Fishes of the World

2nd edition

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A WILEY-INTERSCIENCE PUBLICATION

JOHN WILEY & SONS

New York • Chichester • Brisbane • Toronto • Singapore

Library of Congress Cataloging in Publication Data:

Nelson, Joseph S.
Fishes of the world.

"A Wiley-Interscience publication."
Bibliography: p.
Includes index.
1. Fishes—Classification. I. Title.

QL618.N4 1984 597'.001'2 83-19684
ISBN 0-471-86475-7

Printed in the United States of America

10 9 8 7 6 5 4 3 2 1

Preface

One purpose dominated the writing of the first edition of this book—to present a modern introductory systematic treatment of all major fish groups. The same objective prevailed in doing the research and writing for this enlarged revision. The acceptance of the previous edition as a guide and reference to fish classification by many teachers for courses in ichthyology or fish biology and by many ichthyologists and other zoologists has been very gratifying. Many important works have been published since the last edition, and we have a better understanding of relationships than we had a decade ago; however, only further work will enable us to judge whether all of our new ideas are advances. To some extent, this greater understanding has led us to conclude that many postulated relationships are not as secure as once thought and that more work is needed to resolve differences in conclusions. In this edition I have made a total revision of the classification in light of recent work, given more references to recent systematic works, listed more genera under the families, enlarged many family descriptions, given more biological and systematic information, and attempted to synthesize more of the differing conclusions of various workers. Many new fish figures have also been included.

The introduction deals in an elementary way with various aspects of fish diversity, systematics, and zoogeography. The lower chordates and

fishes are presented in linear order in a manner that would best seem to reflect their postulated evolutionary relationships in a synthetic classification. Alternative schemes of classification in recent literature, primarily cladistic, are referred to often. Evolutionary trends are mentioned for some of the groups. Categories are given down to at least family level and frequently lower. A relatively large number of categories are recognized in order to provide a better presentation of postulated relationships. The categories used, and their endings in parentheses when consistent, are as follows: phylum, subphylum, superclass, grade, subgrade, class, subclass, infraclass, division, subdivision, infradivision, superorder, series, order (*iformes*), suborder (*oidei*), infraorder (*oidea*), superfamily (*oidea*), family (*idae*), subfamily (*inae*), tribe (*ini*), genus, and subgenus. Not all categories are employed within a particular taxon. A dagger denotes those at the level of suborder or higher that do not contain living species. Users who find the number of categories given to be a cumbersome proliferation may wish to use only class, order, suborder, and family (as given in Appendix I).

For each family the most appropriate common name known to me, if any, and a mention of its general range are given. An outline drawing illustrates most of the families, and sometimes more than one is given; it must be remembered, however, that there is much variation in body shape within many of the illustrated groups. A short description is given for most categories; some are inconsistently brief, usually as a consequence of the lack of diagnostic features or my lack of information on them. I have tried to be more consistent in giving information than previously but have also felt it better to explore differing areas of particular interest in a group rather than produce a uniform but limited text. For some families the number of abdominal and caudal vertebrae are given in parentheses after the total vertebral number, for example, 25 (10+15). Interesting life-history or biological notes and the maximum length of the largest species are often given. Estimated numbers of recognized (valid) genera and species are given (in some cases the number of species in each genus is also given). These figures are always for living forms, never fossil unless so stated. The degree of agreement by others with these figures will vary from group to group (in part due to the subjective matter of lumping and splitting); for example, everyone would agree that there are but two valid species of described percopsids, but disagreement can be found on whether there is only one gonorynchid, and considerable disagreement would be found on the number of valid described species of gobiids that should be recognized. I have tried to represent current but conservative thinking in arriving at these numbers. I adhere to the biological species concept, although the evolutionary spe-

