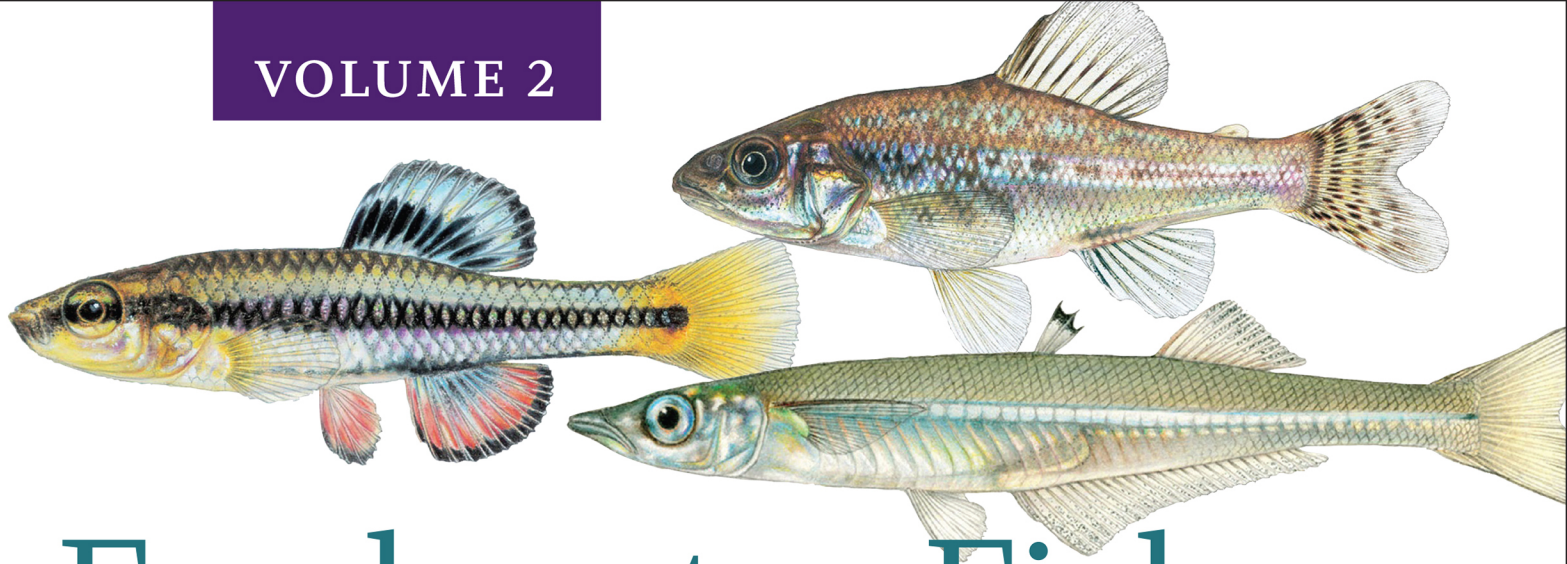
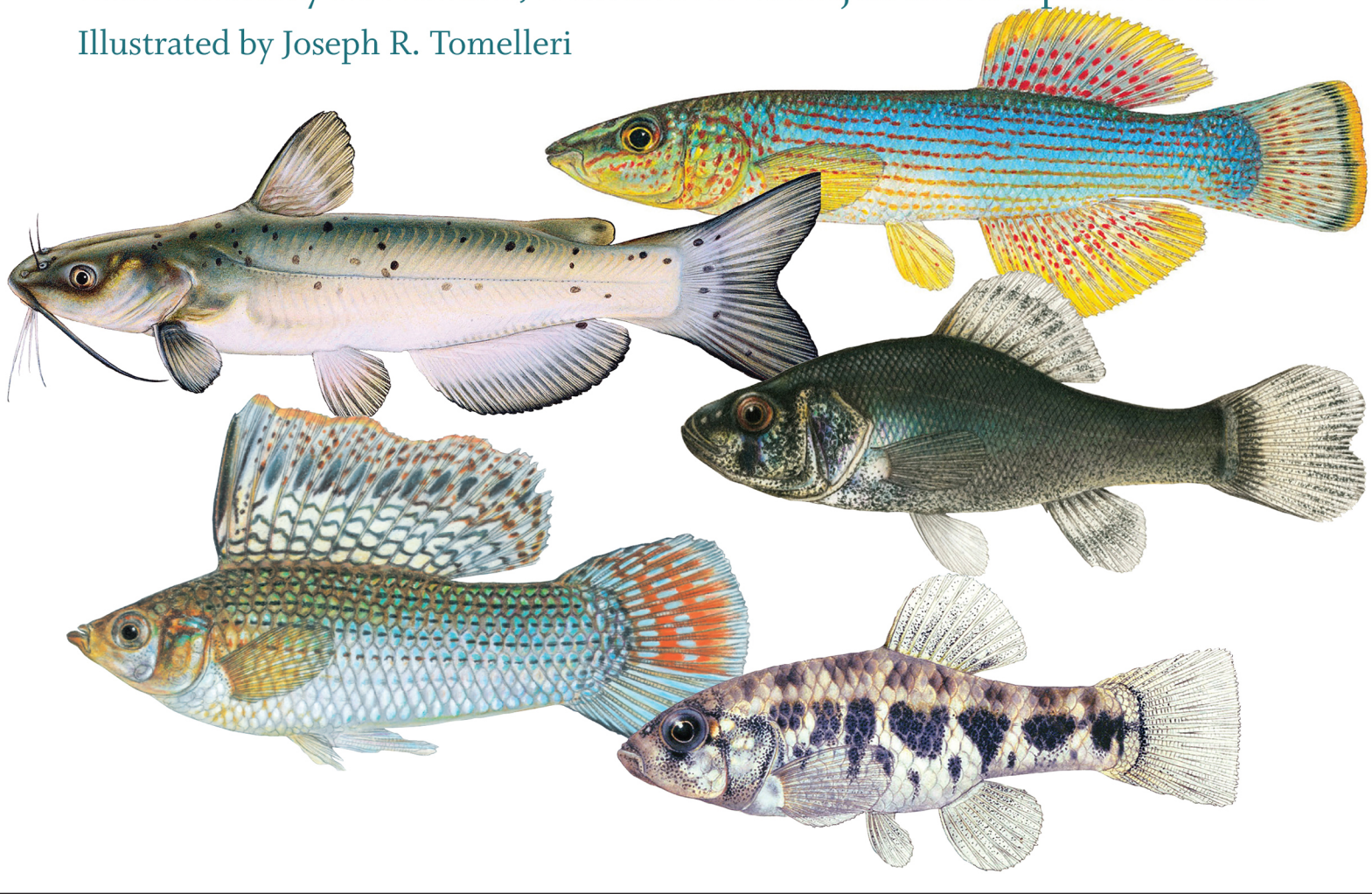
VOLUME 2



