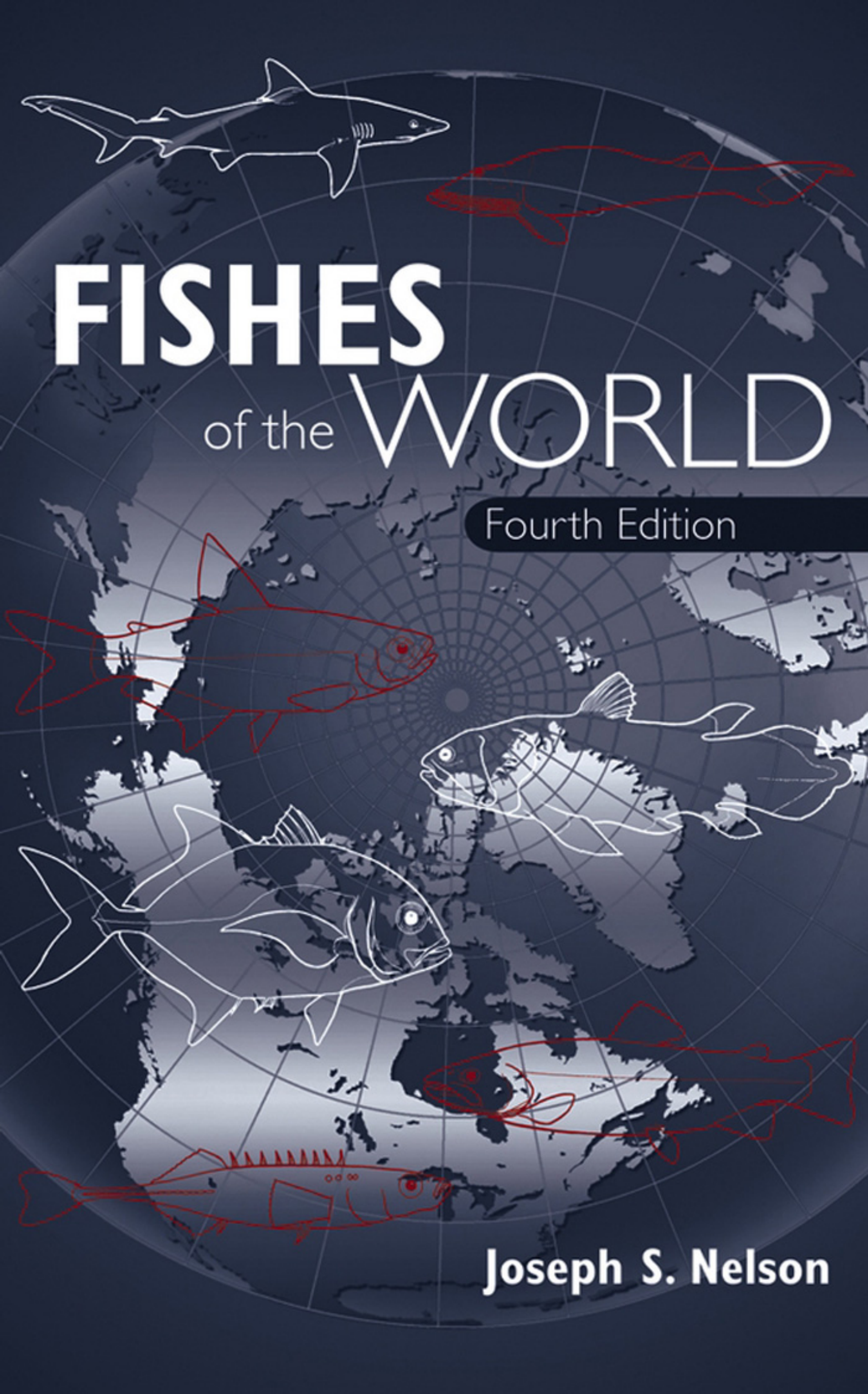

FISHES of the WORLD

Fourth Edition

Joseph S. Nelson

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Preface

One purpose dominated the writing of the previous editions of *Fishes of the World* (Nelson, 1976, 1984, 1994): to present a modern introductory systematic treatment of all major fish groups, both fossil and living. The same objective prevailed in writing this revision. The acceptance of the previous three editions as a guide and reference to the classification of fishes by teachers of courses in ichthyology or fish biology, collection managers, aquarists, and by ichthyologists and other zoologists in general has been increasingly gratifying. Many important works have been published since the last edition (Nelson, 1994), and we think we have a better understanding of relationships than we had a decade ago; however, as in the past, only further work will enable us to judge whether all of our new ideas are advances. Many questions remain. In this edition I have revised the classification in light of recent research, given references to recent systematic works, listed more genera under the families, and given recent systematic information. Some new fish drawings have been added.

The introduction deals in an elementary way with various aspects of fish diversity. In the main text, the lower chordates and fishes appear in linear order in a manner that seems best to reflect their postulated evolutionary relationships. I often present alternative schemes of classification from recent literature. I have given categories down to at least family level and frequently lower. Subfamilies are recognized in many families, but the stability or degree to which we think they are monophyletic varies widely between and within families. In some families the subfamilies appear to be well founded (e.g., Salmoninae). In others, some or all in a family may be weakly founded and the composition of the nominal subfamily is likely to change (e.g., Characinae and Gobiinae).

I recognize a relatively large number of categories 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, class, subclass, infraclass, division, subdivision, superorder, series (these 11 categories are centered in the text), order (iformes), suborder (oidei), infraorder, superfamily (oidea), family (idae), subfamily (inae), tribe (ini), genus, and subgenus. Not all categories are employed within a particular taxon. A dagger (†) denotes those taxa containing only fossil species; it is usually given only for the highest appropriate taxon and not for the lower extinct members of the group. Users who find the number of categories given to be a cumbersome proliferation may wish to use only class, subclass, order, suborder, and family (as given in the Appendix). Not all recognized (named) taxa are assigned rank (e.g., placed in a named category) (the recognition by named category of all branches in a cladistic classification would result in a great proliferation of categories). The following are examples of some major taxa that are part of the classification but for which no formal rank is assigned: Vertebrates (formally the Vertebrata), Neoteleostei, and Acanthomorpha. New in this edition is that a unique number is given for each order and family of living fishes (also given in the Appendix as in past editions) and a common name is given for each order.

For each family with living fishes, I give the most appropriate common name that I know (only a few have been coined and, for some, only a vernacular version of the scientific name is given) and its general range. For many families there is an outline drawing of a member, and sometimes more than one; remember, however, there is much variation in body shape within many of the illustrated groups. Although the outline drawings are based on actual species, details of such variable features as scales are not shown in order to keep the drawings generalized for the family. There is a short description for each family and for many taxa in higher categories; some are inconsistently brief, usually as a consequence of the lack of diagnostic features, especially those features that are external or otherwise easily seen. I have often omitted characters that are difficult to describe briefly, even if diagnostic for the group. For some groups I explore differing areas of interest, rather than trying to produce a uniform but limited text. When given, the numbers of abdominal and caudal vertebrae are placed in parentheses after the total vertebral number—for example, 25 (10 + 15). I often include interesting life-history or biological notes and the maximum length of the largest species. When possible, the length is qualified by giving standard length (SL), fork length (FL), or total length (TL). Also included are estimated numbers of recognized (valid) genera and species (in some cases the number of species in each genus is also given). These figures are always for living forms—never for fossils unless so stated. The degree of agreement with these figures by others 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 one can find disagreement on the number of valid described species of cichlids and gobiids that should be recognized. I have tried to represent current but conservative thinking in arriving at these numbers. In many groups, undescribed species are known to exist; these may be mentioned, but their number is not included in the species total. Priority is given to literature published after 1994 in giving references in the family sections. Nelson (1994) should be referred to for much of the literature forming the basis of earlier editions. I give examples of recognized generic names for each family; if the number is relatively small, I usually list them all. In choosing examples of generic names for large families, I have tried to choose those that represent the following: (1) genera with many species, (2) the type of a subfamilial category or that of a nominal family no longer recognized, (3) genera whose species exhibit some extreme biological diversity, and (4) genera whose species are commonly found or are important in commercial fishery, sports fishery, or aquarium use. Generic synonyms are usually given only for genera recognized as valid in Nelson (1994) but now considered junior synonyms. No attempt is made to recognize all commonly used junior synonyms, as these may easily be found in the very valuable Eschmeyer (1998). I have used Eschmeyer (1998) to verify the spelling of most of the names of extant genera, but time did not permit checking all.

I am assuming 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 (= lacrymal, lacrimal) is the first bone in the series—i.e., it is synonymous with the first suborbital bone. However, proposals to change the name of some bones from that used in previous editions as a result of our better understanding of homologies have not been adopted unless otherwise indicated. For example, as noted in Janvier (1996), what are commonly termed the frontals and parietals in actinopterygians, originally taken from human anatomy, are homologous with the parietals and postparietals, respectively, of early tetrapods.

I have made numerous minor and major changes to the classification presented in the previous edition. As in the last edition, I adopt a cladistic classification. This will provide users with some idea of the hypothesized sister-group relationships and monophyletic groups, and it will help workers in all disciplines of comparative fish biology interpret their work in an evolutionary or historical context. However, I have also tried to make only those changes that seemed well founded. In order to keep the book within reasonable length, I have not always given reasons for the 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 cladistic framework when they seem to be well founded. It is very naive to accept the latest proposals as always being the best in postulating systematic relationships, regardless of the method used and even if the study gives sound comparative information. All new proposals should be critically evaluated. It is good to be innovative in systematic research, but I feel that changes in a classification such as this should be made only when evidence is relatively strong. Of course, researchers in presenting new information will normally be advised to give the implications of their work to classification.

The 515 families with living species recognized in this edition represents an increase from that in the previous three editions. This has resulted, in part, from an increased practice to reject families that are clearly not monophyletic by placing taxa of uncertain familial affinity into separate families. However, it continues to be my belief that in ichthyology we recognize more families than is desirable for the benefit of the nonsystematist, although I do not believe we should necessarily avoid recognizing monotypic families even if their sister group is known. When cladistic relationships are better understood, we may be able to reduce the number of families to a more manageable number while expressing lower relationships with the increased use of subfamily and tribe categories. I have attempted, within the above framework, to keep the number of families from increasing even further and hope to keep instability at the family level to a minimum.

As long as there are active, creative ichthyologists, there will be major disagreements in our classification in the foreseeable future (there is similar 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 questions the value of learning a classification, it should be remembered that classifications 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 information is going to improve.

The primary task of the systematist is to seek an understanding of the evolutionary history of life. The systematist must also deal with such matters as how to spell the names of taxa that have variant names in the literature—a matter that sometimes tries one's patience. It is surely frustrating and confusing, especially for the nonsystematist, to find differences in the spelling of taxonomic names. There are still some problems in agreeing on how certain family names should be spelled (e.g., in family names ending in -ididae vs. –idae; see also discussion under family Lampridae–202). With regard to the latter problem, there is some feeling that it may be more important to have names pronounceable than to be grammatically correct. In this regard, a few of us such as W. N. Eschmeyer and J. R. Paxton, while following provisions of the "International Code of Zoological Nomenclature," hope to arrive at some agreement, eventually!

Although in this edition I have given a common name in English for every family, I cannot state that we have agreement in family common names. Eventually, with the help of such people as K. E. Carpenter and R. Froese, we hope to produce a standardized common name for each family, mainly for the sake of the nonsystematist. In this regard, such publications as *Common and Scientific Names of Fishes from the United States, Canada, and Mexico* (Nelson et al., 2004), FAO species identification guides (edited primarily by K. Carpenter), other FAO publications, and *FishBase* (Froese and Pauly, 2003) are especially useful.

The ichthyologist is a student of fish systematics. A good grounding in many of the sciences is necessary for the future ichthyologists to test the hypotheses we have today. 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 that comprise over one-half of the vertebrate species. The laboratory section of courses usually demonstrates the diversity of fishes and the probable course of evolution, shows systematically important characters, provides insight into how ichthyologists determine which characters to use, and provides training in identification. Emphasis may be given to the local fish fauna, and 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, learn how to hypothesize homologies, attempt to explain the biological significance of differences we consider to be systematically important, and learn how morphology determines function and how ways of life can determine morphology. Fishes provide good examples in showing how natural selection results in diverse adaptations to common functions. Collecting trips, curatorial functions, and special projects (e.g., skeletal preparation and clearing 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 classifications can be critically evaluated are far better than just learning the end results (which are likely to be short-lived). Meetings such as those of the American Society of Ichthyologists and Herpetologists, American Elasmobranch Society, American Fisheries Society, Desert Fishes Council (dedicated to the preservation of America's desert fishes), European Congress of Ichthyology, Indo-Pacific Fish Conference, International Meeting on Mesozoic Fishes, and the Society of Vertebrate Paleontology provide excellent forums for learning and exchanging ideas. It behooves students of ichthyology, both apprentice and professional, to become actively involved in such groups.

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Many individuals helped me in various ways with the preparation of this edition. They are greater in number than given below. I am grateful to them all.

I greatly enjoy and benefit from seeing colleagues at meetings, from students to longtime friends (who sadly grow fewer in number as the years go by). Valuable help was received over the years during visits to museums, and I express my gratitude to museum curators who have been patient with overdue loans while this work was completed. The working interactions, colleagueship, and warmth provided at a 2004 FAO workshop is valued; I thank especially Kent Carpenter, Michel Lamboeuf, FAO, and the staff at the Instituto Español de Oceanografia Laboratory in Tenerife, Spain. I appreciate the thoughtfulness of researchers from around the world who have kindly sent me reprints of their systematic works. I shall be grateful to those who send me referenced corrections and materials for future revisions.

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workers who made available the extremely helpful resources "Catalog of fishes" (especially Bill Eschmeyer) and "FishBase" (especially Rainer Froese and Daniel Pauly). I do not forget those who helped me in various ways with the previous editions, especially Carl L. Hubbs (deceased) and the staff at the Scripps Institution of Oceanography. I value the earlier training from Peter Larkin (deceased), Don McPhail, Tom Northcote (whose darkroom, with Heather's help, led to greater productivity), Ralph Nursall, and Norman Wilimovsky (deceased); I feel a special indebtedness to Casimir Lindsey, teacher, scholar, artist, and friend.

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I appreciate all those who helped with various technical aspects of preparing the manuscript. The Department of Biological Sciences of the University of Alberta generously provided assistance and working space. Patrick Kong of the Department of Biological Sciences prepared the four cladistic charts and the two charts giving the sequence of classes and orders; most of the fish figures, new and old, were prepared by Pauly Wong. The help from Wayne Roberts, collections manager of the University of Alberta Museum of Zoology, is also appreciated. Valued assistance with the manuscript and computer challenges was provided by Claudine B. Nelson and Mark K. Nelson.

The staff at John Wiley & Sons have again, as from the start with the first edition 30 years ago, been extremely helpful, in editorial, design, and production work, and it has been a great pleasure to work with them. In particular for this edition, I thank Jim Harper for his advice and faith in the book. He and Scott Amerman were of immense help and it was always enjoyable talking with them. I also thank Lindsay Orman.

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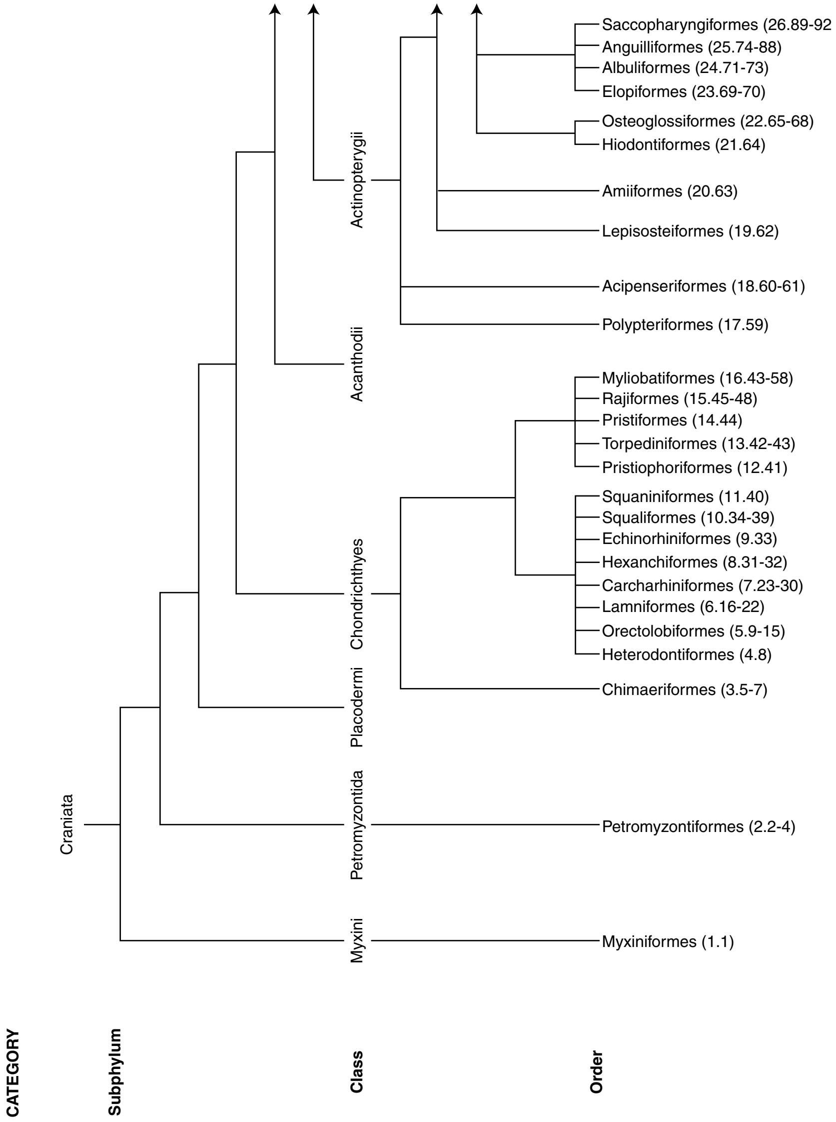
I am grateful to Ed Crossman (deceased), Héctor Espinosa-Pérez, Lloyd Findley, Carter Gilbert, Bob Lea, and Jim Williams, my fellow members on the "Committee on Names of Fishes", a joint committee of the American Fisheries Society and the American Society of Ichthyologists and Herpetologists, in writing the 2004 book "Common and scientific names of fishes from the United States, Canada, and Mexico." Information acquired in writing that book was helpful in writing this one.

One of my greatest professional joys was receiving the Robert H. Gibbs, Jr. Memorial Award, 2002, for "An outstanding body of published work in systematic ichthyology," American Society of Ichthyologists and Herpetologists, presented July 8, 2002, in Kansas City, Missouri (coincidently, where my mother's parents, the Schiesers, were married December 4, 1899). I am pleased to have known Bob Gibbs.

Finally, I thank my wife, Claudine, and children, Brenda, Janice, Mark, and Karen, and grandchildren, Anna and Kaitlind for making it all worthwhile—a work I dedicate to the cherished memory of my parents, Walter Innes Nelson and Mary Elizabeth Nelson (nee Schieser), brothers Walter and Bill, and aunts Anne Sorenson (nee Nelson) and Alice Franks (nee Nelson).

–J. S. N.

SEQUENCE OF CLASSES AND ORDERS (with ordinal number.family numbers used in text)



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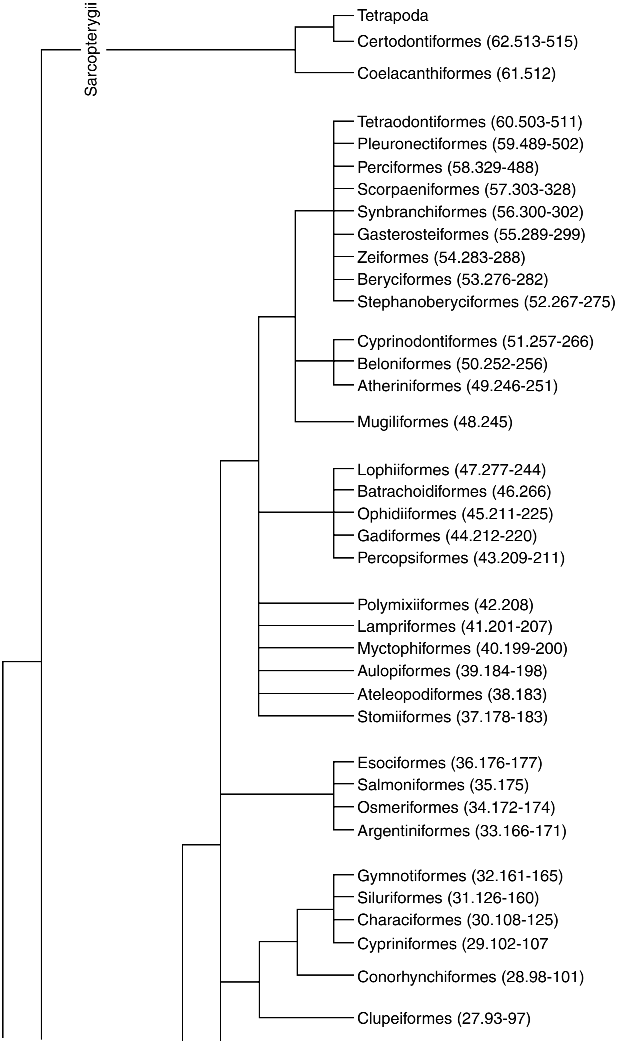


Fishes of the World

Introduction

Fishes exhibit enormous diversity in their morphology, in the habitats they occupy, and in their biology. This diversity is, in part, what makes understanding their evolutionary history and establishing a classification so difficult. From hagfishes and lampreys to sharks, flatfishes, and lungfishes, they include a vast array of distantly related vertebrates. Based on cladistic classification, the ray-finned fishes, the dominant fish group in numbers of species, are more closely related to mammals than they are to sharks. However, although fishes are a heterogeneous assemblage, they exhibit phylogenetic continuity (i.e., they are not a polyphyletic group).

Some people restrict the term "fish" to the jawed bony fishes, namely, among living forms, the Actinopterygii, Latimeriidae, and Dipnoi. Many would also include sharks, rays, and their relatives (a few sharks even have the term "fish" in their common name, e.g., dogfishes). Some, as do I, also include the jawless craniates: hagfishes and lampreys. If we wished to restrict the term to a monophyletic group of what are conventionally called fishes, we would apply it only to the actinopterygians (the ray-finned fishes). Therefore, the term "fishes," as used here, designates an assemblage that is a paraphyletic group (where the most recent common ancestor is included but all descendants from the common ancestor are not—in this case, the tetrapods are excluded), not a monophyletic group (where not only the most recent common ancestor is included, but also all descendants from the common ancestor). We do not give the term "fishes" taxonomic rank. We use it as a matter of convenience, essentially to describe those vertebrates studied by ichthyologists and covered in ichthyological courses. Despite their diversity, fishes can be simply, but artificially, defined as aquatic vertebrates that have gills throughout life and limbs, if any, in the shape of fins.

The body of information known about fishes is vast and includes all facets of biology. Fishes are attractive to researchers because of the wealth of information and diversity still to be found, both in fossil and living (extant) taxa, including basic information on the world's fish faunas. The field of ichthyology, the study of fish systematics, is enormously active and exciting. Many controversies and problems exist, and ichthyologists have numerous opportunities to make discoveries of new taxa, both extinct and extant, and to address phylogenetic and biogeographic questions. This is an exciting time to be studying fish systematics. Many male and female ichthyologists are increasing our knowledge of fish relationships by conducting research on fossil and extant fishes, and for the latter, using molecular and morphological techniques. Some studies are thankfully being done incorporating all such diverse approaches in order to study the evolutionary relationships of fishes. In producing a classification of fishes, we critically examine the phylogenetic research and show the relationships in a way that reflects what are thought to be the most probable hypotheses. However, I feel it better serves the purpose of this book to be more conservative in making changes than a primary researcher should feel in showing the implications of new work.

A friendly word on the terms "fishes" and "fish" and on capitalizing their common names: The term "fishes" is properly used when referring to individuals of more than one species. However, when one is referring to one or more individuals of one species, the term "fish" is appropriate. Hence, it is correct to refer to 100 Rainbow Trout as fish, but to two different trouts, such as one Brook Trout and one Brown Trout, as fishes (the plural form Rainbow Trouts is discouraged). The common names of the three species given in this example (which happen to be in three different genera) were capitalized. Although I uphold the principles of common names in fishes established in 1960 by a joint committee of the American Fisheries Society and the American Society of Ichthyologists and Herpetologists, and explained in Nelson et al. (2004), I deviate in one principle: in this edition the official common name of a species is treated as if it were a proper noun (see Nelson, Starnes, and Warren, 2002).

NUMBERS

The species numbers of fishes given in the text, as in previous editions, are intended to be conservative estimates of valid described species, not of all named species nor of what might be undescribed. They are based, as far as possible, on the latest taxonomic revisions of families and genera and the opinions of the specialists. I regard subspecies as a valid category, with subspecies as a taxon having their own evolutionary history in allopatry and being important in management and conservation efforts. They are not recognized in the species counts. I have concern over efforts to raise, seemingly automatically, all subspecies to species status; however, various workers have appropriately raised many subspecies to, or back to, species status as they have become better understood. Many users will find Eschmeyer (1998) and Froese and Pauly (2003), two Web-based sources that were not available in the first three editions, very useful, as do I, as guides to the taxonomic literature and much more for all extant fish species.

Fishes constitute slightly more than one-half of the total number of approximately 54,711 recognized living vertebrate species. There are descriptions of an estimated 27,977 valid species of fishes compared to 26,734 tetrapods. Many groups of fishes are expanding with newly described species, whereas a few are decreasing because species are being synonymized faster than new ones are described. However, a net increase in species of fish is shown every year, and the number of new species of fishes described annually exceeds that of new tetrapods. The estimated number expected by the end of 2006 is 28,400. The eventual number of extant fish species may be projected to be close to, conservatively, 32,500 (although a change in our species concept will alter this figure and pose problems in making meaningful comparisons). In contrast to amphibians, mammals, and reptiles, 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 there is for birds (even relative to their numbers).

Of the 515 fish families with living species recognized herein, the nine largest (most species-rich) families, each with over 400 species, contain approximately 33% of all species (some 9,302). These families, in order of decreasing numbers of species, are Cyprinidae, Gobiidae, Cichlidae, Characidae, Loricariidae, Balitoridae, Serranidae, Labridae, and Scorpaenidae. Interestingly, about 66% of the species (about 6,106) in these nine largest families are freshwater fishes, whereas only about 43% of all fishes occur in or almost always in freshwater. About 50% of all fish species are in the 26 most species-rich families (each with 222 or more species).

In the present classification, 64 families are monotypic, containing only one species (33 have two species, in one or two genera), while 67 families each have 100 or more species, three of which have over 1,000. Some 151 families have only one genus (with a total of 587 species); the most species rich family with only one genus is the Astroblepidae with 54 species. The average number of species per family is 54, whereas the median number is only 12.

The approximate numbers of recognized extant families, genera, and species in the 62 orders of fishes that contain living representatives is given in the following table. The number of “freshwater species” is an estimate of the species found only, or virtually only, in freshwater (or inland lakes, regardless of salinity); these species may rarely occur in weak brackish water. This number excludes species that are usually diadromous as well as anadromous species that may have landlocked populations. For all such species, the existence of only freshwater would have little or no direct effect on them. The last column, “species using freshwater,” includes those species in the previous column plus those species frequently occurring in freshwater that may otherwise be diadromous or simply entering freshwater in substantial numbers or in a substantial portion of their range. The intent of the last column is to enumerate those species that either would not exist or whose range would be markedly reduced if freshwater habitats were denied them. The category of “Freshwater species” is presented solely to show habitat occurrence; it does not imply biogeographic barriers or dispersal limitations.

Order	Families	Genera	Species	Freshwater Species	Species Using Freshwater
Myxiniformes	1	7	70	0	0
Petromyzontiformes	3	10	38	29	38
Chimaeriformes	3	6	33	0	0
Heterodontiformes	1	1	8	0	0
Orectolobiformes	7	14	32	0	0
Lamniformes	7	10	15	0	0
Carcharhiniformes	8	49	224	1	8
Hexanchiformes	2	4	5	0	0
Echinorhiniformes	1	1	2	0	0
Squaliformes	6	24	97	0	0
Squatiniformes	1	1	15	0	0
Pristiophoriformes	1	2	5	0	1
Torpediniformes	2	11	59	0	0
Pristiformes	1	2	7	0	1
Rajiformes	4	32	285	0	2
Myliobatiformes	10	27	183	23	28
Polypteriformes	1	2	16	16	16
Acipenseriformes	2	6	27	14	27
Lepisosteiformes	1	2	7	6	7
Amiiformes	1	1	1	1	1
Hiodontiformes,	1	1	2	2	2
Osteoglossiformes	4	28	218	218	218
Elopiformes	2	2	8	0	7
Albuliformes	3	8	30	0	0
Anguilliformes	15	141	791	6	26
Saccopharyngiformes	4	5	28	0	0
Clupeiformes	5	84	364	79	85
Gonorynchiformes	4	7	37	31	32
Cypriniformes	6	321	3,268	3,268	3,268
Characiformes	18	270	1,674	1,674	1,674
Siluriformes	35	446	2,867	2,740	2,750
Gymnotiformes	5	30	134	134	134
Argentiniformes	6	57	202	0	0
Osmeriformes	3	22	88	82	86
Salmoniformes	1	11	66	45	66
Esociformes	2	4	10	10	10
Stomiiformes	5	53	391	0	0
Ateleopodiformes	1	4	12	0	0
Aulopiformes	15	44	236	0	0
Myctophiformes	2	35	246	0	0
Lampriformes	7	12	21	0	0
Polymixiiformes	1	1	10	0	0
Percopsiformes	3	7	9	9	9
Gadiformes	9	75	555	1	2
Ophidiiformes	5	100	385	5	6
Batrachoidiformes	1	22	78	6	7
Lophiiformes	18	66	313	0	0
Mugiliformes	1	17	72	1	7

Order	Families	Genera	Species	Freshwater Species	Species Using Freshwater
Atheriniformes	6	48	312	210	240
Beloniformes	5	36	227	98	104
Cyprinodontiformes	10	109	1,013	996	1,008
Stephanoberyciformes	9	28	75	0	0
Beryciformes	7	29	144	0	0
Zeiformes	6	16	32	0	0
Gasterosteiformes	11	71	278	21	43
Synbranchiformes	3	15	99	96	99
Scorpaeniformes	26	279	1,477	60	62
Perciformes	160	1,539	10,033	2,040	2,335
Pleuronectiformes	14	134	678	10	20
Tetraodontiformes	9	101	357	14	22
Coelacanthiformes	1	1	2	0	0
Ceratodontiformes	3	3	6	6	6
Totals	515	4,494	27,977	11,952	12,457

Although various peoples during history have no doubt had an appreciation of species numbers, our current number of known species has grown from about 144 in the days of Pliny, about 77 A.D. (in *Natural History*, Book 32, Chapter 53, lines 142 d-e, Loeb edition); the number 144 is considered more accurate than the number 176 that is given in some translations but may refer to what we think of as genera (pers. comm., Julian Martin, Dept. History and Classics, University of Alberta). The number of species of fishes recognized as valid (ideally, new species less synonymized species) has increased quite dramatically over recent years, as is reflected in the numbers that were given in the previous editions of this book: Nelson (1976), 18,818 in 450 families; Nelson (1984), 21,723 species in 445 families; and Nelson (1994), 24,618 species in 482 families.

IMPORTANCE TO PEOPLE

Fishes, like many other forms of life, are of immense value to humans. They have long been a staple item in the diet of many peoples, leading to the downfall of many species. Today they form an important element in the economy of many nations while giving incalculable recreational and psychological value to the naturalist, sports enthusiast, and home aquarist. Some fishes are dangerous (e.g., poisonous, stinging, shocking, or biting) and are of immense concern in some parts of the world. Fishes are also the subject of international and domestic agreements and disagreements. Many government institutions are devoted to the study of their biology and propagation. Particular aspects of various species lend themselves to studies in behavior, ecology, evolution, genetics, and physiology. They are used as general indicators or summators of pollution, partly to the direct benefit of humans and partly to protect what people consider a valuable and necessary part of their heritage and life. We consider it desirable to maintain the diversity that systematists study, and systematists can play a leading role in protecting this diversity. We recognize the value of and our dependency upon fishes and other organisms, but our threats to the integrity of the environment pose a serious threat to our fishes. There is continuous need for large efforts to do more systematic research and conduct censuses in differing areas. It is a sad commentary on our times that much effort must be spent on designating the status of species: whether they are at risk of becoming endangered or extinct due to human causes. These concerns occupy the attention of many committees and agencies. There are continuing concerns over problems of extinction in both freshwater and marine species, with much conservation effort spent on saving populations and species.

BIOLOGICAL DIVERSITY

Fish behavior is as diverse as fish morphology. Some species travel in schools, while others are highly territorial. Interesting commensal relationships exist with other fishes and other animals. Fishes are adapted to a wide variety of foods. Some are specialized or highly adapted to feed on such items as zooplankton, snails, and coral. Almost all classes of animal and some plants can serve as food. A few species have a parasitic mode of feeding on other species or on the female of their own. Some produce venom, electricity, sound, or light. Most fishes are ectotherms, but some sharks and some scombrids have evolved endothermy for at least part of their body. Internal fertilization occurs in certain species, and females of some of these species provide nutrients to developing embryos. Some exhibit parental care for their offspring, and others scatter millions of eggs to the hazards of predation. Whereas most fishes are gonochoristic (fixed sexual pattern), many are hermaphroditic. Most of the latter are protogynous (vs. protandrous) sequential (vs. synchronous) hermaphrodites, as in labrids, where females change to males. Some fishes have a larval stage and undergo metamorphosis.

Lifespan in fishes may vary from a little over 1 year to about 120 years. A few die relatively soon after a single spawning period (a phenomenon termed semelparity), but individuals of most species normally reproduce for more than one season (iteroparity). Fewer than 1% of fishes are semelparous, and these tend to be diadromous species. Semelparity is known primarily in petromyzontiforms, anguillids, some *Pimephales* (a cyprinid), some populations of osmerids, some galaxioids (e.g., some *Retropinna*), five species of Pacific salmon (*Oncorhynchus*), *Labidesthes sicculus* (an atherinopsid), and a few gobiids. Fishes in all types of aquatic environments may migrate phenomenal distances and use various homing mechanisms, a subject rich in questions for researchers. The larvae and early juveniles of some oceanic species (e.g., flyingfishes and dolphinfishes) regularly inhabit shore waters, whereas the larvae of many shore fishes inhabit oceanic waters. In freshwater, *Oncorhynchus keta* and *O. tshawytscha* migrate 3,000 kilometers (km) up the Yukon River to their spawning grounds without feeding. Other fishes are known to live out their lives in very restricted areas.

HABITAT DIVERSITY

Fishes live in almost every conceivable type of aquatic habitat. They are found at elevations up to 5,200 meters (m) in Tibet, where some nemacheilines live in hot springs, and in South America's Lake Titicaca, the world's highest large lake (3,812 m in elevation), where a group of cyprinodontids have undergone much radiation. Fishes also live in Lake Baikal, the world's deepest lake (at least 1,000 m), and 7,000 m below the surface of the ocean. A few species make short excursions onto land. Some species live in almost pure freshwater of 0.01 parts per thousand (ppt) total dissolved solids (most lakes are between 0.05 and 1 ppt), and others live in very salty lakes of 100 ppt (ocean water is about 34–36 ppt). Subterranean, or hypogean, fishes may be confined to total darkness in caves or other underground areas, or—as in Tibet, China, and India—to fast torrential streams (Proudlove, 2005, discussed these fishes). In Lake Magadi, Kenya, a soda tilapia, known as *Oreochromis alcalicus* or *Alcolapia grahami*, occurs in hot soda lakes that have temperatures as high as 42.5°C (the systematics of these fishes has been studied by L. Seegers and colleagues and their physiology has been studied by C. M. Wood and colleagues). At the other temperature extreme, *Trematomus* lives at about –2°C under the Antarctic ice sheet. Some fishes also live in deep-sea thermal vents in the eastern Pacific Ocean. An individual species may tolerate a wide range of temperatures, in which case it is said to be eurythermal, or a narrow range (stenothermal). Similarly, it may tolerate a wide range of salinity (euryhaline) or only a narrow range (stenohaline). Many species have acquired air-breathing organs, being essentially independent of water for respiration, and live in stagnant, tropical swamps; others demand well-oxygenated waters to sustain life.

MORPHOLOGICAL DIVERSITY

Fishes range in size from an 8–10-millimeter (mm) adult goby in the Indian Ocean (some other groups have some almost equally small species, e.g., cyprinids and schindleriids) to the giant 12-m Whale Shark. They have string-like to ball-shaped bodies. Some species are brilliantly colored; others are drab. Some are sleek and graceful, moving with little resistance through the water (which is 800 times denser than air); others are described by the general public as ugly and grotesque, their livelihood not depending on speed.

Over 50 species of teleosts lack eyes and live in caves (mostly cyprinids, balitorids, siluriforms, amblyopsids, bythitids, and gobiids). Scales may be present or absent in closely related species. Fins may be missing (particularly the pelvic fins, especially in eel-like, burrowing species) or be highly modified into holdfast organs or into lures for attracting prey. Some teleost species lack both the pelvic and pectoral fins and scales. Piscine bodies may be inflatable or encased in inflexible bony armor. Internally, anatomical diversity in hard and soft parts is also enormous. Many bizarre specializations exist. Insights into morphological diversity will be found throughout the text.

CLASSIFICATION AND SYSTEMATICS

Classification is the practice of arranging items into groups or categories, and a classification is the resulting arrangement. Taxa (singular taxon) are groups of organisms recognized in a classification and given biological names (e.g., Salmoniformes, Salmonidae, *Oncorhynchus, Oncorhynchus nerka*). A category is the level or rank at which the taxon is placed (e.g., order, family, genus, species). Generally, the objective in constructing a classification of a group of organisms is to show in a hierarchical system the relationships of the various taxa. We may agree that the kind of relationship we wish to show, as best we can in a listing of names, is an evolutionary one. However, there have been differences of opinion as to what evolutionary relationship means and how it should be determined, and there have also been different ways of expressing evolutionary relationships or phylogeny in a classification. Students working with older literature must be aware of these differences. Classifications are now based, when possible, on postulated genealogical branching points (the cladistic methodology), as attempted in the previous edition (Nelson, 1994) and in this edition. The classification in Nelson (1976, 1984) also considered degrees of divergence.

The fundamental unit in a biological classification is the species, and those involved with constructing classifications must deal with species definitions. I prefer the biological species concept (as a concept, not usually a working definition) (e.g., Nelson, 1999) and regard the species as the only taxonomic unit with evolutionary reality. It is inferred to represent an irreversible evolutionary discontinuity. Of course, in any work such as this, it is not possible in giving estimates of species numbers to expect uniformity of species concepts between workers on different families. Some taxonomists in their revisionary work may adhere to the biological species concept and some may not. Definitions that recognize a species as any terminal clade or as any genetically distinct population would, of course, result in a marked but artificial increase in species numbers that I would prefer not to recognize. Such definitions may result in potentially relatively unstable evolutionary units, and this seems to me to be undesirable to employ in management, systematics, and biology in general (other effective means exist for recognizing differences within a species for any given objective—see also above under "Numbers").

The science of systematics, in studying the relationships of species, is the study of the diversity of organisms in order to understand the evolutionary history of life (practice, methods, and principles thereof). Biological classification is based on systematic studies. Taxonomy is that part of systematics dealing with the theory and practice of describing diversity and erecting classifications. During the past few decades there has been an impressive accumulation of information on extant and fossil material and on morphological and molecular-based phylogenies. More work is needed on species diversity and on analyzing various characters to determine homologies before we reach a sound understanding of how evolution has produced the diversity of fishes that exists. Numerous families of fishes are very poorly classified. In addition, cladograms produced by employing molecular characters and their comparison with morphologically based cladograms promise to give us new insights to aid in our understanding of relationships. Although there is general agreement on many aspects of fish classification, there is also much disagreement. Conflict is especially prominent between some morphological and molecular-based phylogenies, although it is encouraging to see so much agreement in some areas. Reference is made throughout the classification to differences in some of the morphological and molecular-based classifications (see also, for example, under Acanthopterygii). It was not possible to refer to all relevant literature, and in any event, it behooves nonsystematists relating their findings to systematic work to refer back to the primary literature.

The study of fish systematics—ichthyology in the limited sense of the word—has had a long and interesting history. The history of Canadian and American ichthyology is reviewed by J. R. Dymond, G. S. Myers, and C. L. Hubbs in *Copeia* of 1964 (No. 1). In 1997, T. W. Pietsch and W. D. Anderson, Jr., edited the book *Collection Building in Ichthyology and Herpetology*, published by the American Society of Ichthyologists and Herpetologists, which gave good insights into some of the giants of our past. Some of the history of collection building and the challenges facing natural history museums and biodiversity research in Asia are discussed by Matsuura (2000) and Akiyama et al. (2004). During the history of ichthyology, numerous classifications of fishes have been proposed throughout the world. Although our present classifications and methods are improvements over past ones, we should not forget that our current efforts are made far easier by the contributions of past biologists, often working under great difficulty, such as P. Artedi (considered by many as the "Father of Ichthyology"), J. Müller, L. Agassiz, M. E. Bloch, G. Cuvier, A. Valenciennes, P. Bleeker, T. N. Gill, B. A. Boulenger, A. Günther, D. S. Jordan, C. T. Regan, S. Tanaka, K. Matsubara, G. S. Myers, C. L. Hubbs, and D. E. Rosen. Thankfully, there are many active masters still with us. Many younger contemporary ichthyologists are making important contributions, but the field will remain rich in problems for future generations of researchers. Unfortunately, while there is a growing need for a young generation of taxonomists/systematists, there are concerns that this need will not be met unless there are changes in government and public support for future positions.

Students of ichthyology should know the principles and methodology of cladistic (= phylogenetic) systematics and classification, where, in simple terms, the systematist seeks to resolve which two taxa of a group of three or more are each other's closest genealogical relatives. A dichotomously branching cladogram (diagram) is constructed in which paired lineages, called sister groups, are recognized on the basis of sharing derived character states (termed synapomorphies, with a particular derived character state being termed apomorphic; plesiomorphies are the primitive states and do not indicate the existence of sister groups). The sister group possessing more apomorphic character states relative to the other is the derived group, while the other is the primitive one; each is given or is understood to have the same taxonomic rank. A common source of disagreement is over which character states are apomorphic; consequently, a good understanding of the distribution of character states and homology is essential to a cladistic analysis. As with any approach, one must take care that characters are not arbitrarily chosen or their states arbitrarily polarized, consciously or subconsciously, for the express purpose of either producing a change in existing classification or supporting preconceived ideas of relationships (perhaps to provide systematic evidence to support a favored biogeographic hypothesis). In identifying sister groups, cladograms allow the systematist and nonsystematist to focus clearly on questions and test hypotheses concerning the evolution of given traits, whether morphological, behavioral, or physiological.

In a cladistic analysis, there is usually a clear presentation of the character states employed (but, unfortunately for those wishing to appraise the work, characters discarded from analysis are generally not given). Polarity of morphoclines or of character states is determined by evidence from ontogeny or, more usually, by reference to what is called the out-group (the nearest presumed related taxon or taxa—a character state widely distributed in related taxa is taken to be primitive) with the group under consideration being called the in-group. Computer programs assist in analyzing data to construct phylogenetic trees (cladograms).

It is important for nonsystematists who rely on classifications in their studies to remember that in some cladistic studies new classifications are constructed on the basis of only a few weak synapomorphies. In addition, often not all species are examined, resulting in a poor knowledge of character distribution. Such practices are not likely to produce a sound and stable evolutionary classification (certainly not a utilitarian one), any more so than is a synthetic study based on ill-chosen characters or a phenetic study based on overall similarity. Apart from methodological problems or problems resulting from poor practice, there appears in some groups to be such a mosaic of character states of uncertain polarity that a stable cladistic analysis may be difficult to establish.

There are many problems in translating a phylogeny into a classification. Ideally, the classification is based solely on the hypothesized genealogical relations such that one is faithfully derivable from the other. Each taxon is strictly monophyletic, in that all groups sharing a common ancestry and only those groups, including the common ancestor itself, are included in the taxon. In this book, a cladistic classification is employed wherever I feel that there is reasonably sound phylogenetic information to present such a classification, whether based on molecular or morphological data. Where the evidence seems uncertain, I maintain the status quo. There are a great many groups that we know to be paraphyletic, but we lack sufficient evidence to erect monophyletic taxa.

I consider fossils to be critical in understanding evolutionary relationships. Unfortunately, the fossil record in fishes is very incomplete, and many decisions must be made without any evidence from fossils. However, we can answer many critical questions of interrelationships of higher taxa only with a study of new fossils and not, conclusively at least, from extant material. Fossils are ranked along with extant taxa in the classification of this book.

DISTRIBUTION AND BIOGEOGRAPHY

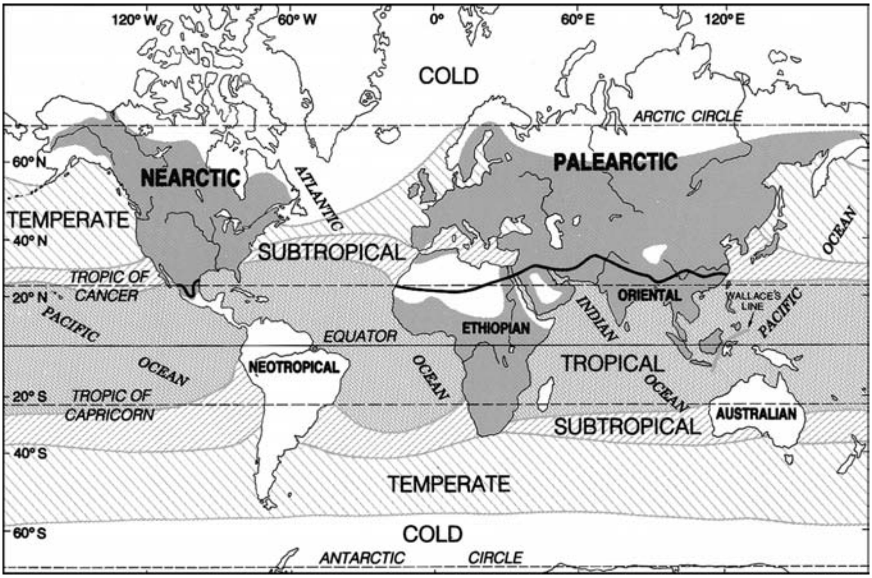
Fishes occur in lakes, streams, estuaries, and oceans throughout the world. In most species of fishes, all individuals live entirely either in fresh or in marine waters. Over 225 species are diadromous, regularly living part of their lives in lakes and rivers and part in the oceans. Among these, most are anadromous, spawning in freshwater but spending much of their time in the sea. A few are catadromous, spawning in the oceans but returning to freshwater. Classification of some species as marine, diadromous, estuarine, or freshwater is impossible, except as a generalization. Just as in an otherwise marine family there may be one species confined to freshwater, so in some species there are populations that occur in an environment opposite that of most others. Individuals of some otherwise marine species ascend rivers for short distances in part of their range, and those of some species that are usually freshwater are anadromous in some areas. Many freshwater and marine species are also common in brackish-water estuaries. It appears to be evolutionarily easier for marine fishes to move into freshwater than for freshwater fishes to move into the oceans. About one-third of the 515 families have at least one species with individuals that spend at least part of their life in freshwater. Berra (2001) gives much information and distribution maps for the freshwater fish families. About 11,952 species, or 43% of all species, normally live exclusively in the freshwater lakes and rivers that cover only 1% of the earth's surface and account for a little less than 0.01% of its water (the mean depth of lakes is only a few meters). About 15,800 species usually live all their lives in the oceans, which cover 70% of the earth's surface and account for 97% of its water, and have a mean depth of about 3,700 m. This descriptive information does not imply restriction to a freshwater or marine habitat, or inability to cross regions of the opposite habitat over long periods of time for all the taxa involved.

Many environmental factors influence just where a certain species will predominate. Competition and other biological interactions may exert a strong influence along with physicochemical factors. In freshwater environments, species may show a preference for lakes or streams. Variations in preferences may exist over the range of a species. Among lakes they may show a preference for deep, cold, oligotrophic lakes or for shallower, warmer, and more productive mesotrophic and eutrophic lakes. In lake waters they may show a preference (horizontal and vertical) for the open-water limnetic zone, the benthic area, or shallow littoral areas. Fishes may even be restricted to certain types of bottom or do best under certain physicochemical conditions. Stream fishes may prefer riffle or quiet areas, and a zonation of species is usually found from the headwaters to the mouth. In the oceans the vast majority of fishes are coastal or littoral. Most of those living beyond the 200-m-deep continental shelf (oceanic species) are deep-sea (mesopelagic, bathypelagic, abyssopelagic, or benthic at various depths); only a small minority regularly live close to the surface in the well-lighted upper 200-m zone (epipelagic), a region much larger in volume than the coastal waters. The epipelagic and mesopelagic fishes, which consist of both large predators and small plankton feeders, are varied, whereas most of the bathypelagic and abyssal fishes are relatively small.

Many species, both geologically young and old, have small ranges; the smallest is perhaps that of the Devils Hole Pupfish, *Cyprinodon diabolis*, found only in one spring in Ash Meadows, Nye County, Nevada. Many areas have a high degree of endemism. Marine fishes face the obvious land barriers (notably the New and Old World land masses) and midocean barriers as well as many ecological and physiological barriers; freshwater species are limited by marine and land barriers. Some species have remarkably large ranges, and it would be interesting to know why some of their relatives have small ranges.

About 130 marine species are known to extend around the world in tropical or subtropical waters. Many genera are represented in both the Pacific and Atlantic, but, almost always, different species are involved. Representatives of many marine genera and of some species occur in the temperate and polar faunas of both hemispheres. Individuals of some of these bipolar or antitropical taxa are surface-bound; others are deepwater. The vast majority of species, however, are tropical; most of the rest occur only in the Northern or only in the Southern Hemisphere. We know little of the abyssal depths and their species composition. Many abyssal species have been found at widely separated localities, which suggests that some may be virtually worldwide. No freshwater species is circumtropical, but two species, *Esox lucius* and *Lota lota*, are circumpolar and several others are almost so. No genus of freshwater fish has an antitropical distribution. Many freshwater fishes have shown a remarkable ability to disperse across newly exposed land areas following glaciation. In addition, they may occur in isolated waters in deserts as a result of a reduction of waters from times when drainage systems were connected.

In both fresh and marine waters, the largest number of species occurs in the tropics. There is a reduction toward the polar areas, although numbers of individuals in certain northern species are large. A great many species of freshwater fishes occur in tropical Africa, southeastern Asia, and the Amazon River—by far the world's largest river. For a tropical region, Central America has relatively few freshwater species because of the physiography and geological history of the area. Most oceanic islands lack indigenous fishes confined to freshwater, and continental areas recently exposed from the last ice age—for example, northern regions of North America, Europe (especially western Europe), and Asia—tend to have a relatively sparse fish fauna. In tropical areas, Africa exhibits the greatest diversity of nonostariophysan freshwater fishes; South America exhibits surprisingly little. In temperate areas, eastern North America shows the greatest diversity in nonostariophysan fishes. In marine waters, the Indo-West Pacific (Red Sea and Indian Ocean to northern Australia and Polynesia) is the richest, with the most species occurring in the New Guinea to Queensland area. In terms of diversity, southeastern Africa and Queensland appear to have the largest number of families of marine shorefish. The West Indian or Caribbean fauna (southern Florida to northern Brazil) is also a rich one. The western African fauna, however, is relatively poor. Arctic and Antarctic faunas are depauperate. In all, the greatest number of fish species in the world inhabit the southeastern Asian region.



Broad surface thermal zones of the ocean, biogeographic regions of the continents, and native distribution of the family Cyprinidae, the most species-rich family of vertebrates. The biogeographical regions express degrees of endemism and are useful indicators of numbers and proportion of endemic organisms. I rarely use the continental regions in the text, and ichthyologists do not use them as much as in former times; the Nearctic and Palearctic are frequently combined into one region, the Holarctic. The thermal divisions of the sea denote tropical (or warm), subtropical, temperate, and cold (or polar) waters; warm temperate is sometimes used for all or part of the subtropical and warmer parts of the temperate (vs. cool temperate) waters. Surface isotherms, used to define thermal regions, are subject to seasonal and annual changes. Major biogeographic regions recognized in the oceans include the Indo-West Pacific, tropical western Atlantic, tropical eastern Atlantic, North Pacific, North Atlantic, and Mediterranean-East Atlantic. Marine oceans share different similarities with one another; for example, in many families the tropical eastern Pacific shows a greater resemblance to the western Atlantic than to the Indo-West Pacific because of the mid-Pacific barrier and the relatively recent marine connection across the Isthmus of Panama. Information on the generalized thermal zones is based partly on Briggs (1974) and modified by numerous other sources. Distribution of the family Cyprinidae, shown by the shaded land area, is based on Berra (2001) and papers in Winfield and Nelson (1991).

The science of biogeography attempts to document the geographic distribution of taxa (descriptive biogeography) and to explain their distributional patterns (interpretive biogeography). It is an active field of study in ichthyology and is rich in problems. There are two extreme approaches to interpretive biogeography. First, ecological biogeography attempts to determine the environmental factors—such as oxygen concentration, temperature, turbidity, salinity, currents, and competition—limiting the distribution of individuals of a species within a body of water or over the range of the species. Second, historical biogeography attempts to explain the origin of distributional patterns and is usually done in conjunction with, and is based upon, systematic studies. Of course, this includes paleontological studies, where the age of fossils must be fairly considered (remembering that fossils indicate minimum ages and that their record is very spotty). Factors such as presumed paleoclimatic changes are often invoked in historical biogeography, especially when postulating that discontinuous distributions result from dispersal events. Aspects of both ecological and historical biogeography, combined with a knowledge of geology, geography, and systematics (usually below the species level), are important in studies of species dispersal following glaciation (such as in northern Eurasia, North America, and New Zealand) or uplift of land from the ocean (Central America, for example), or of dispersal through drainages submerged following glaciation (such as Indonesia).

Various methodological and philosophical approaches are used to explain the origin of distributional patterns of fishes, including areas of endemism. Both dispersal and vicariant events are important. Dispersal is regarded here as the movement, active or passive, of individuals to areas new to the existing population. Barriers of varying effectiveness may be involved as well as varying degrees of chance of reaching particular sites. It is of greatest biogeographic significance if the breeding range of the species is increased. Vicariance is the fragmentation of a former continuous distribution of the ancestral group into geographically separated units through the appearance of a barrier—for example, through plate tectonics. Both dispersal and vicariant approaches are used to explain disjunct distributions (the occurrence of a taxon in different areas with a marked geographical gap between them).

Examples of disjunct distributions include the following: occurrence of *Prosopium coulteri* in western North America and in Lake Superior; *Geotria australis* and *Galaxias maculatus* in Australia, New Zealand, and South America; cottids and agonids in cool temperate waters of the Northern and Southern Hemispheres; characiforms and aplocheiloids in Africa and South America; and osmeriforms in temperate waters of the Northern and Southern Hemispheres. Plate tectonics had a profound effect on the distribution of many freshwater and marine fishes (e.g., it probably explains the occurrence of characiforms in South America and Africa).

Students should read widely on the subject. There are many recent books available on biogeography and numerous articles in such journals as *Cladistics, Journal of Biogeography,* and *Systematic Biology.* The fields of systematics and biogeography are attracting much exciting activity. There is every reason to believe that future ichthyologists will keep the field alive, and that we will achieve a stronger understanding of relationships and explanations of distributional patterns.

Phylum Chordata

Chordates are placed in the superphylum Deuterostomia. The possible relationships of the chordates and deuterostomes to other metazoans are discussed in Halanych (2004). He restricts the taxon of deuterostomes to the chordates and their proposed immediate sister group, a taxon comprising the hemichordates, echinoderms, and the wormlike *Xenoturbella.*

The phylum Chordata has been used by most recent workers to encompass members of the subphyla Urochordata (tunicates or sea-squirts), Cephalochordata (lancelets), and Craniata (fishes, amphibians, reptiles, birds, and mammals). The Cephalochordata and Craniata form a monophyletic group (e.g., Cameron et al., 2000; Halanych, 2004). Much disagreement exists concerning the interrelationships and classification of the Chordata, and the inclusion of the urochordates as sister to the cephalochordates and craniates is not as broadly held as the sister-group relationship of cephalochordates and craniates (Halanych, 2004).

Many exciting fossil finds in recent years reveal what the first fishes may have looked like, and these finds push the fossil record of fishes back into the early Cambrian, far further back than previously known. There is still much difference of opinion on the phylogenetic position of these new Cambrian species, and many new discoveries and changes in early fish systematics may be expected over the next decade. As noted by Halanych (2004), D.-G. (D.) Shu and collaborators have discovered fossil ascidians (e.g., *Cheungkongella*), cephalochordate-like yunnanozoans (*Haikouella* and *Yunnanozoon),* and jawless craniates (*Myllokunmingia,* and its junior synonym *Haikouichthys*) over the last few years that push the origins of these three major taxa at least into the Lower Cambrian (approximately 530–540 million years ago). The Lower Cambrian jawless (agnathan) vertebrate specimens, of about 530 million years age, lacking bone but with well-preserved soft anatomy, were found in Yunnan, China (Janvier, 1999; Shu et al., 1999). Shu et al. (1999), in reporting this discovery, presented a phylogeny suggesting that *Myllokunmingia* is sister to the remaining vertebrates and *Haikouichthys* is sister to a clade with lampreys. Shu et al. (2003a), in describing additional detail from more specimens of *Haikouichthys ercaicunensis,* felt it either formed a trichotomy with hagfishes and all other vertebrates (and possibly is a stem craniate), or that it is the sister group to all other vertebrates except hagfishes, in a position similar to that of *Myllokunmingia.* In further clarification, Xian-guang et al. (2002) described details of a new specimen co-occurring with the nominal *Myllokunmingia fengjiaoa* and *Haikouichthys ercaicunensis* and concluded that all are conspecific; the oldest name *Myllokunmingia fengjiaoa* is appropriate. Characters include filamentous gills, V-shaped myomeres, and a distinct dorsal fin (the latter indicating a more derived condition than in the hagfish). Their phylogenetic analysis suggested that *Myllokunmingia* is either the sister group to the lampreys, or the sister group to the lampreys plus skeletonized vertebrates. Shu et al. (2003b) and Shu and Morris (2003) proposed that the Lower Cambrian yunnanozoans, *Haikouella* and *Yunnanozoon,* are stem-group deuterostomes, and questionably placed them in the phylum Vetulicolia, class Yunnanozoa, family Yunnanozoidae (= Yunnanozoonidae) (with the relationship to fossil calcichordates being unknown). However, in presenting a different interpretation of the possible phylogenetic position of *Haikouella,* Mallatt et al. (2003) interpreted it as not just a nonchordate stem-group deuterostome, but as the immediate sister group of vertebrates.

A classification of the major taxa of the phylum Chordata, as an overview of what follows, is as follows:

Phylum Chordata
  Subphylum Urochordata
  Subphylum Cephalochordata
  Subphylum Craniata
    Superclass Myxinomorphi (with their sister group being the vertebrates, which comprise the following additional six jawless craniate or agnathan taxa and the gnathostomes, each ranked at the same level and sequenced as follows):
    Superclass Petromyzontomorphi
    †Superclass Conodonta
    †Superclass Pteraspidomorphi
    †Superclass Anaspida
    †Superclass Thelodonti
    †Superclass Osteostracomorphi (possible sister group being the gnathostomes, as given below)
    Superclass Gnathostomata (jawed vertebrates)
      †Class Placodermi

Class Chondrichthyes (cartilaginous fishes, e.g., chimaeras, sharks, and rays)
†Class Acanthodii
Class Actinopterygii (ray-finned fishes)
Class Sarcopterygii (includes coelacanths, lungfishes, and tetrapods)

SUBPHYLUM UROCHORDATA (Tunicata: the tunicates)

Their tadpole larvae possess gill slits, dorsal hollow nerve cord, notochord, and a muscular, unsegmented tail; the adults are usually sessile filter feeders and usually lack the preceding features. Feeding is by means of a mucous trap inside the pharynx as in cephalochordates and ammocoete larvae. An endostyle, homologous with the thyroid, is present.

About 1,600 extant species are known.

Class ASCIDIACEA

Larvae free-swimming, tadpolelike (short-lived and nonfeeding); adults sessile benthic, solitary or colonial, and without a tail.

Ascidians are marine and worldwide, extending from the intertidal to well into the abyssal-benthic region.

Class THALIACEA (salps)

Larvae and adults transparent; pelagic (adults may be solitary or colonial). They tend to be planktonic but are generally capable of weak movements. Remarkable life cycles are characteristic of this group, with sexual and asexual reproductive stages occurring.

Order PYROSOMIDA. Marine seas except the Arctic. Tubular colonies with a common atrial chamber. They can emit a strong phosphorescent light. The colonies usually vary in length from about 3 cm to 1 m.

Order DOLIOLIDA (Cyclomyaria). Marine; primarily tropical to temperate. Generally barrel-shaped with eight or nine muscle bands around the body.

Order SALPIDA (Hemimyaria). Marine, all seas. Cylindrical or prism-shaped.

Class APPENDICULARIA (Larvacea)

Pelagic; Arctic to Antarctic. Larval characteristics (such as the tail) are retained in the adult.

SUBPHYLUM CEPHALOCHORDATA (Acrania, in part)

The notochord extends to the anterior end of the body, in front of the brain. No cranium; no vertebrae; no cartilage or bone; heart consisting of a contractile vessel; no red corpuscles; liver diverticulum; segmented musculature; epidermis with a single layer of cells; protonephridia with solenocytes for excretion; endostyle present (with iodine-fixing cells, it may be homologous with the thyroid of vertebrates), produces mucus that entraps food particles; true brain absent, but two pairs of cerebral lobes and nerves present; sexes separate.

About 30 species; no fossil record unless *Pikaia* from the Middle Cambrian Canadian Burgess Shale is a cephalochordate, or possibly some Lower Cambrian fossils from China noted above under phylum Chordata.

Cephalochordates and vertebrates share the following attributes (some also present in the urochordates): notochord present (at least in embryo), a dorsal tubular central nervous system, paired lateral gill slits (at least in embryo), postanal tail, hepatic portal system, and endostyle (homologous with the thyroid).

Order AMPHIOXIFORMES (lancelets). The lancelets (or amphioxus) are small (up to 8 cm long), slender, fishlike animals, probably close to the ancestral vertebrate lineage. They spend most of their time buried in sand or coarse shell gravel and occur primarily in shallow-water tropical and subtropical seas with some species extending into temperate waters as far north as Norway and as far south as New Zealand; they are particularly common off China. Feeding occurs by straining minute organisms from the water that is constantly drawn in through the mouth. A good coverage of lancelets was given in Poss and Boschung (1996) and other articles in the same issue.

Family BRANCHIOSTOMATIDAE. Marine; Atlantic, Indian, and Pacific.

Double row of gonads; metapleural folds symmetrical, located laterally along ventral side and ending near the atriopore, neither fold connected with the median ventral fin.

One genus, *Branchiostoma*, with about 23 species.

Family EPIGONICHTHYIDAE (Asymmetrontidae). Marine; Atlantic, Indian, and Pacific.

Gonads present along right side only; metapleural folds symmetrical, right fold continuous with ventral fin, which passes to the right of the anus, and left fold ending behind atriopore.

One genus, *Epigonichthys* (synonyms *Asymmetron*, *Heteropleuron*), with about seven species, occurring primarily in the Indo-West Pacific.

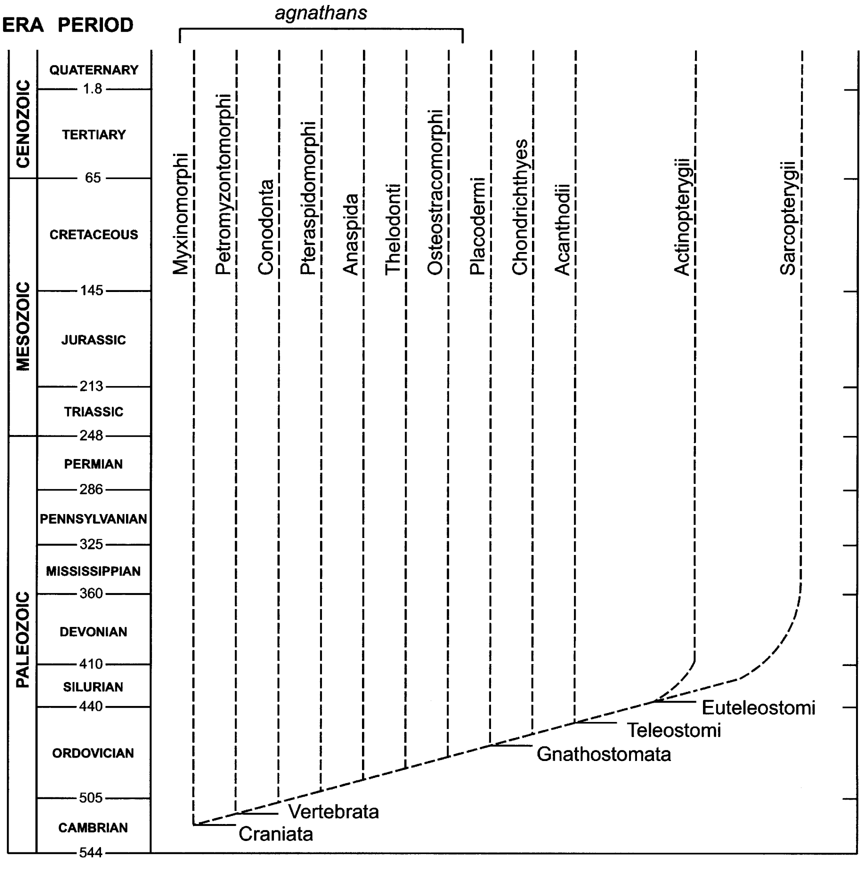
SUBPHYLUM CRANIATA

Notochord never extends in front of brain; cranium present; vertebrae usually present; cartilage or bone or both present; heart chambered; red blood corpuscles usually present; brain well developed; 10 to 12 pairs of cranial nerves; dorsal and ventral nerve roots usually united; nephridia absent; epidermis with several cell layers; endostyle only in larval lampreys (ammocoetes) and transformed into thyroid tissue in all others; sensory capsules present; neural crest formation present. The neural crest is a vertebrate innovation from which the first vertebrate skeletal tissue appears to have arisen (e.g., probably dermal bones, teeth, anterior neurocranium, and visceral arches). Maisey (2001a) reviewed the structure and function of the craniate inner ear and identified 33 apomorphic characters of the membranous labyrinth and associated structures in craniates, gnathostomes, and elasmobranchs.

The classification followed here is based on the cladogram and classification in Donoghue et al. (2000). These authors sequence the following taxa, using their terminology, in a successive sister-group relationship (i.e., each taxon not in the parenthetical comments is sister to, or forms a cladistic node with, all those that follow): Cephalochordata, Myxinoidea (I adopt the name Myxinomorphi, in part to avoid using the ending for superfamilies), Petromyzontida (I adopt the name Petromyzontomorphi), Conodonta, Pteraspidomorphi (with *Astraspis*, Arandaspida, and Heterostraci sequenced in that order), Anaspida, Thelodonti (represented by *Loganellia*), *Eriptychius* and its sister group, the jawed vertebrates (together forming their "Unknown group B"), and their plesion, unnamed group C (herein termed the Osteostracomorphi, with Osteostraci [the best known], Galeaspida, and Pituriaspida). The position of *Eriptychius* is particularly uncertain; it is not considered as sister to the jawed vertebrates in the following discussion (see under Astraspida below). It therefore follows that the sister group of the Gnathostomata (jawed vertebrates) is the Osteostracomorphi (the combined taxon is unnamed). The group that is sister to the Cephalochordata (in the above, Myxinomorphi-Gnathostomata) is called the Craniata, while the sister group to the Myxinomorphi (Petromyzontomorphi-Gnathostomata) is the Vertebrata. The other nodes are unnamed, and in the sequence from Myxini to Osteostracomorphi, I have given these sequenced and named higher taxa the rank of superclass (i.e., the Myxinomorphi, Petromyzontomorphi, Conodonta, Pteraspidomorphi, Anaspida, Thelodonti, and Osteostracomorphi), the same as that of the Gnathostomata. The order in which the main taxa are presented in Janvier (1996) differs in modest detail and is as follows (no sequencing sister-group relationships for successive taxa are implied and the terminology of Donoghue et al., 2000, is used with Janvier's names, if different, in parentheses): Myxinoidea (Hyperotreti), Arandaspida, *Astraspis* (Astraspida), Heterostraci, Anaspida, Petromyzontida (Hyperoartia), Osteostraci, Galeaspida, Pituriaspida, and *Loganellia* (Thelodonti).

The classification used in the previous edition (Nelson,1994), shown immediately below, has thus been considerably changed. The terms Craniata and Vertebrata are no longer used as synonyms (as in Nelson, 1994:23), but are employed, conventionally, at different levels, with Craniata used at the subphylum level and Vertebrata as an unranked taxon within the Craniata.

subphylum Cephalochordata
subphylum Conodontophorida
subphylum Vertebrata (= Craniata)
  superclass Agnatha
    class Myxini
    class Pteraspidomorphi (including the Arandaspidiformes, Pteraspidiformes, and Thelodontiformes)
    class Cephalaspidomorphi (including the Petromyzontiformes, Anaspidiformes, Galeaspidiformes, and the Cephalaspidiformes (=Osteostraci)
  superclass Gnathostomata



One speculative view of the affinities and time of divergence of the major groups of fishes. The approximate age between boundaries of periods is given in millions of years (based on The Geologic Time Scale, 2001, U.S. Geological Survey, Lyn Topinka). The Pennsylvanian and Mississippian (distinct in North America) are together equivalent to the Carboniferous outside North America. The Tertiary is subdivided into the Paleocene, Eocene, Oligocene, Miocene, and Pliocene. Fossils are often dated within the Cretaceous to the following ages in the Late Cretaceous as (oldest to youngest) Cenomanian, Turonian, Coniacian, Santonian, Campanian, and Maastrichtian, and in the Early Cretaceous (from the boundary of the Tithonian of the Jurassic) as Berriasian, Valanginian, Hauterivian, Barremian, Aptian, and Albian (borders the Cenomanian). The terms Late and Early refer to ages, whereas the terms Upper and Lower refer to stratigraphy.

