# INTRODUCTION

In nearly every body of water around the world, the most abundant vertebrate is a fish. From the deepest parts of the ocean to high alpine streams, fishes live and reproduce, sometimes in places where no other vertebrates can survive. Whether peering out from a submarine while conducting deep-sea research, or stopping for a drink of water during a hike in the mountains, explorers, scientists, and naturalists find fishes.

With well over 30,000 species, fishes account for more than half of the total extant vertebrate diversity on Earth—in other words, there are more living species of fishes than of amphibians, turtles, lizards, birds, and mammals combined. Not only are fishes diverse in number of their species, but they are diverse in the habitats in which they live, the foods that they eat, the ways in which they reproduce, communicate, and interact with their environment, and the behaviors that they exhibit. Fishes can also be extremely abundant: the most abundant vertebrates on the planet are the small bristlemouth fishes (Gonostomatidae) that are common throughout the vast open ocean. In some cases abundant fishes such as cods, tunas, salmons, herrings, and anchovies support massive fisheries that feed hundreds of millions of people. By supporting coastal communities and societies, these fisheries (and the fishes they target) have helped shape human history, becoming the foundation for coastal economies and an engine for global exploration and expansion.

## WHAT IS A FISH?

Humans use the term "fish" to refer to several groups of vertebrates that do not have a clear set of diagnostic characteristics unique to them. "Fishes" is not a monophyletic group (i.e., a group made up of an ancestor and all of its descendants) because the tetrapods, which share a common vertebrate ancestor with fishes, are excluded. Thus "fish" typically refers to any vertebrate that is *not* a tetrapod. Fishes (usually) live in water, (usually) obtain oxygen through gills, are (usually) ectothermic (i.e., cold blooded), and (usually) have limbs in the form of fins. Naturally, there are exceptions to each of these rules. Some fishes spend time

out of the water, some breathe air, some are endothermic (i.e., warm blooded), and some have no limbs at all.

While there is no clear set of characteristics that distinguishes all fishes from all other vertebrates, there are four groups that collectively make up the fishes. The extant fishes include the jawless fishes (Agnatha), the cartilaginous fishes (Chondrichthyes), the ray-finned fishes (Actinopterygii), and a small portion of the lobe-finned fishes (Sarcopterygii). Of the extant fishes, the ray-finned fishes are by far the most speciose, accounting for more than 30,000 species, the cartilaginous fishes include about 1,200 species, and the jawless fishes include fewer than 100 species. Only eight species of lobe-finned fishes, two species of coelacanths, and six species of lungfishes are considered by most to be "fishes," while the remaining 28,000 or more sarcopterygian species are tetrapods.

## WHY THIS BOOK?

This book is intended to be a reference text for students and lovers of fishes to assist them in learning the morphology, diagnostic characters, and basic ecology of fishes. It started as a guide to the systematics of fishes, compiled by the senior author for use in ichthyology courses at Scripps Institution of Oceanography and the University of Arizona. It will serve that purpose, but will also provide an entry into the world of fishes for anyone interested in exploring their diversity. To our knowledge, no comparable volume exists. While numerous excellent regional guides to fishes are available (e.g., Eschmeyer and Herald, 1983; Hart, 1973; McEachran and Fechhelm, 1998, 2005; Page and Burr, 2011; Quéro et al., 1990; Robertson and Allen, 2008; Robins and Ray, 1986; Scott and Crossman, 1973; Scott and Scott, 1988; TeeVan et al., 1948–1989; Whitehead et al., 1986), these lack a global perspective. *Fishes of the World* (Nelson, 2006) covers the entire diversity of fishes, including all of the 515 families, but the scope of that impressive work prohibits the illustration of specimens and key characteristics of various groups. Our goal is to give an overview of the global diversity of fishes, together with more detailed accounts and illustrations of the common groups of fishes, as well as those important to humans and those widely discussed in the ichthyological literature.

The general anatomy of fishes is briefly covered, focusing on external features that help to distinguish major groups. These include external body regions, fin types and positions, body shapes, mouth positions, and selected skeletal features. We then provide accounts of approximately 180 groups of fishes, including all currently recognized orders of fishes and a variety of common and diverse families. We start with the jawless fishes (Agnatha) and progress through the cartilaginous fishes (Chondrichthyes), the lobe-finned fishes (Sarcopterygii), and the ray-finned fishes (Actinopterygii).

## SYSTEMATICS OF FISHES

Ichthyologists have been interested in the evolutionary history of fishes for hundreds of years, and classification systems have attempted to capture that history in a hierarchical (Linnaean) system of names. It remains difficult to implement a truly monophyletic classification, one that recognizes only monophyletic groups, for any large group such as

fishes, given both the complexity of the tree of life and our continuing uncertainty as to its form. Traditional classifications recognize several hierarchical levels, but students should keep in mind that a particular level in a classification, such as a family, has little meaning other than that it ideally includes all descendants of a common ancestor (i.e., it recognizes a monophyletic group) that are included in a higher level of the classification. For example, although ichthyologists have designated the two species of fangtooths and the 1,700 species of gobies as the families Anoplogastridae and Gobiidae, respectively, these groups clearly differ greatly in diversity, age, and ecological breadth.