Freshwater Fishes of North America

CHARACIDAE TO POECILIIDAE

Edited by Melvin L. Warren, Jr., and Brooks M. Burr
with Anthony A. Echelle, Bernard R. Kuhajda and Stephen T. Ross
Illustrated by Joseph R. Tomelleri



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Robert C. Cashner (1941–2018)
Friend, teacher, mentor, leader,
and
stellar freshwater ichthyologist.
We miss you, Bob.

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Preface

The North American freshwater fish fauna comprises >1,300 native species in about 50 families. It is the most thoroughly studied and largest temperate fish fauna (Miller et al. 2005; Page & Burr 2011) in the world. In comparison, an analysis and compendium of European freshwater fishes included 546 native species in about 24 families (Kottelat & Freyhof 2007); Europe is about one-third the land area of North America. Australia has nearly 300 freshwater fishes in 35 families (Allen 1989; Allen et al. 2002) in a land area about that of the United States (minus Alaska). This number includes many marine species that enter fresh water, and highly unusual freshwater fish lineages occur there (e.g., Salamanderfish, *Lepidogalaxias salamandroides*; Australian Lungfish, *Neoceratodus forsteri*; and Nurseryfish, *Kurtus gulliveri*). The only other temperate fish fauna that could rival North America is Asia (Lévêque et al. 2008), but reliable information on this vast area and its fishes remains poorly understood by scientists in the New World. Estimates for the country of China range from 920 to 1,010 native species (Kang et al. 2014; M. Kottelat pers. comm.). Unsurprisingly, as for many plant and animal groups, the tropical regions of the world harbor freshwater fish faunas several times larger than those of temperate regions (Lundberg et al. 2000; Agostinho et al. 2005; Berra 2007).