Are agnathans (jawless fishes) monophyletic? This is a bothersome question that concerns one of several major conflicts in fish phylogeny between the results of molecular biology and morphological studies. The term "Agnatha" is no longer used as a taxon name, as it was in the 1994 edition; it applied in a conventional sense to all taxa from Myxini to Pituriaspida, recognized now as a paraphyletic group. However, the term "agnathan" is still a useful one that can be used to describe these jawless fishes. Two groups of jawless fishes that are also considered here to be paraphyletic groups are the cyclostomes and the ostracoderms. The term "cyclostome" is used for the living jawless fishes (hagfishes and lampreys); this group is considered by most paleontologists and others using morphological evidence to be a paraphyletic group, and is so recognized here. However, there is molecular evidence from Mallatt and Sullivan (1998), Mallatt et al. (2001), Kuraku et al. (1999), Delarbre et al. (2002), and Takezaki et al. (2003) that supports the monophyly of cyclostomes (an older idea, termed the "cyclostome hypothesis," and rejecting the hypothesis that lampreys are more closely related to gnathostomes than to hagfishes, termed the "vertebrate hypothesis"). This is a serious conflict with the phylogenetic ideas accepted here and one that must be resolved, ideally by obtaining independent results that are in agreement from both molecular biology and morphological studies, before we can be confident in the basic phylogeny of early craniates. Meyer and Zardoya (2003) suggested the desirability of having larger data sets with greater taxon sampling to better support either the cyclostome hypothesis or the vertebrate (lamprey-gnathostome) hypothesis. It is interesting, though, that lampreys are now placed in the next sequenced group up from hagfishes following Donoghue et al. (2000), rather than in the class Cephalaspidomorphi, and sister to the Anaspidiformes. This suggests that they could have diverged within a relatively short time span. The term "ostracoderm" is used for the fossil armored jawless fishes; this is agreed to be a paraphyletic group but phylogenetically closer to the jawed vertebrates than to either hagfishes or lampreys. Forey (1995) reviewed past theories of relationships of agnathans and gnathostomes and of character evolution.

The paraphyletic jawless fishes (agnathans) are characterized by the following characters: jaws that are derived from gill arches absent (a biting apparatus, not derived from gill arches, is present in some fossil forms and in hagfishes); no pelvic fins; one or two vertical semicircular canals (one canal but two ampullae reported in myxiniforms, at least two in pteraspidiforms); vertebral centra never present (only the notochord); gills covered with endoderm and directed internally; gill arch skeleton fused with neurocranium, external to gill lamellae; gills opening to surface through pores rather than through slits; bony exoskeleton in most.

There are about 17 genera and 108 extant species of extant jawless fishes in four families. The three major clades of craniates with living or extant species—hagfishes, lampreys, and gnathostomes—have a total of about 54,711 species.

SUPERCLASS MYXINOMORPHI

This taxon is thought to be the sister group of vertebrates and to be the basal craniate taxon. Extant hagfishes are excluded from the Vertebrata primarily because they lack arcualia (embryonic or rudimentary vertebral elements). This assumes that hagfishes are not degenerate forms of one of the vertebrate groups, and the evidence supports this assumption.

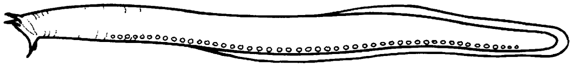
Class MYXINI

Order MYXINIFORMES (Hyperotreti) (1)—hagfishes. One semicircular canal (and one macula); single olfactory capsule with few folds in sensory epithelium, and olfactory nerves with separate bundles; no bone; lens and extrinsic eye muscles absent; 1–16 pairs of external gill openings; adenohypophysis with undifferentiated cellular elements, not divided into distinct regions (unlike in vertebrates); body naked, eel-like; no paired fins; no trace of lateral-line system in adults, neuromasts absent.

Hagfishes are unique among craniates in having only one semicircular canal, which is orientated so that it projects onto all three planes of rotation (lampreys have two and gnathostomes have three) (Jørgensen, 1998; McVean, 1998).

One family (the two subfamilies recognized here are given family status in some works). A probable fossil hagfish, *Myxinikela siroka*, of Pennsylvanian age (about 300,000,000 years ago), described in 1991, is known from a single specimen from Illinois (Bardack, 1998). Janvier (1996) speculated that the fossil *Gilpichthys*, of Mississippian age, might have affinities with the myxiniforms (see also below under Mayomyzontidae).

Family MYXINIDAE (1)—hagfishes. Marine, temperate zones of the world (and Gulfs of Mexico and Panama).



Dorsal fin absent (caudal fin extends onto part of dorsal surface); eyes degenerate; barbels present around biting mouth; teeth only on tongue, plus one on "palate"; dorsal and ventral nerve roots united; nasohypophyseal sac not blind, opening into pharynx; no spiral valve or cilia in intestinal tract; numerous mucous pores along body (shown in sketch); no cerebellum; ovaries and testes in same individual but only one gonad functional; eggs large, yolky, up to 30 per individual; no metamorphosis; low blood pressure. In stating that their eyes are degenerate, it is assumed that hagfishes evolved from an ancestor with eyes, and this is supported by the possible hagfish fossil *Myxinikela*, which is thought to have had relatively well-developed eyes (Bardack, 1998). There is some variation in the structure of their eyes. In *Eptatretus*, generally in shallower water than *Myxine*, the eye has a vitreous body and well-differentiated retina and lies beneath unpigmented skin (presumably the more primitive state), whereas the deepwater *Myxine glutinosa* lacks a vitreous body, has a poorly differentiated retina, and is buried beneath muscle (Locket and Jørgensen, 1998). The external nasohypophyseal opening is terminal, and it is through this opening that respiratory water passes backward to the gills (unlike lampreys).

Hagfishes are scavenger feeders, mostly eating the insides of dying or dead invertebrates and other fishes. They are the only craniate in which the body fluids are isosmotic with seawater. The mucous pores occur in two ventrolateral lines, each with about 70–200 slime glands that contain mucous cells and thread cells. The thread from the discharged thread cell of hagfishes probably gives tensile strength to the slime. The thread cell itself is not known from any other animals. The secreted slime may be important in feeding and for defense, where it may clog the gills of other fishes and cause suffocation. Hagfishes can go through knotting movements to free themselves from entanglement in slime, escape capture, or tear off food. Extensive information on hagfishes is found in Jørgensen et al. (1998). Maximum length is up to about 1.1 m, attained in *Eptatretus carlhubbsi.*

Seven genera with about 70 species. The following classification is based largely on Fernholm (1998), except for the recognition of the genera *Paramyxine* and *Quadratus.*

SUBFAMILY MYXININAE. Efferent branchial ducts open by a common external aperture on each side (i.e., only one pair of branchial openings). The pharyngocutaneous duct, which exits the pharynx behind the gills, is present only on the left side and probably functions to permit the pharynx to be flushed, thus clearing particles too large for the afferent branchial ducts. Four genera and about 25 species.

Myxine. Anal fin ending posterior to branchial aperture; 5 to 7 pairs of gill pouches. Atlantic and Pacific; about 21 species (Wisner and McMillan, 1995, and Fernholm, 1998, recognized 19, but *M. limnosa* is not recognized here for reasons given in Nelson et al., 2004, to which are added three species from Mincarone, 2001a; Mok and Kuo, 2001; and Mok, 2002).

Notomyxine tridentiger. The pharyngocutaneous duct opens separately to the exterior, leaving two apertures on the left side instead of one as in all other Myxininae (in which it opens into the left common branchial aperture). Buenos Aires to Tierra del Fuego.

Neomyxine biniplicata. A pair of short ventrolateral finfolds behind the branchial region (lateral finfolds are absent in other hagfishes). Cook Strait, New Zealand.

Nemamyxine. Anal fin extending anterior to branchial apertures. Two species, one from New Zealand and the other from southern Brazil, Uruguay, and northern Argentina (Mincarone, 2001b).

Subfamily Eptatretinae. Efferent branchial ducts open separately to the exterior with 5–16 external gill openings.

Three genera, *Eptatretus* (synonyms *Bdellostoma* and *Polistotrema,* 33), *Paramyxine* (8), and *Quadratus* (4), with about 45 species (McMillan, 1999; McMillan and Wisner, 2004; Mincarone, 2000; Mincarone and McCosker, 2004; Mok et al., 2001). Fernholm (1998), in recognizing 35 species, treated *Paramyxine* (with species from Japan and Taiwan) as a synonym of *Eptatretus*; however, it continues to be recognized by workers such as Mok (2001) and Mok et al. (2001) and is therefore included here. *Quadratus* was established for species of *Paramyxine* with nonlinear and crowded gill apertures by Wisner (1999), who recognized it in its own subfamily, Quadratinae. Wisner (1999) also placed *Paramyxine* (with gill apertures linear or near linear) in its own subfamily, Paramyxininae (giving three subfamilies rather than the one here). The two new subfamilies were distinguished from the Eptatretinae in having the first efferent branchial duct much longer than the last (versus all being about equal in length). I provisionally recognize the three genera, but place them in the same subfamily because there may be substantial variation in the pattern of the gill apertures (indeed, Fernholm, 1998, preferred regarding *Paramyxine* as synonymous with *Eptatretus* because of uncertainty of the validity of this character).

vertebrates. The following taxa, placed within seven superclasses, are recognized in the clade of vertebrates following Donoghue et al. (2000). This monophyletic group, with members possessing or inferred to be derived from ancestors with such features as a dermal skeleton and neural crest, is not formally ranked. However, for the following classification, it could be recognized as the infraclass Vertebrata.

Many of the earliest vertebrate remains are known from isolated microfossils (microvertebrates, ichthyoliths) such as scales and teeth. Their use in providing information on such things as origin, range, and distribution of taxa and for providing phylogenetic characters are reviewed by Turner (2004), particularly for thelodonts and chondrichthyans. In addition to the vast literature on taxa known only from microfossils, Dr. Susan Turner has published many articles in the Newsletter “Ichthyolith Issues.”

Anatolepis heintzi—*Anatolepis,* known from the Upper Cambrian to Lower Ordovician in Spitsbergen and Greenland, was originally described as an agnathan, but its placement as a vertebrate was later questioned. Smith and Sansom (1995), however, showed that dentine is present in the tubercles, and it is placed in the Vertebrata, but of unknown affinities, and not assigned to any higher taxon.

SUPERCLASS PETROMYZONTOMORPHI

Class PETROMYZONTIDA

Order PETROMYZONTIFORMES (Hyperoartii) (2)—lampreys. Two semicircular canals; seven pairs of external lateral gill openings; eyes well developed in adult, lateral (except in *Mordacia*); single median nostril (nasohypophyseal) opening between eyes with pineal eye behind; body naked, eel-like; no bone; no paired fins; one or two dorsal fins present; tail diphycercal (isocercal) in adults, hypocercal in ammocoete larvae; barbels absent; teeth on oral disc and tongue (except in fossil form); dorsal and ventral nerve roots separated; nasohypophyseal sac with external opening only; spiral valve and cilia in intestinal tract; small cerebellum; sexes separate; eggs small, not yolky, occurring in the hundreds (*Mordacia praecox*) to thousands; larval stage (ammocoete) undergoes radical metamorphosis in freshwater. All lampreys die shortly after spawning.

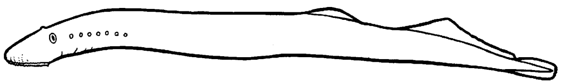
Lampreys are either parasitic or nonparasitic, and both life-history types characterize individuals of closely related species. It is believed that nonparasitic species have been independently derived from a parasitic species. The parasitic phase, after metamorphosis from the ammocoete larvae but before reproducing, goes through a period of feeding on blood from other fishes (very rarely on other animals) by rasping through their skin. The nonparasitic phase reproduces, without feeding, after metamorphosis. It is always confined to freshwater, whereas the parasitic form may be freshwater or anadromous. No parasitic freshwater lampreys are known from the Southern Hemisphere. Maximum length of larvae about 22 cm and parasitic adult about 1.2 m.

The sister group of the petromyzontiforms, previously thought to be myxinids, *Jamoytius kerwoodi,* or anaspidiforms, is now postulated to comprise all the following taxa (including the ostracoderms, i.e., all of the jawless and jawed vertebrates), following Donoghue et al. (2000). They were placed in the Class Cephalaspidomorphi in Nelson (1994).

The phylogenetic study of Gill et al. (2003) found a trichotomy between a monophyletic Northern Hemisphere clade (Petromyzontidae) and the Southern Hemisphere Geotriidae and Mordaciidae, and recommended that all three be treated as separate families. This recommendation is followed here. In the previous edition, all four lineages were recognized as subfamilies within the one family, Petromyzontidae.

Four families, one known only from fossils, and 10 genera with 38 extant species (Renaud, 1997; Gill et al., 2003; Kullander and Fernholm, 2003). Of the 38 species, 29 are confined to freshwater, and 18 feed parasitically as adults (and are generally said to be parasitic, but this usage is correctly understood by ichthyologists as not referring to them as parasites).

Family PETROMYZONTIDAE (2)—northern lampreys. Anadromous and freshwater; cool zones of the Northern Hemisphere, generally north of 30°N.



Three or four lateral circumoral teeth on each side of oral aperture (five or more in other lampreys); dorsal fins continuous or contiguous in mature adults (separate in other lampreys). (Gill et al., 2003, gave four unique characters.)

The following recognition of subfamilies is based on the cladogram of Gill et al. (2003). The subgenera recognized in *Lampetra* in Nelson (1994), with the exception of *Okkelbergia,* are recognized as genera following Renaud (1997) and Gill et al. (2003). The number of species follows Renaud (1997).

Eight genera as follows with 34 species.

SUBFAMILY PETROMYZONTINAE. Median velar tentacles absent (one or two in other lampreys). Two genera as follows.

Ichthyomyzon. Freshwater; eastern North America; three pairs of species (i.e., six species), each pair with an ancestral parasitic species and a nonparasitic derivative.

Petromyzon marinus. Anadromous (landlocked in Great Lakes region); Atlantic drainages of Canada, United States, Iceland, and Europe (including the Mediterranean); parasitic.

SUBFAMILY LAMPETRINAE. Tuberculated or papillose velar tentacles in most (smooth in other lampreys); 60 to 70 trunk myomeres in most (usually fewer than 60 or more than 70 in other lampreys).

Six genera as follows. According to the cladogram of Gill et al. (2003), *Caspiomyzon* is sister to the other five genera and *Tetrapleurodon* is sister to a clade comprising the remaining four genera, in which several nominal species exist that are of uncertain status and are not recognized here; these could be recognized in three sequenced tribes.

Caspiomyzon wagneri. Caspian Sea basin; probably parasitic.

Tetrapleurodon. Freshwater; Rio Lerma system of southern Mexico; nonparasitic and parasitic; two species, *T. geminis* and *T. spadiceus.*

Entosphenus. Anadromous and freshwater; coastal regions of North Pacific in North America and Asia; parasitic and nonparasitic; seven species.

Eudontomyzon. Freshwater; Black Sea drainage (primarily Danube basin), China, and Korea; parasitic and nonparasitic, four species.

Lampetra. Anadromous and freshwater; coastal regions of Europe and North America; parasitic and nonparasitic; seven species (this includes the nonparasitic *L. aepyptera,* southeastern United States, recognized in the subgenus *Okkelbergia* in Nelson, 1994).

Lethenteron. Anadromous and freshwater; circumarctic drainage basins, western Pacific coast south to Japan, coastal regions of western Alaska, eastern North America, and Adriatic Sea basin; parasitic and nonparasitic; six species.

Family GEOTRIIDAE (3)—southern lampreys. Anadromous; Southern Hemisphere, southern Australia, Tasmania, New Zealand, Chile, Argentina, and the Falkland and South Georgia islands.

Teeth on oral disc are spatulate-shaped (pointed or rounded in other lampreys); supraoral lamina (= supraoral plate) with two large centrally located teeth flanked by two lateral flanges; transverse lingual lamina strongly trident, bident at maturity; velar tentacles 23–32; two well-developed diverticula in midgut of ammocoetes; caudal and second dorsal fins well separated in the immature (continuous or contiguous in other lampreys); dorsal fins separate from each other in mature adults; approximately 180 mainly acrocentric chromosomes (Gill et al., 2003, gave 10 unique characters). Parasitic.

One species, *Geotria australis* (e.g., Hubbs and Potter, 1971; Kullander and Fernholm, 2003).

Family MORDACIIDAE (4)—southern topeyed lampreys. Anadromous and freshwater; Southern Hemisphere, southeastern Australia, Tasmania, and southern Chile.

Two discrete supraoral laminae (= supraoral plate); transverse lingual lamina incurved, largest cusps are median and at each lateral edge; velar tentacles fewer than 5; one well-developed diverticulum in midgut of ammocoetes; dorsal fins separate from each other in mature adults; eyes dorsolateral in immature and dorsal in mature (lateral to dorsolateral in other lampreys); 76 metacentric and submetacentric chromosomes (Gill et al., 2003, gave 10 unique characters). Parasitic and nonparasitic.

One genus, *Mordacia*, with three species (e.g., Hubbs and Potter, 1971; Kullander and Fernholm, 2003).

†Family MAYOMYZONTIDAE. Teeth absent.

The only species assigned to this family, *Mayomyzon pieckoensis*, described in 1968, is known from the Pennsylvanian Period (about 300,000,000 years ago) in Illinois from the same geological horizon as the fossil hagfish *Myxinikela* (Bardack, 1998). The specimens are all small in size but have adult characteristics. They are known from marine beds but need not have been marine themselves. Their known character states were compared to other lampreys in Gill et al. (2003).

A second species of fossil lamprey, *Hardistiella montanensis*, from the Mississippian Period (about 320,000,000 years ago) in Montana, is of uncertain relationship to *Mayomyzon*. This species retains a distinct hypocercal tail, has rays in the anal fin, and appears to lack an oral sucker. The number of gill openings cannot be determined. Other fossil agnathans include *Gilpichthys* and *Pipiscius*, but Bardack (1998) feels that they cannot be placed with any known family lineage.

†SUPERCLASS CONODONTA (conodonts)

†Class CONODONTA

The phylogenetic position of conodonts, known in the fossil record from the Cambrian to the Late Triassic and important as biostratigraphic indicators, has long been subject to much speculation. Some earlier workers thought that they might be related to early fishes (and therefore included in the chordates in Nelson, 1976). It has only been since the early 1990s, with the discovery of fossilized soft body parts, evidence of cellular bone, and a study of tooth histology, that convincing evidence has been published that they are craniates (but see Kemp, 2002, for evidence that they do not contain hard tissues characteristic of vertebrates), although I credit a 1987 study of R. J. Krejsa and H. C. Slavkin with providing evidence that they have a relationship to hagfishes. Conodonts were placed between the cephalochordates and the craniates in Nelson (1994), in the subphylum Conodontophorida. Placement here is based on Donoghue et al. (2000), who give a detailed discussion of their anatomy and placement. Conodonts are reviewed by Aldridge and Donoghue (1998), with additional information in Purnell et al. (2000).

†SUPERCLASS PTERASPIDOMORPHI

†Class PTERASPIDOMORPHI (Diplorhina)

Shield made of a large dorsal and ventral median plates; oak leaf–shaped tubercles on dermal bone; true bone cells absent (the acellular nature of the bone may be a primitive rather than a secondary condition, unlike "acellular" bone in higher fishes, which is derived from cellular bone); at least two semicircular canals.

Monophyly of this group was recognized by Blieck et al. (1991) and Gagnier (1993). This has been supported by Janvier (1996) and Donoghue et al. (2000), but they express differing views on the sister-group relations of the Astraspida, Arandaspida, and Heterostraci, here ranked as subclasses. The cladistic results of Donoghue et al. (2000), in finding *Astraspis* to be sister to the Arandaspida and Heterostraci, are followed here.

As with many fossil groups, especially the agnathans, it must be remembered that many character states are poorly known and only inferred (e.g., see descriptions in Janvier, 1996).

†Subclass ASTRASPIDA

Thick, glassy enameloid caps on the tubercles of the ornamentation; eyes small and laterally placed; gill openings at least eight, relatively large and with no cover; paired fins absent (Janvier, 1996).

†Order ASTRASPIDIFORMES. Marine North American and Siberian, Upper Ordovician to Lower Silurian, jawless vertebrates, comprising at least *Astraspis* (including *Pycnaspis*). The poorly known Ordovician *Eriptychius* (placed in the Eriptychiida) (e.g., Gagnier, 1993; Janvier, 1996) is placed here by some; however, Donoghue et al. (2000) raised the possibility, despite incomplete information, that it may be the sister group to the jawed vertebrates (gnathostomes).

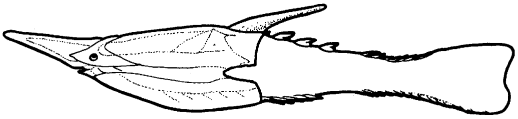
†Subclass ARANDASPIDA

Eyes in extreme anterior position, at tip of head; paired pineal and parapineal openings (the only vertebrate with this condition); at least 10 external branchial openings present (with individual bony covers); paired fins absent (Janvier, 1996).

†Order ARANDASPIDIFORMES. This group is composed of the Ordovician Southern Hemisphere marine taxa as follows: (i) from South America, *Sacabambaspis* and possibly *Andinaspis*, and (ii) from Northern Territories, Australia, *Arandaspis* and possibly *Porophoraspis* (e.g., Gagnier, 1993, 1995).

†Subclass HETEROSTRACI

Pair of external lateral gill openings, emptying from several gill pouches; exoskeleton consisting of head covered in dermal armor consisting of plates of dentine and aspidine, generally with a honeycomb-like structure, covering the branchiocephalic region and body with large scales covering the trunk and tail; eyes lateral, extremely small; sclerotic ring absent; movable paired fins absent; anal fin absent; tail internally hypocercal, externally often symmetrical; perhaps two olfactory capsules (diplorhinal condition) with only an internal opening into the mouth area. Species with interlocking tesserae in the dermal armor are known as the tessellated pteraspidiforms or heterostracans. Maximum length is 1.5 m, usually much smaller. Pteraspidiforms are well known from the Lower Silurian to the Upper Devonian.



Taxa of uncertain affinities, of which some are not definitely known to be heterostracans, include the following (names with endings from Janvier, 1996):

Cardipeltida (e.g., *Cardipeltis*)
Corvaspidida (e.g., *Corvaspis*)
Lepidaspidida (e.g., *Lepidaspis*)
Tesseraspidida (e.g., *Tesseraspis*)
Traquairaspidiformes (e.g., *Phialaspis, Toombsaspis*, and *Traquairaspis*)
Tolypelepidida (e.g., *Athenaegis* and *Tolypelepis*)

Some of these are known as "tessellate heterostracans," known only from fragments and indeed not necessarily heterostracans. Other possible heterostracans include *Aserotaspis* and *Astraspis*.

Karatajute-Talimaa and Smith (2004) established a new order of tesselate pteraspidomorph agnathan, the Tesakoviaspidida, with one family, the Tesakoviaspididae for the Lower Silurian *Tesakoviaspis concentrica* of unique histology (but most closely related to that of the Mongolepidida). Its affinity with such groups as the astraspids is unknown.

†Order CYATHASPIDIFORMES. Ornamentation of longitudinal, dentine ridges (separated by grooves lacking dentine); dorsal shield a single plate. Two major clades are recognized by Janvier (1996), given here as families.

Family AMPHIASPIDIDAE (e.g., with the genera *Eglonaspis, Kureykaspis,* and *Prosarctaspis*).

Family CYATHASPIDIDAE (e.g., with the genera *Anglaspis, Dinaspidella, Irregulareaspis, Poraspis,* and *Torpedaspis*).

Other genera include *Nahanniaspis*, regarded as the sister group of the Cyathaspididae by Janvier (1996).

†Order PTERASPIDIFORMES. Dorsal shield composed of several plates, ornamented, except in psammosteids, with concentric dentine ridges. Five major taxa are given in Janvier (1996), given family rank here, as follows.

Family ANCHIPTERASPIDIDAE (e.g., *Rhachiaspis* and *Ulutitaspis*).

Family PROTASPIDIDAE (e.g., *Cyrtaspidichthys*).

Family PROTOPTERASPIDIDAE (e.g., *Protopteraspis*).

Family PSAMMOSTEIDAE (e.g., *Drepanaspis, Psammolepis,* and *Pycnosteus*).

Family PTERASPIDIDAE (e.g., *Errivaspis, Pteraspis, Rhinopteraspis,* and *Unarkaspis*).

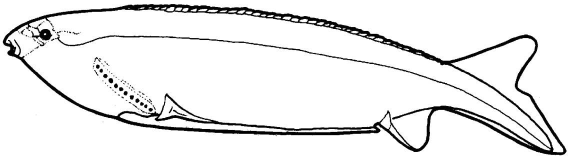
MYOPTERYGIANS. Janvier (1996) uses the term Myopterygii for those vertebrates with radial muscles in fins, innervated heart, muscularized unpaired fins, extrinsic eye muscles, and true paired fins (assumed to be secondarily lost in some taxa). He included in this clade the lampreys, which are excluded here, but, for a monophyletic Myopterygii, excluded the Galeaspida, which here are included and assumed to be part of a monophyletic Osteostracomorphi, and added as synapomorphies cellular bone and an open endolymphatic duct (both being subsequently lost several times). If our phylogenetic hypothesis as presented is correct, pectoral fins originated before pelvic fins. Coates (2003) discussed the possible origin of paired fins, and re-evaluated classical theories of limb evolution (i.e., Gegenbaur's transformational hypothesis of gill arches to limb girdles and the more widely accepted lateral fin-fold).

The term Myopterygii is used to include the following taxa, all forming an hypothesized monophyletic taxon.

†SUPERCLASS ANASPIDA

†Class ANASPIDA

†Order ANASPIDIFORMES (Birkeniae). Six to 15 or more pairs of external lateral gill openings; branchial region posteriorly placed with first gill pouch well behind eye (as in lampreys); eyes large and lateral; tail hypocercal with large epichordal lobe (perhaps in part or entirely corresponding to the posterior dorsal fin); anterior dorsal fin absent, but a series of dorsomedian scutes present; unique pectoral spines or rods present; anal fin reduced or absent; body usually covered with dorsoventrally elongated ornamented scales (which are virtually absent in *Lasanius*); body fusiform and somewhat compressed; mouth terminal; complex dermal head armor present in some; bone cells absent. Maximum length about 15 cm. Silurian (primarily Upper Silurian, although some Late Devonian taxa, e.g., *Endeiolepis* of Quebec, may be anaspidiform), predominantly freshwater.



Genera include *Birkenia, Lasanius, Pharyngolepis,* and *Rhyncholepis* (e.g., Arsenault and Janvier, 1991; Janvier, 1996). *Jamoytius* and *Euphanerops* are regarded as sister taxa to the Anaspida (Donoghue et al., 2000).

†SUPERCLASS THELODONTI

†Class THELODONTI

This group is known primarily from isolated micromeric scales, important for stratigraphic correlations (e.g., Soehn et al., 2001; Turner, 2004; and discussion above under "VERTEBRATES"), although many near complete body fossils are known. Most thelodonts are depressed, with horizontal mouth, asymmetrical tails, one dorsal fin and paired pectoral fin flaps, but species of Furcacaudiformes are compressed, have near tubular mouths, and have a nearly symmetrical tail. Upper Ordovician to Upper Devonian (Turner, 1992). Ordovician genera include *Sandivia* (Karatajute-Talimaa,1997) and *Stroinolepis* (Märss and Karatajute-Talimaa, 2002).

There are questions on the monophyly of thelodonts and their interrelationships. For example, Wilson and Caldwell (1998) placed thelodonts less the Furcacaudiformes in a polytomy with gnathostomes, and the Furcacaudiformes were regarded as a sister group to all. Turner (1991) and others suggested that thelodonts and gnathostomes are closely related. Both taxa share features such as lateral line continuing on body, lining of buccal cavity, pharynx and branchial skeleton with denticles and complex platelets; and Märss and Ritchie (1998) noted that *Shielia taiti* and *Lanarkia* species have pelvic fin flaps and epicercal tails, respectively. Donoghue and Smith (2001) found *Turinia pagei* and the Galeaspida to be sister taxa, and the sister group to the Osteostraci plus jawed vertebrates. In their phylogenetic analysis, Donoghue and Smith (2001) also regarded the thelodonts with a depressed body as a monophyletic group, of which *T. pagei* was the least derived member. The furcacaudiforms were resolved as an unnatural group, one taxon being the sister taxon to the "conventional" thelodont clade, and the other, the sister taxon to this clade plus galeaspids, osteostracans, and jawed vertebrates. However, Donoghue and Smith (2001) had few relevant characters and few species in their analysis, and Wilson and Märss (2004) in their phylogenetic study found evidence that the Thelodonti and the Furcacaudiformes are monophyletic.

I have chosen to follow Donoghue et al. (2000) on the higher classification of craniates and thus place the thelodonts here (with thelodonts as sister to Osteostracomorphi + Gnathostomata), but their position is uncertain, as these authors only used one thelodont taxon, *Loganellia*, in their analysis. The classification below is provisional and follows, as does the orthography, Märss et al. (2002); further changes are expected when cladistic studies such as Wilson and Märss (2004) are conducted with better material. Genera not placed in the following classification include *Apalolepis*, *Stroinolepis*, and *Turinia* (of worldwide distribution [Jiang, 1992]; the internal anatomy of *T. pagei*, with eight pairs of gills and a stomach, is especially well known but remains controversial [Donoghue and Smith, 2001]).

Order LOGANELLIIFORMES. Loganelliidae (= Loganiidae) (*Illoganellia* and *Loganellia*; Karatajute-Talimaa, 1997, revised this family and also placed in it *Angaralepis*, *Paralogania*, and *Sandivia*) and Nunavutiidae (*Nunavutia*).

Order SHIELIIFORMES. Shieliidae (*Paralogania*, *Praetrilogania*, and *Shielia*). *Shielia taiti* has paired fin flaps that are interpreted as pelvic fins (Märss and Ritchie, 1998).

Order PHLEBOLEPIDIFORMES. Phlebolepididae (*Erepsilepis*, *Helenolepis*, and *Phlebolepis*) and Katoporodidae (*Goniporus*, *Katoporodus*, *Overia*, and *Zuegelepis*).

Order THELODONTIFORMES (= Coelolepidiformes). Coelolepididae (*Thelodus*), Lanarkiidae (*Lanarkia* and *Phillipsilepis*), Archipelepididae (*Archipelepis*), Nikoliviidae (*Chattertonodus* and *Nikolivia*), Talivaliidae (*Glacialepis* and *Talivalia*), and provisionally Eestilepididae (*Eestilepis*). Märss and Ritchie (1998) suggested that *Lanarkia horrida* have epicercal, heterocercal tails, and tail fins have scale-covered ray-like supports (as with forktail thelodonts).

Order FURCACAUDIFORMES (forktail thelodonts). Body compressed, eyes lateral and large, branchial openings in an oblique row; stomach present (barrel-shaped); dorsal and ventrolateral fin flaps present in some; caudal fin with large dorsal and ventral lobes and scale covered ray-like fin supports. The lateral line branches to both lobes of tail. Wilson and Caldwell (1993) were the first to interpret a group of thelodonts as having compressed bodies, rather than depressed bodies as in other thelodonts. Furcacaudidae (*Canonia, Cometicercus, Drepanolepis, Furcacauda,* and *Sphenonectris*) and Pezopallichthyidae (*Pezopallichthys*) and provisionally Barlowodidae (*Barlowodus* and *Sophialepis*) (Wilson and Caldwell, 1998; Wilson and Märss, 2004; Märss et al., 2002).

†SUPERCLASS OSTEOSTRACOMORPHI

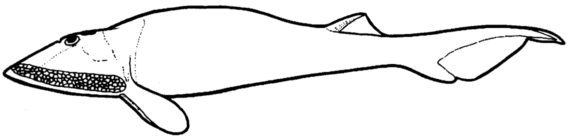
The osteostracomorphs (comprising the cephalaspidiforms or osteostracans, galeaspidiforms, and provisionally the poorly known pituriaspidiforms) are now considered to be the sister group to the jawed vertebrates (gnathostomes) by many researchers. Janvier (2001), in assuming that cephalaspidiforms and galeaspidiforms are the closest well-known outgroups to the gnathostomes and that ostracoderms as a group are more closely related to gnathostomes than to either hagfishes or lampreys, reconstructed the characters of various hypothetical ancestors of certain clades. More systematic work is required to present convincing arguments on possible gill-arch homologies with jaws to have a strong hypothesis on which agnathan group shared a common ancestry with the first jawed vertebrates. There is no evidence of gnathostome-like gill arches in cephalaspidiforms, and the sensory line system is restricted to the head.

†Class CEPHALASPIDOMORPHI (Monorhina)

Two semicircular canals; some bony regions in cephalaspidiforms may have true bone cells; single dorsomedian nostril (nasohypophyseal) opening between eyes with pineal eye behind except in the galeaspidiforms.

†Order CEPHALASPIDIFORMES (Osteostraci). Dorsal and lateral areas of cephalic shield with depressed areas in exoskeleton and associated canals present (this may have been an electric or sensory organ); usually 10 pairs of gill chambers and 10 pairs of external ventral gill openings; branchial region anteriorly placed (first gill opening at least level with eye); eyes dorsal; sclerotic ring present; endolymphatic duct present; tail, assumed to be epicercal, heterocercal, with a pair of horizontal caudal flaps in ventral position; head with complex, ornamented, polygonal interlocking plates; body with dorsoventrally elongated ornamented scales; head depressed anteriorly, triangular posteriorly; body triangular in cross section; mouth ventral; pectoral fins, possibly homologous to gnathostome pectoral fins, present in some (e.g., the basal *Ateleaspis*) but absent in the derived tremataspids; long rostral process present in species of *Boreaspis.* Maximum length about 60 cm, but most are much smaller. Upper Silurian to Upper Devonian, predominantly freshwater. These are the best known of the fossil agnathans. This group is almost always known as the Osteostraci by paleontologists.

In a study of granular labyrinth infillings in such osteostracans as *Waengsjoeaspis nahanniensis* and *Superciliaspis gabrielsei,* Sahney and Wilson (2001) suggested that one function of the endolymphatic pore openings in osteostracans is similar to that in living chondrichthyans, namely that exogenous material gets into the labyrinth of the inner ear by entering through the endolymphatic pores.



Taxa are recognized as non-cornuate (e.g., *Ateleaspis, Hirella,* and *Hemicyclaspis*), or part of a monophyletic clade of cornuate taxa, the Cornuata. Of the latter, several families might be recognized—for example, Benneviaspidae, Cephalaspidae, Dartmuthiidae, Kiaeraspidae, Sclerodidae (= Sclerodontidae), Thyestiidae, Tremataspidae, and Zenaspidae (e.g., Berg, 1940; Janvier, 1985, 1996). Afanassieva (1995) discussed the taxonomy of the *Tremataspis*-like forms and recognized five suborders. As with many groups, there is disagreement on the orthography of the family name (e.g., whether the ending should be –ididae or –idae, as used above). I have made no attempt here to determine which is grammatically correct or which is the traditional usage.

†Order GALEASPIDIFORMES. The cephalic shield, though variable in shape, resembles that of the cephalaspidiforms. Instead of having a minute dorsal nasohypophyseal opening like cephalaspidiforms, galeaspidiforms have a large median dorsal opening in front of the eyes that connects with the paired nasal cavities and with the pharynx. Galeaspidiforms possessed up to 45 pairs of gill compartments, the greatest number among vertebrates (Janvier, 2004), possessed acellular perichondral bone associated with globular calcified cartilage (Zhu and Janvier, 1998), lacked a dorsal and paired fins, and may have had a hypocercal tail. Lower Silurian (*Komoceraspis*) to Upper Devonian of China and northern Vietnam (Jiang, 1992).

Wang (1991, 1995) reviewed various taxa. Jiang (1992) recognized 10 families in a cladogram in a revision of the group.

Many genera have been described (e.g., *Duyunolepis, Eugaleaspis, Hanyangaspis, Huananaspis, Macrothyraspis, Pentathyraspis,* and *Polybranchiaspis*).

†Order PITURIASPIDIFORMES (Pituriaspida). Two species from the Lower Devonian of Australia (Young, 1991).

SUPERCLASS GNATHOSTOMATA — JAWED VERTEBRATES

Jaws present, derived from modified gill arches; endochondral bone present (see Smith and Hall, 1990); paired limbs usually present; three semicircular canals (and two or more maculae); gills covered with ectoderm and directed externally; gill arches not fused with neurocranium, internal to gill lamellae; gills opening to surface in fishes through slits (opercular opening, when present, may be porelike); myelinized nerve fibers. There are many characters that carry over in the transition from jawless fishes to jawed vertebrates that were subsequently modified. For example, the notochord continues to be present in the various lineages of early gnathostomes but in some it is later replaced with vertebral centra, and a bony exoskeleton is present in early gnathostome fossils but absent in higher lineages.

There are many exciting questions on the origin and evolution of characters in the transition from jawless to jawed vertebrates (thought to be from osteostacans to placoderms). One such question concerns the phylogenetic origin of teeth (dentine based versus the horny teeth of lamprey). Smith and Johanson (2003) and Johanson and Smith (2003) suggested that teeth have originated at least twice, in derived placoderms, the arthrodires, and in the placoderm sister clade. However, Young (2003) reviews past conclusions that placoderms have a primitively jawless mouth and concludes that no placoderm had typical teeth, but rather the tooth-like structures are made up of a special dentine unique to placoderms, called semidentine.

In the fossil record, placoderms appear in at least the Middle Silurian (Jiang and Dineley, 1988; Gardiner, 1993) and acanthodians appear in the Lower Silurian (e.g., Zidek, 1993) and possible chondrichthyan scales and denticles are known from the late Ordovician (see section on Chondrichthyes).

Classically, all jawed vertebrates were recognized in two groups, the jawed fishes and the tetrapods. This was recognized in Nelson (1984) in placing all gnathostomes in either the "Grade Pisces" or the "Grade Tetrapoda." It was well recognized some years earlier that although tetrapods form a monophyletic group, the jawed fishes did not. In order to recognize the phylogenetic relationships as generally accepted, Nelson (1994) did not recognize Pisces as a taxon and placed all jawed vertebrates in three taxa, namely in the grades Placodermiomorphi, Chondrichthiomorphi, and Teleostomi (comprising the acanthodians, sarcopterygians, which contains some fishes, and the actinopterygians). While the former taxon Pisces is not monophyletic and no longer recognized in classification, the term "jawed fishes" is still a useful one, even though referring to a paraphyletic group.

The jawed fishes comprise the first two grades and about half of the species of the Teleostomi. In all, there are about 27,869 species of extant jawed fishes and about 54,603 species of extant jawed vertebrates (gnathostomes). This represents an expected disproportional increase in the number of jawed fishes over tetrapods from Nelson (1994), with an estimated 24,535 species of extant jawed fishes and about 48,100 species of extant jawed vertebrates (gnathostomes) (leaving an estimated increase in the number of described species of extant fishes of 3,334, and of extant tetrapods of 2,199). Many new forms of fishes are known that are thought to represent undescribed species, and when these are described the numbers will be substantially higher.

†Grade PLACODERMIOMORPHI

†Class PLACODERMI

Head and shoulder girdle with dermal bony plates (with bone cells); endochondral bone known in some taxa; head shield usually articulated (movable or not) with the trunk shield, with a double cervical joint; gill chamber extending anteriorly under neurocranium and may be covered laterally by dermal bone; probably five gill arches, no good evidence for spiracles; notochord unconstricted with vertebrae consisting only of neural and haemal arches and spines; tail diphycercal or heterocercal; anal fin probably absent. Although many features carry over from the osteostracans and other ostracoderms such as the notochord and head being mostly encased in bone, there are many features that are unique to placoderms. A few Silurian records are known with greatest abundance in Lower to Upper Devonian; there is no clear evidence of placoderms surviving a major extinction event into the Lower Mississippian (see also Carr, 1995; Maisey, 1996).

Most primitive and at least many advanced groups of placoderms were marine. At least some arthrodiriforms, most antiarchiforms, and all phyllolepidiforms are inferred to have been freshwater (e.g., but see Schultze and Cloutier, 1996). Except for the arthrodires, most were bottom-living fish with depressed bodies; only two families had species with compressed bodies. Although placoderms have been found almost worldwide, very few Devonian ones are known from South America (Maisey, 1996). A rapid replacement of placoderms by the chondrichthyans occurred at the end of the Devonian. Maximum length 6 m, but most are much shorter.

There is now strong evidence that placoderms are monophyletic, and five features are given in Goujet and Young (2004) supporting this conclusion. The hypothesis that placoderms are the sister group to all higher gnathostomes (Chondrichthyes, Acanthodii, and the Euteleostomi), as favored by Goujet and Young (2004) and suggested by B. Schaeffer in 1975, is accepted here (that is, placoderms are phylogenetically the sister group of all other jawed vertebrates). Two other hypotheses as discussed by Janvier (1996) and Goujet and Young (2004) are i) placoderms and chondrichthyans are sister taxa, and ii) placoderms and osteichthyans (euteleostomes herein) are sister taxa.

The classification of this group is based primarily on Goujet and Young (2004), except that details for the antiarchs are from the papers noted for that group. The Stensioelliformes from the Lower Devonian (marine) of Germany, and the Pseudopetalichthyiformes, with one family, Paraplesiobatidae, from the Lower Devonian (marine) in Europe are not placed in the present classification.

†Order ACANTHOTHORACIFORMES. Several genera (e.g., *Brindabellaspis, Murrindalaspis, Palaeacanthaspis, Radotina,* and *Romundina*) from Lower Devonian (marine) in Europe, Asia, and Arctic Canada.

Goujet and Young (2004) hypothesized that this taxon, with some of the oldest placoderm fossils, is the basal placoderm group. This taxon thus represents in classification the first known jawed vertebrate. They propose that one pectoral fin element (as opposed to three as in the traditional tribasal theory), an anterior insertion for the internal rectus extra ocular muscle, and two abducens innervated eye muscles may be primitive for placoderms, and hence for all jawed vertebrates.

†Order RHENANIFORMES. One family, Asterosteidae (including *Gemuendina* and *Jagorina),* with a raylike body, and several genera from the Lower to Upper Devonian (marine) in the United States, Bolivia, and Germany.

†Order ANTIARCHIFORMES (antiarchs). Pectoral fin a slender appendage covered by small dermal plates; bottom feeders with mouth subterminal, and eyes dorsal and closely placed; pineal organ between eyes; sockets of the head-body joint on the head shield (opposite to the relationship in arthrodires). Maximum length about 1.2 m.

About seven families are recognized; at least Lower Devonian (but see *Shimenolepis* below) to end of Devonian (perhaps primarily freshwater) on, as a group, all major land masses. Classification based primarily on the phylogeny of Zhu (1996) and Zhu and Janvier (1996) with other details from Burrow and Turner (1999), Johanson (1997a,b), and Young and Zhang (1996). The names Goujet and Young (2004) gave to the two major clades are Yunnanolepida and Euantiarchi. The names used for certain taxa above family level and their rank are provisional.

Suborder Yunnanolepoidei. Zhu (1996) gave the orthography as Yunnanolepidoidei.

Chuchinolepidae—*Chuchinolepis* (synonym *Quijinolepis*).

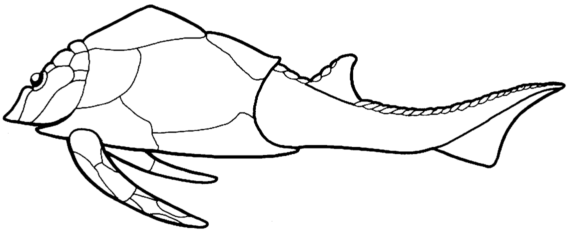
Yunnanolepidae—e.g., *Phymolepis, Yunnanolepis.*

With a number of unassigned genera: e.g., *Heteroyunnanolepis, Shimenolepis* (early Silurian and oldest probable placoderm and thought to be an antiarch, but this is a very poorly known fossil from China as noted by Zhu, 1996:296), and *Zhanjilepis.*

Suborder Bothriolepoidei. Zhu (1996) gave the orthography as Bothriolepidoidei.

Infraorder Sinolepida. Sinolepidae—e.g., *Grenfellaspis* and *Sinolepis.*

Infraorder Euantiarcha



Microbrachiidae—e.g., *Microbrachius.* This and the remaining families are the euantiarcha (those with an articulated pectoral fin).

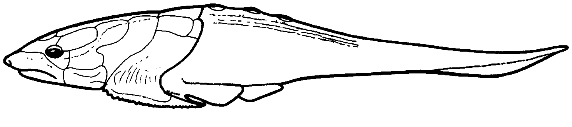
Bothriolepidae—e.g., *Bothriolepis.*

Gerdalepidae—e.g., *Gerdalepis.*

Asterolepidae (= Pterichthyidae) (in figure)—e.g., *Asterolepis, Remigolepis.* Related genera: *Stegolepis.*

With a number of unassigned genera: e.g., *Dianolepis, Minicrania* (sister to the other members of this suborder), and *Pterichthyodes.*

†Order PETALICHTHYIFORMES



A group of low diversity, with several genera (e.g., *Eurycaraspis*, *Lunaspis*, and *Macropetalichthys*, Janvier, 1996) from Lower to Upper Devonian (marine) in North America, Europe, Morocco, Asia, and Australia.

Order PTYCTODONTIFORMES. Large sexually dimorphic pelvic fins with claspers in males (fertilization was probably internal); many resemblances with living holocephalans. One family, Ptyctodontidae (e.g., *Ctenurella* and *Rhamphodopsis*), from Lower Devonian to possibly Lower Mississippian (primarily marine) in North America, Europe, Asia, Libya, Algeria, and Australia (e.g., Forey and Gardiner, 1986; Janvier, 1996).

Order ARTHRODIRIFORMES (arthrodires). Most arthrodires were probably nektonic predators. This group, the largest in number of genera and best known of the placoderms, occurs from Lower Devonian to Lower Mississippian and is found on all major land masses. Several major groups are recognized (e.g., see Goujet and Young, 2004; Janvier, 1996).

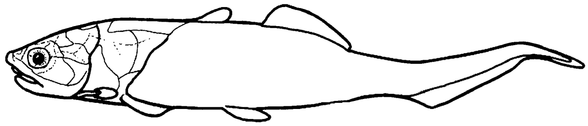
Suborder Actinolepidoidei. Includes Actinolepidae, the most primitive arthrodires, with e.g., *Actinolepis*, *Aethaspis*, *Bollandaspis*, *Eskimaspis*, *Heightingtonaspis*, and *Kujdanowiaspis* (Johnson et al., 2000).

Suborder Phyllolepida. One Middle and Upper Devonian (freshwater) family, Phyllolepidae, with three genera, *Austrophyllolepis*, *Placolepis*, and *Phyllolepis*, known from Antarctica, Australia, Europe, and Greenland (Long, 1984; Ritchie, 1984). The Antarctaspidae may be related to this group.

Suborder Phlyctaeniida

Phlyctaeniidae (e.g., *Arctolepis*–in figure) and Groenlandasididae.

Suborder Brachythoraci. Includes the Eubrachythoraci with, based on information in Carr (2004), two major subgroups, the pachyosteomorphs and the coccosteomorphs. The brachythoracoids of the late Devonian were the first large marine vertebrate predators, with *Dunkleosteus* with large blade-like jawbones getting to be at least 6 m in length (e.g., Young, 2003).



Other arthrodires, whether belonging in the above groups or not, include: Buchanosteidae (a basal brachythoracid group, Carr, 2003), Camuropiscidae (e.g., *Camuropiscis*), Coccosteidae (e.g., *Coccosteus,* in figure), Dinichthyidae (Carr and Hlavin, 1995, moved several genera from this family into other families), Dunkleosteidae (e.g., *Dunkleosteus, Eastmanosteus*), *Hadrosteus,* Mylostomatidae, Panxiosteidae, Selenosteidae, Titanichthyidae, and Wuttagoonaspidae.

GRADE CHONDRICHTHIOMORPHI

One class, Chondrichthyes.

Class CHONDRICHTHYES—cartilaginous fishes

Prismatic endoskeletal calcification; dermal skeleton consisting of denticles (placoid scales); skull lacks sutures in living forms; teeth are usually not fused to jaws and are replaced serially; fin rays soft, unsegmented (termed ceratotrichia); nasal openings on each side usually single (imperfectly divided by a flap into incurrent and excurrent openings) and more or less ventral; biting edge of upper jaw formed by palatoquadrate (and lower jaw by Meckel's cartilage); endolymphatic duct present; swim bladder and lung absent; intestinal spiral valve present; internal fertilization in at least all known taxa, fossil and extant, by means of claspers (of males, derived from pelvic axis and termed myxopterigia) that are inserted in the female cloaca and oviduct(s); gestation periods of two years are known, the longest of any vertebrate; usually high blood concentration of urea and trimethylamine oxide (converted from toxic ammonia), which allows water to be drawn freely into the body. Characters supporting a monophyletic Chondrichthyes (holocephalans and elasmobranchs) are given in Maisey (2001b), Didier (1995), Janvier (1996), and Grogan and Lund (2004), and unique shared characters of the spermatozoa are given in Jamieson (1991). The two key synapomorphies are the prismatic endoskeletal calcification and pelvic claspers (Grogan and Lund, 2004).

The various means of jaw suspension of chondrichthyans is of much interest. Grogan and Lund (1999) concluded that autodiastyly is the ancestral condition from which holostyly and hyostyly (and from it, two types of amphistyly) are derived. However, Maisey (2001b:282) and Maisey and Anderson (2001:712) found that *Pucapampella* (discussed below), considered a basal chondrichthyan, has a suspensory hyomandibula; therefore, autodiastyly may be the primitive pattern only for holocephalans. Chimaeroids exhibit holostyly (which has evolved several times in gnathostomes) in which the upper jaw (palatoquadrate) is completely fused to the cranium. Elasmobranchs, with hyostyly or amphistyly, however, have an upper jaw that is suspended from the cranium by muscles and ligaments and variously braced to the cranium by processes of the palatoquadrate, cranium, and/or modified pharyngeal arches.

Although chondrichthyans have internal fertilization, there is much diversity both in where the last stages of embryonic development occurs (viviparity and oviparity) and in the source of fetal nutrition (lecithotrophy and matrotrophy) (there is some gradation between the various modes) (described in Hamlett, 1999, 2005, and Carrier et al., 2004). Unfortunately, there are also differences as well as confusion in the literature in the appropriate terms to be used for the various phenomena. The terminology followed here is that as clarified in Hamlett (2005) and Musick and Ellis (2005); the latter authors gave a phylogenetic analysis of the occurrence of the many reproductive modes. For reasons explained in Musick and Ellis (2005) it is probable that viviparity is the primitive mode of reproduction in chondrichthyans (Grogan and Lund, 2004, originally proposed this idea on the balance of Paleozoic evidence and from their Montana fossil site). To enlarge upon the above-mentioned diversity, based on Musick and Ellis (2005), in embryonic development, chondrichthyans exhibit both i) viviparity, in which developing eggs are retained in the female and free-swimming young are born, and ii) oviparity, in which fertilized eggs (in leatherlike egg cases termed mermaid purses) are deposited with hatching being external to the female. The various ways of obtaining nutrition are as follows:

A. All nutrition from the yolk sac—most chondrichthyan embryos, like those of actinopterygians, are lecithotrophic, obtaining all nutrition from the yolk sac. In this category, there can be either:

i) yolk sac viviparity or lecithotrophic viviparity (formerly known as ovoviviparity)—the most common state in Chondrichthyes (occurring in at least some members of all living orders of elasmobranchs except Heterodontiformes, Lamniformes, and Rajiformes).

ii) yolk sac oviparity or lecithotrophic oviparity—occurs in all living holocephalans, some selachians (e.g., all Heterodontiformes), and all Rajidae. All members exhibiting oviparity are lecithotrophic.

B. Some nutrition from the female (directly or indirectly)—In contrast to the above, some chondrichthyan embryos, where there is viviparity, obtain at least some nutrition from the female, either from uterine secretions, ova, siblings, or a placenta in what is termed:

iii) matrotrophy—There are several versions of this, including:

Nutrition from uterine secretions (histotrophy)—there is either limited histotrophy which occurs in many squaliform and carchariniform sharks, or lipid histotrophy in the myliobatiforms.

Nutrition from eating unfertilized eggs (oophagy)—all Lamniformes and some Carchariniformes. In *Carcharias taurus*, the largest embryo eats all smaller embryos and then feeds on unfertilized eggs.

Nutrition from a placenta—in some Carchariniformes.

Two main evolutionary lines are recognized: the holocephalans (see below under Holocephali for use of this name) and elasmobranchs (ranked as subclasses). They are considered here as belonging to a monophyletic unit (as supported by, e.g., Lund and Grogan, 1997a; Grogan et al., 1999). The ancestral group of chondrichthyans is unknown, although *Pucapampella,* discussed below, is a possible candidate. There has been a great increase in our knowledge of chondrichthyan diversity, especially of Paleozoic taxa, over the last few decades, and the future challenge will be to produce sound phylogenies and classifications to recognize this diversity.

A good fossil record is known from the Devonian onwards (e.g., Ginter, 2004). However, the oldest chondrichthyan fossil remains may be of scales or dermal denticles of late Ordovician age (about 455 million years ago); the tooth record goes back to the earliest Devonian (about 418 million years ago) while the oldest, intact shark fossil is said to be almost 409 million years old (early Devonian), a specimen of a small species known as *Doliodus problematicus,* with large, paired pectoral-fin spines (Miller et al., 2003). However, the Early Devonian *Pucapampella*-like taxon from South Africa (Maisey and Anderson, 2001), appears to be older than *Doliodus.* Turner (2004) placed *D. problematicus* in the order Omalodontiformes (her Omalodontida) and family Protodontidae and noted similarities in their teeth with teeth of *Antarctilamna* (see Xenacanthiformes).

The Middle Devonian *Pucapampella* from Bolivia, the earliest chondrichthyan in which the braincase can be studied in detail, may be a primitive stem chondrichthyan whose phylogenetic position lies before the divergence of holocephalans and elasmobranchs (Maisey, 2001b). The primitive gnathostome features of *Pucapampella,* e.g., ventral otic fissure present, prominent dorsal sellae, and endolymphatic ducts enclosed by the dorsal posterior fontanelle (endolymphatic fossa absent), are discussed by Maisey (2001b, 2004a). The ventral braincase of the early Devonian *Pucapampella*-like taxon from South Africa is described by Maisey and Anderson (2001). In addition, Maisey (2004a) reviews the endocranial morphology of chondrichthyans and discusses its phylogenetic potential.

Groups thought to be related to the chondrichthyans but not otherwise classified include the Mongolepidida, with the genera *Mongolepis, Teslepis, Sodolepis,* and *Udalepis,* known from scales found from the Lower Silurian in central Asia (Karatajute-Talimaa, 1995), and Kannathalepididae (*Kannathalepis* and *Frigorilepis*) and Wellingtonellidae (Märss et al., 2002). Additional early and poorly known fossil remains (e.g., *Emsolepis*) are discussed in Turner (2004).

Last and Stevens (1994) is an excellent book on Indo-Pacific taxa. There are several multiauthored sources reviewing our knowledge of chondrichthyan biology. Hamlett (1999) presents a systems approach to the anatomy and physiology of sharks and rays, in which Compagno (1999) discusses neoselachian phylogeny and body form and gives a checklist of living species of elasmobranchs. Carrier et al. (2004) review what we know of chondrichthyan phylogeny, zoogeography, and overall biology. Hamlett (2005) emphasizes reproductive biology, corrects many past errors in the literature, and reviews phylogeny. Finally, the FAO series such as Compagno (2001) and the various “Species identification guides” describe the biology and distribution of the species and give keys to species identification.

Extant taxa constitute 14 orders, 54 families, 184 genera, and about 970 species (with many known but undescribed species).

Subclass HOLOCEPHALI (= Subclass Euchondrocephali of Grogan and Lund, 2000)

Gill cover over the four gill openings, leaving one opening on each side; palatoquadrate fused to cranium (holostylic) in living forms (see above under Chondrichthyes for more detail); complete hyoid arch (with pharyngohyal present), followed by five gill arches; no hyomandibular in suspensorium; branchial basket mostly beneath the neurocranium; no spiracle opening; teeth as a few grinding plates in extant and a few fossil forms (e.g., eugeneodontiforms, *Helodus*, petalodonts, orodonts, debeeriids, gregoriids); no cloaca, separate anal and urogenital openings; skin in adult naked in extant forms (specialized denticles and scales in many fossil forms); no stomach; no ribs; males of at least extant species with clasping organ on head (better termed a tentaculum or cephalic structure in fossils—see Grogan and Lund, 2004, and Grogan and Lund, 2004b) (in addition to the pelvic claspers). It is recognized that this description is very incomplete for the vast diversity of fossil taxa. Late Devonian to present (major reduction in diversity after the Permian).

The higher classification of this group is based in part on the phylogenetic works of Grogan and Lund (2000, 2004), but much detail of the composition of various taxa is based on Stahl (1999), who presents a different view of relationships (valuable criticisms of the latter work are provided by de Carvalho, 2004a). Didier (1995, 2004) also presented new insights into the phylogeny of this group and reviewed past works. Our understanding of the phylogenetic relationships of this group is very uncertain and major changes are expected. The following table compares the higher classification adopted in Nelson (1994) with that of Stahl (1999) and Grogan and Lund (2000, 2004). Users must be aware of the unfortunate use of different terms to describe the various taxa of these non-elasmobranch chondrichthyans (as seen below; especially that use of the term Holocephali is used for the sister group of Elasmobranchii and in a different sense from the works noted below). The principle adopted in this book continues to be to retain familiar names for similar or identical taxa under the belief that stability in such names better serves the general user as well as the systematic audience. As stated in the 1994 edition, "I retain the well-known term Holocephali, believing it undesirable to change the names of higher categories just because they become descriptively inaccurate with new finds," and this view is also adopted by de Carvalho (2004a) in his critique of recent phylogenetic work on holocephalans.

Nelson (1994)	Stahl (1999)	Grogan and Lund (2000, 2004)
Subclass Holocephali	Subterbranchialia	Euchondrocephali
Superorder Paraselachimorpha (iniopterygians to helodontiforms)	Iniopterygiia	Paraselachii
Superorder Holocephalimorpha	Holocephali (all others)	Holocephali (differs from Stahl)

The cladogram of Stahl (1999:45), as seen in the above table, separates her subclass Subterbranchialia into two clades, the Iniopterygiia and the Holocephali (different usage than given herein), with the following sequenced in the latter clade: Chondrenchelyidae, Helodontidae, Psammodontidae, Copodontidae, Cochliodontiformes, Menaspiformes, and Chimaeriformes. Grogan and Lund (2004) comment on their differences with Stahl (1999). In their Paraselachii they place *Orodus*, petalodonts, helodonts, and other basal euchondrocephalans, debeeriids, iniopterygians, and edestids, while in their Holocephali they placed chondrenchelyids, *Squaloraja*, cochliodonts, and derivatives.

Other taxa belonging to the Holocephali (the Euchondrocephali of Grogan and Lund) that are not otherwise mentioned include the autodiastylic Harpacanthidae (Lund and Grogan, 2004a) and Gregoriidae (with *Bealbonn*, *Gregorius*, and *Strianta*) (Lund and Grogan, 2004b). Cladistic analysis shows that the Gregoriidae have a basal position relative to the *Orodus* + *Helodus*—Petalodontiform clade (Lund and Grogan, 2004a,b). The previously recognized fossil *Desmiodus*, order Desmiodontiformes (e.g., Cappetta et al., 1993; Nelson, 1994), is taxonomically invalid and *nomina dubia* (Lund and Grogan, 2004b:520).

†Superorder PARASELACHIMORPHA

Dentition similar to selachians and palatoquadrate fused to neurocranium in some forms and not in others; continuously growing cuboidal scales in some.

†Order ORODONTIFORMES. Only family, Orodontidae. (e.g., *Hercynolepis* and *Orodus*) (Cappetta et al., 1993).

†Order PETALODONTIFORMES. About four families, Belantseidae (e.g., *Belantsea* and *Ctenoptychius*), Janassidae, Petalodontidae (e.g., *Polyrhizodus*), and Pristodontidae (Lund, 1989). Cappetta et al. (1993:598) gave reasons for recognizing only two families. Some members, such as *Janassa*, are raylike in body form. The phylogenetic position of this group is particularly uncertain.

†Order HELODONTIFORMES. Known primarily from teeth and tooth plates. One family. Helodontidae, with one genus, *Helodus* (synonym *Pleurodus*) (Stahl, 1999). Upper Devonian to Lower Permian.

†Order INIOPTERYGIFORMES. Two families, Iniopterygidae (including *Iniopteryx* and *Promyxele*) and Sibyrhynchidae (Cappetta et al., 1993; Stahl, 1999). This taxon was considered to be sister to all other members of Holocephali as herein defined by Stahl (1999), who used the term Holocephali for said sister group and the R. Zangerl term Subterbranchialia for the entire group, but as sister to Debeeriidae by Lund and Grogan (2004a). The iniopterygiforms were first described in 1973 and are known from the Pennsylvanian Period in North America (Stahl, 1980; Zangerl, 1981).

†Order DEBEERIIFORMES. One family, Debeeriidae, with two genera, *Debeerius* and *Heteropetalus* (Grogan and Lund, 2000). Upper Mississippian. In appearing intermediate in morphology to chimaeroid and selachian body plans, the cranial and postcranial morphology of *Debeerius* suggests affinity with the cochliodonts and chimaeriforms, the heterodont dentition is similar to selachians, yet this paraselachian appears to have the fundamental jaw suspension of gnathostomes (autodiastyly but a derived form of autodiastyly) (Grogan and Lund, 2000).

†Order EUGENEODONTIFORMES. Position uncertain. Four families, Agassizodontidae (including Helicoprionidae), Caseodontidae (e.g., *Fadenia* and *Ornithoprion*), Edestidae (e.g., *Lestrodus*), and Eugeneodontidae (e.g., *Bobbodus* and *Gilliodus*) (Cappetta et al., 1993).

Superorder HOLOCEPHALIMORPHA—Subclass HOLOCEPHALI of Grogan & Lund (2000, 2004)

Dentition consisting of a few large permanent grinding tooth plates (selachianlike anterior teeth may also be present); palatoquadrate fused to neurocranium (holostyly); dorsal fin spine usually present. This diagnosis is very imperfect; some assumed members are known only from isolated tooth plates.

†Order PSAMMODONTIFORMES. Position uncertain. Known only from isolated tooth plates. One family, Psammodontidae (e.g., *Archaeobatis, Lagarodus,* and *Psammodus*) (Stahl, 1999; Elliott et al., 2004). Upper Devonian to Lower Carboniferous.

†Order COPODONTIFORMES. Position uncertain. Known only from tooth plates. One family, Copodontidae (e.g., *Copodus*) (Stahl, 1999). Carboniferous.

Of the following taxa, Grogan and Lund (2004) suggested that chondrenchelyiforms and menaspiforms are sister taxa as are cochliodontiforms and chimaeriforms, with all four being sister to the squalorajiforms, and all five taxa being placed in the Cochliodontomorpha.

†Order SQUALORAJIFORMES. Body depressed. One family, Squalorajidae, and one genus, *Squaloraja* (Stahl, 1999). Lower Jurassic. Stahl (1999) recognized this taxon as one of four suborders of Chimaeriformes and sequenced it between the Echinochimaeroidei and Myriacanthoidei.

†Order CHONDRENCHELYIFORMES. Body elongate, biserial pectoral fin, and long lower jaw. One family, Chondrenchelyidae (e.g., *Chondrenchelys, Harpagofututor,* and *Platyxystrodus*) (Stahl, 1999). Lower Carboniferous.

†Order MENASPIFORMES. Three families, Deltoptychiidae, with *Deltoptychius,* Menaspidae, with *Menaspis,* and Traquairiidae, with *Traquairius* (Stahl, 1999). Lower Carboniferous (Mississippian) to Upper Permian.

†Order COCHLIODONTIFORMES. Known primarily from teeth and tooth plates. Two families, Cochliodontidae (e.g., *Cochliodus, Deltodus, Poecilodus,* and

Sandalodus) and Psephodontidae (with *Psephodus*) (Stahl, 1999). Upper Devonian to Permian.

Order CHIMAERIFORMES (3)—chimaeras. Three families, six genera, and 33 species. Stahl (1999) recognized four suborders of chimaeriforms; her Squalorajoidei are recognized here as more basal following Grogan and Lund (2004).

†Suborder Echinochimaeroidei. Position uncertain. One family, Echinochimaeridae, with one genus, *Echinochimaera.* Mississippian. Differs from the chimaeroids in having a dermal cranial armor of denticles, placoid squamation, a tuberculated first dorsal spine, and no frontal clasper in males (Lund, 1986; Stahl, 1999).

†Suborder Myriacanthoidei. Two families, Chimaeropsidae, with one genus, *Chimaeropsis,* and Myriacanthidae (e.g., *Acanthorhina, Agkistracanthus, Halonodon,* and *Myriacanthus*) (Stahl, 1999). Upper Triassic to Jurassic.

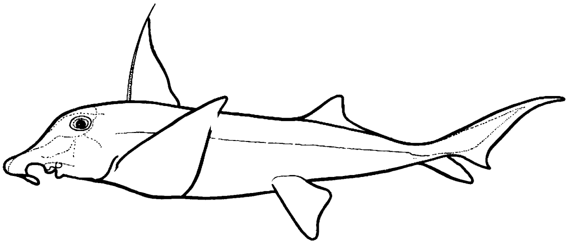
Suborder Chimaeroidei (chimaeras). Two dorsal fins, the first erectile, with short base, and preceded by an erectile spine, the second nonerectile, low, and with long base; mouth inferior. In living forms, at least, fertilization is internal; the deposited egg is encased in a brown horny capsule. Water for breathing is chiefly taken in through the nostrils. Maximum length about 1.5 m.

Six extant genera with about 33 species (listed in Compagno, 2005; Didier, 2004, with several undescribed species). Lower Jurassic to present. Fossil taxa, all in the extant families, are given with the families.

Didier (1995), in a phylogenetic analysis of living taxa based on morphological characters, gave synapomorphic characters for the higher taxa and reviewed ideas on the origin of the Holocephali.

Superfamily Callorhinchoidea (Callorhynchoidea)

Family CALLORHINCHIDAE (Callorhynchidae) (5)—plownose chimaeras. Marine, continental and insular shelves and uppermost slopes; Southern Hemisphere (e.g., off southern South America, New Zealand, southern Australia, southern Africa).



Snout with elongate, flexible, hooklike process; lateral line canals closed; eyes small; tail heterocercal. Egg capsule large, ovoid (typically 27 cm X 13 cm), with wide, ribbed lateral web.

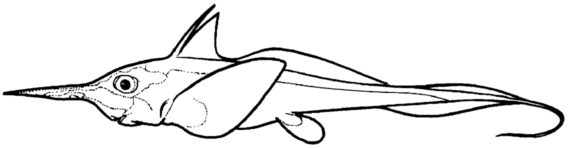
Fossil Callorhinchidae (earliest in Jurassic) include: *Brachymylus, Ischyodus,* and *Pachymylus,* with *Edaphodon* placed in its own subfamily, Edaphodontinae, by Stahl (1999), with possibly also in this family the Jurassic *Eomanodon* and *Ganodus.* In addition, fossils of the genus *Callorhinchus* are known from the Eocene of Antarctica (Kriwet and Ga´zdzicki, 2003).

One genus, *Callorhinchus,* with three species (Didier, 1995, 1998, 2004).

Change in orthography of family name to conform with generic name (Eschmeyer, 1998).

Superfamily Chimaeroidea

Family RHINOCHIMAERIDAE (6)—longnose chimaeras. Marine, deep oceanic, continental and insular slopes; Atlantic, Indian, and Pacific.

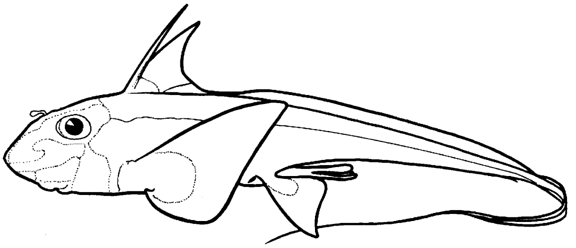


Snout long, fleshy, and pointed, not hooklike; lateral line canals are open grooves; tail diphycercal; anal fin separated from caudal in *Neoharriotta* and joined with it in the other genera. Egg capsule ovoid (pear-like) (typically 15 cm × 6 cm), with ribbed lateral web.

Fossil Rhinochimaeridae (earliest in Jurassic) include *Amylodon* and *Elasmodus.*

Three genera, *Harriotta* (2), *Neoharriotta* (3), and *Rhinochimaera* (3), with about eight species (Compagno et al., 1990; Didier, 1995, 2004; Didier and Stehmann, 1996; Didier and Nakaya, 1999). Didier (1995, 2004) placed *Harriotta* and *Neoharriotta,* with thick tooth plates, in the subfamily Harriottinae, and *Rhinochimaera,* with smooth, thin tooth plates in the subfamily Rhinochimaerinae.

Family CHIMAERIDAE (7)—shortnose chimaeras or ratfishes. Marine; Atlantic and Pacific.



Snout (rostrum) short, fleshy, and rounded; lateral line canals are open grooves with those on snout widened; tail diphycercal. Egg capsule relatively small (typically 17 cm × 2.5 cm), spindle-shaped with distinct dorsal keel and little or no lateral web. A poison gland is associated with the dorsal spine, and the venom is painful to humans. Maximum total length about 1.4 m, attained in *Chimaera lignaria,* probably the largest extant chimaeroid.

Fossil Chimaeridae (earliest in Cretaceous), include *Belgorodon.* In addition, fossils of the genus *Chimaera* are known from the Late Cretaceous and Eocene of Antarctica (Stahl, 1999; Stahl and Chatterjee, 1999).

Two genera, *Chimaera* (with a notch separating the anal fin from the caudal fin) and *Hydrolagus* (with anal fin joined to caudal fin), and about 22 species. *Chimaera* has seven species that occur in the northern Atlantic, off South Africa, Japan and northern China, Australia, and New Zealand, whereas *Hydrolagus* has about 16 species that occur primarily in the northern and southwestern Atlantic, off South Africa, and in many areas in the Pacific (e.g., southern Alaska to southern California, Japan, Australia, and New Zealand) (Didier, 1995, 1998, 2002, 2004; Soto and Vooren, 2004). Most species are in the western Pacific off Japan and New Zealand. The allocation of some species to the above genera on the basis of the anal fin character is subject to change (Hardy and Stehmann, 1990; Didier, 2004). Several undescribed species are known from Australia and New Zealand (Didier, 1998, 2002, 2004; Compagno, 2005).