cies concept of Wiley (1981:24–25) would be acceptable. I reject any redefinition of a species, however, which would essentially equate it with that of a subspecies or of any other lower recognizable unit. Examples of recognized generic names are given for each family; if the number is relatively small I have tried to list them all. (When this is not done it is usually because there is doubt about which of a number of nominal generic names should be recognized.) In choosing examples of generic names to list for large families I have tried to choose those that represent the following: (1) especially speciose genera, (2) the type of a subfamilial category or that of a nominal family not recognized here, (3) genera whose species exhibit some extreme biological diversity, and (4) genera whose species are commonly found or are important in commercial, sports fishery, or aquarium use. Names preceded by an equal sign and placed in parentheses after a generic name, in what is an unconventional practice, denote a variety of things: junior synonyms (objective or subjective and sometimes regarded as subgenera), junior homonyms, and names found in the literature which have been emended. This is done only when I feel that a name is relatively well known or was used as a valid generic name in the previous edition, and no attempt has been made to recognize all commonly used junior synonyms.

It is assumed that a knowledge of fish anatomy, if not already acquired, will be obtained elsewhere. (In the osteological descriptions I use the terms circumorbital, infraorbital, and suborbital synonymously and the lachrymal is the first bone in the series—i.e., it is synonymous with the first suborbital bone.) I originally hoped to include a section on fish osteology, but this idea has been put aside temporarily at least. The generalized maps in Appendix II are based primarily on the acknowledged sources. Limits are often based on scattered populations of one species. The maps are intended to show basic distributions only and are not necessarily accurate in detail.

Numerous minor and major changes have been made in the classification of the previous edition. For example, the Myxini are recognized as the most primitive fish group, and the Ostariophysi are changed in position and in internal classification. These and many of the other changes do not meet with universal acceptance. In order to keep the book within reasonable length I have not always given reasons for decisions in making changes. However, in preparing this edition I have again attempted to be relatively conservative in making changes while, at the same time, accepting new and often radically different schemes, or parts thereof, within a synthetic framework when they seem to be well founded. (I hasten, however, to beg forgiveness for overlooking or misjudging those references that I ought not to have.) It is very naive to accept the latest

proposals as the best in postulating systematic relationships, regardless of the methodology used and even if the study gives sound comparative information. All new proposals should be critically evaluated. It is good to be innovative in doing systematic research but changes in a classification such as this, I feel, should be made only when the evidence for it is relatively strong.

As long as there are active, creative ichthyologists there will be major disagreements in our classification in the foreseeable future (similarly there is disagreement in almost all important fields of biology). Fish classification is in a dynamic state, and the student pursuing ichthyology will find that all groups can be reworked. There are many challenges, both in developing the theory of classification and in its actual practice. Because particular classifications eventually become obsolete (as will most biological information), they should be regarded as frameworks that will provide a basis for building as advances are made. If, however, anyone should question the value of learning a classification, it should be remembered that they are useful vehicles on which to base an understanding of biology. We do not stop using objects or acquiring the present state of knowledge merely because our technical knowledge is going to improve.

The spelling of some names above the generic level has been changed from the previous edition following Steyskal (1980) except for the following: Dasyatidae (vs. Dasyatididae), Carapidae (vs. Carapodidae), Anarhichadidae (vs. Anarhichantidae), and provisionally Grammidae (vs. Grammatidae). The decision to change family names in order to make them grammatically correct according to the stem of the generic name, strictly following the International Code of Zoological Nomenclature, was taken reluctantly. I originally felt it best to continue to use spellings that are in general usage, in the interests of stability, even if they are grammatically incorrect. However, ichthyologists appear to be accepting the spirit of Steyskal's proposals and probably will continue to do so (although some of the same ichthyologists do not accept the code's recommendations regarding the use of the terminal ending of *i* or *ii* in spelling masculine patronyms). I therefore have followed the proposals, except where valid reasons were given to me for not doing so, even when an awkward-sounding name is the result (e.g., Echeneididae). Unfortunately, there continues to be disagreement over various spellings in the modern literature.

