
Probathic[a]	69	—	—	—	—	—	—	—	—	—	—	—	69
Rhynchobathic	—	—	—	1	—	—	—	—	—	—	—	—	1
Anguilloid	—	—	2	—	—	—	—	—	—	—	—	—	2
Aquilopelagic	—	—	—	—	40	—	—	—	—	—	—	—	40
Planktitrophic[a]	—	—	—	—	9	—	—	—	—	—	—	—	9
Microceanic	—	—	—	1	—	—	—	—	—	9	—	—	10
Macroceanic	3	—	—	8	—	1	—	—	—	—	—	—	12
Tachypelagic	—	—	—	4	—	—	—	—	—	—	—	—	4
Planktipelagic[a]	—	—	—	2	—	1	—	—	—	—	—	—	3
Archipelagic	—	—	—	1	—	—	—	—	—	—	—	—	1
Total	293	9	7	14	232	45	10	296	72	143	22	58	

Note: The number of species in the subtypes of ecomorphotypes are italicized.

[a] New ecomorphotype or subtype designated in this chapter.

them to be more closely aligned to the littoral ecomorphotype due to their morphology, despite having a much reduced ventral caudal-fin lobe. Four littoral subtypes were identified by Compagno (1990) that represent specialized forms of the littoral ecomorphotype:

- **Teuthitrophic** sharks are specialist cephalopod predators. They possess small mouths; small, comb-like upper teeth; and erect, pointed lower teeth. There are four species of teuthitrophic sharks: the triakid monotypic genus *Furgaleus* and three from the family Hemigaleidae (i.e., both weasel sharks in the genus *Hemigaleus* and the Atlantic Weasel Shark, *Paragaleus pectoralis*). The two other *Paragaleus* species with comb-like upper teeth are also likely teuthitrophic, but their diet has not yet been investigated.
- **Cancritrophic** sharks are specialist crustacean predators. They possess strong jaws with small cutting and/or crushing teeth and primarily feed on benthic crustaceans. There are 28 species of cancitrophic sharks, all from the family Triakidae (i.e., all 27 species of *Mustelus* and the Flapnose Houndshark, *Scylliogaleus quecketti*). Species of the genus *Triakis* and *Hemitriakis* could also be considered cancritrophic, but their dietary compositions are more varied.
- **Eurytrophic** sharks are large, omnivorous predators that are trending toward being apex predators. They possess large jaws with cutting teeth and are opportunistic predators. Two species are classed as eurytrophic, the Tiger Shark (*Galeocerdo cuvier*) and the Bull Shark (*Carcharhinus leucas*). The Broadnose Sevengill Shark (*Notorynchus cepedianus*) and

the Bluntnose Sixgill Shark (*Hexanchus griseus*) have also been included in this ecomorphotype by Compagno (1990) and Lucifora *et al.* (2011), respectively. Although these species superficially align with the littoral ecomorphotype, their possession of large gill slits, large teeth, and softer muscle should preclude them from any of the littoral subtypes.

- **Sphyrnid** sharks are littoral sharks with a specialized cephalofoil in the form of a hammer-shaped head. This cephalofoil increases their sensory field and separates the eyes for a more enhanced binocular field (Compagno 1990). The nine species in the family Sphyrnidae belong to this littoral subtype.

Herein, we define a new subtype of littoral sharks, which includes the two species of Odontaspididae and the monotypic Carchariidae: **odontobenthic**. This littoral subtype is characterized by its large slender teeth with small lateral cusplets, small to large circular eyes, and long gill slits. These characters distinguish them from the other littoral species and, as such, warrant a separate subtype. They occur in coastal waters down to the lower continental slope.

The **probenthic** ecomorphotype was considered by Compagno (1990) to be the least divergent and closest to the littoral ecomorphotype, occurring in similar habitats but differing in spending more time on the substrate. Probenthic species are unspecialized bottom-dwelling sharks with the following characters: stocky, cylindrical, or moderately flattened bodies; short body cavities; muscular pectoral fins with distally expanded radials; dorsally elevated eyes; strongly calcified skeletons; and tough skin with enlarged denticles. There is also a trend toward smaller mouths, with larger spiracles or a longer first pair of gill slits to complement suction ventilation through the mouth. Most probenthic species are found on the insular and continental shelf, are nocturnal, and rest on the bottom during the day. The 85 species of probenthic sharks include all members of the Brachaeluridae (blind sharks, two species), Ginglymostomatidae (nurse sharks, four species), Heterodontidae (nine species), and Stegostomatidae (Zebra Shark, one species), as well as some pentanchid (29 species) and scyliorhinid (34 species) catsharks. The probenthic catsharks include all species in the pentanchid genera *Asymbolus*, *Figaro*, *Galeus*, *Haploblepharus*, and *Poroderma* and in the scyliorhinid genera *Akheilos*, *Cephaloscyllium*, and *Scyliorhinus*. The Whitetip Reef Shark (*Triaenodon obesus*) shares many characteristics of probenthic species but is retained as a littoral species based on its general morphology being better aligned with that ecomorphotype.

The **leptobenthic** ecomorphotype is similar to the probenthic type but is more derived (advanced). These bottom-dwelling sharks share many of the characteristics of probenthic sharks but differ in being slenderer with elongate precaudal tails. The 56 species of leptobenthic sharks include all members of the Hemiscylliidae (17 species), Parascylliidae (collared carpetsharks, eight species), and Proscylliidae (finback catsharks, six species). They also include all species of the pentanchid genera *Halaelurus* and *Holohalaelurus* and all species in the scyliorhinid genera *Atelomycterus*, *Aulohalaelurus*, and *Schroederichthys*. It is important to note that there is a gradient between probenthic and leptobenthic species, with a gray area regarding which ecomorphotype some species belong to. For example, *Atelomycterus* species could be classified as slightly elongate probenthic species or slightly less elongate leptobenthic species.

Some sharks with probenthic and leptobenthic ecomorphotypes display a trend toward a flattening of the head and body and an increasing width of the pectoral fins. The pentanchid genus *Halaelurus* provides a good example of the head becoming more flattened and the scyliorhinid genus *Cephaloscyllium* a good example of both head and body becoming more flattened. Another group of bottom-dwelling sharks has adapted further on this body plan, resulting in a greatly flattened head and body and enlarged pectoral fins. This is the **squatinobenthic** ecomorphotype. Sharks with this morphotype also possess a terminal mouth, with narrow, pointed teeth and protrusible jaws. Their morphology enables these ambush predators to remain well camouflaged on the sea floor until unsuspecting prey approaches close enough to be engulfed by their protrusible jaws. Prey items include relatively large, active prey. They include all members of the Squatinidae (22 species) and the Orectolobidae (12 species).

A superficially similar, but fundamentally distinct, body form is the **rhinobenthic** ecomorphotype. In these species, the head and body are flattened and the paired fins are enlarged, as in squatinobenthic sharks; however, rhinobenthic species differ in having a very long snout extending well ahead of a small, ventrally positioned mouth. The jaws have small crushing teeth used for feeding primarily on benthic crustaceans. The caudal fin remains the primary source of propulsion, as in sharks. There are 67 species of rhinobenthic elasmobranchs, which are comprised of all shark-like rays in the families Glaucostegidae (six species), Platyrhinidae (five species), Rhinidae (11 species), Rhinobatidae (35 species), Trygonorrhinidae (eight species), and Zanobatidae (two species). The **pristobenthic** ecomorphotype is a closely related and more specialized form than the rhinobenthic ecomorphotype. These species possess a greatly elongated rostrum, edged with numerous sharp rostral teeth, which are used to detect and remove prey from the substrate and/or as a weapon to stun and kill prey, including fishes and sometimes invertebrates. Pristobenthic species include all five species of Pristidae and all 10 species of Pristiophoridae. These are a prime example of convergent evolution in elasmobranchs, where two unrelated groups, the shark family Pristiophoridae and the ray family Pristidae, have independently evolved a specialized saw-like rostrum.

The **torpedobenthic** ecomorphotype is similar to the rhinobenthic type in having caudal propulsion but differs in having an expanded pectoral disc, with powerful electric organs. The electric organs are used for stunning and killing prey and for defense against predators. Torpedobenthic species occur mostly on insular and continental shelves, but some species extend onto the upper continental slope. They are benthic and feed on smaller invertebrates, with the exception of the larger torpedo rays of the genus *Tetronarce* that are semi-pelagic and swim up into the water column seeking larger active prey. The 58 species of torpedobenthic rays are all restricted to the torpediniform families: Hypnidae (Coffin Ray, one species), Narcinidae (30 species), Narkidae (sleeper rays, nine species), and Torpedinidae (18 species). Several torpedobenthic species are the only known blind elasmobranchs (Compagno 1990).