Subclass ELASMOBRANCHII

Five to seven separate gill openings on each side; dorsal fin(s) and spines, if present, are rigid; males without clasper organ on head; dermal placoid scales usually present; palatoquadrate (upper jaw) not fused to cranium (suspension amphistylic or hyostylic); branchial basket mostly behind the neurocranium; tooth replacement relatively rapid; teeth numerous; some ribs usually present; spiracle opening (remains of hyoidean gill slit) usually present. As noted in Maisey (2001b), in modern elasmobranchs the anterior and posterior semicircular canals are separated dorsally (they are variously united dorsally in chimaeroids, sarcopterygians, and actinopterygians). Silurian to present.

Elasmobranchs are typically predaceous fishes that use both smell and sight for obtaining their food.

This subclass is recognized with three lineages ranked as infraclasses, only one of which has extant members. The first two superorders may be the most primitive chondrichthyans. Some Paleozoic taxa, not otherwise mentioned, that are too poorly known to properly classify include the following taxa:

†***Plesioselachus.*** A Late Devonian stem-group elasmobranch with amphistylic jaw suspension and thought to have a single dorsal fin and no anal fin (Anderson et al., 1999).

†**Squatinactiformes**. One family, Squatinactidae, with the Mississippian *Squatinactis* from Montana which resembles the extant *Squatina* in some body form features (e.g., Zangerl, 1981). Placed in the Cladodontiformes in Lund (1990).

†**Protacrodontiformes**. Includes the Tamiobatidae and shows some similarity to the Orodontidae and Ctenacanthiformes (e.g., Zangerl, 1981).

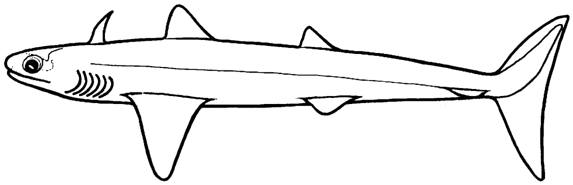
†Infraclass CLADOSELACHIMORPHA

Cladodont-type tooth (tall central cusp and one or more pairs of lateral cusps on a broad base); claspers usually absent; no anal fin; paired fins in shape of triangular flaps; radials of fins unsegmented and extending almost to the edge of the fin.

Devonian to Pennsylvanian fossil groups, too poorly known to be properly classified but possibly belonging to the cladoselachimorphs (see Cappetta et al., 1993, for a provisional classification), including "*Cladodus*" (a series of unrelated species, placed in the family Cladodontidae), *Coronodus*, Symmoriidae (e.g., *Cobelodus*, *Denaea*, and *Symmorium*), Falcatidae (*Damocles* and *Falcatus*), and Stethacanthidae (e.g., *Orestiacanthus* and *Stethacanthus*) (e.g., Lund, 1990). Coates and Sequeira (2001) described new morphological features of *Stethacanthus*.

†Order CLADOSELACHIFORMES. Two dorsal fins, at least a spine associated with the first. One family.

Family CLADOSELACHIDAE. Upper Devonian to Mississippian.



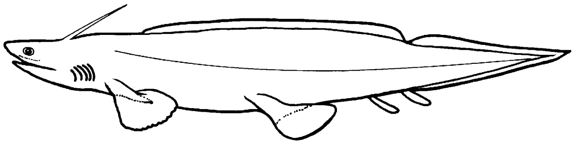
Maximum length about 2 m. Includes the well-known *Cladoselache*.

†Infraclass XENACANTHIMORPHA (Pleuracanthodii)

†Order XENACANTHIFORMES. Pleuracanth-type tooth (three cusps of variable size, usually two prominent lateral cusps and a smaller median one). Claspers in male; elongate dorsal fin base; diphycercal or heterocercal tail; two anal fins; cephalic spine; radials of pectorals jointed and ending well before fin margin.

The Lebachacanthidae and Diplodoselachidae are also in this group, with the latter being the stem xenacanthiform (Soler-Gijón, 2004). Ginter (2004) discussed the origin of the xenacanthiforms and discussed the *Antarctilamna-Wellerodus* group, *Diplodus*, the possibly related *Bransonella*, *Jalodus*, and Phoebodontiformes, and the distant Omalodontiformes.

Family XENACANTHIDAE. Freshwater; Lower Devonian to Triassic.



For example, *Orthacanthus, Pleuracanthus, Triodus,* and *Xenacanthus.*

Infraclass EUSELACHII (sharks and rays, and related fossils)

Sharks, with lateral gill openings, anterior edge of the pectoral fin not attached to the side of the head, and pectoral girdle halves not joined dorsally, are regarded here as forming a separate taxon from the rays (including skates), which have ventral gill openings, anterior edge of the enlarged pectoral fin attached to the side of the head (forming the disc in most species), and pectoral girdle halves joined dorsally.

There are currently two conflicting hypotheses regarding the phylogenetic relationships of euselachians, one based on morphological evidence and one based on molecular evidence (interestingly, older non-cladistic morphological studies showed the same conflict, some placing rays within sharks and others not). This conflict is common in fish systematics. In the present case, following Compagno's (1973, 1977) work, there was growing acceptance that while sharks and rays form a monophyletic group, sharks were a paraphyletic group without the inclusion of rays. Compagno (2001), Shirai (1992a, 1996), and de Carvalho (1996) agreed that rays (batoids or rajiforms) and pristiophoriforms are sister taxa and that both belong in the squalomorph clade.

A comparison of the revised higher classification of the elasmobranch division Neoselachii herein of de Carvalho (1996) (his infraclass Neoselachii) and of Shirai (1996) is given on the next page (for Shirai's Squalea, unless otherwise stated, the orders have one family). The higher classification by Compagno (2001) for his cohort Neoselachii is based on a consensus of his earlier works and of de Carvalho (1996) and Shirai (1996) in giving superorder Squalomorphi with the orders Hexanchiformes (including the Chlamydoselachiformes), Squaliformes, Squatiniformes, Pristiophoriformes, and Rajiformes and the superorder Galeomorphi (as recognized herein) (note that Compagno's sequencing of the two extant euselachian superorders is reversed from the others). The equivalency of some taxa recognized herein is given in parentheses.

However, while the above studies of de Carvalho (1996) and Shirai (1996) present sound morphological studies and analyses, it may be premature to follow their cladistic implications. The cytogenetic data reviewed by Schwartz and Maddock (2002) and the molecular studies of Arnason et al. (2001) and Douady et al. (2003) presented preliminary evidence supporting the monophyly of sharks (without rays), and strong evidence for the same conclusion

de Carvalho (1996)	Shirai (1996)
Division Galeomorphii (= superorder Galeomorphi)	Superorder Galea (= superorder Galeomorphi)
Division Squalea (= superorder Squalomorphi + subdivision Batoidea)	Superorder Squalea (= superorder Squalomorphi + subdivision Batoidea)
Superorder Notidanoidea	Order Chlamydoselachiformes
Order Hexanchiformes	Order Hexanchiformes (two families)
Superorder Echinorhinoidea	Order Echinorhiniformes
Order Echinorhiniformes	Order Dalatiiformes (four families)
Superorder Squaloidea	Order Centrophoriformes
Order Squaliformes	Order Squaliformes
Superorder Hypnosqualea	–
Order Squatiniformes	Order Squatiniformes
Order Pristiophoriformes	Order Pristiophoriformes
Order Rajiformes	Order Rajiformes (four suborders and 12 families)

was given by Maisey et al. (2004) and Naylor et al. (2005). This conclusion was accepted in McEachran and Aschliman (2004), Musick et al. (2004), and Musick and Ellis (2005). With both modern sharks and rays going back to at least the Early Jurassic, I accept that the paleontological evidence can be best interpreted to support the hypothesis of Maisey et al. (2004) and that proposal is accepted here. Maisey et al. (2004) discussed the conflict between the molecular- and morphological-based trees, and they regarded the stratagraphic data as highly congruent with the molecular data; in addition, they regard the batoids as basal to the modern sharks. There are thus two current hypotheses expressing the relationships of sharks and rays:

i) the hypnosqualean hypothesis—the batoids (rays) are sister to the Pristiophoriformes and that clade (coined the Pristiorajea by de Carvalho, 1996) is sister to the squatiniformes (the resulting clade being the Hypnosqualea), and all share a common ancestry with the Squaliformes.

ii) the selachian/batoid (shark/ray) hypothesis—the sharks, as conventionally defined, are monophyletic without the inclusion of the rays.

The latter hypothesis is accepted here. Although I normally feel it best to accept the implications of morphological data for classifications when there is a conflict with molecular evidence, in this case with such apparently strong conflicting evidence, I prefer to recognize sharks and rays in separate taxa (as done, for example, in Berg, 1940, and Nelson, 1976, 1984), pending further work. However, the cladistic results of de Carvalho (1996) and Shirai (1996) may yet warrant changing our classification. If the molecular evidence is correct, then the morphological features used to argue for a monophyletic Hypnosqualea would be the result of convergence (i.e., there would be much homoplasy in the morphological data).

Regardless of which system is employed and whether a different taxonomic rearrangement is used, for common names, the terms shark or selachian (non-batoids) and rays or batoids still seem appropriate to use, as opposed to using the term sharks to include rays as given in Compagno (2001). This follows the principle of keeping common names as stable as possible; thus scientific names are intended to apply to monophyletic taxa while common names are intended only to refer to classical recognized groups, monophyletic or not. The rankings assigned to various taxa and the terms applied, unfortunately and especially so for the non-taxonomist, vary in the literature, more so with the euselachians than with most fish groups. In addition, the content of some taxa varies as well with authors. Some of this is the result of the uncertainty of the current state of our knowledge of the phylogeny of the group. In order to better express relationships, the classification presented here recognizes more categories than some users may wish to use. Users wishing to recognize fewer categories may do so by recognizing only the classical and more familiar taxonomic names and, in reducing the number of categories, changing the category names of the retained taxa (e.g., to subclass Euselachii and superorder Selachii).

Teeth are especially important in the fossil record of sharks and exhibit much variation between taxa. Many publications describe the teeth of living and fossil taxa, for example, works by S. P. Applegate. R. Lund, and J. G. Maisey have worked on the taxonomy and systematics of fossil elasmobranchs. A general review of some aspects of shark behavior and acoustical biology may be found in Myrberg and Nelson (1990) and Myrberg (2001). Schwartz and Maddock (2002) review the cytogenetic data of euselachians. See "Chondrichthyes" above for references giving major revisions to our knowledge of chondrichthyans and explanations to the many terms describing the reproductive phenomena oviparity and viviparity with their many variations as differing means of supplying nutrients to the embryo. Many websites give information on sharks and rays (e.g., http://www.flmnh.ufl.edu/fish/).

Thirteen orders, 51 families, 178 genera, and about 937 species of extant elasmobranchs or euselachians. Some 403 species are sharks and 534 are skates and rays. At least 28 species of sharks and rays are known primarily from freshwater. There are many species of sharks and rays yet to be described, with the rays still outnumbering the sharks. The current classification of euselachians is very split compared to that of other fishes. The mean number of species per family is 18 and the median number is 5.3. About 50% of the species of sharks and rays are in four of the 51 families, Rajidae, Scyliorhinidae, Dasyatidae, and Carcharhinidae, and about one-fifth of the families (11) are monotypic, having only one species in each.

An overview of the higher categories of living (extant) euselachians adopted here is as follows:

Division Neoselachii
Subdivision Selachii (sharks)
    Superorder Galeomorphi
        Order Heterodontiformes (one family)
        Order Orectolobiformes (seven families)

Order Lamniformes (seven families)
Order Carcharhiniformes (eight families)
Superorder Squalomorphi
Order Hexanchiformes (two families)
Order Echinorhiniformes (one family)
Order Squaliformes (six families)
Order Squatiniformes (one family)
Order Pristiophoriformes (one family)
Subdivision Batoidea (rays)
Order Torpediniformes (two families)
Order Pristiformes (one family)
Order Rajiformes (four families)
Order Myliobatiformes (ten families)

†Order CTENACANTHIFORMES. Two dorsal fins, each with a spine; anal fin near caudal fin; cladodont-type tooth (as with many fossil taxa, there are no synapomorphic characters to show monophyly). Maximum length about 2.5 m.

Three families (Zangerl, 1981; Cappetta, 1987; Cappetta et al., 1993). Middle Devonian to Triassic. Unassigned genera include *Acronemus* and *Carinacanthus.*

Family CTENACANTHIDAE. Upper Devonian and Mississippian.
e.g., *Ctenacanthus* and *Goodrichthys.*

Family BANDRINGIDAE. Pennsylvanian.
Primarily freshwater. Snout elongated; caudal fin externally heterocercal.
e.g., *Bandringa.*

Family PHOEBODONTIDAE. Middle Devonian to Upper Triassic.
e.g., *Phoebodus.*

†Division HYBODONTA

Order HYBODONTIFORMES. Hybodontids have the features given above for the ctenacanthiforms. They differ, among other features, in their internal fin structure. Males have hooked cephalic spines above the eye that may have functioned as claspers during copulation. Hybodonts might have been as diverse in feeding and related behavioral strategies as is found among living sharks and rays (Maisey and de Carvalho, 1997). Some were several meters long, others only about 15 cm.

Hybodonts are probably the closest extinct sister group to the neoselachians (Maisey et al., 2004), and this has been expressed here by giving the two groups equal rank. As noted by Maisey et al. (2004), of all elasmobranchs, only these two lineages, the hybodonts and neoselachians, are known to have survived well into the Mesozoic (the other lineages becoming extinct in the Paleozoic, many in the Permo-Triassic mass extinction and the others during the Triassic). Only the neoselachians survived into the Cenozoic. Cappetta (1987) and Cappetta et al. (1993) recognized several families for the taxa given below.

One (Hybodontidae) or more families with the following generic examples from Maisey (1982, 1989, 1991), Cappetta (1987), and Cappetta et al. (1993): *Acrodus, Asteracanthus, Hamiltonichthys, Hybodus, Lissodus, Lonchidion* (see Arratia et al., 2002), *Palaeobates, Polyacrodus, Protacrodus, Pseudodalatias, Ptychodus, Steinbachodus,* and *Tribodus.* Mississippian to Cretaceous (the dominant selachians of the Triassic and Jurassic).

Division NEOSELACHII

Includes all modern sharks and rays. Two clades of sharks are recognized, the Galeomorphi and the Squalomorphi (ranked as superorders). Compagno (2001), which is followed here for most of the general classification, placed the squalomorphs before the galeomorphs. The opposite arrangement is followed here, after de Carvalho (1996) and Shirai (1996). Since this is a two-node system there are no phylogenetic implications in this difference. The arrangement also places the rays at the end as has been conventional in past classifications. The continued recognition of the rays (batoids) as separate from the sharks is discussed above under Euselachii. The neoselachian fossil record extends back to the Early Jurassic, and Maisey et al. (2004) gave a list of the earliest records of their modern taxa.

Subdivision SELACHII (sharks) (Selachimorpha, Pleurotremata)

Gill openings mainly lateral; anterior edge of pectoral fin not attached to side of head; anal fin present or absent; pectoral girdle halves not joined dorsally (but scapulocoracoids fused ventrally in both sharks and rays). These features, while not representing shared derived features of the clade, do serve to distinguish sharks from rays. See above under Infraclass Euselachii for reasons why the sharks and rays, unlike in the 1994 edition, are placed in separate taxa of equal rank.

Two superorders, the Galeomorphi, with four orders, and the Squalomorphi with five orders, and a total of 34 families, 106 genera, and 403 species.

Superorder GALEOMORPHI

Anal fin present (members of the other superorder with living species, the Squalomorphi, lack the anal fin, except for the Hexanchiformes). The recognition of galeomorphs as a monophyletic group follows the many works of Leonard J.V. Compagno (e.g., Compagno 1988, 2001).

The composition is the same as the division Galeomorphii of de Carvalho (1996), superorder Galea of Shirai (1996), and superorder Galeomorphi of Compagno (2001); all have the same four orders as here. The sequencing of the orders is based on de Carvalho (1996), Goto (2001), and Musick and Ellis (2005), where the Heterodontiformes (the most primitive galeomorphs) are sister to the other three orders and the Orectolobiformes are sister to the

Lamniformes and Carcharhiniformes. The classification, information on distribution, and much of the other information are based on Compagno (1999, 2001, 2005).

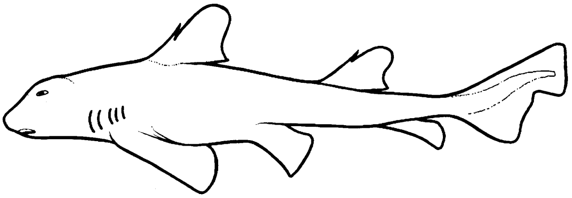
Four orders, 23 families, 74 genera, and 279 species.

The following fossil family may belong to the Galeomorphi (Cappetta, 1987). Palaeospinacidae. Lower Triassic to the Paleocene. Includes *Nemacanthus, Palaeospinax, Paraorthacodus,* and *Synechodus.*

Order HETERODONTIFORMES (4)—bullhead sharks. Two dorsal fins, each with a spine (other galeomorphs lack dorsal fin spines); anal fin present; head elevated with crests above eyes; five gill slits, first the largest and posteriormost two or three behind pectoral fin origin; spiracle present but small; eyes dorsolateral, without nictitating fold; nostrils connected with mouth by deep groove. Vertebrae 103–123. Oviparous, screw-shaped egg cases.

One family (Compagno, 2001).

Family HETERODONTIDAE (8)—bullhead sharks. Marine, tropical to warm temperate, continental and insular shelves (primarily continental versus oceanic islands) and uppermost slopes (0–275 m, most shallower than 100 m); western Indian (Arabian Peninsula to South Africa) and Pacific (western Pacific from Japan to Tasmania and New Zealand, eastern Pacific from California to Galapagos Islands and Peru).



See order for family description. Maximum length 1.6 m, attained in *Heterodontus portusjacksoni,* most under 1 m. Also known as horn sharks or Port Jackson sharks.

One genus, *Heterodontus,* with eight species and one undescribed (Compagno, 2001, 2005).

Order ORECTOLOBIFORMES (5)—carpet sharks. Two dorsal fins, without spines; anal fin present; five gill slits, broad, last two to four above or behind pectoral fin origin; spiracles present, small to large, and close behind and about level with eyes; eyes usually dorsolateral on head (lateral in *Nebrius, Stegostoma,* and *Rhincodon*); eyes without nictitating membrane; mouth small to large, well in front of the eyes; nostrils longitudinal on snout, with prominent nasoral grooves and barbels in most.

Seven families, 14 genera, and 32 species (Compagno, 2001, 2005). Goto (2001), who gave a cladistic analysis of this order, gave keys to the families and the genera, placed the families Stegostomatidae and Ginglymostomatidae in synonymy with Rhincodontidae, and thus recognized only five families. The recognition of the two suborders follows Goto (2001).

Suborder Parascyllioidei. Spiracles minute, without gill filaments; fifth (and last) gill opening large; origin of anal fin well in front of origin of second dorsal fin.

Family PARASCYLLIIDAE (9)—collared carpet sharks. Marine, tropical to temperate continental to slopes (1–435 m); western Pacific (Australia to Japan).

Vertebrae 159–199. Maximum length 3.3 m, in *Cirrhoscyllium expolitum*, most under 0.9 m.

Two genera, *Cirrhoscyllium* (3, South China Sea to Japan) and *Parascyllium* (4, Australia), with seven species (Compagno, 2001, 2005).

Suborder Orectoloboidei. Spiracles moderate to large, with gill filaments; fifth (and last) gill opening moderate in size; origin of anal fin behind origin of second dorsal fin.

Family BRACHAELURIDAE (10)—blind sharks. Marine, tropical to temperate continental shelf, primarily coastal (0–137 m); western South Pacific (off east coast of Australia).

Spiracles large; nasal barbels very long; eyes dorsolateral. The common name comes from the habit of one of the species of closing its eyelids when removed from the water. Vertebrae 117–142. Maximum length about 1.2 m, attained in *Brachaelurus waddi.*

Two monotypic genera, *Brachaelurus* and *Heteroscyllium* (Compagno, 2001, 2005). Both species are placed in *Brachaelurus* in Goto (2001).

Family ORECTOLOBIDAE (11)—wobbegongs. Marine, tropical to warm temperate continental shelf (0–110 m); western Pacific (Japan to southern Australia).

Head and body depressed; mouth nearly terminal; skin flaps along side of head and long barbels; spiracles large; enlarged fanglike teeth at symphysis of upper and lower jaws. Vertebrae 149–158. Maximum length about 3.2 m, attained in *Orectolobus maculatus.*

Three genera, *Eucrossorhinus* (1), *Orectolobus* (synonym *Crossorhinus*) (4 and several undescribed), and *Sutorectus* (1), with six species (Compagno, 2001, 2005).

Family HEMISCYLLIIDAE (12)—bamboo sharks. Marine, tropical and subtropical, continental shelves (usually close inshore, up to about 100 m); Indo-West Pacific (Madagascar to Japan and Australia).

Nasal barbels short; spiracles large; anal fin low and rounded, origin well behind origin of second dorsal fin. Vertebrae 151–192. Maximum length about 1.0 m, attained in *Chiloscyllium punctatum* and *Hemiscyllium ocellatum*, most under 70 cm.

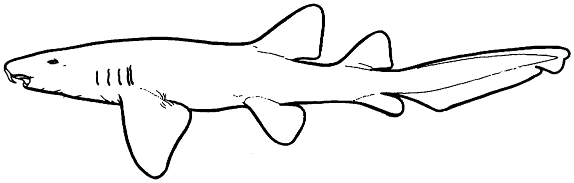
Two genera, *Chiloscyllium* (7) and *Hemiscyllium* (5, primarily western Pacific, the long-tailed carpet sharks), with 12 species (Compagno, 2001, 2005).

Family STEGOSTOMATIDAE (13)—zebra sharks. Marine, primarily tropical inshore over continental and insular shelves (0–62 m); Indo-West Pacific (from Red Sea and off eastern Africa to southern Japan, northern Australia, and New Caledonia).

Spiracles moderate in size and behind the eye; eyes lateral on head; caudal fin unusually long, almost as long as rest of shark. Vertebrae 207–243. Maximum length possibly 3.5 m, usually under 2.5 m.

One species, *Stegostoma fasciatum*, Zebra Shark (Compagno, 2001, 2005).

Family GINGLYMOSTOMATIDAE (14)—nurse sharks. Marine, tropical and subtropical inshore over continental and insular shelves (0 to about 100 m); western Atlantic (northern USA to southern Brazil), eastern Atlantic primarily off Africa, Indo-West and central Pacific (Africa to southern Japan, northern Australia, and Tahiti), and eastern Pacific (Mexico to Peru).

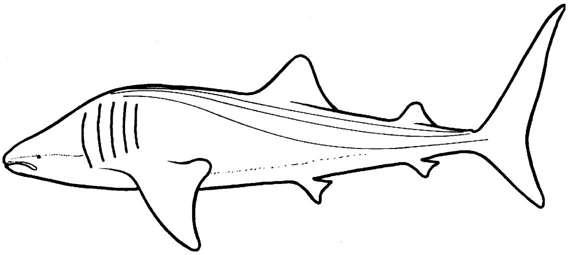


Spiracles small (smaller than the eyes), behind the eyes; eyes lateral on head in *Nebrius*; nostrils with short to moderately long barbels; no lobe and groove around outer edges of nostrils; fourth and fifth gill slits almost overlapping. Vertebrae 135–195.

Maximum length about 3 m, attained in *Ginglymostoma cirratum* and *Nebrius ferrugineus*.

Three monotypic genera, *Ginglymostoma*, *Nebrius*, and *Pseudoginglymostoma* (Compagno, 2001, 2005).

Family RHINCODONTIDAE (Rhiniodontidae) (15)—whale sharks. Marine, tropical to warm temperate coastal and oceanic (0–700 m); circumglobal Atlantic, Indian, and Pacific.



Mouth exceptionally large and virtually terminal; gill openings exceptionally large, fifth well separated from fourth; eyes lateral; gill rakers elongate, plankton feeders; teeth reduced but numerous tooth rows; spiracles relatively small. Vertebrae 174. Maximum length at least 12 m, probably over 14 m, and perhaps up to 18 m (Colman, 1997). Even at 12 m, this is the world's largest fish.

One species *Rhincodon typus,* Whale Shark (Compagno, 2001, 2005). Generic synonym: *Rhiniodon.*

Order LAMNIFORMES (6)—mackerel sharks. Two dorsal fins, without spines; anal fin present; five gill slits, broad, last two may be above pectoral fin origin; spiracles usually present, small and behind eyes; eyes usually lateral (dorsolateral in *Carcharias*); eyes without nictitating membrane; barbels absent; mouth large and extending well behind eyes; spiral intestinal valve of ring type (appearing as a stack of rings), with 19–55 turns.

Seven families with 10 genera and 15 species (Compagno, 2001).

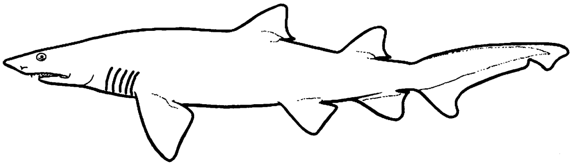
The following fossil taxa, known primarily from teeth, are recognized in Lamniformes by Cappetta (1987).

Cretoxyrhinidae. Lower Cretaceous to Paleocene. Includes *Cretodus, Cretoxyrhina, Leptostyrax, Paraisurus,* and *Protolamna.*

Otodontidae. Paleocene to Pliocene. Includes *Carcharocles* and *Otodus.*

Anacoracidae. Lower to Upper Cretaceous. Includes *Pseudocorax* and S*qualicorax.*

Family ODONTASPIDIDAE (16)—sand tiger sharks. Marine, tropical to temperate continental and insular shelves to deep slopes (1 to about 1600 m) with one species oceanic; Atlantic, Indian, and Pacific.

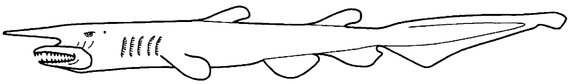


Gill openings all in front of pectoral fin, relatively large but not extending onto dorsal surface of head; eyes relatively small; caudal peduncle without a lateral keel; caudal fin asymmetrical with relatively short ventral lobe. Vertebrae 156–183. Maximum length 4.1 m, attained in *Odontaspis ferox* (the other two species reach over 3 m).

Fossil taxa include *Eugomphodus* (synonym *Synodontaspis*). *Carcharias* and *Odontaspis* have been separate since the Cretaceous, and it has been suggested that they be placed in separate families, although this is not followed by Compagno (2001:57) pending further study.

Two genera, *Carcharias* (1) and *Odontaspis* (2), with three species (Compagno, 2001, 2005).

Family MITSUKURINIDAE (17)—goblin sharks. Marine, outer continental and upper slopes and seamounts (100–1300 m, usually 270–960 m); scattered in eastern Atlantic (France to South Africa), western Atlantic (Gulf of Mexico and Guiana to French Guyana), western Indian (primarily South Africa), western Pacific (Japan, Australia, and New Zealand), and eastern Pacific (southern California).

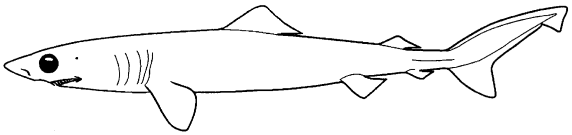


Snout with a greatly elongated and flattened bladelike projection; jaws very protrusible; precaudal pit absent; eyes small; caudal fin long but ventral lobe not developed. Vertebrae 122–125. Maximum length 3.8 m.

Fossils include species of *Anomotodon* (Lower Cretaceous to at least the Eocene) and *Scapanorhynchus* (Lower Cretaceous to Upper Cretaceous), and there are also fossils of *Mitsukurina* extending back to the Eocene (Cappetta, 1987). Some authors have considered *Mitsukurina* and *Scapanorhynchus* to be congeneric, the latter name having priority.

One species, *Mitsukurina owstoni,* Goblin Shark (Compagno, 2001, 2005). The one worldwide species occurs on the Pacific side in North America over the continental shelf, but on the Atlantic side it is known only from the northern Gulf of Mexico from about 1000 m (Parsons et al., 2002).

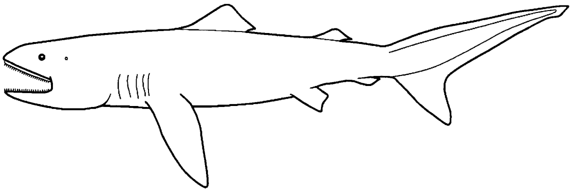
Family PSEUDOCARCHARIIDAE (18)—crocodile sharks. Marine, tropical to subtropical, inshore (rarely) to oceanic and circumglobal (surface to at least 590 m); scattered localities, western Atlantic (Brazil), eastern Atlantic (Cape Verde Islands to South Africa), western Indian (primarily southern Africa), parts of eastern Indian, western Pacific (southern Japan to northern Australia, North Island of New Zealand, and Hawaii), much of open Pacific (Hawaii to North and South America), and eastern Pacific (Baja California to Peru).



Eyes exceptionally large; gill openings extending onto dorsal surface of head; caudal peduncle with upper and lower precaudal pits and with low lateral keel; caudal fin asymmetrical with moderate lower lobe. Vertebrae 146–158. Maximum length 1.1 m.

One species, *Pseudocarcharias kamoharai,* Crocodile Shark (Compagno, 2001, 2005).

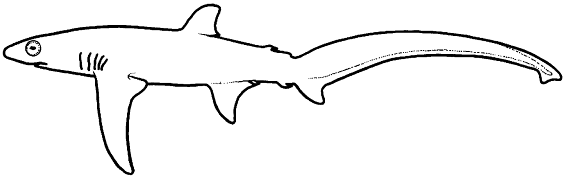
Family MEGACHASMIDAE (19)—megamouth sharks. Marine, tropical to warm temperate, coastal (as shallow as 5 m) and oceanic (epipelagic from 8–166 m depth), probably circumtropical; Atlantic (Brazil and Senegal), Indian (western Australia), and Pacific (Japan, Philippines, Indonesia, Hawaiian Islands, and southern California).



Head elongated, about length of trunk; mouth exceptionally large, terminal; snout short and broadly rounded; gill openings moderately long but not extending onto dorsal surface of head and with last two over pectoral fin base; teeth small, in numerous rows; gill rakers unique, of fingerlike dermal papillae; precaudal pits present. Vertebrae 151. Maximum length 5.5 m. This is one of the three species of gigantic filter-feeding sharks. First found in 1976 and described in 1983, the one species of this family was known up to 2004 from only 24 specimens (see http://www.flmnh.ufl.edu/fish/ under "shark" for updates). It is the only shark thought to be subject to attacks from the semiparasitic shark *Isistius brasiliensis.*

One species, *Megachasma pelagios*, Megamouth Shark (Compagno, 2001, 2005).

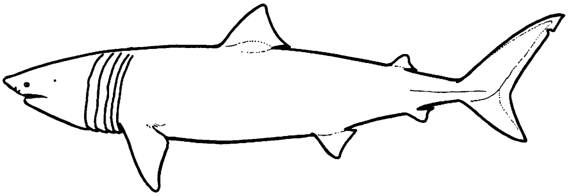
Family ALOPIIDAE (20)—thresher sharks. Marine, tropical to cold temperate, coastal and oceanic (surface–at least 500 m); scattered across Atlantic, Indian, and Pacific.



Upper lobe of caudal fin long and curving, about as long as rest of shark; last two gill openings above pectoral fin base; gill openings short; mouth small; pectoral fins long and narrow; eyes large; precaudal pits present. Vertebrae 282–477 (most variation is in the number of caudal vertebrae; *Alopias vulpinus* has the greatest number, 453–477). Maximum length at least 5.7 m, attained in *Alopias vulpinus*, the Pelagic Thresher, the species with the largest range.

One genus, *Alopias*, with three species (Compagno, 2001, 2005).

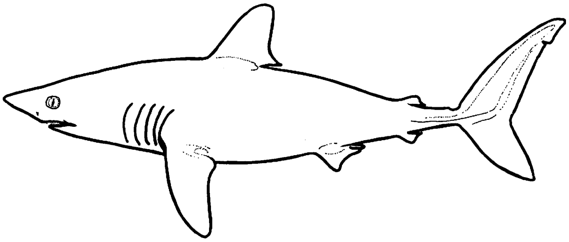
Family CETORHINIDAE (21)—basking sharks. Marine, warm temperate (rarely subtropical) to cool temperate, continental and insular shelves, possibly oceanic (usually in shallow water); Atlantic (including the Mediterranean and western Barents Sea), Indian (only off western Australia), and Pacific.



Gill openings exceptionally large, extending almost to the top of the head; teeth small and numerous; mouth large; eyes small; gill rakers elongate (hairlike), modified dermal denticles (occasionally shed in this plankton feeder); caudal fin nearly symmetrical and caudal peduncle with strong lateral keel. Vertebrae 109–116. Maximum length perhaps up to 15.2 m, at least 10 m. One of the three species of gigantic filter-feeding sharks, this is the world's second-largest fish species.

One species, *Cetorhinus maximus*, Basking Shark (Compagno, 2001, 2005).

Family LAMNIDAE (22)—mackerel sharks. Marine, tropical to cool temperate, continental and insular waters (to about 1,200 m) and oceanic; Atlantic, Indian, and Pacific.



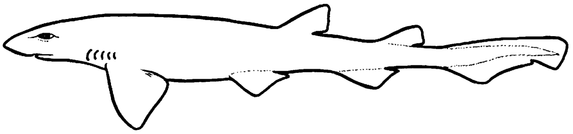
Gill openings large, barely extending onto dorsal surface of head; teeth relatively few and enlarged; gill rakers absent; caudal fin nearly symmetrical and caudal peduncle with strong lateral keel and precaudal pits. Vertebrae 153–197. Maximum length at least 6.0 m, attained in *Carcharodon carcharias* (White Shark, also known as the Great White Shark, e.g., in FAO publications) (Compagno, 2001). This species is responsible for the majority of attacks on humans in many areas (e.g., for this and other information see Myrberg and Nelson, 1990; Ellis and McCosker, 1991; Klimley and Ainsley, 1996; Compagno, 2001; see also the International Shark Attack File [ISAF] at http://www.flmnh.ufl.edu/fish/). The White Shark has one of the widest ranges of all elasmobranchs.

Three genera, *Carcharodon* (1, *C. carcharias*, White Shark), *Isurus* (2, makos), and *Lamna* (2, Salmon Shark and Porbeagle), with five species (Compagno, 2001, 2005). Fossils include the giant late Pliocene *Carcharodon megalodon*, Megatooth Shark or Megalodon, which reached a length of up to 11–20 m (Compagno, 2001).

Order CARCHARHINIFORMES (7)—ground sharks. Two dorsal fins (one dorsal fin in the scyliorhinid *Pentanchus profundicolus*, the Onefin Cat Shark, from the Philippines), without spines; anal fin present; five gill slits, with the last one to three over the pectoral fin; gill rakers absent; mouth extending behind eyes; eyes with nictitating fold or membrane (lower eyelid, described in detail in Compagno, 1988); spiracles usually absent; intestinal valve of spiral or scroll type (described in Compagno, 1988:79–80). Development may be oviparous, ovoviparous, or viviparous.

Eight families, 49 genera, and at least 224 species (Compagno, 1999). The classification of this order is based on Compagno (1999).

Family SCYLIORHINIDAE (23)—cat sharks. Marine, temperate to tropical; continental and insular shelves and slopes; circumglobal, Atlantic, Indian, and Pacific.



First dorsal fin base opposite or behind pelvic fin base (in front of pelvic fin base in all others); nictitating eyelids rudimentary; spiracles present; intestine with spiral valve. Maximum length at least 1.6 m, attained in *Scyliorhinus stellaris.*

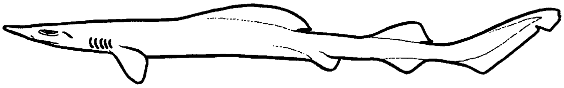
Sixteen genera, *Apristurus* (31, and about 13 undescribed species), *Asymbolus* (8), *Atelomycterus* (3), *Aulohalaelurus* (2), *Bythaelurus* (6), *Cephaloscyllium* (7, with up to 11 undescribed species), *Cephalurus* (1), *Galeus* (16), *Halaelurus* (5), *Haploblepharus* (3), *Holohalaelurus* (3), *Parmaturus* (5), *Pentanchus* (1), *Poroderma* (2), *Schroederichthys* (5), and *Scyliorhinus* (15), with at least 113 species (and more than 25 undescribed species) (Compagno, 2005).

Family PROSCYLLIIDAE (24)—finback cat sharks. Marine, warm temperate to tropical, continental shelves and slopes; western North Atlantic (between Florida and Cuba) and Indo-West Pacific.

Nictitating eyelids rudimentary; spiracles present; posterior teeth comblike; labial furrows (at corner of mouth) short or absent. Maximum length 1 m, attained in *Gollum attenuatus.*

Three genera, *Ctenacis* (1), *Eridacnis* (3), and *Proscyllium* (1), with five species (Compagno, 1999, 2005).

Family PSEUDOTRIAKIDAE (25)—false cat sharks. Marine, continental and insular slopes; part of North Atlantic, western Indian, and western and central Pacific (including to New Zealand).



First dorsal fin low, elongate, and keel-like; nictitating eyelids rudimentary; spiracles large; tooth rows exceptionally numerous, posterior teeth comblike; intestine with spiral valve. Maximum length 2.9 m.

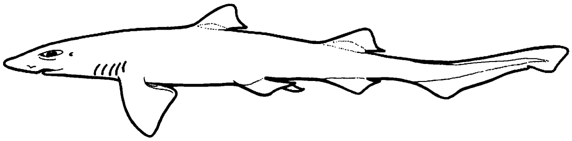
Two monotypic genera, *Gollum* (2 undescribed species are known) and *Pseudotriakis* (Compagno, 1999, 2005).

Family LEPTOCHARIIDAE (26)—barbeled hound sharks. Marine, continental shelf; eastern Atlantic off Africa.

Labial furrows (at corner of mouth) very long; anterior nasal flaps formed into slender barbels; nictitating eyelids internal; spiracles small; intestine with spiral valve. Maximum length 8.2 m. The one species appears to be closely related to the triakids and, perhaps, should be included in it.

One species, *Leptocharias smithii,* Barbeled Hound Shark (Compagno, 1999, 2005).

Family TRIAKIDAE (27)—hound sharks. Marine, rarely in freshwater, tropical to cool temperate, continental and insular shelves and slopes; circumglobal, Atlantic, Indian, and Pacific.



Labial furrows moderately long; anterior nasal flaps usually not slender or barbel-like; spiracles present; intestine with spiral valve. Maximum length 2.4 m, attained in *Triakis maculata.*

Nine genera with at least 38 species (Compagno, 1999, 2005). Compagno (1988) recognized two subfamilies and they are provisionally recognized here:

SUBFAMILY TRIAKINAE. Relatively large nasal flaps. *Mustelus* (at least 22, smoothhounds), *Scylliogaleus* (1), and *Triakis* (5, leopard sharks, including *Cazon*), with 28 species. *Mustelus canis* enters freshwater for short periods in the western Atlantic.

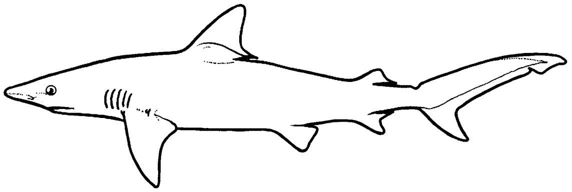
SUBFAMILY GALEORHININAE. Small or barbel-like nasal flaps. *Furgaleus* (1), *Galeorhinus* (1), *Gogolia* (1), *Hemitriakis* (4), *Hypogaleus* (1), and *Iago* (2), with 10 species.

Family HEMIGALEIDAE (28)—weasel sharks. Marine, continental shelves; eastern tropical Atlantic (and possibly New England) and Indo-West Pacific.

Dorsal fin margin undulated; precaudal pit present; nictitating membrane internal; spiracles small; labial furrows moderately long; intestine with spiral valve. Maximum length 2.4 m, attained in *Hemipristis elongatus.*

Four genera, *Chaenogaleus* (1), *Hemigaleus* (1), *Hemipristis* (1), and *Paragaleus* (4), with seven species (Compagno, 1999, 2005).

Family CARCHARHINIDAE (29)—requiem sharks. Marine, occasionally in freshwater rivers and lakes, tropical to warm temperate, continental and insular shelves and slopes and oceanic; circumglobal, Atlantic, Indian, and Pacific.



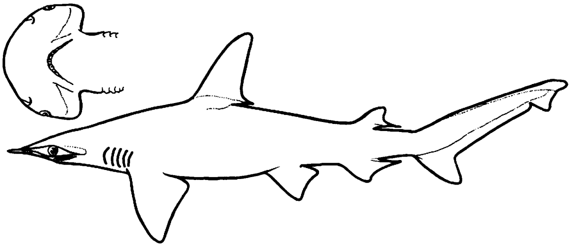
Dorsal fin margin undulated; precaudal pit present; spiracles usually absent; nictitating eyelids internal; intestine with scroll valve, lacking spiral valve. Maximum length at least 7.4 m, attained in *Galeocerdo cuvier.*

Seven species enter freshwater, with extended movements by *Carcharhinus leucas* (Bull Shark) and *Glyphis gangeticus* (Ganges Shark) (the latter may be confined to fresh and brackish water).

In the 1994 edition, sphryrnids (hammerhead sharks) were placed in this family because independent evidence based on morphological and molecular data suggested that the Carcharhinidae were not monophyletic unless sphryrnids were included in the family (Compagno, 1988:403; Naylor, 1992). Naylor (1992) did not, however, have data from *Scoliodon*, the taxon Compagno (1988) thought to be the sister group of sphryrnids. Carcharinids and sphryrnids are now, as classically done, recognized in separate families as in Compagno (1999, 2005) until better evidence of their interrelationships is published (however, Musick and Ellis, 2005, placed sphryrnids within carcharinids).

Twelve genera, *Carcharhinus* (30), *Galeocerdo* (1, Tiger Shark), *Glyphis* (3, river sharks), *Isogomphodon* (1), *Lamiopsis* (1), *Loxodon* (1), *Nasolamia* (1), *Negaprion* (2, lemon sharks), *Prionace* (1, Blue Shark), *Rhizoprionodon* (7), *Scoliodon* (1), and *Triaenodon* (1), with at least 50 species (several undescribed species are known) (Compagno, 1999, 2005).

Family SPHYRNIDAE (30)—hammerhead sharks. Marine (occasionally brackish), tropical to warm temperate, primarily continental shelf; Atlantic, Indian, and Pacific.



Lateral, bladelike extensions to the head (with eyes and nasal openings farther apart than in other sharks, perhaps conferring an advantage in homing in on food); spiracles absent. The head extensions range from being narrow and winglike in the Indo-West Pacific *Eusphyra blochii* to being evenly rounded and spadelike in the New World *Sphyrna tiburo* (shown in above figure). Large individuals are very dangerous and there are many records of fatal attacks on humans. Maximum length 6.1 m, attained in *S. mokarran.*

Two genera, *Eusphyra* (1) and *Sphyrna* (7), with eight species (Compagno, 1999, 2005).

Superorder SQUALOMORPHI

The composition of this superorder differs from the division Squalea of de Carvalho (1996) and superorder Squalea of Shirai (1996) (see above under infraclass Euselachii for a discussion of differing hypotheses on the interrelationships of sharks and rays). Major differences between these two authors and the present work are as given in table form below (suborders not given, but the number of families recognized by the author is given in parentheses; unless stated otherwise, one family is recognized in the order) except that their Rajiformes are not recognized here in this superorder but are placed in a separate taxon. J.G. Maisey in 1980 recognized this group by its unique form of jaw articulation, the orbitostylic jaw articulation, hence the group can be referred to as the orbitostylic sharks.

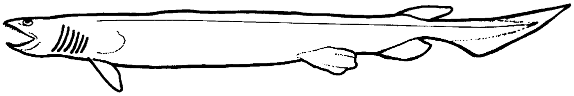
de Carvalho (1996)	Shirai (1996)	Herein
Superorder Notidanoidea	Order Chlamydoselachiformes	Order Hexanchiformes (2)
Order Hexanchiformes (2)	Order Hexanchiformes	
Superorder Echinorhinoidea		
Order Echinorhiniformes	Order Echinorhiniformes	Order Echinorhiniformes
Superorder Squaloidea	Order Dalatiiformes (4)	Order Squaliformes (6)
Order Squaliformes (6)	Order Centrophoriformes	
Superorder Hypnosqualea	Order Squaliformes	
Order Squatiniformes	Order Squatiniformes	Order Squatiniformes
Order Pristiophoriformes	Order Pristiophoriformes	Order Pristiophoriformes
Order Rajiformes (unstated)	Order Rajiformes (12)	

Five orders, 11 families, 32 genera, and 124 species.

Order HEXANCHIFORMES (Notidanoidei) (8)—six-gill sharks. One dorsal fin, without spine; anal fin present; six or seven gill slits; eyes without nictitating fold; spiracle present but small, well behind eye. The homology of the extra arches is discussed by Shirai (1992b).

Two families with four genera and five species. Shirai (1992a, 1996) considered *Chlamydoselachus* to be sister to all remaining euselachians, and he thus placed it in a separate order from the Hexanchiformes. The evidence of de Carvalho (1996) that it and the Hexanchidae are sister taxa is accepted here. Fossil forms include the Lower Jurassic to Paleocene Orthacodontidae with one genus, *Sphenodus* (synonym *Orthacodus*) (Cappetta, 1987), Jurassic *Notidanoides* (the formerly recognized generic name *Notidanus* is invalid) (Maisey, 1986a), Late Cretaceous to Eocene *Notidanodon* (Cione, 1996), and perhaps, unexpectedly, Devonian teeth placed in the family Mcmurdodontidae (Turner and Young, 1987).

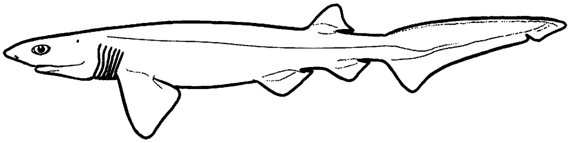
Family CHLAMYDOSELACHIDAE (31)—frill sharks. Marine, continental and insular slopes, occasionally on shelves; scattered in western North Atlantic, eastern Atlantic (Norway to around South Africa), southwestern Indian, western Pacific (Japan to New Zealand), and eastern Pacific (California and Chile).



Six gill openings, margin of first gill continuous across throat; mouth terminal; teeth alike on upper and lower jaws, with three elongate cusps; lateral-line canal open; body very elongate. Maximum length about 1.9 m.

One species, *Chlamydoselachus anguineus*, Frill Shark; possibly an undescribed species off southern Africa (Compagno, 1999, 2005).

Family HEXANCHIDAE (32)—cow sharks. Marine, temperate to tropical, continental and insular shelves and slopes; circumglobal, Atlantic, Indian, and Pacific.



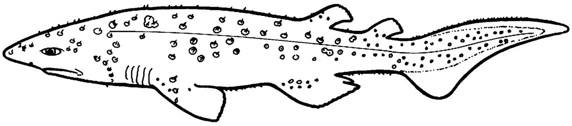
Six or seven gill openings, margin of first gill not continuous across throat; mouth ventral; teeth in upper jaw different from those in lower jaw; lateral-line canal open in *Notorynchus*. Maximum length about 4.7 m, attained in *Hexanchus griseus*.

The braincase of *Notorynchus* is described by Maisey (2004b), based on high-resolution scanning and digital imaging. This study also gives new phylogenetic information on the elasmobranch braincase in fossils.

Three genera and four species (Compagno, 1999, 2005): *Hexanchus* (2) with six gill openings, and *Heptranchias perlo* (sometimes placed in its own family Heptranchiidae) and *Notorynchus cepedianus* (sometimes placed in its own family Notorynchidae) with seven gill openings.

Order ECHINORHINIFORMES (9)—bramble sharks. Bramble sharks are placed in their own order by de Carvalho (1996) based on several characters that he feels suggest that this taxon is sister to all remaining sharks (Squaliformes, Squatiniformes, and Pristiopriformes) and to the rays (batoids). They are treated in their own order here but the noted sister-group relationship is not adopted (see under infraclass Euselachii). The only family was recognized in the Squaliformes in the last edition and in Compagno (1999).

Family ECHINORHINIDAE (33)—bramble sharks. Marine, cool to warm temperate, continental and insular shelves and slopes and some sea mounts; Atlantic, western Indian, and Pacific.



Both dorsal fins small and spineless, first dorsal fin originating over or behind pelvic fin origin (some other sharks such as the dalatiid *Isistius* have posteriorly placed dorsal fins, but they are not as far back); pelvic fins larger than second dorsal fin; body with coarse denticles; teeth alike in both jaws, rows linearly arranged; last gill slit distinctly larger than others; spiracles minute and well behind eyes; lateral-line canal open; caudal fin without a subterminal notch. Maximum length up to 2 m.

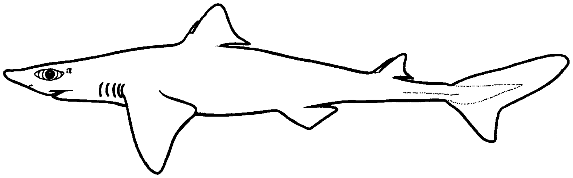
One genus, *Echinorhinus*, with two species (Compagno, 1999, 2005), *E. brucus* (shown in figure) in parts of the Atlantic (commonest in eastern Atlantic), Indian, and western Pacific with denticles relatively few and large, and *E. cookei* in parts of the Pacific with denticles relatively numerous and small.

Order SQUALIFORMES (10)—dogfish sharks.
Two dorsal fins, with or without spines; anal fin absent; five gill slits; spiracles present; nictitating lower eyelid absent; lateral-line canal closed (as it is in most euselachians).

The Echinorhinidae, placed in this order in Nelson (1994), is now placed in its own order following de Carvalho (1996). Three of the families now recognized were regarded as subfamilies of Dalatiidae in Nelson (1994) (see Dalatiidae).

Six families, 24 genera, and at least 97 species.

Family SQUALIDAE (34)—dogfish sharks. Marine, cool temperate to tropical, circumglobal on continental and insular shelves and slopes and on sea mounts; Atlantic, Indian, and Pacific.



Both dorsal fins with spines and spines not grooved; teeth on lower jaw not much larger than those on upper jaw; upper precaudal pit usually present; caudal peduncle with a pair of lateral keels.

The Spiny Dogfish, *Squalus acanthias*, is one of the most cosmopolitan fish species, being widespread in the Northern and Southern Hemispheres but virtually absent in tropical waters and the Indian Ocean. This family was placed in its own order, Squaliformes, in Shirai (1992a, 1996) and regarded as the sister group to all remaining euselachians.

Two genera, *Cirrhigaleus* (2) and *Squalus* (8, and six undescibed species), with at least 10 species (Compagno, 2005).

Family CENTROPHORIDAE (35)—gulper sharks. Marine, warm temperate to tropical, continental and insular outer shelves and slopes; Atlantic, Indian, and Pacific (absent in eastern Pacific).

Both dorsal fins with spines and both spines grooved; teeth on lower jaw larger than those on upper jaw; precaudal pits and lateral keels absent on caudal peduncle.

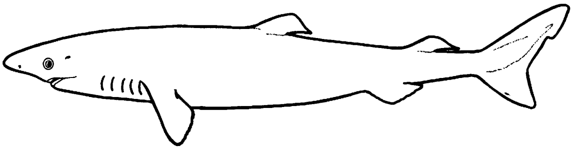
Two genera, *Centrophorus* (10) and *Deania* (4), with 14 species (Compagno, 1999, 2005).

Family ETMOPTERIDAE (36)—lantern sharks. Marine, tropical to temperate, continental and insular slopes (rarely on shelves), a few oceanic; parts of the Atlantic (extending north to Iceland), Indian, and Pacific.

Both dorsal fins with spines and both spines grooved; caudal fin with subterminal notch; luminous organs usually present on body. These are small sharks, the maximum length is under 90 cm in most species.

Five genera, *Aculeola* (1), *Centroscyllium* (7), *Etmopterus* (31, with three undescribed species), *Miroscyllium* (1), and *Trigonognathus* (1), with 41 species (Shirai, 1992a; Shirai and Okamura, 1992; Compagno, 1999, 2005).

Family SOMNIOSIDAE (37)—sleeper sharks. Marine, Arctic to sub-Antarctic, continental and insular slopes (on shelves in Arctic and sub-Antarctic), some oceanic; Atlantic, Indian, and Pacific.



Dorsal fins usually without spines (present in a few species but small and in both fins); lateral ridge present on abdomen between pectoral and pelvic fins; luminous organs present in most.

Seven genera, *Centroscymnus* (2), *Centroselachus* (1), *Proscymnodon* (2), *Scymnodalatias* (4), *Scymnodon* (1), *Somniosus* (including *Rhinoscymnus*, 5), and *Zameus* (2), with 17 species (Compagno, 2005). *Somniosus* is in both the Arctic and sub-Antarctic and extends onto inner shelves.

Family OXYNOTIDAE (38)—rough sharks. Marine, continental and insular shelves and slopes; eastern Atlantic (including Mediterranean), western Atlantic, and western Pacific.

Body very high and compressed, triangular in cross section; dorsal fins very high, each with a large spine that may be concealed by the fin; origin of first dorsal fin may extend far forward over gill openings; lateral ridge present on abdomen between pectoral and pelvic fins; skin very rough; luminous organs present.

One genus, *Oxynotus*, with five species (Compagno, 2005).

Family DALATIIDAE (39)—kitefin sharks. Marine, tropical to temperate, continental and insular shelves and slopes and oceanic; Atlantic, Indian, and Pacific.

Dorsal fins without spines, except species of *Squaliolus* have a spine in the first dorsal fin; luminous organs present, appearing as black dots mainly on ventral surface (Shirai, 1992a).

One species of this group, *Squaliolus laticaudus*, and the proscylliid *Eridacnis radcliffei* are the smallest known sharks, reaching only about 25 cm in total length (Compagno, 1984a, b). The small and pelagic cookiecutter sharks of the genus *Isistius*, with modifications to their feeding apparatus, cause crater-like wounds in other fishes and cetaceans (Shirai and Nakaya, 1992).

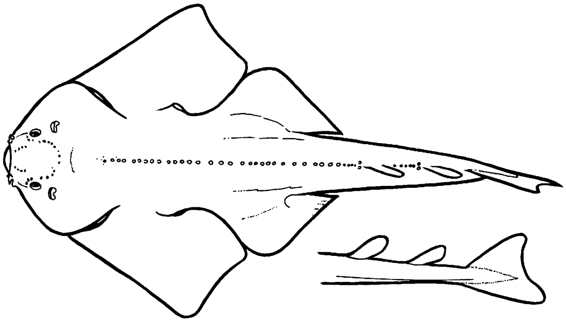
In Nelson (1994), the Etmopteridae, Somniosidae, and Oxynotidae were recognized as subfamilies of the Dalatiidae.

Seven genera, *Dalatias* (1), *Euprotomicroides* (1), *Euprotomicrus* (1), *Heteroscymnoides* (1), *Isistius* (perhaps 3, cookiecutter sharks), *Mollisquama* (1), and *Squaliolus* (2), with about 10 species (Compagno, 2005).

†Order PROTOSPINACIFORMES. One family, Protospinasidae, with one genus, *Protospinax*, Upper Jurassic, Bavaria. The position of this fossil was resolved by de Carvalho and Maisey (1996) based on new material and cladistic analysis. Their re-evaluation was based on a revised data matrix, largely from Shirai (1992a), with some differing interpretations of Shirai's characters. Their study supported Shirai's hypnosqualean group and they formally recognized the group as the Superorder Hypnosqualea, with *Protospinax* as sister to the living hypnosqualeans (i.e., all remaing neoselachians in the present classification). Although this phylogeny is not followed here, *Protospinax* is regarded as sister to the remaining squalomorphs, the squatinids and pristiophorids.

Order SQUATINIFORMES (11)—angel sharks.

Family SQUATINIDAE (40)—angel sharks. Marine, temperate to tropical, continental shelves and upper slopes; Atlantic, southwestern Indian, and Pacific.



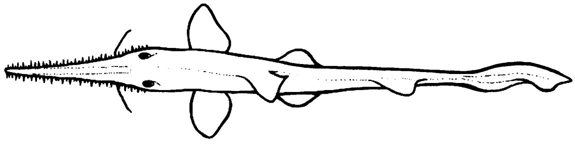
Body raylike; eyes dorsal; two spineless dorsal fins; no anal fin; five gill openings; spiracle large; mouth almost terminal; nostrils terminal with barbels on anterior margin. Maximum length up to 2 m.

Squatina and the remaining euselachians (the pristiophorids and the batoids), termed the Hypnosqualean group, were regarded as a clade by Shirai (1992c, 1996) and by de Carvalho (1996).

One genus, *Squatina*, with 15 species (Compagno, 1984a, 1999, 2005; Shirai, 1992c).

Order PRISTIOPHORIFORMES (12)—saw sharks.

Family PRISTIOPHORIDAE (41)—saw sharks. Marine (rarely in estuaries), temperate to tropical, continental and insular shelves and slopes; western Atlantic in region of Bahamas, Florida, and Cuba, southwestern Indian off South Africa, and western Pacific from southern Australia to Japan.



Body sharklike; snout produced in a long flat blade with teeth on each side (teeth unequal in size, usually alternating large and small, and weakly embedded); one pair of long barbels; no dorsal fin spines (sometimes present as internal rudiments); anal fin absent; spiracles large. Maximum length 1.4 m.

Two genera, *Pliotrema* (1, six gill openings) and *Pristiophorus* (4, and four undescribed species, five gill openings), with five species (Compagno, 1984a, 1999, 2005).

Subdivision BATOIDEA (rays) (Hypotremata; Superorder Batidoidimorpha of Nelson, 1984; Order Rajiformes of Nelson, 1994)

Gill openings ventral; anterior edge of the greatly enlarged pectoral fin attached to side of head, anterior to the gill openings; anal fin absent; eyes and spiracles on dorsal surface; anterior vertebrae fused to form a synarcual; suprascapulae of pectoral girdles joined dorsally over vertebral column and articulating with column or synarcual or fused with synarcual; nictitating membrane absent, cornea attached directly to skin around the eyes; body generally strongly depressed; jaws protrusible in most; teeth pavementlike; in most, water for breathing taken in chiefly through the spiracle rather than the mouth (except for those living off the bottom); most rays give birth to live young (however, the skates are oviparous, i.e., egg layers, and have eggs encased in a horny capsule); the snout may function as an electroreceptive organ (as in all elasmobranchs). McEachran and Aschliman (2004) comment on the diversity of claspers in batoids and suggest that they offer potential in resolving interrelationships. Two basic shapes are apparent in external form: Rajiformes have claspers that are long, slender, and depressed distally while the other batoids, as far as studied, have claspers that are short, stout, and cylindrical to moderately depressed.

Monophyly of the batoids seems well established, but their internal interrelationships remain very uncertain. Although McEachran and Aschliman (2004) regard their classification as a working hypothesis, it is an advance over the largely phenetic classification presented in Compagno (1999) and that of earlier authors. McEachran and Aschliman (2004) examined more morphological characters in more representatives of genera than previously done. They also used basal taxa as out-groups as a result of other recent studies. While batoids are regarded as monophyletic, there is much controversy as to whether modern sharks are monophyletic without the inclusion of rays (i.e., whether rays are an offshoot of a branch of sharks or whether both modern sharks and rays are sister taxa). This disagreement is discussed above under the infraclass Euselachii, and reasons are given there for accepting the hypothesis that modern sharks and rays are separate groups.

Many different views have been proposed on batoid interrelationships, with various taxa seen as the basal group (these ideas are briefly reviewed in McEachran and Aschliman, 2004). The higher classification given here is based on McEachran and Aschliman (2004), while the number of species given in each genus follows Compagno (1999, 2005), unless otherwise noted.

Although most batoids have a strongly depressed body, some are relatively shark-like. The phylogenetic study of McEachran and Aschliman (2004) showed that the depressed, disclike body characteristic of most higher rays was probably independently achieved in two lineages. The depressed body of rajids was probably derived from a more robust-bodied rhinobatidlike ancestor, while the depressed body of higher myliobatiforms was probably derived from a robust-bodied platyrhinidlike ancestor.

The table on the following page compares the classifications of Nelson's (1994) order Rajiformes, Compagno's (1999) unranked group of rays or batoids, McEachran and Aschliman's (2004) cohort Batoidea, and the one employed here as the subdivision Batoidea, closely reflecting that of McEachran and Aschliman (2004). Compagno (2005), with all rays or batoids placed in his order Rajiformes, closely followed Compagno (1999) in the sequence of family level taxa; however, Compagno (2005) recognized the Rhynchobatidae and the orders of Compagno (1999) are ranked as suborders with additional suborders given. Indentations of taxa reflect differing ranks.

The common names skate and ray are sometimes used to refer to mutually exclusive groups (where skates would be a monophyletic group but rays would be a paraphyletic group). However, I prefer to use the term ray as a collective name for all members of the following four orders of batoids. Thus, skates, in the strictest sense, are members of one particular family of rays, the Rajidae. In this usage, both names refer to monophyletic groups, but skates are a subset of the rays, just as are sawfishes and stingrays. Skates (Rajiformes) differ from the other rays in many features in morphology and biology.

Fossil batoids are known as far back as the Jurassic in Europe and Argentina and include taxa such as *Asterodermus, Belemnobatis,* and *Spathobatis* (Cappetta, 1987; Cione, 1999); the latter two genera may be sister taxa and were found by Brito and Seret (1996) to be basal batoids, supporting an earlier view of J. G. Maisey. The following poorly known fossil batoids from the Cretaceous are described in Cappetta (1987): i) Cyclobatidae—Upper Cretaceous rays from Lebanon, and ii) Sclerorhynchidae—Lower to Upper Cretaceous rays resembling pristiophorids and pristids including *Ankistrorhynchus, Ganopristis, Ischyrhiza,* and *Sclerorhynchus.* The study of Kriwet (2004a) provided insight into possible relationships of this group with other batoids. He concluded from his

Nelson (1994)	Compagno (1999)	McEachran and Aschliman (2004)	Herein
Pristoidei	Pristiformes	Torpediniformes	Torpediniformes
Pristidae	Pristidae	Torpedinidae	Torpedinidae
Torpedinoidei	Rhiniformes	Narcinidae	Narcinidae
Torpedinidae	Rhinidae	Pristiformes	Pristiformes
Narcinidae	Rhinobatiformes	Pristidae	Pristidae
Rajoidei	Rhinobatidae	Rajiformes	Rajiformes
Rhinidae	Platyrhinidae	Rhinobatidae	Rhinidae
Rhinobatidae	Zanobatidae	Rajidae	Rhynchobatidae
Rajidae	Torpediniformes	Myliobatiformes	Rhinobatidae
Myliobatoidei	Narcinidae	Platyrhinoidei	Rajidae
Plesiobatidae	Narkidae	Platyrhinidae	Myliobatiformes
Hexatrygonidae	Hypnidae	Zanobatoidei	Platyrhinoidei
Dasyatidae	Torpedinidae	Zanobatidae	Platyrhinidae
Urolophidae	Rajiformes	Myliobatoidei	Zanobatoidei
Gymnuridae	Arhynchobatidae	Hexatrygonidae	Zanobatidae
Myliobatidae	Rajidae	Urolophidae	Myliobatoidei
	Anacanthobatidae	Urytrygonidae	Hexatrygonidae
	Myliobatiformes	Dasyatidae	Plesiobatidae
	Plesiobatidae	Potamotrygonidae	Urolophidae
	Hexatrygonidae	Gymnuridae	Urytrygonidae
	Urolophidae	Myliobatidae	Dasyatidae
	Potamotrygonidae		Potamotrygonidae
	Dasyatidae		Gymnuridae
	Gymnuridae		Myliobatidae
	Myliobatidae		
	Rhinopteridae		
	Mobulidae		

analysis that the Pristiorajea (of de Carvalho, 1996, the Pristiophoriformes + batoids in the hypnosqualean hypothesis—see above under “infraclass Euselachii”) is a monophyletic clade, with Sclerorhynchidae being the sister group to pristiforms and all remaining pristiorajeans. These results require further study to verify monophyly and to resolve the conflict they present with the classification adopted herein. Brito and Seret (1996) discuss the possible relations and implications to our views on batoid classification of the Lower Cretaceous fossil *Iansan*, from Brazil, with the rhinobatids and other taxa.

Four orders, 17 families, 72 genera, and at least 534 species.

Order TORPEDINIFORMES (13)—electric rays. Powerful electric organs, derived from branchial muscles in head region (strongest discharges in the Torpedinidae); skin soft and loose; eyes small to obsolete; caudal fin well developed; dorsal fins 0–2. Electrical production is largely for feeding and defense.

Torpedininforms are regarded as the basal batoid group and sister to the remaining members of this order (McEachran and Aschliman, 2004). Several species are blind.

Two families, 11 genera with about 59 species. McEachran and Aschliman (2004) recognized the monophyly of these taxa as shown.

Family TORPEDINIDAE (42)—torpedo electric rays. Marine, continental and insular shelves and slopes; Atlantic (including Mediterranean Sea), Indian, and Pacific.

Disc truncate or emarginate anteriorly; jaws extremely slender; no labial cartilages; rostrum reduced.

Two genera with 22 species.

SUBFAMILY TORPEDININAE (TORPEDO ELECTRIC RAYS). Tail and dorsal and caudal fins well developed. This taxon is ranked as a separate family by some workers (e.g., Compagno, 2005).

One genus, *Torpedo* (including *Tetronarce*), with about 21 species (plus two doubtfully valid ones and several undescribed species) (Compagno, 1999, 2005; de Carvalho et al., 2002).

SUBFAMILY HYPNINAE (COFFIN RAYS). Tail and dorsal and caudal fins very small. Continental shelf and uppermost slope, off Australia. This taxon is ranked as a separate family by some workers (e.g., Compagno, 2005).

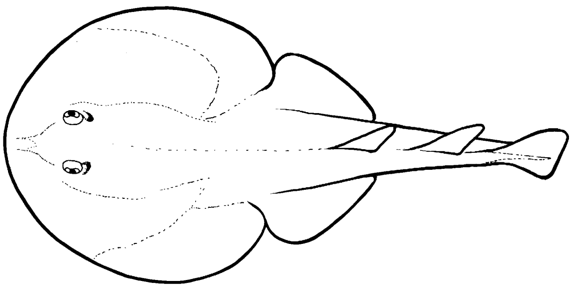
One species, *Hypnos monopterygius* (Compagno, 1999, 2005).

Family NARCINIDAE (43)—numbfishes. Marine, tropical to warm temperate, continental and insular shelves and uppermost slopes; Atlantic, Indian, and Pacific.

Disc rounded anteriorly; jaws stout; strong labial cartilages; rostrum present.

Nine genera with at least 37 species. Several undescribed species are known to exist.

SUBFAMILY NARCININAE (NUMBFISHES). Deep groove around mouth and lips; jaws long and strongly protractile; rostrum broad; usually two dorsal fins. This taxon is ranked as a separate family by some workers (e.g., Compagno, 2005).



Four genera, *Benthobatis* (4), *Diplobatis* (4), *Discopyge* (1), and *Narcine* (17), with 26 species and many undescribed species (de Carvalho, 1999; de Carvalho et al., 2002, 2003; de Carvalho and Randall, 2003; Compagno, 1999, 2005). Four species of *Diplobatis* are recognized based on McEachran and de

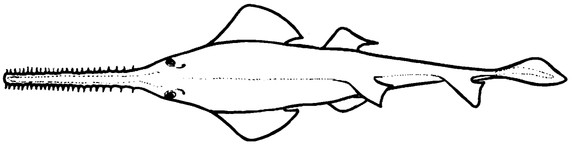
Carvalho's (2003:518–20) recognition of two subspecies of *Diplobatis pictus* (Compagno, 2005) as species.

SUBFAMILY NARKINAE (SLEEPER RAYS). Shallow groove around mouth; jaws short and weakly protractile; rostrum narrow; usually a single dorsal fin. Indo-West Pacific. This taxon is ranked as a separate family by some workers (e.g., Compagno, 2005).

Five genera (validity of *Crassinarke* and its species is questionable), *Crassinarke* (1), *Heteronarce* (4), *Narke* (3), *Temera* (1), and *Typhlonarke* (2), with 11 species (Compagno, 1999, 2005).

Order PRISTIFORMES (14)—sawfishes. One family.

Family PRISTIDAE (44)—sawfishes. Marine (rarely occurring in freshwater and ascending rivers), circumtropical, continental shelves; Atlantic, Indian, and Pacific.



Snout produced in a long flat blade with teeth on each side (teeth of equal size and embedded in deep sockets); barbels absent; body somewhat sharklike, although the head is depressed; two distinct dorsal fins and a caudal fin. Maximum length over 6 m.

Two genera, *Anoxypristis* (1) and *Pristis* (4–7), with about seven species (de Carvalho and McEachran, 2003; Compagno, 1999, 2005).

Order RAJIFORMES (15)—skates. Caudal fin moderately well developed, reduced, or absent; tail extremely slender; dorsal fins 0–2; most with prickles or thorns (derived from placoid scales) on skin, often with a row along midline of back; claspers long, slender, and depressed distally. Oviparous, with eggs encased in horny capsule with four long tips.

Members of this order were placed in the suborder Rajoidei with the same three families in the 1994 edition. McEachran and Aschliman (2004) recognized only two families, the Rhinobatidae and Rajidae, with the two rhinid genera being listed as *incertae sedis* because of their uncertain relationships (see below under Rhinidae). McEachran and Konstantinou (1996) discuss the taxonomic occurrence and variation of alar and malar thorns in skates.

For a discussion of the terms "skates and rays" see above under Cohort Batoidea.

Four families, 32 genera, and 285 species.

Family RHINIDAE (45)—bowmouth guitarfishes. Marine, continental shelves; Indo-West Pacific.

Body intermediate between sharklike and skatelike (family called "sharkrays" in Compagno, 2005); caudal fin large, bilobed; origin of first dorsal over or in front of pelvics; snout and anterior part of head broadly rounded, with deep indentation separating it from pectoral-fin origin. Maximum total length at least 270 cm.

Rhina and *Rhynchobatus* (see next family) were placed together in family Rhinidae in Nelson (1994) and Compagno (1999), but the latter recognized the family in its own order, Rhiniformes. It was recognized that there was only weak evidence that the two genera formed a monophyletic group. McEachran and Aschliman (2004) suggested that *Rhina* and *Rhynchobatus* are successive sister groups of the remaining rajiforms, and placed the two genera as *incertae sedis,* until they could be examined in better detail, under the order Rajiformes. The present treatment in placing them in separate families follows Compagno (2005), who placed them in separate suborders, somewhat reflecting the view of McEachran and Aschliman (2004).