It is the eventual hope to produce a standardized common name for each family. This will be achieved in the future with the help of such people as Drs. R. M. Bailey, C. R. Robins, and W. Fischer. In this regard, such publications as "A list of common and scientific names of fishes from the United States and Canada" (Robins et al., 1980) and "FAO species

identification sheets for fishery purposes" (edited primarily by W. Fischer) are especially useful.

The ichthyologist is a student of fish systematics. Ichthyology courses may be designed for students interested in ichthyology or fisheries biology as a career and for the general biology student wishing to learn something of those animals who comprise one-half of the species of vertebrates. The laboratories usually demonstrate the diversity of fishes and their probable course of evolution, show systematically important characters, provide insight into how ichthyologists determine which characters to use, and provide training in identification. Stress may be given to the local fish fauna. For this purpose there are many fine regional books. However, it is desirable to have a broad look at fish classification and to place one's local fauna in perspective to all fishes. Depending on the time available, students may, for example, attempt to explain the biological significance of the differences we consider to be systematically important and to learn how morphology determines function and how ways of life can determine morphology. Fishes provide good examples in showing how diverse adaptations to common functions can be brought about by natural selection. Collecting trips, curatorial functions, and special projects (e.g., skeletal preparation and cleaning and staining specimens) may also be involved. The laboratory can be a good place to discuss taxonomic problems as well. The student of ichthyology must be well versed in the methods and theories of systematic biology. An understanding of how systematic relationships are postulated (hypothesized) and knowing the strengths and weaknesses of various approaches so that classification can be critically evaluated are far better than just learning the end results (which are likely to be short-lived). Meetings such as the American Society of Ichthyologists and Herpetologists and the Congress of European Ichthyologists provide excellent forums for learning and exchanging ideas.

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November 1983

Acknowledgments

I am grateful to many individuals who have helped me in various ways with the preparation of this edition. I apologize to those I do not name here.

Much literature and research work was done at the Carl L. Hubbs Library and the Vertebrate Museum at Scripps Institution of Oceanography. I thank Laura Hubbs, Betty Shor, and Dick Rosenblatt, who made my trips to San Diego that much more enjoyable. The friendliness and help received during visits to many other museums, especially that from Bob Carveth, Graham Hardy, and Don McAllister, and, in addition, that from Wayne Roberts of the University of Alberta Museum of Zoology at my own university, are valued. I express my gratitude to the many museum curators and colleagues who have been so patient with overdue loans and collaborative research projects, respectively, while this work was completed. I appreciate the thoughtfulness of researchers from around the world who have kindly sent me reprints of or references to their systematic works. Many have taken time at meetings to discuss their work with me. I shall be thankful to those who send me referenced corrections and materials for future revisions.

I have benefited from comments and information from many individuals, including students and professors. It would be difficult to know where to stop if I attempted to name them (some are mentioned in the

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Introduction

Fish exhibit enormous diversity in their morphology, in the habitats they occupy, and in their biology. Unlike the other commonly recognized vertebrate groups, fish are a heterogeneous assemblage. From lamprey and hagfish to lungfish and flatfish, they include a vast array of distantly related vertebrates. Many are even more closely related to mammals than to certain other fish. Despite this diversity and the dilemma that evolution does not always make definitions easy, fish can be simply defined as aquatic poikilotherm vertebrates that have gills throughout life and limbs,if any, in the shape of fins. The body of information known about them is so vast that their study can include all facets of biology. On the other hand, they are attractive to the researcher because of the wealth of information still to be found. The field of ichthyology, the study of fish systematics, is enormously active and exciting. Many controversies exist and ichthyologists are split on fundamental issues on principles of zoogeography and systematics.

