THE DIVERSITY OF FISHES

BIOLOGY, EVOLUTION AND ECOLOGY

DOUGLAS E. FACEY
BRIAN W. BOWEN
BRUCE B. COLLETTE
GENE S. HELFMAN

THIRD EDITION

WILEY

The Diversity of Fishes

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Biology, Evolution and Ecology

Third Edition

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To our parents, for their encouragement of our nascent interest in things biological;
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Preface to the Third Edition

Thank you to all who helped make the first two editions of *The Diversity of Fishes* successful. We greatly appreciate the feedback and suggestions from those who have used them. And to those who have been asking us about an update – thanks for your patience. Here is what you can expect in the third edition.

- We have done our best to update information while recognizing that no textbook can represent the most current information in any large field. This book is intended as a starting point, not the final destination. Therefore, we encourage those using the text to consult more current sources for updated information.
- This edition includes more color photographs to better demonstrate the diversity and beauty of fishes that attract many to the field. We include photographs from public agencies, in part to acknowledge the valuable contributions to Ichthyology of those in natural resources and management organizations.
- Reorganization and consolidation of some topics has reduced the total number of chapters to 22.
- Each chapter begins with a Summary that provides a broad overview of the content of that chapter. This may be particularly useful for those using the text for a course and who do not intend to utilize some chapters in detail – students can read the summary of each of those chapters.
- Molecular genetics has transformed many aspects of ichthyology over the last few decades, and this is reflected throughout the text. Important concepts are introduced in Chapters 1 and 2, supported by an Appendix of terminology at the end of the book, and specific contributions of molecular genetics to the field of ichthyology are included in many chapters.
- Structure and function are addressed together rather than treated in separate chapters. For example, Chapter 3 addresses structure and function of the head (e.g. bones, muscles, breathing, jaw suspension, feeding, dentition), and Chapter 4 addresses structure and function of the trunk (e.g. bones, muscles, integument, scales, fins, locomotion).
- In chapters addressing the history of the fishes (Chapter 11) and systematics of the major groups of fishes (Chapters 12–15), we have largely adopted the approach of Nelson et al. (2016), which includes consideration of molecular phylogenetics. However, we have retained the approach of Nelson (2006) where conclusions from molecular data are quite different from those based on morphological evidence (see Chapter 15, for example). We note differences between the approaches and encourage readers to consult current sources for updated information and perspectives, as our collective understanding of the relationships among groups of fishes continues to evolve.
- Fishes as predators and prey are considered together in one chapter (Chapter 16). Many fishes are both predators and prey, and many physical and behavioral adaptations are rather similar and, in some cases, may have developed in response to one another.
- Our chapter on Zoogeography and Phylogeography (Chapter 19) uses global maps that more accurately represent the comparative sizes of oceans and landmasses than maps used in prior editions.
- Fish populations are covered in Chapter 20, including Population Ecology, Population Dynamics and Regulation, and Population Genetics.
- Fish interactions with other species within fish assemblages and broader communities, and their impacts on ecosystems are addressed in Chapter 21. This is a long chapter but avoids the redundancy of addressing similar types of interactions and impacts in multiple chapters.
- As in the past, we conclude with a chapter on Conservation (Chapter 22), but this now includes Conservation Genetics.

Preface to the Second Edition

The first edition of *The diversity of fishes* was successful beyond our wildest dreams. We have received constant and mostly positive feedback from readers, including much constructive criticism, all of which convinces us that the approach we have taken is satisfactory to ichthyological students, teachers, and researchers. Wiley-Blackwell has validated that impression: by their calculations, *The diversity of fishes* is the most widely adopted ichthyology textbook in the world.

However, ichthyology is an active science, and a great deal of growth has occurred since this book was first published in 1997. Updates and improvements are justified by active and exciting research in all relevant areas, including a wealth of new discoveries (e.g., a second coelacanth species, 33 more megamouth specimens, several new record tiniest fishes, and exciting fossil discoveries including some that push back the origin of fishes many million years and another involving a missing link between fishes and amphibians), application of new technologies (molecular genetics, transgenic fish), and increased emphasis on conservation issues (e.g., Helfman 2007). Websites on fishes were essentially nonexistent when the first edition was being produced; websites now dominate as an instant source of information. Many of the volumes we used as primary references have themselves been revised. Reflective of these changes, and of shortcomings in the first edition, is the addition of a new chapter and author. Genetics received insufficient coverage, a gross omission that has been corrected by Brian Bowen's contribution of a chapter devoted to that subject and by his suggested improvements to many other chapters. Brian's contributions were aided by extensive and constructive comments from Matthew Craig, Daryl Parkyn, Luiz Rocha, and Robert Toonen. He is especially grateful to John Avise, Robert Chapman, and John Musick for their guidance and mentorship during his professional career, and most of all to his wife, RuthEllen, for her forbearance and support.

Among the advances made in the decade following our initial publication, a great deal has been discovered about the phylogeny of major groups, especially among jawless fishes, sarcopterygians, early actinopterygians, and holocephalans. In almost all taxa, the fossil record has expanded, prompting reanalysis and sometimes culminating in conflicting interpretations of new findings. A basic textbook is not the appropriate place to attempt to summarize or critique the arguments, opinions, and interpretations. We have decided to accept one general compilation and synthesis. As in the 1997 edition, where we adopted with little adjustment the conclusions and terminology of Nelson (1996), we here follow Nelson (2006), who reviews the recent discoveries and clearly presents and assesses the many alternative hypotheses about most groups. Instructors who used our first edition will have to join us in learning and disseminating many changed names as well as rearrangements among taxa within and among phylogenies, especially Chapters 11–13. Science is continually self-correcting. We should applaud the advances and resist the temptation to comfortably retain familiar names and concepts that have been modified in light of improved knowledge.

Also, we have now adopted the accepted practice of capitalizing common names.

Acknowledgments

Thanks especially to the many students and professionals who corrected errors in the first edition (J. Andrew, A. Clarke, D. Hall, G.D. Johnson, H. Mattingly, P. Motta, L.R. Parenti, C. Reynolds, C. Scharpf, E. Schultz, M.L.J. Stiassny, and S. Vives proved particularly alert editors). Their suggestions alone led to many changes, to which we have added literally hundreds of new examples, facts, and updates. Wiley-Blackwell has provided a website for this second edition, www.wiley.com/go/helfman, through which we hope to again correct and update the information provided here. We encourage any and all to inform us wherever they encounter real or apparent errors of any kind in this text. Please write directly to us. Chief responsibilities fell on GSH for Chapters 1, 8–15, and 18–26 (genehelfman@gmail.com); on BBC for Chapters 2–4 and 16 (collettb@si.edu); on DEF for Chapters 5–7 (dfacey@smcvt.edu), and on BWB for Chapter 17 (bbowen@hawaii.edu). Once again and more than anything, we want to get it right.

Preface to the First Edition

Two types of people are likely to pick up this book, those with an interest in fishes and those with a fascination for fishes. This book is written by the latter, directed at the former, with the intent of turning interest into fascination.