The **rajobenthic** ecomorphotype is a more specialized form of ray, where there is an increased trend toward pectoral-fin propulsion and the caudal fin is either small or absent. Rajobenthic rays have been one of the most successful colonizers of benthic habitats, ranging from freshwater rivers and lakes (i.e., most Potamotrygonidae and several Dasyatidae) to the abyssal plains (e.g., some skates). A total of 487 species, representing ~40% of all elasmobranch species, are rajobenthic. They include all species of skates of the families Anacanthobatidae (14 species), Arhynchobatidae (107 species), Gurgesiellidae (12 species), and Rajidae (156 species). All skates possess a long slender tail with a caudal fin, except the leg skates, and most have two small dorsal fins, except the leg skates and several species of *Gurgesiella*. Also included are the Hexatrygonidae (one species), Plesiobatidae (one species), Urolophidae (28 species), and Urotrygonidae (round rays, 16 species), which have a moderately long tail with a prominent caudal sting(s) and a small but distinct caudal fin. The Gymnuridae (butterfly rays, 12 species) are rajobenthic rays with a lozenge-shaped disc and a very thin, short tail. The Potamotrygonidae (39 species) and all but one species of Dasyatidae (94 species) are rajobenthic and have moderately long to extremely long and filamentous tails, with prominent caudal stings and round- to oval-shaped pectoral discs. One species of dasyatid ray, the Pelagic Stingray (*Pteroplatytrygon violacea*), has a body form superficially similar to that of other dasyatids but, as the common name implies, has adapted to a completely pelagic lifestyle. Compagno (1990) noted that this species is secondarily oceanic and maintained it as a rajobenthic species. However, the Pelagic Stingray is a truly pelagic species (e.g., Veras *et al.* 2014; Wilson and Beckett 1970), so grouping it as rajobenthic is not reflective of the lifestyle of this species. We propose a new morphotype, **rajopelagic**, to better reflect the pelagic nature of this myliobatoid ray.

Although some littoral, leptobenthic, and probenthic sharks descend onto the upper continental slope, other sharks have successfully colonized the deep sea. Compagno (1990) placed these species into a **bathic** ecomorphotype, comprised of "squaloids and hexanchoids." Lucifora *et al.* (2011), who assigned all shark species to one of the ecomorphotypes defined by Compagno (1990), also included many deepwater pentanchids and members of the family Pseudotriakidae (false catsharks) in the bathic ecomorphotype. However, most of these species have short trunks, small denticles, and a more calcified skeleton, and some do not have uniform dark coloration. These characters differ from those defined for the bathic ecomorphotype by Compagno (1990), with bathic sharks having softer skin, flaccid muscles, large and rough denticles, weak skeletal calcification, uniform dark coloration, and long trunks with huge oily livers. Thus, deepwater sharks are divided into three different ecomorphotypes to better categorize them. First, the **bathic** ecomorphotype is retained from its description in Compagno (1990), as defined above, with the addition of lacking an anal fin. A total of 93 species of squaliform sharks are assigned to this ecomorphotype: Centrophoridae (16 species), Dalatiidae (kitefin sharks, one species), Echinorhinidae (two species), Etmopteridae (52 species), Oxynotidae (rough sharks, five species), and Somniosidae (sleeper sharks, 17 species). Four of the lanternsharks (*Etmopterus*) are also secondarily microceanic (see later).

Second, a new ecomorphotype is herein defined for the six species of hexanchid sharks: **hexanchobenthic**. Most species occur in deepwater, except for the Broadnose Sevengill Shark, which is restricted to the coastal shelf, and adult females of the Bluntnose Sixgill Shark, which move inshore seasonally to pup. Hexanchobenthic sharks possess large gill slits (in six or seven pairs), an asymmetrical caudal fin with an elongate upper lobe, a single dorsal fin, and large compressed comb-like teeth in the lower jaw. Finally, an ecomorphotype is defined for deepwater bottom-dwelling sharks that largely resemble probenthic species but differ in having generally softer bodies, weaker calcification of the skeleton, and typically less muscular pectoral fins. These sharks are placed in the new **probathic** ecomorphotype. Probathic sharks include three species of pseudotriakid sharks—all species of *Planonasus* (two species) and *Pseudotriakis* (one species)—and 66 species of pentanchid sharks, including all species of the genera *Apristurus* (39 species), *Bythaelurus* (14 species), *Cephalurus* (one species), *Parmaturus* (11 species), and *Pentanchus* (one species).

Compagno (1990) allocated the genera *Apristurus* and *Pentanchus* to the separate and more specialized **rhynchobathic** ecomorphotype. These were defined as having a short body cavity with large oily liver; soft body and skin; dark coloration; an elongate, paddle-like snout; and protrusible jaws. The other extant shark assigned to this ecomorphotype was the Goblin Shark (*Mitsukurina owstoni*). However, *Apristurus* and *Pentanchus* differ markedly from *Mitsukurina*, most notably in having oval versus circular eyes; short versus long gill slits; very small, cuspidate teeth versus large, slender teeth; slightly protrusible versus highly protrusible jaws; and dark versus pale coloration. Also, although some *Apristurus* species have very elongate snouts (i.e., the *longicephalus* subgroup, such as the Longfin Catshark, *Apristurus herklotsi*), many species have shorter snouts (e.g., Humpback Catshark, *Apristurus gibbosus*). The snouts of these species do not approach the length of the paddle-like snout that Goblin Sharks possess. Thus, we consider the Goblin Shark as the sole species assigned to the **rhynchobathic** ecomorphotype, which is redefined as possessing an elongate and paddle-like snout; long, slender teeth; long gill slits; soft skin; pale coloration; and highly protrusible jaws.

Compagno (1990) introduced an **anoxybathic** ecomorphotype for the several sharks that have elongated gill regions and expanded gill filaments (e.g., *Cephalurus*, some *Parmaturus*, some *Iago* species). Species of this ecomorphotype can live in low oxygen and/or high salinity and temperature environments. We consider these species as secondarily anoxybathic, while maintaining their primary ecomorphotype of littoral (for the Bigeye Houndshark, *Iago omanensis*) and probathic (for the Lollipop Catshark, *Cephalurus cephalus*, and Filetail Catshark, *Parmaturus xaniurus*). As such, anoxybathic is not included as a primary ecomorphotype or subtype in our system.

The frill sharks, genus *Chlamydoselachus*, have an elongate body cavity and a very short, snake-like head. Compagno (1990) placed this genus in the aptly named **anguilloid** ecomorphotype. It is likely an offshoot of the littoral–hexanchobenthic ecomorphotype but differs in its eel-like body plan.

The pelagic realm is home to the **aquilopelagic** morphotype, which encompasses rays that have narrowly angular and expanded, wing-like pectoral fins that have a strong junction with the body. This morphology allows for active, bird-like propulsion by flapping the pectoral fins in unison. There are 40 species of aquilopelagic rays, comprised of all species in the families Aetobatidae (five species), Mobulidae (devil rays, nine species), Myliobatidae (eagle rays, 18 species), and Rhinopteridae (cownose rays, eight species). We define a specialized subtype of aquilopelagic rays, the **planktitrophic** subtype, to encompass the nine mobulid species, which possess elongate cephalic lobes that they use to direct plankton into their mouths.

The **microceanic** ecomorphotype is a group of highly derived sharks and is an extension of the bathic ecomorphotype that has specialized features for a pelagic lifestyle. These small species have big eyes, bulbous snouts, slender and cylindrical bodies, large oily livers, and very small fins, and they often have symmetrical caudal fins for better propulsion. There are 10 species of microceanic sharks, comprised of nine species of Dalatiidae (genera *Euprotomicroides*, *Euprotomicrus*, *Heteroscymnoides*, *Isistius*, *Mollisquama*, and *Squaliolus*) and the monotypic Pseudocarchariidae (crocodile sharks). In addition, four etmopterid species, genus *Etmopterus*, are secondarily microceanic, as they have been caught well off the bottom, but are considered primarily bathic, as they are mostly recorded near the bottom.

The **macroceanic** ecomorphotype includes large, open-ocean species that mostly have firm bodies, thin skin, and narrow, blade-like pectoral fins. The 12 macroceanic sharks include all members of the families Alopiidae (thresher sharks, three species), Megachasmidae (one species), Cetorhinidae (one species), and Rhincodontidae (one species), four species of Lamnidae, and three species of Carcharhinidae. Two of the macroceanic carcharhinids are truly oceanic: the Oceanic Whitetip Shark (*Carcharhinus longimanus*) and the Blue Shark (*Prionace glauca*). The third carcharhinid, the Silky Shark (*Carcharhinus falciformis*), is also pelagic and can be found well offshore, but it is most often found over deep water close to land. There are three subtypes that represent specialized forms of macroceanic sharks:

- **Tachypelagic** sharks have a tuna-like, fusiform body; lunate caudal fins; and large keels on caudal peduncle. These species are very fast swimmers and can maintain elevated body temperatures, making them efficient predators, feeding on small to moderate-sized active prey. The four lamnid species, both *Isurus* and both *Lamna* species, are tachypelagic. This was considered a major ecomorphotype by Compagno (1990), but we consider it a subtype of the macroceanic ecomorphotype.
- **Planktipelagic** sharks, defined herein, have a huge mouth, long to extremely long gill slits, small circular eyes, and numerous, tiny teeth. They are slow swimmers that feed on plankton. The Whale Shark, Basking Shark, and Megamouth Shark (*Megachasma pelagios*) are the three planktipelagic sharks.
- **Alopipelagic** sharks, defined herein, have an extremely elongate, whip-like, upper caudal-fin lobe. These agile macroceanic species use their long tails to herd and stun small fishes. The Alopiidae species are the three alopipelagic sharks.