In the mid-1970s, knowledge of North American freshwater fishes was confined to a few specialists, but even so for many species (and families) little was available on natural history or ecology. In 1980 a landmark volume was published that used spot distribution maps to illustrate the ranges of all freshwater fish species in the United States and Canada (Lee et al. 1980 et seq.). That volume made available to the lay public as well as specialists a level of knowledge of the North American freshwater fish fauna theretofore unknown. Shortly thereafter a physician from Forsythe, Missouri, combined his hobby of scuba diving and snorkeling with photography and revealed—new even to specialists—the incredible colors of the North American native fish fauna, especially in their brightest breeding condition, as well as some of their unique and fascinating natural histories. William N. Roston eventually traveled the continent looking for clear water and fish to photograph in their natural environment (never in aquaria). A number of his photographs are used in this volume.

From the 1970s through the 1990s numerous books focused on fish faunas of individual states (e.g., Alabama, Arkansas, California, Idaho, Illinois, Kansas, Mississippi, Missouri, New Mexico, Ohio, Tennessee, Virginia, Washington, West Virginia, and Wisconsin) as well as Canada, making even more detail on fishes available to the public. These works allowed for the first complete identification guide to all freshwater fishes in the United States and Canada (Page & Burr 1991, revised 2011). Nevertheless, it was not until the *Freshwater Fishes of Mexico* (Miller et al. 2005, 2009) was published that it was possible for us to consider editing this three-volume work on the natural history, ecology, and conservation of North American freshwater fishes. We are indebted to a large community of ichthyologists, fisheries biologists, and other workers in related fields (e.g., genetics, physiology, behavior, ecology) who have investigated the details of the lives of fishes in such a way that much technical information can now be synthesized in one place and again made available to the public and other specialists.

Even though our overarching goal was to synthesize as much information as possible on North American freshwater

fishes, the job of gathering information is far from complete. In editing this work and writing synthesis chapters of our own, we were struck at once by the incredible natural history and taxonomic diversity among our native freshwater fishes, but also by the large and critical information gaps that remain. Unfortunately, for many species (and nearly entire families), the syntheses presented here are (or are close to being) obituaries (e.g., Miller et al. 1989; Minckley & Deacon 1991; Warren et al. 2000; Brouder & Scheurer 2007; Jelks et al. 2008; Burkhead 2012). For many species and groups, the biological information needed to help recover them, to slow population declines, or to prevent extinction is simply unavailable. That said, the most critical component of conserving North American freshwater fishes is the prevention of habitat loss and degradation by humans, not the lack of biological information. Fishes in this fauna have an incredible tenacity for life, whether we completely understand their biology or not, but we as coinhabitants of the North American continent need to provide them the opportunity to endure. We hope that this work helps stem the high rates of population decline and extinction being experienced across the North American fish fauna. We also hope this work stimulates a whole new generation of ichthyologists and fisheries researchers to further expand our knowledge and appreciation of the natural history, ecology, and conservation of the great freshwater fish fauna of North America.

AREA AND BREADTH OF COVERAGE

The area of coverage encompasses fishes in fresh waters of North America, including Canada, the coterminous United States, and Mexico, south generally to the Isthmus of Tehuantepec. For some families, authors extended the southern boundary to include fishes of the Yucatan Peninsula region. Within the covered area, all native North American fishes, emphasizing the level of genus, are included that primarily inhabit and reproduce in fresh water and that primarily inhabit marine or estuarine systems but are frequent or even permanent components of some freshwater fish assemblages. Some primarily marine fishes (across 11 families) are included because they are naturally established and reproduce in fresh waters (e.g., Atlantic Needlefish, *Strongylura marina*, Collette & Walsh, this volume). Others are included because young and adults penetrate deeply into freshwater systems and reproduce or are suspected of reproducing in fresh waters (e.g., Hogchoker, *Trinectes maculatus*), and still others simply occur with such high frequency in freshwater habitats that they likely are important functionally in those ecosystems (e.g., Striped Mullet, *Mugil cephalus*, Powers, this volume). Admittedly, some degree of arbitrariness was unavoidable in the inclusion or exclusion of marine species in a work about freshwater fishes, but the arbitrariness reflects a biologically real gray area among fishes at the interface of freshwater and saltwater systems (e.g., coastal Largemouth Bass, *Micropterus salmoides*; Gulf Pipefish, *Syngnathus scovelli*; Atlantic Needlefish, *Strongylura marina*, Collette & Walsh, this volume).