Our two major themes are adaptation and diversity. These themes recur throughout the chapters. Wherever possible, we have attempted to understand the adaptive significance of an anatomical, physiological, ecological, or behavioral trait, pointing out how the trait affects an individual's probability of surviving and reproducing. Our focus on diversity has prompted us to provide numerous lists of species that display particular traits, emphasizing the parallel evolution that has occurred repeatedly in the history of fishes, as different lineages exposed to similar selection pressures have converged on similar adaptations.

The intended audience of this book is the senior undergraduate or graduate student taking an introductory course in ichthyology, although we also hope that the more seasoned professional will find it a useful review and reference for many topics. We have written this book assuming that the student has had an introductory course in comparative anatomy of the vertebrates, with at least background knowledge in the workings of evolution. To understand ichthyology, or any natural science, a person should have a solid foundation in evolutionary theory. This book is not the place to review much more than some basic ideas about how evolutionary processes operate and their application to fishes, and we strongly encourage all students to take a course in evolution. Although a good comparative anatomy or evolution course will have treated fish anatomy and systematics at some length, we go into considerable detail in our introductory chapters on the anatomy and systematics of fishes. The nomenclature introduced in these early chapters is critical to understanding much of the information presented later in the book; extra care spent reading those chapters will reduce confusion about terminology used in most other chapters.

More than 27,000 species of fishes are alive at present. Students at the introductory level are likely to be overwhelmed by the diversity of taxa and of unfamiliar names. To facilitate this introduction, we have been selectively inconsistent in our use of scientific versus common names. Some common names are likely to be familiar to most readers, such as salmons, minnows, tunas, and freshwater sunfishes; for these and many others, we have used the common family designation freely. For other, less familiar groups (e.g., Sundaland noodlefishes, trahiras, morwongs), we are as likely to use scientific as common names. Many fish families have no common English name and for these we use the Anglicized scientific designation (e.g., cichlids, galaxiids, labrisomids). In all cases, the first time a family is encountered in a chapter we give the scientific family name in parentheses after the common name. Both scientific and common designations for families are also listed in the index. As per an accepted convention, where lists of families occur, taxa are listed in phylogenetic order. We follow Nelson et al. (1994, now updated) on names of North American fishes and Robins et al. (1991, also now updated) on classification and names of families and of higher taxa. In the few instances where we disagree with these sources, we have tried to explain our rationale.

Any textbook is a compilation of facts. Every statement of fact results from the research efforts of usually several people, often over several years. Students often lose sight of the origins of this information, namely the effort that has gone into verifying an observation, repeating an experiment, or making the countless measurements necessary to establish the validity of a fact. An entire dissertation, representing 3–5 or more years of intensive work, may be distilled down to a single sentence in a textbook. It is our hope that as you read through the chapters in this book, you will not only appreciate the diversity of adaptation in fishes, but also consider the many ichthyologists who have put their fascination to practical use to obtain the facts and ideas we have compiled here. To acknowledge these efforts, and because it is just good scientific practice, we have gone to considerable lengths to cite the sources of our information in the text, which correspond to the entries in the lengthy bibliography at the end of the book. This will make it possible for the reader to go to a cited work and learn the details of a study that we can only treat superficially. Additionally, the end of each chapter contains a list of supplemental readings, including books or longer review articles that can provide an interested reader with a much greater understanding of the subjects covered in the chapter.

This book is not designed as a text for a course in fisheries science. It contains relatively little material directly relevant to such applied aspects of ichthyology as commercial or sport fisheries or aquaculture; several good text and reference books deal specifically with those topics (for starters, see the edited volumes by Lackey & Nielsen 1980, Nielsen & Johnson 1983, Schreck & Moyle 1990, and Kohler & Hubert 1993). We recognize however that many students in a college-level ichthyology class are training to become professionals in those or related disciplines. Our objectives here are to provide such readers with enough information on the general aspects of ichthyology to make informed, biologically sound judgments and decisions, and to gain a larger appreciation of the diversity of fishes beyond the relatively small number of species with which fisheries professionals often deal.

Adaptations versus adaptationists

Our emphasis throughout this text on evolved traits and the selection pressures responsible for them does not mean that we view every characteristic of a fish as an adaptation. It is important to realize that a living animal is the result of past evolutionary events, and that animals will be adapted to current environmental forces only if those forces are similar to what has happened to the individual's ancestors in the past. Such phylogenetic constraints arise from the long-term history of a species. Tunas are masters of the open sea as a result of a streamlined morphology, large locomotory muscle mass connected via efficient tendons to fused tail bones, and highly efficient respiratory and circulatory systems. But they rely on water flowing passively into their mouths and over their gills to breathe and have reduced the branchiostegal bones in the throat region that help pump water over their gills. Tunas are, therefore, constrained phylogenetically from using habitats or foraging modes that require them to stop and hover, because by ceasing swimming they would also cease breathing.

Animals are also imperfect because characteristics that have evolved in response to one set of selective pressures often create problems with respect to other pressures. Everything in life involves a trade-off, another recurring theme in this text. The elongate pectoral fins ("wings") of a flyingfish allow the animal to glide over the water's surface faster than it can swim through the much denser water medium. However, the added surface area of the enlarged fins creates drag when the fish is swimming. This drag increases costs in terms of a need for larger muscles to push the body through the water, requiring greater food intake, time spent feeding, etc. The final mix of traits evolved in a species represents a compromise involving often-conflicting demands placed on an organism. Because of phylogenetic constraints, trade-offs, and other factors, some fishes and some characteristics of fishes appear to be and are poorly adapted. Our emphasis in this book is on traits for which function has been adequately demonstrated or appears obvious. Skepticism about apparent adaptations can only lead to greater understanding of the complexities of the evolutionary process. We encourage and try to practice such skepticism.

Acknowledgments

This book results from effort expended and information acquired over most of our professional lives. Each of us has been tutored, coaxed, aided, and instructed by many fellow scientists. A few people have been particularly instrumental in facilitating our careers as ichthyologists and deserve special thanks: George Barlow, John Heiser, Bill McFarland, and Jack Randall for GSH; Ed Raney, Bob Gibbs, Ernie Lachner, and Dan Cohen for BBC; Gary Grossman and George LaBar for DEF. The help of many others is acknowledged and deeply appreciated, although they go unmentioned here.

Specific aid in the production of this book has come from an additional host of colleagues. Students in our ichthyology classes have written term papers that served as literature surveys for many of the topics treated here; they have also critiqued drafts of chapters. Many colleagues have answered questions, commented on chapters and chapter sections, loaned photographs, and sent us reprints, requested and volunteered. Singling out a few who have been particularly helpful, we thank C. Barbour, J. Beets, W. Bemis, T. Berra, J. Briggs, E. Brothers, S. Concelman, J. Crim, D. Evans, S. Hales, B. Hall, C. Jeffrey, D. Johnson, G. Lauder, C. Lowe, D. Mann, D. Martin, A. McCune, J. Meyer, J. Miller, J. Moore, L. Parenti, L. Privitera, T. Targett, B. Thompson, P. Wainwright, J. Webb, S. Weitzman, D. Winkelman, J. Willis, and G. Wippelhauser. Joe Nelson provided us logistic aid and an early draft of the classification incorporated into the 3rd edition of his indispensable *Fishes of the world*. Often animated and frequently heated discussions with ichthyological colleagues at annual meetings of the American Society of Ichthyologists and Herpetologists have been invaluable for separating fact from conventional wisdom. Gretchen Hummelman and Natasha Rajack labored long and hard over copyright permissions and many other details. Academic departmental administrators gave us encouragement and made funds and personnel available at several crucial junctures during production. At the University of Georgia we thank J. Willis (Zoology), R. Damian (Cell biology), and G. Barrett, R. Carroll, and R. Pulliam (Ecology) for their support. At St. Michael's College, we thank D. Bean (Biology). The personnel of Blackwell Science, especially Heather Garrison, Jane Humphreys, Debra Lance, Simon Rallison, Jennifer Rosenblum, and Gail Segal, exhibited patience and professionalism at all stages of production.