The **archipelagic** ecomorphotype, as defined by Compagno (1990), includes super predators that attain a large size; have a tuna-like, fusiform body; and have powerful jaws with large serrated teeth. The only extant species that is archipelagic is the White Shark, which mostly occurs inshore but sometimes well offshore. It preys on large, active prey, such as other sharks, rays, large teleosts, pinnipeds, and cetaceans, but it also has a propensity to scavenge. The only other marine animal that matches the White Shark in its food habits is the larger killer whale *Orcinus orca*. Archipelagic sharks are similar to tachypelagic sharks in their morphology but differ in occurring mostly on insular and continental shelves.

Compagno (1990) also included key extinct elasmobranch species in the ecomorphotypes he defined, providing excellent insight into the evolution of elasmobranch ecomorphotypes. For example, the Miocene superpredator Megalodon (*Otodus megalodon*) had the archipelagic ecomorphotype. Characterizing elasmobranchs by their ecomorphotypes provides a more holistic view of diversity by considering not just phylogenetic position but also their body form, habitat, and behavior.

2.4 ZOOGEOGRAPHIC PATTERNS

To investigate the broad zoogeographic patterns of sharks and rays, the geographic areas in which each of the 1202 species occurs were recorded. Seven broad geographic regions were used: Eastern Pacific, Western Pacific, Indian, Eastern Atlantic, Western Atlantic, Southern Ocean circumpolar region, and Arctic circumpolar region. Subregions within these broad regions were defined, except for the two polar regions. For the Atlantic and Pacific regions, the subregions used were Northern, Central, and Southern, and for the Indian region the subregions used were Western, Eastern, and Northern. The Eastern Atlantic also includes the Mediterranean Sea as a separate subregion. These subregions broadly follow the FAO Fishing Areas (http://www.fao.org/fishery/area/search/en), except for including the Northern Indian Ocean as separate from the Western and Eastern Indian oceans.

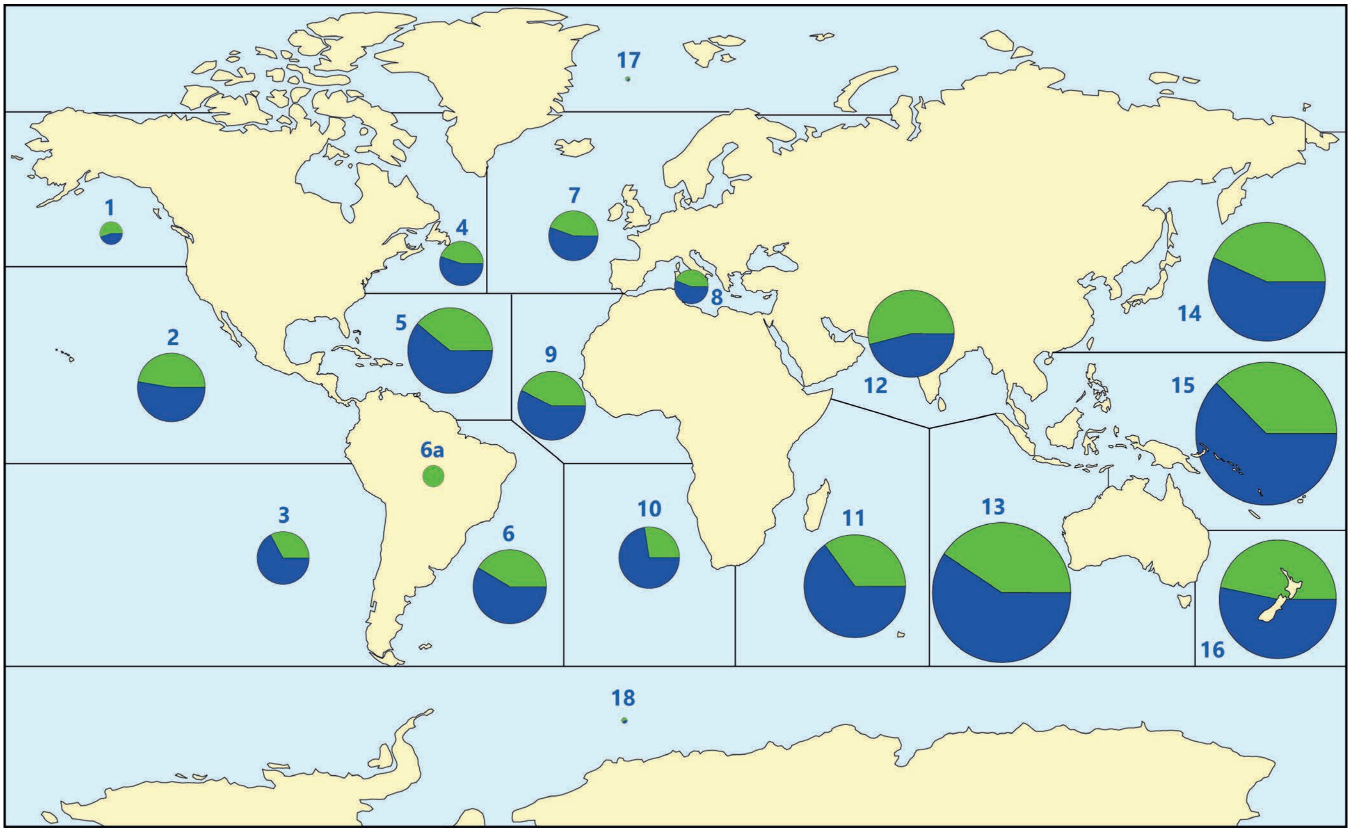

FIGURE 2.10 Map showing the 18 subregions to which each species was assigned. Each subregion is overlaid with a catch composition pie chart showing the proportion of skates and rays (green) and sharks (blue). The size of each pie chart is scaled to the number of species in that subregion. Subregions: (1) Eastern North Pacific; (2) Eastern Central Pacific; (3) Eastern South Pacific; (4) Western North Atlantic; (5) Western Central Atlantic; (6) Western South Atlantic (6a, South American freshwater); (7) Eastern North Atlantic; (8) Mediterranean; (9) Eastern Central Atlantic; (10) Eastern South Atlantic; (11) Western Indian; (12) Northern Indian; (13) Eastern Indian; (14) Western North Pacific; (15) Western Central Pacific; (16) Western South Pacific; (17) Arctic Seas; (18) Antarctic Sea.

The approximate boundaries of the 18 subregions and respective pie charts displaying the proportion of sharks and rays present, with the size of the pie charts scaled by the number of species present in each region, are shown in Figure 2.10. The South American obligate freshwater species are plotted separately, as they occur inland, often thousands of kilometers from the sea. The Indian and Western Pacific (i.e., Indo-West Pacific) contains the highest number of elasmobranchs, with 64% of species occurring in this region, with 45% of the species being found in the West Pacific and 41% in the Indian Ocean. The Southern Ocean and Artic regions have a depauperate elasmobranch fauna, with only seven and 11 species, respectively. The subregions with the greatest diversity of elasmobranchs are the Eastern Indian Ocean and Western Central Pacific, with 25% and 26%, respectively, of species occurring there.

The high diversity in these subregions is driven by the overlap with the megadiverse Coral Triangle region (see Barber 2009). Other than the polar regions, the lowest diversity of elasmobranchs was recorded in the Eastern North Pacific, Western North Atlantic, and Eastern North Atlantic, with 4%, 8%, and 9% of species occurring there, respectively. A greater number of sharks occur in most subregions compared to rays, except in the Northern Indian Ocean, Eastern North Pacific, and in the South American freshwater region, where more rays occur.

Many elasmobranchs are found in relatively narrow geographic ranges. About 53% of all species occur in only a single subregion, and 24% occur in only two subregions. More than half of the species in each elasmobranch order occur in only a single region, except for the Hexanchiformes (frill, sixgill, and sevengill sharks) and Lamniformes (mackerel sharks), with only one and no species, respectively, found in a single region. Most of the species of the Squatiniformes (angel sharks), Rajiformes (skates), Heterodontiformes (horn sharks), and Rhinopristiformes (sawfishes, guitarfishes, and wedgefishes) are found in a single region: 91%, 79%, 78%, and 78%, respectively. Thus, most elasmobranch groups have relatively narrow distributions, with only a few orders having a global distribution.