In organizing this guide, we have had to face a host of perplexing and often conflicting hypotheses of fish relationships. For chondrichthyan fishes we have elected to follow a somewhat traditional classification of their diversity based primarily on Nelson (2006). Our organization of the ray-finned fishes largely follows the classification provided in Helfman and Collette (2011), which is, in turn, based largely on Nelson (2006), as modified by Wiley and Johnson (2010). Within the Percomorpha, a large group of ray-finned fishes whose relationships remain poorly understood, we have followed the taxonomic levels of Wiley and Johnson (2010) rather than those of Helfman and Collette (2011). In some cases we have modified these classification schemes based on well corroborated studies. However, we have not implemented some recent and radically different classification schemes (e.g., Betancur et al., 2013; Near et al., 2013). We find it difficult and in fact unnecessary to implement certain changes in percomorph classification at this time, and instead treat its hypothesized members in a more or less traditional manner.

Until very recently, our understanding of fish relationships was based almost exclusively on morphological features. With the advent of modern molecular methods, the study of the evolutionary relationships of fishes has grown exponentially, with new studies of various groups appearing at a nearly overwhelming pace. In many cases, the hypotheses generated by these studies conflict with long-held concepts of fish relationships, some to small degrees, others to very great degrees. Too often, these molecular-based phylogenetic hypotheses are not supported by morphology, as the number of molecular-based hypotheses have far outpaced the ability of morphologists to fully explore them (Hastings, 2011). Students of fishes should remember that these published phylogenies are merely hypotheses of relationships, and are subject to testing and refuting. As a consequence of this burgeoning of new ideas about fish relationships, the time is ripe for a morphological renaissance in ichthyology. Emerging molecular hypotheses provide a wealth of testable hypotheses for students with knowledge and expertise in morphology as we continue to refine our understanding of the fish tree of life.

## ABOUT THIS BOOK

While ichthyology students often learn regional fish faunas through a series of local field trips, appreciation of the true diversity of fishes is more readily gained by a survey of a wide diversity of preserved specimens from a variety of habitats and from different geographic regions. Consequently our approach in this guide has been to include images of represen-

tative preserved specimens, labeled with the most important and easily visible diagnostic characters for the group to which they belong. For several groups, we provide images of more than one species, and in some cases, additional anatomical details to document variation within the group. Each photograph in this book is of a specimen archived in a natural history collection. Because our illustrations are of museum specimens, some are damaged, with broken fins or twisted bodies. This is especially true of many fishes of the deep-sea groups, as they are fragile and frequently damaged by nets during collection. In addition, the preservation methods used by fish collections (fixation in 10% formalin and transfer to alcohol for long-term storage) do not retain the bright colors typical of many living fishes. However, a vast number of images of living and freshly caught fishes are available on the internet, and students are encouraged to use one of the common search engines to locate additional images of groups of fishes of particular interest.

Almost all of the images in this guide are of specimens archived at the Scripps Institution of Oceanography Marine Vertebrate Collection (SIO). Details on the collecting locality and other information for each of these specimens are available online at https://scripps.ucsd.edu/collections/mv/. The Marine Vertebrate Collection is an extraordinary resource with over 2,000,000 specimens of fishes from all over the world. This inventory, supplemented by a few specimens from other collections, permitted us to provide coverage of all 78 currently recognized orders of fishes, as well as an additional 92 families of diverse, common, or otherwise interesting groups. While we have a slight bias towards groups found in North American waters, we also illustrate groups from other areas where possible. We are indebted to fish collections at other institutions for a few of the illustrated specimens. These include the Academy of Natural Sciences of Philadelphia (ANSP), California Academy of Sciences (CAS), Cornell University (CU), Tulane University (TU), the University of Arizona (UAZ), and the University of Michigan (UMMZ), as well as our colleague Dave Ebert (DE).

Each primary account also includes an estimate of the group's diversity based on Eschmeyer and Fong (2013), the approximate distribution of the group (the continents or oceans where they are found), the habitats in which they normally occur (freshwater, coastal marine, oceanic zone), and the portion of the water column where they typically reside (pelagic, neritic, demersal, or benthic). The Remarks section includes information such as the phylogenetic relationships of the group, their reproductive strategies and food preferences, their importance to humans, and in some cases the conservation status of the group. Additional details on the biology of most fishes can be found in the online resource Fishbase (Froese and Pauly, 2000; www.fishbase.org/home.htm). Finally, each account includes a list of some of the most important guides for identification, classic references on the systematics and biology of the group, and recent studies of their phylogeny. We owe a deep debt of gratitude to the late Joseph S. Nelson and his compendium, *Fishes of the World,* now in its fourth edition (2006). This work proved especially useful in compiling key characters for the groups of fishes represented herein. We also benefitted greatly from several classic references on fishes, too numerous to mention here, as well as a number of online resources, especially Eschmeyer's Catalog of Fishes (Eschmeyer, 2013; http://researcharchive.calacademy.org/

research/Ichthyology/catalog/fishcatmain.asp). Additional details on the biology of most fishes can be found in standard ichthyology texts (e.g., Bond, 1996; Bone and Moore, 2008; Helfman et al., 2009; Moyle and Cech, 2004).

Fishes are fascinating animals and have held our interest for most of our lives. We hope that this general survey of the most speciose group of vertebrates on the planet will provide others a greater appreciation of the amazing diversity of fishes, stimulating interest in them and all things ichthyological.

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