Finally, a note on the accuracy of the information contained in this text. As Nelson Hairston Sr. has so aptly pointed out, "Statements in textbooks develop a life independent of their validity." We have gone to considerable lengths to get our facts straight, or to admit where uncertainties lie. We accept full responsibility for the inevitable errors that do appear, and we welcome hearing about them. Please write directly to us with any corrections or comments. Chief responsibilities fell on GSH for Chapters 1, 8–15, and 17–25; on BBC for Chapters 2–4 and 16; and on DEF for Chapters 5–7.

Acknowledgments

Thank you to the many students and colleagues who provided constructive feedback on the first two editions. We hope that we were able to honor most of your suggestions in the preparation of this third edition.

We are profoundly grateful to colleagues who provided advice, reviews, encouragement, and logistic support during construction of the third edition, including A.M. Friedlander, M.A. Hixon, G. Orti, J.E. Randall, L.A. Rocha, R.J. Toonen. and the ToBo Lab at Hawai'i Institute of Marine Biology. Special thanks to R.C. Thomson for reviewing Chapter 2 (Phylogenetic Procedures), J. Webb for specific feedback on Chapter 6 (Nervous System and Sensory Organs), M. Wilson for clarifying some questions regarding Nelson et al. (2016), and to R. Hayden and the editing team at Wiley.

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Douglas Facey (dfacey@smcvt.edu) reorganized the topics and updated content throughout the book. Brian Bowen (bbowen@hawaii.edu) provided molecular genetics content and updates throughout the text, and also provided editorial input on multiple chapters. Bruce Collette (collettb@si.edu) assisted with updates of systematics in Chapters 11–15. Gene Helfman (genehelfman@gmail.com) took the lead role on the first two editions and provided editorial feedback on most chapters of this current edition.

About the Companion Website

This book is accompanied by a companion website.

www.wiley.com/go/facey/diversityfishes3

Resources include:

- Figures and tables from the book
- Links to supplementary, supporting content

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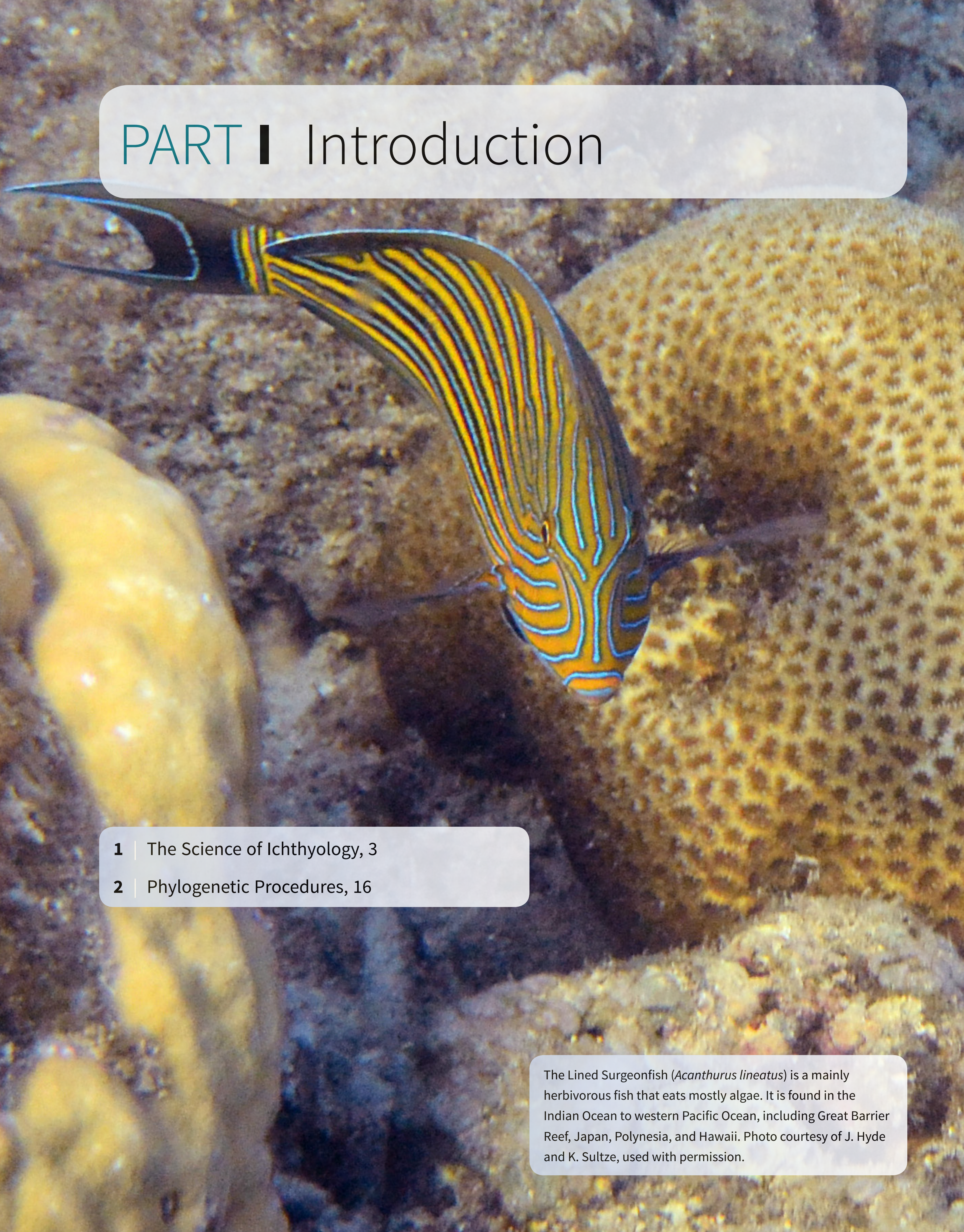
2 | Phylogenetic Procedures, 16



The Lined Surgeonfish (*Acanthurus lineatus*) is a mainly herbivorous fish that eats mostly algae. It is found in the Indian Ocean to western Pacific Ocean, including Great Barrier Reef, Japan, Polynesia, and Hawaii. Photo courtesy of J. Hyde and K. Sultze, used with permission.

CHAPTER 1

The Science of Ichthyology

Summary

Fishes account for more than half of all living vertebrates and exhibit remarkable evolution and diversity. There are over 35,000 living species of fishes (approaching 36,000 as we prepare this edition), of which over 100 are jawless (hagfishes, lampreys), approximately 1100 are cartilaginous (sharks, skates, rays), and the remaining are bony fishes.