Only about 4% of species (*n* = 50) occur in five or more of the geographic regions. These wide-ranging species include all but three species of Lamniformes, four of the seven species of Hexanchiformes, 11 species of Squaliformes (dogfish sharks), four of the nine species of Mobulidae, and 15 species of Carcharhiniformes (ground sharks). The groups that have no wide-ranging species are the Pristiophoriformes (sawsharks), Heterodontiformes, Squatiniformes, and Torpediniformes (electric rays). Also noteworthy is that only one of the 294 species of Rajiformes, one of the 70 species of Rhinopristiformes, and one of the 45 species of Orectolobiformes (carpetsharks) have occurred in five or more regions. Overall, only a small proportion of elasmobranchs are widely distributed across the world's oceans.

Few regions have been found to have far less unique genera (i.e., genera that are only found within that region). For example, the Eastern Pacific and Eastern Atlantic regions have only four and three unique genera present, respectively, compared to the Western Atlantic, Indian, and West Pacific, which have 11 to 13 genera. The high number of unique genera in the Western Atlantic includes four of the five genera of the Potamotrygonidae, the freshwater rays, which occur in the South American River systems. Although most of these genera are only represented by one or two species, they highlight the evolutionary distinctiveness of faunal assemblages in the different regions. This is also true for the higher diversity of elasmobranchs observed in the Indian and West Pacific regions and is further highlighted by the greater number of genera that have their full complement of species present (i.e., 70 and 66 genera, respectively). Thus, about a third of all elasmobranch genera are fully represented in these two regions compared to less than 17% in the other regions.

The Lamniformes, Rajiformes, and Squaliformes are the only orders found in all seven regions. The remaining orders are found in the five non-polar regions, except for Heterodontiformes, which are absent from the Atlantic regions, and the Pristiophoriformes, which are absent from the Eastern Pacific. For all orders, except the Lamniformes, most of their species occur in the Indian and West Pacific regions. This is particularly evident in the Orectolobiformes, where 27 and 33 of the 45 known species occur in the Indian and West Pacific, respectively, versus less than four in the Atlantic and Eastern Pacific regions.

The diversity of elasmobranchs follows a trend similar to that of other marine organisms in having a center of diversity in the central Indo-West Pacific where the Coral Triangle is located (Barber 2009). The poorest diversity is found in the polar regions and in the Eastern Pacific and North Atlantic.

2.5 CONCLUSIONS

Taxonomy is a foundation for all other life sciences. Without taxonomy, there would be no uniformity or consistency in the naming and classification of species globally. This confusion would result in a greatly reduced understanding and management of biodiversity. Despite the strict rules, taxonomy is dynamic. Taxonomic decisions are based on the best information available at the time of any study. Technology is continually advancing, providing new and improved tools for taxonomic studies, such as micro-CT scanning and molecular tools, but the fundamental conventions set in stone centuries ago by Linnaeus still apply and must be adhered to. New information (e.g., more specimens available for examination) can sometimes lead to a different conclusion. Although it can be frustrating to see names or classifications change, there is a process involved and rules to follow. Continuing to refine our understanding of biodiversity in the natural world is essential; however, the reality of obtaining resources for taxonomic studies, particularly alpha-taxonomy, is extremely difficult. Furthermore, the number of trained taxonomists is decreasing, with many of the most prolific elasmobranch taxonomists retiring over the last decade. The number of new species is showing the opposite trend, increasing rapidly since the onset of the 21st century, showing that there are still many species yet to be discovered and named.

These issues raise several questions about the future of this fundamental science. Are we providing the right environment for the future taxonomists to become established or even be found? The difficulty in obtaining resources for taxonomic work makes this difficult to achieve. A quarter of the total elasmobranch species have been described since 2000. What would have been the ramifications of these species not being named? Conservation status could not have been assessed formally. Given that many of the taxonomists involved in these species' descriptions are now retired, there is concern about what the future holds for elasmobranch taxonomy. Thankfully, several younger taxonomists are becoming established who will hopefully continue the legacy of others.

Regarding the pioneers of elasmobranch taxonomy, special recognition must be given to Dr. Leonard J.V. Compagno. His contributions to elasmobranch taxonomy are unrivaled. His *magnum opus* was his *Sharks of the Order Carcharhiniformes*, first published in 1988, which was based on his PhD thesis from 1979. With the material he had at the time and without the use of molecular tools or digital imagery, Compagno provided an excellent, full account of members of this order. The phylogenetic classification he developed is exceptionally well supported by modern molecular analyses. More relevant to this chapter was his 1990 paper published in *Environmental Biology of Fishes* (Compagno 1990), which detailed the life-history styles of elasmobranchs. The ecomorphotype section of this chapter was largely drawn from this paper. One section of the Abstract struck a particular chord, where he stated, "The success and importance of cartilaginous fishes is largely underrated by marine biologists and by the public, and requires new and 'heretical' emphasis to overcome the present inadequacies of chondrichthyian [*sic*] research and the problems of overexploitation that cartilaginous fishes face." To see how far elasmobranch research has come over the last three decades is testament to the pioneers such as Leonard Compagno. Yet, although we have come so far, much more work is needed to ensure we conserve not only individual species of elasmobranchs but also their incredible diversity.

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3 How to Build a Shark

Biomechanics and Bioinspiration

E.W. Misty Paig-Tran, Marianne E. Porter, Lara A. Ferry, and Lisa B. Whitenack

CONTENTS

ABSTRACT

Chondrichthyan fishes have a suite of morphological adaptations that affect their biomechanical performance. Many of these adaptations are not found in other extant fishes, and, even within the chondrichthyans, there is no one-size-fits-all metric that applies. Chondrichthyans come in a variety of shapes and sizes, from typical streamline-shaped sharks to the dorsally flattened, pancake skates and rays to the alien ratfishes with whip-like tails and large pectoral fins. This variation enables sharks and their relatives to inhabit surface waters and the deep oceans, warm tropical coral reefs and cold arctic waters. This chapter summarizes the biomechanical principles that shape chondrichthyan form and function in an easy-to-digest format. Topics covered include feeding (mechanical performance of teeth and jaws, suction performance, and mechanisms of filtration), swimming (contributions of the vertebrae, fins, and scales), and bioinspiration (new products and technologies inspired by shark performance). Scientists reading this chapter will gain a deeper understanding for how physics and anatomy shape performance and will be able to identify how biomechanics can inform ecology, physiology, and even conservation research of chondrichthyans.

3.1 INTRODUCTION

> Science isn't about the things but about the relationships among the things.
>
> **Steven Vogel, *The Life of a Leaf* (2012)**

Steven Vogel was a master of explaining biomechanics in a clear and entertaining way. Vogel used simple, humorous language to facilitate understanding of fundamental, but inherently difficult, biomechanical principles. The inherent difficulty in understanding biomechanics led to the efforts of Vogel to simplify the complex principles by using a simpler and humorous language, a style he utilized in order to facilitate understanding the fundamentals. It was the intent of the writers of this chapter to pay tribute to his influence by continuing to use a similar writing style that will differ from the tone taken in the rest of this text. We offer this tribute to Dr. Vogel.

One thing Shark Week has taught us is that people are generally fascinated by sharks. The programming that millions watch each year features sharks voraciously feeding, energetically swimming, and even jumping clear out of the water. We also occasionally get to experience the joy on researchers' faces when they are finally able to answer those "why" or "how" questions that keep them trudging through the endless sea of grant proposals and paperwork that make "aha!" research moments possible. Those "why" and "how" questions run the gamut from understanding shark reproduction and physiology to ecology and habitat use. One only needs to read the Contents of this book to appreciate the variety and scope of scientific inquiry. Chondrichthyans, in various forms, have been successfully swimming around the world's oceans for more than 450 million years, well before dinosaurs, before trees, before insects, and long before humans (Andreev *et al.* 2015; Burrow *et al.* 2019; Ginter 2004; Sansom *et al.* 2012; Turner 2004). This begs another "why" question: "Why have chondrichthyans existed for so long?" The success of chondrichthyans can be attributed to many things, but oceanographer Matt Hooper (played by Richard Dreyfuss) from *Jaws* provides a simplistic summary: "Mr. Vaughan, what we are dealing with here is a perfect engine, er ... an eating machine. It's really a miracle of evolution. All this machine does is swim and eat and make little sharks and that's all." Although we know that there is much more to the evolutionary success of chondrichthyans, Hooper's description does hint at something important: Extant (living) chondrichthyans are the result of 450 million years of trial and error.

Enter the realm of comparative biomechanics—the application of principles from physics and engineering to understand biological variation and performance. Essentially, this is the study of how to build an organism that can truly withstand the test of evolutionary time. How would *you* build a shark? There are many parts to consider and a slew of jobs for those parts to do. These various parts must somehow work together to accomplish specific jobs; after all, the "relationship among the things" is just as important as the things themselves. Here, we explore aspects of swimming and feeding, such as the skeletal composition and kinematics of motion, that contribute to being a successful predator. We also look to elasmobranchs for biological inspiration. We are all awed by sharks, and scientists and engineers are able to learn from their impressive performance metrics to develop products and technologies for human benefit.