Each taxonomic chapter focuses on a family or in some cases two families of North American freshwater fishes with emphasis on the natural history, biology, evolution, and conservation of each genus in the family. Because of the timing of preparation of the volumes, the sequence of the families generally follows the arrangement of Page et al. (2013), Nelson (2006), and Nelson et al. (2016), but we acknowledge the phylogeny of Ray-finned Fishes and Spiny-rayed Fishes by Near et al. (2012b, 2013) and the expansion of that work by Betancur-R. et al. (2013ab, 2017) as the most comprehensive and defensible to date and present these sequences herein for North American fishes we cover (Tables P.1 and P.2). In Volume 1, taxonomic chapters covered the Lampreys (Petromyzontidae) through the Suckers (Catostomidae) with one exception. Taxonomic chapters in Volume 2 cover the Characins (Characidae) through the Livebearers (Poecilidae) with one exception, and in Volume 3, the Sticklebacks through the American Soles (Achiriidae). Because of extenuating circumstances, the chapters on Herrings (Clupeidae; originally slated for Volume 1) and Trouts and Salmons (Salmonidae; originally slated for Volume 2) will appear in Volume 3.

METHODS

Sources. We encouraged authors to use only peer-reviewed publications in this work, but in many cases, information was only available in unpublished dissertations, theses, or even reports. We clearly indicate those unpublished sources as such in the literature cited.

Scientific and common names. For scientific and common names of taxa (e.g., species, genera, families, orders), we used Nelson (2006), Page et al. (2013), Nelson et al. (2016), and occasionally FishBase (Froese & Pauly 2019) as guides. Our order of presentation of families generally follows that of Nelson (2006), Page et al. (2013), and Nelson et al. (2016), but as noted previously, Near et al. (2012b, 2013) presented a phylogeny of Ray-finned Fishes (Actinopterygii) and Spiny-rayed Fishes (Acanthomorpha) based on 9–10 nuclear genes and 579 fish species. Using

Table P.1. Phylogenetic sequence, clade names, orders, and family names of Ray-finned Fishes (Actinopterygii) and Spiny-rayed Fishes (Acanthopterygii) represented in North American fresh waters. The sequence follows the phylogenetic trees recovered from analysis of 9–10 nuclear genes and 579 fish species (modified from Near et al. 2012b, 2013). The designation at the ordinal level of incerti ordis indicates the broader relationships of the family are to date undefined.

Clade Name	Order and Family (common name)
Actinopterygii	
Actinopteri	
	Acipenseriformes
	Acipenseridae (Sturgeons)
	Polyodontidae (Paddlefishes)
Neopterygii	
Holostei	
	Amiiformes
	Amiidae (Bowfins)
	Lepisosteiformes
	Lepisosteidae (Gars)
Teleostei	
Elopomorpha	
	Anguilliformes
	Anguillidae (Freshwater Eels)
Osteoglossocephala	
Osteoglossomorpha	
	Hiodontiformes
	Hiodontidae (Mooneyes)
Clupeocephala	
Otocephala	
	Clupeiformes
	Clupeidae (Herrings)
	Engraulidae (Anchovies)
Ostariophysi	
Otophysi	
	Cypriniformes
	Catostomidae (Suckers)
	Cyprinidae (Carps and Minnows)
	Characiformes
	Characidae (Characins)
	Siluriformes
	Ariidae (Sea Catfishes)
	Heptapteridae (Seven-finned Catfishes)
	Ictaluridae (North American Catfishes)
Euteleostei	
	Salmoniformes
	Salmonidae (Trouts and Salmons)
	Esociformes
	Esocidae (Pikes and Mudminnows)
	Osmeriformes
	Osmeridae (Smelts)
Neoteleostei	
Eurypterygii	
Ctenosquamata	
Acanthomorpha	
	Percopsiformes
	Amblyopsidae (Cavefishes)
	Aphredoderidae (Pirate Perches)
	Percopsidae (Trout-Perches)
	Gadiformes
	Gadidae (Cods)