A fish can be defined as an aquatic vertebrate with gills and with limbs in the shape of fins. There are, however, exceptions to such general rules, including hagfishes (nonvertebrate craniates) and some fishes that have lost their paired fins over evolutionary time (e.g. moray eels). Included in this definition is a tremendous diversity of sizes (from 8 mm gobies and minnows to the 12 + m Whale Shark), shapes, ecological functions, life history scenarios, anatomical specializations, and evolutionary histories.

Our current understanding of the relationships among the major extant lineages of fishes and other vertebrates shows that fishes include members of four different classes of vertebrates. The hagfishes (class Myxini) are craniates but not vertebrates. The major groups of living vertebrates include the lampreys (class Petromyzontida), sharks and other cartilaginous fishes (class Chondrichthyes), and the bony fishes and their descendants (class Osteichthyes). The Osteichthyes include the subclass Sarcopterygii (the lobe-finned fishes and their tetrapod descendants) and the subclass Actinopterygii (the ray-finned fishes).

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The Diversity of Fishes

Superlative Fishes

A Brief History of Ichthyology

Introduction to Fish Genetics

Additional Sources of Information

Supplementary Reading

The Diversity of Fishes: Biology, Evolution and Ecology, Third Edition. Douglas E. Facey, Brian W. Bowen, Bruce B. Collette, and Gene S. Helfman.

Companion website: www.wiley.com/go/facey/diversityfishes3

Most (about 60%) living fishes are primarily marine, and the remainder live in freshwater; about 1% move between salt and freshwater as a normal part of their life cycle. The greatest diversity of fishes is found in the tropics, particularly the Indo-West Pacific region for marine fishes and tropical South America, Africa, and Southeast Asia for freshwater species.

Unusual adaptations among fishes include African lungfishes that can survive buried in dry mud for up to 4 years, Antarctic fishes that produce their own antifreeze compounds, deep-sea fishes that can swallow prey larger than themselves (some deep-sea fishes exist as small males that are entirely parasitic on larger females), species that live less than a year and other species that may live hundreds of years, fishes that change sex from female to male or vice versa, sharks that provide nutrition for developing young via a complex placenta, fishes that create an electric field around themselves and detect biologically significant disturbances of the field, light-emitting fishes, warm-blooded fishes, and at least one group, the coelacanths, that was thought to have gone extinct with the dinosaurs.

Historically important contributions to ichthyology were made by Linnaeus, Peter Artedi, Georges Cuvier, Achille Valenciennes, Albert Günther, David Starr Jordan, B. W. Evermann, C. Tate Regan, and Leo S. Berg, among many others.

Genetics and molecular techniques have become integral and essential components to understanding fish biology, evolution, and ecology. In many cases, similarities in DNA probably more accurately reflect evolutionary relationships among groups than do morphological similarities.

The literature on fishes is voluminous, including college-level textbooks, popular and technical books, and websites that contain information on particular geographic regions, taxonomic groups, or species sought by anglers or best suited for aquarium keeping or aquaculture. Scientific journals with a local, national, or international focus are produced in many countries. Another valuable source of knowledge is public aquaria. Observing fishes by snorkel or scuba diving will provide anyone interested in fishes with indispensable, first-hand knowledge and appreciation.

We encourage anyone interested in fishes to observe them closely and carefully, both in captivity and in their natural habitats. They are truly fascinating animals.

Introduction

We recognize the formal common names of fish species as proper names, and therefore they will be capitalized throughout this book. Hence, a green sunfish could be any sunfish (family Centrarchidae) that has a somewhat green color, whereas Green Sunfish refers only to *Lepomis cyanellus*. However, bluefin tuna is not capitalized because it could refer to any of the following three species: the Atlantic Bluefin Tuna (*Thunnus thynnus*), the Pacific Bluefin Tuna (*Thunnus orientalis*), and the Southern Bluefin Tuna (*Thunnus maccoyii*).

Fishes make up more than half of the over 60,000 species of living vertebrates. Along with this remarkable taxonomic diversity comes an equally impressive habitat diversity. Fishes are the cradle of vertebrate biodiversity, dating back more than 500 million years, giving rise to the amphibians, dinosaurs, modern reptiles, birds, and mammals, including you. Millions of years before humans emerged from Africa to spread across the planet, fish species had already attained global distributions in the planet's oceans, lakes, and rivers. Diminutive killifish flourish in the highest lakes of the Andes (Lake Titicaca at 3812 m elevation), and ghostly snailfish forage in utter darkness of the deepest ocean abyss (Mariana Trench at 8000 m depth), very near the physiological limit for life under pressure. In a good year, anchovies of the genus *Engraulis* will vastly outnumber humans, foraging for plankton in schools that can span 50 km. The largest fish, the Whale Shark (*Rhincodon typus*), can exceed 12 meters in length, whereas the minnow *Paedocypris progenetica* in the swamps of Sumatra measures less than 1 cm. From ice-covered polar oceans to oxygen-depleted swamps, from the deepest ocean to desert ponds that dry up for years, and through all the more benign environments in between, fishes have been the ecologically dominant vertebrates in aquatic habitats through much of the history of complex life. To colonize and thrive in such a variety of environments, fishes have evolved striking anatomical, physiological, behavioral, and ecological adaptations.

With an excellent fossil record, fishes are showcases of the evolutionary process, exemplifying the intimate relationship between form and function, between habitat and adaptation. These themes are the foundations for our journey through the diversity of fishes. However, a shadow darkens this narrative: some killifish species in Lake Titicaca are extinct due to introduced trout, anchovies are harvested in the millions of tons to supply fish oil, and the whale shark is no match for human impacts on the global environment. We hope that an appreciation for the diversity of fishes brings a mandate to protect this diversity, so that future generations of fishes can continue to generate remarkable adaptations, and future generations of students can appreciate this majesty.

What Is a Fish?

It may be unrealistic to define a "fish," given the diversity of adaptations that characterizes the multiple classes and thousands of species alive today, each with a unique evolutionary history going back over half a billion years. By recognizing this diversity, one can define a fish as an aquatic chordate with gills and often with paired limbs in the shape of fins. The term "fish" is not a formal taxonomic category but a convenient term for a variety of aquatic organisms as diverse as jawless hagfishes and lampreys; cartilaginous sharks and rays; primitive bony fishes such as lungfishes, sturgeons, and gars; and advanced ray-finned fishes.

Definitions are hazardous in science because exceptions may be viewed as falsifications of the definition (see Berra 2001). Exceptions to the preceding definitions do not negate them, but instead, reveal adaptations arising through powerful selection pressures. Hence the loss of scales and fins in eel-shaped fishes tell us that these structures are not beneficial to fishes with an elongate body. Similarly, although most fishes are ectothermic (the same temperature as the surrounding water), heterothermy (partial warm-blooded physiology) in tunas, lamnid sharks, and opahs indicates the metabolic benefits of elevated body temperature to continuously moving predators in open sea environments. Lungs or other air-breathing structures in lungfishes, gars, African catfishes, and gouramis demonstrate adaptations to environmental conditions where gills are insufficient for transferring adequate oxygen to the blood. Deviations from the definition of "fish" are not invalidations of the definition but are lessons about evolutionary innovations.