3.2 MOVING THE MACHINE

3.2.1 How to Swim

Chondrichthyans come in a variety of shapes and sizes, ranging from typical streamline-shaped sharks to the dorsally flattened, pancake-like skates and rays to the alien ratfishes, with their whip-like tails and large pectoral fins (Figure 3.1). Differences in shapes, among other things, provide clues about how these fishes move their bodies (Irschick *et al.* 2017). Intuitively, we would not expect a Round Stingray (*Urobatis halleri*) to be faster in the water column than a torpedo-shaped Shortfin Mako (*Isurus oxyrinchus*). A shortened, "winged" Oceanic Manta Ray (*Mobula birostris*) has greater control over its steering compared to an elongated and stiff Basking Shark (*Cetorhinus maximus*). And, so, we acknowledge that there are certain swimming principles that are universal and help guide our quest to build a proper shark (or ray, skate, or chimaera). Before we can fully assess performance in sharks (or any of their relatives), we must first deal with the business of defining the metrics we will use for our assessments. As such, we first address four specific topics from physics that aid in our discussion about the movement of sharks in a fluid environment 50 times more viscous than air. These topics are *buoyancy*, *lift*, *drag*, and *thrust* (Figure 3.2).

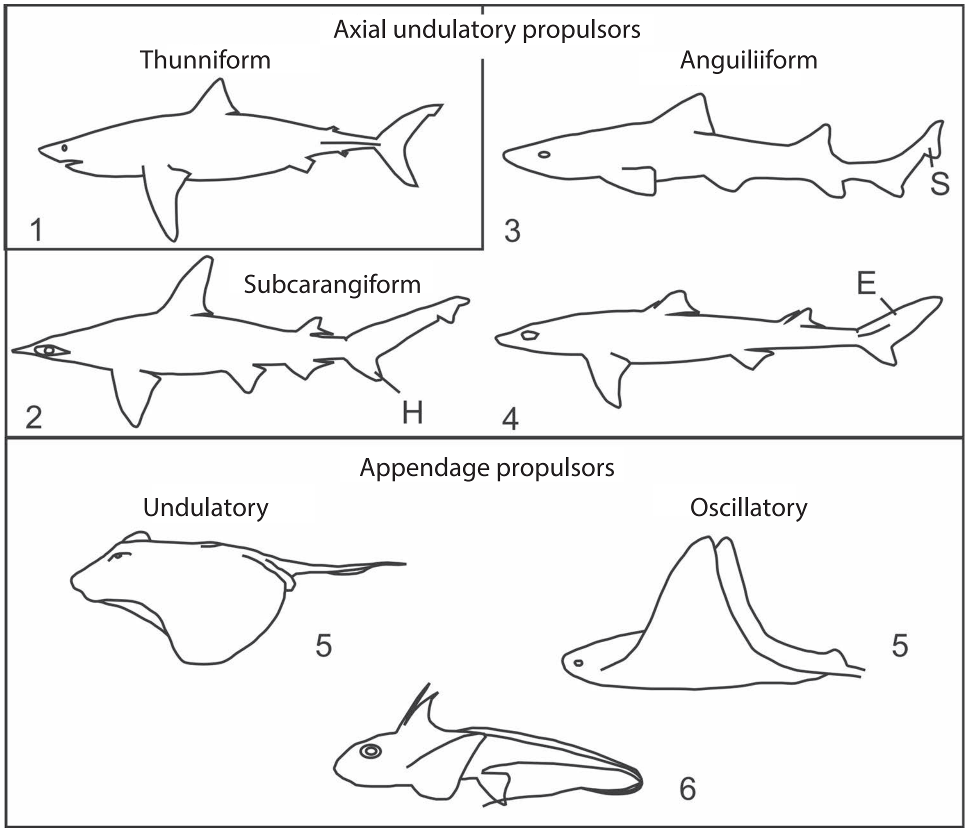

FIGURE 3.1 Propulsion mechanisms in chondrichthyans. Numbers indicate body groups mentioned in text. E, epicaudal lobe; H, hypochordal lobe; S, subterminal lobe. (Figure from Wilga and Lauder 2004, based on Webb 1984 and Webb and Blake 1985.)

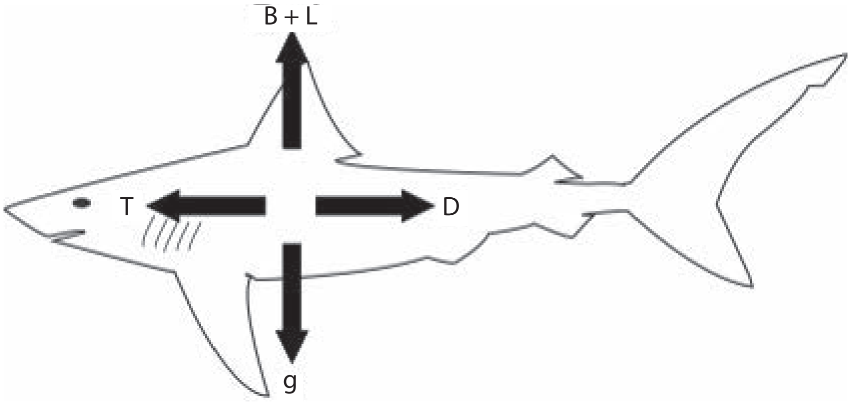

FIGURE 3.2 Forces affecting sharks as they move through their environment. B, buoyancy; D, drag; g, gravity; L, lift; T, thrust.

3.2.2 BUOYANCY

Consider a rubber duck floating peacefully in your bath water. How does this duck come to float at the surface? The learned scholar might answer this question by stating that the object at float is less dense than the water. But, what is density exactly? Stated in another way, one might simply say that the object weighs less than the same volume of water that has been displaced. As such, the less dense object experiences a lifting force that pushes the object to the surface—a positive buoyancy. On the other hand, a piece of granite dropped in water will sink immediately, and we can conclude that the rock has a density greater than a volume of water equal to its own—a negative buoyancy. Of course, if an object is experiencing neither a floating or a sinking effect, we can conclude that the density of the object is equal to the same volume of water—a neutrally buoyant object. Sharks, in particular, are equipped with buoyant livers that help counteract the sinking force that is associated with possessing skeletal tissues that are denser than the surrounding water. Sharks (and their relatives) overall are less dense than other fishes because their skeletons are composed entirely of cartilage and not bone; however, they do still have a tendency to sink to the bottom (for more information, see Baldridge 1970; Bone and Roberts 1969;

Iosilevskii and Papastamatiou 2016; Wetherbee and Nichols 2000). This is hugely helpful for a stingray that likes to be buried in the sand, but not so helpful for a Blacktip Reef Shark (*Carcharhinus melanopterus*) that needs to swim through the shallow coral reef.

3.2.3 LIFT

Lift sounds like it should be associated with an upward direction. In physics, it has a very particular definition that has nothing to do with elevation (up or down). Buoyancy is a form of lift, but the two terms are not necessarily interchangeable. Picture a solid object in water—for our purposes, let us envision a plastic toy shark. The water (the fluid) flows around the body of the toy. Let us imagine this flow is happening in a singular direction, from the shark's head toward the tail. Lift is defined as a force perpendicular (at a right angle) to this fluid flow. If the shark is swimming in a steady, level position, this fluid moves around the shark horizontally and so the lift force will be directed in an upward direction, counteracting the force of gravity. However, if the shark shifts its body position from the horizontal, so too will the direction of the lift force (remember it is perpendicular to the flow). But, sharks can generate lift in other ways. Not only are they able to generate lift using flows moving around their torso (or, as we like to refer to it, the torpedo portion of the shark), but they also tend to have sizable pectoral fins that add to lift.

Let us back up a moment and provide a visual. Sharks are very much akin to airplanes. How so? Picture a small, single engine airplane (not the cushy jet engines of the 21st century). The shape of the wings is hugely important to creating lift for the small plane. Closer inspection of the wings reveals that the anterior top portion (the front and top end) of the wing is quite rounded, whereas the bottom is much less curved (Figure 3.3). As air hits the wing, the flow moving over the curved portion on top will move faster than the air moving beneath the wing. Thanks to Bernoulli's principle, we know that there is an inverse relationship between the velocity of a fluid streamline and the pressure. The faster streamline above the wing creates a pressure differential, such that lower pressure is generated above the wing. The plane will then move toward the lower pressure, creating lift.