NUMBERS

Fishes constitute almost half the total number of vertebrates. An estimated 21,723 living species compared with 21,450 extant tetrapods (a

total of about 43,173 recognized vertebrate species) have been described. Other workers, for various reasons, have arrived at different estimates, most of which range between 17,000 and 30,000, for the numbers of currently recognized fish species. The number arrived at here is somewhat larger than Cohen's (1970) 20,600 (mean of his extremes). Some groups are expanding with newly described species, whereas others are decreasing, for species are being synonymized faster than the new ones are described. However, a net increase is shown every year, and the number of new species of fishes described annually exceeds that of the new tetrapods. Bird and mammal species are not likely to rise much above the present 12,600. Amphibians and reptiles may increase significantly (perhaps at a relatively slow rate because herpetologists are far fewer than other vertebrate systematists). The eventual number of extant fish species may be close to 28,000. In contrast to amphibians, reptiles, and mammals, the known diversity of living fishes exceeds that of known fossil taxa. On the other hand, there is a much richer and more informative fossil fish record than is known for birds (even relative to their numbers).

Of the 445 fish families with living species recognized herein, the seven largest contain approximately 30% of the species (some 6411). These families, in order of numbers of species, are Cyprinidae, Gobiidae, Characidae, Cichlidae, Labridae, Loricariidae, and Serranidae. Interestingly, about 63% of the species in the seven largest families are freshwater ones (in contrast, about 39% of all fishes occur in or almost always in fresh water).

In the present classification some 66 families contain only one species, while 57 families have 100 or more species recognized in them, of which two have over 1000. The average number of species per family is 49, whereas the median number is only 10.

In most fish groups it appears that the number of taxa at any one level is not randomly distributed in the taxa at the next highest level within any one group; that is, the majority of lower-level taxa (e.g., species) are found in a relatively few higher-level taxa (e.g., genera) within that particular lineage (e.g., family). This does not seem to be an artifact of the classification, although some workers prefer to split some very speciose groups into groups more equal in size, while others lump monotypic offshoots with the ancestral family. It does not seem to be an artifact of a synthetic versus a cladistic classification either, although the details would vary. This observation, which is also apparent in other vertebrate groups (e.g., *Rana* and *Bufo* contain a disproportionately high number of amphibians as colubrids do for reptiles), may mean that there is a nonrandom relationship between the amount of diversity and divergence

within a lineage. However, it is not clear to me what statistical test would be appropriate in this problem to determine whether or not there actually is randomness in the distribution of taxa; speculating on the biological meaning if it is nonrandom is another matter.

Approximate numbers of recognized extant families, genera, and species in the 50 orders of fishes that contain living representatives. The number of freshwater species is an estimate of the species always or almost always confined to fresh water (or inland lakes, regardless of salinity). It basically includes all species in Darlington's (1957) primary division families, most in his secondary division families, and many in his peripheral division families. It excludes commonly diadromous fishes that may have landlocked populations.

Order	Families	Genera	Species	Freshwater species
Myxiniformes	1	6	32	0
Petromyzontiformes	1*	6	41	32
Chimaeriformes	3	6	30	0
Hexanchiformes	2	4	5	0
Heterodontiformes	1	1	8	0
Lamniformes	7	65	239	0
Squaliformes	3	21	87	0
Rajiformes	9	54	424	14
Ceratodontiformes	1	1	1	1
Lepidosireniformes	2	2	5	5
Coelacanthiformes	1	1	1	0
Polypteriformes	1	2	11	11
Acipenseriformes	2	6	25	15
Lepisosteiformes	1	1	7	7
Amiiformes	1	1	1	1
Osteoglossiformes	6	26	206	206
Elopiformes	3	4	11	0
Notacanthiformes	3	6	25	0
Anguilliformes	19	147	597	0
Clupeiformes	4	68	331	26
Gonorynchiformes	4	7	27	25
Cypriniformes	6	256	2,422	2,422
Characiformes	10	252	1,335	1,335
Siluriformes	31	400	2,211	2,155
Gymnotiformes	6	23	55	55
Salmoniformes	15	90	320	95

(*Continued*)