Vertebrate Classes

When we (the authors) were first learning our fishes, many textbooks listed five classes of vertebrates: Pisces (all fishes) and four classes of tetrapods – the amphibians, reptiles, birds, and mammals. But Nelson (1969) demonstrated that this five-class system was biased by a human perspective that overemphasized differences among tetrapods while neglecting many of the profound differences among the different evolutionary lineages of fishes. This approach minimized the large morphological and evolutionary gap between the jawless fishes (lampreys and hagfishes) and other groups of fishes and exaggerated the more recently evolutionary divergences between bony fishes and tetrapods. Thus "Pisces" was not a monophyletic group with a single evolutionary history but rather a term used for convenience to describe all non-tetrapod vertebrates, which included several groups that are not closely related to one another (see Chapter 11). More recently, however, modern phylogenetics with an emphasis on utilizing DNA-based molecular appraisals of evolutionary lineages has yielded a more accurate view of the relationships among the major groups of vertebrates (Fig. 1.1).

The great diversity of fishes includes several major branches, and there is some difference of opinion among experts regarding the major taxonomic groupings. Nelson et al. (2016) and our previous edition recognized five classes that included fishes. Nelson et al. (2016) recognize four classes, whereas Eschmeyer and Fong (2017) recognize eight. There is general agreement that the jawless hagfishes and lampreys each belong in their own class, with hagfishes not quite qualifying as vertebrates (hence the term "craniate"). Nelson et al. (2016) put all cartilaginous fishes with jaws in one class (Chondrichthyes), whereas Eschmeyer and Fong consider the Holocephalans (ratfishes, chimaeras) as a class apart from the sharks, skates, and rays (Euselachii). Nelson et al. 2016 consider all jawed, bony fishes (and their descendants, including tetrapods) as members of the class Osteichthyes, with the Sarcopterygii (lobe-fins) and Actinopterygii (ray-fins) as separate subclasses. (These each had separate class status in Nelson 2006.) Eschmeyer and Fong separate the lobe-finned fishes (and their descendants) into three classes and consider all ray-finned fishes as members of a single class. The differences are due to somewhat different interpretations of the level of differences among groups – but should not cause undue concern or confusion to

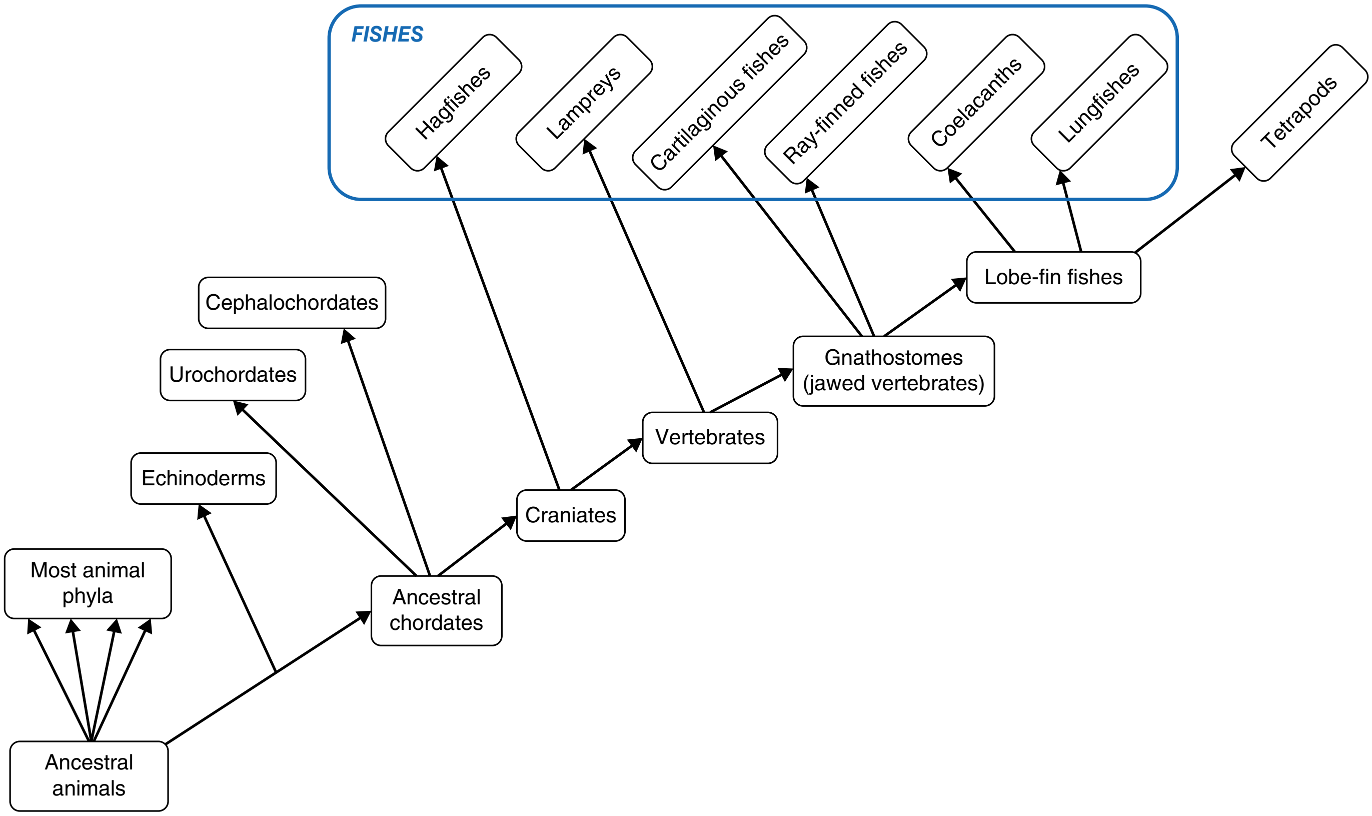


FIGURE 1.1 A cladogram showing the relationships of the major groups of chordates. Note that the fishes represent several major groups, and that the tetrapods are derived from a branch of the lobe-finned fishes.