(*continued*)

Table P.1, continued

Clade Name		Order and Family (common name)
	Acanthopterygii	
	Percomorpha	
		Syngnathiformes
		Syngnathidae (Pipefishes and Seahorses)
		Gobiiformes
		Gobiidae (Gobies)
		Eleotridae (Sleepers)
		Synbranchiformes
		Synbranchidae (Swamp Eels)
		Pleuronectiformes
		Achiridae (American Soles)
		Paralichthyidae (Sand Flounders)
		Pleuronectidae (Righteye Flounders)
	Ovalentaria	
		Atheriniformes
		Atherinopsidae (New World Silversides)
		Beloniformes
		Belonidae (Needlefishes)
		Hemiramphidae (Halfbeaks)
		Cyprinodontiformes
		Rivulidae (New World Rivulines)
		Goodeidae (Goodeids)
		Profundulidae (Middle American Killifishes)
		Cyprinodontidae (Pupfishes)
		Fundulidae (Topminnows)
		Poeciliidae (Livebearers)
		incerti ordinis
		Cichlidae (Cichlids and Tilapias)
		incerti ordinis
		Mugilidae (Mullets)
		Embiotocidae (Surfperches)
		incerti ordinis
		Gobiesocidae (Clingfishes)
	Unnamed clade	
		Centrarchiformes
		Centrarchidae (Sunfishes)
		Perciformes
		Percidae (Perches)
		Cottidae (Sculpins)
		Gasterosteidae (Sticklebacks)
	Unnamed clade	
		incerti ordinis
		Moronidae (Temperate Basses)
	Unnamed clade	incerti ordinis
		Sciaenidae (Drums)

and expanding and updating the Near et al. (2013) data, Betancur-R. et al. (2013ab, 2017) analyzed relationships of nearly 2,000 bony fish taxa using multi-locus trees. The results clearly indicate convergence on a well-resolved phylogeny for most fishes. We accept those works as definitive (Tables P.1 and P.2) but did not follow that phylogenetic sequence because of timing of volume preparation. Authors give the complete scientific and common name in the chapters on first mention of the species and thereafter use either or both. Authors were free to deviate from these primary sources for common and scientific names for newly described species and higher taxa or because of differing or new systematic evidence (or taxonomic opinion) as well as for clarity. We capitalized the common names, if available, of all species, families, orders, and higher taxonomic categories (e.g., Ray-finned Fishes for

Table P.2. Phylogenetic classification of Ray-finned Fishes (Actinopterygii) represented in North American fresh waters. The sequence follows the phylogenetic tree recovered from analysis of multiple locus DNA sequence data for nearly 2,000 fish taxa (Betancur-R. et al. 2013ab, 2017). The designation at the ordinal level of incerti ordinis indicates the broader relationships of the family are to date undefined.