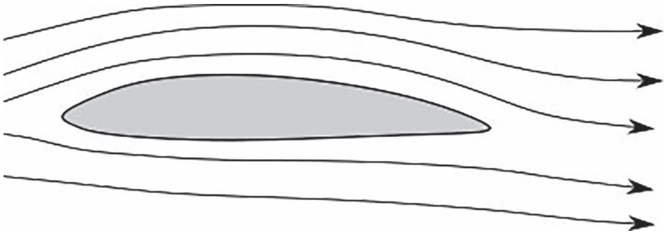

FIGURE 3.3 Simplified diagram of fluid flowing around a shark pectoral fin. The pectoral fin acts as a hydrofoil (gray), and water must flow around it (arrows). Because the upper surface is more curved than the lower surface, the streamlines move faster than those below the fin. Faster velocities above the fin also lead to decreased pressure above the fin; slower velocities below the fin lead to increased pressure below the fin. The fin moves toward the lower pressure, producing lift.

Many shark fins have shapes similar to airplane wings, at least this is the case with many of the varieties of sharks found continually cruising the seas. Fluids do not usually move around a shark fin (or airplane wing) in an organized manner, and substantial turbulence is created. This turbulence, described as vorticity shedding, is important for lift and also thrust. We will return to this point in Section 3.2.5. Nevertheless, for our purposes, airplane wings are a suitable comparison to use when thinking broadly about fin contribution to lift. We suggest reviewing additional texts on comparative biomechanics by Steven Vogel for further insight (Vogel 1988, 1996, 2000, 2013).

It is important to note that shark pectoral fins work somewhat differently than aeronautical devices in that they are not creating lift during normal, steady, horizontal swimming; rather, they are responsible for generating lift during rising (positive lift) or sinking (negative lift) maneuvers (Wilga and Lauder 2000, 2001). The shark's body (or fuselage, if we are still imagining an aircraft) in relation to the flow direction that contributes greatest to overall lift and during horizontal swimming is actually held in a slightly negative angle (Wilga and Lauder 2002). Nevertheless, the fin angle is not static and can be dynamically adjusted to increase maneuverability. If the angle of the pectoral fin increases, it will produce vorticity that is shed in the downward direction (positive lift). If the angle of the fin decreases, vorticity will shed toward the dorsal direction, and the shark will move toward the bottom (negative lift).

The pectoral fins and body orientation do not fully account for lift generation. The heterocercal tail in sharks also works to propel the fish not just forward but also upward in the water column (Ferry and Lauder 1996; Flammang *et al.* 2011). This occurs through a complex mechanism of vortex shedding, and this shedding produces not only lift but also thrust. We will return to this point shortly.

3.2.4 DRAG

Lift forces are always accompanied by drag forces. Shark fins are described as hydrofoils (Figure 3.3), or a streamlined shape that generates more lift than drag—the topic of this section. Drag is somewhat more complicated to deal with than lift; however, we can simplify it to suit our purposes. Returning to our shark toy example, we are dealing with a solid–fluid drag force, the solid being the shark toy and the fluid the water. One way of defining drag is to describe a force that is acting in opposition to the relative motion of an object in a fluid. Stating this another way, drag force is parallel to the flow direction. For example, if our shark is swimming forward (a forward force), then the drag force would be in the opposing direction of the forward movement, slowing the shark down.

In a laminar flow (flow where streamlines do not cross), drag force is proportional to velocity. That is to say, as velocity of a fluid increases, so does the drag force. Put another way, increased drag forces will slow down the fluid velocity relative to the solid object—in turn, our shark slows down. The viscous friction is responsible for drag, but sharks do not swim in laminar flows. They swim in chaotic, turbulent waters. And, in turbulent flows, drag is not ruled by the viscosity. Not to worry. It turns out that dealing with turbulent drag is also rather easy. Turbulent drag is proportional to the squared velocity. We return to our previous claim that drag is rather complex in nature. There are many types of drag, including viscous pressure drag, skin friction drag, lift-induced drag, and wave drag. For our purposes, this is as far as we will take this topic, although we do suggest a textbook on comparative biomechanics to learn more—might we once again suggest one written by Dr. Vogel (2013)?

3.2.5 THRUST

Finally, we turn our attention to the main event—*thrust*, or as we like to refer to it, "moving the machine." We know sharks are capable of fast starts and high speeds. Most readers can correctly identify that this forward movement is thrust. The propulsive force that moves a shark is generated by the tail. As the caudal fin is moved from side to side, the shark is propelled forward—either smoothly or as a burst of impressive speed. However, this is not the full story.

Imagine a plastic shark tail oscillating back and forth in a flow tank. As the tail moves from one side to the next, vortices (rings) are produced and shed, producing a wake. This wake is angled in a lateral and downward direction (a downwash), also in effect creating lift. One may envision that the size and overall strength of vorticity of these shedding rings might be different in their size scale, depending on if they are being produced by the larger, dorsal lobe of the caudal fin or the smaller, ventral lobe. This is indeed the case for models of shark tails. Two vortices are produced, one by the upper caudal lobe and one by the lower caudal lobe. The two vortices form a linked ring structure consisting of one large, outer vortex and one smaller, weaker inner vortex (Flammang *et al.* 2011). The vortices shed at the end of the tail beat in a lateral and somewhat downward direction, producing some amount of lift and thrust.

But, a live shark tail takes this process of shedding vortices in a different direction than the shark model. Flammang *et al.* (2011) demonstrated that model shark tails are not as dynamic as live shark tails and, as such, work in a different way (Figure 3.4). Similar to the plastic shark tail, a live shark caudal fin will also produce a series of vortices; however, the inner ring is shed at a more extreme downward directed angle. The downward-directed vortices create a wake that generates more lift than the plastic shark fin. Rather than two unequally sized vortices, the live shark sheds dual ring vortices that are more proportional in size and vorticity, with the smaller rings displaying the highest velocity jets—creating more thrust (Flammang *et al.* 2011).

It turns out that live sharks also have one more strategy for modulating both lift and thrust: musculature that can change the stiffness of the caudal fin. The radialis muscle inserts directly into the cross-fiber array of collagen fibers in the shark skin, stiffening the tail on the side in the direction of motion (Flammang *et al.* 2011). In effect, this stiffening helps to oppose hydrodynamic loading and can modulate both the fin angle and stiffness, creating a system where the shark can dynamically adjust the vortex wake produced as they swim and, in turn, the lift and thrust being generated (Flammang 2014; Flammang *et al.* 2011). This dynamic modulation results in the two linked ring vortices shedding not just at the end of the tail beat but also at the half beat (the mid-swing of the tail). It is the change in tail stiffness, not the change in angle, that results in the additional vorticity shedding at the half beat. The extra vorticity results in more continuous thrust, allowing a shark to hold a steady position better than most bony fishes (Flammang *et al.* 2011). Evidence of this is on full display at local aquariums when comparing the motions of bony fishes and sharks swimming. One can easily identify the characteristic minor accelerations at the end of every tail beat, resulting in the bobbing forward and backward motion displayed by bony fishes. Sharks, on the other hand, tend to swim in a more fluid and seamless manner, with no bobbing about.

Although the tail is the main thrust producer on our generic shark, other fins can contribute to thrust production. The dorsal fins in sharks have been shown to contribute to both stabilization and thrust. Maia *et al.* (2017) showed that both dorsal fins in the Whitespotted Bamboo Shark (*Chiloscyllium plagiosum*) and the second dorsal fin in Spiny Dogfish (*Squalus acanthias*) contribute to thrust through accelerations during steady swimming. Maia and Wilga (2016) demonstrated that Spiny Dogfish dorsal fins are not passive stabilizers but instead have a dual dorsal fin function controlled via dorsal fin epaxial musculature. The first dorsal fin moves independently from the body, especially at decreased speeds, to stabilize the body position during steady swimming, while the second dorsal fin moves in phase with the body undulations, working as a thrust producer. Most stingrays do not have a thrust-generating caudal fin; instead, they create thrust production via their pectoral fins, either via coordinated vertical oscillations (flapping; Myliobatidae) or via undulations (s-curve; Dasyatidae) (Figure 3.1) (Blevins and Lauder 2012; Fish *et al.* 2018). The mechanics of this thrust production stems from the generation of leading-edge vortices that create low-pressure regions at the anterior edge, enhancing thrust in both fast- and slow-swimming rays (Bottom *et al.* 2016). However, the torpedo rays (e.g., Brazilian Electric Rays, *Narcine brasiliensis*) swim using their caudal fins in a manner similar to that of sharks. These negatively buoyant rays use their caudal fin to produce thrust, while their body disc produces lift and controls the speed and angle of a glide (Rosenblum *et al.* 2011). Some stingrays and skates are capable of substrate locomotion through pelvic fin punting (Bilecenoglu and Ekstrom 2013; Lucifora and Vassallo 2002; Macesic and Kajiura 2010; Macesic *et al.* 2013), and Epaulette Sharks (*Hemiscyllium ocellatum*) are famous for their ability to "walk," both in a benthic environment and as a fish out of water over air-exposed coral clumps (Goto *et al.* 1999; Pridmore 1994; Travis 2020).