TABLE 1.1 **The diversity of living fishes. Below is a brief listing of higher taxonomic categories of the Phylum Chordata, including living fishes, in phylogenetic order. This list is meant as an introduction to major groups of living fishes as they will be discussed in the initial two sections of this book. Many intermediate taxonomic levels, such as infraclasses, subdivisions, and series, are not presented here; they will be detailed when the actual groups are discussed in Part III. Only a few representatives of interesting or diverse groups are listed. Taxa mainly according to Nelson et al. 2016.**

<table>
<tr><td>PHYLUM CHORDATA</td></tr>
<tr><td style="padding-left:1em">Subphylum Cephalochordata – lancelets</td></tr>
<tr><td style="padding-left:1em">Subphylum Craniata</td></tr>
<tr><td style="padding-left:2em">Infraphylum Myxinomorphi</td></tr>
<tr><td style="padding-left:4em">Class Myxini – hagfishes</td></tr>
<tr><td style="padding-left:2em">Infraphylum Vertebrata</td></tr>
<tr><td style="padding-left:3em">Superclass Petromyzontomorphi</td></tr>
<tr><td style="padding-left:4em">Class Petromyzontida – lampreys</td></tr>
<tr><td style="padding-left:3em">Superclass Gnathostomata – jawed vertebrates</td></tr>
<tr><td style="padding-left:5em">Class Chondrichthyes – cartilaginous fishes</td></tr>
<tr><td style="padding-left:6em">Subclass Holocephali – chimaeras</td></tr>
<tr><td style="padding-left:6em">Subclass Euselachii – sharklike fishes</td></tr>
<tr><td style="padding-left:8em">Infraclass Elasmobranchii –extant sharks and rays</td></tr>
<tr><td style="padding-left:4em">Grade Teleostomi</td></tr>
<tr><td style="padding-left:5em">Class Osteichthyes - bony fishes and tetrapod descendants</td></tr>
<tr><td style="padding-left:6em">Subclass Sarcopterygii – lobe-finned fishes and relatives (includes Infraclass Tetrapoda), but only fishes listed here</td></tr>
<tr><td style="padding-left:8em">Infraclass Actinistia (Coelacanthimorpha) – coelacanths</td></tr>
<tr><td style="padding-left:8em">Infraclass Dipnomorpha – lungfishes</td></tr>
<tr><td style="padding-left:6em">Subclass Actinopterygii – ray-finned fishes</td></tr>
<tr><td style="padding-left:8em">Infraclass Cladistia – bichirs</td></tr>
<tr><td style="padding-left:8em">Infraclass Chondrostei – paddlefishes, sturgeons</td></tr>
<tr><td style="padding-left:7em">Neopterygii – unranked clade including Holosteans and Teleosts</td></tr>
<tr><td style="padding-left:8em">Infraclass Holostei</td></tr>
<tr><td style="padding-left:9em">Division Ginglymodi – includes gars</td></tr>
<tr><td style="padding-left:9em">Division Halecomorphi – includes Bowfin</td></tr>
<tr><td style="padding-left:8em">Infraclass Teleosteomorpha</td></tr>
<tr><td style="padding-left:9em">Division Teleostei</td></tr>
<tr><td style="padding-left:10em">Cohort Elopomorpha – tarpons, bonefishes, eels</td></tr>
<tr><td style="padding-left:10em">Cohort Osteoglossomorpha – bonytongues</td></tr>
<tr><td style="padding-left:10em">Cohort Otocephala</td></tr>
<tr><td style="padding-left:11em">Superorder Clupeomorpha – herrings</td></tr>
<tr><td style="padding-left:11em">Superorder Ostariophysi – minnows, suckers, characins, loaches, catfishes</td></tr>
<tr><td style="padding-left:10em">Cohort Euteleostei – further derived bony fishes</td></tr>
<tr><td style="padding-left:11em">Superorder Protacanthopterygii – salmons, smelts, pikes, stomiiforms (bristlemouths, marine hatchetfishes, dragonfishes</td></tr>
<tr><td style="padding-left:11em">Superorder Ateleopodomorpha - jellynose fishes</td></tr>
<tr><td style="padding-left:11em">Superorder Cyclosquamata - greeneyes, lizardfishes</td></tr>
<tr><td style="padding-left:11em">Superorder Scopelomorpha - lanternfishes</td></tr>
<tr><td style="padding-left:11em">Superorder Lampriomorpha - opahs, oarfishes</td></tr>
<tr><td style="padding-left:11em">Superorder Paracanthopterygii - troutperches, cods, toadfishes, anglerfishes</td></tr>
<tr><td style="padding-left:11em">Superorder Acanthopterygii - spiny rayed fishes: mullets, silversides, killifishes, squirrelfishes, sticklebacks, scorpionfishes, basses, perches, tunas, flatfishes, pufferfishes, and many others</td></tr>
</table>

students of ichthyology. Our understanding of fishes continues to evolve, as do the fishes themselves. In this text, we follow Nelson et al. (2016) and recognize four classes: Myxini, Petromyzontida, Chondrichthyes, and Osteichthyes (which includes the subclasses Sarcopterygii and Actinopterygii, Table 1.1).

Regardless of differences in higher taxonomic rankings, it is worth noting that in all interpretations of the phylogeny of major groups of vertebrates, the tetrapods (amphibians, reptiles, birds, and mammals, including humans) are a subgroup of the lobe-fins. This means that lungfishes and coelacanths are more closely related to you than they are to an Atlantic Bluefin Tuna or a Largemouth Bass. And all of the bony fishes are more closely related to you than they are to sharks, which are in a completely different class representing jawed vertebrates that have a skeleton of calcified cartilage instead of bone.

The Diversity of Fishes

There are well over 35,000 living species of fishes (Eschmeyer & Fong 2017), with the number approaching 36,000 as we complete this update of our text. (Among ichthyologists, the word "**fish**" is used to refer to a single individual or multiple individuals of a single species, whereas "**fishes**" is plural for more than one species, see Fig. 1.2). The great majority of these species are bony fishes with jaws, but there are also many jawless fishes (hagfishes and lampreys) and cartilaginous fishes with jaws (sharks, skates, rays, and chimaeras). Increased study of remote habitats, combined with modern genetic techniques, helps to continuously add new species to our lists – 7841 new species of fishes were described between 1998 and 2017 (Eschmeyer & Fong 2017). Consult the online *Catalog of Fishes* for updated information, including lists by major taxa.

One reason for the enormous diversity of fishes is the diversity of habitats in which fishes are successful. Water covers about 71% of the earth's surface, and in many places is very deep so the total volume of potential habitats is enormous. Fishes occupy nearly all aquatic habitats that have liquid water throughout the year, including thermal and alkaline springs, hypersaline lakes, sunless caves, anoxic swamps, temporary ponds, torrential rivers, wave-swept coasts, high-altitude and high-latitude environments, open expanses of large lakes