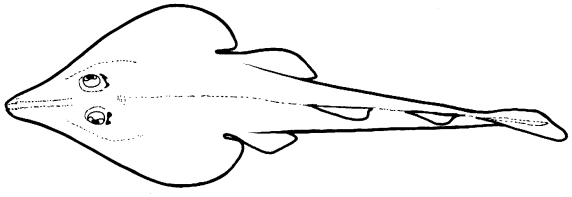
One monotypic genus, *Rhina* (Compagno, 2005; Compagno and Last, 1999).

Family RHYNCHOBATIDAE (46)—wedgefishes. Marine, continental shelves; eastern Atlantic (off Africa) and Indo-West Pacific.

Body intermediate between sharklike and skatelike; caudal fin large, bilobed; origin of first dorsal over or in front of pelvics; snout and anterior part of head broadly angular and wedge-shaped, with shallow indentation separating it from pectoral-fin origin. Maximum total length at least 300 cm. See family Rhinidae above for systematic notes.

One genus, *Rhynchobatus,* with four species (Compagno, 2005; Compagno and Last, 1999).

Family RHINOBATIDAE (47)—guitarfishes. Marine (rarely entering estuaries and freshwater), tropical to temperate, continental shelves and uppermost slopes; Atlantic, Indian, and Pacific.

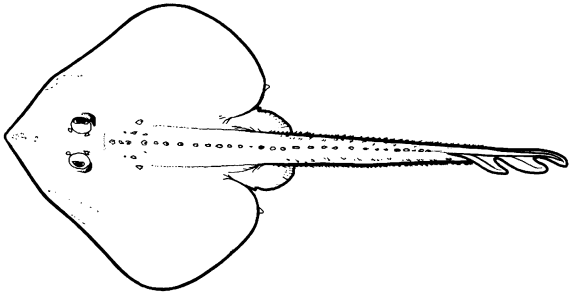


Body intermediate between sharklike and skatelike; tail stout, not definitely marked off from body; two distinct dorsal fins and a caudal fin, the latter not bilobed; origin of first dorsal behind pelvics; denticles over body form a row on midline of back; tail without spine.

Compagno (1999) recognized this family, along with two other (herein placed in the Myliobatiformes), in the order Rhinobatiformes. McEachran and Aschliman (2004) followed here; note that monophyly of the family and placement relative to Rajidae are uncertain.

Four genera, *Aptychotrema* (3), *Rhinobatos* (including *Acroteriobatus* and *Glaucostegus,* 35), *Trygonorrhina* (1), and *Zapteryx* (3), with 42 species (Compagno, 1999, 2005; Last, 2004; Last et al., 2004).

Family RAJIDAE (48)—skates. Marine, tropical to polar seas, shallow to deep-water; Atlantic, Indian, and Pacific.



Caudal fin moderately well developed, reduced, or absent; tail extremely slender; weak electric organs derived from caudal muscles; dorsal fins 0–2; most with prickles on skin, often with a row along midline of back. Eggs encased in horny capsule with four long tips. Maximum total length about 2.5 m.

The Arhynchobatinae (softnose skates) and the rajines *Anacanthobatis* and *Cruriraja,* are recognized as separate families from Rajidae by Compagno (1999, 2005), the Arhynchobatidae (softnose skates) and Anacanthobatidae (legskates), respectively. They are classified here following McEachran and Aschliman (2004), in whose cladogram *Anacanthobatis* and *Cruriraja* form a monophyletic group but one which is nested within the Rajinae. McEachran and Dunn (1998) give a detailed analysis of rajid interrelationships.

Twenty-six genera and 238 species.

SUBFAMILY RAJINAE (HARDNOSE SKATES). Fifteen genera, *Amblyraja* (10), *Anacanthobatis* (10), *Breviraja* (6), *Cruriraja* (8), *Dactylobatus* (2), *Dipturus* (31, with many undescibed species), *Fenestraja* (8), *Gurgesiella* (3), *Leucoraja* (12), *Malacoraja* (3), *Neoraja* (5), *Okamejei* (14), *Raja* (12, and 15 or so additional valid species currently in Raja, but probably requiring new genera, based on McEachran and Dunn, 1998, and Compagno, 1999, 2005), *Rajella* (15), and *Rostroraja* (1), with at least 155 species, and many undescribed species (Compagno, 1999, 2005; McEachran and Last, 2004).

SUBFAMILY ARHYNCHOBATINAE (SOFTNOSE SKATES). Eleven genera, *Arhynchobatis* (1), *Atlantoraja* (3), *Bathyraja* (43), *Irolita* (1), *Notoraja* (at least 6), *Pavoraja* (at least 2), *Psammobatis* (8), *Pseudoraja* (1), *Rhinoraja* (13), *Rioraja* (1), and *Sympterygia* (4), with at least 83 species (Compagno, 1999, 2005; Stevenson et al., 2004; Díaz de Astarloa et al., 2004).

Order MYLIOBATIFORMES (16)—stingrays. Monophyly of this taxon is recognized after McEachran and Aschliman (2004). There has been strong support for monophyly of this order as well based on the earlier works of Nishida (1990), Lovejoy (1996), and McEachran et al. (1996). Platyrhinids and *Zanobatus* are thought to form successive sister taxa to the myliobatoids (McEachran and Aschliman, 2004). Most members have enlarged brain development.

Ten families with 27 genera and 183 species

Suborder Platyrhinoidei

Family PLATYRHINIDAE (49)—thornbacks. Marine, continental shelves; tropical to cool-temperate, North Pacific (off Asia and North America, in Mexico and California).

Round or heart-shaped pectoral disc; long, stout shark-like tails with two large dorsal fins well anterior on the tail; strong thorns (derived from placoid scales) on dorsal surface of the disc and tail.

The family was redefined by de Carvalho (2004b) and the newly described Late Cretaceous fossil *Tethybatis*, known from articulated remains from Italy, was placed within it.

Two genera, *Platyrhina* (2, the fanrays) and *Platyrhinoidis* (1), with three species (Compagno, 1999, 2005; Compagno and Last, 1999).

Suborder Zanobatoidei

Family ZANOBATIDAE (50)—panrays. Marine; tropical, eastern Atlantic (off Africa) and possibly Indian.

Similar in appearance to the Platyrhinidae.

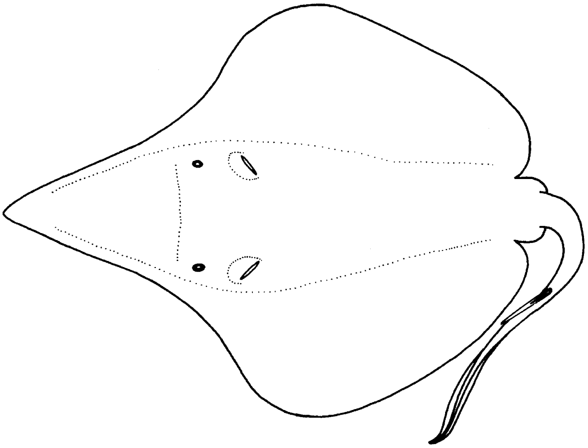
One genus, *Zanobatus*, with possibly two species (Compagno, 1999, 2005).

Suborder Myliobatoidei. Monophyly of this clade has been further established by de Carvalho et al. (2004). They recognized this group, at the ordinal level (Myliobatiformes) following Compagno (1973), as having numerous synapomorphies such as a serrated caudal spine and lacking thoracic ribs. They present a revised classification but agree with many past conclusions, e.g., Hexatrygonidae is sister to the remaining taxa and the families Gymnuridae and Myliobatidae (the pelagic stingrays) are sister groups; for an example of differences, see below under Dasyatidae. The fossil record, extending primarily from the Paleocene to the Miocene but known from the Early Cretaceous to the Quaternary, is reviewed by de Carvalho et al. (2004); fossils include the freshwater *Asterotrygon* and *Heliobatis* (the latter in its own family, Heliobatidae) of the Eocene Green River Formation of Wyoming.

The de Carvalho et al. (2004) paper is a highly informative model study. It very nicely showed the problems that exist in studying elasmobranch phylogeny, where there is much character conflict, and cladogram results are sensitive to changes in character coding. These are the same problems that exist in many studies of fishes but are not usually made transparent.

Superfamily Hexatrygonoidea

Family HEXATRYGONIDAE (51)—sixgill stingrays. Marine, continental and insular slopes; Indo-West Pacific (South Africa to Hawaii).



Six gill openings and six gill arches; snout elongate, thin (depressed), translucent; no supraorbital crests on cranium; spiracles large, well behind eyes, with external flaplike valve (the spiracle of other rays is closed by an internal valve); brain very small, posteriorly placed in large cranial cavity; tail with one or two serrate spines; disc longer than broad; nostrils wide apart, anterior nasal flaps short, not joined to form a broad nasal curtain that reaches the mouth.

McEachran et al. (1996) placed *Plesiobatis* and *Urolophus* (they included *Trygonoptera* as a synonym) in this family as *incertae sedis.*

Probably only one valid species, *Hexatrygon bickelli,* described in 1980 (Smith and Heemstra, 1986; Compagno, 1999, 2005).

Superfamily Urolophoidea

Family PLESIOBATIDAE (52)—deepwater stingrays. Marine; continental and insular slopes, Indo-West Pacific (South Africa to Hawaii).

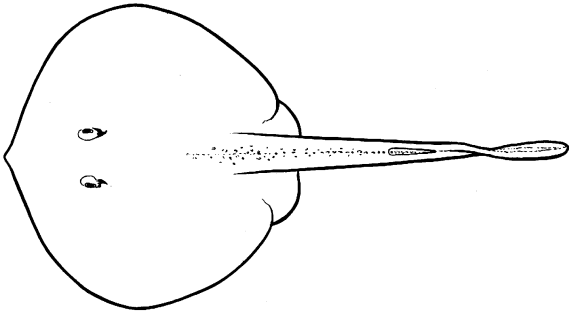
Nasal curtain incompletely united, not reaching the mouth (true also for *Hexatrygon,* which has six gill arches). Maximum length 2.7 m (Smith and Heemstra, 1986).

This family (as Plesiobatididae) was established by Nishida (1990) for the species *Plesiobatis daviesi,* recognized prior to that in the genus *Urotrygon.* For alternate family placement see Hexatrygonidae above and Urolophidae below. The family is recognized here as done in the 1994 edition until analysis involving more species better clarifies relationships of the one included species.

The common name for family in Compagno (1999, 2005) is giant stingarees.

One species, *Plesiobatis daviesi* (Compagno, 1999, 2005).

Family UROLOPHIDAE (53)—round stingrays. Marine, continental shelves and upper slopes; western Pacific.



Disc less than 1.3 times as broad as long; caudal fin small but well-developed; dorsal fin present in some species (e.g., *Trygonoptera,* of Australia); tail moderately long with a barbed spine.

The family Urolophidae was formerly recognized as also including *Urobatis* and *Urotrygon* (e.g., by Nelson, 1994, although *Urobatis* was not listed but was regarded as a synonym of *Urolophus,* by Nelson et al., 2004, and by Compagno, 1999). McEachran et al. (1996) placed *Urobatis* and *Urotrygon* of North, Central, and South America and species of *Urolophus* from the same area, in their own family, the Urotrygonidae, and this is followed here. However, McEachran et al. (1996) regarded Indo-Pacific *Urolophus* as *incertae sedis* in the Hexatrygonidae and did not recognize the family Urolophidae. Subsequently, McEachran and Aschliman (2004) recognized the family but, unlike here, as also including the species *Plesiobatis daviesi*; de Carvalho et al. (2004) included only the following two genera. Family members are also known as stingarees.

Two genera, *Trygonoptera* (4) and *Urolophus* (20), with at least 24 species (Compagno, 2005; Séret and Last, 2003).

Superfamily Urotrygonoidea

Family UROTRYGONIDAE (54)—American round stingrays. Marine, tropical to warm temperate, continental shelves; western Atlantic and eastern Pacific.

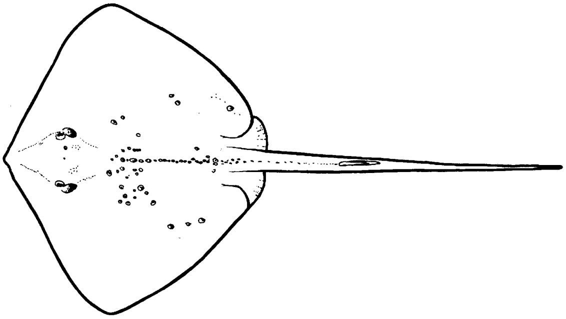
Disc not more than 1.3 times as broad as long; tail slender and about as long as disc length, without dorsal fin but with one or more long, poisonous spines; caudal fin distinct.

This family, as noted above, was included in the Urolophidae in Nelson (1994).

Two genera, *Urobatis* (6) and *Urotrygon* (10), with 16 species (Compagno, 2005).

Superfamily Dasyatoidea

Family DASYATIDAE (Trygonidae) (55)—whiptail stingrays. Marine (continental and insular shelves and uppermost slopes, one species oceanic), brackish, and freshwater, tropical to warm temperate; Atlantic (including the Mediterranean Sea), Indian, and Pacific.



Disc not more than 1.3 times as broad as long; no caudal fin; tail long (distance from cloaca to tip much longer than breadth of disc), very slender to whiplike, without dorsal fin but tail with one or more long, poisonous spines; caudal fin absent.

A few species of *Dasyatis* and *Himantura* and *Pastinachus sephen* occur in tropical to warm-temperate rivers and lakes. *Pteroplatytrygon violacea,* often placed in *Dasyatis,* is oceanic. McEachran and Aschliman (2004) provisionally recognized only three genera in the family, placing *Pastinachus* and *Urogymnus,* as well as *Dasyatis kuhlii* as *incertae sedis* in the superfamily Dasyatoidea, as were the Indo-West Pacific species of *Himantura* as *incertae sedis* (the two amphi-American species of *Himantura* were placed within the Potamotrygonidae). The study of de Carvalho et al. (2004) placed the dasyatid genera *Dasyatis, Himantura, Pastinachus* (but not included in their analysis), *Pteroplatytrygon, and Taeniura* as *incertae sedis* at a node sister to the clade comprising Gymnuridae and Myliobatidae; the family Dasyatidae was thus not recognized. Compagno (2005) anticipates that species of *Taeniura* and the two Western Hemisphere species of *Himantura* may belong in the Potamotrygonidae (see also Potamotrygonidae below).

Six genera, *Dasyatis* (at least 38, synonyms include *Trygon* and *Urolophoides*), *Himantura* (at least 23, but see above note), *Pastinachus* (1, synonym *Hypolophus*), *Pteroplatytrygon* (1), *Taeniura* (3), and *Urogymnus* (2), with at least 68 species (Compagno, 1999, 2005).

Family POTAMOTRYGONIDAE (56)—river stingrays. Freshwater; South America (Atlantic, including Caribbean, drainage).

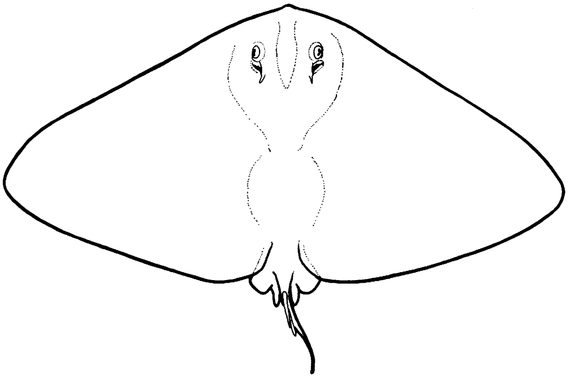
Long, median, anteriorly directed process from the pelvic girdle; angular cartilages present (except *Paratrygon*), within hyomandibular-Meckelian ligament;

adaptation to freshwater as evidenced by rectal gland (used for salt secretion) reduced and low urea concentration in body fluids. Most species are quite colorful on the dorsal surface. A detailed study was given by de Carvalho et al. (2004). Maximum length over 100 cm.

Additional species may belong in this family that are here retained in the Dasyatidae pending further research to clarify their relationships. The species in question are the three marine species of *Taeniura,* occurring in the eastern Atlantic (and Mediterranean) and Indo-West Pacific, and two marine species of the large genus *Himantura, H. pacificus* (Pacific off Central America and northern South America) and *H. schmardae* (Atlantic off southern North America and northern South America) which were placed in the Potamotrygonidae by Lovejoy (1996) and followed by McEachran et al. (1996). However, McEachran and Aschliman (2004) retained *Taeniura* in the Dasyatidae (see also above under Dasyatidae). The taxon Potamotrygonidae was regarded as a subfamily of Dasyatidae in Nelson (1994). Eocene fossils of this family are known, and de Carvalho et al. (2004) and Brito and Deynat (2004) hypothesized that the family arose in the Late Cretaceaous or Early Tertiary.

Three genera, *Paratrygon* (1), *Plesiotrygon* (1), *Potamotrygon* (at least 18), with 20 species (Rosa, 1991; de Carvalho et al., 2003; Compagno, 1999, 2005).

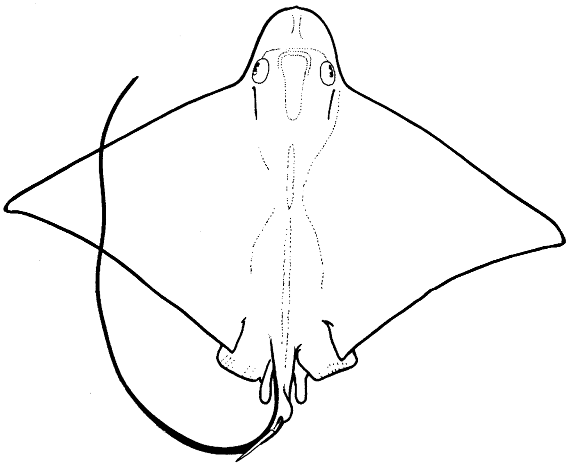
Family GYMNURIDAE (57)—butterfly rays. Marine; tropical to temperate, continental shelves, Atlantic, Indian, and Pacific.



Disc extremely broad (more than 1.5 times as broad as long); dorsal fin and tail spines present (and poisonous) or absent; tail short (distance from cloaca to tip much shorter than breadth of disc); no caudal fin.

Possibly two genera, *Aetoplatea* (2) and *Gymnura* (at least 9), with at least 11 species (Compagno, 1999, 2005).

Family MYLIOBATIDAE (58)—eagle rays. Marine; tropical to warm temperate, continental and insular shelves to offshore but not oceanic, Atlantic, Indian, and Pacific.



Distinct but small dorsal fin present; most species with one or more long poisonous spines on tail; no caudal fin; head elevated above disc; eyes and spiracles lateral on head; gill openings about length of eye to much longer; tail much longer than disc; small dorsal fin; pectoral fins reduced or absent opposite the eyes, but with an anterior subdivision that unites below the tip of the snout forming a subrostral lobe. Some are famous for their ability to leap high into the air from the water.

Monophyly of this family is recognized in McEachran et al. (1996), although they gave it as a subfamily of Dasyatidae, and in de Carvalho et al. (2004) and McEachran and Aschliman (2004). Although available evidence suggests that the Myliobatinae as given below are paraphyletic, the three subfamilies given below (accorded family status in Compagno, 1999, 2005) are recognized as given in Nelson (1994) because of their phenetic distinctiveness, until more species are used in a cladistic analysis.

Three subfamilies, seven genera, and 37 species.

Subfamily Myliobatinae (eagle rays). Anterior face of cranium nearly straight; subrostral fin not incised.

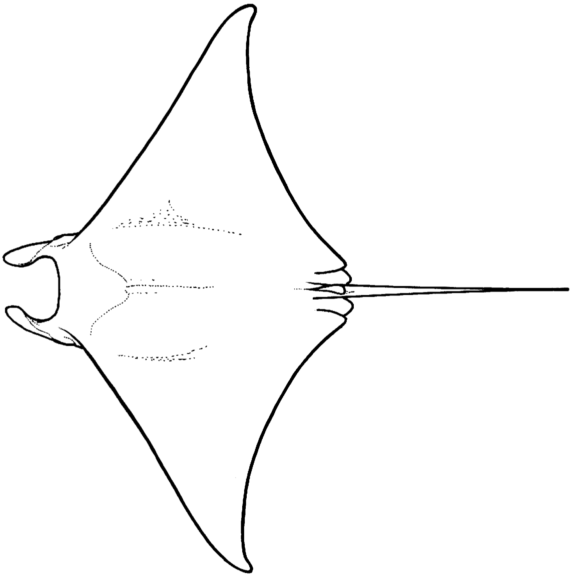
Four genera, *Aetobatus* (3), *Aetomylaeus* (4), *Myliobatis* (at least 11), and *Pteromylaeus* (2), with at least 20 species (Compagno, 1999).

Subfamily Rhinopterinae (cownose rays). Marine; tropical to warm temperate, continental shelves, Atlantic, Indian, and Pacific.

Anterior face of cranium concave; subrostral fin incised (bilobed).

One genus, *Rhinoptera*, with at least seven species (Compagno, 1999, 2005).

Subfamily Mobulinae (devil rays). Marine; tropical to warm temperate, inshore and oceanic, Atlantic, Indian, and Pacific.



Members of this family are the only living vertebrates with three pairs of functional limbs. The cephalic pair assist in feeding and are the anterior subdivision of the pectorals.

Some mantas grow to a width of about 6.1 m and a weight of more than 1,360 kg; largest members of the superorder (and, like the Whale Shark and Basking Shark, are zooplanktophagous, straining their food out of the water).

Two genera, *Manta* (perhaps 1, Manta) and *Mobula* (9, devil rays), with about 10 species (Compagno, 1999, 2005).

Grade TELEOSTOMI

The following three classes, the Acanthodii, Actinopterygii, and Sarcopterygii (with acanthodians being the sister-group to the latter two), account for the remaining vertebrates and are thought to form a monophyletic group termed the Teleostomi (and used previously in Nelson, 1994). The alignment of acanthodians with the others is based on their sharing three otoliths with the Actinopterygii, although their otoliths do differ in appearance and composition (a distinction must be made between the sandy statoconia of early fossil taxa and solid otoliths). As typically found in actinopterygians, there is, on each side, one otolith presumably in each of the three membranous sacs of the labyrinth of the inner ear; the three otoliths are the sagitta, usually the largest, in the sacculus; the asteriscus, in the lagena; and the lapillus, in the utriculus. In sarcopterygians there are two otoliths in dipnoans and one in *Latimeria*; tetrapods have secondarily derived statoconia (minute calcareous crystals = otoliths of some authors) similar to the statoconia in agnathans and most chondrichthyans. Arratia et al. (2001) gave further details, emphasizing details of the vertebral column and associated elements in these three groups. Homologies of the palatoquadrate and associated dermal bones and evolutionary trends in the teleostomes are given by Arratia and Schultze (1991). In this edition, unlike in Nelson (1994), I have placed Sarcopterygii at the end, as seems more logical considering that its characters have a more derived state than in Actinopterygii (and this sequence was also followed in Arratia et al., 2001:160). This revision is not due to any change in our view of vertebrate phylogeny. Furthermore, regardless of one's preference, since these two classes form a monophyletic group, there is no phylogenetic difference in these two alternatives. For another view of relationships, see Arnason et al. (2001) and Venkatesh et al. (2001), who challenged our current view of higher relationships based on morphological and paleontological studies that took us away from earlier concepts of relationships for which these molecular studies now find some support. The implications of their findings are not followed here pending comprehensive supporting studies.

The names Acanthodii and Actinopterygii (originating with E. D. Cope in 1871) have each changed little in meaning over time. However, the terms Teleostomi (originating with C. L. Bonaparte in 1836), Osteichthyes (originating with T. H. Huxley in 1880), and Sarcopterygii have each been used for different taxa over time (the dates given are from the unpublished manuscript of the deceased D. E. McAllister, 1989, "A working list of fishes of the world"). I retain the terms Teleostomi and Sarcopterygii as taxonomic names, but as noted below (after the class Acanthodii under the heading Euteleostomi), I do not use the term Osteichthyes in a formal taxonomic sense. Use of the term Teleostomi is noted above. Sarcopterygii, as used here, applies to a monophyletic taxon that includes the tetrapods (following Wiley, 1979, and Rosen et al., 1981). This term (Sarcopterygii) was used by A. S. Romer to include only fishes conventionally called crossopterygians and dipnoans (the lobe-finned fishes).

The Teleostomi and its three classes contain about 53,633 extant valid species (with no extant acanthodians, 26,891 actinopterygians, and 26,742 sarcopterygians). Within the paraphyletic osteichthyans (bony fishes), there are some 46 orders, 457 families, 4,293 genera, and 26,899 species (numbers apply to extant members).

†Class ACANTHODII

Dermal and perichondral bone present, endochondral bone absent; jaws formed by palatoquadrate and Meckel's cartilage, both uncalcified, calcified, or with perichondral ossification; mandibular arch (palatoquadrate) probably closely associated with hyoid arch, with the spiracular gill cleft (homologous with spiracle of other fishes and eustachian tube of tetrapods) virtually closed;

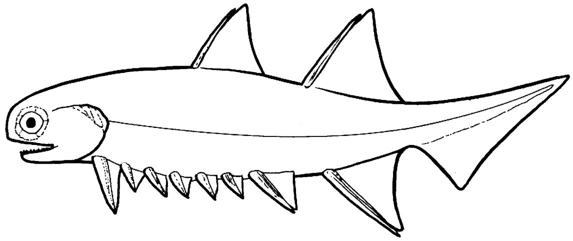
ornamented platelike dermal cover over gill chamber (associated with hyoid arch) in most species; five gill arches; notochord persistent; neural and haemal arches present but vertebral centra lacking; rhombic to teardrop-shaped dermal scales present on body and fins; body scales usually grew by addition of concentric layers; stout spines present before the dorsal, anal, and paired fins; up to six paired spines present between the pectorals and pelvics in many, with small spines in a prepectoral series present in some species; caudal fin epicercal heterocercal. Burrow (2004) reviews the acanthodians with dentigerous jaw bones and gives references to the recent acanthodian literature. Species of climatiiforms and acanthodiforms have a double mandibular joint. Late Ordovician (as microfossils) to Early Permian (Zidek, 1993; Janvier, 1966; Hanke and Wilson, 2004). Articulated remains from Late Silurian to Early Permian.

The acanthodians, with their large eyes, terminal or near terminal mouth, and small nasal capsules, mostly were mid- and surface-water feeders. Many were microphagous while others, especially the ischnacanthiforms, ate fishes and invertebrates. Acanthodians are known from both freshwater and marine environments; the Mississippian to Permian *Acanthodes* is known from both. They are the earliest well-known true jawed fishes, but the earliest specimens are poorly known and represented by isolated microremains. Maximum length is estimated at about 2.5 m; most are less than 20 cm.

Various views have existed on acanthodian relationships. D. M. S. Watson in 1937, in his review of the group, felt that they were the most primitive known gnathostomes. He placed them in the Aphetohyoidea, along with several other groups, a taxon with equal rank as the Pisces. In many classifications of the 1930s to 1950s, they were placed in the class Placodermi. Berg (1940) recognized acanthodians in their own class and placed them immediately before his class Elasmobranchii. A. S. Romer, in his classic 1966 "Vertebrate paleontology," provisionally considered them as the most primitive subclass of the osteichthyans because of certain resemblances to the actinopterygians. Important contributors to acanthodian classification in the 1970s included R. H. Denison, E. Jarvik, and R. S. Miles. Authors have variously proposed that they are i) most closely related to the elasmobranchs, ii) the sister group to chondrichthyans, placoderms, and osteichthyans, or—the modern view presented here—iii) the sister group to the remaining vertebrates, the Euteleostomi (Sarcopterygii and Actinopterygii).

As shown in Hanke and Wilson (2004), in a cladistic analysis of the group, acanthodians are more diverse than previously appreciated, and the conventional three-order classification likely is an oversimplification. Of particular interest, they describe two new taxa (*Obtusacanthus* and *Lupopsyroides*) which show primitive gnathostome features yet have some characters similar to those of acanthodians, but not assignable to any known higher taxon. Therefore, as a working classification, and rather than making unstable piecemeal changes as a result of recent work (e.g., Warren et al., 2000, and Zajíc, 1995, who described the new family Howittacanthidae, and many other new contributions), I maintain the groups as given in Nelson (1994), with nine recognized families in three orders, based primarily on Long (1986, 1989). Taxa regarded as acanthodian or possibly having some acanthodian affinity but not assigned to present taxa include *Granulacanthus joenelsoni* (Hanke et al., 2001) and *Obtusacanthus* and *Lupopsyroides*, with *Lupopsyrus pygmaeus* being considered as the basal-most acanthodian (Hanke and Wilson, 2004). Other acanthodian genera shown in their cladogram, such as *Cassidiceps* and *Paucicanthus*, do not conveniently fit within the present acanthodian classification scheme. Spiny sharks such as *Antarctilamna* and *Doliodus*, putative chondrichthyans such as *Altholepis*, *Seretolepis*, *Polymerolepis*, and several new taxa now known from articulated material from northern Canada and Russia require additional study before a formal revision of the Acanthodii should be attempted.

†Order CLIMATIIFORMES. Most with ornamented dermal bones in ventral portion of shoulder girdle (other acanthodians possess only endoskeletal elements); two dorsal fins, each with a spine; intermediate (prepelvic) paired spines between the pectoral and pelvic fins in most taxa, up to six pairs in climatiids and perhaps absent in some *Culmacanthus* and *Acritolepis* (the latter might better be placed in the Ischnacanthiformes, Burrow, 2004); teeth absent or, if present, not fused to jaws. Mid-Silurian to Pennsylvanian (North and South America, Greenland, Europe, Asia, Australia, and Antarctica).



Five provisionally recognized families: Climatiidae—e.g., *Brachyacanthus*, *Climatius* (usually reached only 7.5 cm, shown in figure), *Parexus* (had exceptionally long first dorsal spines), and *Vernicomacanthus*; Culmacanthidae (*Culmacanthus*); Diplacanthidae (*Diplacanthus*, *Gladiobranchus*, and *Uraniacanthus*, and *Tetanopsyrus*, revised by Hanke et al., 2001, is provisionally retained in this family); Gyracanthidae (e.g., *Gyracanthides*, with chondrichthyan-like scales); and Euthacanthidae (e.g., *Euthacanthus*). Other genera not placed above include *Nostolepis*. The climatiiforms as presently classified may be paraphyletic (Hanke and Wilson, 2004) and the order is far more diverse than previously known.

†Order ACANTHODIFORMES. One posterior dorsal fin with spine; teeth absent; gill rakers well developed in later members of the clade (probably adapted for filter-feeding); prepelvic spines absent or limited to one pair in the Mesacanthidae. Lower Devonian to Lower Permian (North America, Europe, Asia, South Africa, Australia, and Antarctica).

Three families, Mesacanthidae (e.g., *Mesacanthus* and *Melanoacanthus*), Cheiracanthidae (e.g., *Carycinacanthus*, *Cheiracanthus*, and *Homalacanthus*), and Acanthodidae, in which the pelvic fins when present are closer to the pectoral fins than to the anal fin (e.g., *Acanthodes*, *Acanthodopsis* (Burrow, 2004), *Howittacanthus*, and *Traquairichthys*, which lacks the pelvic fins).

†Order ISCHNACANTHIFORMES. Two dorsal fins, each with a spine; teeth fixed to strong dermal jaw bones that attach to the oral border of the meckelian cartilage and palatoquadrate; no prepelvic spines between the pectoral and pelvic fin spines. Many known only from isolated jaws and tooth whorls, and in some cases, isolated elements have been combined to create species based on faunal association in the absence of articulated remains. Upper Silurian to Pennsylvanian (North and South America, Europe, Australia, Antarctica, and Asia).

Two families, Ischnacanthidae (e.g., *Atopacanthus*, *Ischnacanthus*, *Marsdenius*, and *Xylacanthus*) and Poracanthodidae (*Poracanthodes*) (Burrow, 2004).

EUTELEOSTOMI—(OSTEICHTHYES OF ROSEN ET AL., 1981) (INCLUDES ACTINOPTERYGII + SARCOPTERYGII) (THE BONY VERTEBRATES). The remaining two monophyletic classes of the teleostomes together are thought to also form a monophyletic group, termed in the 1994 edition and here the Euteleostomi. The taxon Euteleostomi would be in a category between grade and class, such as subgrade. This taxon includes the paraphyletic bony fishes, consisting of some sarcopterygians (the lobe-finned fishes) and all actinopterygians. These fishes were placed in the class Osteichthyes in Nelson (1984) and in most earlier works (see Nelson, 1984, for its definition). The taxon Euteleostomi also includes the remaining sarcopterygians, consisting of the monophyletic tetrapods. Rather than dropping the term Osteichthyes in a taxonomic sense, as I do, an alternative use of the term would be to apply it in a cladistic sense for the monophyletic sarcopterygians plus actinopterygians as used by Rosen et al. (1981) and subsequently by many vertebrate paleontologists (e.g., Janvier, 1996, and Ahlberg, 2001) and some others. This, I feel, is unfortunate. To avoid any confusion by all readers, familiar or not with recent works, the term Osteichthyes (clearly not a monophyletic group in older usage), used for so long for the largest group of fishes, ought not be used in such a different sense so as to include a group of about equal size. Following this principle allows us to use the term "osteichthyan" when referring to the higher group of fishes formerly recognized in Osteichthyes (i.e., osteichthyans lack polydactylous limbs and have gills throughout life). The term Euosteichthyes was used by Wiley (1979) for what are given here as euteleostomes less the coelacanthiforms.

Members of this taxon of two classes may be characterized as follows: skeleton, in part at least, with bone (endochondral or membrane bone); skull with sutures; swim bladder or functional lung usually present; intestinal spiral valve in only a few lower groups; low blood concentration of urea and trimethylamine oxide (except in dipnoans and *Latimeria*)—osmotic balance maintained only by an energy-demanding transfer process.

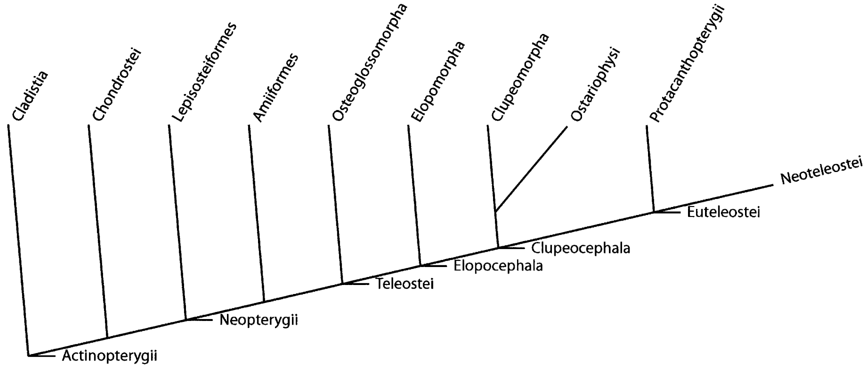
An overview of the classification of the Euteleostomi given here is as follows:

Class Actinopterygii
  Subclass Cladistia
  Subclass Chondrostei
  Subclass Neopterygii
Class Sarcopterygii
  Subclass Coelacanthimorpha (Actinistia)
  Subclass unnamed (Porolepimorpha and Dipnoi)
  Subclass Rhizodontimorpha
  Subclass Osteolepimorpha
  Subclass Tetrapoda

As noted above under grade Teleostomi, the sequence of the two classes in this classification has been reversed from that given in Nelson (1994). I end with tetrapods, that divergent sideline within the fishes that ascends onto land and into the air and secondarily returns to water.

Class ACTINOPTERYGII—the ray-finned fishes

Scales ganoid, cycloid, or ctenoid (scales absent in many groups); spiracle usually absent; pectoral radials (actinosts) attached to the scapulo-coracoid complex except in Polypteriformes; interopercle and branchiostegal rays usually present; gular plate usually absent; internal nostrils absent; nostrils relatively high up on head. The condition of the neural spines shows basic differences within the actinopterygians. In chondrosteans, some taxa possess paired neural spines throughout the vertebral column, the assumed primitive state; others, including *Polypterus*, have median neural spines in the caudal region; most teleosts have median neural spines anteriorly.



Cladogram showing the relationships of the extant actinopterygians as presented here. The Clupeomorpha and Ostariophysi compose the subdivision Ostarioclupeomorpha (= Otocephala), sister to the Euteleostei. See text for the many fossil clades omitted.

The class Actinopterygii, one of the major vertebrate taxa, is not diagnosed by strong derived character sets, but is nevertheless thought to be monophyletic. The earliest fossil remains are of scales of the Late Silurian *Andreolepis, Ligulalepis, Naxilepis, Lophosteus,* and *Orvikuina*; in addition, there is Devonian material of, for example, *Cheirolepis, Dialipina, Howqualepis, Limnomis,* and *Moythomasia* (including an Early Devonian endocranium of a specimen tentatively assigned to the actinopterygian genus *Ligulalepsis,* Basden and Young, 2001), and Carboniferous material of, for example, *Aesopichthys, Cyranorhis, Discoserra, Guildayichthys, Kalops, Melanecta, Mesopoma, Mimia, Proceramala, Wendyichthys,* and *Woodichthys* (Cloutier and Arratia, 2004). Photographs and descriptions of many fossil taxa are given in Frickhinger (1991).

Actinopterygii are the sister taxon of the Sarcopterygii. We infer that at some time there was a common ancestor of both of these major lineages, and there are some interesting fossils, such as *Psarolepis,* that show combinations of actinopterygian and sarcopterygian characters (Cloutier and Arratia, 2004; Zhu and Yu, 2004). Genera *incertae sedis* include the Cretaceous *Diplospondichthys,* known from the same locality as the acanthomorph *Spinocaudichthys* (Filleul and Dutheil, 2004).

The early diversification of actinopterygians was reviewed by Cloutier and Arratia (2004). That paper gave a historical review of our phylogenetic hypotheses and general understanding of relationships, and discussed the taxa involved and the many contributions of other workers, past and present. Lauder and Liem (1983) gave an earlier valuable review of the actinopterygians. Springer and Johnson (2004) have produced a valuable monograph with many anatomical drawings giving insights into the relationships of teleostome fishes, with emphasis to the Actinopterygii, and especially to the acanthomorphs. It has not been possible to do justice to this work in this edition.

A major problem in understanding actinopterygian phylogeny is, as noted by Cloutier and Arratia (2004), that we still have much to learn about the homologies of various characters. Much more work is needed in studying fossils in a cladistic context and in knowing more on the origin and development of characters.

Actinopterygians are recognized here with three subclasses, 44 orders, 453 families, 4,289 genera, and 26,891 species. About 44% of the species are known only or almost only from freshwater.

Subclass CLADISTIA

Order POLYPTERIFORMES (Brachiopterygii) (17)—bichirs. This taxon has been thought by some workers to be a member of the Sarcopterygii or at least to be more closely related to them than to the Actinopterygii; they are regarded here as the sister group of all other actinopterygians. This latter view, with some recent support from Britz and Bartsch (2003) and possibly Venkatesh et al. (2001), seems with other comprehensive studies to be better supported than the hypothesis accepted in Nelson (1994) that they represent the earliest chondrostean lineage with surviving members.

Family POLYPTERIDAE (59)—bichirs. Freshwater; Africa.

Rhombic ganoid scales; spiracular opening large but canal lost; dorsal fin consisting of 5–18 finlets, each with a single spine to which is attached one or more soft rays; pectoral fin rays supported by numerous ossified radials which attach to a cartilaginous plate and two rods, thence to the scapula and coracoid; a pair of gular plates, no branchiostegals; maxilla firmly united to skull; intestine with spiral valve; lungs partially used in respiration; vertebrae with ossified centra and neural canal. Polypterids have many primitive characters that are unknown in other living Actinopterygii and many autapomorphies (Britz and Johnson, 2003). Among the latter, they have only four rather than the usual five gill arches. Of various hypotheses concerning the homology of the posteriormost arch of polypterids, Britz and Johnson (2003) make a convincing argument that it represents the fourth arch of other Actinopterygii and that the fifth arch is absent. Britz and Bartsch (2003) discussed rib homology in gnathostomes and the unique rib type of polypterids. Maximum length about 90 cm, most species less than 30 cm.

Two genera with at least 16 extant species. In addition, there are fossils in Africa back to the middle Cretaceous and, perhaps, from the Late Cretaceous and Early Paleocene in South America (e.g., *Dagetella, Latinopollis,* a replacement name for *Pollia, Sainthilairia,* and *Serenoichthys*) (references to studies of fossils and extant forms, other than those already given, include Gayet et al., 1995; Dutheil, 1999; Murray, A. M. 2000; Stewart, 2001; and Gayet et al., 2002).

*Erpetoichthys (*synonym *Calamoichthys) calabaricus* (reedfish or ropefish). Body eel-like; pelvics absent. Confined to coastal areas adjacent to the Gulf of Guinea. Although previous editions (Nelson, 1984, 1994), for stability, favored retaining *Calamoichthys* as the valid generic name over the technically correct *Erpetoichthys,* I now use *Erpetoichthys* based on Eschmeyer (1998, Online).

Polypterus (bichirs). Body elongate; pelvics present. At least 15 species (e.g., Gosse, 1988; Hanssens et al., 1995; Daget et al., 2001; Britz, 2004a). There is need for a revision to determine how many of the additional nominal species might be valid.

Subclass CHONDROSTEI

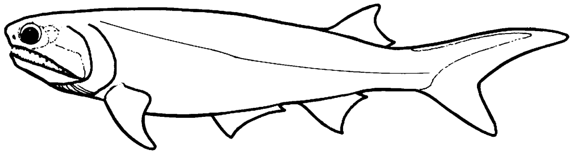
Interopercle absent; premaxilla and maxilla rigidly attached to the ectopterygoid and dermopalatine; spiracle usually present; myodome absent in the most primitive taxa.

The classification of this group is very insecure. It is a group of great structural diversity, and evidence is lacking for monophyly not only for this subclass but also for most of the groups herein recognized. Given the many phylogenetic uncertainties that exist on the relationships of many taxa, I have not made many changes to the classification of this taxon from that used in Nelson (1994), except for the exclusion of the Polypteriformes. As noted by Cloutier and Arratia (2004) and other authors, the selection of outgroups and the varied inclusion of extant and fossil taxa play a significant role in phylogenetic analyses. There is great need for extensive work, involving both fossil and extant material, such as that done by Grande and Bemis (1991, 1996, 1998).

The arrangement of fossil taxa given by Cloutier and Arratia (2004) is a good hypothesis to follow. The sister group to the remaining actinopterygians is thought to be *Dialipina* (based also on a 1997 work of L. Taverne and a 2001 work by H.-P. Schultz and S. L. Cumbaa), followed in a successive comblike branching pattern, with each group sister to all remainging taxa, by perhaps i) Cheirolepididae, ii) *Mimia* and *Moythomasia,* iii) *Osorioichthys* and *Kentuckia,* and continuing. No phylogenetic classification is attempted here, and for convenience only for this classification, chondrosteans are shown as the sister group of neopterygians until more convincing evidence to the contrary is available. An early chondrostean family not otherwise classified here is Haplolepidae (with two Pennsylvanian genera, *Haplolepis* and *Pyritocephalus*).

Extant taxa in two families, six genera, and 27 species.

†Order CHEIROLEPIDIFORMES. Includes only the one family, the Devonian Cheirolepididae with the one genus, *Cheirolepis.* One species, *C. canadensis,* may hold the record for having the largest number of pelvic fin rays, up to 124, as noted in a 1996 paper by G. Arratia and R. Cloutier. Although classified here within the chondrosteans, this taxon, after *Dialipina,* is probably the sister group for all remaining actinopterygians (e.g., Cloutier and Arratia, 2004).



†Order PALAEONISCIFORMES. In many primitive palaeoniscids, the cheekbones form a solid unit (the maxilla, preopercles, and suborbitals are firmly united), the hyomandibular is oblique, the eyes are large and far forward, and the tail is strongly heterocercal. More advanced forms had a hyomandibular in the vertical plane and a breakup of the cheekbones. This permitted more flexibility in the oral-branchial chamber. The dorsal lobe of the tail became reduced to an abbreviated heterocercal tail. Numerous other evolutionary trends can be noted in proceeding from the chondrostean level of organization to the holostean level.

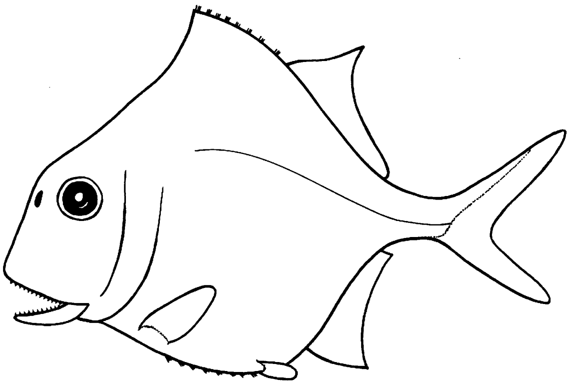
Coccolepis. incertae sedis. The morphology of *Coccolepis bucklandi* was described by Hilton et al. (2004).

Suborder Palaeoniscoidei. Families or genera placed in this heterogenous group of primitive chondrosteans include Aeduellidae, Acrolepidae (with, for example, *Acrolepis* and possibly *Boreosomus* and *Pteronisculus*), Amblypteridae (*Amblypterus* and *Paramblypterus*) (Dietze, 2000), Birgeriidae (e.g., *Birgeria*), *Canobius*, Commentryidae, Elonichthyidae, Palaeoniscidae, Pygopteridae, Rhabdolepidae (includes the Devonian *Osorioichthys*), Rhadinichthyidae and the related Aesopichthyidae (Poplin and Lund, 2000; Cloutier and Arratia, 2004), and Stegotrachelidae (with, e.g., the Devonian *Stegotrachelus* and *Tegeolepis*).

Suborder Redfieldioidei. Body fusiform; mouth terminal or subterminal; dorsal and anal fins positioned far back, opposite one another, and with fin rays more numerous than radials; branchiostegal rays reduced to one or two platelike bones; single external naris surrounded by a distinctive "premaxilla," rostral, nasal, and adnasal bones. Triassic and Lower Jurassic, freshwater.

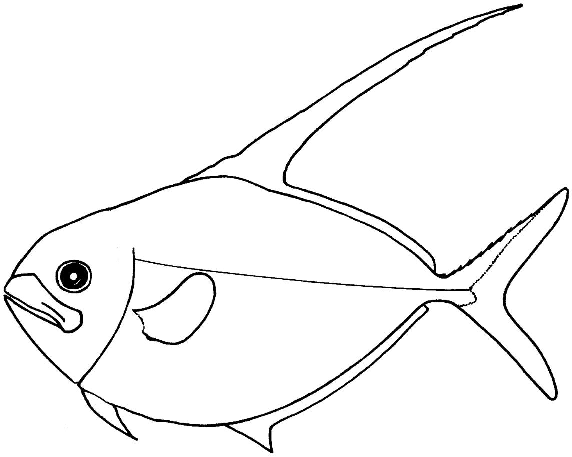
About 15 genera, herein treated as belonging to one family, Redfieldiidae (e.g., *Brookvalia, Dictyopyge, Helichthys, Redfieldius,* and *Schizurichthys*).

Suborder Platysomoidei. Body deep and compressed (zeidlike).



Three families, Bobastraniidae, Chirodontidae, and Platysomidae. Marine and freshwater. Mississippian to Lower Triassic.

Suborder Dorypteroidei. Body deep and mostly scaleless; pelvic fin in front of pectorals (jugular); caudal peduncle very narrow.



One Upper Permian genus, *Dorypterus.*

†Order TARRASIIFORMES. Dorsal and anal fins continuous with the diphycercal caudal fin; pelvic fins absent; scales variously reduced or absent; body elongate; pectoral fins with a rounded fleshy lobe; frontal bones distinct (e.g., Taverne, 1996). Mississippian.

†Order GUILDAYICHTHYIFORMES. Highly compressed, discoidal bodies, tall rhombic "ganoid" scales with peg-and-socket joints. Marine fishes of Mississippian age.

Lund (2000) found in a cladistic analysis a stable sister group relationship between *Polypterus* and the Guildayichthyiformes as a crown group within the Paleozoic Actinopterygii, and he rediagnosed the Cladistia as a superorder to reflect this relationship. However, I follow the placement of Cloutier and Arratia (2004) in showing a close relationship with the Tarrasiidae and Guildayichthyidae.

Two genera, *Guildayichthys* and *Discoserra,* from Montana (Lund, 2000).

†Order PHANERORHYNCHIFORMES. Body superficially like that of a sturgeon.

One Pennsylvanian genus, *Phanerorhynchus.*

†Order SAURICHTHYIFORMES. Triassic and Jurassic. One family, Saurichthyidae (e.g., *Acidorhynchus* (synonyms *Belonorhynchus* and *Saurorhynchus*) and *Saurichthys*).

Order ACIPENSERIFORMES (18)—sturgeons. Caudal fin heterocercal; myodome and preopercle reduced or absent; gulars absent; skeleton largely cartilaginous; fin rays more numerous than their basals; intestine with spiral valve. Grande and Bemis (1991) give derived characters for this order and for the taxa of the suborder Acipenseroidei. Their classification, in their detailed osteological study, is followed here.

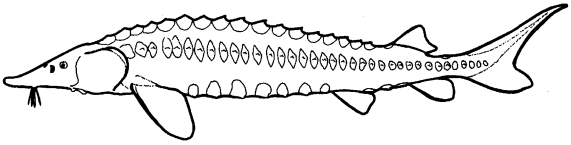
Extant representatives in two families with six genera and 27 species (Grande and Bemis, 1996; Bemis et al., 1997).

†Family PEIPIAOSTEIDAE. *Incertae sedis.* Two genera, *Peipiaosteus* and *Stichopterus,* and probably *Spherosteus* and *Yanosteus,* extending back to the Upper Jurassic (Grande and Bemis, 1996; Bemis et al., 1997).

†Suborder Chondrosteoidei. One family, Chondrosteidae (mouth subterminal), with *Chondrosteus* and *Strongylosteus,* and perhaps *Gyrosteus* from the Jurassic of Europe. The chondrosteids are considered to be the primitive sister group of the acipenseroids (Grande and Bemis, 1991, 1996).

Suborder Acipenseroidei. Opercle lost, gill cover made up primarily by the subopercle; one to three elements that may be homologous to the branchiostegal rays of other actinopterygians; endocranium with an extensive rostrum.

Family ACIPENSERIDAE (60)—sturgeons. Anadromous and freshwater; Northern Hemisphere.



Five rows of bony scutes or plates on body; four barbels in front of mouth; mouth inferior and protrusible; gill rakers fewer than 50; teeth absent in adults; pectoral fin with anterior spinous ray made up of fused rays; swim bladder large. The freshwater Kaluga, *Huso dauricus,* and the anadromous Beluga, *H. huso,* are among the largest if not the largest fish in freshwater. *H. huso* definitely reaches 4.2 m, and longer lengths have been reported for both species.

Four genera with 25 species (Bemis et al., 1997; Birstein and Bemis, 1997). Many of the species are difficult to identify. The historical biogeography of sturgeons is explored in Choudhury and Dick (1998). One fossil genus, the Upper Cretaceous *Protoscaphirhynchus,* from Montana.

SUBFAMILY ACIPENSERINAE. Three genera in two tribes (Grande and Bemis, 1996; Bemis et al., 1997), although this arrangement may be incorrect (Birstein et al., 2002).

TRIBE ACIPENSERINI. Spiracle present; snout and caudal peduncle subconical.

Acipenser. Range of family. Gill membranes joined to isthmus, mouth transverse. Seventeen species (five of which occur in North America).

TRIBE SCAPHIRHYNCHINI. Spiracle absent; snout depressed.

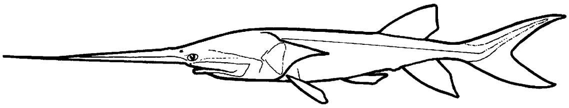
Pseudoscaphirhynchus. Aral Sea basin. Caudal peduncle short, slightly depressed, and not completely armored. Three species.

Scaphirhynchus. Mississippi basin. Caudal peduncle long, depressed, and completely armored. Three species.

SUBFAMILY HUSINAE

Huso. Adriatic Sea to Caspian Basin; Amur River. Gill membranes joined to one another, mouth crescentic. Two species.

Family POLYODONTIDAE (61)—paddlefishes. Freshwater, rarely brackish; China and United States.



Snout paddlelike; body lacking the large scutes of acipenserids but with small "scales" in some regions, such as the caudal peduncle and caudal fin, and large *Psephurus* with trunk "scales"; minute barbels on snout; gill rakers long and in the hundreds in the plankton-feeding *Polyodon* (shorter and fewer in number in *Psephurus*); teeth minute; spiracle present; gill cover greatly produced posteriorly. Maximum length perhaps up to 3 m, attained in *Psephurus gladius.*

Fossil taxa are *Protopsephurus* (Lower Cretaceous, China, the oldest and most primitive paddlefish known and sister to all other members, Grande et al., 2002), *Paleopsephurus* (Lower and Upper Cretaceous, freshwater, Montana and Wyoming, and considered to be the primitive sister group to the remaining polyodontid taxa), *Crossopholis* (Lower Eocene, freshwater, Wyoming, and the sister group to *Polyodon*), and *Polyodon tuberculata* (lower Paleocene, freshwater, Montana). Grande and Bemis (1991, 1996) and Grande et al. (2002) described this family and its included taxa.

Two living species.

Polyodon spathula. United States (Mississippi drainage). The Paddlefish, plankton-feeding, with a nonprotrusible mouth.

Psephurus gladius. China (Yangtze River and lower reaches of some other rivers and adjacent sea). The Chinese Paddlefish, piscivorous, with a protrusible mouth.

†Order PTYCHOLEPIFORMES. Triassic and Jurassic. North America.

†Order PHOLIDOPLEURIFORMES. Triassic. One family, Pholidopleuridae (e.g., *Australosomus* and *Pholidopleurus*).

†Order PERLEIDIFORMES. Triassic and Lower Jurassic. Example families placed in this artificial group are Cephaloxenidae, Colobodontidae, Platysiagidae, Peltopleuridae, Cleithrolepidae, and Perleididae (e.g., *Aetheodontus*, *Dipteronotus*, and *Meridensia*, e.g., Tintori, 1990; Bürgin, 1992). Tintori and Sassi (1992) provided evidence for a sequenced ranking of *Australosomus*, Peltopleuriformes (with *Peltopleurus*, *Habroichthys*, and *Thoracopterus*, placed in the family Thoracopteridae and thought to be capable of gliding), *Cleithrolepis*, *Perleidus*, *Luganoia*, and the Neopterygii. Further studies on members placed here include that of Bürgin (1996), Lombardo and Tintori (2004), and Mutter (2004).

†Order LUGANOIIFORMES. Triassic.

Subclass NEOPTERYGII

Fin rays equal in number to their supports in dorsal and anal fins; premaxilla with internal process lining the anterior part of nasal pit; symplectic developed as an outgrowth of hyomandibular cartilage. In addition, the spermatozoa of neopterygians has lost a plesiomorphic feature of vertebrates—the acrosome (several species, however, have acrosome-like structures) (Jamieson, 1991).

It is generally agreed that the neopterygian fishes are a monophyletic group. However, there is much uncertainty about the relationships of the basal taxa, and much more work will be required before even a reasonable phylogenetic hypothesis of relationships of the basal groups can be put forth. The fossil record extends as far back as the Late Permian with *Acentrophorus.*

An overview of the classification adopted here is as follows (the Halecostomi and Halecomorphi are not named in the main classification):

Class Actinopterygii
  Subclass Cladistia
  Subclass Chondrostei
  Subclass Neopterygii

Halecostomi (halecostomes)—for such extinct taxa as Macrosemiiformes, Semionotiformes, and Pycnodontiformes and the following coordinate taxa. In some earlier works this was viewed as sister to the Ginglymodi (for Lepisosteidae) (as adopted in Nelson, 1984). Arratia (2004) reviewed the early fossil taxa.

Halecomorphi (halecomorphs)—for Amiiformes and related fossil taxa and the remainder. This assumes that Amiiformes and some other groups are sister to the teleosts, whereas some evidence exists supporting the older view that Amiiformes and Lepisosteiformes form a monophyletic group, the holosteans. Grande and Bemis (1998) and Arratia (2004) discussed the membership. See below for mention of disagreement as to whether the Osteoglossomorpha or the Elopomorpha are the most primitive extant taxa.

Division Teleostei
    Subdivision Osteoglossomorpha
  Elopocephalans
    Subdivision Elopomorpha
   Clupeocephalans
    Subdivision Ostarioclupeomorpha (= Otocephala)
    Subdivision Euteleostei

The view expressed in the present classification that chondrosteans and neopterygians are coordinate taxa is regarded as a working hypothesis. However, the conclusions, with respect to extant groups, that amiiforms and the teleosts are sister groups with lepisosteids being their primitive sister group requires further testing in the face of some molecular data supporting that, among living neopterygians, amiids and lepisosteids may form a clade separate from teleosts (comprising the one-time recognized Holostei).

Arratia (2004) gave an insightful evaluation of our understanding of halecomorph and teleost phylogeny. This work nicely shows what we know and what remains uncertain. Arratia (2001) introduced the term Teleostomorpha for the taxon including the Teleostei (with *Pholidophorus* as the primitive sister taxa) and stem-based fossils and used the term Teleocephala of de Pinna (1996a) for the included taxon covering everything sister to the Ichthyodeciformes. She further explored this concept of relationships in Arratia (2004). These taxa are not formally introduced into classification here pending more work on the basal groups involved.

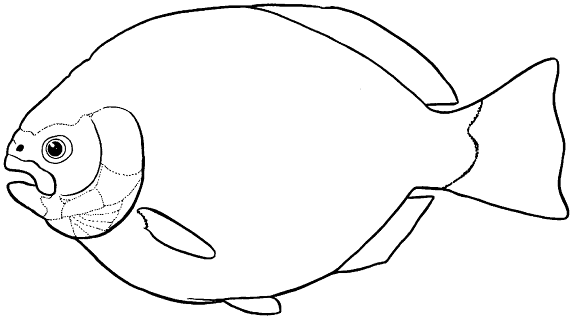
There are many neopterygian taxa of uncertain position. For example, Nursall and Capasso (2004) described a fascinating fossil from the upper Middle Cretaceous of Lebanon (*Gebrayelichthys uyenois*, the Archangelfish). It is a highly compressed fish placed in its own family, Gebrayelichthyidae.

The next orders given below up to Teleostei were generally regarded as the holosteans, of which the last, the Pachycormiformes, is the hypothesized sister group to the teleosts (see Arratia, 2001, for other possible candidate groups—Amiiformes, Lepisosteiformes, *Dapedium*, Pycnodontiformes, Pachycormiformes, and Aspidorhynchiformes). These following orders are not placed in higher categories to indicate any particular hypothesized phylogenetic position. Rather, the subclass Neopterygii is recognized with one division—the monophyletic Teleostei—with several orders sequenced before it.

†Order MACROSEMIIFORMES. One family, Macrosemiidae, Jurassic and Lower Cretaceous, known from Europe and Mexico (González-Rodríguez et al., 2004; González-Rodríguez and Reynoso, 2004).

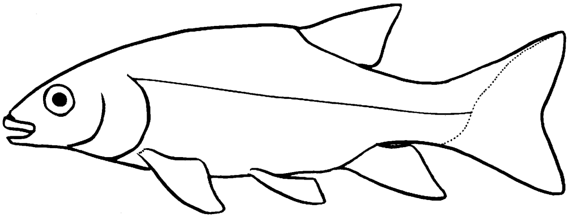
†Order SEMIONOTIFORMES. Extant gar and the fossil Semionotidae are often recognized in the same order, either under the ordinal name Lepisosteiformes or Semionotiformes (e.g., Nelson, 1976, 1994). In contrast, I placed them in separate orders in Nelson (1984) and do so now following the scholarly and highly detailed work of Grande and Bemis (1998). Their ongoing studies may yet result in further changes.

†Family DAPEDIIDAE. Position uncertain.



Body deep; dorsal and anal fins long; gular present. Upper Triassic to Lower Jurassic; in marine and freshwater deposits; North America, Europe, and India. E.g., *Dapedium.*

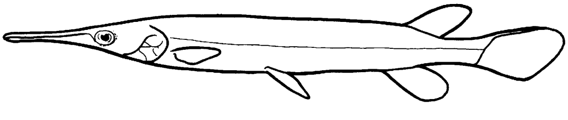
†Family SEMIONOTIDAE (Lepidotidae). Dorsal ridge scales present; epiotic with a large posteriorly directed process; mouth small; body fusiform; dorsal and anal fins short. Triassic to Cretaceous.



Genera include *Lepidotes Paralepidotus,* and *Semionotus* (e.g., Tintori, 1996). Among the many genera excluded is *Acentrophorus,* known from the Late Permian, and not assigned here to any higher taxon.

Order LEPISOSTEIFORMES (19)—gars.

Family LEPISOSTEIDAE (62)—gars. Freshwater, occasionally brackish, very rarely in marine water; eastern North America, Central America (south to Costa Rica), and Cuba.



Body and jaws elongate; mouth with needlelike teeth; abbreviated heterocercal tail; heavy ganoid scales, about 50–65 along lateral line; dorsal fin far back, with few rays; three branchiostegal rays; interoperculum absent; two or more supratemporal bones on each side; maxilla small and immobile; supramaxilla absent; myodome absent; vomer paired; swim bladder vascularized (thus permitting aerial respiration); vertebrae opisthocoelous (anterior end convex, posterior end concave, as in some reptiles and unlike all other fish except the blenny *Andamia*).

The heavily armored predaceous gars usually occur in shallow, weedy areas. Maximum length about 3.0 m, attained in *Atractosteus spatula.*

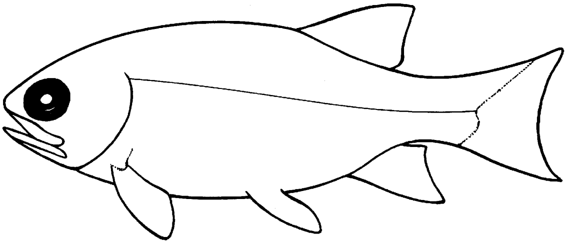
The northernmost limit is reached by *Lepisosteus osseus* in southern Quebec; the southernmost limit is reached by *A. tropicus* in Costa Rica. This is also the only species that ranges to Pacific slope drainages (from southern Mexico to Honduras). *Atractosteus tristoechus* is known to enter marine water around Cuba and the Isle of Pines.

Two genera, *Lepisosteus* and *Atractosteus,* with seven species (e.g., Nelson et al., 2004, which lists six of the seven). *Lepisosteus* has four species, with about 14–33 small, pear-shaped gill rakers, and *Atractosteus* has three species, with about 59–81 large, laterally compressed gill rakers. Fossil species (primarily Cretaceous and Eocene) of *Lepisosteus* are known from North America, South America, Europe, and India (extant species are restricted to North America); fossil species of *Atractosteus* are known from North America, South America, Europe, and Africa (extant species are restricted to North America, Cuba, and Central America). Many fossil genera, e.g., *Masillosteus, Obaichthys,* and *Oniichthys* (e.g., Micklich and Klappert, 2001).

†Order PYCNODONTIFORMES. Position uncertain. Upper Triassic to Eocene. This group of reef- or lagoon-dwelling fishes lived primarily around the Tethys Sea and its extensions as the Atlantic opened during the Jurassic. Well-known fossil sites such as Monte Bolca in northern Italy and Solnhofen in southern Germany have added many of the specimens. Extensive research on the systematics of this group has been done by J. Ralph Nursall and Francisco J. Poyato-Ariza. Poyato-Ariza and Wenz (2002) presented a cladistic analysis on the interrelationships of the pycnodontiforms and revised systematic paleontology.

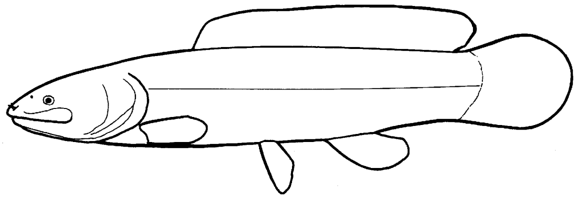
The families recognized in recent literature are Gibbodontidae, Gyrodontidae (e.g., *Gyrodus,*), Mesturidae, Brembodontidae, Pycnodontidae (with several subfamilies such as Nursalliinae and Proscinetinae), Coccodontidae (with *Coccodus* the only benthic member of the order), Hadrodontidae, and Trewavasiidae (Nursall, 1996, 1999a, b; Kriwet, 1999, 2004b; Poyato-Ariza and Wenz, 2002, 2004).

Order AMIIFORMES (20)—bowfins



Taxa that belong to or are related to this group, and placed in the Halecomorphi (ranked as subdivision) in the monumental work of Grande and Bemis (1998), include (with rankings of Grande and Bemis, 1998) order Parasemionotiformes (Parasemionotidae—includes *Parasemionotus,* in above figure, and *Watsonulus*), Ionoscopiformes (Ionoscopidae, Oshuniidae, and Ophiopsidae), and Amiiformes (Caturidae, Liodesmidae, Sinamiidae, and Amiidae) (for more information see Maisey, 1991; Lambers, 1995; Grande and Bemis, 1998; Arratia, 2004). Most amiids were apparently freshwater, while most non-amiids were marine.

Family AMIIDAE (63)—bowfins. Freshwater; eastern North America.

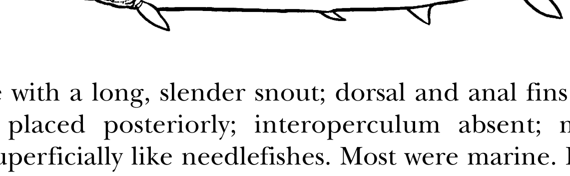


Caudal fin abbreviate heterocercal; dorsal fin base long, with about 48 rays; large median gular plate and 10–13 branchiostegal rays; swim bladder can function as a lung; no pyloric caeca. Maximum length about 90 cm.

One species, *Amia calva.* Fossil amiids (e.g., *Amia, Amiopsis, Calamopleurus, Cyclurus, Solnhofenamia,* and *Vidalamia*) are known primarily from freshwater deposits from throughout much of the world; the oldest fossils are of Jurassic age (Maisey, 1991; Grande and Bemis, 1998, 1999; Forey and Grande, 1998). Four subfamilies are recognized by Grande and Bemis (1998), and that work should be consulted for its wealth of information on recent advances on both the extant *Amia* and on the fossil taxa (including advances in biogeography such as the exciting biogeographical history of members of the subfamily Vidalamiinae).

†Order ASPIDORHYNCHIFORMES. Position uncertain. One family.

Family ASPIDORHYNCHIDAE. Upper Jurassic and Cretaceous.



Body elongate with a long, slender snout; dorsal and anal fins opposite one another and placed posteriorly; interoperculum absent; maxillae free. Appearance superficially like needlefishes. Most were marine. Lengths up to 1 m. Brito (1999) presented strong evidence from the caudal skeleton that these fishes are in fact teleosts.

Three genera, *Aspidorhynchus, Belonostomus,* and *Vinctifer* (Maisey, 1991:170–89; Brito, 1999; Arratia, 2004).

†Order PACHYCORMIFORMES. One family. The pelvic fin appears to be absent in many pachycormids.

Family PACHYCORMIDAE. Jurassic to Upper Cretaceous.

Genera include *Asthenocormus, Euthynotus, Hypsocormus, Leedsichthys* (which reached an exceptionally large size), *Orthocormus, Pachycormus, Prosauropsis,* and *Protosphyraena* (e.g., Arratia and Lambers, 1996; Liston, 2004; Arratia, 2004).

Division TELEOSTEI

It is agreed that there is a higher taxon that is monophyletic comprising all remaining fishes, supported by morphological evidence, but there is need for convincing molecular evidence that is in agreement to support this conclusion of its monophyly. There is, however, some disagreement on the boundaries of the Teleostei when fossil taxa such as Pycnodontiformes, Aspidorhynchiformes, Pachycormiformes, Pholidophoriformes, and Leptolepidiformes and others are considered (hence arguments of teleost monophyly must be carefully framed). A summary of some earlier work on teleost monophyly and boundaries is given in Nelson (1994) and de Pinna (1996a), and a summary of recent works can be found in Arratia (1997, 1999, 2004). At least 27 anatomical synapomorphies were found by de Pinna (1996a) to support monophyly of the group when defined as the most inclusive group of actinopterygians not including *Amia* and relatives (the Halecomorphi) and *Lepisosteus* and relatives (the Ginglymodi). G. Arratia has added immensely to our understanding of the basal members and their phylogeny (e.g., Arratia, 1997, 1999, 2004), but, as she makes clear, we require a much better understanding of characters and their homology before we can erect a sound classification.

Patterson and Rosen (1977) defined the teleosts as a group of halecostomes with the ural neural arches elongated as uroneurals, basibranchial toothplates unpaired, and premaxilla mobile. In addition, the teleost urohyal is distinctive, being formed as an unpaired ossification of the tendon of the sternohyoideus muscle (Arratia and Schultze, 1990). Given the comblike cladogram presented in Arratia and Schultze (1987), with amiiforms and pachycormids progressing toward the teleost level, it is difficult to establish any one place in the transition as the place where teleosts begin; it depends on what characters are employed to define them. Arratia and Schultze (1987) include the pachycormids in the teleosts, whereas, in the strictest sense, it is used by some for groups above the level of *Pholidophorus.*

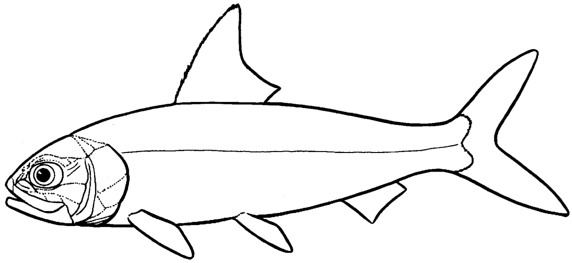
In the following classification, I will give several groups of primitive fossil teleosts first. These are followed by the four lineages, including all living teleosts (collectively termed the Teleocephala by de Pinna, 1996a), given as subdivisions, the Osteoglossomorpha, Elopomorpha, Ostarioclupeomorpha

(= Otocephala), and Euteleostei. These taxa are sequenced according to the sister-group relationships postulated by Patterson and Rosen (1977) (with redefinition of their Euteleostei), with the Elopomorpha, Ostarioclupeomorpha, and Euteleostei composing the Elopocephala, and the Ostarioclupeomorpha and Euteleostei composing the Clupeocephala. Arratia (1991) challenged the view that osteoglossomorphs are more primitive than elopomorphs on the grounds that the caudal skeleton of *Elops* is more primitive than that of the osteoglossomorphs. Subsequent detailed work of Arratia (1997, 1999, 2004, and others) further supported the view that elopomorphs are the living sister group of all other living teleosts. However, this in turn has been challenged by Patterson (1998) (but see the rebuttal by Arratia, 1998) and particularly by the works of Filleul (2000), Inoue and Miya (2001), Inoue et al. (2003), and Wang et al. (2003). There are challenges in the two main hypotheses presented, and while I favor the arguments presented by the works of G. Arratia, I have not changed the classification pending better resolution of remaining questions.