It is worth noting that the basic principles discussed above are not the only variables that bear consideration when designing a shark. True nautical vessels have a variety of other

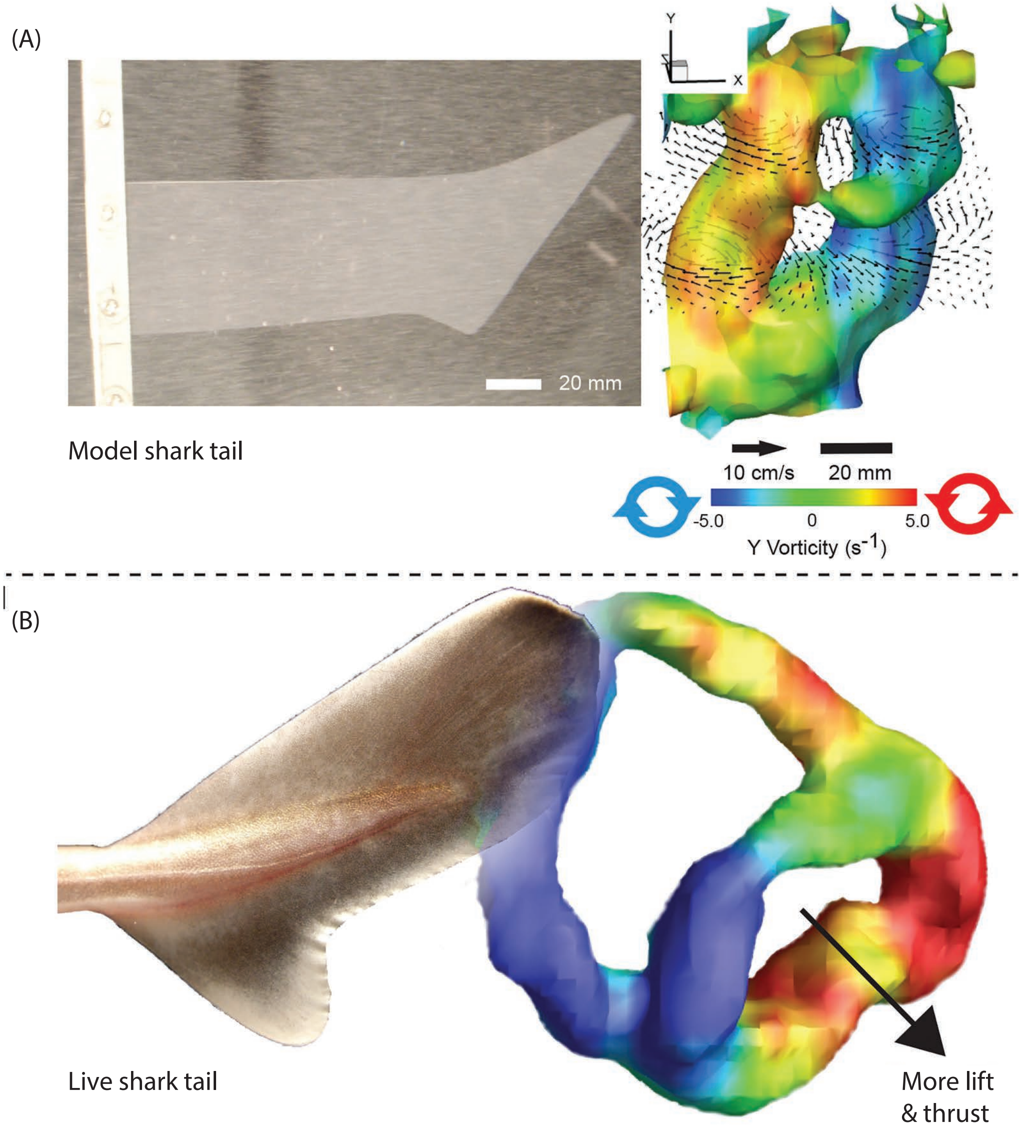

FIGURE 3.4 Vorticity produced by (A) a model shark tail and (B) a live shark. Dual linked vortices generated by the model shark tail are oriented laterally, and the linked vortices from the live shark are oriented in a more ventral direction. (Figure from Flammang *et al.* 2011; modified and used with permission of Brooke Flammang.)

considerations, including Reynolds number, a dimensionless number that describes the ratio of initial (turbulent) forces to viscous (laminar) forces in a fluid (we will return to this in Section 3.7.2); Strouhal number, a dimensionless number that describes the frequency of vortex shedding; and vorticity, the formation and motion of vortex rings. Nevertheless, the basic principles discussed above should help to demystify the basic forces acting upon a swimming shark.

3.2.6 Stabilizing and Turning the Machine

Another critical element for swimming is, of course, steering. Lift and thrust are important factors for moving forward and staying afloat, but what good are either of these things if your steering is not finely tuned (Figure 3.5)? Perhaps it is best to imagine a Blacktip Reef Shark (*Carcharhinus melanopterus*) navigating its complex environment. The shark must be nimble and reactive to avoid collisions with corals or other marine fauna. So, we can introduce an imaginary line through the fish that runs from the front of the head to the tail, in the same direction that we discussed drag and thrust. First, we will imagine our shark is oriented in a normal, steady swimming, horizontal position. If the shark was to elevate one pectoral fin toward its dorsal surface, the opposite fin would naturally move toward the ventral surface. This is referred to as *roll* (Figure 3.5).

Now let us imagine that the shark is actively hunting. It is perhaps convenient to imagine the wonderful cephalofoil of a hammerhead. As the hammerhead searches for its prey, the cephalofoil swings from one side to the next. This side-to-side motion of the head is referred to as *yaw* (Figure 3.5). Finally, the elevation of the shark's snout is referred to as *pitch*

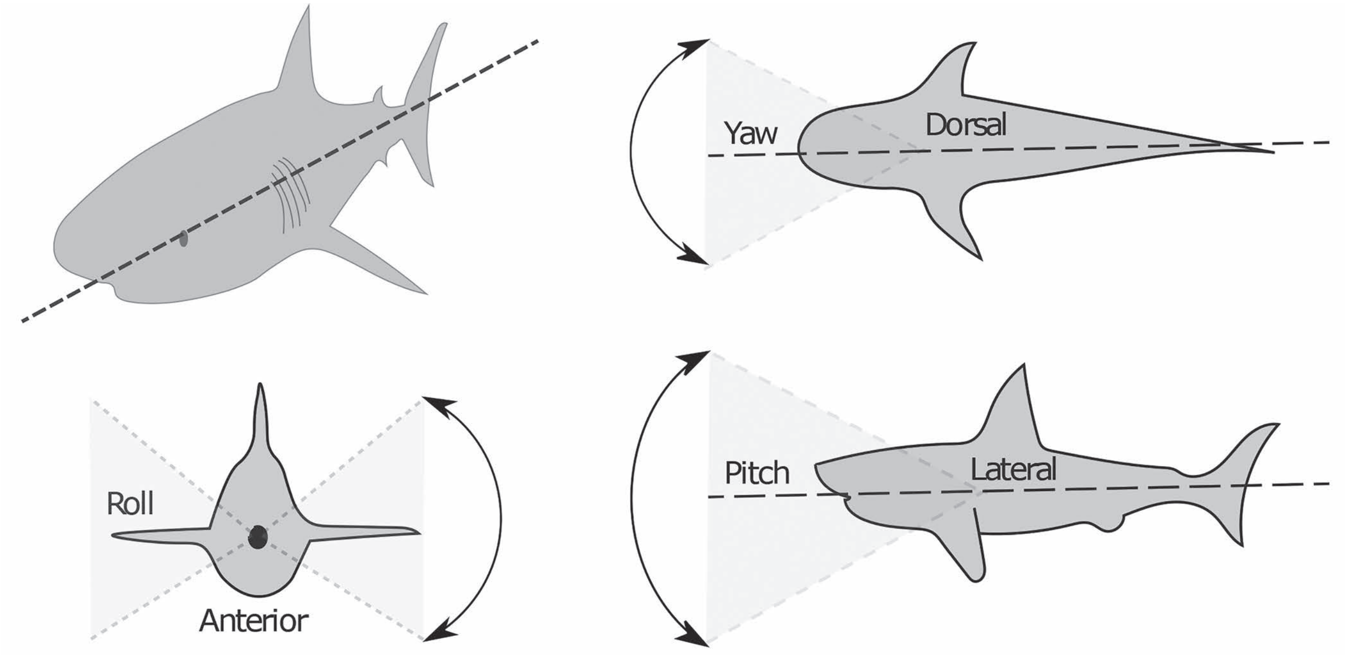

FIGURE 3.5 Illustrations of yaw, roll, and pitch in a shark. Gray areas and arrows indicate the direction of motion around the central axis.