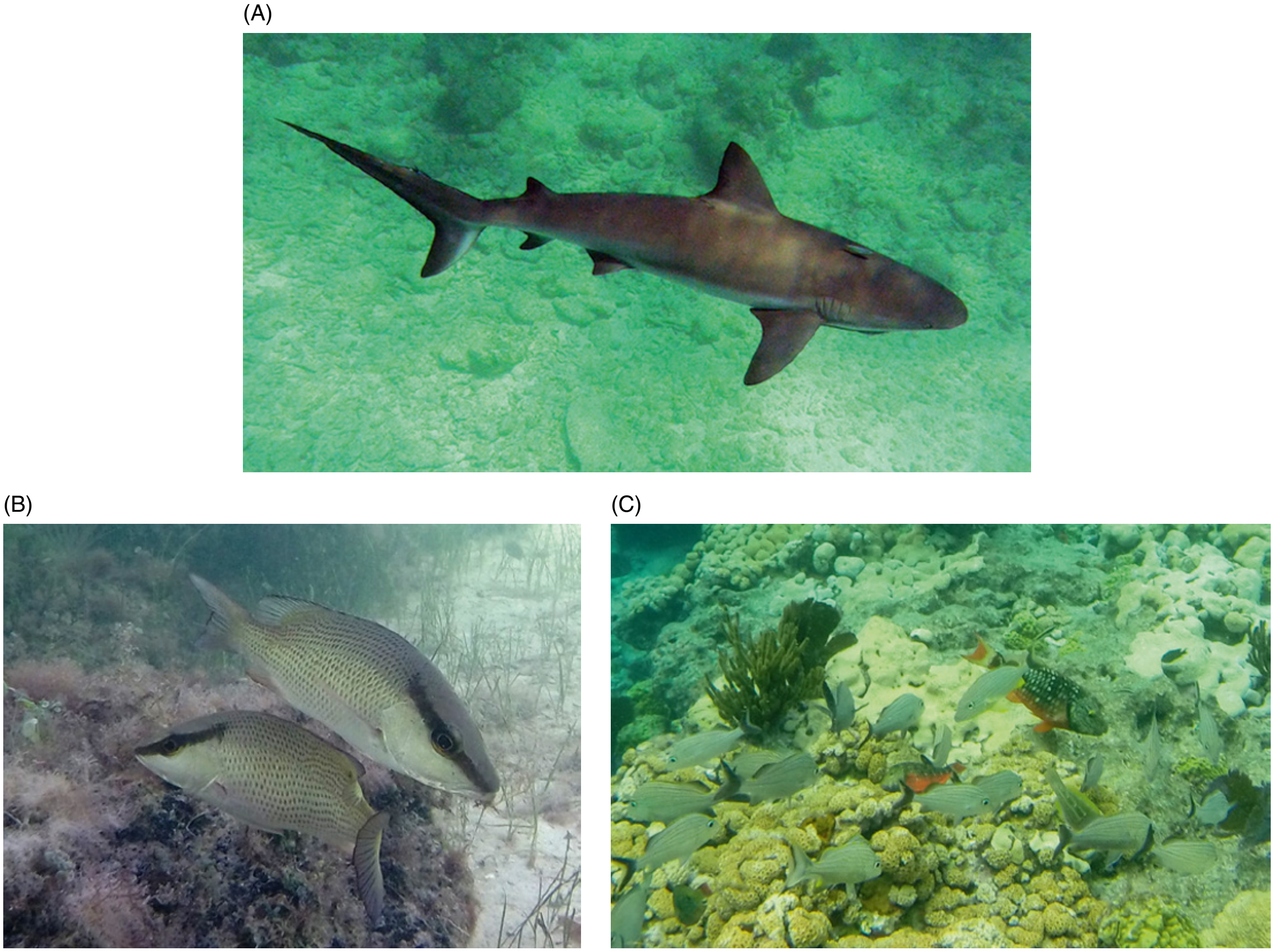


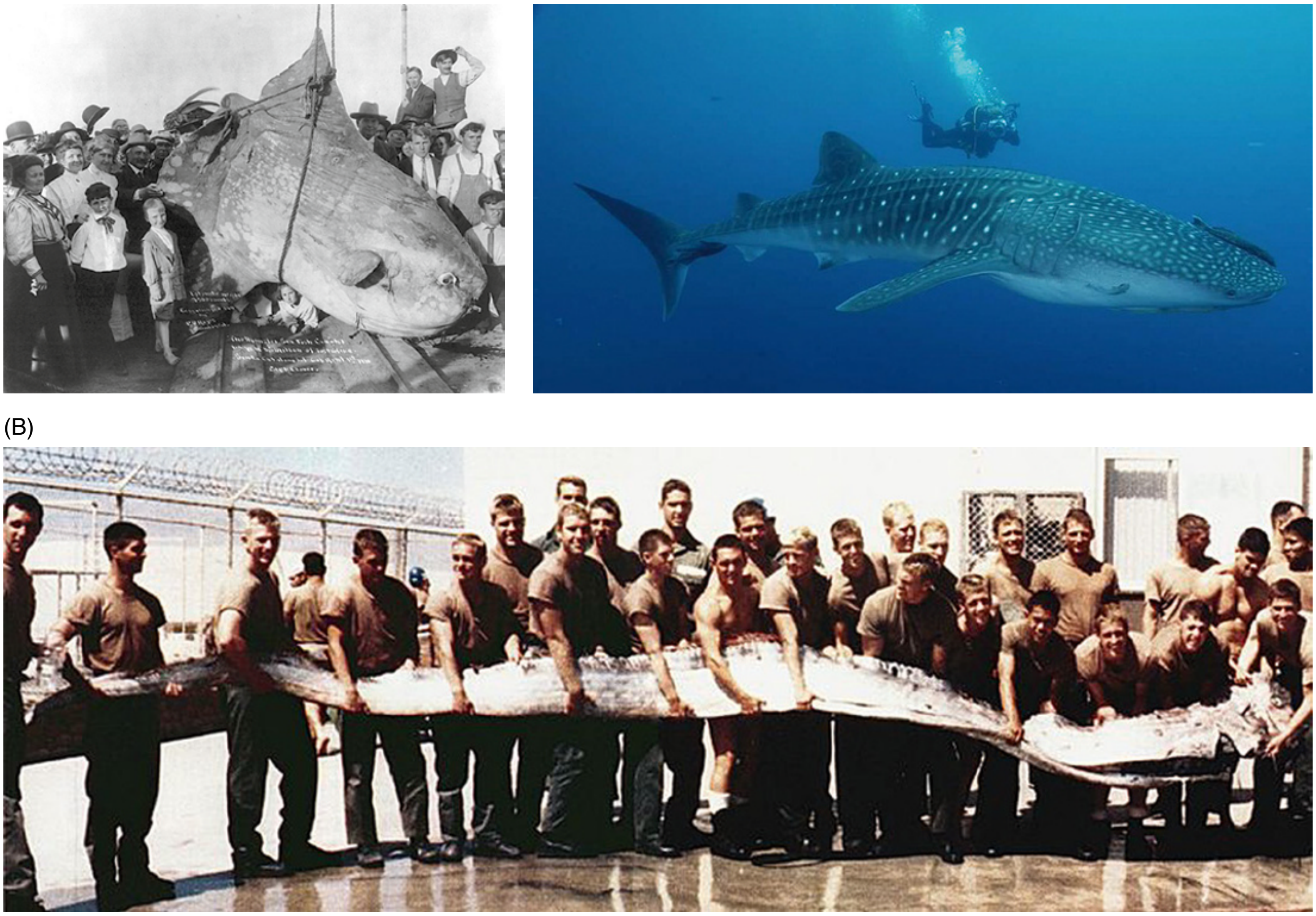
FIGURE 1.2 Fish versus fishes. By convention, "fish" refers to one or more individuals of a single species. "Fishes" is used when discussing more than one species, regardless of the number of individuals involved. (A) One fish, (B) two fish, (C) multiple fishes. (A) G. Helfman (Author); (B, C) D. Facey (Author).

and oceans, and deep ocean areas with no sunlight, low temperatures, and intense pressure. The altitudinal record is set by some nemacheiline river loaches that inhabit Tibetan hot springs at elevations of 5200 m; the record for unheated waters is Lake Titicaca in northern South America, where killifishes and pupfishes live at an altitude of 3812 m. The deepest living fishes are snailfishes and cusk-eels, which occur 8000 m down in the deep sea. When broken down by major habitats, a bit under 60% of fish species live in seawater, about 1% move between freshwater and the sea during their life cycles, and the rest live in freshwater. The highest diversities are found in the tropics. The Indo-West Pacific region known as the Coral Triangle (between Philippines, Indonesia, and New Guinea) has the highest marine diversity with an estimated 4000 species (Allen & Erdmann 2012), whereas South America, Africa, and Southeast Asia, in that order, contain the most species of freshwater fishes (Berra 2001; Lévêque et al. 2008).