Teleosts probably arose in the middle or late Triassic, about 220–200 million years ago. They have a rich fossil record (e.g., Patterson, 1993; Arratia, 1997, 1999, 2004). Several early fossil groups of uncertain relationships and not otherwise mentioned are given in Nelson (1994:89) and the above works of G. Arratia.

Teleosts are the most species-rich and diversified group of all the vertebrates. They dominate in the world's rivers, lakes, and oceans. About 26,840 extant species, about 96% of all extant fishes, placed in 40 orders, 448 families, and 4,278 genera.

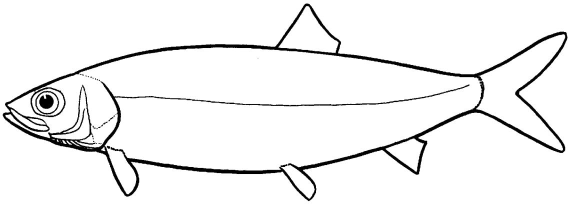
†Order PHOLIDOPHORIFORMES. Position uncertain. Probably not monophyletic, possibly polyphyletic (e.g., Arratia, 2004, and reference to her 2000 study). Some members of this group may have shared a common ancestry with the leptolepidiforms in the Triassic and, independently, the elopomorph and osteoglossomorph teleostean lines in the Triassic or Jurassic. All major teleostean lines radiate in the Cretaceous.



Families perhaps belonging here include Archaeomaenidae, Ichthyokentemidae, Oligopleuridae, Pholidophoridae (i.e., *Eurycormus*), and Pleuropholidae.

†Order LEPTOLEPIDIFORMES. Position uncertain.

Family LEPTOLEPIDIDAE. Probably marine, Triassic to Cretaceous.



This family is probably polyphyletic (e.g., Maisey, 1991:272–73).

†Order TSELFATIIFORMES. Position uncertain. Body deep; mouth bordered by premaxilla and maxilla; dorsal fin extending along most of back; pectoral fins inserted high on body; pelvics absent or present with six or seven rays; caudal fin deeply forked with 18 principal rays; palate toothed; most fin rays unsegmented. Cretaceous.

Much work on this group has been conducted by L. Taverne (e.g., Taverne, 2000). Taverne and Gayet (2004) found evidence placing this assemblage in the Clupeocephala. It is maintained in its position here pending a cladistic analysis with better understanding of the characters involved. The orthography of the ordinal name has been corrected from that used in Nelson (1994) by adding "*iformes*" to the stem of the type genus, *Tselfatia*. This error originated in Nelson (1976) in spelling the subordinal name "Tselfatoidei" rather than Tselfatioidei.

Plethodidae (= Bananogmiidae)—e.g., *Plethodus.*

Protobramidae—e.g., *Abisaadichthys*, *Eusebichthys*, and *Protobrama.*

Tselfatiidae—e.g., *Tselfatia.*

Subdivision OSTEOGLOSSOMORPHA

Two orders and five families. Britz (2004) made some interesting finds on their reproduction and early life history. Most osteoglossomorphs exhibit some kind of parental care (mouthbrooding occurs in *Osteoglossum* and *Scleropages*). Unlike most teleosts, adult osteoglossomorphs, except *Pantodon* and *Hiodon*, which do not exhibit parental care, possess only the left ovary, the right being absent. Of two major studies of this group, Li and Wilson (1996) and Hilton (2003), I am more impressed with the similarities in their conclusions than in the differences.

†Order ICHTHYODECTIFORMES. Position and monophyly uncertain. An endoskeletal ethmo-palatine bone in floor of nasal capsule; uroneurals covering lateral faces of preural centra; anal fin long, usually with 24–37 rays and opposite the posteriorly situated dorsal fin of 10–18 rays. Most were marine and probably predators of other fishes. The predaceous *Gillicus* reached 1.5 m, and *Xiphactinus* reached at least 4 m. Maisey (1991:190–207) reviewed this order.

Allothrissopidae. E.g., *Allothrissops,* Upper Jurassic, and perhaps *Pachythrissops* and *Tharsis. Eubiodectes* (lowermost Upper Cretaceous) and *Thrissops* (Upper Jurassic) may be related to this group.

Occithrissopidae. One genus, *Occithrissops.* This middle Jurassic teleost is the oldest known ichthyodectiform.

Cladocyclidae. Three genera, *Cladocyclus, Chiromystus* (recognized as a valid genus, distinct from *Cladocyclus,* by Maisey, 1991:190-207), and *Chirocentrites.* Lower Cretaceous to lowermost Upper Cretaceous.

Saurodontidae. Two Cretaceous genera, *Saurodon* and *Saurocephalus.*

Ichthyodectidae. Three genera, *Gillicus, Ichthyodectus,* and *Xiphactinus,* from the Lower to the Upper Cretaceous.

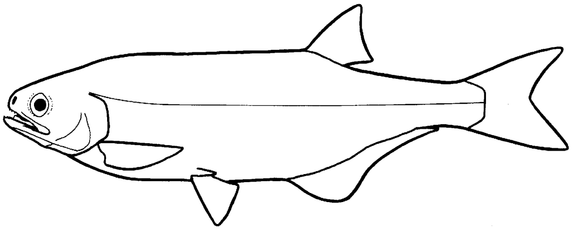
†Order LYCOPTERIFORMES. *Incertae sedis.*

†Family LYCOPTERIDAE. Upper Jurassic to Lower Cretaceous; freshwater; eastern Asia.

Includes the well-known genus *Lycoptera.* Li and Wilson (1996), on the basis of four synapomrphies, regarded the Lycopteridae as stem-group osteoglossomorphs, sister to all extant clades. In what I regard as a minor difference, Hilton (2003) placed it *incertae sedis,* finding it to be either the sister group of all other osteoglossomorphs he sampled or of *Eohiodon* + *Hiodon.*

Order HIODONTIFORMES (21)—mooneyes. Placement of the Hiodontidae in its own order rather than in the Osteoglossiformes, as formerly done (Nelson, 1994), follows Li and Wilson (1996) and Hilton (2003).

Family HIODONTIDAE (64)—mooneyes. Freshwater; North America (primarily Mackenzie, Saskatchewan, Mississippi, and St. Lawrence river systems).



Anal fin moderately long (23–33 rays) and not confluent with the well-developed forked caudal fin; pelvic fins distinct, with seven rays; 7–10 branchiostegal rays; subopercular present; lateral line scales about 54–61. Length up to 51 cm.

Two species: *Hiodon tergisus* (Mooneye) with 11 or 12 principal dorsal fin rays and ventral keel not extending in front of pelvic fins; and *Hiodon alosoides* (Goldeye) with 9 or 10 principal dorsal fin rays and ventral keel extending in front of pelvics.

Several species of the fossil *Eohiodon* are known from Eocene deposits in western North America. Other fossil hiodontid genera are *Plesiolycoptera* and *Yanbiania* of the Cretaceous of China (Li and Wilson, 1996; Li et al., 1997).

Order OSTEOGLOSSIFORMES (22)—bonytongues. Intestine passes posteriorly to left of esophagus and stomach; parasphenoid and tongue bones usually with well-developed teeth and forming a shearing bite (mesopterygoid and usually the ectopterygoid also toothed); premaxilla small and fixed to the skull; no supramaxilla; caudal fin skeleton with large first ural centrum and no urodermals, one or more epurals fused with uroneurals; caudal fin with 16 or fewer branched rays; nasal capsule rigid, no antorbital-supraorbital system for pumping water over olfactory epithelium; epipleural intermuscular bones absent; one or two pyloric caeca, one caecum in *Pantodon* and two in other osteoglossiforms.

Two monophyletic clades are recognized—the osteoglossoids and the notopteroids. Evidence, summarized in Lauder and Liem (1983), that the Osteoglossinae and *Pantodon* form a monophyletic clade and that the notopterids and mormyroids form a monophyletic clade was confirmed by Li and Wilson (1996) and is accepted here.

The osteoglossomorph *Ostariostoma* from Upper Cretaceous or lower Paleocene freshwater deposits of Montana assigned to the family Ostariostomidae was placed by Li and Wilson (1996) in their suborder Notopteroidei (they provisionally also included the Paleocene *Thaumaturus*), but found to be the sister group of all non-hiodontiform osteoglossomorphs by Hilton (2003). Subsequently, the latter position was accorded to the Early Cretaceous *Xixiaichthys* from China by Zhang (2004). The Cretaceous *Palaeonotopterus* from Morocco was considered to be related to either mormyrids or notopterids by Cavin and Forey (2001) (however, a 2004 paper by L. Taverne suggests that more phylogenetic work is needed before we can be confident of relationships).

The phylogeny of Li and Wilson (1996) suggested that in classification the Osteoglossidae be placed in the suborder Osteoglossoidei, and that Notopteridae, Mormyridae, and Gymnarchidae be placed in the suborder Notopteroidei. However, Hilton (2003) found that mormyrids are the sister group of notopterids + osteoglossids. I have not used the categories of suborder or superfamily to express relationships.

Four families, 28 genera, and about 218 species. All species occur in freshwater; only some notopterids enter brackish water.

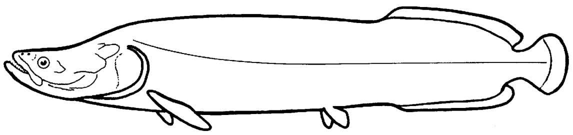
Family OSTEOGLOSSIDAE (65)—osteoglossids or bonytongues. Freshwater; circumtropical, South America, Africa, and Southeast Asia to northern Australia.

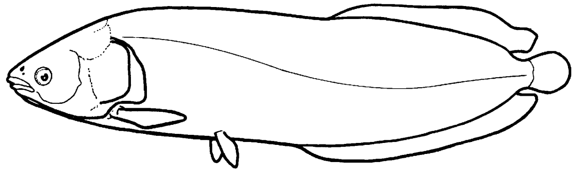
Maxilla toothed; no intracranial penetration of swim bladder; six pelvic rays; pelvic fins distinctly behind base of pectoral fins; some possess a suprabranchial organ and can utilize atmospheric air; lateral line scales 21–55; 60–100 vertebrae.

Most osteoglossids are omnivorous or carnivorous.

Five genera and eight species. A number of fossils are recognized: e.g., *Phareodus* from the Eocene of Wyoming, and *Brychaetus* of the Paleocene and Eocene of Europe and Africa. Additional fossils are given in Li and Wilson (1996), Hilton (2003), and Zhang (2004).

Subfamily Heterotidinae. No mandibular barbels; branchiostegal rays 10 or 11 (*Arapaima*) or 7–9 (*Heterotis*).

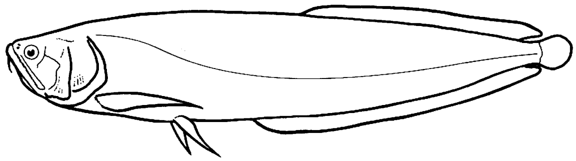




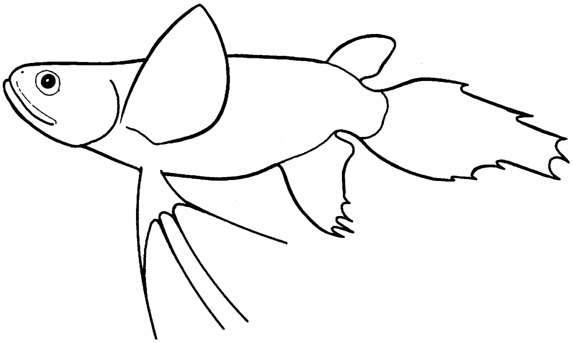
Two species, *Arapaima gigas* (Pirarucú) of South America (upper figure) and *Heterotis niloticus,* which lacks parasphenoid teeth and has reduced tongue teeth, of western Africa (lower figure above). *A. gigas* of South America, one of the world's largest species of scaled freshwater fish, grows to about 2–2½ m in length, although larger specimens probably existed before the modern fisheries. *Heterotis niloticus,* which grows to 98 cm in length, has a unique spiralled epibranchial organ that aids in concentrating and swallowing food.

Subfamily Osteoglossinae. *Osteoglossum* and *Scleropages* have mandibular barbels present; 10–17 branchiostegal rays.

Osteoglossum bicirrhosum (silver aruana, arowana, or arawana) and *O. ferreirai* (Black Aruana) of South America have 42–57 dorsal fin rays.

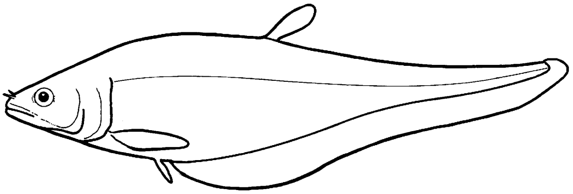


Scleropages jardinii of northern Australia and New Guinea, *S. leichardti* of the Fitzroy River in Queensland, Australia, and *S. formosus* of Southeast Asia (including Sumatra and Borneo) have about 20 dorsal fin rays. Three other valid species may constitute *S. formosus* and have been formally described by Pouyaud et al. (2003).



Pantodon buchholzi (Butterflyfish, shown above) of tropical western Africa, formerly recognized in its own family, Pantodontidae, has pelvic fins located under the pectoral fins; swim bladder that can act as an air-breathing organ; eight branchiostegal rays; greatly enlarged pectoral fins; suboperculum absent; interoperculum sometimes absent; 30 vertebrae. Length up to 10 cm.

Family NOTOPTERIDAE (66)—featherfin knifefishes or Old World knifefishes. Freshwater, sometimes brackish; Africa to Southeast Asia.



Maxilla toothed; anterior prongs of the swim bladder pass forward to the ear lateral to the skull (intracranially in *Xenomystus* and *Papyrocranus*) (also true for mormyrids); anal fin long (94–141 rays or 100 or more rays in anal and caudal combined) and confluent with a reduced caudal fin; dorsal fin small to absent; pectoral fin rays 11–17; pelvic fins small (3–6 rays) to absent; subopercular absent; lateral line scales 120–180; ventral scutes 25–52; vertebrae 66–86. Body color uniform, with numerous small spots, with wavy stripes, or with large ocellated spots above anal fin. Length perhaps up to 1.5 m in *Chitala chitala* and *C. lopis.*

Four genera and eight species (Roberts, 1992).

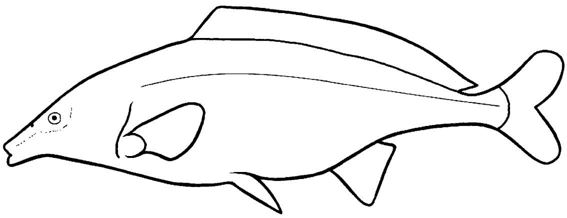
Chitala. Craniodorsal profile concave (vs. convex, straight, or slightly concave). Formerly ranked as a subgenus of *Notopterus.* Four species, Pakistan and India to Sumatra and Borneo.

Notopterus. Mandible with two rows (vs. one or none) of strongly developed serrations. One species, southern and Southeast Asia from India to Sumatra and Java.

Papyrocranus. Pelvic fin absent (vs. present with 3–6 rays); well-developed intracranial extensions of the swimbladder. Two species, West Africa, primarily from Senegal to Nigeria, and the Congo Basin.

Xenomystus. Dorsal fin absent (vs. present with 6–11 rays along a short base); branchiostegal rays 3 (vs. 6–9); gill rakers rudimentary (vs. 10–15). One species, tropical Africa (primarily Nile, Chad, Niger, and Congo basins).

Family MORMYRIDAE (67)—elephantfishes. Freshwater; tropical Africa and Nile.



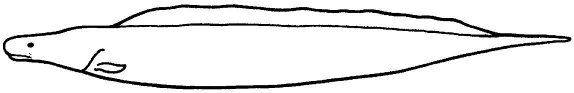
Anal, caudal, and pelvic fins present; caudal peduncle narrow; caudal fin deeply forked; teeth present on parasphenoid and tongue; 6–8 branchiostegal rays; dorsal fin rays 12–91; anal fin rays 20–70; dorsal and anal fins usually opposite and placed back on body; vertebrae 37–64.

The mouth is extremely variable in mormyrids. In some there is a very elongate proboscislike snout with a terminal mouth (e.g., *Gnathonemus curvirostris*); in a few there is an elongate lower jaw (e.g., *Gnathonemus petersii*), whereas in others there is a rounded snout with an undershot mouth (e.g., *Marcusenius*). The fish shown above has a moderately developed proboscislike snout. Some bottom-feeding mormyrids have a chin barbel that is absent in the midwater species. Length reported up to 1.5 m; the maximum length in most species is 9–50 cm.

Some mormyrids and the one gymnarchid are known to transmit weak electric currents and to be capable of detecting extremely weak charges. They are primarily nocturnal fishes and may use these currents to locate objects. Mormyrids, at least, appear to have considerable learning ability. Their brain size (largely cerebellum), relative to body weight, is comparable to that of humans. There is evidence that the family Mormyridae is paraphyletic without the inclusion of *Gymnarchus*; both groups share the following: maxilla toothless; enormous cerebellum; eyes usually small; electric organs derived from caudal muscles; intracranial penetration of swim bladder; flagellum lost in spermatozoa (Jamieson, 1991).

About 18 genera (e.g., *Brienomyrus, Campylomormyrus, Gnathonemus, Hippopotamyrus, Hyperopisus, Marcusenius, Mormyrops, Mormyrus, Petrocephalus, Pollimyrus,* and *Stomatorhinus*) and about 201 species (Kramer and van der Bank, 2000; Kramer et al., 2004).

Family GYMNARCHIDAE (68)—aba. Freshwater; tropical Africa and Nile.



Anal, caudal, and pelvic fins absent; teeth absent from parasphenoid and tongue; four branchiostegal rays; elongate body; long dorsal fin (183–230 rays), which can be used for locomotion. They can move forward or backward equally well by passing reversible wavelike movements along the fin while keeping the body rigid. Vertebrae 114–120. Length reported up to 1.5 m but usually less than 0.9 m.

One species, *Gymnarchus niloticus* (Aba).

ELOPOCEPHALANS. The remaining three subdivisions, the Elopomorpha, Ostarioclupeomorpha (= Otocephala), and Euteleostei, are placed in the unranked taxon Elopocephala. However, as noted above, there are strong arguments by Arratia (1997, 1999, 2004) that the Elopomorpha are more primitive than the Osteoglossomorpha, but counterarguments exist by others that the Osteoglossomorpha may be the most primitive, an arrangement shown in Nelson (1994), based on Patterson and Rosen (1997). I have thus opted to maintain the classification previously given until we have clearer resolution of this problem.

†Family ARARIPICHTHYIDAE. Position uncertain.

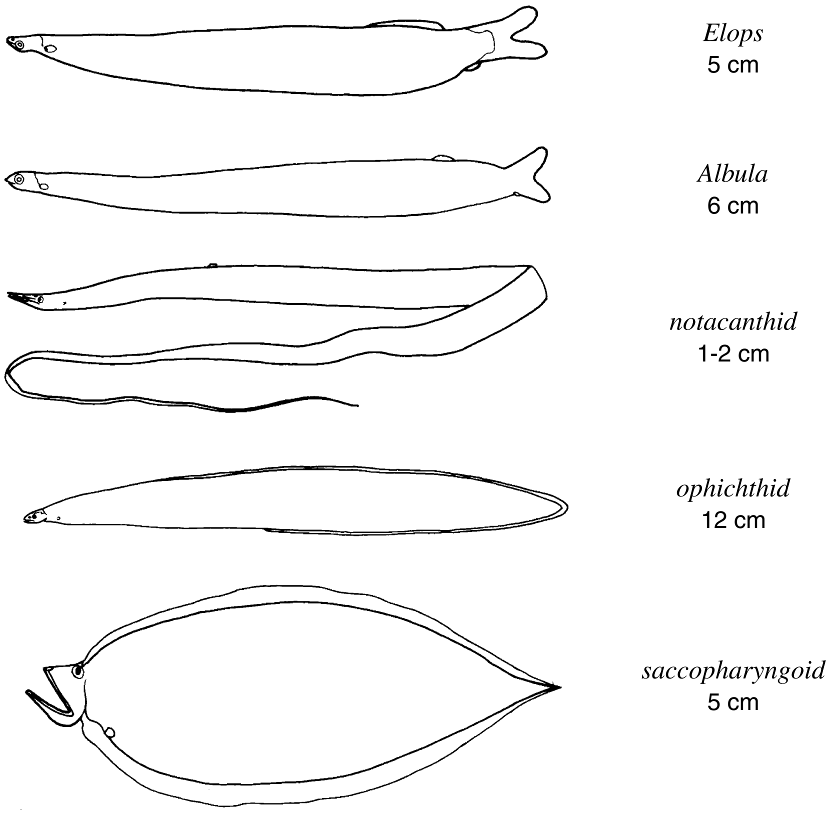
Body deep; dorsal and anal fins with long base; pelvic fins and skeleton absent; pectoral fins attached low on body; caudal fin forked; teeth in jaws absent; premaxilla protractile and forming border of upper jaw; supramaxilla present; supraorbitals absent.

J. G. Maisey and S. Blum in Maisey (1991:208–15) note many similarities between this taxon and the lampriforms. However, they do not find evidence to support earlier suggestions that it is an acanthopterygian or a beryciform. They also cast doubt on original reports that it had spiny fin rays.

One genus, *Araripichthys*, marine, from the Lower Cretaceous in Brazil.

Subdivision ELOPOMORPHA

Leptocephalus larva (ribbonlike, totally unlike the adult); swim bladder not connected with ear (in *Megalops*, however, it does lie against the skull); no *recessus lateralis*; hypurals, when present, on three or more centra; branchiostegal rays usually more than 15; parasphenoid toothed (except in some notacanthoids). During metamorphosis from the leptocephalus to the juvenile body form, the fish shrinks greatly in length. Larvae commonly reach 10 cm and may be as long as 2 m. Böhlke (1989, vol. 2) gave keys and descriptions for the leptocephali of this group.



Representatives of some elopomorph leptocephalus larvae. Typical maximum length given.

Some historical notes on the classification of the elopomorphs are given in Nelson (1994), and older classifications based on adult characters recognized markedly different relationships of the taxa given here. The relationship between the members of this group is based largely on the common occurrence of a leptocephalus larval stage. Not all authors accept the larva as a valid indicator of affinity. As with many fish taxa, there is controversy as to whether the elopomorphs are monophyletic or not and, if they are, as to what the interrelationships are. For example, rather than the leptocephalus larvae representing a derived condition, W. H. Hulet and C. R. Robins, in Böhlke (1989:669–77), believe it to be a primitive condition and therefore of limited systematic significance. Forey et al. (1996) concluded that elopomorphs and anguilliforms, as shown here, are monophyletic; their classification differs little from that herein. Recently, Filleul and Lavoué (2001) felt that the morphological characters used to support the monophyly of the Elopomorpha are mostly weak and proposed a new hypothesis of relationships based on nucleotidic sequences of ribosomal RNA 18S, 16S, and 12S. They concluded that the Elopomorpha are not monophyletic, and considered elopiforms, anguilliforms, albuliforms, and notacanthiforms as four monophyletic, *incertae sedis* taxa among basal teleosts. However, Wang et al. (2003), in an analysis of 12S rRNA sequences, confirmed a monophyletic Elopomorpha, and concluded that *Elops* and *Megalops* share a common ancestor and are clustered at the bottom of Elopomorpha, and that *Albula* and *Notacanthus* share a common ancestor forming the sister group to Anguilliformes, but that the Congroidei are not monophyletic and neither are the Anguilliformes without the Saccopharyngiformes. Inoue et al. (2004) also demonstrated the monopoly of the Elopomorpha. However, it is still possible that our concept of elopomorphs will change, or at least our view of interrelationships, when more morphological studies are done employing both fossil and extant taxa and more out-groups, combined with extensive molecular studies. However, for the present edition, I have made no higher-level changes from that given in Nelson (1994).

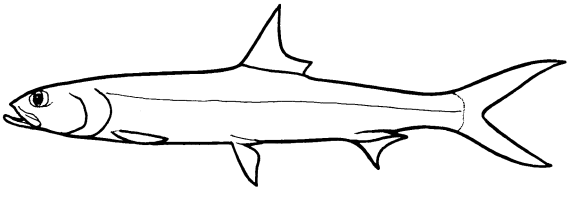
Of the fossil taxa, *Eichstaettia* and the possibly related *Leptolepides* (Arratia, 1991) may be the most primitive known elopomorph fossils. Other fossil elopomorphs not mentioned below include Anaethalionidae with *Anaethalion* (oldest record is Late Jurassic), *Davichthys*, *Lebonichthys*, and *Brannerion* and *Osmeroides* (both albuloids); these and others are reviewed by Forey et al. (1996).

Four orders, 24 families, 156 genera, and about 856 species. All but six species are marine or primarily marine.

Order ELOPIFORMES (23)—tenpounders. Pelvic fins abdominal; body slender, usually compressed; gill openings wide; caudal fin deeply forked; caudal fin with seven hypurals; scales cycloid; mesocoracoid and postcleithra present; gular plate well developed (median); branchiostegal rays 23–35; mouth bordered by premaxilla and toothed maxilla; upper jaw extending past eye; tip of snout not overhanging mouth (mouth terminal or superior); no sensory canal extending onto the small premaxilla. Leptocephali small, maximum length about 5 cm, with a well-developed, forked, caudal fin, a posterior dorsal fin (pelvic fins in older larvae), and about 53–86 myomeres (see D. G. Smith, pp. 961–72, in Böhlke, 1989).

Two families, two genera, and about eight species.

Family ELOPIDAE (69)—tenpounders (ladyfishes). Mainly marine (rarely brackish and freshwater); tropical and subtropical oceans.

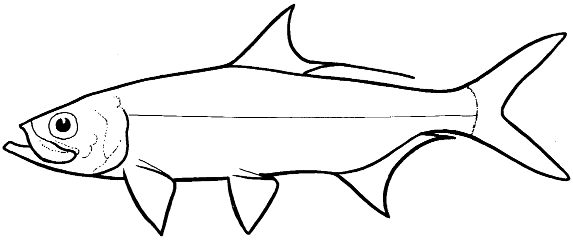


Body rounded (little compressed); mouth terminal; pseudobranchiae large; branchiostegal rays 27–35; dorsal fin rays usually 20–25, the last ray not elongate; anal fin rays usually 13–18; pelvic rays usually 12–16, no conus arteriosus;

lateral line tubes unbranched; lateral line scales usually 95–120; insertion of pelvic fin beneath or posterior to origin of dorsal fin; vertebrae 63–79. Maximum length 1.0 m, attained in *Elops machnata.*

One genus, *Elops,* with about six species (e.g., Smith, 2003). The taxonomy of this genus is poorly known, and some authors recognize fewer species.

Family MEGALOPIDAE (70)—tarpons. Mainly marine (enters freshwater); tropical and subtropical oceans.



Body compressed; mouth terminal or superior; pseudobranchiae absent; branchiostegal rays 23–27; dorsal fin rays 13–21, the last ray elongate; anal fin rays usually 22–29; pelvic rays 10 or 11; conus arteriosus present; lateral line tubes branched (radiating over surface of lateral line scales); only elopiform with the swim bladder lying against the skull (there is no intimate association between the swim bladder and the perilymphatic cavity as in clupeoids and notopteroids). Maximum length about 2.4 m, attained in *Megalops atlanticus.*

Two species, *Megalops cyprinoides* of the Indo-West Pacific (Africa to Society Islands) and *Megalops atlanticus* (= *Tarpon atlanticus*) of the western Atlantic (North Carolina, rarely north to Nova Scotia, to Brazil and offshore) and off tropical West Africa (rarely to southern Europe). The two species can be distinguished as follows:

Megalops cyprinoides. Insertion of pelvic fin beneath origin of dorsal fin; dorsal fin rays 17–21; lateral line scales 37–42; vertebrae 67 or 68; expanded arm of the intercalar forming the entire wall of the large periotic bulla.
Megalops atlanticus. Insertion of pelvic fin in advance of origin of dorsal fin; dorsal fin rays 13–16; lateral line scales 41–48; vertebrae 53–57; intercalar does not form part of lateral wall of periotic cavity.

Order ALBULIFORMES (24)—bonefishes. Mandibular sensory canal lying in an open groove in the dentary and angular bones (in all other elopomorphs the groove is roofed; in *Albula* there is a small roof in the angular).

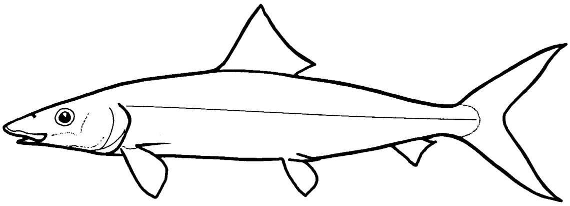
Three families, eight genera, and about 30 species.

Suborder Albuloidei. Body herringlike; gular plate reduced to a thin median splint or absent; pelvic rays 10–14; mouth bordered primarily by the premaxilla (maxilla toothed only in Pterothrissinae); upper jaw not extending as far as front of eye; tip of snout overhanging mouth (mouth inferior); caudal fin with six hypurals; infraorbital lateral line canal extending onto premaxilla, which is rare among living teleosteans; branchiostegal rays 6–16.

Family ALBULIDAE (71)—bonefishes. Marine; tropical seas.

Maximum length about 105 cm, attained in *Albula vulpes.*

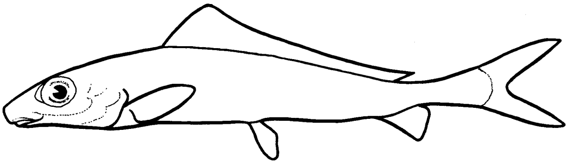
SUBFAMILY ALBULINAE. Most tropical seas (rarely brackish and freshwater).



Dorsal fin base short, 16–21 rays (last ray of dorsal fin prolonged into a filament in *Albula nemoptera*); branchiostegal rays 10–16; gill rakers 15–17; lateral line scales 66–84; vertebrae 69–80; small median gular plate; maxilla and basihyal toothless; crushing dentition on parasphenoid.

One genus, *Albula,* and at least three species (e.g., Smith, 2003; see Nelson et al., 2004:194, for a discussion from the literature concerning number of valid species of *Albula* that may be recognized).

SUBFAMILY PTEROTHRISSINAE. Eastern Atlantic (Gulf of Guinea) and Japan.



Dorsal fin base long, about 55–65 rays; branchiostegal rays 6; lateral line scales 85–112; vertebrae about 107; gular plate absent; maxilla each with six or seven small teeth.

One genus, *Istieus* (synonym *Pterothrissus*), with two species: *I. belloci* from tropical west Africa and *I. gissu* from Japan. C. R. Robins (in Böhlke, 1989:9–23) noted the 1973 evidence of P. L. Forey for synonymizing the genus *Istieus,* based on fossil species, with the similar extant species.

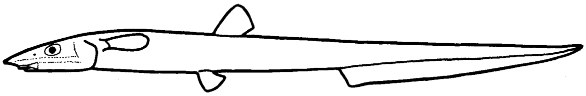
Suborder Notacanthoidei (Lyopomi and Heteromi). Body eel-like; posteriorly directed spine on dorsal edge of rear of maxilla; premaxilla and maxilla bordering upper jaw; gill membranes separate; pectoral fins relatively high on body; pelvic fins abdominal, with 7–11 rays (the two fins are usually connected by a membrane); anal fin base long and merged with what remains of the caudal fin; caudal fin skeleton reduced or absent; tail easily regenerated when lost (analogous to loss of tail in lizards?); branchiostegal rays 5–23; swim bladder present. Some have photophores.

D. G. Smith (in Böhlke, 1989:955–59) described the leptocephalus larva. The 300 or more myomeres are V-shaped. A normal caudal fin is absent but there is a postcaudal filament. The dorsal fin is short, consisting of about 10 rays, and is located in the anterior half of the body. Older larvae have small pelvic fins. The larvae, which can be exceptionally large, reach a length of up to 2 m before metamorphosis. Generic names applied to notacanthoid larvae include *Tilurus* and *Tiluropsis.*

Members of this deep-sea order have been taken between 125 and 4,900 m, but most seem to occur at depths of 450–2,500 m.

Six genera with about 25 species (e.g., Sulak, 1977; Smith, 2003).

Family HALOSAURIDAE (72)—halosaurs. Deep-sea; worldwide.



Maxilla and premaxilla toothed; branchiostegal membranes completely separate, rays 9–23; dorsal fin entirely anterior to anus, with 9–13 soft rays, no spines; lateral line cavernous and extending full length of body, lateroventrally; scales relatively large, fewer than 30 longitudinal rows on each side.

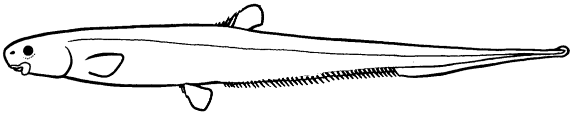
Three genera with 15 species. *Halosaurus,* with eight species, occurs in many areas of the Atlantic, Indian, and Pacific, usually confined to continental margins. *Halosauropsis macrochir* is in the Atlantic, western Pacific, and Indian. *Aldrovandia,* with six species, is in the Atlantic, Indian, and western and central Pacific. In addition, some fossils, such as the Upper Cretaceous *Echidnocephalus,* are known.

Family NOTACANTHIDAE (73)—spiny eels. Deep-sea; worldwide.

Branchiostegal membranes at least partly joined; at least part of the dorsal fin posterior to the anus; lateral line not cavernous and well up on the side; scales relatively small, more than 50 longitudinal rows occur on each side; some with the unique feature of having as many as three spinelike rays in each pelvic fin.

Three genera with 10 species.

Lipogenys. Mouth small, toothless, and suctorial; lower jaw short, lying within the suckerlike opening; branchiostegal rays 5–7; gill rakers absent; pectoral girdle somewhat degenerate, cleithrum and supracleithrum absent; dorsal fin base short, with 9–12 rays (the first few spinelike); anal fin base long, with the first 32–44 rays spinelike, total rays about 116–136; pyloric caeca 5–7; vertebrae about 228–234.



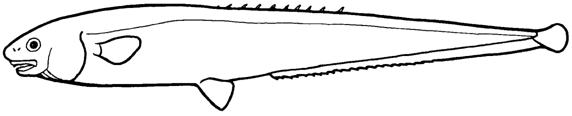
One species, *Lipogenys gilli,* deep-sea, in the western North Atlantic and off Japan (Nakabo et al., 1991).

In contrast to the above taxon, the following two genera have mouth normal in size, maxilla toothless but premaxilla and dentary are toothed; branchiostegal rays 6–13; well-developed gill rakers; cleithrum and supracleithrum well ossified.

Polyacanthonotus. Dorsal fin with 26–41 isolated spines and no conspicuous soft rays; vertebrae 224–290.

Three species known from the southern Bering Sea, North Pacific, New Zealand, Caribbean, Mediterranean, and North Atlantic in 500–3,753 m depth (Sulak et al., 1984; Crabtree et al., 1985).

Notacanthus. Dorsal fin with 6–15 isolated spines and no conspicuous soft rays.



Six species and probably worldwide.

Order ANGUILLIFORMES (Apodes) (25)—eels. Pelvic fins and skeleton absent; pectoral fins and girdle absent in some; pectoral fins, when present, at least midlateral in position or higher and skeleton lacking bony connection to skull (posttemporal absent); dorsal and anal fins confluent with caudal fin (caudal fin rayless or lost in some); scales usually absent or, if present, cycloid and embedded; body very elongate (eel-like); gill openings usually narrow; gill region elongate and gills displaced posteriorly; gill rakers absent; pyloric caeca absent; maxilla toothed, bordering mouth; the two premaxillae (rarely absent), the vomer (usually), and the ethmoid united into a single bone; branchiostegal rays 6–49; swim bladder present, duct usually present; oviducts absent; opisthotic, orbitosphenoid, mesocoracoid, gular plate, posttemporal, postcleithra, supramaxilla, and extrascapular bones absent; ossified symplectic absent (cartilaginous one present in Synaphobranchidae); hyomandibular united with quadrate; ribs present or absent. All or most of the gonads are in the tail (post anal) in some groups (e. g., Heterenchelyidae and Synaphobranchidae) (Fishelson, 1994). C. R. Robins (in Böhlke, 1989:9–23) and other chapters in Böhlke (1989) discussed the various characters. C. R. Robins (above C. R. Robins article, pp. 15–17) discussed some fossils previously thought to be anguilliforms, including *Anguillavus,* which has pelvic fins. L. Taverne in 2004 described a primitive Cretaceous fossil, *Libanechelys,* that lacked the pelvic girdle.

Eels are primarily specialized for wedging through small openings. Some, in addition, are adapted to burrowing in soft substrates or to a pelagic existence.

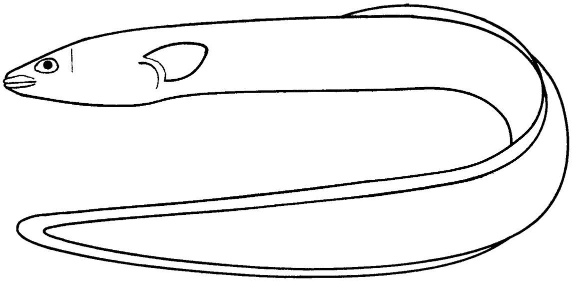
The leptocephalus larva of anguilliforms differs from that of elopiforms and notacanthiforms (but not saccopharyngiforms) in having the caudal fin small and round, continuous with the dorsal and anal fins (note: the many-rayed dorsal and anal fins are usually very inconspicuous) (as with notacanthiforms and saccopharyngiforms, there are usually more than 100 myomeres). Considerable morphological diversity exists among the pelagic leptocephalus larvae, more so than among the adults. Selective pressures on larval characters have generally been different than on adult characters (as is true for most marine larvae); the larvae and adults give the appearance of having evolved independently. Problems still exist in determining which leptocephali are the young of which adult. Most leptocephali are less than 20 cm long before metamorphosis (when there is a loss of certain characters and a contraction in length), but a few are known to exceed 50 cm. Further information on eel leptocephali and keys to their identification may be found in Böhlke (1989, vol. 2). Most of the family chapters are authored by David G. Smith, who has done much work on these larvae. Extensive work has also been done by such workers as Peter H. J. Castle.

The recognition of three suborders follows C. R. Robins (Böhlke, 1989:9–23). Fifteen families, with 141 genera, and about 791 species. Members of several families occur in freshwater, and about six species are known only from freshwater.

Suborder Anguilloidei. Frontals divided (sutured).

Three families, five genera, and about 29 species.

Family ANGUILLIDAE (74)—freshwater eels. Usually catadromous; tropical and temperate seas except eastern Pacific and southern Atlantic.



Minute scales present; gill opening crescentic, lateral; lateral line complete on body and head; pectoral fins well developed; vertebrae 100–119.

Adult anguillids live in freshwater or in estuaries. They stop feeding at maturity, when they move from freshwater out to sea. The leptocephali move back to coastal areas, undergo metamorphosis, and enter freshwater as elvers. The North American (*Anguilla rostrata*) and European (*A. anguilla*) freshwater eels spawn in the Sargasso Sea area. The relationship between these two species is uncertain, and some authors regard them as conspecific. It seems most probable that they represent separate species. Despite much effort, many mysteries remain concerning the life history of *A. rostrata.* For example, adults have only very rarely been taken in the open ocean after they leave the estuaries on their spawning migration. It was not until 1977 that the first evidence of adults occurring off the continental shelf was obtained when two were photographed on the bottom at about 2,000 m depth near the Bahamas.

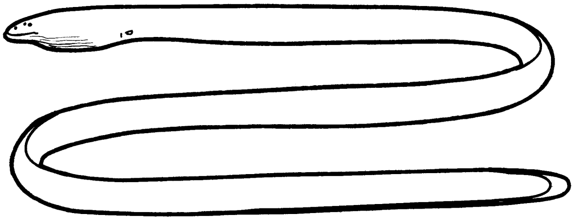
One genus, *Anguilla,* with 15 species (D. G. Smith, in Böhlke, 1989:24–47).

Family HETERENCHELYIDAE (75)—mud eels. Marine; tropical, Atlantic (and Mediterranean) and eastern Pacific.

Pectoral fin absent; mouth large; scales absent; gill openings low on body; dorsal fin origin over gill opening; lateral line obsolete. Members of this family appear to burrow (head first).

Two genera, *Panturichthys* (dermal crest on top of head, inner row of maxillary teeth complete or nearly so, and 109–136 vertebrae) with four species and *Pythonichthys* (synonym *Heterenchelys*) (no crest, inner row of maxillary teeth incomplete, and 141–227 vertebrae) also with four species (e.g., D. G. Smith, in Böhlke, 1989:48–54).

Family MORINGUIDAE (76)—spaghetti eels. Marine, rarely in freshwater; tropical, Indo-Pacific and western Atlantic.



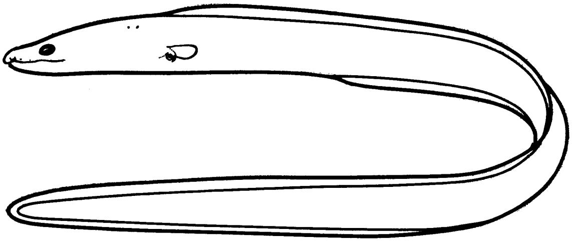
Body extremely elongate; scales absent; gill openings low on body; dorsal and anal fins reduced to low folds, posteriorly; pectoral fin small to feeble; eyes small and covered with skin; vertebrae 98–180. Many of their features are adaptations to their fossorial life (they burrow head first). *Moringua* has been found in freshwater.

Two genera, *Moringua* and *Neoconger,* with roughly six species (D. G. Smith, in Böhlke, 1989:55–71).

Suborder Muraenoidei. Frontals divided (sutured); marked reduction in gill-arch elements and lateral line; scales absent; eyes of normal size.

Three families, 24 genera, and about 207 species.

Family CHLOPSIDAE (Xenocongridae) (77)—false morays. Marine; tropical and subtropical, Atlantic, Indian, and Pacific.



Gill openings restricted to small roundish lateral openings; lateral line pores on head but not on body; one or two branchial pores; pectoral fins absent in some (e.g., in the six species of *Chlopsis* and the similar appearing *Robinsia catherinae*); posterior nostril displaced ventrally, all but *Kaupichthys nuchalis* of the western Atlantic with posterior nostril opening into the lip; vertebrae usually 100–150.

Eight genera, *Boehlkenchelys, Catesbya, Chilorhinus, Chlopsis, Kaupichthys, Powellichthys, Robinsia,* and *Xenoconger,* with 18 species (e.g., D. G. Smith in Böhlke, 1989:72–97; Tighe, 1992; Tighe and McCosker, 2003).

Family MYROCONGRIDAE (78)—myroconger eels. Marine; eastern tropical Atlantic, St. Helena, and Pacific.

Gill openings small but not greatly restricted; body strongly compressed; pectoral fin present; posterior nostril high on head, level with upper margin of eye; lateral line incomplete, 5–7 pores at anterior end of canal in branchial region above pectoral fin.

One genus, *Myroconger,* with four species (D. G. Smith in Böhlke, 1989:89–103; Castle and Bearez, 1995).

Family MURAENIDAE (Heteromyridae) (79)—moray eels. Marine, some species in or occasionally entering freshwater; tropical and temperate seas.

Gill openings restricted to small roundish lateral openings; lateral line pores on head but not on body; two branchial pores; gill arches reduced; fourth branchial arch strengthened and supporting pharyngeal jaws; pectorals absent (some other eels have lost the pectoral fin, but only morays have a greatly reduced fin in the larval stage—Smith, 1979); posterior nostril high in head (usually above front portion of eye); most with long fanglike teeth; vertebrae usually 110–200. Maximum length 3.0 m.

Some morays, such as species of *Gymnothorax,* are involved in ciguatera fish poisoning, which occurs largely between 35°N and 34°S and results from eating any one of a large variety of marine fish species that are ciguatoxic. It is suspected that plant-feeding fishes acquire the toxicity first by feeding on a certain algae, especially some dinoflagellates; they then pass it on to carnivorous fishes that are the most likely to be poisonous (e.g., *Sphyraena, Caranx, Mycteroperca,* and *Lutjanus*).

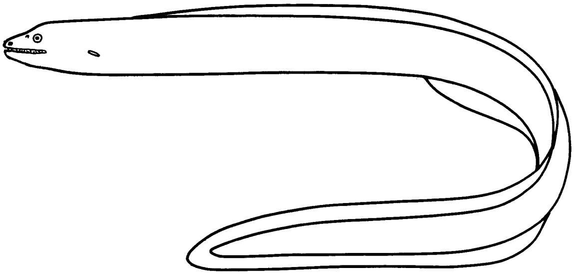
About 15 genera with about 185 species (E. B. Böhlke, J. E. McCosker, and J. E. Böhlke in Böhlke, 1989:104–206; Böhlke and Randall, 2000; Böhlke and McCosker, 2001; Smith, 2002).

SUBFAMILY UROPTERYGIINAE. Ossified hypobranchials in first and second arches; vertical fins reduced, rays confined to tip of tail (the dorsal and anal fins in the larvae are also confined to the posterior end).

Four genera, *Anarchias, Channomuraena, Scuticaria,* and *Uropterygius.*

SUBFAMILY MURAENINAE. No ossified hypobranchials; vertical fins not confined to tip of tail (usually the dorsal fin origin is above the gill opening or forward, but in three species it begins over the anus or behind).

T. J. Miller, in a 1987 article in *Copeia,* described knotting behavior as a mode of feeding in species of *Echidna* and *Gymnothorax* (in aquarium observations), otherwise known in fishes only in hagfishes. The eels also employed rotational feeding, known also in *Anguilla. Gymnothorax polyuranodon* regularly occurs in freshwater in Indonesia and perhaps in Fiji and part of Australia.



About 11 genera, *Echidna, Enchelycore, Enchelynassa, Gymnomuraena, Gymnothorax* (synonyms *Lycodontis, Rabula*), *Monopenchelys, Muraena, Rhinomuraena, Siderea, Strophidon,* and *Thyrsoidea* (synonym *Evenchelys*).

Suborder Congroidei. Frontals fused; scales present only in some synaphobranchids.

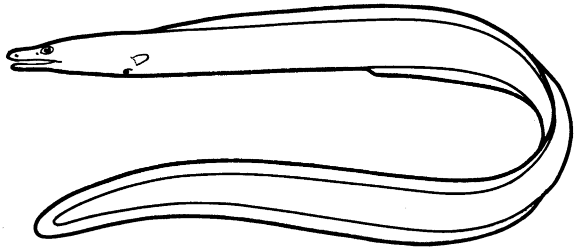
Nine families, 112 genera, and about 555 species.

Family SYNAPHOBRANCHIDAE (80)—cutthroat eels. Marine; Atlantic, Indian, and Pacific.

Gill openings low on body, at or below insertion of pectoral fin (this fin is absent in a few species); vertebrae 110–205; third hypobranchial directed forward from midline, meets third ceratobranchial at a sharp angle; larvae with diagonally elongated eyes (termed telescopic), lens at anterodorsal end.

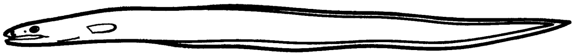
Ten genera and about 32 species (C. H. Robins and C. R. Robins in Böhlke, 1989:207–53; Chen and Mok, 1995; Sulak and Shcherbachev, 1997).

SUBFAMILY ILYOPHINAE (DYSOMMATINAE) (ARROWTOOTH EELS OR MUSTARD EELS). Lower jaw shorter than upper; body scaleless (except in some *Ilyophis*); pectoral fin absent in some species of *Dysomma* and the monotypic *Thermobiotes*; head shape depressed and relatively rounded; some teeth relatively long.



Seven genera, *Atractodenchelys, Dysomma, Dysommina, Ilyophis, Linkenchelys, Meadia,* and *Thermobiotes.*

SUBFAMILY SYNAPHOBRANCHINAE (CUTTHROAT EELS). Lower jaw longer than upper; body scaled (usually naked in *Haptenchelys texis*); head shape compressed and relatively pointed; teeth small and needlelike; branchial apertures confluent or only slightly separated in most; ventral region dark-colored and dorsal region pale.



Two genera, *Haptenchelys* (one species) and *Synaphobranchus* (about eight species).

SUBFAMILY SIMENCHELYINAE (SNUBNOSE PARASITIC EEL). Body especially slimy, with scales embedded in skin; snout blunt and rounded with terminal slitlike mouth; pectoral fin moderate in size; palatopterygoid arch (arcade) complete (absent or only a splinterlike pterygoid present in members of the other subfamilies). Maximum length about 60 cm.

This eel occurs between 365 and 2,620 m. It is essentially worldwide from tropical to temperate latitudes. Although this eel is reported to be a scavenger on other fishes (especially halibut), little is known of its feeding habits and food. Adults probably cut or rasp chunks of tissue from moribund fishes and feed on invertebrates.

One species, *Simenchelys parasiticus.*

Family OPHICHTHIDAE (81)—snake eels and worm eels. Marine, some species in or occasionally entering freshwater; coastal areas of tropical to warm temperate oceans, rarely in midwater.

Posterior nostril usually within or piercing the upper lip; tongue not free; branchiostegal rays numerous (15–49 pairs) and overlapping along the midventral line, forming a basketlike structure termed a "jugostegalia" in the ventral wall of the throat; neural spines poorly developed or absent; hyomandibulae usually vertical or backwardly inclined (inclined obliquely forward in *Benthenchelys*); pectoral fins present or absent; vertebrae 110–270.

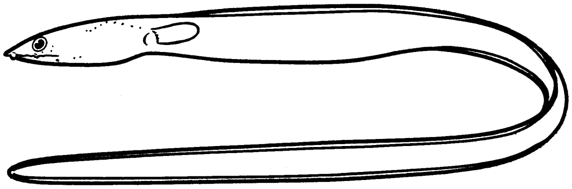
Ophichthids, with their stiffened tail, burrow tail first; they are thought to move through the sediment equally well going forward or backward (unlike the head-burrowing heterenchelyids and moringuids). Some members are especially sharp-tailed, an adaptation for rapid burrowing.

Fifty-two genera with about 290 species (e.g., J. E. McCosker, E. B. Böhlke, and J. E. Böhlke in Böhlke, 1989:254–412; Castle and McCosker, 1999; McCosker and Rosenblatt, 1998; McCosker and Chen; 2000; McCosker and Randall. 2001; McCosker and Robertson, 2001).

SUBFAMILY MYROPHINAE (WORM EELS). Gill openings midlateral, opening constricted; caudal fin rays conspicuous, but still confluent with dorsal and anal fins, tail tip flexible; pectoral fin present or absent; coloration uniform, often darkened dorsally.

Eleven genera, *Benthenchelys, Ahlia, Asarcenchelys, Glenoglossa* (the glossohyal of the tongue is modified into a lure), *Mixomyrophis, Muraenichthys, Myrophis, Neenchelys, Pseudomyrophis, Schismorhynchus,* and *Schultzidia.*

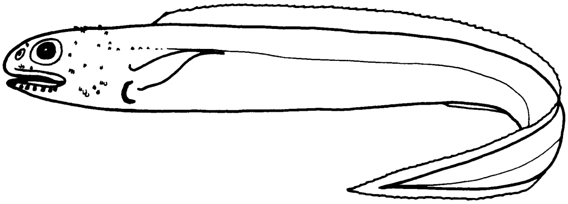
SUBFAMILY OPHICHTHINAE (SNAKE EELS). Gill openings midlateral to entirely ventral, unconstricted; tail tip is a hard or fleshy finless point, rudimentary rays visible in some genera; pectoral fin present or absent, anal fin absent in some, dorsal fin absent in some and all fins absent in *Apterichtus, Cirricaecula,* and *Ichthyapus*; coloration variable (usually spotted or striped) or uniform.



Forty-one genera—e.g., *Apterichtus* (synonym *Verma*), *Bascanichthys, Caecula, Callechelys, Cirrhimuraena, Dalophis* (freshwater in Africa), *Echelus, Echiophis,* *Ethadophis*, *Lamnostoma* (with four western Pacific species generally found in freshwater), *Letharchus*, *Myrichthys*, *Mystriophis*, *Ophichthus*, *Phaenomonas*, *Pisodonophis*, and *Yirrkala*

Family COLOCONGRIDAE (82)—shorttail eels. Marine; Atlantic, Indian, and western Pacific.

Body stubby and snout blunt (this is the least elongate anguilliform); lateral line complete, most pores in short tubes; anus well behind midlength; pectoral fin well developed; vomerine teeth absent; vertebrae 142–163.



One genus, *Coloconger*, with about five species (D. G. Smith in Böhlke, 1989:413–19).

Family DERICHTHYIDAE (83)—longneck eels. Marine; Atlantic, Indian, and Pacific.

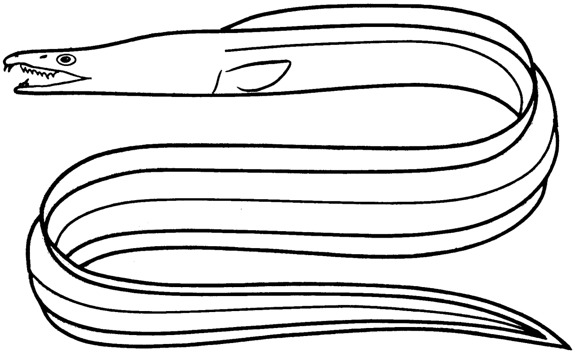
Series of parallel striations on the head forming part of a sensory system; branchial region not expanded, with body behind gill opening somewhat compressed; pectoral fins present; dorsal fin origin behind tip of pectoral fin; anus well behind midlength; lateral line virtually complete; vertebrae 125–160; adults mesopelagic to bathypelagic. Maximum length about 60 cm.

Two genera, the monotypic *Derichthys* with a short snout and *Nessorhamphus* containing two species with relatively long snouts (C. H. Robins in Böhlke, 1989:420–31).

Family MURAENESOCIDAE (84)—pike congers. Marine; tropical, Atlantic, Indian, and Pacific.

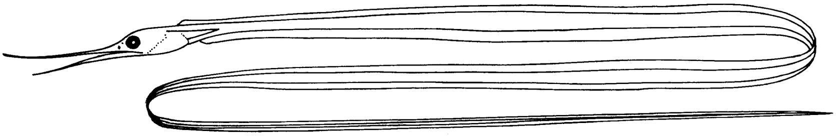
Teeth well developed, especially on the vomer; pectorals well developed; eyes large and covered with skin; dorsal fin origin over or slightly before pectoral base; lateral line conspicuous; vertebrae 120-216.

As noted by D. G. Smith, in Böhlke (1989:432–40), this family is poorly diagnosed and is of uncertain affinity.



Four genera, *Congresox*, *Cynoponticus*, *Muraenesox*, and probably *Sauromuraenesox*, with about eight species.

Family NEMICHTHYIDAE (85)—snipe eels. Marine (bathy- and mesopelagic); Atlantic, Indian, and Pacific



Extremely long, nonocclusible upper and lower jaws (except in fully mature males), with upper jaw longer than lower; body very elongate; pectoral fin present; dorsal and anal fins confluent with caudal; eyes large; preopercle absent; frontals only partially fused in some; lateral line complete; anus a short distance behind pectoral fin (*Avocettina*) or under pectoral fin (the other two genera); vertebrae 170–220 in *Labichthys* and *Avocettina* to over 750 in *Nemichthys* (species of this genus have a caudal filament that is frequently lost and thus precludes accurate counts).

Male snipe eels undergo a marked transformation at sexual maturity with, for example, the jaws undergoing a drastic shortening and loss of teeth. The two sexes of some species were at one time placed in separate genera and even in separate suborders.

Three genera, *Avocettina* (about four species), *Labichthys* (two species), and *Nemichthys* (three species), with about nine species (D. G. Smith and J. G. Nielsen in Böhlke, 1989:441–59).

Family CONGRIDAE (86)—conger eels. Marine; tropical to temperate, Atlantic, Indian, and Pacific.

Lateral line complete; pectoral fin usually present; branchiostegal rays 8–22; vertebrae 105–225.

Three subfamilies with 32 genera and roughly 160 species (e.g., D. G. Smith in Böhlke, 1989:460–567; Castle and Randall, 1999; Smith and Karmovskaya, 2003; Greenfield and Niesz, 2004).

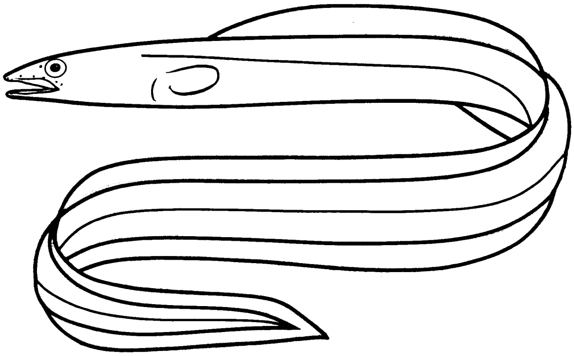
SUBFAMILY HETEROCONGRINAE (GARDEN EELS). Dorsal and anal fin rays unsegmented; pectoral fin minute or absent; body very elongate and slender; mouth short and lower jaw projecting beyond upper. Garden eels have the interesting habit of hovering above their sand burrows in large colonies (giving the appearance of a garden), with their tail down and the body relatively straight up.

Two genera, *Gorgasia* and *Heteroconger.*

SUBFAMILY BATHYMYRINAE. Dorsal and anal fin rays unsegmented; pectoral fin well developed; posterior nostril below mideye level.

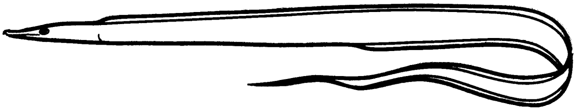
About five genera, *Ariosoma, Bathymyrus, Chiloconger, Parabathymyrus,* and *Paraconger.*

SUBFAMILY CONGRINAE. Dorsal and anal fin rays segmented; pectoral fin well developed; posterior nostril at or above mideye level.



About 25 genera—e.g., *Acromycter, Conger* (= the older but suppressed generic name *Leptocephalus*), *Gavialiceps, Gnathophis, Hildebrandia, Lumiconger* (a luminescent eel off northern Australia described in 1984), *Macrocephenchelys* (this genus was once placed in its own family), *Rhechias, Rhynchoconger, Uroconger,* and *Xenomystax.*

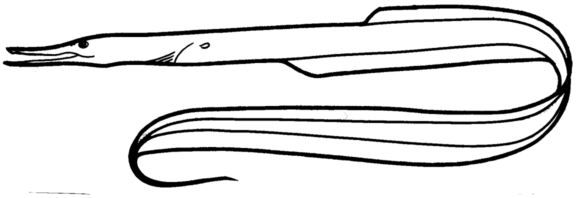
Family NETTASTOMATIDAE (87)—duckbill eels. Marine; Atlantic, Indian, and Pacific.



Head and snout elongate and narrow; mouth enlarged; tail greatly attenuated; pectoral fin usually absent in adults (present only in *Hoplunnis*); vertebrae usually 190–280. Maximum length about 1 m. This family of tropical and warm temperate waters is poorly known; it is thought to be most closely related to the *Uroconger* line of congrids.

Six genera, *Facciolella, Hoplunnis, Nettastoma, Nettenchelys, Saurenchelys,* and *Venefica,* with about 38 species (e.g., D. G. Smith in Böhlke, 1989:568–612; Karmovskaya, 1999).

Family SERRIVOMERIDAE (88)—sawtooth eels. Marine; midwater (pelagic) tropical to temperate, Atlantic, Indian, and Pacific.



Jaws extremely elongate and slender; vomerine teeth in two or more rows; gill openings connected ventrally; branchiostegal rays 6 or 7; color usually blackish with silvery sides; vertebrae 137–170.

Two genera, *Serrivomer* (about nine species, dorsal-fin origin slightly posterior to anus) and the monotypic *Stemonidium* (dorsal-fin origin over or slightly anterior to anus), with about 10 species (K. A. Tighe in Böhlke, 1989:613–27).

Order SACCOPHARYNGIFORMES (26)—sackpharynx fishes. Highly aberrant fishes, lacking symplectic bone, opercular bones, branchiostegal rays, scales, pelvic fins, ribs, pyloric caeca, and swim bladder; caudal fin absent or rudimentary; gill openings ventral; dorsal and anal fins long; jaws and hyomandibular greatly elongate, attached to neurocranium by only one condyle; leptocephalus larvae deep-bodied with myomeres V-shaped and not W-shaped. Like anguilliforms, they may spawn once and die.

C. R. Robins, in Böhlke (1989:9–23), gave reasons for including Cyematidae in this order rather than in the anguilliforms, where it was previously placed (see also D. G. Smith in Böhlke, 1989:629–35).

Four families, five genera, and 28 species.

Suborder Cyematoidei

Family CYEMATIDAE (89)—bobtail snipe eels. Marine (bathypelagic); Atlantic, Indian, and Pacific.

Body relatively short, compressed; lateral line pores absent; eye small to vestigial; maxillae present; caudal fin present, tip of tail blunt. This family shows less reduction in characters than do the other saccopharyngiforms. Maximum length about 15 cm.

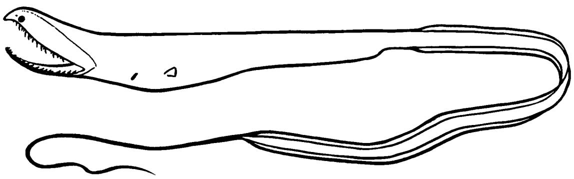
Two monotypic genera—*Cyema* (body black; long, nonocclusible upper and lower jaws) and *Neocyema* (body bright red; pectoral skeleton absent, although a rayless fin is present—probably neotenic).

Suborder Saccopharyngoidei (Lyomeri). Quadrate greatly elongate; pharynx highly distensible (accommodating extremely large prey).

The species of this suborder are perhaps the most anatomically modified of all vertebrate species. Some earlier authors (e.g., V. V. Tchernavin) have questioned whether they are true bony fishes at all.

Three families, three genera, and 26 species (e.g., E. Bertelsen, J. G. Nielsen, and D. G. Smith in Böhlke, 1989:636–55, and references below).

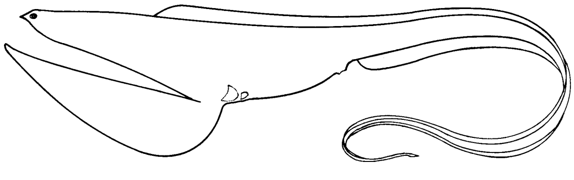
Family SACCOPHARYNGIDAE (90)—swallowers. Marine; Atlantic, Indian, and Pacific.



Gill openings closer to end of snout than to anus; mouth large; jaws with curved teeth; pectoral fins well developed; vomer and parasphenoid absent; vertebrae about 150–300. Maximum length about 2 m, including the long slender tail.

One genus, *Saccopharynx*, with about10 species (Tighe and Nielsen, 2000).

Family EURYPHARYNGIDAE (91)—gulpers or pelican eels. Marine; tropical and temperate, Atlantic, Indian, and Pacific.



Gill openings small, closer to anus than to end of snout; only teleost with five gill arches and six visceral clefts; mouth enormous; jaws with numerous minute teeth; pectoral fins minute; vertebrae 100–125. Maximum length about 75 cm.

One species, *Eurypharynx pelecanoides* (Nielsen et al., 1989).

Family MONOGNATHIDAE (92)—onejaw gulpers. Marine; Atlantic and Pacific.

Upper jaw absent (i.e., no maxilla or premaxilla); pectoral fins absent; dorsal and anal fins without skeletal supports; rostral fang with connected glands. Maximum length 15.9 cm. Most of the 70 known specimens were taken below 2,000 m.

One genus, *Monognathus*, with about 15 species (Nielsen and Hartel, 1996).

CLUPEOCEPHALANS. The remaining two subdivisions, the Ostarioclupeomorpha (= Otocephala) and Euteleostei, are placed together as sister groups in the taxon Clupeocephala following Patterson and Rosen (1977). However, the Clupeocephala are not given formal rank here.

†Order CROSSOGNATHIFORMES. Position uncertain. Taverne (1989) established this taxon for the Crossognathidae and Pachyrhizodontoidei, two groups previously thought to have differing affinities with the Elopomorpha. However, Taverne (1989) considered this order to be the primitive sister group of the clupeomorphs and euteleosts within the Clupeocephala.

This is a marine group, known from the Cretaceous (Lower and Upper) with one genus extending to the middle Eocene. Fossils are found primarily in Europe, North America, South America, and Australia. The following classification is based on Taverne (1989) and his other works.

Suborder Crossognathoidei. Premaxillae very small; palate without teeth and jaw teeth small; palatine very elongate.

Family CROSSOGNATHIDAE Two genera, *Apsopelix* and *Crossognathus*.

Suborder Pachyrhizodontoidei. Antorbital lost or completely fused with the first infraorbital; never more than six hypurals.

Family NOTELOPIDAE One genus, *Notelops*.

Family PACHYRHIZONTIDAE Six genera, *Elopopsis, Greenwoodella, Pachyrhizodontus, Pachyrhizodus, Platinx* (the only crossognathiform from Paleocene-Eocene), and *Rhacolepis*

Subdivision OSTARIOCLUPEOMORPHA (= OTOCEPHALA)

Strong phylogenetic evidence exists for a sister-group relationship between Clupeomorpha and Ostariophysi, based on both molecular and morphological evidence (e.g., Lê et al., 1993; Lecointre and Nelson, 1996; Arratia, 1997, 1999, 2004; Zaragueta-Bagils et al., 2002). However, some molecular work conflicts with this relationship and continued studies are warranted. The study of T. Grande and de Pinna (2004), while not supporting or refuting a Clupeomorpha/Ostariophysi relationship, examined the evolution of the Weberian apparatus within a phylogenetic context (and components of the complex are found in clupeoids), and gives a character plot of various shared features concerning the Weberian apparatus. In some older works, several features were thought to demonstrate an affinity between the Gonorynchiformes and the Clupeiformes, and gonorynchiforms were thought by some, before cladistic analysis, to represent an evolutionary link between clupeiforms (where many earlier workers placed them) and other ostariophysans.

The next two superorders, Clupeomorpha and Ostariophysi, with six orders, are recognized in this clade, and they are sister to the Euteleostei. The name used for this subdivision, Ostarioclupeomorpha (a taxon-based name), is from page 170 of the 1996 doctoral dissertation of Gloria Arratia (published as Arratia, 1997:153); the widely used synonym, Otocephala (an apomorphic-based name), is from Johnson and Patterson (1996).

Superorder CLUPEOMORPHA

Otophysic (ear-swim bladder) connection comprising a pair of anterior extensions of the swim bladder that enter the skull through the exoccipital and extend into the prootic and often into the pterotics within the lateral wall of the braincase to connect with the utriculus of the inner ear (unlike that occurring in any other group); second hypural fused at base to first ural centrum in all stages of development, but the first hypural free at its base from first ural centrum (autogenous); single pelvic scute present at insertion of the pelvic fin (inconspicuous in adult *Chirocentrus*) and most species with series of median scutes along abdomen before and behind pelvic fin; branchiostegal rays usually fewer than 7, rarely up to 20; body compressed in most; pneumatic duct extending from swim bladder to gut at or near stomach (opening into the dorsal wall of the stomach, relatively anteriorly, in most Engraulidae, Pristigasteridae, and in *Dussumieria*, and in some the duct extends from the swim bladder to the anus); jaws not protrusible; usually two supramaxillae. The first two diagnostic characters are described in Patterson and Rosen (1977).

Several lines of clupeomorphs, both fossil and extant, have members that are double-armored; that is, they have predorsal as well as ventral scutes. In some of these there are only one or two predorsal scutes (double-armored engraulids of the Indo-Pacific), while in others there is a series (*Paraclupea, Diplomystus, Ellimmichthys, Knightia, Hyperlophus, Potamalosa, Ethmidium, Gosiutichthys,* and *Clupanodon*). The double-armored feature has evolved (or possibly been lost) independently several times.

The Lower Cretaceous *Erichalcis* is a clupeomorph of uncertain position. The Upper Cretaceous *Ornategulum* is probably a preclupeomorph. Forey (2004) considered the Lower Cretaceous *Spratticeps* as sister to the extant Clupeiformes plus fossils such as *Santanaclupea*. The higher classification of this taxon has not changed much from that presented by Grande (1985).

Five families, 84 genera, and about 364 species. About half the species are Indo-West Pacific, and almost one-quarter are in the western Atlantic. About 79 species occur primarily in freshwater.

†Order ELLIMMICHTHYIFORMES. No recessus lateralis (infraorbital canal not merging with preopercular canal but extending through dermosphenotic); lateral line complete; patch of teeth on the parasphenoid similar to that in *Osteoglossum*; large foramen in the anterior ceratohyal; parietals meeting at the midline between the supraoccipital and the frontals.

The recognition of this order and its one family follows Grande (1985).

†Family PARACLUPEIDAE (= Ellimmichthyidae). Lower Cretaceous to Middle Eocene; freshwater and marine.

Subrectangular dorsal scutes; ventral scutes extending from isthmus to anus; pelvic fin, as far as known, in advance of dorsal fin; two supramaxillary bones; parhypural fused to first preural centrum; lateral line complete. Some species had a very deep body.

The classification follows Forey (2004); Zaragüeta Bagils (2004) noted some biogeographical questions and gave stratigraphic and geographic occurrence for the genera and species.

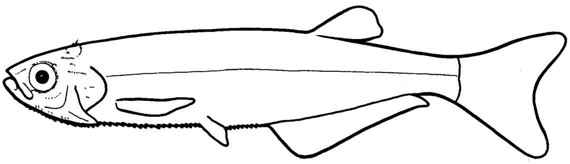
Seven fossil genera, recognized in two lineages (Chang and Grande, 1997; Chang and Maisey, 2003; Forey, 2004): i) *Armigatus, Diplomystus, Sorbinichthys,* and *Triplomystus,* and ii) *Paraclupea, Ellimma,* and *Ellimmichthys.*

Order CLUPEIFORMES (27)—herrings. Recessus lateralis present (part of the otophysic connection in which various sensory canals merge within a chamber in the otic region of the neurocranium, not known in any other group); parasphenoid teeth absent; no large foramen on the anterior ceratohyal; parietals separated by the supraoccipital; no leptocephalus larvae. Most are plankton feeders, with long and sometimes very numerous gill rakers that serve as straining devices. This group is very important in the world's commercial fisheries.