Class Subclass Infraclass Megacohort	Superorder	Order	Family (common name)
Actinopteri			
Chondrostei		Acipenseriformes	Acipenseridae (Sturgeons)
Neopterygii			Polyodontidae (Paddlefishes)
Holostei		Amiiformes	Amiidae (Bowfins)
		Lepisosteiformes	Lepisosteidae (Gars)
Teleostei			
Elopocephali		Anguilliformes	Anguillidae (Freshwater Eels)
Osteoglossocephalai		Hiodontiformes	Hiodontidae (Mooneyes)
		Clupeiformes	Clupeidae (Herrings)
			Engraulidae (Anchovies)
	Cypriniphysae	Cypriniformes	Catostomidae (Suckers)
			Cyprinidae (Carps and Minnows)
		Characiformes	Characidae (Characins)
	Siluriphysae	Siluriformes	Ariidae (Sea Catfishes)
			Heptapteridae (Seven-finned Catfishes)
			Ictaluridae (North American Catfishes)
		Salmoniformes	Salmonidae (Trouts and Salmons)
		Esociformes	Esocidae (Pikes)
			Umbridae (Mudminnows)
		Osmeriformes	Osmeridae (Smelts)
		Percopsiformes	Amblyopsidae (Cavefishes)
			Aphredoderidae (Pirate Perches)
			Percopsidae (Trout-perches)
		Gadiformes	Gadidae (Cods and Cuskfishes)
		Gobiiformes	Eleotridae (Sleepers)
			Gobiidae (Gobies)
		Syngnathiformes	Syngnathidae (Pipefishes and Seahorses)
		Synbranchiformes	Synbranchidae (Swamp Eels)
		Pleuronectiformes	Achiridae (American Soles)
			Paralichthyidae (Sand Flounders)
			Pleuronectidae (Righteye Flounders)
		incerti ordinis	Embiotocidae (Surfperches)
	Atherinomorphae	Atheriniformes	Atherinopsidae (New World Silversides)
	Cichlomorphae	Cichliformes	Cichlidae (Cichlids and Tilapias)
	Atherinomorphae	Beloniformes	Belonidae (Needlefishes)
			Hemiramphidae (Halfbeaks)
	Atherinomorphae	Cyprinodontiformes	Cyprinodontidae (Pupfishes)
			Fundulidae (Topminnows)
			Poeciliidae (Livebearers)
			Goodeidae (Goodeids)
			Profundulidae (Middle American Killifishes)
			"Rivulidae" (New World Rivulines)
	Mugilomorphae	Mugiliformes	Mugilidae (Mullets)
	Blenniimorphae	Gobiesociformes	Gobiesocidae (Clingfishes)
		incerti ordinis	Moronidae (Temperate Basses)
		incerti ordinis	Sciaendae (Drums)
		Centrarchiformes	Centrarchidae (Sunfishes)
			Elassomatidae (Pygmy Sunfishes)
		Perciformes	Percidae (Perches)
			Gasterosteidae (Sticklebacks)
			Cottidae (Sculpins)

Actinopterygii, Catfishes for Siluriformes, North American Catfishes for Ictaluridae, Channel Catfish for *Ictalurus punctatus*) (see Nelson et al. 2002). We encouraged authors to use the common name in lieu of scientific names after first mention because common names are descriptive and colorful and are increasingly more stable through time than scientific names. We did not capitalize colloquial, nonstandard, or semi-technical, but informal, common names for groups of fish (e.g., bass, blackbass, brook lamprey, buffalo, bullhead, carp, carpsucker, chub, crappie, dace, darter, jumprock, killifish, madtom, minnow, molly, mosquitofish, pickerel, pikeminnow, piranha, redhorse, salmon, shad, shiner, splitfin, trout).

Fossil taxa. We indicated fossil taxa by a dagger (†) placed before the genus name. In general, we followed Walker et al. (2012) for designation of geologic time (period, epoch, age) in millions of years ago (mya), but the original references should be consulted to determine how the geological formations were dated or how fossil dates were estimated.

Length abbreviations and museum acronyms. We abbreviated standard length (SL), total length (TL), and fork length (FL) throughout. Museum acronyms followed Sabaj Pérez (2016).

Distributional maps. We provided to authors shaded maps for each genus showing the estimated native freshwater range (unless indicated otherwise) of the genus in North America. For genera with expansive marine ranges, the freshwater and near-shore marine range is given, not the entire marine range. Although we took care to make the maps as accurate as possible, the scale of the maps and shading of the range obviated pin-point accuracy. Also, for many fishes that have been widely introduced, the native range can only be estimated from often limited historical data.

TAXONOMIC CHAPTER ORGANIZATION

Each taxonomic chapter contains 13 major sections and various numbers of subsections. For some families, little to nothing may be known about certain sectional and subsectional topics, and in those cases, the paucity or lack of information is generally acknowledged.

Even in a work this large and broad ranging, we came to realize early on that some important topics could not be covered adequately when our focus was largely at the level of genus. Hence, contributors did not cover the zoogeography of species within each family. The zoogeography of North American freshwater fishes would require another volume to update and reassess information previously synthesized on that topic (e.g., Hocutt & Wiley 1986; Mayden 1992; Ross 2013; Ross & Matthews 2014). Likewise, contributors did not include tools or aids in identification of species (e.g., illustrated keys) because identification is most often a species-level exercise and it is so well covered in numerous state and regional fish books, including Canada (Scott & Crossman 1973) and Mexico (Miller et al. 2005, 2009; see also literature guide sections in each taxonomic chapter) as well as in a field guide for North American freshwater fishes north of Mexico (Page & Burr 2011). Another important, but large topic not covered in detail is the area of fishing statistics, which again is deserving of a separate synthesis (see commercial importance sections for some details). We describe the content of major sections and subsections in each chapter as follows:

Chapter introduction. In an initial section, contributing authors introduce the family to the reader by relating the scientific and common names of the fishes, highlighting some specialized or unusual features of the group, and for those families with a large number of marine species or those not wholly endemic to fresh waters of North America, placing the focal taxa in context of the diversity and geographic distribution of the entire family.