Order	Families	Genera	Species	Freshwater species
Stomiiformes	9	53	248	0
Aulopiformes	12	40	188	0
Myctophiformes	2	35	241	0
Percopsiformes	3	6	9	9
Gadiformes	7	76	414	1
Ophidiiformes	4	86	294	4
Batrachoidiformes	1	19	64	5
Lophiiformes	16	64	265	0
Gobiesociformes	2	36	114	2
Cyprinodontiformes	13	120	845	675
Atheriniformes	5	48	235	85
Lampriformes	11	20	39	0
Beryciformes	14	38	164	0
Zeiformes	6	21	36	0
Gasterosteiformes	3	8	10	2
Indostomiformes	1	1	1	1
Pegasiformes	1	1	5	0
Syngnathiformes	6	63	257	3
Dactylopteriformes	1	4	4	0
Synbranchiformes	1	4	15	11
Scorpaeniformes	20	269	1,160	90
Perciformes	150	1,367	7,791	1,107
Pleuronectiformes	6	117	538	3
Tetraodontiformes	8	92	329	8
Totals	445	4,044	21,723	8,411

Numbers of species of fishes in Canada and the United States as determined from Robins et al. (1980), excluding species introduced into the two countries, occurring in freshwater (FW; the number in parentheses indicates those species found only in fresh water in the area and is given only if not all are normally confined to fresh water); the Atlantic Ocean and eastern Arctic (Atl.); the Pacific Ocean and western Arctic (Pac.); those in both the Atlantic and Pacific Oceans (Atl. and Pac.), whether or not introduced into one from the other; and the total number occurring in the area. Species in the ocean which occur to as deep as the edge of the continental shelf (200 m depth) are included. Species with at least some individuals occurring both in fresh water and in the ocean (e.g., diadromous ones) are included in each of the four habitat categories. The number of fish families (Fam.) represented in the various orders are as recognized in this book.

Order	Fam.	Species				
		FW	Atl.	Pac.	Atl. and Pac.	Total
Myxiniformes	1	0	1	2	0	3
Petromyzontiformes	1	17 (13)	1	3	0	17
Chimaeriformes	1	0	0	1	0	1
Hexanchiformes	2	0	1	3	1	3
Heterodontiformes	1	0	0	1	0	1
Lamniformes	7	1 (0)	35	26	14	47
Squaliformes	2	0	9	4	1	12
Rajiformes	7	1 (0)	30	22	1	51
Acipenseriformes	2	8 (4)	2	2	0	8
Lepisosteiformes	1	5	0	0	0	5
Amiiformes	1	1	0	0	0	1
Osteoglossiformes	1	2	0	0	0	2
Elopiformes	2	3	3	2	1	4
Notacanthiformes	1	0	1	0	0	1
Anguilliformes	9	1 (0)	60	8	1	67
Clupeiformes	2	11 (0)	33	11	3	41
Cypriniformes	2	273	0	0	0	273
Characiformes	1	1	0	0	0	1
Siluriformes	2	40 (39)	2	1	0	42
Salmoniformes	7	53 (35)	12	21	6	62
Stomiiformes	2	0	0	2	0	2
Aulopiformes	7	0	14	5	2	17
Myctophiformes	1	0	0	9	0	9
Percopsiformes	3	9	0	0	0	9
Gadiformes	3	2 (1)	24	7	1	31
Ophidiiformes	3	0	19	4	0	23
Batrachoidiformes	1	0	4	2	0	6
Lophiiformes	6	0	17	3	0	20
Gobiesociformes	1	0	3	6	0	9
Cyprinodontiformes	6	59 (44)	41	12	3	94
Atheriniformes	1	3 (2)	7	3	0	12
Lampriformes	5	0	8	7	4	11
Beryciformes	2	0	12	0	0	12
Zeiformes	3	0	5	1	0	6
Gasterosteiformes	2	4 (1)	4	3	2	6
Syngnathiformes	4	1 (0)	27	8	1	34
Dactylopteriformes	1	0	1	0	0	1

(*Continued*)