Five families, 84 genera, and about 364 species.

Suborder Denticipitoidei

Family DENTICIPITIDAE (93)—denticle herrings. Freshwater; coastal rivers of Nigeria and Cameroon, Africa.



Denticles (odontodes) on all roofing bones of skull; no supramaxillae; four or five branchiostegal rays, first (median) pair with denticles on anterior edge; ventral half of head with "furred" appearance from small denticles; lateral line complete; ventral scutes present; 16 principal caudal fin rays; caudal skeleton with one uroneural (other clupeomorphs have three) and parhypural fused to first preural centrum; *recessus lateralis* relatively primitive, incomplete in not having a separate opening for the supraorbital laterosensory canal. Scales in lateral line 37–40 and vertebrae 40–41 in the living species. Maximum length 6 cm.

The one fossil species, *Palaeodenticeps tanganikae,* probably of Miocene Age, is known from Tanzania, Africa.

One species, *Denticeps clupeoides* (note that the family name is not spelled Denticepitidae).

Suborder Clupeoidei. Lateral line not extending onto body (a canal does extend beyond the gill cover and branches over one or two scales, but there are no pored lateral-line scales); 19 principal caudal fin rays; first uroneural fused to first preural centrum (located in front of the reduced first ural centrum, which is fused to the second hypural in all clupeomorphs); parhypural usually separate from the first preural centrum. Yolk segmented (also in Bothidae). There is much diversity in the swim bladder of clupeoids, with the extreme specializations found in the pristigasterids.

The classification of this suborder is based primarily on Grande (1985), Whitehead (1985), and Whitehead et al. (1988). Grande (1985) and Grande and Nelson (1985) gave an elevated rank to many of the groups. They recognized three superfamilies in this suborder: Engrauloidea with two families (vs. one family and two subfamilies), Pristigasteroidea with two families (vs. one family and two subfamilies), and Clupeoidea (with the sister families Chirocentidae and Clupeidae as given here). Thus, the same phylogenetic arrangement is adopted here while maintaining the family names as generally recognized. Di Dario (2002) presented evidence from new characters that Pristigasteridae may be the basal group of Clupeoidei and sister to a clade comprising Clupeidae + Engraulidae; the implications of this possible phylogeny in finding new characters to test the possible sister-group relationship between Clupeomorpha and Ostariophysi were given.

Family PRISTIGASTERIDAE (94)—longfin herrings. Primarily marine, some freshwater in South America and southeast Asia; Atlantic, Indian, and Pacific in tropical and some subtropical seas.

Mouth usually superior, otherwise terminal; jaw teeth small, canines only in *Chirocentrodon*; abdominal scutes present; anal fin long, 30–92 rays; six branchiostegal rays; scales in lateral series about 35–55; vertebrae usually 40–55, up to 62 in *Raconda.* Pelvic fins are absent in several species as noted below. Grande (1985) recognized this taxon on the basis of having the predorsal bones orientated either vertically or inclined anterodorsally (vs. being inclined posterodorsally as in nearly all other teleosts) and no notch in third hypural of the caudal skeleton (vs. having a distinct notch that creates a gap with the second hypural as in most clupeomorphs). He recognized this group as a superfamily, giving family status to the following subfamilies and noted that *Ilisha,* as recognized here, is not monophyletic. Maximum length about 55 cm SL, attained in *Pellona flavipinnis* of South America; most under 25 cm.

Nine genera with 34 species (e.g., Whitehead, 1985; Randall, 1994; Munroe, 1999, 2003a; de Pinna and Di Dario, 2003). Four species are freshwater; the rest are marine, occasionally entering brackish water.

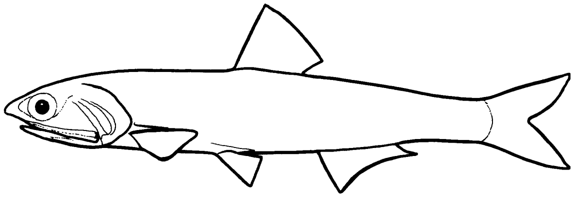
SUBFAMILY PELLONINAE. Grande (1985) recognized this group on the basis of having the maxillary-premaxillary gap covered by bone, either a toothed hypomaxilla bone or an extension of the maxilla (vs. having a gap as in other clupeomorphs; the hypomaxilla is a bone that is part of the gape of the upper jaw and situated behind the premaxilla, it is also found in *Harengula*). The pelvic fin is absent in the two small species of *Neoopisthopterus* and in the single species of *Pliosteostoma.* The one small species of *Chirocentrodon* has strong conical teeth and caninelike teeth in front (there are also teeth in the gap separating the premaxillae).

Five genera, *Chirocentrodon, Ilisha, Neoopisthopterus, Pellona,* and *Pliosteostoma,* with 23 species.

SUBFAMILY PRISTIGASTERINAE. Grande (1985) recognized this group on the basis of having a bony process on the first pleural rib that articulates with the shoulder girdle (not known from any other teleost except *Ilisha africana,* which Grande would place in this taxon). The pelvic fin is absent in the six species of *Opisthopterus,* the three of *Odontognathus,* the single species of *Raconda* (which also lacks the dorsal fin), and usually in the single species of the exceptionally deep-bodied Amazonian *Pristigaster.*

Four genera, *Odontognathus, Opisthopterus, Pristigaster,* and *Raconda,* with 11 species.

Family ENGRAULIDAE (Engraulididae and Stolephoridae) (95)—anchovies. Marine, occasionally freshwater; Atlantic, Indian, and Pacific.



Suspensorium inclined forward with head of hyomandibular well in front of quadrate, hind tip of upper jaw (maxilla) extending well behind eye in most species and jaw articulation well behind eye; mesethmoid projecting in front of vomer and supporting a paired sensory rostral organ; snout blunt, prominent, projecting beyond tip of lower jaw in most species (only just beyond in some Old World anchovies); gill rakers 10–50 or more on lower limb of first arch, 90 or more (100 or more on both limbs) in *Anchovia;* teeth on jaws absent to well developed; 7–19 branchiostegal rays; scales in lateral series usually 30–60; vertebrae usually 38–49, more in *Coilia;* body often translucent and with a silver stripe down the side in some. Luminescent organs occur in *Coilia dussumieri* (found from coastal India to Java).

Most species feed on plankton (a few by filter-feeding), but a few large species are piscivorous. Most of the freshwater species occur in South America. The maximum size is 37 cm, attained by *Thryssa scratchleyi* of rivers in Papua New Guinea and those entering the Gulf of Carpentria; most species under 20 cm.

The generic composition of the two subfamilies follows Grande (1985) and Grande and Nelson (1985); however, they gave family status to these two subfamilies. Whitehead et al. (1988) gave keys to the genera and descriptions of the species. In contrast to the clupeids, surprisingly few fossil anchovies are known, the oldest of the four known species being only of Miocene age (Grande and Nelson, 1985).

Sixteen genera with 139 species. About 17 species are freshwater, occasionally entering brackish water; the others are marine, rarely entering freshwater.

SUBFAMILY COILIINAE. Scutes present in front of pelvic fin and behind pelvic fin (prepelvic scutes absent in some *Coilia*); anal fin long, 27–81 rays (*Coilia*, with the anal fin joined to the caudal fin, has 80 to about 115 rays). In addition, Grande (1985) recognized this group as being monophyletic on the basis of having lost the peg on the proximal end of the uppermost ray of the lower caudal lobe (a dorsal peg is present on the upper-middle caudal ray; in most other clupeoids there is a two-peg arrangement on the two middle rays); and loss or poor development of a notch on the distal end of the third hypural (similar to pristigasterids). *Coilia* (the rattailed anchovies) has an exceptionally long tapering body. Most species other than the 13 of *Coilia* have a terminal or superior mouth, quite different in appearance from that of other anchovies; in the extreme form the mouth may be highly oblique with the lower jaw projecting beyond the upper (e.g., *Papuengraulis micropinna* with its minute dorsal fin, and *Setipinna breviceps*).

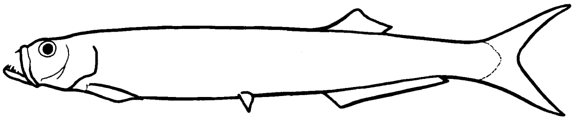
Five Indo-West Pacific genera found in eastern Africa, Asia, and Australia, *Coilia*, *Lycothrissa*, *Papuengraulis*, *Setipinna*, and *Thryssa* (includes the subgenus *Thrissina*), with about 47 species (Grande, 1985; Whitehead et al. 1988).

SUBFAMILY ENGRAULINAE. Scutes present in front of pelvic fin only in *Encrasicholina* and *Stolephorus*, absent behind pelvic fin; anal fin usually short, usually 13–37 rays.

Most members of this subfamily are confined to North, Central, and South America. Some species of *Engraulis* and species of two other genera occur elsewhere. The diminutive and scaleless *Amazonsprattus scintilla* of Brazil, the smallest-known clupeomorph and reaching only 19.5 mm standard length, probably belongs in this subfamily.

Eleven genera, *Amazonsprattus*, *Anchoa*, *Anchovia*, *Anchoviella*, *Cetengraulis*, *Encrasicholina*, *Engraulis*, *Jurengraulis*, *Lycengraulis*, *Pterengraulis*, and *Stolephorus*, with about 92 species (Grande, 1985; Whitehead et al. 1988; Kullander and Ferraris, 2003; Nizinski and Munroe, 2003).

Family CHIROCENTRIDAE (96)—wolf herrings. Marine; Indian (west to South Africa and the Red Sea) and western Pacific (Japan to Queensland, Australia).



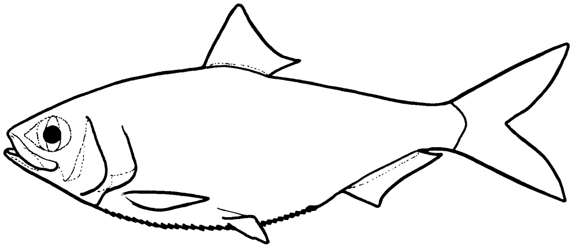
Body elongate and highly compressed; fanglike teeth in the jaws (highly predacious fish); spiral valve in intestine; 17–22 gill rakers; no pyloric caeca; scales small; dorsal fin with 16–19 rays; anal fin with 30–35 rays; pelvic fins small, with six or seven rays; pectoral fin with 13–15 rays; eight branchiostegal rays; pelvic scute highly reduced in adults; other abdominal scutes absent; vertebrae 69–75 (42–45 abdominal and 27–31 caudal).

Wolf herrings are voracious carnivores, unlike other clupeoids. Maximum length 100 cm.

The Chinese fossil *Mesoclupea* is sometimes placed in this family, but Grande (1985) questions that it is a clupeomorph. The only fossil fish recognized in the family is the Upper Cretaceous *Gastroclupea* from Bolivia.

Two species, *Chirocentrus dorab* and the very similar *C. nudus* (Whitehead, 1985; Munroe et al., 1999).

Family CLUPEIDAE (97)—herrings (shads, sprats, sardines, pilchards, and menhadens). Primarily marine, some freshwater and anadromous; worldwide (mostly tropical).



Two long, rodlike postcleithra in most; mouth usually terminal or nearly so or somewhat superior, usually inferior only in Dorosomatinae; teeth small or absent; abdominal scutes usually present—the Dussumieriinae (round herrings) usually lack abdominal scutes, except for a single pelvic scute; anal fin usually with 12–29 rays, up to 38 in Dorosomatinae; scales in lateral series about 40–50; usually 5–10 branchiostegal rays; vertebrae usually 37–59. There is much variation in body shape (from rounded to compressed). Maximum length 60 cm, attained in *Tenualosa ilisha* of India and Myanmar (marine and anadromous); most species less than 25 cm.

A valuable commercial fishery exists for clupeids in many parts of the world. Most species form schools and swim near the surface, usually in coastal waters, feeding on plankton.

Six subfamilies. The pristigasterids and *Congothrissa* were formerly given subfamily status within the clupeids. As Grande (1985) notes, the monophyly and interrelationships of at least the subfamilies Clupeinae, Alosinae, and Dorosomatinae are uncertain. About 57 genera and 188 species. About 57 species are freshwater, occasionally entering brackish water; many others occur in the Caspian Sea, are anadromous, or otherwise extend into freshwater but are primarily marine.

SUBFAMILY DUSSUMIERIINAE (ROUND HERRINGS). Pelvic scute W-shaped and no other scutes along abdomen (in other clupeids the pelvic scute, located just before the pelvic fin, has lateral ascending arms, and other scutes are usually present in front of and behind the pelvic scute).

Whitehead (1985:27) recognized *Dussumieria* and *Etrumeus* with 11–18 branchiostegal rays in the tribe Dussumieriini, and *Jenkinsia* and *Spratelloides* with 6 or 7 branchiostegal rays in the tribe Spratelloidini.

Four genera, *Dussumieria, Etrumeus, Jenkinsia,* and *Spratelloides,* with 12 species.

SUBFAMILY SUNDASALANGINAE (SUNDALAND NOODLEFISHES). Body transparent, elongate, and scaleless; adipose fin absent; olfactory organs each with a single nasal opening; pelvic fin with five rays; dorsal and anal fins posteriorly placed, dorsal with 11–15 rays and anal with 15–21 rays; pectoral fin rayless; vertebrae 37–43. Maximum length about 28 mm standard length (SL). Freshwater; Borneo, Laos, and Thailand.

These miniature, paedomorphic fishes, first described by T. R. Roberts in 1981, were formally placed in the Osmeriformes, in their own family Sundasalangidae. They were shown to be clupeiforms by Siebert (1997), who found a prootic bulla and a *recessus lateralis*; he suggested on the basis of caudal skeleton consolidation a relationship to *Jenkinsia.* On this basis, they are provisionally placed in the Clupeidae as a separate subfamily, but recognition as a separate family of clupeiforms, Sundasalangidae, as preferred by Britz and Kottelat (1999a), is certainly appropriate.

One genus, *Sundasalanx,* with about seven species (Siebert, 1997; Britz and Kottelat, 1999a).

SUBFAMILY PELLONULINAE (FRESHWATER HERRINGS). Usually only one supramaxilla (anterior one lost); pre- and post-pelvic scutes reduced to absent; scutes present before dorsal fin in some. Most species occur in freshwater, but some are in marine waters; found only in Africa, off India, in Southeast Asia, and in Australia, with most species in lakes and rivers of West Africa.

The double-armored fossil *Knightia,* known from presumed freshwater deposits of the Middle Paleocene to Middle Eocene from western North America and China, is provisionally retained in this subfamily. The monotypic *Congothrissa* of the Zaire system was originally placed in its own family, Congothrissidae.

Twenty-three genera (e.g., *Clupeichthys, Clupeoides, Congothrissa, Cynothrissa, Ehirava, Hyperlophus, Limnothrissa, Microthrissa, Pellonula, Potamalosa, Potamothrissa, Spratellomorpha,* and *Stolothrissa*) with about 44 species.

SUBFAMILY CLUPEINAE. Two supramaxillae present. Fossils include *Gosiutichthys* of Wyoming.

Sixteen genera (e.g., *Amblygaster, Clupea, Clupeonella, Escualosa, Harengula, Herklotsichthys, Lile, Opisthonema, Sardina, Sardinella, Sardinops,* and *Sprattus*) with 72 species.

SUBFAMILY ALOSINAE (SHADS). Upper jaw with a distinct median notch or cleft; mouth terminal; jaw teeth small or absent; strong scutes along abdomen and, in *Ethmidium,* before dorsal fin. Species may be marine, freshwater, or anadromous.

Seven genera, *Alosa*, *Brevoortia*, *Ethmalosa*, *Ethmidium*, *Gudusia*, *Hilsa*, and *Tenualosa*, with 31 species. Almost half of the species belong to *Alosa*.

SUBFAMILY DOROSOMATINAE (GIZZARD SHADS). Upper jaw with a distinct median notch or cleft; mouth usually inferior, lower jaw flared outward; no teeth; strong scutes along abdomen and, in *Clupanodon*, before dorsal fin; last dorsal fin ray filamentous in most; gill rakers long and numerous; stomach muscular, gizzard-like, and intestine after second and last flexure with a loop; pharyngeal pouches near the fourth epibranchials that may concentrate food from the exceptionally large number of gill rakers. Species may be marine, anadromous, or freshwater. *Dorosoma* is found only in North and Central America, while the others are Indo-West Pacific (marine and freshwater).

Six genera, *Anodontostoma*, *Clupanodon*, *Dorosoma*, *Gonialosa*, *Konosirus*, and *Nematalosa*, with 22 species.

Superorder OSTARIOPHYSI

Basisphenoid absent; orbitosphenoid present, except in gonorynchiforms; mesocoracoid usually present; dermopalatine absent; postcleithrum absent in gonorynchiforms and siluriforms, one in most cypriniforms, and three in some characiforms and gymnotiforms; swim bladder present (except in *Gonorynchus*) and usually divided into a smaller anterior chamber, which is partially or completely covered by a silvery peritoneal tunic and a larger posterior chamber (reduced or absent in some groups); minute, unicellular, horny projections, termed “unculi,” commonly present on various body parts (e.g., mouth region or ventral surface of paired fins), known only from ostariophysans; multicellular horny tubercles (= breeding or nuptial tubercles or pearl organs) with keratinous cap well developed; upper jaw protractile in many species; pelvic fins, if present, abdominal. An extensive survey of the subterranean species (hypogean) is given by Proudlove (2005).

Fishes of this group possess a fright reaction elicited by an alarm substance. This was first documented by Karl von Frisch in 1938 and described in detail by Wolfgang Pfeiffer in 1963 and 1977. The alarm substance (Schreckstoff) is a pheromone that is chemically similar or identical in all ostariophysans and is produced from epidermal club cells. Injuries to the skin release the alarm substance, which is detected by the sense of smell and causes a fright reaction in nearby members of the same species (or sometimes in related species). Some members of this superorder lack the fright reaction but possess an alarm substance (e.g., Serrasalminae) or lack both the alarm substance and the fright reaction to alarm substances of other species (e.g., Loricariidae and Gymnotiformes).

The recognition of five major lineages and their sequencing follows Fink and Fink (1981), although they recognized the siluriforms and gymnotiforms as suborders of the order Siluriformes. They postulated, as is still accepted, gymnotiforms to be siluriform derivatives and characiforms to be the primitive sister group of both, with cypriniforms being more primitive than this assemblage.

This superorder is divided into two series, the Anotophysi and the Otophysi. As a word of warning, in older literature the term Ostariophysi is restricted to what is herein recognized as the Otophysi.

Five orders, 68 families, 1,075 genera, and about 7,931 species. The four largest families—Cyprinidae, Characidae, Loricariidae, and Balitoridae—account for 4,656 (or 59%) of the species. The ostariophysans contain about 28% of the known fish species in the world while accounting for about 68% of the freshwater species. They are present on all continents and major land masses except Antarctica, Greenland, and New Zealand (Australia has a few catfishes secondarily derived from marine groups). About 123 species are marine (the chanid, the gonorynchids, half of the plotosids, and most ariids).

Series ANOTOPHYSI

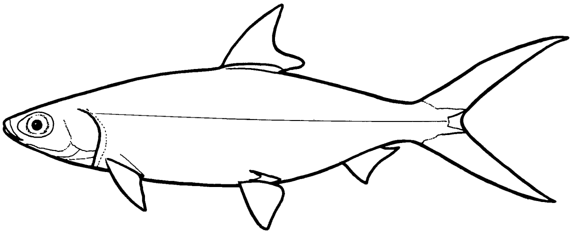
Order GONORYNCHIFORMES (28)—milkfishes. Orbitosphenoid absent; parietals small; quadrate condyle far forward; teeth absent on fifth ceratobranchial; first three vertebrae specialized and associated with one or more cephalic ribs (this represents a primitive Weberian apparatus, as shown in 1970 by D. E. Rosen and P. H. Greenwood); suprabranchial (= epibranchial) organ present (consisting of lateral pouches in the posterior part of the branchial chamber behind the fourth epibranchials); mouth small; jaws toothless; no postcleithra; 5–7 hypural plates.

Monophyly has been shown by T. Grande and Poyato-Ariza (1995, 1999). The classification of this order is based on the cladistic analysis of fossil and extant material by Grande and Poyato-Ariza (1999). The latter study was also used as the basis for the biogeographical study of Grande (1999a). Many Cretaceous gonorynchiform taxa have been described by Louis Taverne from Italy as follows: *Apulichthys* (considered to be the primitive sister group to all other gonorynchoids), *Lecceichthys* (in 1998 and considered to be the sister to *Notogoneus* and *Gonorynchus*), and *Sorbininardus* (in 1999 and placed in its own family, Sorbininardidae, and order, Sorbininardiformes, and considered primitive and sister to the Gonorynchiformes).

Four families, seven genera, and about 37 species (of which 31 are freshwater).

Suborder Chanoidei. Early Cretaceous fossils of gonorynchiforms represent some of the earliest well-known clupeocephalans, including *Aethalinopsis* (Belgium), regarded as sister to Chanidae (Grande and Poyato-Ariza, 1999).

Family CHANIDAE (98)—milkfishes. Marine and brackish (occasionally freshwater); tropical and subtropical Indian and Pacific (rare in eastern Pacific from southern California to Peru).



Mouth cleft small; jaws without teeth. The following two subfamilies are recognized following Poyato-Ariza (1996a) and Grande and Poyato-Ariza (1999).

†SUBFAMILY RUBIESICHTHYINAE. Two Early Cretaceous fossil genera, *Gordichthys* (Spain) and *Rubiesichthys* (Spain) (Poyato-Ariza, 1996b).

SUBFAMILY CHANINAE. Body compressed; mouth terminal; nonprotractile upper jaw; cycloid scales, 78–90 in lateral line; dorsal fin rays 13–17; anal fin rays 9–11; pelvic fin rays 10–12; branchiostegal rays four; swim bladder present.

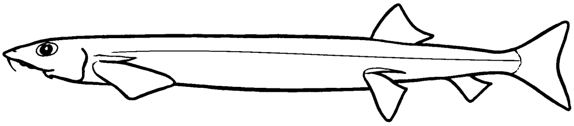
Milkfish spawn in the ocean, but metamorphosis from the ribbonlike larval stage occurs in brackish water. They are of considerable importance as a food fish in Southeast Asia. In the Philippines (where they are known as bangos, bangus, or sabalo), Indonesia, and Taiwan, especially, there is an extensive fishpond culture for them. Young are caught close to shore and reared in coastal ponds. Breeding, however, does not occur in the ponds. Females are highly fecund and can lay millions of eggs. Adults feed primarily on algae. Maximum length 1.8 m, usually 1.0 m.

Early Cretaceous fossil genera include *Dastilbe* (Brazil and Equatorial Guinea), *Parachanos* (Gabon), and *Tharrhias* (Brazil, and sister to *Chanos*).

One species, *Chanos chanos* (e.g., Poyato-Ariza, 1996a).

Suborder Gonorynchoidei

Family GONORYNCHIDAE (99)—beaked sandfishes. Marine; Indo-Pacific, rare in southern Atlantic (e.g., St. Helena).



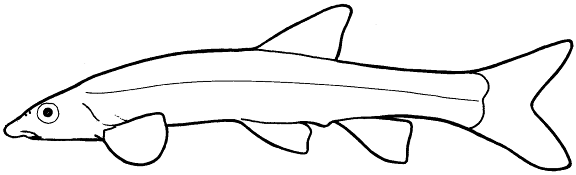
Body elongate; mouth inferior; protractile upper jaw; single barbel at tip of pointed snout; ctenoid scales on body and head, about 140–170 in lateral line; dorsal (11–13 rays) and anal (9 or 10 rays) fins posteriorly placed; branchiostegal rays four or five; no swim bladder. Maximum length 60 cm.

Fossil gonorynchid genera include *Notogoneus* (North America, Europe, Australia, some freshwater, Late Cretaceous to Oligocene, sister to *Gonorynchus*) and the Cretaceous *Charitosomus* (Germany, Lebanon), *Judeichthys* (Israel), *Ramallichthys* (Israel), and *Charitopsis* (Lebanon) (Poyato-Ariza,1996; Grande, 1996, 1999a; Grande and Grande, 1999; Grande and Poyato-Ariza, 1999.

One genus, *Gonorynchus*, with five species (Grande, 1999b). Unlike in Nelson (1994), the correct generic spelling is *Gonorynchus* (not *Gonorhynchus*) and the correct family spelling is Gonorynchidae (not Gonorhynchidae), according to Eschmeyer (1998 and Online version, January 2005).

Suborder Knerioidei. Branchiostegal rays usually three; swim bladder present and used in respiration in some species at least; supraoccipital with prominent cartilaginous margin.

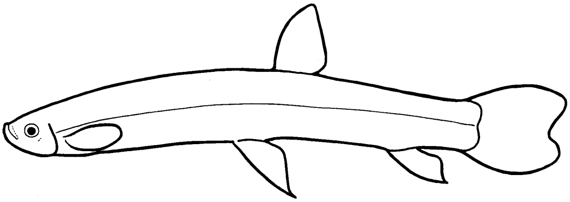
Family KNERIIDAE (100)—knerias. Freshwater; tropical Africa and Nile.



Mouth inferior or subterminal; protractile upper jaw; pelvic rays 6–9. *Kneria* and *Parakneria* have cycloid scales and a lateral line, whereas the small and transparent species of the monotypic *Cromeria* and *Grasseichthys* have a naked body and lack a lateral line. Maximum length about 15 cm (attained in *Parakneria marmorata* of Angola).

Four genera with 30 species, *Cromeria nilotica, Grasseichthys gabonensis, Kneria* (13 species), and *Parakneria* (15 species) (Poll, 1984a, b; Seegers, 1995). *Cromeria* and *Grasseichthys* were recognized in separate families (i.e., Cromeriidae, Grasseichthyidae) by Poll (1984a) and Poll and Gosse (1995). However, Grande (1994) considered all part of a monophyletic group and placed *Cromeria* and *Grasseichthys* in one clade and *Kneria* and *Parakneria* in the other. Grande and Poyato-Ariza (1999) supported these relationships, and in addition, showed that *Phractolaemus* is the sister group these four genera; however, unlike these authors, I do not place *Phractolaemus* in its own subfamily within the Kneriidae.

Family PHRACTOLAEMIDAE (101)—snake mudheads. Freshwater; tropical Africa (Niger Delta and Malebopool and Zaire systems).



Mouth superior; quadrate positioned near anterior tip of head; protractile upper jaw; pelvic rays six; cycloid scales; body elongate; dorsal and anal fin rays about six; esophagus with numerous folds; swim bladder divided into numerous small alveoli and adapted to airbreathing; single median abdominal vein resulting from fusion of the iliac veins. Maximum length about 16 cm.

One species, *Phractolaemus ansorgii* (D. F. E. Thys van den Audenaerde, in Daget et al, 1984; Poll and Gosse, 1995). It is also known as the African Mudminnow.

Series OTOPHYSI

Distinctive modification of anterior four or five vertebrae; movable bony ossicles connect the swim bladder to the inner ear for sound transmission. These ossicles are known as the Weberian ossicles, and their ligaments and the associated vertebrae are the Weberian apparatus. Wilhelm Harder, in his 1975 book *Anatomy of Fishes,* regards the fully functional Weberian apparatus as consisting of the stato-acoustic organ, swim bladder, Weberian ossicles (named in honor of E. Weber who described them in 1820), portions of the anterior part of the vertebral column, and some muscles and ligaments. The morphology, development, and evolution of the Weberian apparatus, with emphasis on catfishes, is provided by Chardon et al. (2003). In otophysans there is also fusion of the second hypural with the terminal centrum.

Early fossils (going back to the Early Cretaceous), probably or possibly otophysans, some were marine, include *Chanoides, Clupavus, Lusitanichthys, Salminops,* and *Satanichthys* (Patterson,1984a, b; Filleul and Maisey, 2004).

Fink and Fink (1981, 1996) gave strong morphological evidence for the phylogenetic relationships of the Otophysi (comprising herein four orders, the Cypriniformes, Characiformes, Siluriformes, and Gymnotiformes). Their results show, of the major clades, the fossil *Chanoides* to be sister to all remaining members of otophysans (placed in the Cypriniphysi), with the Cypriniformes being the primitive sister taxa to the remaining three groups (the Characiphysi), and Characiformes being sister to the clade (the Siluriphysi) of Siluriformes and its sister group the Gymnotiformes. Dimmick and Larson (1996) provided strong support for this phylogenetic hypothesis (as opposed to earlier views postulating different relationships). These authors used a combined analysis of molecular (from 160 phylogenetically informative sites from nuclear-encoded ribosomal RNA and 208 phylogenetically informative sites from the mitochondrial genes encoding ribosomal RNA and the valine transfer RNA) and 85 morphological characters and found generally high congruence between the molecular and morphological data in supporting our view of a sister-group relationship between the Gymnotiformes and Siluriformes, which together form a sister group to the Characiformes, with the separation of the Cypriniformes from all other otophysans representing the earliest phylogenetic split within the Otophysi. However, the molecular data analyzed separately produced a topology that differs from the analysis of the combined data, for example, in grouping the Characiformes and the Gymnotiformes as sister taxa (an earlier view). In their paper they examined the sources of the taxonomic incongruence between the molecular and morphological data, and concluded that the morphological characters are significantly less homoplastic than those from nuclear encoded rRNA, which are significantly less homoplastic than those from mitochondrial DNA (this is an area that requires much consideration, given the great many studies of other groups showing an inconsistency between molecular and morphological data).

Dimmick and Larson (1996) also discussed the biogeographic implications of the above postulated relationships (for an alternative biogeographic analysis, where Siluriformes are considered sister to a clade of Characiformes and Gymnotiformes, see Briggs, 2005).

Four orders, 64 families, 1,068 genera, and 7,894 species.

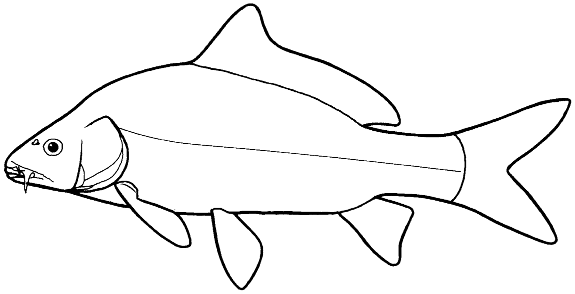
Order CYPRINIFORMES (29)—carps. Kinethmoid present (a median bone between ascending processes of premaxillae); palatine articulating in a socket of the endopterygoid; fifth ceratobranchial (the pharyngeal bone) enlarged, with teeth ankylosed to the bone (bound by collagenous fibers to the bone in other ostariophysans with teeth, pharyngeal teeth absent in gyrinocheilids); pharyngeal teeth opposed to enlarged posterior process of basioccipital bone (which encloses the dorsal aorta) rather than to upper pharyngeal elements, the basioccipital process against which the pharyngeal teeth press usually covered by a pad (tough horny pad in cyprinids, soft pad in catostomids); ascending process to premaxillae; upper jaw usually protractile; mouth (jaws and palate) always toothless; adipose fin absent (except in some cobitoids); head almost always scaleless; branchiostegal rays three; spinelike rays in dorsal fin of some species.

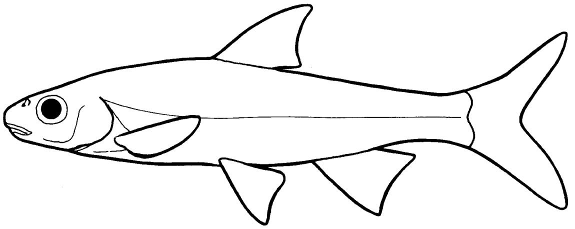
Ordinal status is given here following Fink and Fink (1981). I accept their conclusion that cypriniforms are cladistically more primitive than characiforms and therefore regard Cyprinoidea as more primitive than Cobitoidea. Siebert (1987) gave valuable insights into family interrelationships. More work is needed, for example, to test the tentative findings of Liu et al. (2002), which suggest differing relationships than those conventionally held. Many exciting studies are currently underway. Our understanding of cypriniform biodiversity and systematics should greatly increase over the next several years, in particular by studies being done by many specialists involved with the Assembling the Tree of Life (Cypriniformes) program funded by the U.S. National Science Foundation and coordinated by Dr Richard Mayden of Saint Louis University, Saint Louis, Missouri.

Six families, 321 genera, and about 3,268 species. The greatest diversity is in southeastern Asia. Cypriniforms are absent from Australia and South America. Members of this order are popular aquarium fishes, especially the minnows and loaches.

Superfamily Cyprinoidea

Family CYPRINIDAE (102)—minnows or carps. Freshwater, very rarely occurring in brackish water; North America (northern Canada to southern Mexico), Africa, and Eurasia.





Pharyngeal teeth in one to three rows, never more than eight teeth in any row; lips usually thin, not with plicae or papillae (however, mouth sometimes suckerlike as in *Garra* and *Labeo*); barbels present or absent; upper jaw usually bordered only by premaxilla (i.e., maxilla entirely or almost entirely excluded from gape); upper jaw usually protrusible; spinelike rays in dorsal fin in some. *Pectenocypris balaena* of Borneo, a phytoplankton feeder, has over 200 gill rakers. The largest species are the tetraploid barbine *Catlocarpio siamensis* of Thailand, which is known to reach at least 2.5 m and probably 3 m, and *Tor putitora* of the Brahmaputra River (eastern India), which reaches about 2.7 m; other large Asian species (2 m or larger) include *Elopichthys bambusa* and *Barbus esocinus.* The largest North American cyprinid is *Ptychocheilus lucius* of the Colorado River. Many species are under 5 cm, and the smallest cyprinid and the smallest freshwater fish is *Danionella translucida,* from lower Myanmar, in which females are ripe at 10–11 mm and the longest specimen known is 12 mm, with *D. mirifer* of upper Myanmar being only slightly larger, reaching up to 14 mm (Britz, 2003).

The family Cyprinidae is the largest family of freshwater fishes and, with the possible exception of Gobiidae, the largest family of vertebrates. It may be artificially large relative, especially, to characiform and siluriform families. The common name for the family most frequently used in North America is minnow, while in Eurasia it is carp; another common family name is dace (a term used for several unrelated subtaxa). Other common names associated with species of this family, and sometimes with those of other families, are chub and shiner; additional common names are given with some of the genera below, but in some cases these names are also used for members of other genera, and other names may also be used for species of the genus.

Various members of this family are important as food fish, as aquarium fish, and in biological research. Species particularly widely used include the

Common Carp (and koi) *Cyprinus carpio*, Goldfish *Carassius auratus*, and Zebra Danio or zebrafish *Danio* (*Brachydanio*) *rerio*. The latter species, a popular aquarium fish that is being used extensively in developmental (embryological) and genetic research.

The earliest definite cyprinid fossils are of Eocene age from Asia; the earliest European and North American ones are of Oligocene age. Cavender (1991) presents reasons for believing that cyprinids were absent from North America in the Eocene, a time when other otophysans were present (catostomids, hypsidorids, and ictalurids). Major extinctions occurred about 40 and 38 million years ago (Eocene) in the North American faunas when a marked global cooling occurred. Taiwan, which has few fossil fishes, has Pliocene fossil teeth of several species (Tao and Hu, 2001).

Much information on this family is found in Winfield and Nelson (1991). Gilbert (1998) gives a type catalogue of recent and fossil taxa.

The recognition and composition of the subfamilies is based on that followed by Arai and Kato (2003) (these taxa were given, for example, in a 1984 work by X. L. Chen and coauthors and in 1987 by Y. Wu). Previously I had used a less split classification based largely on the chapters in Winfield and Nelson (1991) by G. J. Howes and W. J. Rainboth. Cavender (1991) and Cavender and Coburn (1992) preferred to recognize two subfamilies: those with "head usually kept relatively rigid when feeding and having relatively slow swimming movements in feeding" (Cyprininae, as also given in Nelson, 1994), and those with a "head lifting mechanism when feeding and often feeding with rapid swimming movements" (Leuciscinae, six subfamilies of Nelson, 1994). The monophyly of the nominal subfamilies is uncertain, and the interrelationships of the subfamilies are in question. Species are being described and genera revised on a broad front. For example, Kottelat (2000a) described 15 species from Laos, the genus *Danio* was phylogenetically studied by Fang (2003), and *Labeo* was revised by Jayaram and Dhas (2000). There are studies in North America on phylogenetic relationships, and some resulting in former nominal subspecies being elevated to species rank.

About 220 genera and about 2,420 species.

SUBFAMILY ACHEILOGNATHINAE. Ovipositor in females (eggs usually laid in mantle cavity of clams). Eurasia (including Japan, absent from central Asia). Three genera, *Acheilognathus*, *Rhodeus* (bitterlings), and *Tanakia*.

SUBFAMILY CULTRINAE. Belly keel-like, body compressed. Eastern Asia. For example, *Chanodichthys*, *Culter*, *Erythroculter*, *Hemiculter*, and *Parabramis*.

SUBFAMILY CYPRININAE. For example, *Carassius* (Crucian Carp and Goldfish) and *Cyprinus* (e.g., Common Carp, koi).

SUBFAMILY BARBINAE. *Barbus* (barbels, barbs), *Diptychus*, *Pseudobarbus*, *Puntius*, *Schizothorax* (this and its relatives, known as snow trouts, occur at high elevations) and *Sinocyclocheilus* (with many cave species in China).

SUBFAMILY LABEONINAE. *Labeo* and *Osteochilus.* Fossil *Labeo* are noted in Africa by Stewart (2001).

SUBFAMILY SQUALIOBARBINAE. *Ctenopharyngodon* (*C. idella,* Grass Carp), *Mylopharyngodon,* and *Squaliobarbus.*

SUBFAMILY TINCINAE. *Tinca* (*T. tinca,* Tench)

SUBFAMILY XENOCYPRINAE. Pharyngeal teeth compressed, six teeth in main row. For example, *Aristichthys, Hypophthalmichthys* (Bighead Carp and Silver Carp, introduced into North America, India, and Southeast Asia), and *Xenocypris.* Miocene fossils include *Eoxenocypris* and *Xenocyproides* (Chang et al., 1996).

SUBFAMILY GOBIONINAE. Eurasia. All genera except *Gobio* (gudgeons) restricted to eastern Asia (including Japan). For example, *Coreius, Gnathopogon, Gobio, Gobiobotia, Microphysogobio, Pseudogobio, Pseudorasbora, Romanogobio, Sarcocheilichthys* (type of the nominal subfamily Sarcocheilichthyinae), *Saurogobio,* and *Squalidus.*

SUBFAMILY RASBORINAE (= DANIONINAE). Africa and southern Eurasia, including Indonesia. The composition and monophyly of this group are uncertain. For example, *Amblypharyngodon, Aspidoparia, Barilius, Chela, Danio* (synonym *Brachydanio*), *Danionella, Engraulicypris, Esomus, Leptocypris, Macrochirichthys, Mesobola, Neobola, Opsaridium, Opsariichthys, Opsarius, Oxygaster, Raiamas, Rasbora, Rastrineobola, Salmostoma, Tanichthys, Thryssocypris,* and *Zacco.*

SUBFAMILY LEUCISCINAE. North America and Eurasia (except, e.g., India and Southeast Asia). Several monophyletic lineages are recognized within this taxon, but the subfamily itself may not be monophyletic. In current taxonomy the genus *Phoxinus* is recognized as being in both the Nearctic and Palearctic (Holarctic). North American genera include *Acrocheilus, Agosia, Algansea, Aztecula, Campostoma, Clinostomus, Couesius, Cyprinella, Dionda, Eremichthys, Erimonax, Erimystax, Exoglossum, Gila, Hemitremia, Hesperoleucus, Hybognathus, Hybopsis, Iotichthys, Lavinia, Lepidomeda, Luxilus, Lythrurus, Macrhybopsis, Margariscus, Meda, Moapa, Mylocheilus, Mylopharodon, Nocomis, Notemigonus* (may have affinity with Alburninae), *Notropis, Opsopoeodus, Oregonichthys, Orthodon, Phenacobius, Pimephales, Plagopterus, Platygobio, Pogonichthys, Pteronotropis, Ptychocheilus, Relictus, Rhinichthys, Richardsonius, Semotilus, Snyderichthys,* and *Yuriria* (based on Nelson et al., 2004).

Old world genera probably in this clade include *Aaptosyax* (a large Mekong River fish), *Abramis* (bream), *Alburnoides, Alburnus* (bleak) (type genus of the subfamily Alburninae, recognized in Nelson, 1994), *Aspius, Blicca, Chalcalburnus, Chondrostoma* (nase), *Elopichthys, Eupallasella, Leuciscus* (e.g., ide, formerly in the genus *Idus*), *Luciobrama, Luciocyprinus, Oreoleuciscus, Pelecus, Pseudophoxinus, Rutilus* (roach), *Scardinius* (rudd), *Tribolodon,* and *Vimba.*

Other cyprinid genera not assigned here to subfamily include *Acrossocheilus, Balantiocheilos, Bangana, Boraras, Capoeta, Catlocarpio, Cirrhinus, Crossocheilus,* *Cyclocheilichthys, Cyprinion, Epalzeorhynchos* (in the aquarium trade these are called "sharks" including the flying fox; some species of *Labeo* and of other genera are also called "sharks"), *Garra, Gibelion, Gymnocypris, Hampala, Oreinus, Phreatichthys, Poropuntius, Rectoris, Rohtee, Semiplotus, Tor,* and *Varicorhinus.*

Family PSILORHYNCHIDAE (103)—mountain carps. Freshwater mountain streams; Nepal and adjacent India to western Myanmar (former Burma).

Mouth small, subterminal; jaws with sharp horny edges, lips fleshy; barbels absent; gill openings narrow; ventral surface of head flattened; dorsal fin with 10–12 rays (7—9 branched) and anal fin with five branched rays; pectoral fin with at least four unbranched rays; lateral line complete, with 31–50 scales; pharyngeal bone with one row of four teeth; swim bladder reduced. Maximum length about 8 cm. Given in Nelson (1994) as a subfamily of Cyprinidae.

Two genera, *Psilorhynchoides* and *Psilorhynchus,* with six species (Yazdani et al., 1993; Vishwanath and Manojkumar,1995).

Superfamily Cobitoidea. The arrangement of families follows Siebert (1987). The composition and interrelationships of the Cobitidae and Balitoridae (= Homalopteridae) are based primarily on Sawada (1982). Prior to his work, the Nemacheilinae was recognized as a subfamily of Cobitidae (vs. Balitoridae). The cobitids and balitorids are recognized as a monophyletic group by Sawada (1982), in part, because the opisthotic is absent and the orbitosphenoid is in contact with the supraethmoid-ethmoid complex.

Four families, 99 genera, and 842 species.

Family GYRINOCHEILIDAE (104)—algae eaters. Freshwater mountain streams; Southeast Asia.

Pharyngeal teeth absent; ventral mouth modified into a sucking organ for attaching onto objects; gill slit consisting of two small openings, inhalent aperture entering into gill chamber above the exhalent aperture; no barbels; number of gill rakers about 140; lateral line scales 39–43. Feeds exclusively on algae. Size up to 30 cm. These fishes are used extensively in home aquaria. Whether or not cladistic analysis will show this family to be valid or not is uncertain; however, of the five cypriniform families, this is the smallest and the only one to get smaller from numbers in Nelson (1994).

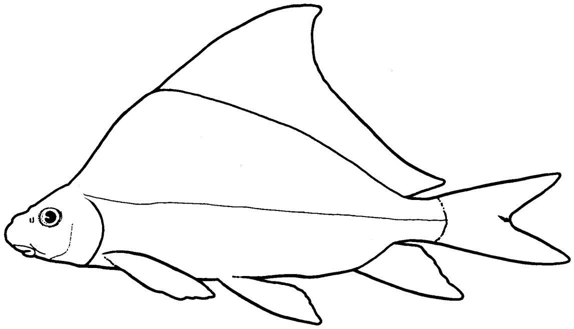
One genus, *Gyrinocheilus,* with three species (Roberts and Kottelat, 1993).

Family CATOSTOMIDAE (105)—suckers. Freshwater; China, northeastern Siberia, North America.

One row of 16 or more pharyngeal teeth; lips usually thick and fleshy with plicae or papillae; upper jaw usually bordered by premaxilla and maxilla; tetraploids. Maximum length about 1.0 m, less than 60 cm for most species.

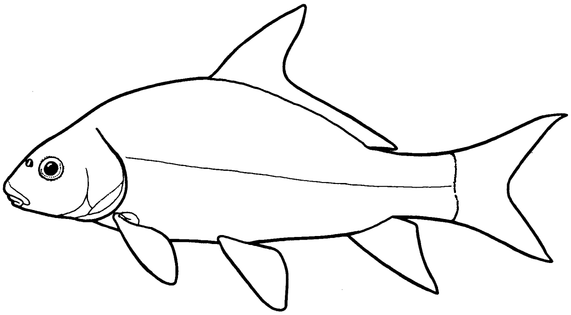
Thirteen genera with 72 species (about 45 species placed in the genera *Catostomus* and *Moxostoma*). In Nelson (1994), three subfamilies were recognized following Smith (1992); currently four subfamilies are provisionally recognized based on Harris and Mayden (2001) and Harris et al. (2002). Much in the phylogeny of the latter two studies, however, is in agreement with that in Smith (1992). Fossil genera include the Eocene-Oligocene ictiobines *Amyzon* and *Vasnetzovia* (Wilson, 1977; Bruner, 1991a; Smith, 1992). Smith (1992:800) reviews the Asian and North American fossil record. Bruner (1991b) gives a bibliography to the family, and Gilbert (1998) gives a type catalogue of recent and fossil taxa.

SUBFAMILY MYXOCYPRININAE. Twelve to 14 anal rays; 52–57 dorsal rays; 47–55 lateral line scales. Juveniles with a relatively deep body as shown in figure.



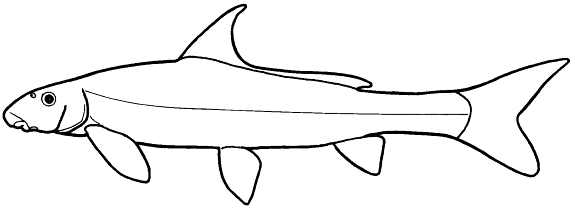
One species, *Myxocyprinus asiaticus*, primarily in Yangtse and Hwang Ho drainages, eastern China.

SUBFAMILY ICTIOBINAE. Seven to 11 anal rays; 22–32 dorsal rays; 33–43 lateral line scales; 115–190 pharyngeal teeth (the highest of all catostomids). Canada to Guatemala (absent from Pacific drainages). Northernmost species is *Carpiodes cyprinus* (North Saskatchewan and Red Deer rivers, Alberta); southernmost is *Ictiobus meridionalis* (Guatemala).



Two genera, *Carpiodes* (3, quillback and carpsuckers) and *Ictiobus* (5, buffaloes), with eight species.

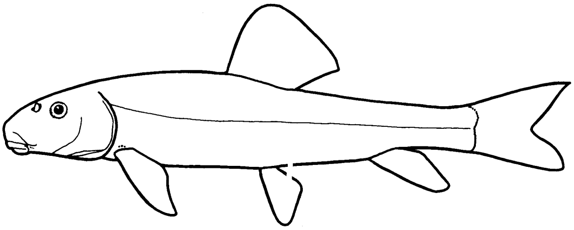
Subfamily Cycleptinae. Seven anal rays; 28–37 dorsal rays; 51–59 lateral line scales.



One genus, *Cycleptus* (blue suckers), with two species, Mississippi and adjacent gulf coastal drainages of southern United States and Mexico.

Subfamily Catostominae. Seven anal rays; 10–18 dorsal rays; 30–120 lateral line scales. Northeastern Siberia, Alaska, and northern Canada to Mexico. Northernmost species is *Catostomus catostomus* (rivers adjacent to Arctic coastline); southernmost is probably *Moxostoma congestum* (northeastern Mexico).

Nine genera and 61 species.



tribe catostomini. Lateral line present; more than 50 lateral line scales. Most suckers are benthic feeders and have a ventral mouth, but species of *Chasmistes* (lake suckers) are midwater planktivores and have a large, terminal mouth.

Most of the species live in western North America. Two are particularly widespread: *Catostomus catostomus* (Longnose Sucker) extends from New York to eastern Siberia and *C. commersonii* (White Sucker) extends from Georgia to British Columbia.

Four genera, *Catostomus* (24, with the subgenera *Catostomus* and *Pantosteus*), *Chasmistes* (4), *Deltistes* (1), and *Xyrauchen* (1), with 30 species. The genus *Catostomus* may be paraphyletic (Harris et al., 2002). Whereas Nelson et al. (2004) listed four species of *Chasmistes,* it is possible that there are five, if *Chasmistes fecundus* (Webug Sucker), Utah Lake, Utah, should be found to be valid as suggested by Cook (2001). This nominal species has had a confused nomenclatural history with specimens regarded as being of hybrid origin (Gilbert, 1998; Cook, 2001).

TRIBE ERIMYZONINAE *incertae sedis.* Lateral line is incomplete or absent. Two genera, *Erimyzon* (3, chubsuckers) and *Minytrema* (1), with four species, eastern Canada and United States.

TRIBE THOBURNIINAE. Swimbladder with one or two chambers. Two genera, *Hypentelium* (3, hog suckers) and *Thoburnia* (3, paraphyletic if all species included), with six species, eastern Canada and United States.

TRIBE MOXOSTOMATINI. Lateral line present; fewer than 50 lateral line scales. Most of the species live in eastern and central Canada and United States and in Mexico. One, *Moxostoma macrolepidotum,* which is particularly widespread, extends from easternmost United States to Alberta. One genus, *Moxostoma* (synonyms *Lagochila,* based on Smith, 1992, and *Scartomyzon,* based on Harris et al., 2002) (redhorses and jumprocks), with 21 species. The extinct Harelip Sucker, *Moxostoma lacerum* (*Lagochila lacera*), has not been collected for over 100 years and is not included in the generic species counts.

Family COBITIDAE (106)—loaches. Freshwater; Eurasia and Morocco.

Body wormlike to fusiform; mouth subterminal; 3–6 pairs of barbels present; erectile spine below eye (anterior in *Acantopsis*); one row of pharyngeal teeth. Greatest diversity in southern Asia; bottom dwellers. Maximum length about 40 cm. Popular aquarium species belong to such genera as *Acantopsis* (horseface loach), *Pangio* (e.g., kuhli or coolie loaches), *Botia* (e.g., clown, skunk, and zebra loaches), and *Misgurnus* (e.g., weatherfishes, including a color form of the Japanese weather loach called the golden dojo).

The accepted spelling of the family name is Cobitidae, not Cobitididae as introduced into the literature in 1980 (Opinion 1500 of the International Commission on Zoological Nomenclature, 1988, stemming from a case published in the Bulletin of Zoological Nomenclature in December 1986 by Maurice Kottelat).

About 26 genera and about 177 species.

SUBFAMILY COBITINAE. One pair of rostral barbels (rarely absent); cephalic lateral line system conspicuous; caudal fin usually rounded or slightly emarginate (forked in *Acantopsis* and some *Lepidocephalichthys*) Eurasia and Morocco.

About 19 genera, e.g., *Acanthopsis, Acanthopsoides, Acantophthalmus, Acantopsis, Cobitis, Enobarbus, Kichulchoia, Kottelatlimia, Lepidocephalichthys, Lepidocephalus, Misgurnus, Neoeucirrhichthys, Niwaella, Pangio, Serpenticobitis,* and *Somileptus,* with about 130 species (e.g., Kottelat et al., 1993, 1998; Roberts, 1997).

SUBFAMILY BOTIINAE. Two pairs of rostral barbels; cephalic lateral line system inconspicuous; caudal fin deeply forked; body compressed. Asia, from India to China and Japan, including Sumatra, Java, and Borneo.

About seven genera, *Botia* (7), *Chromobotia* (1), *Leptobotia* (13), *Parabotia* (7), *Sinibotia* (5), *Syncrossus* (5), and *Yasuhikotakia* (9), with about 47 species (Kottelat, 1998, 2004).

Family BALITORIDAE (Homalopteridae) (107)—river loaches. Freshwater; Eurasia.

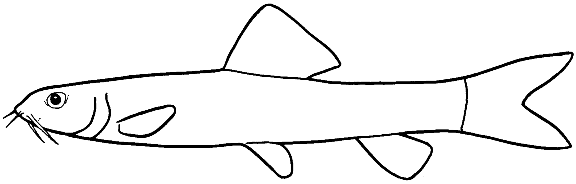
Three or more pairs of barbels present near mouth.

Recognition of Nemacheilinae and Balitorinae as comprising a monophyletic lineage follows Sawada (1982). According to this author, balitorids may be recognized as a separate lineage from cobitids by differences in the Weberian apparatus (e.g., by the Y-shaped tripus, the most posterior element of the Weberian ossicles).

About 59 genera and about 590 species. The number of estimated valid species is approximate; there is much need for a systematic revision to determine how many nominal species are valid. Species are being described at a rapid rate and many undescribed species probably yet exist.

SUBFAMILY NEMACHEILINAE. Prepalatine present; no spine under or before eye; two pairs of rostral barbels and one pair of maxillary barbels; body elongate, rounded, or compressed; mouth subterminal; single unbranched ray in pectoral and pelvic fins; adipose-like fin present in some; scales present or absent. Several cave species are known from Iran, India, China, Thailand, and Malaysia (e.g., Proudlove, 2005).

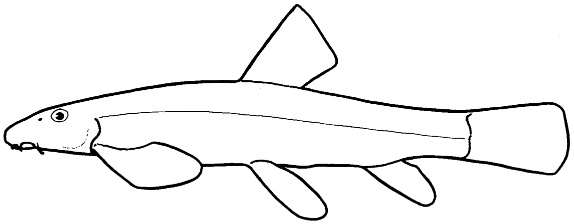
These loaches occur throughout much of Eurasia. Most species are in the India subcontinent, Indochina, and China.

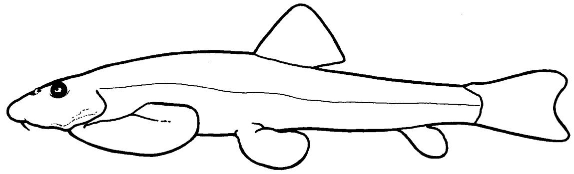


At least 30 genera, e.g., *Aborichthys, Acanthocobitis, Adiposia, Barbatula, Eonemachilus, Heminoemacheilus, Lefua, Nemacheilus, Neonoemacheilus, Oreonectes, Orthrias, Paracobitis, Schistura* (which contains the majority of species), *Traccatichthys, Triplophysa, Vaillantella* (the long-finned loaches with 50–60 dorsal fin rays and probably belonging in this subfamily), and *Yunnanilus,* with at least 420 species (e.g., Sawada, 1982; Kottelat, 1998, 2000a; Freyhof and Serov, 2001; Vishwanath and Laisram, 2001). *Ellopostoma,* of uncertain relationships, was placed in this subfamily by Tan and Lim (2002). Kottelat (1990a) gives a synonymy of the 31 named genera he recognized pending a phylogenetic study.

Subfamily Balitorinae (flat loaches). Exoccipitals separated from each other; interhyal absent; mesocoracoid fused with an enlarged cleithrum; three or more pairs of barbels present; gill opening restricted or not; paired fins enlarged with adhesive pads on ventral surface, orientated horizontally; pelvic fin separated or united under belly. These fishes, commonly known as the hillstream loaches, have the body and head flattened, mouth subterminal, and paired fins adapted as adhesive organs. They are found in fast-flowing mountain streams from India through Southeast Asia including Sumatra, Java, and Borneo, to China and Taiwan.

In Nelson (1994) I recognized two tribes (that in earlier literature had been recognized as distinct at the family or subfamily level), the balitorines (= homalopterines) (with two or more unbranched anterior rays in both pectoral and pelvic fins) and gastromyzontines (single unbranched anterior ray in pectoral and pelvic fins). I now put all members together at the subfamily level only pending better cladistic resolution of relationships of the species.





About 29 genera, e.g., *Annamia, Balitora* (upper figure), *Balitoropsis, Beaufortia, Bhavania, Crossostoma, Cryptotora, Erromyzon, Gastromyzon* (lower figure), *Glaniopsis, Hemimyzon, Homaloptera, Katibasia, Lepturichthys, Protomyzon, Sewellia, Sinogastromyzon,* and *Travancoria,* with at least 170 species (e.g., Tan and Martin-Smith, 1998; Freyhof, 2003; Freyhof and Serov, 2000; Kottelat, 1988, 1998, 2000a, 2001a,b, 2004b).

Order CHARACIFORMES (30)—characins. Teeth usually well developed (most are carnivores); adipose fin usually present; body almost always scaled (scales almost totally lacking in adults of the characid tetra *Gymnocharacinus bergii* of Argentina, which also lacks an adipose fin and is the most southerly known characiform); ctenoid or ctenoidlike scales in some; pelvic fin present (with 5–12 rays); anal fin short to moderately long (fewer than 45 rays); lateral line often decurved, sometimes incomplete; upper jaw usually not truly protractile; pharyngeal teeth usually present, but not usually specialized as in cypriniforms (anostomids have highly modified pharyngeal teeth); barbels absent; branchiostegal rays 3–5; usually three postcleithra; first hypural separated from the centrum by a gap in adults (most other primitive teleosts lack such a gap); usually 19 principal caudal fin rays. Some characiforms lack the adipose fin (it may be present or absent among congeneric species). Maximum length about 1.4 m, attained by *Hydrocynus goliath* of the Congo. At the opposite extreme, many members are under 3 cm, and the smallest reach a maximum size of about 13 mm. Some members of this order are extremely colorful (many are silvery). Many species are popular aquarium fishes (often known as tetras). In South America, many are also important food fishes (e.g., *Brycon*).

The classification of this large assemblage of poorly known species, with much morphological diversity and where convergent evolution is common, has undergone much change as a result of the works noted below. However, there is the need for much more work to establish phylogenetic relationships. Fossils include *Paleohoplias* and *Tiupampichthys* from South America (Gayet et al., 2003), *Eocitharinus* (possibly in Citharinoidei) and *Mahengecharax* (and possibly sister to the Alestiidae) from Africa (Murray, 2003a, b), and *Sorbinicharax* (of the fossil family Sorbinicharacidae) (Taverne, 2003). Of particular interest, the early Cretaceous (Albion) *Santanichthys* of Brazil, although having two supramaxillary bones (unlike all other ostariophysans which lack the supramaxillary), is considered, with reservation, to be the oldest characiform (and otophysan) and was probably either marine or brackish water (Filleul and Maisey, 2004). Phylogenetic concepts within this ordered are reviewed by Vari (1998).

Eighteen families with about 270 genera and at least 1674 species. All extant characins are confined to fresh water. At least 209 species occur in Africa, with the remainder in southwestern United States, Mexico, and Central and South America. The African members comprise three lineages—the citharinoids, the alestiids, and the one species of *Hepsetus*. As noted below, numbers of species for Central and South America taxa follow Reis et al. (2003); some species have been described after this work but are not given here.

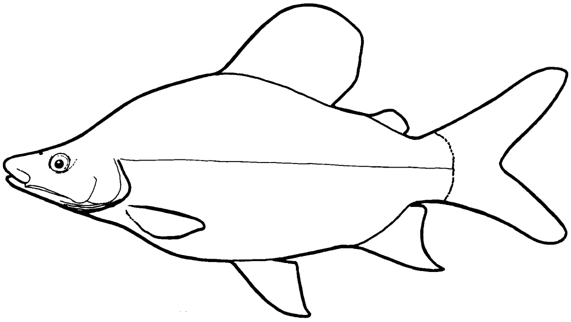
The classification down to family level follows Buckup (1998) and that work should be consulted for details of the synapomorphies of the various clades. The family descriptions below do not necessarily give diagnostic features. This is the sister group to the remaining two orders (see above under Otophysi).

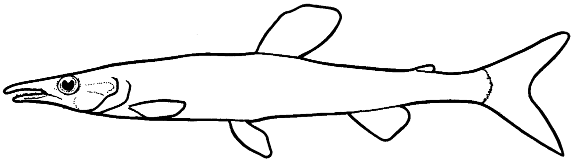
Suborder Citharinoidei. Teeth bicuspidate; second and third postcleithra fused; neural arch of fourth vertebra autogenous; premaxillary ascending process absent; scales ctenoid (cycloid in *Citharinus*); pelvic fin rays relatively numerous.

Fink and Fink (1981) and Buckup (1998) postulated this group to be the primitive sister group to all other characiforms, with *Xenocharax* being the most primitive member.

Twenty genera and about 98 species.

Family DISTICHODONTIDAE (108)—distichodontids. Freshwater, Africa.

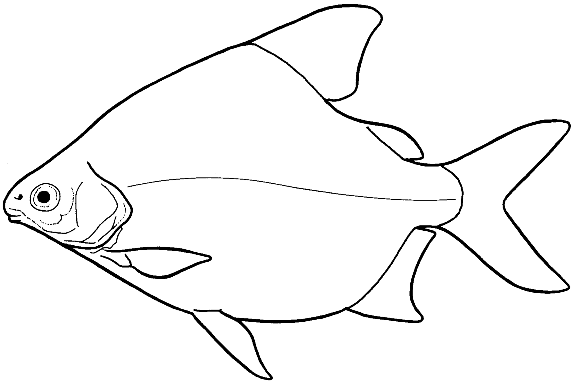




There are two evolutionary grades. One consists of those members with nonprotractile upper jaws, which are micropredators and herbivores; their body shape is variable, ranging from deep (as in upper figure) to shallow. The other consists of species with a movable upper jaw, which are carnivores, eating the fins of other fishes or the whole fish; their body is usually elongate (as in lower figure). This latter group was frequently recognized as a subfamily or family (Ichthyboridae). Maximum length 83 cm, attained in *Distichodus niloticus.*

Seventeen genera, *Belonophago, Congocharax, Distichodus, Dundocharax, Eugnathichthys, Hemigrammocharax, Hemistichodus, Ichthyborus, Mesoborus, Microstomatichthyoborus, Nannaethiops, Nannocharax, Neolebias, Paradistichodus, Paraphago, Phago,* and *Xenocharax,* with about 90 species (J. Daget and J. P. Gosse in Daget et al., 1984:184–211).

Family CITHARINIDAE (109)—citharinids. Freshwater; Africa.



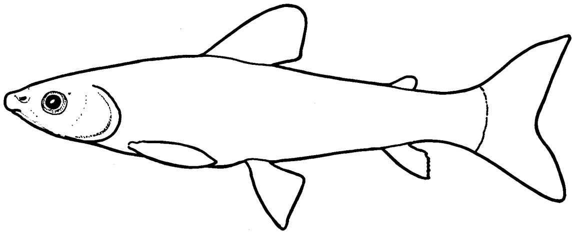
Maxilla reduced and lacking teeth; body deep; dorsal and anal fins relatively long, dorsal with 16–24 rays and anal with 19–31 rays. Maximum length about 84 cm.

Three genera, *Citharinus* with six species and the monotypic *Citharinops* and *Citharidium* (J. Daget in Daget et al. 1984:212–16).

Suborder Characoidei

Superfamily Parodontoidea

Family PARODONTIDAE (110)—parodontids. Freshwater, benthic; mountain streams of eastern Panama and most of South America.



Peculiar fishes with ventral mouths and teeth modified for scraping algae off rocks; premaxillaries highly mobile and greatly enlarged; adipose eyelid absent; lateral line scales 35–43; pectoral fins expanded and flattened; vertebrae 35–41. Maximum length usually 15 cm.

Formerly considered a subfamily of Hemiodontidae. Recognized here following Buckup (1998) as forming a polytomy with two other clades of the Charocoidei, the Anostomoidea and all other characiforms (his clade 9, recognized in six superfamilies and 11 families).

Three genera, *Apareiodon* (8), *Parodon* (10), and *Saccodon* (3), with about 21 species, and several undescribed species (Pavanelli, 2003).

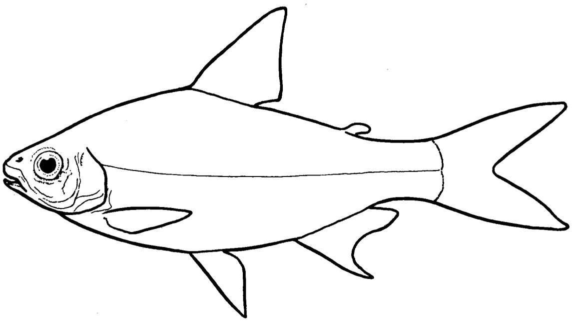
Superfamily Anostomoidea.

Unnamed clade of Family CURIMATIDAE + Family PROCHILODONTIDAE. Large sac-like muscular epibranchial organ that extends dorsal to the medial elements of the dorsal portions of the gill arches; reduction or loss of dentition on the fifth upper pharyngeal tooth plate and loss on the ceratobranchial. Typically detritivorous.

The two families included here were recognized by Vari (1983, 1989). Many of the synapomorphies he listed to indicate that they form a monophyletic clade are associated with food gathering and manipulation. The two families were recognized in Nelson (1994) as subfamilies of the Curimatidae.

About 11 genera and 116 species.

Family CURIMATIDAE (111)—toothless characiforms. Freshwater; southern Costa Rica to northern Argentina.

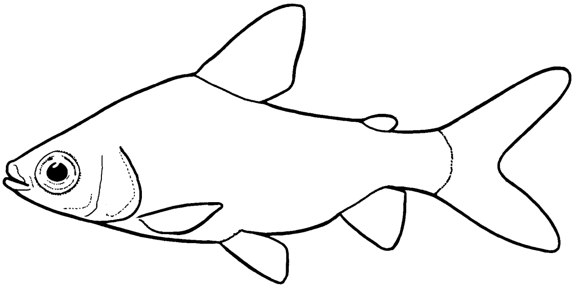


Jaw teeth absent (*Anodus* is the only other characiform lacking jaw teeth); enlarged lagenar capsule; gill rakers absent or poorly developed; four branchiostegal rays; branchiostegal membranes united to isthmus; vertebrae usually 30–36.

Body form ranges from fusiform to deep-bodied and compressed; most are mulletlike in shape. Curimatids are microphagous fishes. Maximum length about 32 cm, attained in *Curimata mivartii.*

Eight genera, *Curimata* (synonym *Acuticurimata*), *Curimatella, Curimatopsis, Cyphocharax, Potamorhina* (synonyms *Gasterotomus, Suprasinelepichthys*), *Psectrogaster, Pseudocurimata,* and *Steindachnerina* (synonyms *Cruxentina, Curimatorbis*), with about 95 species (e.g., Vari, 1991, 1992a, b, 2003a). The eight genera that are currently recognized are keyed in Vari (1992b).

Family PROCHILODONTIDAE (112)—flannel-mouth characiforms. Freshwater; South America, primarily the northern half, south to Ecuador and Brazil.



Mouth protractile, forming a sucking disc (lips enlarged); jaw teeth present, numerous and small; predorsal spine present. Superficially resemble the cyprinid *Labeo.* Maximum length 74 cm TL., attained in *Prochilodus lineatus.*

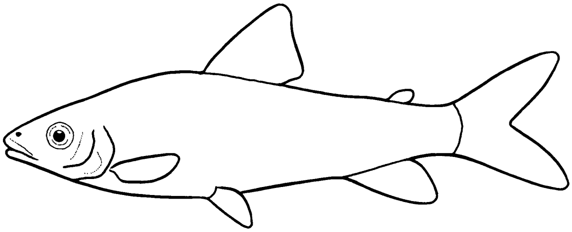
Three genera, *Ichthyoelephas* (2), *Prochilodus* (13), and *Semaprochilodus* (6), with about 21 species (Vari, 1983; Castro and Vari, 2003).

Unnamed clade of Family ANOSTOMIDAE + Family CHILODONTIDAE. Mandible relatively short; upper and lower pharyngeal dentition enlarged; two or more cusps on all pharyngeal teeth; single tooth row on each jaw.

Many of the species swim in an oblique head-down position, hence the common name headstanders for the group. Most species are herbivores or detritovores.

The two families recognized here are thought to form a monophyletic clade (Vari, 1983).

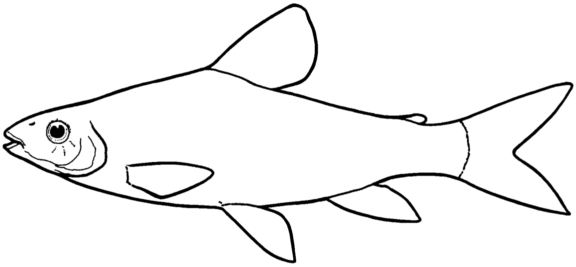
Family ANOSTOMIDAE (113)—toothed headstanders. Freshwater; southern Central America and South America.



Mouth small, nonproctractile (upturned in many species); series of only three or four teeth in upper and lower jaws; premaxilla (especially the ascending process) enlarged, much larger than the maxilla (which is excluded from the gape), and with enlarged teeth; body usually elongate; anal fin short, usually with fewer than 11 branched rays. Maximum length 80 cm SL.

Twelve genera, *Abramites* (2), *Anostomoides* (2), *Anostomus* (7), *Gnathodolus* (1), *Laemolyta* (10), *Leporellus* (3), *Leporinus* (87), *Pseudanos* (3), *Rhytiodus* (4), *Sartor* (3), *Schizodon* (14), and *Synaptolaemus* (1), with at least 137 species (Garavello and Britski, 2003).

Family CHILODONTIDAE (114)—headstanders. Freshwater; northern South America.



Premaxilla relatively small, maxilla much enlarged; uppermost of three postcleithra typical of the order missing; 7–10 branched dorsal fin rays; lateral line scales about 25–31; sixth lateral-line scale smaller than the other scales; highly modified pharyngeal apparatus; single series of relatively small teeth movably attached to jaws. Maximum length 18 cm.

Two genera, *Caenotropus* (3) and *Chilodus* (4), with seven species (Vari and Raredon, 2003).

Superfamily Crenuchoidea

Family CRENUCHIDAE (115)—South American darters. Freshwater; eastern Panama and South America.

Paired foramina in the frontal bones, posterodorsally to the orbits (pronounced in Crenuchinae but very small in the Characidiinae). Crenunchids are relatively small, usually under 10 cm SL.

Both subfamilies were recognized a subfamilies of a large Characidae in Nelson (1994); they are placed here as a monophyletic group in the family Crenuchidae following Buckup (1998, 2003).

Twelve genera and 74 species.