Some fishes have adapted to life in water with little oxygen and can breathe air (see Chapter 3). There are even some species that make occasional excursions onto land (see Chapter 7). And we must not forget that over 530 million years of evolutionary adaptations have permitted some descendants of early lobe-finned fishes to become permanently terrestrial – but we call them tetrapods, reserving the term "fish" for those still mainly restricted to aquatic habitats.

Fishes show great variation in body length, ranging more than 1000-fold. The world's smallest fishes – and vertebrates – mature at around 7–8 mm and include the previously mentioned Indonesian minnow, *P. progenetica*, and two gobioids, *Trimmatom nanus* from the Indian Ocean and *Schindleria brevipinguis* from Australia's Great Barrier Reef. Parasitic males of a deep-sea anglerfish *Photocorynus spiniceps* mature at 6.2 mm, although females are 10 times that length. The world's longest cartilaginous fish is the Whale Shark *R. typus*, which can exceed 12 m, whereas the longest bony fish is the 8 m long (or longer) Oarfish *Regalecus glesne*. Body masses top out at 34,000 kg for whale sharks and 2300 kg for the Ocean Sunfish *Mola mola* (Fig. 1.3). Diversity in form includes relatively fishlike shapes such as minnows, trouts, perches, basses, and tunas, but also such unexpected shapes as boxlike trunkfishes, elongate eels

(A) (C)



(B)

FIGURE 1.3 Some very large fishes. (A) The Ocean Sunfish (*Mola mola*) is estimated to be the heaviest of the bony fishes, with some estimated to weigh up to over 2000 kg . The Library of Congress / Public Domain. (B) The Oarfish (*Regalecus glesne*) is probably the longest bony fish in the world (can exceed 10 m) and is responsible for many reports of sea monsters . Photo by Wm. Leo Smith / Wikimedia Commons / Public Domain. (C) The Whale Shark (*Rhincodon typus*), a filter-feeding cartilaginous fish that can exceed 12 m and 21 tons, is the largest of the living fishes on the planet. Crystaldive / Wikimedia Commons / CC BY-SA 4.0.

and catfishes, globose lumpsuckers and frogfishes, rectangular ocean sunfishes, question-mark-shaped seahorses, and flattened and circular flatfishes and batfishes, in addition to the exceptionally bizarre fishes of the deep sea.

Superlative Fishes

A large part of ichthyology's fascination is the spectacular diversity of fishes. As a few examples:

- Coelacanths, an offshoot of the lineage that gave rise to the amphibians (and subsequently to all tetrapods), were thought to have died out with the dinosaurs at the end of the Cretaceous Period, about 65 million years ago. However, in 1938, fishers in South Africa trawled up a live Coelacanth. This fortuitous capture of a "living fossil" not only rekindled debates about the evolution of vertebrates but underscored the international and political nature of conservation efforts (see Chapter 13).
- Lungfishes can live in a state of dry "suspended animation" for up to 4 years, burying themselves in the mud and becoming dormant when their ponds dry up and reviving quickly when immersed in water (see Chapters 3, 13).
- Some Antarctic fishes don't freeze because their blood contains antifreeze proteins that prevent ice crystal growth. Some Antarctic fishes have no hemoglobin, and thus have clear blood (see Chapter 10).
- Deep-sea fishes include many forms that can swallow prey larger than themselves. Some deep-sea anglerfishes are characterized by females that are 10 times larger than males, the males existing as small parasites permanently fused to the side of the female, living off her bloodstream (see Chapter 10).
- Fishes grow throughout their lives, changing their ecological role several times. In some fishes, differences between larvae and adults are so pronounced that many larvae were originally thought to be entirely different species (see Chapter 9).
- Fishes have maximum life spans of as little as 10 weeks (African killifishes and Great Barrier Reef pygmy gobies) and as long as 400 years (Greenland shark; Neilsen et al. 2016). Several teleost fishes can live past 100 years (Randall & Delbeek 2009). Some short-lived species are annuals, surviving drought as eggs that hatch with the advent of rains. Longer-lived species may not begin reproducing until they are 20 or more years old (see Chapter 8).
- Gender in many fishes is flexible. Some species are simultaneously male and female, whereas others change from male to female or from female to male (see Chapter 8). Fishes, therefore, are the original genderfluid vertebrates and demonstrate that nature includes a broad range of gender identities.
- Fishes engage in parental care that ranges from simple nest guarding to mouth brooding to the production of external or internal body substances upon which young feed. Many sharks have a placental structure as complex as any found in mammals. Egg-laying fishes may construct nests by themselves, whereas some species deposit eggs in the siphon of living clams, on the undersides of leaves of terrestrial plants, or in the nests of other fishes (see Chapter 17).
- Many fishes can detect biologically meaningful, minute quantities of electricity, which they use to navigate and sense prey, competitors, or predators. Some groups can produce an electrical field and detect disturbances to the field, whereas others produce large high-voltage pulses to deter predators or stun prey (see Chapters 4, 16).
- Some fishes can produce light; this ability has evolved independently in different lineages and can be produced either by the fish itself or by symbiotic bacteria (see Chapter 10).
- Although the blood of most fishes is the same temperature as the water surrounding them, some pelagic fishes maintain body temperatures warmer than their surroundings and have circulatory systems that use countercurrent flow to conserve metabolic heat (see Chapter 7).
- Predatory tactics include attracting prey with lures made of modified body parts or by feigning death. Fishes include specialists that feed on ectoparasites, feces, blood, fins, scales, young, and eyes of other fishes (see Chapter 16).
- Fishes can erect spines or inflate themselves with water to deter predators. In turn, the ligamentous and levering arrangement of mouth bones allows some fishes to increase mouth volume by as much as 40-fold (see Chapters 3, 16).
- Some of the most dramatic demonstrations of evolution result from studies of fishes. Both natural and sexual selection have been experimentally manipulated in Guppy, swordtails, and sticklebacks, among others. These investigations show how competition, predation, and mate choice lead to adaptive alterations in body shape and armor, body color, vision, and feeding habits and locales (see Chapters 16, 20). Fishing has also proven to be a powerful evolutionary force, affecting the ages and sizes at which fish reproduce, body shape, and behavior (see Chapter 22).

Fishes have become increasingly important as model organisms for vertebrate research. Because of small size, ease of care, rapid growth and short generation times, and larval anatomical features, such species as Medaka, *Oryzias latipes*, and Zebrafish, *Danio rerio*, are used in studies of toxicology, pharmacology, neurobiology, developmental biology, cancer and other medical research, aging, genomics, and recombinant DNA methodology (e.g. Shima & Mitani 2004; Collins et al. 2010; Chang et al. 2013).