(Figure 3.5). For example, the snout may point in the direction of the dorsal surface or orient downward toward the substratum. These three basic maneuvers are critical for underwater locomotion and can be finely tuned for great maneuverability through complex ecosystems.

Now that we have some useful terminology in hand, we are ready to learn how to steer a shark. There are two pieces to this puzzle that we must consider as a shark turns: the first is to study the contribution of the fins and the second is to examine the body motion.

Let us examine the role of pectoral fins for turning. While watching sharks swimming in an aquarium, you may notice that the pectoral fins seem to move during turning maneuvers. Using video reconstruction of moving morphology to quantify three-dimensional (3D) kinematics of pectoral fins during turning, Hoffmann and colleagues (2019) found that Pacific Spiny Dogfish (*Squalus suckleyi*) moved their pectoral fins on the inside of the turn in protraction (move fin toward head), supination (move ventral surface of fin toward head), and depression (move fin to ventral midline). As the amount of rotation in protraction and depression increased, so too did the drag, due to the greater surface area of the fin angled perpendicular to the water flow. In addition, the angular velocity (change of an angle from one time step to the next, over a time period, expressed as °/s) of the turns increased. What does this mean? Essentially, Pacific Spiny Dogfish have great control over their pectoral fins and operate them as a human would a kayak paddle; the inside fin is placed down into the water, creating a pivot point that enables the animal to increase the speed of a turn. This technique is not unique to Pacific Spiny Dogfish. Bonnethead (*Sphyrna tiburo*) turning maneuvers are also controlled by the pectoral fin on the inside of the turn, protracting, pronating, and depressing (Hoffmann and Porter 2019). Bonnethead turns were found to have the greatest angular velocity when pectoral fin depression was also greatest. Like Pacific Spiny Dogfish, Bonnethead pectoral fins move most in the axis of depression, but Bonnetheads also use another strategy quite similar to that of short-track speed skaters. When approaching a turn at increased speeds during a race, speed skaters tend to touch their hand to the ground. Similarly, Bonnetheads have been observed to retract, supinate, and elevate the inside pectoral fin, then quickly touch the substrate during a turn by pronating and depressing the fin (Hoffmann and Porter 2019). This type of turning maneuver may be useful for benthic-associated elasmobranchs like omnivorous Bonnetheads (Leigh *et al.* 2018, 2021).

Let us take a look at the body during a turn. To date, turning has been studied in over 14 shark and ray species (see summary table in Hoffmann and Porter 2019). We are particularly interested in how much bend the body of a shark undergoes. Several studies have used a bending coefficient (BC) to quantify the maximum body curvature achieved during a turn (Azizi and Landberg 2002; Brainerd and Patek 1998; Hoffmann and Porter 2019; Kajiura *et al.* 2003; Porter *et al.* 2009, 2011). This coefficient takes into account the minimum distance from the head to the caudal fin (L_1) relative to the total length (TL) of the shark ($1 - L_1/TL$). When the bending coefficient is 1, the shark nose is touching the tail, and when values are closer to 0, the body is straightened.

How much does a shark bend? Can the nose of the shark actually touch the tail during natural turning? It turns out small sharks in the family Hemiscylliidae are the true winners (Porter *et al.* 2009). In lab experiments, the Epaulette Shark has been the most flexible (BC = 0.9) of all the sharks examined, and they nearly touched their noses to the tips of the tails during turning. The Epaulettes are followed closely by the Brownbanded Bamboo Shark (*Chiloscyllium punctatum*) (BC = 0.8) and the Whitespotted Bamboo Shark (BC = 0.75). Do sharks always bend fully while turning? Probably not. The motivational state of the animal likely impacts any performance metrics measured in the lab and also observed in the wild. For example, Bonnetheads produced bending coefficients of 0.37 during routine turning in a tank, but when an electrical stimulus elicited turning the distance between the head and the tail was much smaller (BC = 0.59) (Hoffmann and Porter 2019; Kajiura *et al.* 2003). In other words, the amount that the shark bends is variable and so is the speed of turning. Among sharks, the Pacific Spiny Dogfish is relatively slow during routine turning (27.4°/s) (Hoffmann *et al.* 2019). In contrast, the Spiny Dogfish turn was 706°/s in a slow escape response, and this number nearly doubled (1221°/s) in a fast escape (Domenici *et al.* 2004). Like sharks, batoids also show variation while turning. The oscillatory rays have the quickest turns of the batoids (24.8°/s), followed by the undulatory rays (20.1°/s) (Parson *et al.* 2011), and the Oceanic Manta Ray has the slowest turns (18.3°/s) (Fish *et al.* 2018).

Body anatomy matters when considering maneuvering. The shape of the body and the morphology of the vertebral column are two important factors to consider when studying turning or maneuvering. After examining 16 morphological variables from the axial skeleton and precaudal vertebrae, Porter *et al.* (2009) found that the second moment of area (a structural predictor of stiffness) of the vertebral centra was the best predictor of body curvature during a turn, followed by length and transverse height. Following the vertebral morphology, the next most significant variables determining the curvature during a turn were total length, a two-dimensional measure of shape (fineness ratio, which is the ratio of body length to body width), and body width. Additionally, magnitude and timing of body flexion are the primary variables controlling turning performance (Porter *et al.* 2011). Taken together, sharks operate as a dynamic rudder during turning; the body flexes first at the tail to start a turn and then the flexion moves forward.

Shape affects the swimming kinematics of sharks and their relatives. When building a shark, we must consider whether the same mechanisms for generating lift and drag or roll and yaw apply to strangely shaped elasmobranchs, such as Frilled Sharks (*Chlamydoselachus anguineus*), chimaeras, and sawfishes. Few studies examine locomotion in these groups, although one particular family of sharks provides some insight. Hammerhead species, with their cephalofoil heads, are a great group to examine as we integrate the topics of buoyancy, lift, drag, and thrust. Some hammerheads (Bonnetheads and Scalloped Hammerheads, *Sphyrna lewini*) yaw their cephalofoil and do not roll their bodies during turning maneuvers (Kajiura *et al.* 2003). However, they do use their large dorsal fins to take advantage of both roll and lift (Payne *et al.* 2016). Great Hammerheads (*Sphyrna mokarran*) will roll between 50° and 75° to engage their dorsal fin as a lifting body and also to reduce drag. More recently, Scalloped Hammerheads were found to use this same tactic, but they change the amount of roll depending on the time of day—sharks swim with average roll angles of 41° during the day but 60° at night (Royer *et al.* 2020). The use of computational fluid dynamics to model flow around shark heads revealed that hammerheads of various species experience greater drag on their cephalofoil, resulting in a tenfold increase in energetic cost compared with carcharhinid species lacking the broadened head structure (Gaylord *et al.* 2020). They also found that the hammerhead cephalofoil does not provide much lift when the head is held parallel to the flow, but Kajiura *et al.* (2003) showed that, during maneuvering, differences in water velocity across a model cephalofoil should result in increased lift on the outside edge of the head during a turn. When measured using physical 3D-printed models of Scalloped Hammerhead and Bonnethead, lift generated by the cephalofoil increased as the angle of attack increased (Kazemi *et al.* 2018).

3.2.7 MECHANICAL TESTING OF CARTILAGINOUS VERTEBRAE

When considering shark swimming, we must remember that a series of cartilaginous vertebrae run the length of the animal and experience bending forces. How do those vertebrae deal with those forces? A common tool for explaining cartilage to non–shark scientists is to ask one to touch their bendable ears or stiff bridge and less stiff tip of their nose. We can learn a lot about a material just by poking and stretching it. For example, we often focus on the mechanical performance of cartilage when compressing, pulling (tension), bending (a combination of both compression and tension), and shearing, as discussed later in this chapter (Section 3.6.2). These poking and pulling experiments all fall into the realm of mechanical testing. During a mechanical test, a force or load (N) is applied to a sample, such as elasmobranch cartilage of some measured size. As the load is applied, the cartilage will change length (l), either shortening in compression or lengthening in tension. The size of the starting sample matters here, because bigger samples will require more force to change, so standardization is key. We can do this by applying the force over a specified cross-sectional area (stress, σ) and looking at the changed length relative to the starting length (strain, ε) (Figure 3.6). Now we can plot the changes in stress and strain relative to each other and generate a stress–strain curve. These curves allow us to learn quite a bit about material properties (a physical property that does not depend on the amount of the material used). The slope of the curve (stress–strain) tells us how well the material resists forces; we call this *stiffness* (E) and report these values in pascals (Pa). The peak of the curve is the combination of *maximum stress* (Pa) and *strain* (%) the material can withstand before failure, termed *maximum strength* (Pa) and *strain at failure* (%), respectively. The area under the curve is called *toughness* ($N \cdot m \cdot m^{-3}$ or $J \cdot m^{-3}$) and speaks to the ability of the material to absorb energy without rupturing.

Although the maxima can tell us about the maximal performance capabilities of a material, failing biological materials are not particularly useful for most organisms. Many