SUBFAMILY CRENUCHINAE. Enlarged lateral frontal foramina (Buckup, 1998, lists an additional synapomorphic features supporting monophyly for this taxon). *Poecilocharax* lacks an adipose fin. Maximum length only 5.7 cm TL. Northern South America.

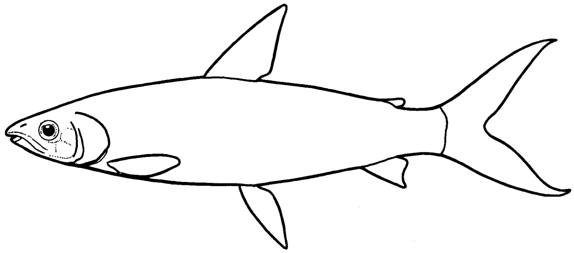
Two genera, *Crenuchus* (1) and *Poecilocharax* (2), with three species.

SUBFAMILY CHARACIDIINAE. Anal fin with fewer than 14 rays. Buckup (1993a), lists some 13 synapomorphic features supporting monophyly for this taxon and provides a diagnosis for the then known genera and species. Eastern Panama and South America south to northern Argentina and Uruguay). Some species of *Characidium* have the remarkable ability to climb waterfalls by using their paired fins to cling to the underside of rocks (Buckup et al., 2000). As noted by these authors, some species of *Awaous* and reportedly of Trichomycteridae, Astroblepidae, Rivulidae, and Balitoridae are able to surmount waterfalls (adult *Entosphenus* and juvenile *Galaxias* apparently can also surmount falls and/or dams).

Ten genera, *Ammocryptocharax* (4), *Characidium* (47), *Elachocharax* (4), *Geryichthys* (1), *Klausewitzia* (1), *Leptocharacidium* (1), *Melanocharacidium* (8), *Microcharacidium* (2 plus 1 incertae sedis), *Odontocharacidium* (1, recognized as *Klausewitzia aphanes* in Nelson, 1994), and *Skiotocharax* (1), with about 71 species (Buckup, 1993b, 2003).

Superfamily Hemiodontoidea

Family HEMIODONTIDAE (116)—hemiodontids. Freshwater, usually pelagic; northern South America, south to the Paraná-Paraguay Basin.



Body subcylindrical to fusiform (and fast swimming fishes); adipose eyelid well developed; teeth absent on lower jaw in adults; gill membranes free; adipose eyelid present; lateral line scales 50–125; pectoral fin rays 18–23; 9–11 branched pelvic rays; most species with round spot on side of mid-body and stripe along lower lobe of caudal fin; vertebrae 40–45. Langeani (1998) lists synapomorphies for the family and its lower taxa. Maximum length about 30 cm SL.

Five genera with about 28 species, with several undescribed species (Langeani, 2003).

SUBFAMILY ANODONTINAE. *Anodus* has jaw teeth absent; numerous elongate gill rakers, up to 200 on first arch (more than any other characoid) depending on fish size; pharyngeal structures specialized for filter feeding on plankton, while *Micromischodus sugillatus* is the only hemiodontid with teeth on lower jaw throughout life.

Two genera, *Anodus* (2, synonym *Eigenmannina*) and *Micromischodus* (1), with three species (Langeani, 2003).

SUBFAMILY HEMIODONTINAE

TRIBE HEMIODONTINI. One genus, *Hemiodus* (synonyms *Hemiodopsis* and *Pterohemiodus*), with about 18 species (Langeani, 2003).

TRIBE BIVIBRANCHIINI. The only characiform with a highly protrusible upper jaw with a unique mechanism of protrusion (especially pronounced in *Bivibranchia*); premaxilla minute and firmly attached to anterior end of maxilla. *Bivibranchia* also has a number of other derived modifications, including a unique elaboration of the glossopharyngeal and vagus nerves.

Two genera, *Argonectes* (2) and *Bivibranchia* (synonym *Atomaster*, 5), with about seven species (Langeani, 2003).

Superfamily Alestioidea

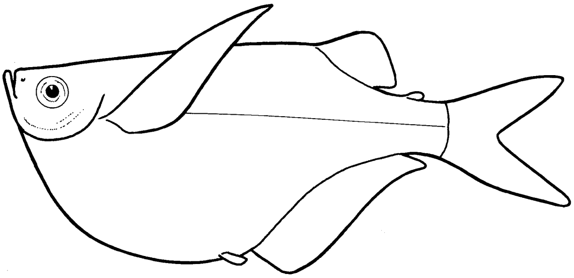
Family ALESTIIDAE (ALESTIDAE) (117)—African tetras. Freshwater; Africa.

Considered a subfamily of Characidae in Nelson (1994) and Weitzman and Malabarba (1998), but Buckup (1998) gave reasons for recognition as a separate family.

About 18 genera, e.g., *Alestes, Brycinus, Bryconaethiops, Clupeocharax, Hemigrammopetersius, Hydrocynus, Ladigesia, Micralestes, Nannopetersius, Petersius, Phenacogrammus, Rhabdalestes,* and *Tricuspidalestes,* with about 110 species (Géry, 1995; Murray and Stewart, 2002).

Superfamily Characoidea

Family GASTEROPELECIDAE (118)—freshwater hatchetfishes. Freshwater; Panama and South America (absent in Chile).



Strongly compressed head and body with protruding bony and muscular breast region; lateral line extremely short, extending to tail, or curved downward to approach origin of anal fin; dorsal fin rays 10–17; anal fin rays 22–44; pelvic fins and associated bones minute: four or five branchiostegal rays; adipose fin present (in larger species) or absent (in smaller species); frontal bone bearing a strong longitudinal ridge; posttemporal and supracleithrum fused into a single bone; cleithra of each side fused; no postcleithra. Maximum length about 6.8 cm SL.

These fishes are capable of jumping out of the water and making short flights.

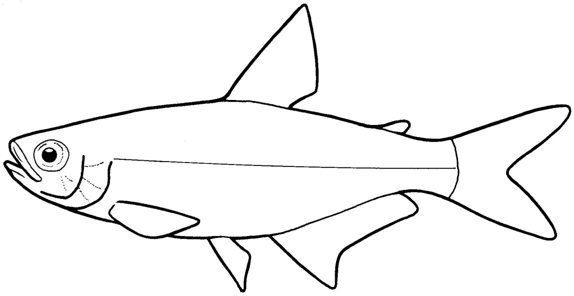
Three genera, *Carnegiella* (4), *Gasteropelecus* (3), and *Thoracocharax* (2), with nine species (Weitzman and Palmer, 2003).

Family CHARACIDAE (119)—characins. Freshwater; southwestern Texas, Mexico, and Central and South America.

This large and diversified family includes the potentially dangerous piranhas (*Serrasalmus*), many fishes that are widely used in home aquaria and as food, a blind cavefish in Mexico (*Astyanax jordani* and *Astyanax sp*) and Brazil (*Stygichthys typhlops*) (Proudlove, 2005), and a species that has dispersed into Texas, United States (*Astyanax mexicanus*).

The composition of this family has greatly changed with the removal of the formerly recognized subfamilies Crenuchinae and Characidiinae, now recognized in the family Crenuchidae, and the removal of African taxa (the formerly recognized Alestiinae, now a family). This now leaves the osteoglossids as the only completely freshwater fish family indigenous to both Africa and

South America (some nandids enter brackish water, and cyprinodontids and cichlids have a few members that enter marine water).



A large number of taxa are *incertae sedis*; as stated by Reis et al. (2003:212), it is preferred to emphasize that the relationships of many characids are poorly known to recognizing artificial subfamilies. Reis et al. (2003:104–105) listed nine species as *incertae sedis* in Characidae and Reis et al. (2003:106–169), in a multi-authored chapter headed by F. C. T. Lima, listed 88 genera containing 620 species as *incertae sedis* (some of these genera, not assigned to subfamilies, may not be monophyletic). As noted by the authors, 47 of the 88 genera are monophyletic and another 23 contain two or three species. Some of the 88 genera (with numbers of species) include *Astyanax* (86, see note below), *Bramocharax* (4), *Bryconamericus* (51), *Bryconops* (16), *Creagrutus* (64), *Engraulisoma* (1), *Exodon* (1), *Gymnocharacinus* (1), *Gymnocorymbus* (3, black tetras), *Hemibrycon* (19), *Hemigrammus* (43, figure above), *Hyphessobrycon* (97, synonyms include *Megalamphodus*), *Inpaichthys* (1), *Jupiaba* (21), *Knodus* (16), *Lignobrycon* (1), *Moenkhausia* (58), *Oligosarcus* (15), *Paracheirodon* (3, recognized at one time in *Hyphessobrycon*, cardinal, green neon, and neon tetras), *Paragoniates* (1), *Prionobrama* (2), *Pristella* (1), *Probolodus* (1), *Rachoviscus* (2), *Salminus* (2), *Stygichthys* (1), *Triportheus* (13), *Tyttobrycon* (4), and *Xenagoniates* (1). The genus *Astyanax*, the most species rich of the order, requires much work. There have been many changes in the species recognized in this genus over the last several years as recognized in Reis et al. (2003). For example, *A. jordani* of Mexico (originally described in *Anoptichthys*), often treated as a synonym of *A. mexicanus*, is recognized as valid; and *A. fasciatus*, described from Brazil, has recently not been recognized as occurring as far north as Mexico, but with treating *A. aeneus* as a synonym it is again recognized as being in Mexico (more work may yet change our understanding of species boundaries and thus distribution).

Information on the subfamilies listed below and considered to be monophyletic by Reis et al. (2003:170—230) is from the individual chapters written by specialists as follows: Agoniatinae (F. C. T. Lima and A. Zanata), Clupeacharacinae (F. C. T. Lima), Iguanodectinae (C. Moreira), Bryconinae (F. C. T. Lima), Serrasalminae (M. Jégu), Aphyocharacinae (R. S. Lima), Characinae (C. A. S. Lucena and N. A. Menezes), Stethaprioninae (R. E. Reis), Tetragonopterinae (R. E. Reis), Rhoadsiinae (A. R. Cardosa), Cheirodontinae (L. R. Malabarba), and Glandulocaudinae (S. H. Weitzman).

SUBFAMILY AGONIATINAE. South America (primarily in the Amazon basin). Resemble clupeiforms in body shape and color. One genus, *Agoniates*, with two species (F. C. T. Lima and A. Zanata, p 170, in Reis et al., 2003).

SUBFAMILY CLUPEACHARACINAE. South America. Elongate body with midventral keel and long anal fin. One species, *Clupeacharax anchoveoides* (F. C. T. Lima, p 171, in Reis et al., 2003).

SUBFAMILY IGUANODECTINAE. South America. Two genera, *Iguanodectes* (8) and *Piabucus* (3), with 11 species (C. Moreira, pp 172—173, in Reis et al., 2003).

SUBFAMILY BRYCONINAE. Southern Mexico (i.e., *Brycon guatemalensis*) to Argentina. Maximum length about 70 cm SL. Three genera, *Brycon* (41), *Chilobrycon* (1), and *Henochilus* (1), with about 43 species (F. C. T. Lima, pp 174—181, in Reis et al., 2003).

SUBFAMILY SERRASALMINAE. South America (introduced to other areas) (pacus, silver dollars, and piranhas). Maximum length about 80 cm SL. Fifteen genera, e.g., *Acnodon* (3), *Catoprion* (1), *Colossoma* (1), *Metynnis* (11), *Mylesinus* (3), *Myleus* (15), *Pristobrycon* (5), *Pygocentrus* (4), *Serrasalmus* (28), and *Tometes* (2), with about 80 species (M. Jégu, pp 182—196, in Reis et al., 2003). Lundberg et al. (1986) described fossils of a living species of *Colossoma* from the Miocene, suggesting a very conservative history for a specialized herbivorous fish.

SUBFAMILY APHYOCHARACINAE. South America. One genus, *Aphyocharax*, with 10 species (R. S. Lima, pp 197—199, in Reis et al., 2003).

SUBFAMILY CHARACINAE. Southern Mexico to South America (to la Plata basin). Maximum length 24 cm SL. Twelve genera, e.g., *Acestrocephalus* (4), *Charax* (16), *Cynopotamus* (11), *Phenacogaster* (10), *Priocharax* (2), and *Roeboides* (20), and 70 species (C. A. S. Lucena and N. A. Menezes, pp 200—208, in Reis et al., 2003).

SUBFAMILY STETHAPRIONINAE (SILVER DOLLAR TETRAS). South America (mainly Colombia to Argentina). Body deep; anteriorly directed spine preceding the first dorsal-fin ray. Maximum length 9 cm. Four genera, *Brachychalcinus* (5), *Orthospinus* (1), *Poptella* (4), and *Stethaprion* (2), with 12 species (R. E. Reis, pp 209—211, in Reis et al., 2003).

SUBFAMILY TETRAGONOPTERINAE. South America. Body deep; long anal fin base. Most genera previously placed in this subfamily, as in Nelson (1994), are now placed as *incertae sedis* in Characidae because there is no evidence that they formed a monophyletic group. One genus, *Tetragonopterus*, with two species (R. E. Reis, p 212, in Reis et al., 2003).

SUBFAMILY RHOADSIINAE. Nicaragua and Costa Rica to Ecuador and Peru. Longest dorsal-fin ray may reach caudal fin in adult males. Maximum length 13.6 cm SL. Three genera, *Carlana* (1), *Parastremma* (3), and *Rhoadsia* (2), with six species (A. R. Cardosa, pp 213—214, in Reis et al., 2003).

SUBFAMILY CHEIRODONTINAE. Costa Rica and South America (to northern Argentina and including Trinidad). Two tribes are recognized: Cheirodontini with secondary sexual specializations in males of the ventral procurrent caudal-fin rays, and Compsurini, which are inseminators, where sperm is apparently transferred to the ovaries of females. Maximum length 6 cm, attained in *Spintherobolus papilliferus.* Fifteen genera, e.g., *Cheirodon* (7), *Compsura* (2), *Odontostilbe* (10), *Serrapinnus* (7), and *Spintherobolus* (4), with about 46 species (L. R. Malabarba, pp 215—221, in Reis et al., 2003).

SUBFAMILY GLANDULOCAUDINAE. Costa Rica and South America (to northern Argentina and including Trinidad). Males with a putative pheromone pumping mechanism in the caudal region; internal fertilization in all known species are inseminators, as are those of the above-mentioned members of the tribe Compsurini, but with differing details. Nineteen genera, e.g., *Argopleura* (4), *Corynopoma* (1), *Diapoma* (2), *Gephyrocharax* (12), *Glandulocauda* (2), *Mimagoniates* (6), *Pseudocorynopoma* (2), *Tyttocharax* (3), and *Xenurobrycon* (4), with 50 species (and many undescribed species) (S. H. Weitzman, pp 222–230, in Reis et al., 2003).

In all, the family contains about 165 genera and over 962 species.

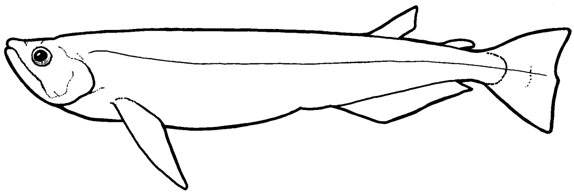
Superfamily Cynodontoidea. The genera in the two families recognized here following Buckup (1998) were placed in the Characidae, subfamily Characinae in Nelson (1994).

Family ACESTRORHYNCHIDAE (120)—acestrorhynchids. Freshwater; South America (greatest diversity in Orinoco and Amazon basins).

Body elongate, pikelike body, and covered with small scales. Maximum length 40 cm SL.

One genus, *Acestrorhynchus*, with 15 species (Menezes, 2003).

Family CYNODONTIDAE (121)—cynodontids. Freshwater; South America.

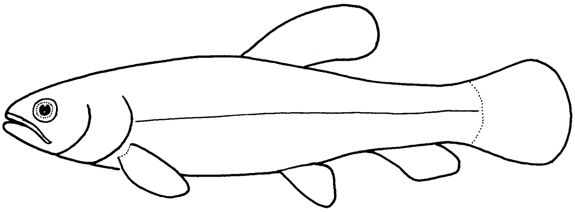


Mouth oblique; well-developed canines (saberlike in some); pectoral fins relatively large. Maximum length 65 cm. Two subfamilies are recognized, Cynodontinae for *Cynodon*, *Hydrolycus*, and *Rhaphiodon* with the largest species and those with the longest canines, and Roestinae for *Gilbertolus* and *Roestes*.

Five genera, *Cynodon* (3), *Gilbertolus* (3), *Hydrolycus* (4), *Rhaphiodon* (1, upper figure), and *Roestes* (3), with 14 species (Toledo-Piza, 2003).

Superfamily Erythrinoidea

Family ERYTHRINIDAE (122)—trahiras. Freshwater; South America.



Gape long, extending beyond anterior margin of orbit; body cylindrical; five branchiostegal rays; pectoral fin rays relatively few, 9–14; dorsal fin with 8–15 rays (plus three rudimentary ones), origin in front of anal fin and usually over pelvic fins (males of *Erythrinus* can have an elongated dorsal fin); anal fin short, 10–11 rays; adipose fin absent; caudal fin rounded; scales relatively large, 34–47 in lateral line; numerous teeth on palate.

Some are predators. Some can breathe air and move across land between ponds. They show some resemblance to *Amia* in body shape. Maximum length about 1.0 m, attained in *Hoplias lacerdae* and *H. macrophthalmus.*

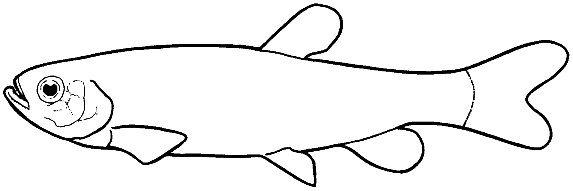
Three genera, *Erythrinus* (2), *Hoplerythrinus* (3), and *Hoplias* (9), with about 14 species (Oyakawa, 2003).

Family LEBIASINIDAE (123)—pencil fishes. Freshwater; Costa Rica, Panama, and South America.

Gape short, usually not reaching orbit; three or four branchiostegal rays; adipose fin present or absent; anal fin with 8–14 rays; dorsal fin in front of anal fin, usually over pelvic fins (often behind in the Pyrrhulinini, which also have an elongate upper caudal fin lobe); scales large, 17–33 in longitudinal series.

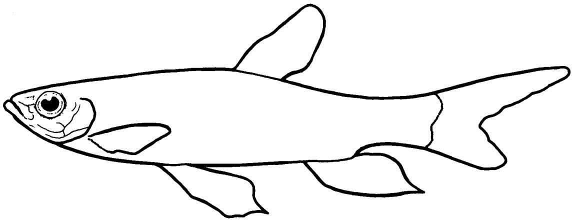
Two subfamilies with seven genera (*Derhamia* with one species is not assigned to subfamily) and 61 species (Weitzman and Weitzman, 2003).

SUBFAMILY LEBIASININAE. Four branchiostegal rays; maxilla relatively long.



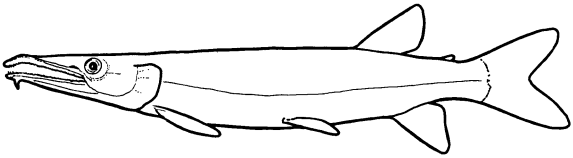
Two genera, *Lebiasina* (8) and *Piabucina* (9), with about 17 species.

SUBFAMILY PYRRHULININAE. Three branchiostegal rays; maxilla short.



Two tribes are recognized: Pyrrhulinini, with about 27 species, in *Copeina* (2), *Copella* (8), and *Pyrrhulina* (17); and Nannostomini, which contains the one genus of pencilfishes, proper, *Nannostomus* (16, synonym *Poecilobrycon*).

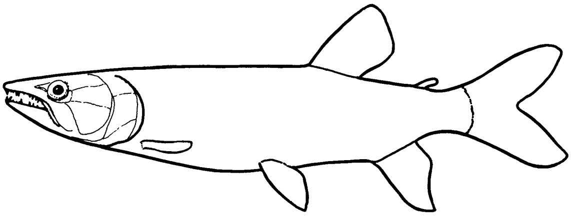
Family CTENOLUCIIDAE (124)—pike-characids. Freshwater; Panama and South America.



Elongate pikelike body, including having anal fin and usually the dorsal fin set far back on body; carnivorous; scales spinoid; pelvic fin with eight rays. Maximum length at least 67.5 cm SL.

Two genera, *Boulengerella* (5) and *Ctenolucius* (2), with seven species (Vari, 1995, 2003b).

Family HEPSETIDAE (125)—African pikes. Freshwater; tropical Africa.



Elongate pikelike body; long snout and large mouth with a few large canines and smaller pointed teeth; dorsal fin with seven rays placed before origin of anal fin which has nine rays (each also with two rudimentary rays); pelvic fin with nine rays; lateral line scales 49–58, cycloid; adipose fin present. Maximum length 65 cm SL. Eggs are laid in a nest of floating foam. This species is considered to be a gamefish.

One species, *Hepsetus odoe* (T. R. Roberts in Daget et al., 1984:138–39; Poll and Gosse, 1995; Skelton, 2001).

Order SILURIFORMES (Nematognathi) (31)—catfishes. Symplectic, subopercular, basihyal, and intermuscular bones absent; parietals probably present but fused to supraoccipital; mesopterygoid very reduced; preopercle and interopercle relatively small; posttemporal probably fused to supracleithrum but thought by some to be present as a separate element in many families; vomer usually toothed (as is the pterygoid and palatine); dorsal- and anal-fin pterygiophores lacking middle radial ossification (as is also true for gymnotiforms), distal radial also absent in silurids; adipose fin usually present; spine-like (= spinous) rays often present at the front of the dorsal and pectoral fins (referred to as spines in family descriptions) (the dorsal fin of most catfishes technically has two spines—the first being very short and forming a locking mechanism for the second spine, which is usually the only one referred to in the family descriptions); body naked or covered with bony plates; normally up to four pairs of barbels on head, one nasal, one maxillary, and two on chin (i.e., on the lower jaw or mandible), the nasal and chin barbels may be variously absent; maxilla toothless and rudimentary (except in Diplomystidae and the extinct Hypsidoridae), supporting a barbel; principal caudal fin rays 18 or fewer (most with 17); caudal skeleton varying between having six separate hypural plates to complete fusion of caudal elements; eyes usually small (barbels are important in detecting food); air-breathing organs in Clariidae and Heteropneustidae. Vertebrae are as few as 15 in some pangasiids to over 100 in some clariids, not including the Weberian vertebrae (G. Arratia in Arratia et al., 2003:127). In contrast to other teleosts, where the urohyal forms as an unpaired ossification of the tendon of the sternohyoideus muscle, in siluriforms there is what is called a "parurohyal" that results from paired ossifications of the tendons, which then fuse in early ontogeny (Arratia et al., 2003). The Weberian apparatus of catfishes is described in detail by Chardon et al. (2003). The many cave species are listed in Proudlove (2005).

Several species of the catfish order are known to be poisonous or venomous (Perrière and Goudey-Perrière, 2003, give a detailed review). They can inflict severe wounds with their spines (primarily those of the pectoral fin) and inject a poison produced by glandular cells in the epidermal tissue covering the spines. Most species are passive stingers (e.g., *Noturus*). Some, such as *Heteropneustes fossilis* of India, which has a painful and potentially dangerous sting, have an aggressive behavior with records of attacks on humans and other fishes. Stings from *Plotosus lineatus* may result in death.

In many areas catfishes are a popular sports fish and a valued food item. They are also widely used as a tropical aquarium fish. All members of this order are appropriately referred to as catfishes, despite attempts for marketing purposes to restrict use of the term to one family (Nelson et al., 2002). The largest catfish is *Silurus glanis* which commonly reaches 3 m in length; a pangasiid and pimelodid are also known to reach exceptionally large sizes. Many catfishes have a maximum length of under 12 cm.

Despite considerable progress in determining the phylogenetic relationships of catfishes and monophyly of taxa since the 1994 edition (see references below), there are still many questions on the classification of catfishes, and disagreement exists on the interrelationships of some families. Much exciting work is currently being done. Our understanding of catfish biodiversity should greatly increase over the next several years, in particular by studies being done by many specialists involved with the "All Catfish Species (Siluriformes) Inventory" funded by the U.S. National Science Foundation and coordinated by Dr. Lawrence M. Page, University of Florida Museum of Natural History. It should be noted that the extensive and pioneering efforts of Carl H. Eigenmann and his wife Rosa Smith on South American catfishes, while based on still earlier works of others, provided the basis for the later works of W. A. Gosline and G. S. Myers and for more recent studies.

Extensive information on all aspects of catfishes may be found in various chapters in Arratia et al. (2003); for example, apart from papers cited below, chapters 1 and 4 by Gloria Arratia give, respectively, an overview of the catfish head skeleton and of the postcranial skeleton, and chapter 5 by B. G. Kapoor, B. Khanna, R. Diogo, E. Parmentier, and M. Chardon reviews the internal anatomy.

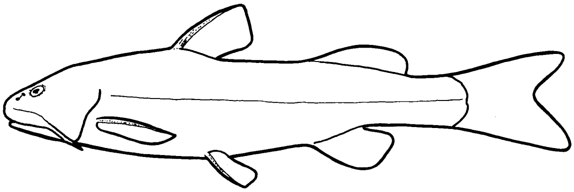
Thirty-five families with about 446 genera and about 2,867 species. Of these, about 1,727 species (excluding strictly marine ones of Ariidae) occur in the Americas. Two families, Ariidae and Plotosidae, consist largely of marine species (about 117 species), but they have representatives that are frequently found in brackish and coastal waters and sometimes only in freshwater. Other catfish families are freshwater, although some have species that can invade brackish water. At least 200 undescribed species are known and many others no doubt exist. With the inclusion of Eocene or Oligocene fossils from Antarctica (Grande and Eastman, 1986), catfishes are known from all continents. The sister group of the siluriforms is the gymnotiforms (see above under Otophysi). As noted by C. J. Ferraris, Jr. in Reis et al. (2003:254), *Conorhynchos conirostris* of Brazil does not appear to be assignable to any family and is placed *incertae sedis,* but not included in the above counts. A new family of catfishes has been described by Rodiles-Hernandez et al. (2005), the Lacantuniidae, erected for the new species *Lacantunia enigmatica,* known from the Río Lacantún, tributary to the Río Usumacinta, Chiapas, southern Mexico (this was described too late to be incorporated in the classification).

The classification down to family level is based on de Pinna (1998) and that work, based largely on his 1993 unpublished Ph.D. dissertation, should be consulted for details of the synapomorphies of the various clades. Some deviations from de Pinna (1998) include provisionally retaining the sister taxa Clariidae and Heteropneustidae as separate families and in provisionally treating the family Bagridae as monophyletic. Valuable reviews of past classifications, as well as information on the groups, are found in de Pinna (1998), Diogo (2003a), and Teugels (2003). The family descriptions below do not necessarily give diagnostic features. A detailed review of higher-level names was given by Ferraris and de Pinna (1999).

The fossil record, extending back to the Late Cretaceous (and fossils are known from all continents except, apparently, Australia), is reviewed in Gayet and Meunier (2003). That work should be consulted for the many fossils known from the families classified below. Some fossil taxa not placed in the families below include †Family Andinichthyidae, Lower Maastrichtian of the Late Cretaceous to Paleocene in Bolivia with *Andinichthys, Incaichthys,* and *Hoffstetterichthys*; the taxon Arioida, Late Campanian and Maastrichtian of the Late Cretaceous in Bolivia; and the genera, some of which may belong in the Arioida (in the sense used by J. G. Lundberg in 1993), *Bucklandium, Fajumia,* and "titanoglanis" (Gayet and Meunier, 2003) (the Eocene "titanoglanis," awaiting a valid generic name, from the Eocene of Arkansas, as noted in the 1993 description by J. G. Lundberg, probably should be placed in its own family).

Superfamily Diplomystoidea. This is the primitive sister group of all other catfishes (de Pinna, 1998).

Family DIPLOMYSTIDAE (126)—velvet catfishes. Freshwater; southern South America, Chile and Argentina.



The only extant catfish family with teeth on a well-developed maxilla, 18 principal caudal fin rays, and lagenar otolith equal in size to or larger than the utricular otolith. There are only maxillary barbels present; skin covered with papillae, no bony plates; dorsal fin with spine and 6 or 7 soft rays; anal fin with 9–12 principal rays; adipose fin present; pectoral fin with spine. Maximum length 32 cm SL.

Two genera, *Diplomystes* (3) and *Olivaichthys* (3), and six species (Arratia, 1987; Ferraris, 2003; Lundberg et al., 2004).

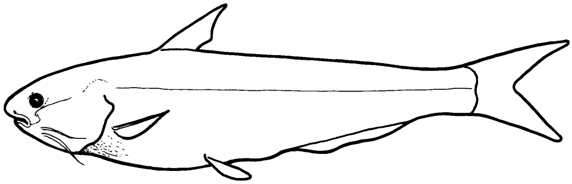
Superfamily Cetopsoidea. The one family forms a trichotomy with the hypsidorids and all remaining catfishes (de Pinna, 1998). The Helogeneidae and Cetopsidae (as recognized in Nelson, 1994) were united by de Pinna and Vari (1995) and this combination was followed in de Pinna, 1998.

Family CETOPSIDAE (127)—whalelike catfishes. Freshwater; South America.

Body naked; three pairs of barbels (no nasals); anal fin with long base, usually 20—49 rays; body naked and lacking bony plates; pectoral and dorsal fins lacking spines (except in a few cetopsines).

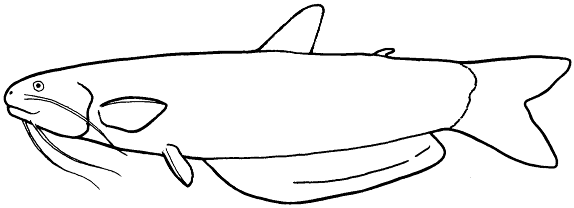
Seven genera (see below) with 23 species (Vari and Ferraris, 2003).

SUBFAMILY CETOPSINAE. No adipose fin; swim bladder highly reduced and enclosed in bony capsule; dorsal fin far forward. Maximum length about 26 cm SL.



Six genera, *Bathycetopsis* (1), *Cetopsis* (2), *Denticetopsis* (2), *Hemicetopsis* (1), *Paracetopsis* (1, synonym *Cetopsogiton*), and *Pseudocetopsis* (12), with about 19 species (Vari and Ferraris, 2003). Vari et al. (2005) made generic changes and described new species, giving a total of 37 (this study was received too late to make changes).

SUBFAMILY HELOGENEINAE. Dorsal fin base short, with about five soft rays and no spine; no spine in pectoral fin; adipose fin, if present, small (present or absent within some species); caudal fin with 15 or 16 principal rays; 12 or 13 branchiostegal rays; vertebrae 41–45 (including the 5 Weberian vertebrae). Maximum length about 7 cm SL.



One genus, *Helogenes* (synonym *Leyvaichthys*), with four species (Vari and Ferraris, 2003).

†*Superfamily Hypsidoroidea*

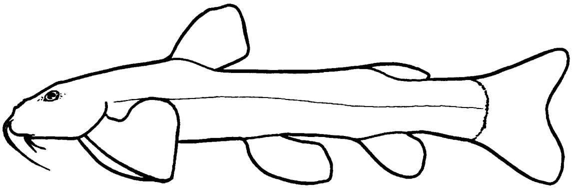
†Family HYPSIDORIDAE

Teeth on a well-developed maxilla (similar to the condition in diplomystids); one suprapreopercle; six infraorbital bones; 17 principal caudal fin rays.

Two species, *Hypsidoris farsonensis* from the Early Middle Eocene of Wyoming and *H. oregonensis* from the Middle Eocene of Oregon (Grande and de Pinna, 1998).

Superfamily Loricarioidea. Seven families with 156 genera and 1,187 species.

Family AMPHILIIDAE (128)—loach catfishes. Freshwater; tropical Africa.



Three pairs of barbels (nasal barbels absent); dorsal and anal fin bases short; dorsal and pectoral fin spine absent (weakly developed in Leptoglaninae and *Trachyglanis*); adipose fin present (with a short spine, modified scute, in *Trachyglanis*); pterygoid and posttemporal absent. Widespread in tropical Africa but commonest in streams at high elevations; most of the species can cling to rocks in fast-flowing streams. Maximum length 19 cm, but most species are less than 12 cm.

Twelve genera with 66 species (Diogo, 2003b; Teugels, 2003; Roberts, 2003). There has been doubt about the content of this family as recognized, but evidence for monophyly of this family and of its three subfamilies was given by Diogo (2003b).

SUBFAMILY AMPHILIINAE. Body relatively short, appearing similar to homalopterids; bony plates and nuchal shield absent; mouth subterminal.

Two genera, *Amphilius* (22) and *Paramphilius* (4) with 26 species.

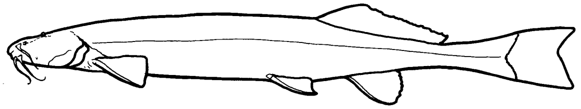
SUBFAMILY LEPTOGLANINAE. Maxilla exceptionally elongated; proximal radials completely fused (versus not fused as is the primitive condition found in most siluriforms).

Five genera, *Dolichamphilius* (2), *Leptoglanis* (1), *Psammphiletria* (2), *Tetracamphilius* (4), and *Zaireichthys* (7), with 16 species.

SUBFAMILY DOUMEINAE. Body elongate; bony plates often developed along body, nuchal shield present; mouth inferior.

Five genera, *Andersonia* (1), *Belonoglanis* (2), *Doumea* (5), *Phractura* (12), and *Trachyglanis* (4), and with 24 species.

Family TRICHOMYCTERIDAE (Pygidiidae) (129)—pencil catfishes or parasitic catfishes. Freshwater; Costa Rica, Panama, and throughout South America.



Body naked and elongate; chin (mental) barbels usually absent, nasal barbel usually present, usually two pairs of maxillary barbels; usually no adipose fin;

opercle usually with spines. Pelvic fins have been lost in at least three lineages—*Eremophilus*, Glanapteryginae, and *Miuroglanis*.

The common name "parasitic catfishes" is derived from the habits found in species of two subfamilies. Members of the Vandelliinae are hematophagous and pierce the skin of living fishes or other animals and gorge themselves on blood; some live on blood obtained within the gill cavities of other fishes. In addition, individuals of *Vandellia* (a candiru) of Brazil are known to enter the urethra of humans with serious consequences for both the fish and the person (see review by de Carvalho, 2003, of a book on the candiru). Members of the Stegophilinae feed on the mucus and scales of other fishes. This family and the Nematogenyidae are probably sister groups (de Pinna, 1998).

Eight subfamilies provisionally recognized, with about 41 genera and 201 species, are recognized as follows (de Pinna, 1998; de Pinna and Wosiacki, 2003; Teugals, 2003).

SUBFAMILY COPIONODONTINAE. Adipose fin well developed; origin of dorsal fin in anterior half of body; maxilla articulating with lower jaw. Two genera, *Copionodon* (3) and *Glaphyropoma* (1), with four species from northeastern Brazil (de Pinna and Wosiacki, 2003). This group and the Trichogeninae may be part of a trichotomy with the remaining trichomycterids (de Pinna, 1998).

SUBFAMILY TRICHOGENINAE. Anal fin long, with more than 30 rays. One species, *Trichogenes longipinnis*, from southeastern Brazil (de Pinna and Wosiacki, 2003).

SUBFAMILY TRICHOMYCTERINAE. Eight genera, *Bullockia* (1), *Eremophilus* (1), *Hatcheria* (1), *Ituglanis* (11), *Rhizosomichthys* (1), *Scleronema* (3), *Silvinichthys* (1), and *Trichomycterus* (about 120), with about 139 species (de Pinna and Wosiacki, 2003; Wosiacki and Garavello, 2004). They occur from near sea level to 4,500 m elevation. Some of the species in the unusually widespread genus *Trichomycterus* can inhabit torrential streams. One species, *T. catamarcensis* from the Andes of Argentina, lacks the pelvic fins and girdle. This subfamily is a non-monophyletic assemblage, in need of revision (de Pinna, 1998).

SUBFAMILY VANDELLIINAE. About four genera, *Paracanthopoma* (1), *Paravandellia* (2, synonyms *Branchioica* and *Pleurophysus*), *Plectrochilus* (3), and *Vandellia* (3), with about nine species (de Pinna and Wosiacki, 2003; Teugals, 2003).

SUBFAMILY STEGOPHILINAE. About 12 genera (e.g., *Acanthopoma*, *Henonemus*, *Homodiaetus*, *Ochmacanthus*, *Parastegophilus*, *Pareiodon*, *Schultzichthys*, and *Stegophilus*) with about 26 species (de Pinna and Wosiacki, 2003; Teugals, 2003).

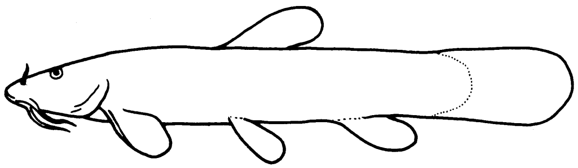
SUBFAMILY TRIDENTINAE. Anal fin relatively long, more than 15 fin rays. About four genera, *Miuroglanis* (1), *Tridens* (1), *Tridensimilis* (2), and *Tridentopsis* (3), with about seven species (de Pinna and Wosiacki, 2003; Teugals, 2003).

SUBFAMILY GLANAPTERYGINAE. Pectoral fin with three or four rays; principal caudal-fin rays 11 or fewer; pelvic skeleton and fin present or absent within

Glanapteryx anguilla, both absent in the other species; dorsal fin present in only the two species of *Listrura*; anal fin absent in *G. anguilla*; hypurals completely fused. They have a transparent body and are sand-dwelling. Four genera, *Glanapteryx* (2), *Listrura* (4), *Pygidianops* (1), and *Typhlobelus* (2), with about nine species (de Pinna and Wosiacki, 2003; Teugals, 2003).

SUBFAMILY SARCOGLANIDINAE. Six genera, *Ammoglanis*, *Malacoglanis*, *Microcambeva*, *Sarcoglanis*, *Stauroglanis*, and *Stenolicmus*, all monotypic to date but undescribed species are known (de Pinna and Wosiacki, 2003; Teugals, 2003). Poorly known and specialized minute catfishes known only from a few specimens from the Amazon Basin.

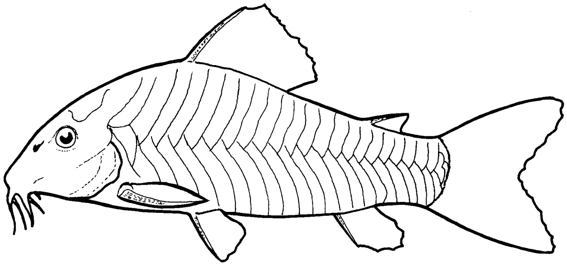
Family NEMATOGENYIDAE (130)—mountain catfishes. Freshwater; central Chile.



Body naked and elongate; three pairs of barbels present, chin (mental) barbel, single maxillary barbel, and a short nasal barbel on each side; no adipose fin; opercle lacking spines; dorsal fin in midbody, over pelvic fin origin; pectoral spine serrated on posterior margin. This family and the Trichomycteridae are probably sister groups (de Pinna, 1998).

One species, *Nematogenys inermis* (de Pinna, 2003; Teugals, 2003).

Family CALLICHTHYIDAE (131)—callichthyid armored catfishes. Freshwater; Panama and South America.



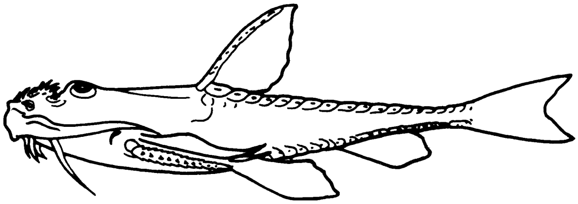
Body with two rows of overlapping bony plates on each side; swim bladder encased in bone; mouth small and ventral; one or two pairs of well-developed barbels present, and shorter processes usually on upper jaw and on lower jaw; dorsal and pectoral fins with strong spine; spine at anterior border of adipose fin. Some species can move short distances on land by utilizing air in vascular hindgut.

Two subfamilies with eight genera and about 177 species (Reis, 2003c). Reis (1998) discussed the fossil record and biogeography of this taxon.

SUBFAMILY CALLICHTHYINAE. Snout area depressed. Five genera, *Callichthys* (2), *Dianema* (2), *Hoplosternum* (3, synonym *Cataphractops*), *Lepthoplosternum* (4), and *Megalechis* (2), with 13 species (Reis, 2003c).

SUBFAMILY CORYDORADINAE. Snout area compressed or rounded. Three genera, *Aspidoras* (about 18 species), *Brochis* (3), and *Corydoras* (about 143 species), with about 164 species (Reis, 2003c).

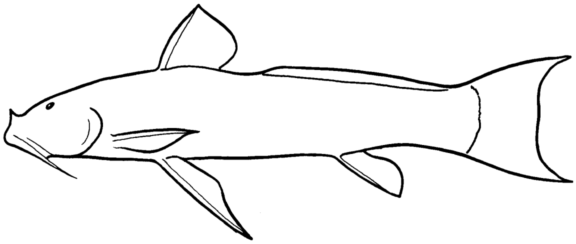
Family SCOLOPLACIDAE (132)—spiny dwarf catfishes. Freshwater; South America (Peru, Bolivia, Brazil, and Paraguay).



Body with two bilateral series of odontode-bearing plates and one midventral series of plates; rostral plate with numerous recurved odontodes; odontodes on many other parts of body; dorsal fin with stout smooth spine and 3–5 soft rays; anal fin with 5 or 6 soft rays; adipose fin absent; caudal fin with 10–12 principal rays; vomer absent; exoccipitals absent. Maximum length about 20 mm SL. This is the second-most recent family of catfish to be discovered in the sense that the first species in it was not described until 1976 (Lacantuniidae is the most recent of extant fish families).

One genus, *Scoloplax*, with four species (Schaefer, 2003a).

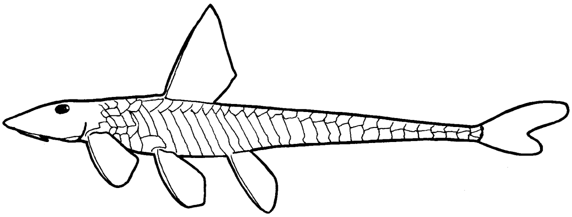
Family ASTROBLEPIDAE (Argidae) (133)—climbing catfishes. Freshwater; Panama and South America (Andean region).



Body naked or almost naked; suctorial mouth disc present as in virtually all loricariids; two pairs of barbels present, maxillary and nasal; adipose fin present or absent; dorsal fin with a spine and 6 or 7 soft rays; dorsal fin spine lacking locking mechanism (a locking mechanism is present in the related callichthyids and loricariids); anal fin with 4–6 rays; relatively short intestine; 34 vertebrae (17 + 17). Some members are able to live in torrential mountain streams, up to 3500 m, and climb the faces of waterfalls. Maximum length about 30 cm.

One genus, *Astroblepus*, with up to 54 species (Schaefer, 2003b).

Family LORICARIIDAE (134)—suckermouth armored catfishes. Freshwater; Costa Rica, Panama and South America.



Body with bony plates; mouth ventral, with or without noticeable barbels; ventral lip papillose; adipose fin, when present, usually with a spine at anterior border; relatively long intestine; 23–38 vertebrae. Members of this family may be found from low elevations to swift-flowing streams up to 3,000 m. "Pleco" or "plecostomus" is a name used in the aquarium trade for species in several genera of this family.

This is the largest family of catfishes, with more species being described every year. The recognition of six families and their composition is based on de Pinna (1998) and Reis et al. (2003), which in turn closely followed, with modifications, the classical study of Isbrücker (1980) (who with his co-authors such as Hans Nijssen added much to our knowledge). In Nelson (1994), *Lithogenes* was placed in the Astroblepidae.

About 92 genera and about 684 species, with one of the species *incertae sedis* from that in the following list (Reis et al., 2003:318–400). Information on the subfamilies listed below is from the individual chapters in Reis et al. (2003:170–230) written by specialists as follows: Neoplecostominae (C. J. Ferraris, Jr.), Hypoptopomatinae (S. A. Schaefer), Loricariinae (C. J. Ferraris, Jr.), Ancistrinae (S. Fisch-Muller), and Hypostominae (C. Weber). Changes in the composition of the subfamilies Ancistrinae and Hypoptopomatinae is expected with the work of J. W. Armbruster, as well as the description of new species (e.g., Armbruster and Provenzano, 2000).

SUBFAMILY LITHOGENEINAE. Two species, *Lithogenes valencia* (described in 2003 and may be extinct) and *L. villosus* (Provenzano et al., 2003).

SUBFAMILY NEOPLECOSTOMINAE. *Neoplecostomus*, with seven species in southeastern Brazil.

SUBFAMILY HYPOPTOPOMATINAE. Sixteen genera, e.g., *Acestridium*, *Hisonotus*, *Hypoptopoma*, *Microlepidogaster*, *Otocinclus*, *Otothyris*, *Oxyropsis*, and *Parotocinclus*, with 79 species.

SUBFAMILY LORICARIINAE. About 31 genera, e.g., *Crossoloricaria, Farlowella, Harttia, Loricaria, Loricariichthys, Pseudohemiodon, Reganella, Rineloricaria, Spatuloricaria,* and *Sturisoma,* with 209 species.

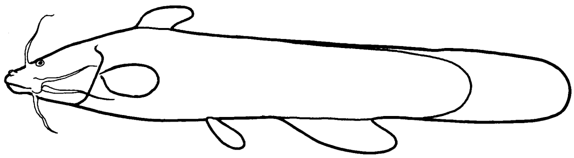
SUBFAMILY ANCISTRINAE. About 27 genera, e.g., *Ancistrus* (synonym *Xenocara*), *Chaetostoma, Hemiancistrus, Hypancistrus, Lasiancistrus, Lithoxus, Megalancistrus, Panaque, Peckoltia, Pseudacanthicus,* and *Pseudancistrus,* with 217 species.

SUBFAMILY HYPOSTOMINAE. About 16 genera, e.g., *Delturus, Glyptoperichthys, Hemipsilichthys, Hypostomus* (synonyms *Cochliodon* and *Plecostomus*) (*H. watwata* lives in brackish water), *Liposarcus, Pogonopoma, Pterygoplichthys, Rhinelepis,* and *Squaliforma,* with 169 species.

Superfamily Sisoroidea. This taxon is sister to the Loricarioidea and the amblycipitids are sister to the remaining families of sisoroids (de Pinna, 1996b, 1998). The phylogenetic study of de Pinna (1996b) found that the Erethistidae is the sister group of the Aspredinidae, with the Sisoridae being the sister group of the clade formed by these two families. This was supported in the study of Diogo et al. (2001, 2003). For details of the synapomorphies of the various clades see de Pinna (1996b) and Diogo et al. (2001, 2002, 2003).

Five families, 41 or 42 genera, and 230 species.

Family AMBLYCIPITIDAE (135)—torrent catfishes. Freshwater; southern and eastern Asia (Pakistan across northern India to Malaysia and to Korea and southern Japan).



Dorsal fin covered by thick skin; adipose fin present, confluent with caudal fin in some species; dorsal fin base short, spine in fin weak; anal fin base short, with 9–18 rays; four pairs of barbels; lateral line poorly developed or absent. These small fish inhabit swift streams.

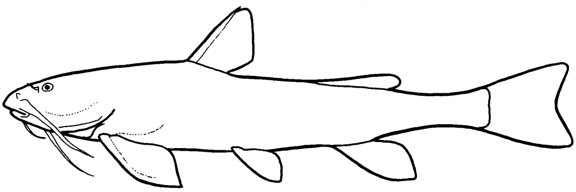
Three genera, *Amblyceps* (11), *Liobagrus* (13), and *Xiurenbagrus* (2), with about 26 species (Chen and Lundberg, 1995; Ng and Kottelat, 2000a; Ng, 2001).

Family AKYSIDAE (136)—stream catfishes. Freshwater; southeastern Asia.

Dorsal fin with a strong spine and a short base, usually four or five soft rays.

Four genera (given below) with at least 42 species. The two subfamilies were ranked as families in Nelson (1994). The family is sister to the clade of Sisoridae, Erethistidae, and Aspredinidae (de Pinna, 1996b, 1998).

SUBFAMILY AKYSINAE. Body with unculiferous tubercles arranged in longitudinal rows, a median middorsal row and usually four lateral rows; dorsal fin with usually five soft rays; adipose fin present and moderate; pectoral fin with strong spine, anterior margin with notch visible dorsally and usually serrated posteriorly; gill openings relatively narrow; eyes small; four pairs of barbels.

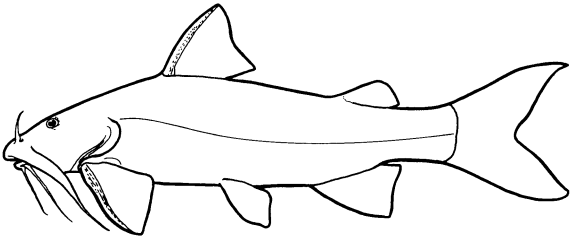


One genus, *Akysis* with at least 24 species (Ng and Kottelat, 1998, 2004; Ng and Freyhof, 2003; Ng and Siebert, 2004).

SUBFAMILY PARAKYSINAE. Dorsal fin with 4 soft rays; pectoral spine nonserrate; anal fin with 8–13 soft rays; four pairs of barbels, mandibular barbels usually with short accessory barbels; gill rakers absent; lateral-line pores absent; head and body covered with rounded tubercles, arranged in longitudinal rows (*Acrochordonichthys* and *Breitensteinia*) or evenly distributed and not in rows (*Parakysis*); adipose fin absent (*Breitensteinia* and *Parakysis*) or present and long (*Acrochordonichthys*); eyes minute; vertebrae 30–32 (abdominals 16–19). Primarily Malay Peninsula, Sumatra, Sarawak, and western and southern Borneo.

Three genera, *Acrochordonichthys* (10), *Breitensteinia* (3), and *Parakysis* (5), with 18 species (Ng and Ng, 2001; Vidthayanon and Ng, 2003; Ng and Siebert, 1998; Ng and Kottelat, 2003).

Family SISORIDAE (Bagariidae) (137)—sisorid catfishes. Freshwater; southern Asia (from Turkey and Syria to South China and Borneo, primarily in Oriental region).



Body usually with small unculiferous tubercles; adipose fin present (confluent with caudal in some genera and consisting of a small spine in the elongate *Sisor*); dorsal fin base short, fin with or without a spine; adhesive apparatus in thoracic region present or absent; four pairs of barbels (however, the monotypic *Sisor* has one maxillary pair and five pairs on the lower jaw). Mostly small forms occurring in mountain rapids; maximum length 2 m.

The compostion of this family as recognized in Nelson (1994) was changed by de Pinna (1996b), who separated off six taxa into a new family, Erethistidae.

Seventeen genera with at least 112 species (de Pinna, 1996b; Roberts and Ferraris, 1998; Roberts, 2001; Diogo et al, 2002; Diogo, 2003).

SUBFAMILY SISORINAE. Six genera, *Ayarnangra, Bagarius, Gagata, Gogangra, Nangra,* and *Sisor,* with about 23 species.

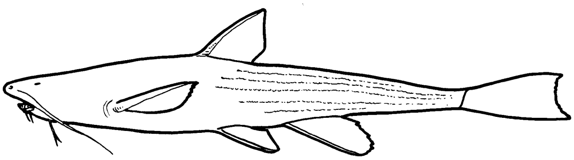
SUBFAMILY GLYPTOSTERNINAE. Eleven genera, *Coraglanis, Euchiloglanis, Exostoma, Glaridoglanis, Glyptosternon, Glyptothorax, Myersglanis, Oreoglanis, Pareuchiloglanis, Pseudecheneis,* and *Pseudexostoma,* with about 89 species.

Family ERETHISTIDAE (138)—erethistid catfishes. Freshwater; southern Asia.

The family Erethistidae was established by de Pinna (1996b) to include genera previously placed in Sisoridae. Two subfamilies were recognized, Continae, for genus *Conta,* and Erethistinae, for the other five genera. See above under superfamily Sisoroidea.

Six genera, *Caelatoglanis, Conta, Erethistes, Erethistoides, Hara, and Pseudolaguvia,* with about 14 species (de Pinna, 1996b; Diogo et al., 2003; Britz and Ferraris, 2003; Ng and Kottelat, 2005).

Family ASPREDINIDAE (139)—banjo catfishes. Freshwater (some brackish); tropical South America.



Body naked except for large tubercles arranged in longitudinal rows; no adipose fin; body depressed anteriorly; opercular aperture reduced to a slit; dorsal spine-locking mechanism absent in most species; 10 or fewer caudal fin rays. Maximum length about 38 cm SL, attained in *Aspredo aspredo*; most species less than 15 cm.

Twelve genera with 36 species (de Pinna, 1998; Diogo et al., 2001; Friel and Lundberg, 1996; Friel, 2003). Much information from these studies was based on the 1994 Ph.D. dissertation of John Friel of Duke University. *Micromyzon akamai* (Friel and Lundberg, 1996) lacks eyes. *Acanthobunocephalus* may be sister to the remaining taxa (and hence would not belong in the subfamily Bunocephalinae).

SUBFAMILY BUNOCEPHALINAE. *Acanthobunocephalus, Amaralia,* and *Bunocephalus,* with 16 species.

SUBFAMILY ASPREDININAE. Four genera, *Aspredinichthys, Aspredo, Platystacus,* and *Pterobunocephalus,* with six species.

SUBFAMILY HOPLOMYZONTINAE. Five genera, *Dupouyichthys*, *Ernstichthys*, *Hoplomyzon*, *Micromyzon*, and *Xyliphius*, with 14 species.

Superfamily Pseudopimelodoidea. This taxon is sister to Sisoroidea + Loricarioidea (de Pinna 1998). The composition of the family Pimelodidae has been greatly changed from that recognized in Nelson (1994), where three subfamilies were recognized: Rhamdiinae, Pimelodinae, and Pseudopimelodinae after the important studies of Lundberg et al. (1991a, b). These subfamilies were also recognized in de Pinna (1998); the changes are based on the cladogram of de Pinna (1998:289) and are described in Diogo (2003) and Shibatta (2003a,b). However, Diogo et al. (2004a) concluded that the Pseudopimelodidae, Heptapteridae, Pimelodidae constitute a monophyletic assemblage (thus recognized the subfamilies Pseudopimelodinae, Pimelodinae and Heptapterinae), contradicting the hypothesis that the former family Pimelodidae is a polyphyletic group. Further analysis of the conclusion is required.

Family PSEUDOPIMELODIDAE (140)—bumblebee catfishes. Freshwater; South America.

Wide mouth; small eyes; barbels short. Some are popular aquarium fishes, noted for their body coloration of dark brown blotches. Formerly part of Pimelodidae.

Five genera, *Batrochoglanis* (4), *Cephalosilurus* (4), *Lophiosilurus* (1), *Microglanis* (12), *Pseudopimelodus* (5), with 26 species (Shibatta, 2003a,b).

Superfamily Heptapteroidea. The sister group of the heptapterids is regarded by de Pinna (1998) to be a clade comprising those families given below from Cranoglanididae onwards. However, whether or not bagrids or some bagrids are related to heptapterids is considered here as uncertain. For further details see below in family Bagridae, superfamily Bagroidea. Further research is needed to improve our understanding of the phylogenetic relationships of the group.

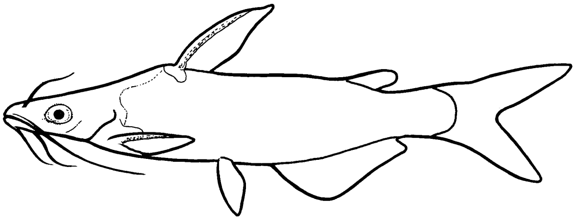
Family HEPTAPTERIDAE (141)—heptapterids. Freshwater; Mexico to South America.

Skin usually naked; three pairs of barbels; adipose fin large; caudal fin deeply forked. Unfortunately for field identification, members of this family cannot always be separated from members of the former Pimelodidae by external features (the above features are not unique to this family); synapomorphies are given in Lundberg et al, 1991a; de Pinna, 1998; Bockmann and Guazzelli, 2003; Shibatta, 2003a. This family is equivalent to the previously recognized Rhamdiinae (placed in Pimelodidae, with the nominal genera listed in Lundberg et al., 1991a:198) plus the Heptapterinae of de Pinna (1998). The diversity of this group is especially poorly known and perhaps 50 species are yet to be described (Bockmann and Guazzelli, 2003).

About 25 genera, e.g., *Acentronichthys*, *Brachyglanis*, *Brachyrhamdia*, *Cetopsorhambia*, *Chasmocranus*, *Gladioglanis*, *Goeldiella*, *Heptapterus*, *Imparfinis*, *Leptorhamdia, Pimelodella* (synonyms *Caecorhamdella* and *Typhlobagrus*), *Rhamdella, Rhamdia,* and *Taunayia,* with roughly 175 species (Shibatta, 2003a; Bockmann and Guazzelli, 2003; Weber et al., 2003; Trajano et al., 2004).

Superfamily Cranoglanidoidea

Family CRANOGLANIDIDAE (142)—armorhead catfishes. Freshwater; Asia, China and Vietnam (mainly large rivers).

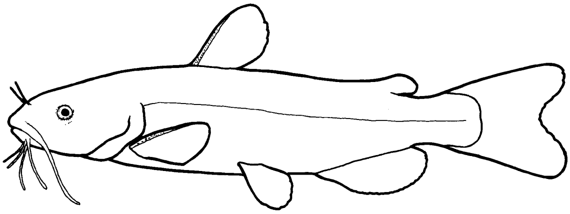


Dorsal fin short, six (rarely five) branched rays and one spine; anal fin with 35–41 rays; pectoral with a spine; each pelvic fin with 12–14 rays; caudal fin deeply forked; eyes large; body compressed and naked; rough bony plates on top of head; vomer without teeth; four pairs of barbels. Similar to *Pseudobagrus.*

One genus, *Cranoglanis,* and three species (Teugels, 2003).

Superfamily Ictaluroidea

Family ICTALURIDAE (Ameiuridae) (143)—North American catfishes. Freshwater; North America (southern Canada to Guatemala).



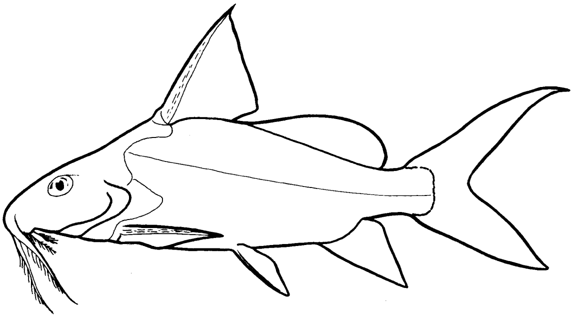
Four pairs of barbels on head; skin naked; dorsal (except in *Prietella*) and pectoral fins with a spine; dorsal fin usually with six soft rays; palate toothless except in fossil *Astephus.* Four species of blind (eyeless) catfishes are known; two (*Satan* and *Trogloglanis*) from deep artesian wells and associated ditches near San Antonio, Texas, and two (*Prietella*) from northeastern Mexico. Monophyly and phylogenetic relations of the genera were shown by Lundberg (1992) and relationships among species of *Ameiurus* discussed in (Hardman and Page, 2003). Maximum length about 1.6 m, attained in *Ictalurus furcatus* and *Pylodictis olivaris.*

Seven genera, *Ameiurus* (7, bullheads), *Ictalurus* (9, five of which occur only in Mexico and Guatemala, channel catfishes), *Noturus* (25, including one recently extinct, stonecat and madtoms which have a poison gland at base of pectoral spine); *Prietella* (2), *Pylodictis* (1, Flathead Catfish), *Satan* (1), and *Trogloglanis* (1), with a total of about 46 species (including one recently extinct) (Nelson et al., 2004). Gilbert (1998) gives a type catalogue of recent and fossil taxa.

Superfamily Doradoidea. Ariidae was placed in Doradoidea in de Pinna (1998), but it is moved to the Bagroidea as sister to Claroteidae based on M. de Pinna (pers. comm., 2005). Diogo et al. (2004b) provided further support for the hypothesis that the Doradidae and the Auchenipteridae are closely related.

Three families, 61 genera, and 345 species.

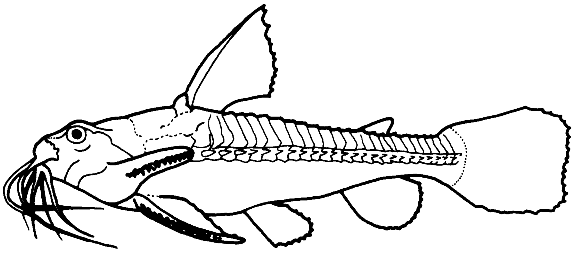
Family MOCHOKIDAE (144)—squeakers or upside-down catfishes. Freshwater; Africa.



Adipose fin usually very large; anal fin with fewer than 10 rays; dorsal and pectoral fin spines usually strong and with a locking mechanism; three pairs of barbels, nasal barbels absent and mandibular barbels may have numerous branches; some with lips and part of barbels modified into an oral sucker (*Atopochilus, Chiloglanis,* and *Euchilichthys*); the two species of *Mochokus* of the Nile system have a rayed adipose fin. Maximum length 72 cm. Monophyly was addressed by Mo (1991).

Eleven genera, e.g., *Ancharius, Atopochilus, Chiloglanis, Euchilichthys, Microsynodontis, Mochokus* (synonym *Acanthocleithron*), and *Synodontis,* with 179 species (e.g., Teugels, 2003).

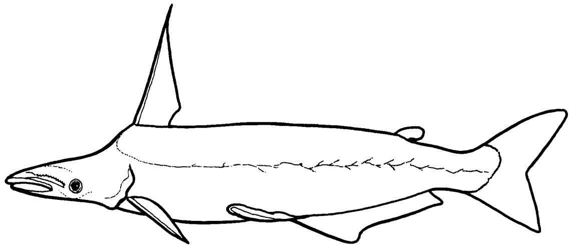
Family DORADIDAE (145)—thorny catfishes. Freshwater; South America (primarily in Brazil, Peru, and the Guianas).

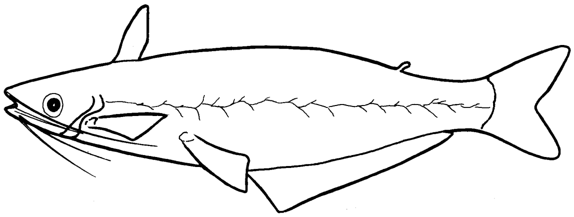


Body with a row of lateral bony plates, most with spines. *Liosomadoras morrowi* lacks lateral bony plates and *Doraops zuloagai* has them only on the posterior portion of the body. Three pairs of barbels (no nasals), mandibular barbels with branches in some; dorsal fin with spine and 4–6 soft rays; adipose fin usually present. Doradids are also called "talking catfishes" because of their sound production, made either by movements of the pectoral spine or by vibrating the swim bladder. Maximum length about 120 cm FL.

About 30 genera, e.g., *Acanthodoras, Agamyxis, Amblydoras, Anadoras, Doraops, Doras, Hassar, Hemidoras, Leptodoras, Liosomadoras, Megalodoras, Nemadoras, Opsodoras, Oxydoras, Physopyxis, Platydoras, Pseudodoras, Pterodoras, Scorpiodoras,* and *Tachydoras,* with about 72 species (Sabaj and Ferraris, 2003).

Family AUCHENIPTERIDAE (146)—driftwood catfishes. Freshwater (one species in brackish water); Panama and tropical South America (to Argentina).





Body naked (dorsal region of body between head and dorsal fin with sutured bony plates beneath the skin); usually three pairs of barbels (nasal barbels absent), maxillary pair longest; strong spine in pectoral and dorsal fins; adipose fin present but small, rarely absent. Internal insemination probably in all species.

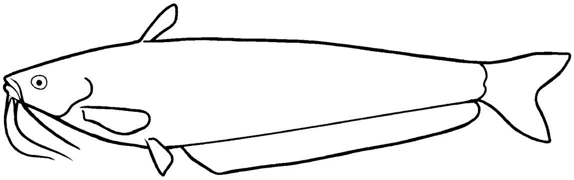
This family now includes the previously recognized family Ageneiosidae (the bottlenose or barbelless catfishes with *Ageneiosus* and *Tetranematichthys*) (Ferraris, 2003b). Two subfamilies with 20 genera and about 94 species (Ferraris, 2003b).

SUBFAMILY CENTROMOCHLINAE. Soares-Porto (1998) gave details on the synapomorphies in showing monophyly and relationships of this group. Four genera, *Centromochlus* (10), *Gelanoglanis* (2), *Glanidium* (6), and *Tatia* (13), with 31 species (Ferraris, 2003b).

SUBFAMILY AUCHENIPTERINAE. About 16 genera, e.g., *Ageneiosus* (upper figure), *Auchenipterus* (lower figure), *Epapterus, Tetranematichthys, Trachelyichthys, Trachelyopterus,* and *Trachycorystes,* with 63 species (Ferraris, 2003b).

Superfamily Siluroidea. Seven families, 45 genera, and 275 species.

Family SILURIDAE (147)—sheatfishes. Freshwater; Europe and Asia.



Dorsal fin usually with fewer than seven rays, sometimes absent, not preceded by a spine; adipose fin absent; pelvic fins small, sometimes absent; anal fin base very elongate, 41–110 rays; nasal barbel absent, one or two pairs of barbels on lower jaw, and maxillary barbels usually elongate. Monophyly of this family has been established by Bornbusch (1995) on the basis of such characters as the autopalatine reduced to a small nodule.

The largest species of siluriform is the commercially important European wels, *Silurus glanis*, which commonly reaches 3 m (maximum recorded length is 5 m and weight 330 kg). This species is native in Europe, east of the Rhine, and in some areas occurs in brackish water and in inland saline seas.

At least 11 genera, *Belodontichthys*, *Ceratoglanis*, *Hemisilurus*, *Hito*, *Kryptopterus* (glass catfish), *Micronema*, *Ompok*, *Pterocryptis*, *Silurichthys*, *Silurus* (*Parasilurus* may be a synonym), and *Wallago*, with about 97 species (Bornbusch, 1995; Rainboth, 1996; Teugels, 2003). Only two species, both in the large genus *Silurus*, occur in Europe.

Family MALAPTERURIDAE (148)—electric catfishes. Freshwater; tropical Africa and Nile.

Electrogenic organ present, derived from anterior body musculature and lining the body cavity; dorsal fin absent; fin spines absent; adipose fin far back; caudal fin rounded; three pairs of barbels (nasal pair absent); pectoral girdle loosely attached to skull; swimbladder with an elongate posterior chamber, two chambers in *Malapterurus* and three in *Paradoxoglanis*. Produce strong stunning electrical current; some other catfishes have electroreceptive systems, but only malapterurids have a well-developed electrogenic organ. Maximum length about 1.0 m SL (all species of *Paradoxoglanis* are much smaller).

Two genera, *Malapterurus* (16) and *Paradoxoglanis* (3), with 19 species (Norris, 2002) (this family has had a large increase in species recognized since Nelson, 1994, with 14 new species described in Norris, 2002).

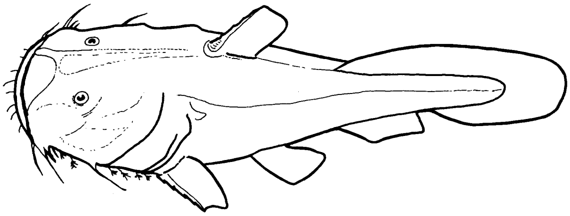
Family AUCHENOGLANIDIDAE (149)—auchenoglanidids. Freshwater; Africa.

Anterior nostrils on anteroventral side of upper lip; caudal fin rounded.

Often formerly placed in the Bagridae (as in Nelson, 1994), this taxon was considered a subfamily of Claroteidae by Mo (1991) as followed by Teugels (2003), but recognized by de Pinna (1998), as here, as a sister group to Malapteruridae.

Six genera, *Anaspidoglanis, Auchenoglanis, Liauchenoglanis, Notoglanidium, Parauchenoglanis,* and *Platyglanis,* with about 28 species (Teugels, 2003; Geerinckx et al., 2004).

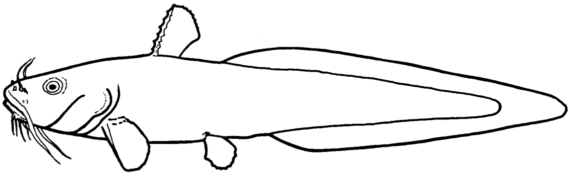
Family CHACIDAE (150)—squarehead, angler, or frogmouth catfishes. Freshwater; eastern India to Borneo.



Head broad, long, and depressed; body compressed posteriorly; mouth terminal, very wide; three or four pairs of small barbels (nasals if present, minute); eyes very small; dorsal fin with one short spine and four soft rays; anal fin with 8–10 soft rays; pectoral fin with one serrated spine and four or five soft rays; pelvic fins large, with six rays; adipose fin confluent with caudal fin; gill rakers absent; branchiostegal rays 6–8; vertebrae 31–35 (14–16 abdominals). Maximum length about 24 cm. On occasions, *Chaca* uses its maxillary barbels to lure prey fish closer to its large mouth. Diogo et al. (2004c), found new autapomorphies, and in addition their study further supported there being a close relationship between the chacids, the plotosids and the clariids.

One genus, *Chaca,* with three species (Brown and Ferraris, 1988; Teugels, 2003).

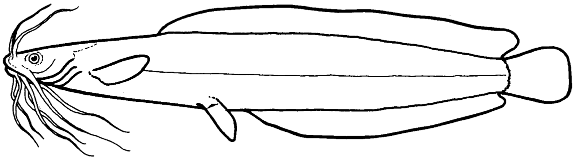
Family PLOTOSIDAE (151)—eeltail catfishes. Marine, brackish, and freshwater; Indian Ocean and western Pacific from Japan to Australia and Fiji.



Body eel-like, tail pointed or bluntly rounded; usually four pairs of barbels; no adipose fin; caudodorsal fin rays may extend far forward (i.e., two dorsal fins, the second of which is confluent with the caudal), and lower procurrent caudal rays join the long anal fin to form a continuous fin; branchiostegal rays 7–14. As with some other catfishes, some of these can inflict painful wounds.

Ten genera, *Anodontiglanis* (1), *Cnidoglanis* (3), *Euristhmus* (2), *Neosiluroides* (1), *Neosilurus* (12), *Oloplotosus* (3), *Paraplotosus* (2), *Plotosus* (7), *Porochilus* (2), and *Tandanus* (2), with about 35 species (Allen and Feinberg, 1998; Ng and Sparks, 2002; Teugels, 2003). About half of the species are freshwater and occur in Australia and New Guinea.