Diversity and distribution. Contributing authors summarize the general diversity of the focal family, including a discussion of each genus, its native distribution, the number of species in each genus, and evidence of polytypy or phylogeographic structure. Contributing authors also included a non-native distribution subsection, if information was available, outlining introductions outside the native range and, if known, the effects of the taxa as non-natives.

Phylogenetic relationships. Contributing authors cover all phylogenetic hypotheses (those based on cladistic methodologies) for the focal family (inter- and intrafamilial) identifying, if possible, the sister-group of the family and then detailing the relationships of all genera within the family.

Fossil record. Contributing authors summarize the fossil history, if any, for the focal family. Minimally the section synthesizes information on each known fossil genus in the family and the number of extinct fossil species in each genus. Ages or approximate ages are given when known.

Morphology. Contributing authors synthesize information on morphological structures with an emphasis on diversity in morphology across family members and specialized, unusual, and unique features. In the introductory subsection, contributing authors describe the general physiognomy of the respective family (e.g., body shape; fin shape, type, relative size, and placement; mouth size and placement; scale type, color, and pigmentation patterns).

In other subsections, contributing authors detail unusual or specialized external and internal anatomical characteristics (e.g., reproductive anatomy, sensory organs, functional biology, and eco-morphology).

Genetics. Contributing authors synthesize genetic-based studies focusing on topics such as karyology, phylogeography, infraspecific variation, and hybridization and introgression. They also present studies employing genes or gene products to determine phylogeny in the phylogenetic relationships section.

Physiology. Contributing authors highlight the incredible diversity of physiological traits exemplified by fishes in each family. When information is available, the sections include syntheses on tolerances to and effects of water temperature, dissolved oxygen, pH, salinity, and turbidity. Contributing authors also highlight other specialized physiological adaptations of each family (e.g., swimming performance, sensory physiology, chemical ecology, bioenergetics, and metabolism).

Behavior. Contributing authors cover nonreproductive-associated behaviors in this section. These include behavioral areas such as aggression, dominance, learning, memory, migratory and nonmigratory movement, diel activity, schooling behavior, foraging behavior, alarm signaling, patch choice, and any other unique or specialized behavior.

Reproduction. Contributing authors synthesize features of the reproductive cycle, including reproductive behaviors. The section focuses on topics such as age and size at maturity; sexual dimorphism; spawning migrations, cues, and sites; pre-spawning and spawning behaviors; male and female reproductive allocation; parental care; unusual mating systems; and embryo and larval development.

Ecology. Contributing authors focus on habitat, diet (particularly diet breadth and specializations), predation, and parasitism but also when possible range across topics from autecology to the functional importance of individual taxa in communities and ecosystems.

Conservation. Contributing authors discuss imperiled fishes in the focal family and the likely reasons for their decline. Contributing authors incorporate the best available information and summarize the reasons for declines or anticipated declines.

Commercial importance. Contributing authors cover economic importance and values of taxa in the focal family. This includes the importance in historic or present commercial fisheries, cultural significance, aquaculture, sport fisheries, and the aquarium trade.

Literature guide. In the final section, contributing authors point the reader to major sources of information on the family. In particular, detailed family, species, or topic-specific treatments are referenced.

Melvin L. Warren, Jr.
Brooks M. Burr

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COLOR PLATES AND PHOTOGRAPHS

We used color drawings by Joe Tomelleri, the premier fish artist in North America, to illustrate as many North American genera as possible. The colors are as seen on the fishes when they are first removed from the water, and many were drawn when at their peak breeding colors. Joe's fish portraits are done in Berol Prismacolor pencils, and using those pencils Joe is renowned for precisely portraying life color, scale and fin-ray counts, and a full spread of the fins. We express our appreciation to Joe for granting us a generous licensing arrangement for use of his drawings.

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