Family CLARIIDAE (152)—airbreathing catfishes. Freshwater; Africa, Syria, and southern and western Asia (Philippines to Java).

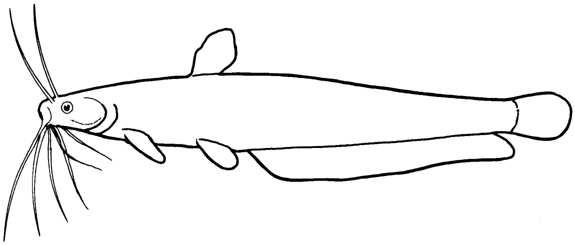


Dorsal fin base very long, usually with more than 30 rays, not preceded by a spine, separate or continuous with caudal fin; pectoral and pelvic fins variously absent in some species; caudal fin rounded; gill openings wide; usually four pairs of barbels; air-breathing labyrinthic organ arising from gill arches .

Some members of this family can move short distances over land. One species of walking catfish, the widespread *Clarias batrachus* has been introduced into southern Florida waters, where it thrives. Members of three African genera (*Gymnallabes*, *Channallabes*, and *Dolichallabes*) have a marked burrowing habit, have small eyes, and reduced or absent pectoral and pelvic fins. *Uegitglanis* (sometimes placed in Uegitglanididae) of Somali Republic, *Horaglanis* of India, and one species of *Clarias* in southwestern Africa are blind (Proudlove, 2005). Clariidae and Heteropneustidae are sister taxa (e.g., Mo, 1991; Teugels and Adriaens, 2003) and could be recognized as subfamilies, but I provisionally retain them as separate families.

About 14 genera, *Bathyclarias* (possibly 12, Africa), *Channallabes* (1, Africa), *Clariallabes* (16, Africa), *Clarias* (32, Africa and probably synonym *Xenoclarias* 1, Africa, and 8, Asia), *Dinotopterus* (1, Africa), *Dolichallabes* (1, Africa), *Encheloclarias* (6, SE Asia), *Gymnallabes* (3, Africa), *Heterobranchus* (4, Africa), *Horaglanis* (1, India), *Platyallabes* (1, Africa), *Platyclarias* (1, Africa), *Tanganikallabes* (1, Africa), and *Uegitglanis* (1, Africa), with about 90 species (Teugels and Adriaens, 2003). The greatest diversity occurs in Africa.

Family HETEROPNEUSTIDAE (Saccobranchidae) (153)—airsac catfishes. Freshwater; Pakistan to Thailand (primarily India, Ceylon, and Myanmar).



Body elongate, compressed; head greatly depressed, strongly resembling that of clariids; four pairs of barbels; long air sac, serving as a lung, extends posteriorly from the gill chamber; dorsal fin short, without a spine; adipose fin absent or represented as a low ridge.

The pectoral spines have an associated venom gland, and the fish is considered dangerous to persons wading in its territory. Clariidae and Heteropneustidae are sister taxa (e.g., Mo, 1991; Teugels and Adriaens, 2003) and could be recognized as subfamilies, but I provisionally retain them as separate families.

One genus, *Heteropneustes*, and about three species (Menon, 1999; Rema Devi and Raghunathan, 1999).

Superfamily Bagroidea. Seven families, 96 genera, and 551 species.

Family AUSTROGLANIDAE (154)—austroglanids. Freshwater; southern Africa.

Three pairs of barbels (nasal pair absent); strong dorsal and pectoral spines; adipose fin small.

Formerly placed in Bagridae, but recognized in a separate family by Mo (1991) and de Pinna (1998).

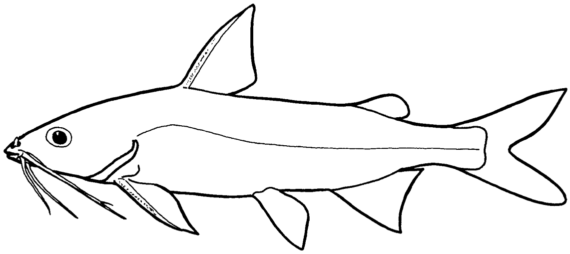
One genus, *Austroglanis*, with three species (Teugels, 2003).

Family CLAROTEIDAE (155)—claroteids. Freshwater; Africa.

Dentary at the symphysis with a ventral process; body moderately elongate; four pairs of barbels; dorsal and pectoral fins with strong spines; adipose fin present. Formerly placed in Bargidae, but recognized in a separate family by Mo (1991). The Auchenoglanididae were included as a subfamily of Claroteidae by Mo (1991) as followed by Teugels (2003), but recognized by de Pinna (1998), as here, as a sister group to Malapteruridae.

Seven genera, *Amarginops*, *Bathybagrus*, *Chrysichthys*, *Clarotes*, *Gephyroglanis*, *Lophiobagrus*, and *Phyllonemus*, with as many as 59 species (Teugels, 2003, based on Mo, 1991).

Family ARIIDAE (Tachysuridae) (156)—sea catfishes. Mainly marine (to 100 m depth), many fresh or brackish water; worldwide, tropical to warm temperate.



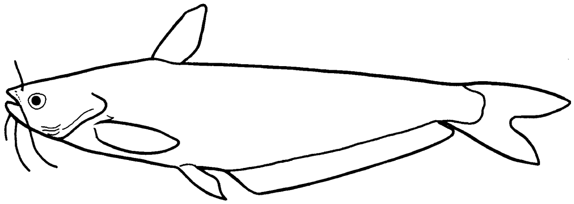
Caudal fin deeply forked; adipose fin present; usually three pairs of barbels, rarely two (no nasal barbels); some bony plates on head and near dorsal fin origin; pectoral and dorsal fins with a spine; anal fin with 14–40 soft rays; in most, if not all species, the male carries the relatively large eggs in its mouth until hatching.

Many species of the sea catfishes enter freshwater and some only occur in freshwater. For example, in the United States, Mexico, and Central and South America about 43 species of the genera *Ariopsis* (*A. felis*), *Arius, Aspistor, Bagre, Cathorops, Galeichthys, Genidens, Hexanematichthys, Notarius,* and *Potamarius* occur in freshwater (some exclusively) or at least extend into brackish water river mouths from the ocean (Marceniuk and Ferraris, 2003, using a classification that is based on the 2003 doctoral dissertation of the senior author; Nelson et al., 2004). The divergent *Doiichthys* from freshwater in New Guinea has sometimes been placed in its own family, Doiichthyidae.

Ariidae were placed in Doradoidea in de Pinna (1998), but it is moved to the Bagroidea as sister to Claroteidae based on M. de Pinna (pers. comm., 2005).

About 21 genera, *Ariopsis, Arius* (synonym *Tachysurus*), *Aspistor, Bagre, Batrachocephalus, Cathorops, Cinetodus, Cochlefelis, Doiichthys Galeichthys, Genidens, Hemipimelodus, Hexanematichthys* (synonym *Selenaspis* and possibly *Sciades*), *Ketengus, Nedystoma, Netuma, Notarius* (synonym *Sciadeops*), *Osteogeneiosus, Paradiplomystes, Potamarius,* and *Tetranesodon,* with about 150 species (Marceniuk and Ferraris, 2003; Teugels, 2003).

Family SCHILBEIDAE (SCHILBIDAE) (157)—schilbeid catfishes. Freshwater; Africa and southern Asia.



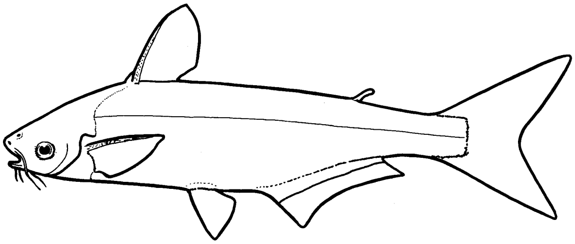
Dorsal fin usually present (with short base and a spine, absent in *Ailia* and *Parailia*); adipose fin usually present; anal fin base very long, not confluent with caudal, 24–90 rays; usually four pairs of barbels. The pelvic fin is occasionally absent in species of several genera. Members of this family tend to swim in open water.

It is interesting here to note that, as with some other family names, there is disagreement on the correct spelling. Rules concerning determining the correct formation of family names are given in the code of the International Commission of Zoological Nomenclature (ICZN), as presented in the fourth edition of the "International Code of Zoological Nomenclature" (the Code), primarily in Articles 29 and 35. Normally the rules are easy to interpret and apply, but occasionally that is not the case, with multiple spellings existing in the literature until agreement is reached (in the meantime this may cause unfortunate confusion in the literature, especially for non-taxonomists). In this case, the spellings Schilbeidae and Schilbidae occur for the same taxon in the literature. I have been guilty of using both (Schilbeidae in Nelson, 1976, 1994, and Schilbidae in Nelson, 1984). While informed specialists disagree on the correct formation and usage, I prefer Schilbeidae as does Eschmeyer (1998), and that seems to be the prevailing usage (although Ferraris and de Pinna, 1999, recommended the spelling Schilbidae).

The Schilbeidae are probably monophyletic with a close relationship with the Pangasiidae (Diogo et al., 2004d). *Horabagrus* with two species in Southeast Asia (e.g., Ng, 2003) is of uncertain phylogenetic relations and is provisionally put here (as it was in Teugels, 2003, presumably based on Mo, 1991). Jayaram (2005) recognized it in its own subfamily. It was shown in de Pinna (1998) as sister to the clade comprising Pangasiidae and higher, therefore requiring a separate family should that relationship be confirmed.

About 15 genera, with five in Africa, *Irvineia, Parailia, Siluranodon, Pareutropius,* and *Schilbe,* with 34 species, and ten genera in Asia, *Ailia, Ailiichthys* (probably a synonym of *Ailia*), *Clupisoma, Eutropiichthys, Laides, Platytropius, Proeutropiichthys,* and *Pseudeutropius,* plus provisionally retained here the Asian genus *Silonia* (2, not listed in this family by Diogo et al., 2004) and the above mentioned *Horabagrus,* with 22 species in Asia, and with 56 species for the family (Diogo et al., 2004d; Teugels, 2003, for species numbers, except for *Horabagrus).*

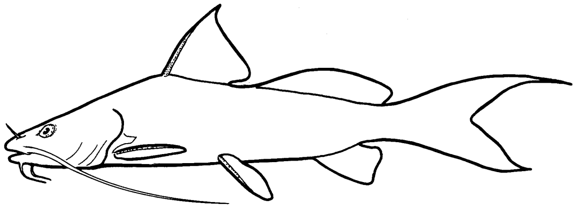
Family PANGASIIDAE (158)—shark catfishes. Freshwater; southern Asia (Pakistan to Borneo).

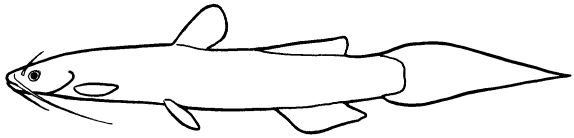


Usually two pairs of barbels (maxillary and one pair of mandibular or mental barbels present, nasal barbels always absent, only maxillary barbels in adult *Pangasianodon gigas*); body compressed; adipose fin present, small, never confluent with caudal fin; dorsal fin far forward with one or two spines and 5–7 soft rays; anal fin with 26–46 rays; vertebrae 39–52. Maximum length about 3 m and maximum weight 300 kg, attained in the plant-eating, toothless (in adults) *Pangasianodon gigas.*

Three genera, *Helicophagus* (3), *Pangasianodon* (2), and *Pangasius* (23), with 28 species (Rainboth, 1996; Teugels, 2003).

Family BAGRIDAE (159)—bagrid catfishes. Freshwater; Africa and Asia (to Japan and Borneo).





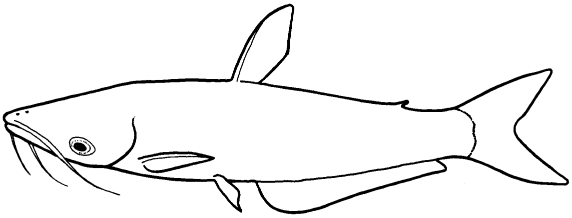
Dorsal fin preceded by a spine, usually with 6 or 7 soft rays (rarely 8–20) (except in *Olyra,* which lacks a spine and has seven or eight soft rays); adipose fin present and highly variable in size between species; pectoral spine serrated; body naked; usually four pairs of well-developed barbels. Some species are kept as aquarium fishes, while others are large and important as food fishes. Maximum length about 1.5 m.

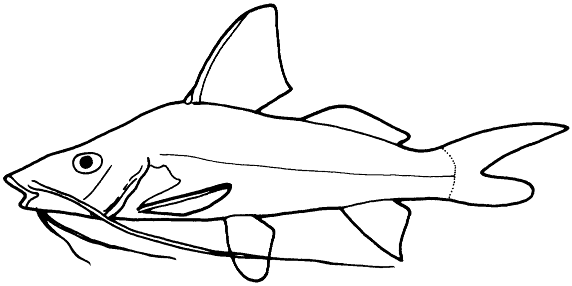
The family is very different from that recognized in Nelson (1994) as a result of studies by Mo (1991), de Pinna (1998), and Ng (2003); e.g., the family Olyridae has been included here. Mo (1991) divided the family as recognized in Nelson (1994) into three families, the Claroteidae (with two subfamilies, Claroteinae and Auchenoglaninae, Africa), Austroglanididae (one genus, Africa), and Bagridae (the African *Bagrus* and the Asian genera and including *Olyra,* the only genus of Olyridae). The recognition of two subfamilies by Mo (1991), Bagrinae for 16 genera, and Ritinae for *Nanobagrus* and *Rita,* was supported by Ng (2003).

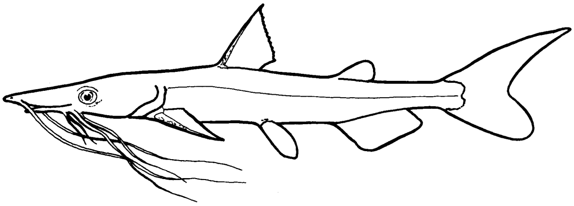
Two major unresolved questions concern this family: is it monophyletic and what are its relationships to other catfishes? Our confidence in its composition and placement is unsatisfactory. Its composition here and assumed monophyly is recognized following Mo (1991) and Ng (2003). However, de Pinna (1998), as shown in Ng (2003:449), recognized most of the genera, occurring in Asia, as sister to the Heptapteridae and others, of the genera *Bagrus* (the type genus of the family), *Hemibagrus, Sperata,* and as sister to these, *Mystus,* in a separate group and sister to the New World family Pimelodidae. See also above under superfamily Heptapteroidea.

About 18 genera, e.g., *Bagrichthys, Bagroides, Bagrus, Batasio, Hemileiocassis, Hyalobagrus, Hemibagrus, Leiocassis, Mystus, Nanobagrus, Neotropius, Olyra* (shown in the lower figure), *Pelteobagrus, Pseudobagrus, Pseudomystus, Rama, Rita,* and *Sperata,* with about 170 species (Teugels, 2003:323; Ng, 2003).

Family PIMELODIDAE (160)—long-whiskered catfishes. Freshwater; Panama and South America (north to southernmost Mexico).







Body naked; adipose fin present; three pairs of barbels (no nasal barbels); pectoral and dorsal fin spines present or absent; adipose fin well developed. Maximum length about 2.8 m FL, attained in *Brachyplatystoma filamentosum.*

This family now includes the previously recognized family Hypophthalmidae (lookdown catfishes or loweye catfishes with four species of *Hypophthalmus,* thought to be most closely related to *Parapimelodus,* part of the *Pimelodus* group) (de Pinna, 1998; Lundberg and Littmann, 2003). Also, in Nelson (1994), three subfamilies were recognized, Rhamdiinae, Pimelodinae, and Pseudopimelodinae, with members of the first and last now placed elsewhere. See above under superfamily Pseudopimelodoidea for further notes.

About 31 genera, e.g., *Brachyplatystoma, Calophysus, Goslinia, Hypophthalmus* (shown in upper figure), *Luciopimelodus, Parapimelodus, Phractocephalus, Pimelodina, Pimelodus* (middle figure), *Sorubim* (lower figure), *Sorubimichthys,* and *Zungaro* (synonym *Paulicea*), and at least 85 species (de Pinna, 1998; Lundberg and Littmann, 2003). The listed works discuss various lineages of this family.

Order GYMNOTIFORMES (32)—American knifefishes.

Body eel-like (compressed or cylindrical); pelvic girdle and fins absent; dorsal fin absent (but see family Apteronotidae); anal fin extremely long (more than 100 rays and extending from near pectoral-fin origin to near posterior tip of body) and employed in forward and backward movements; caudal fin absent or greatly reduced (present only in the apteronotids); restricted gill openings; anal opening under head or pectorals; basal pterygiophores to anal fin with only one section (radial) and a hemispherical cartilaginous head that articulates the fin rays (allowing them to move in a circular motion); electric organs present; suboperculum absent; palatine not ossified; maxilla rudimentary (except *Electrophorus*). The electric organs are derived from muscle cells in most groups (myogenic), or from nerve cells in adult apteronotids (neurogenic). Like catfishes, gymnotiforms are nocturnal. They probably arose in the Neotropical region. They are thought, on the basis of a cladistic study by Fink and Fink (1981, 1996), to be the sister group to the siluriforms (see above under Otophysi).

Five families, 30 genera, and about 134 species (at least 38 additional species are being described giving at least 173 species known, and many additional species no doubt remain to be discovered) (Albert and Crampton, 2005). The classification follows Albert and Campos-da-Paz (1998), Albert (2001), and Albert and Crampton (2005). See family Sternopygidae below for the only known fossil species.

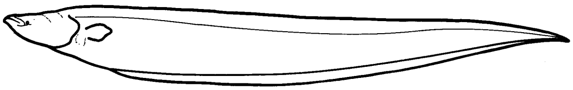
Suborder Gymnotoidei. One family, two genera, *Gymnotus* (32) and the monotypic *Electrophorus*, with 33 species (Albert and Crampton, 2005).

Family GYMNOTIDAE (161)—nakedback knifefishes.

Freshwater; North (southern Mexico only), Central, and South America.

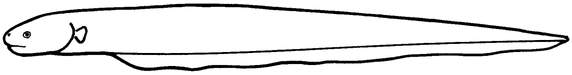
Body rounded or partially so (adult body depth greater than half the body width at the anal-fin origin); body cavity very long with 31–51 (more than 100 in *Electrophorus*) precaudal vertebrae. Maximum length about 2.2 m TL, attained in *Electrophorus electricus*; species of *Gymnotus* reach up to 100 cm. The common name in English for the family is appropriate for the order but is retained here.

Gymnotus (banded knifefishes).



Small scales present; mouth superior; anal fin terminating at a point near the tip of the tail; body subcylindrical; weak electrical discharge. The genus *Gymnotus*, currently with 32 species (Campos-da-Paz, 2003; Albert and Crampton, 2003a, 2005) is substantially more diverse than previously recognized (e.g., Nelson, 1994, recognized only three species). This is the most

widespread genus of the order, extending from southern Mexico (*G. maculosus*) to Argentina (*G. inaequilabeatus*); also in Trinidad (*G. carapo*).
Electrophorus electricus (electric eel).

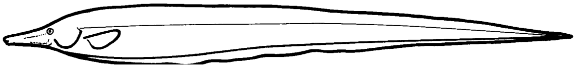


This species was formerly recognized in the family Electrophoridae (electric knifefish), but was placed with the gymnotids in its own suborder; placement here in the same family with *Gymnotus* is based on studies demonstrating their close relationship (Albert and Campos-da-Paz, 1998; Albert, 2001). *Electrophorus* is unique among gymnotiforms in having large electric organs producing lethal discharges (up to 600 volts) for stunning prey (high voltage, low amperage), vascularized oral respiratory organ (they can breathe air), and continuous addition of vertebrae throughout life. In addition: scales absent; mouth terminal; anal fin continuing to the tip of the tail; body rounded. Northern South America (primarily Orinoco and Amazon River basins).

Suborder Sternopygoidei. Body compressed (rarely cylindrical); precaudal vertebrae 12–26 (except *Sternopygus*, which can have as many as 30). Four families, 28 genera, and 101 species.

Superfamily Rhamphichthyoidea

Family RHAMPHICHTHYIDAE (162)—sand knifefishes. Freshwater; South America.



Teeth absent on oral jaws; snout elongate; nostrils relatively close together. The common name tubesnout knifefishes may also used for this group.

Three genera, *Gymnorhamphichthys* (4), *Iracema* (1), and *Rhamphichthys* (7), with 12 species (Ferraris, 2003c; Albert and Crampton, 2005).

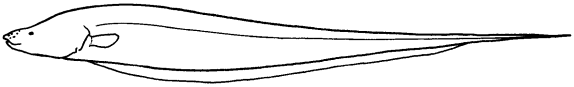
Family HYPOPOMIDAE (163)—bluntnose knifefishes. Freshwater; Panama and South America.

Teeth absent on oral jaws; snout relatively short, not tubular; nostrils well separated; anal-fin origin below or posterior to pectoral-fin base. Maximum length only 35 cm, attained in *Brachyhypopomus brevirostris*; the smallest gymnotiform is *Hypopygus lepturus,* reaching only 9 cm TL. The common names grass and leaf knifefishes may also be used for this group.

Seven genera, *Brachyhypopomus* (7), *Hypopomus* (1, synonym *Parupygus*), *Hypopygus* (2), *Microsternarchus* (1), *Racenisia* (1), *Steatogenys* (3), and *Stegostenopos* (1), with 16 species (Albert and Crampton, 2003b, 2005).

Superfamily Apteronotoidea (Sinusoidea)

Family STERNOPYGIDAE (164)—glass knifefishes. Freshwater; Panama and South America.

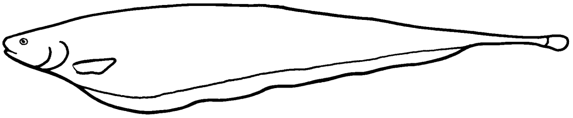


Villiform teeth present on the upper and lower jaws; infraorbital bone series complete, bones enlarged, partial cylinders with slender osseous arches, and with an enlarged sensory canal; snout relatively short; eye relatively large (diameter equal to or greater than distance between nares); anal-fin origin at isthmus. *Eigenmannia vicentespelaea* of Brazil is the only cave-inhabiting gymnotiform (Proudlove, 2005). Maximum length 140 cm, attained in *Sternopygus macrurus.*

The only known fossil, *Humboldtichthys* (formerly *Ellisella*) *kirschbaumi,* known from the Upper Miocene of Bolivia, belongs to this family; as with living gymnotiforms, it could regenerate its caudal skeleton (Gayet and Meunier, 2000; Albert and Crampton, 2005). Species are also known as rattail knifefishes.

Five genera, *Archolaemus* (1), *Distocyclus* (2), *Eigenmannia* (8), *Rhabdolichops* (8), and *Sternopygus* (9), with about 28 species (Albert, 2003a; Albert and Crampton, 2005).

Family APTERONOTIDAE (165)—ghost knifefishes. Freshwater; Panama and South America.



Small caudal fin (with fin rays) present that is not united to the anal fin; fleshy dorsal organ (a longitudinal strip attached to posterodorsal midline, resembling an adipose fin); neurogenic electric organ in adults. Maximum length 1.3 m, attained in *Apteronotus magdalenesis.*

Thirteen genera (with another being described), *Adontosternarchus* (4), *Apteronotus* (19, synonyms *Tembeassu* and *Ubidia*), *Compsaraia* (1), *Magosternarchus* (2), *Megadontognathus* (2), *Orthosternarchus* (1), *Parapteronotus* (1), *Platyurosternarchus* (1), *Porotergus* (2), *Sternarchella* (4), *Sternarchogiton* (1), *Sternarchorhamphus* (1), and *Sternarchorhynchus* (6), with about 45 species (Albert, 2001, 2003b; Albert and Crampton, 2005). The genus *Apteronotus* is artificial and six of the 19 species do not belong in it (Albert and Crampton, 2005).

Subdivision EUTELEOSTEI

This taxon contains all the remaining teleost fishes. There is less than desirable convincing evidence that it is monophyletic, although, as noted by Johnson and Patterson (1996), monophyly is supported by the pattern of supraneural development and presence of a stegural and caudal median cartilages in the caudal skeleton.

Formerly, in Nelson (1994), the Ostariophysi was recognized here at the start of the Euteleostei as suggested by Rosen (1973a) and subsequently by others. However, the Ostariophysi is probably the sister group of the Clupeiformes and it is now placed above in the subdivision Ostarioclupeomorpha (= Otocephala). A critique of problems in euteleostean phylogeny may be found in Johnson and Patterson (1996). Much more work remains to be done before a sound classification of euteleosts can be given.

Twenty-eight orders, 346 families, 2,935 genera, and 17,419 species.

Superorder PROTACANTHOPTERYGII

As stated in Nelson (1994) and still regarded as true, the classification of the protacanthopterygians has been and continues to be unstable, largely because the many characters exhibit a mosaic distribution, show reduction, are otherwise highly modified, or are primitive for the euteleosts. The composition of this assemblage over the past many decades has undergone much reduction, largely as a result of Rosen (1973a). In Nelson (1984) I recognized it with the one order, Salmoniformes, containing four suborders, and in Nelson (1994) with a differing arrangement but with the same content placed in three orders. Much of the work immediately prior to Johnson and Patterson (1996), and employed in Nelson (1994), was by W. L. Fink, D. E. Rosen, and C. P. J. Sanford. Herein, I follow many of the conclusions in the detailed work of Johnson and Patterson (1996) for relationships within the orders. However, because of much continuing disagreement about higher relations, I choose to not change the overall composition followed in Nelson (1994), but the ordinal recognition and sequence are changed. It will be important for all future researchers to carefully study Johnson and Patterson (1996) and the more recent works, mostly molecular, that arrive at differing conclusions. I also encourage careful study of Williams (1987), who indeed may have been correct in certain conclusions not commonly acknowledged (it is unfortunate that his work was not fully published). Nelson (1994) reviewed some of the history of the classification of this group, summarizing some of the conclusions of those with differing views of its classification, such as Williams (1987).

The most major deviation here from Johnson and Patterson (1996) is that they regarded the Esociformes as sister to the Neoteleostei (i.e., not as protacanthopterygians). Although not conclusive, Williams (1987), Arratia (1997, 1999), Zaragueta-Bagils et al. (2002), and López et al. (2004) found esociforms and salmoniforms to be sister taxa; while such a relationship is not formally expressed here, the arrangement is not incompatible with it either. A comparison of the arrangement of Johnson and Patterson (1996) and that given here is as follows:

Four orders with 12 families, 94 genera, and about 366 species.

Johnson and Patterson (1996)	Herein
Euteleostei	Euteleostei
Protacanthopterygii	Protacanthopterygii
Argentiniformes	Argentiniformes
Salmoniformes	Osmeriformes
Salmonoidei	Salmoniformes
Osmeroidei	Esociformes
Neognathi	Neoteleostei—for remaining euteleosts
Esociformes	
Neoteleostei	

Order ARGENTINIFORMES (33)—marine smelts. Complex posterior branchial structure ("epibranchial" organ), termed the "crumenal organ" (Johnson and Patterson, 1996, discussed this and other characters).

Greenwood and Rosen (1971) recognized the two suborders given here as each other's closest relatives; they were included in their suborder Argentinoidei, as two superfamilies, Argentinoidea and Alepocephaloidea, as given in Nelson (1994). The recognition of this taxon at the ordinal level with two suborders follows Johnson and Patterson (1996). Possible fossil groups include the family Pattersonellidae described by L. Taverne in 1982.

Six families, 57 genera, and about 202 species.

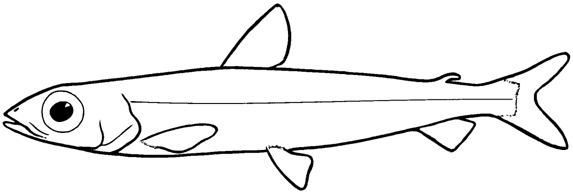
Suborder Argentinoidei. Adipose fin usually present; caudal fin forked; dorsal fin near body center; maxillae and premaxillae (when present) toothless; supramaxilla absent; mouth usually small; branchiostegal rays 2–7; lateral line scales 40–70; swim bladder, when present, physoclistous; mesocoracoid present or absent. Many are bathypelagic. Color usually silvery. Hatch from small eggs (about 1–3 mm diameter) with larval development gradual and transformation to demersal juvenile.

The classification of this taxon is based on Johnson and Patterson (1996:308–309); other references include Kobyliansky (1990, 1998), Mecklenburg et al. (2002), and Carter and Hartel (2003). Johnson and Patterson (1996) and Patterson and Johnson (1997a, b) noted errors involved in an earlier cladistic study of D. P. Begle.

Nineteen genera and about 72 species.

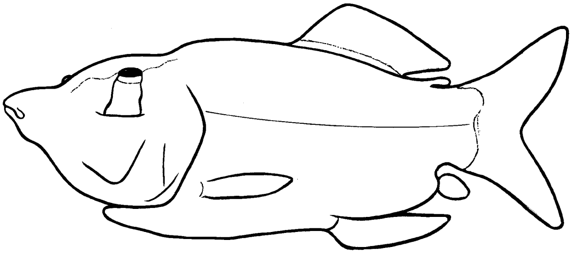
Family ARGENTINIDAE (166)—argentines or herring smelts. Marine; Atlantic, Indian, and Pacific.

Eyes not tubular; adipose fin over anal fin base; postcleithra and mesocoracoid present; dorsal fin origin in front of pelvics; pectoral fin base on ventrolateral surface; dorsal fin rays 10–14; anal fin rays 10–17; pectoral fin rays 11–25; pelvic fin rays 10–15; branchiostegal rays 4–6; vertebrae 43–70 (most with 46–55).



Two genera, *Argentina* and *Glossanodon,* with about 23 species.

Family OPISTHOPROCTIDAE (167)—barreleyes or spookfishes. Marine; tropical to temperate, Atlantic, Indian, and Pacific.



Eyes usually tubular; pectoral fin base on side; pelvic fin base on side in some; adipose fin in some; photophores in some; most lack swim bladder; frontals fused; parietals not meeting on midline (true also for bathylagids); branchiostegal rays 2–4.

Six genera, *Bathylychnops, Dolichopteryx, Macropinna, Opisthoproctus, Rhynchohyalus,* and *Winteria,* with about 11 species.

Family MICROSTOMATIDAE (168)—pencilsmelts. Marine; tropical to temperate seas, Atlantic, Indian, and Pacific (extending from the subarctic to the Antarctic).

Eleven genera and about 38 species.

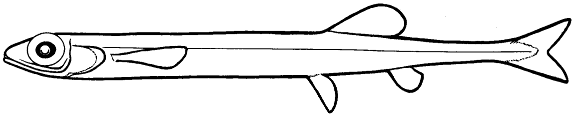
SUBFAMILY MICROSTOMATINAE (PENCILSMELTS). Lateral line and lateral-line scales extending onto tail; postcleithra present; mesocoracoid absent; pectoral fin base on side; dorsal fin rays 9–12; anal fin rays 7–10; pectoral fin rays 7–14;

pelvic fin rays 8–12; branchiostegal rays 3 or 4; vertebrae 41–50. Primarily tropical to temperate latitudes.

Three genera with about 18 species.

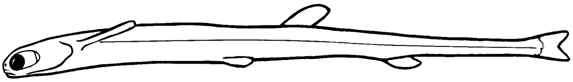
Nansenia. Adipose fin present; dorsal fin in front of pelvics. Fourteen species found from the subarctic to the subantarctic.

Microstoma. No adipose fin; dorsal fin behind pelvics.



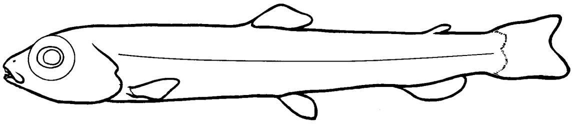
One or two species.

Xenophthalmichthys. No adipose fin; dorsal fin origin behind pelvic fin insertion; eyes tubular (protruding anteriorly); pectoral fin base well up on side, fin with 7 rays; pelvic fin with 7 or 8 rays.



One or two species.

Subfamily Bathylaginae (deepsea smelts). Adipose fin present or absent; postcleithra and mesocoracoid absent; pectoral fin base near ventral surface; dorsal fin rays 6–13; anal fin rays 10–28; pectoral fin rays 7–16; pelvic fin rays 6–11; branchiostegal rays 2; vertebrae 38–55. Extending from the subarctic to the Antarctic.



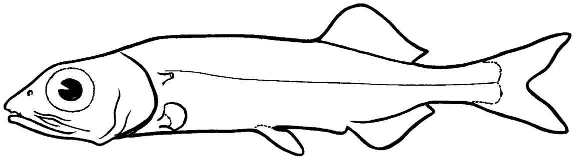
Eight genera, *Bathylagichthys, Bathylagoides, Bathylagus, Dolicholagus, Leuroglossus, Lipolagus, Melanolagus,* and *Pseudobathylagus,* with about 20 species.

Suborder Alepocephaloidei. Dorsal fin inserted well back on body; no adipose fin; upper jaw with teeth except in *Leptochilichthys*; one or two supramaxillae; mouth usually large; no swim bladder; mesocoracoid present; dark-colored fishes. Hatch from large eggs with direct development.

The classification of this taxon is based on Johnson and Patterson (1996: 311–312). They and Patterson and Johnson (1997a, b) noted errors involved in an earlier cladistic study of D. P. Begle. Inoue et al. (2003) placed this taxon in the Ostarioclupeomorpha (= Otocephala) based on molecular characters.

About 38 genera with 130 species.

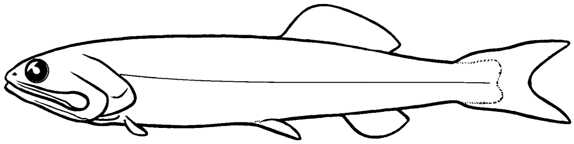
Family PLATYTROCTIDAE (Searsiidae) (169)—tubeshoulders. Marine; all oceans (absent from Mediterranean).



Black shoulder sac apparatus located under shoulder girdle produces blue-green luminous fluid, conspicuous opening through tubular papilla just below lateral line; light organs present in many species (directed horizontally in young and ventrally in adults); subcutaneous canal system, usually connected to scale pockets by pores; pectoral fin rays 14–28; pelvic fin rays 6–10, pelvic fins absent in *Platytroctes apus*; swim bladder absent; branchiostegal rays 4–8; vertebrae 40–52. Maximum length about 30 cm. Most species occur between 300–1,000 m.

Thirteen genera, *Barbantus, Holtbyrnia, Maulisia, Mirorictus, Normichthys, Paraholtbyrnia, Pellisolus, Persparsia, Platytroctes, Sagamichthys, Searsia, Searsioides,* and *Tragularius,* with 37 species (Matsui and Rosenblatt, 1987).

Family BATHYLACONIDAE (170)—bathylaconids. Marine; tropical to temperate latitudes, circumglobal.

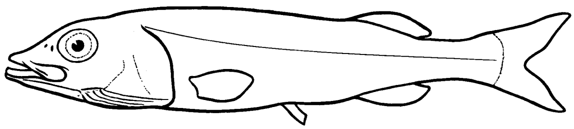


Premaxilla minute, maxilla extending well behind eyes; pectoral fin rays 4–11 (higher in *Herwigia*); branchiostegal rays 7–10, upper ones forming part of posterior gill cover; large cycloid scales.

Regarded as a subfamily of Alepocephalidae in Nelson (1994).

Two genera, *Bathylaco* and *Herwigia,* with three species known from few specimens from circumtropical waters (e.g., Iwamoto et al., 1976; Carter and Hartel, 2003).

Family ALEPOCEPHALIDAE (171)—slickheads. Deep-sea; all oceans.



Teeth usually small; gill rakers long and numerous; shoulder sac apparatus absent; photophores present; pectoral fin rays 7–18; branchiostegal rays 5–8 (12 in the pikelike *Bathyprion*); scales absent in some. Most commonly found below 1000 m.

Leptochilichthys, with three species, deep-sea, rare but widespread, was placed in its own family, Leptochilichthyidae, in Nelson (1994).

About 23 genera (e.g., *Alepocephalus*, *Asquamiceps*, *Aulastomatomorpha*, *Bajacalifornia*, *Bathyprion*, *Bathytroctes*, *Bellocia*, *Conocara*, *Ericara*, *Leptochilichthys*, *Leptoderma*, *Narcetes*, *Photostylus*, *Rinoctes*, *Rouleina*, *Talismania*, and *Xenodermichthys*) with at least 90 species (e.g., Markle and Merrett, 1980; Markle and Sazonov, 1996; Sazonov, 1999; Mecklenburg et al. (2002).

Order OSMERIFORMES (34)—freshwater smelts. Posterior shaft of vomer short; mesopterygoid teeth reduced (absent in *Lepidogalaxias*); articular absent or reduced; pterosphenoid usually with ventral flange; maxilla included in gape of mouth (the toothless maxilla is excluded from the gape in *Prototroctes* and *Lovettia* and almost so in *Aplochiton*); adipose fin present or absent; radii absent on scales; loss of basisphenoid and orbitosphenoid bones.

Osmeriforms spawn in freshwater except for *Osmerus eperlanus*, and perhaps one or two salangines; only some salangines and *Nesogalaxias* occur in tropical regions.

The classification of this taxon, with the removal of the Argentinoidei as given in Nelson (1994), is based on Johnson and Patterson (1996:307). However, they recognized it at the subordinal level and as sister to Salmonoidei (placing both suborders in the order Salmoniformes). López et al. (2004) gave molecular evidence supporting a close relationship of this order with Stomiiformes and of their Osmeroidei (recognized as Osmeridae here) with Retropinnidae.

Possible fossils include the piscivorous marine Late Cretaceous *Spaniodon* (Taverne and Filleul, 2003).

Recognized with two superfamiles, 3 families, 22 genera, and 88 species.

Superfamily Osmeroidea. Egg surrounded by an adhesive anchor membrane. The Sundasalangidae, previously placed with this group, is placed in the Clupeidae.

Family OSMERIDAE (172)—smelts. Marine, anadromous, and coastal freshwater; Northern Hemisphere in Arctic, Atlantic, and Pacific.

Palatine bone dumbbell shaped; notch in dorsal margin of opercle; pelvic axillary process absent; adipose fin present; lateral line present, but usually incomplete; dorsal fin rays 7–14; anal fin rays usually 11–17, but up to 23 in *Mallotus*; pelvic fin rays eight (one additional short ray in *Mallotus*); principal caudal rays 19 (17 branched), caudal fin forked; branchiostegal rays 5–10; teeth on premaxilla, maxilla, dentary, and inner mouth bones in extant species; mesocoracoid present; pyloric caeca 0–11, over 300 in *Plecoglossus*; vertebrae 51–78. Color silvery. Maximum length about 40 cm; most species less than 20 cm.

The oldest fossil osmerid is the Paleocene freshwater *Speirsaenigma lindoei* from Alberta, whose closest living relative appears to be *Plecoglossus altivelis* (Wilson and Williams, 1991); other fossils include the European *Enoplophthalmus.*

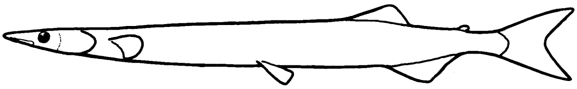
Three subfamilies recognized after Johnson and Patterson (1996), with 11 genera, and about 31 species.

SUBFAMILY HYPOMESINAE. One genus, *Hypomesus,* with about six species (Saruwatari et al., 1997).

SUBFAMILY PLECOGLOSSINAE. One genus, *Plecoglossus.* The one species, *Plecoglossus altivelis* (Ayu), an anadromous and freshwater fish from Japan, Korea, Taiwan, and China, differs from other osmerids in having more than 300 pyloric caeca. Most Ayu live only one year, dying after spawning. Anadromous individuals spawn in the lower reaches of rivers with the newly hatched fish drifting into the ocean. This is a commercially important fish, as are some other smelt, and it is also produced in aquaculture.

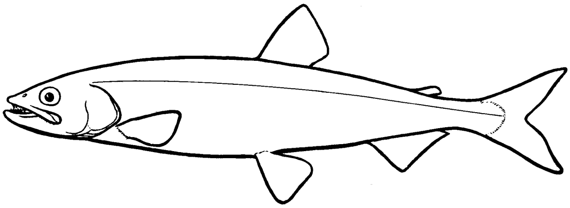
SUBFAMILY OSMERINAE

TRIBE SALANGINI. Five genera, *Mallotus* (Capelin), *Neosalanx, Protosalanx, Salangichthys,* and *Salanx* (shown in figure), with about 16 species.



Mallotus villosus is circumpolar, occurring almost throughout the range of the family. The last four genera of about 15 species, anadromous and freshwater occurring in Sakhalin, Japan, Korea, China, to northern Vietnam, were previously placed in a separate family, Salangidae (icefishes or noodlefishes).

TRIBE OSMERINI



Four genera, *Allosmerus, Osmerus, Spirinchus,* and *Thaleichthys* (Eulachon).

Superfamily Galaxioidea. Usually no pyloric caeca; no mesocoracoid; no supramaxillae; 18 or fewer principal caudal fin rays; no upturned vertebrae. These cold-water fishes form the dominant element in the freshwater fish fauna of the Southern Hemisphere.

Eleven genera and about 57 species. The recognition of two families and their compostion with two subfamilies of Galaxiidae follows Johnson and Patterson (1996). For various controversies in our knowledge of relationships of this group see the discussion below under family Galaxiidae. In addition, Waters et al. (2002), in their mitochondrial DNA analysis, dispute the conclusions of Johnson and Patterson (1996) based on osteology and conclude that retropinnids and osmerids are sister taxa. The conclusions of Waters et al. (2002) are not accepted here, even if compatible with life history stratagies of the taxa; discussed reasons for disagreement between molecular and morphological data matrices and their paper is recommended reading for all ichthyologists.

Family RETROPINNIDAE (173)—New Zealand smelts. Freshwater and brackish water (some partially marine); New Zealand, Chatham Islands, southeastern Australia, and Tasmania.

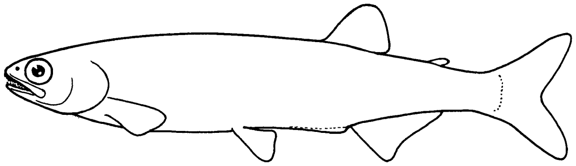
Adipose fin present; caudal fin forked, with 16 branched rays; cycloid scales present, but no lateral line on body; small horny keel along midventral abdomen, in front of anus; vomerine, palatine, and basibranchial teeth present; branchiostegal rays usually five or six; pyloric caeca absent; only left gonad present; cucumber odor to body in most species when captured (this has also been detected in some osmerids).

Three genera with about five species.

SUBFAMILY PROTOTROCTINAE (SOUTHERN GRAYLINGS). Dorsal fin forward, above pelvic fin; maxilla toothless; horny shelf surrounding lower jaw; vertebrae 62–72. Length up to 35 cm.

One species, *Prototroctes maraena*, in southeastern Australia and Tasmania. Another species of this genus in New Zealand is apparently now extinct (McDowall, 1990).

SUBFAMILY RETROPINNINAE (SOUTHERN SMELTS). Dorsal fin posterior to pelvics and a little in front of anal fin origin; maxilla sometimes with teeth; vertebrae 45–63. Maximum length about 15 cm, usually less than 10 cm. These small silvery fishes occur in coastal seas, estuaries and lowland rivers, and inland lakes and rivers.



Two genera, *Retropinna* and *Stokellia*, with about four species. *Retropinna* has about three highly variable species, one in Australia (southern Queensland to eastern South Australia), one in Tasmania, and one in New Zealand (including the Chatham Islands; in some areas of New Zealand, both diadromous and lake-resident forms occur, and in at least one drainage there appears to be reproductive separation of the two forms); *Stokellia anisodon* is endemic to the South Island of New Zealand (McDowall, 1990).

Family GALAXIIDAE (174)—galaxiids. Freshwater and diadromous; Australia, New Zealand, New Caledonia, southernmost Africa, and southern South America.

Vomer toothless; hypurals 5; principal caudal fin rays 16 or fewer.

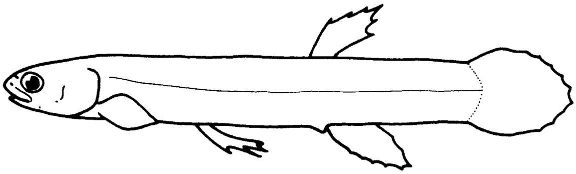
There is still disagreement on the classification of this group. *Lepidogalaxias* has many unique features and its phylogenetic relationships have been subject to much debate. Johnson and Patterson (1996) presented strong evidence that *Lepidogalaxias salamandroides* (recognized in its own family, Lepidogalaxiidae, in Nelson, 1994) and the other galaxiids form a monophyletic group (however, in their cladogram, a number of characters in *Lepidogalaxias* were interpreted as reversals). Although separate families could still be maintained, I also now place the former Lepidogalaxiidae and Galaxiidae into synonymy and have adopted most aspects of their cladogram in the present classification. They present strong evidence of a sister-group relationship between *Lepidogalaxias* and *Lovettia* (placing both in their subfamily Lepidogalaxiinae); however, I choose to maintain the same relationships as given in Nelson (1994), but downgrading of group names, given the suggestive evidence of Williams (1996) that *Lovettia* and *Aplochiton* may form a clade (they were placed in their own family, Aplochitonidae, in some works, e.g., Williams, 1997). Williams (1997) regarded *Lepidogalaxias* as the sister group to his Galaxiidae + Aplochitonidae. Waters et al. (2000) argued that it is not a galaxiid, and that an esocoid relationship might be possible (at least they could not reject such a hypothesis), a view suggested by D. E. Rosen in 1974; they also found in their analysis *Galaxias* to be polyphyletic (whether this is troublesome for molecular or morphological analysis I leave to future investigators, but *Galaxias* is here regarded as monophyletic). Much of what we know about galaxiids is due to the work of R. M. McDowall.

Anderson (1998) described a possible galaxiid, *Stompooria,* from the Late Cretaceous in South Africa; he also notes other papers on fossil *Galaxias* from New Zealand.

Eight genera and 52 species.

SUBFAMILY LEPIDOGALAXIINAE. Body elongate and slender; dorsal fin posterior to pelvic fin, above anal fin; no adipose fin; dorsal fin rays 5–7; anal fin rays 11 or 12; scales very thin; males with modified anal fin rays and a sheath of scales over anal fin base; gill rakers 4–7; eyes lacking eye muscles (in compensation for the inability to rotate the eye in its socket, the fish has an unusual ability to bend its neck downwards and sideways); vertebrae 44–47. Freshwater; southwestern Australia.

This species survives drought periods by burrowing into damp sand. Fertilization is internal (fertilized eggs are laid). Maximum length about 6.7 cm SL.



One species, *Lepidogalaxias salamandroides* (Salamanderfish) (Berra, 1997; Berra and Pusey, 1997).

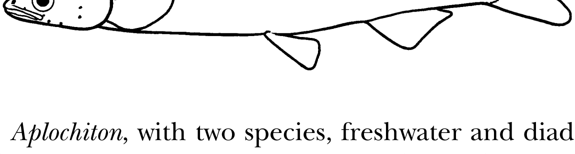
SUBFAMILY GALAXIIDAE. Caudal fin with 12–14 branched rays; scales absent, but lateral line present; no horny keel along abdomen; maxillary, vomerine, palatine, and basibranchial teeth absent; gonads paired; cucumber odor absent. Freshwater and diadromous; Australia, New Zealand, New Caledonia, southernmost Africa, and southern South America.

Seven genera and about 51 species.

TRIBE LOVETTIINAE. Adipose fin reduced but present; dorsal fin anteriorly placed, above pelvic fin, with 7–9 rays; caudal fin forked; branchiostegal rays usually 5 or 6; pyloric caeca absent; maxilla excluded from gape; postcleithrum present; vertebrae 52–58. Maximum length about 7.7 cm.

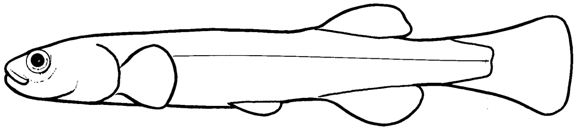
One species, *Lovettia sealii*, anadromous, known only from Tasmania (McDowall, 1990). *Lovettia* and a few *Galaxias* constitute the Tasmanian whitebait fishery.

TRIBE APLOCHITONINAE. Adipose fin present; dorsal fin anteriorly placed, above pelvic fin, with 11–14 rays; caudal fin forked; branchiostegal rays 3 or 4; pyloric caeca long, 1 or 2; maxilla almost excluded from gape; postcleithrum absent; vertebrae 64–73. Maximum length 38 cm, attained in *Aplochiton taeniatus*



One genus, *Aplochiton*, with two species, freshwater and diadromous, from southern Chile, parts of western Argentina in the Andes, Tierra del Fuego, and the Falkland Islands (= Malvinas Islands) (McDowall, 1990).

TRIBE GALAXIINAE. No adipose fin; dorsal fin posteriorly placed near tail (originating above pelvics in *Paragalaxias*); caudal fin usually truncate to emarginate (forked or rounded in some); pelvic fins absent in most *Neochanna*; branchiostegal rays 5–9; pyloric caeca 0–6 (usually 2); vertebrae 37–66.



Most members are confined to freshwater, although some species are partially anadromous, having larvae that descend streams after hatching and spend some time in the ocean. The 16-cm *Galaxias maculatus* is peculiar among galaxiids in that ripe adults in New Zealand usually migrate down streams and spawn in estuarine grasses in the upper tidal flats at spring tides. The eggs usually hatch after two weeks in future high tides when they are reimmersed in water and the larvae are washed out to sea (they have been found as far as 700 km from shore). The species is marginally catadromous (with a lunar rhythm), although landlocked populations are known. The juveniles of several species of *Galaxias* can move up damp rock faces or dams and *G. brevipinnis* of New Zealand is particularly good in moving upstream in rapid waters. Species of *Neochanna* (mudfishes) can live in swamps and are able to aestivate during dry periods. The term whitebait is applied to the transparent young that move from the sea into rivers at approximately six months of age. In New Zealand, several species of *Galaxias* constitute the whitebait commercial and recreational fishery.

Maximum length 58 cm, attained in *Galaxias argenteus* of New Zealand; most species are less than 20 cm.

Five genera, *Brachygalaxias, Galaxias* (synonym *Nesogalaxias*), *Galaxiella, Neochanna,* and *Paragalaxias,* with about 48 species (e.g., McDowall, 1990, 1997, 2003; McDowall and Wallis, 1996; McDowall and Chadderton, 1999; Waters et al., 2000; Ling and Gleeson, 2001; Wallis et al., 2001; McDowall and Waters, 2002). Species abundance is greatest in Australia, especially in Tasmania and southeastern Australia, and in New Zealand. The variable *Galaxias zebratus* occurs in South Africa (two or more species may be represented, McDowell, 2001), and the only species of *Nesogalaxias* occurs in the uplands of New Caledonia. The most widespread species, *G. maculatus,* occurs in Australia, Tasmania, Lord Howe Island, New Zealand, Chatham Islands, and southern South America (Chile, Patagonia, Tierra del Fuego, and Falkland Islands). Berra (2001) and Wallis and Waters (2003) gave details on the distribution of galaxiid fishes.

Order SALMONIFORMES (35)—trouts. This taxon is restricted to the family Salmonidae. Cretaceous fossils that may be related to salmoniforms include *Kermichthys* and *Paravinciguerria,* studied by L. Taverne in the 1990s.

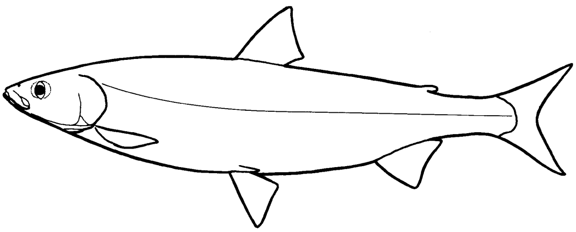
Family SALMONIDAE (175)—salmonids. Freshwater and anadromous; Northern Hemisphere.

Deep posterior myodome with eye musculature passing through and attaching to trunk muscles; adipose fin present; mesocoracoid present; gill membranes extending far forward, free from isthmus; pelvic axillary process present; last three vertebrae turned up; 11–210 pyloric caeca; 7–20 branchiostegal rays; vertebrae 50–75; tetraploid karyotype; parr marks in young of most species. Maximum length up to 1.5 m. This family has high value in sport and commercial fisheries.

The biological diversity in this family is greater than is recognized in our current taxonomy with its nomenclatural limits. Many biological species exist that are not named (e.g., of whitefishes and char). However, there is a serious problem of how many nominal species to recognize as valid (according to various species definitions). Some workers might combine various species (for an example, see Nelson et al., 2004:208–209), which others might split. I have opted to not change the species numbers recognized in Nelson (1994) pending more comprehensive studies. The classification of this group is as presented in Nelson (1994), based largely on the works of A. W. Kendall, Jr., and R. J. Behnke in 1984, C. P. J. Sanford in 1990, and R. F. Stearley and G. R. Smith in 1993. These studies agree that the sequenced cladistic relationships remain as Coregoninae, Thymallinae, and Salmoninae, with the latter two constituting a monophyletic group. Some authors prefer to recognize two of the subfamilies at the family level, e.g., Coregonidae and Salmonidae (containing the subfamilies Thymallinae and Salmoninae) (e.g., Johnson and Patterson, 1996; Sanford, 2000), or all three at the family level (e.g., Reshetnikov et al., 1997). This is a subjective matter, and I prefer to maintain the one family. While it is almost an impossible task, it is important to attempt some uniformity in principles of establishing family limits across orders, while respecting the desire to maintain some historical uniformity and consider the levels used by the specialists. A listing of species by broad geographic areas is found in Kottelat (1997), Reshetnikov et al. (1997), and Nelson et al. (2004).

Three subfamilies with 11 genera and about 66 species.

SUBFAMILY COREGONINAE. Fewer than 16 dorsal fin rays; scales large, fewer than 110 along lateral line; no teeth on maxilla; vomer usually small and without teeth; orbitosphenoid present; suprapreopercular absent. Three genera and about 32 species.



New insights into the relationships of coregonines is being provided by research using techniques of molecular biology (e.g., isozymes and mitochondrial DNA). The results of various workers do not always agree, but studies suggest that the subgenus of ciscoes (*Leucichthys*) is not monophyletic and that *Stenodus* falls within *Coregonus* (Hamada et al., 1998). Sanford (2000) gave seven morphological characters supporting monophyly of his Stenodinae, with the one species, and considered it sister to *Coregonus* + *Prosopium*. As with Nelson et al. (2004), I prefer to retain recognition of *Stenodus* until additional evidence is published on its sister-group relationship (within *Coregonus* or not).

Prosopium (round whitefishes). Small mouth with weak or no teeth; single flap between nostrils; basibranchial plate present; young with parr marks. Freshwater; northern Northern Hemisphere; six species. One species occurs in both northern North America and Siberia; three are endemic to Bear Lake, Utah-Idaho, one of which is ciscolike.

Coregonus (lake whitefishes and ciscoes). Small mouth with weak or no teeth; two flaps between nostrils; no basibranchial plate; young without parr marks. Freshwater (occasionally anadromous along Arctic coastline), northern Northern Hemisphere; 25 species (eight lake whitefishes and 17 ciscoes).

The two subgenera are probably not strictly monophyletic. In North America there is good separation between the two groups in gill-raker number; the lake whitefishes almost always have 35 or fewer gill rakers, the ciscoes 36 or more. In Eurasia, however, one lake whitefish (*C. muksun*) usually has 51–56 gill rakers, whereas one cisco (*C. tugun*) has 25–39.

Subgenus *Coregonus* (lake whitefishes). Mouth subterminal; maxillae usually not extending beyond front margin of eye. Bottom and plankton feeders.

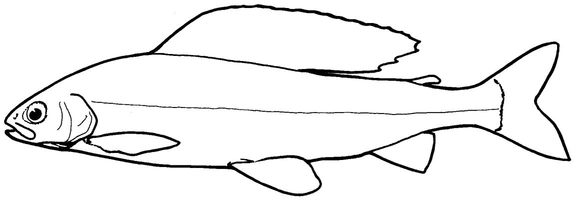
Circumpolar, but most species in northwestern Eurasia. The dominant ones are *C. lavaretus* complex in Eurasia and *C. clupeaformis* complex in North America.

Subgenus *Leucichthys* (ciscoes). Mouth superior or terminal; maxillae normally extending beyond front margin of eye. Usually plankton feeders.

Circumpolar, but most species in eastern North America in Great Lakes.

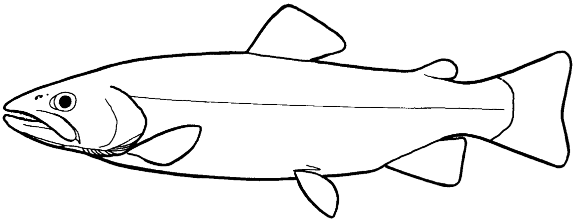
Stenodus leucichthys (Inconnu). Large mouth with many small teeth on jaws, vomer, and palatine; two flaps between nostrils. Anadromous; Arctic Asia and North America.

SUBFAMILY THYMALLINAE. More than 17 dorsal fin rays; teeth on maxilla; orbitosphenoid absent; suprapreopercular absent.



One genus, *Thymallus* (graylings), freshwater; Northern Hemisphere; four or five species—one in Europe, two in Mongolia, one variable species widespread across northern Asia and North America, and possibly one from the Khor River (Amur Basin). Affinities between North American and Eurasian grayling are covered by Stamford and Taylor (2004).

SUBFAMILY SALMONINAE. Fewer than 16 dorsal fin rays; scales small, more than 110 along lateral line; teeth on maxilla; orbitosphenoid present (sometimes absent in *Salvethymus svetovidovi*); suprapreopercular present. Seven genera and about 30 species. For a discussion of North American species see Behnke (2002).



Certain species, such as *Salvelinus fontinalis*, *Salmo trutta*, and *Oncorhynchus mykiss* (synonym *Salmo gairdnerii*), have been introduced virtually throughout the world.

Fossils include i) the Eocene *Eosalmo*, the oldest salmonine and the primitive sister group to all other salmonines (Wilson and Williams, 1992; Stearley and Smith, 1993); ii) the large Miocene *Oncorhynchus rastrosus* from Oregon and California, which had over 100 gill rakers; and iii) the southernmost occurring (historically) salmonid, the Pliocene *Oncorhynchus australis* of Mexico (Stearley and Smith, 1993). These fossils demonstrate that *Oncorhynchus* arose at least six million years ago.

Brachymystax lenok (lenok). Freshwater; northern Asia to Korea (Holcík et al., 1988).

Acantholingua. Freshwater; one species in one lake in the former Yugoslavia.

Salmothymus (synonym *Platysalmo*). Freshwater; with about three species—two in the southern part of the former Yugoslavia and one in Turkey.

Hucho (huchen or taimen). Freshwater and anadromous; northern Asia to Japan, Danube basin of Europe; two or three species (Holcík et al., 1988). The subgenus *Parahucho*, erected by V. D. Vladykov in 1963, should be recognized if studies confirm that *Hucho* is otherwise paraphyletic as suggested in a 1995 molecular study by R. B. Phillips and colleagues.

Salvelinus (chars or charrs). Biological information on the species of this genus and some problems of char taxonomy are presented by Behnke (2002).

Subgenus *Salvethymus*. One species, *S. svetovidovi* (Longfin Char), described by I. A. Chereshnev and M. B. Skopets in 1990, known only from Lake

El'gygytgyn, a cold, clear, ultraoligotrophic lake formed in a meteorite crater about 3.5 million years ago and having been a refugium during the Pleistocene glaciation. This planktivore is unique among salmonines in several features—for example, it has an unusually high number of gill rakers and a very reduced orbitosphenoid (sometimes absent) and basisphenoid. Reasons for not recognizing *Salvethymus* at the generic level, as proposed by Chereshnev and Skopets (they also recognized *Baione* and *Cristivomer* as genera), are given in Nelson (1994), based on a 1989 paper by R. J. Behnke.

Subgenus Baione. Two species, *Salvelinus fontinalis*, Brook Trout (freshwater and anadromous, eastern North America), and *S. namaycush*, Lake Trout (freshwater, northern North America, recognized by some in the subgenus or genus *Cristivomer*).

Subgenus Salvelinus. Freshwater and anadromous; Northern Hemisphere. About eight species (e.g., Arctic Char, Dolly Varden, and Bull Trout). Perhaps the northernmost record for any freshwater fish is that for anadromous and freshwater Arctic Char in Lake Hazen, Ellesmere Island, Canada. The work of Stearley and Smith (1993) suggested that several species recognized here belong in the *Baione* lineage; for example, in their cladogram, Bull Trout and Lake Trout are sister species. E. B. Taylor and colleagues have done many studies on hybridization and its significance in char species (e.g., Taylor, 2004).

Salmo (Atlantic trouts). Freshwater and anadromous; North Atlantic basin (northeastern North America and Europe) and European Arctic. Fall spawning. About five species (e.g., Atlantic Salmon and Brown Trout, both with anadromous and freshwater populations).

Oncorhynchus (Pacific trouts and Pacific salmon). About 11 species.

Subgenus Rhabdofario (Pacific trouts). Freshwater and anadromous; North Pacific basin (eastern slopes of parts of the Rocky Mountains in North America) and south to Mexico and Arizona. Spring spawning; unlike Pacific salmon, anadromous individuals do not necessarily die after spawning. Four species—Mexican Golden Trout, Cutthroat Trout, Gila Trout, and Rainbow Trout (Behnke, 2002)—listed respectively from primitive to advanced with rainbow trout being the sister group to the Pacific salmon (Stearley and Smith, 1993). There is much diversity in the western trouts, and there is disagreement on what constitutes a species or a subspecies; recognizing only four species of Pacific trout is a very conservative taxonomic treatment.

It has long been recognized that Pacific trout and Pacific salmon share a close relationship; cladistically, they form a monophyletic group. The relationships of the species of Pacific trout and the endemic Japanese salmon are poorly known. Stearley and Smith (1993) provide evidence that the subgenus *Rhabdofario*, as recognized here for Pacific trout, is paraphyletic, with the four extant species forming separate branches on a comblike cladogram. Pending more evidence to the contrary, I prefer to recognize the Pacific trout in their own subgenus.

Subgenus Oncorhynchus (Pacific salmon). Usually anadromous, occasionally freshwater; North Pacific coastal areas from Taiwan (with the native *O. masou formosanus*) and Japan to California and adjacent parts of Arctic Ocean. Fall spawning. Six or seven species (five occur in Asia and North America, one or two being endemic to far east Asia).

Pacific salmon comprise an important fishery, and a great deal is known of their biology. They are a rich source of material for studies in raciation. They have a strong homing ability, usually returning to their natal streams for spawning. *Oncorhynchus masou* (Masu Salmon or Cherry Salmon) and *O. rhodurus* (Amago) are the most "troutlike"; the latter nominal species is probably conspecific with *O. masou*—both occur only in far eastern Asia. *O. kisutch* (Coho Salmon) and *O. tshawytscha* (Chinook Salmon) are somewhat intermediate between the Japanese endemics and the next three species. *Oncorhynchus keta* (Chum Salmon) and *O. gorbuscha* (Pink Salmon) usually spawn in the lower reaches of rivers and are the most "marinelike." Individuals of *O. gorbuscha* have a rigid two-year life span, with one or the other or both of the even- and odd-year stocks existing allochronously in the same stream. Individuals of other species have variable lifespans: those of *O. nerka* (Sockeye Salmon) live as long as eight years in their northern range (Alaska). In this species the anadromous form (sockeye) has, throughout most of its range, given rise to freshwater populations (kokanee), which occur in sympatry or allopatry (usually in "landlocked" lakes) with the parental anadromous form. All individuals of the last five species and all anadromous individuals die after spawning; some non-anadromous *O. masou* may repeat spawn.

Order ESOCIFORMES (Haplomi, Esocae) (36)—pikes. Maxilla toothless but in gape of mouth; no adipose fin; dorsal and anal fins located posteriorly; no breeding tubercules; no pyloric caeca; no mesocoracoid.

Four genera and at least 10 species.

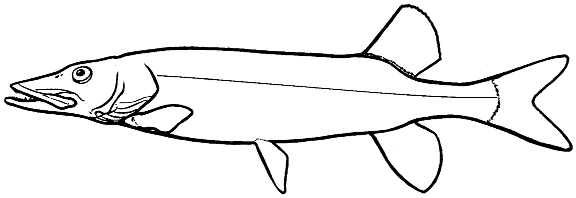
This group includes the extinct family Palaeoesocidae with the Eocene *Palaeoesox* and the Paleocene-Eocene *Boltyshia.*

The evidence for monophyly of this taxon is strong. However, now with the work of López et al. (2000, 2004), we have serious doubts about the monophyly of the two families. They found *Dallia* and *Novumbra* to be more closely related to *Esox* than to *Umbra,* with *Novumbra* being sister to *Esox.* Their proposed classification would thus be:

Esocidae—*Esox, Novumbra,* and *Dallia*
Umbridae—*Umbra*

I have not adopted this change; more work must be done on how anatomical characters might be reinterpreted to agree, or not, with their results and on the effect of rooting their trees differently depending on assumptions of out-groups.

Family ESOCIDAE (176)—pikes. Freshwater; Northern Hemisphere.



Snout produced; caudal fin forked, with 40–50 rays (17 branched, rarely 16); lateral line complete; infraorbital canal with eight or more pores; branchiostegal rays 10–20; nasals present; vertebrae 43–67. Maximum length 1.4 m, obtained in *Esox masquinongy.*

The oldest members of the family are fossil species of the Late Cretaceous *Estesox* and *Oldmanesox.* The oldest known fossil *Esox* species, *E. tiemani,* is from Paleocene formations of about 62 million years ago in Alberta and are relatively similar in appearance to *E. lucius,* more so than Tertiary *Esox* species from Eurasia. L. Grande (1999) reviews both fossil and extant species. The oldest pike found outside North America is from the early Eocene of China (Chang and Zhou, 2002). Much of our knowledge on the fossil species comes from the work of M. V. H. Wilson.

One genus, *Esox,* with one circumpolar species (*E. lucius,* the Northern Pike), one species in Siberia (*E. reicherti,* the Amur Pike), and three species restricted to eastern North America (*E. masquinongy,* the Muskellunge, *E. niger,* the Chain Pickerel, and *E. americanus,* with two subspecies, the Redfin Pickerel and the Grass Pickerel) (L. Grande, 1999; T. Grande et al., 2004). Grande et al. (2004) and López et al. (2004) found strong support for the monophyly of the genus, and for the monophyly of the subgenera *Esox* (i.e., pikes) and *Kenoza* (i.e., pickerels). Much of our knowledge on the species of this family comes from the extensive work of E. J. Crossman and colleagues.

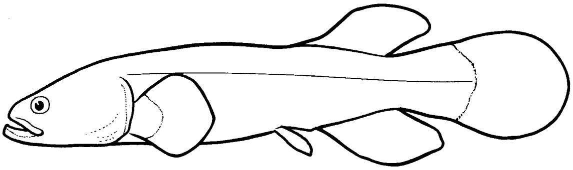
Family UMBRIDAE (177)—mudminnows. Freshwater; parts of Northern Hemisphere.

Snout not produced; caudal fin rounded, with 20–30 rays (8–19 branched); lateral line faint or absent; infraorbital canal with three or fewer pores; branchiostegal rays 5–8; nasals absent; vertebrae 32–42. Maximum length 20 cm.

For a review of past differences of opinion on the relationships of the genera, see Nelson (1994); for an alternate proposal that would restrict this family to one genus, *Umbra,* see above under order Esociformes.

Three genera with at least five species. Fossils include *Proumbra* of Oligocene in western Siberia, and *Novumbra* of Oligocene in Oregon.

Dallia. Pectoral fin rays 29–38; pelvic rays usually two or three (rarely none or one); dorsal fin rays 10–16; anal fin rays 11–16; lateral scales 76–100; vertebrae 40–42; Baudelot's ligament ossified (only esociform with it ossified); intercalar and postcleithrum absent; much of pectoral skeleton unossified (all based on *Dallia pectoralis*, in the strict sense).

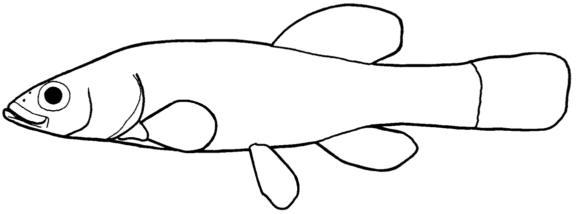


One to three species, *D. pectoralis* (Alaska Blackfish), in northeastern-most Siberia and Alaska and the nominal species *D. admirabilis* and *D. delicatissima* from northeastern Siberia (pelvic fin rays absent in some specimens of the latter). Mecklenburg et al. (2002) recognized all nominal species as synonyms of *D. pectoralis*, but noted those workers recognizing three species.

Novumbra. Pectoral fin rays 18–23; pelvic fin rays six or seven; dorsal fin rays 12–15; anal fin rays 11–13; lateral scales 52–58; vertebrae 37–40.

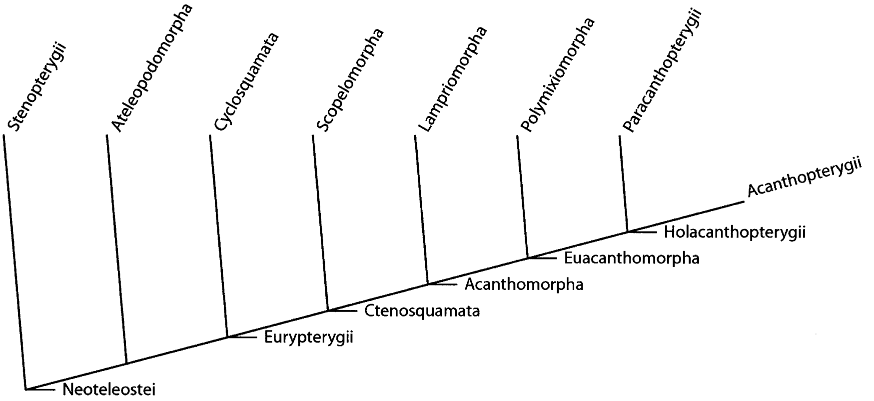
One species, *Novumbra hubbsi*, confined to the Olympic Peninsula in western Washington, occurring primarily in the Chehalis system.

Umbra. Pectoral fin rays 11–16; pelvic fin rays 5–7; dorsal fin rays 13–17; anal fin rays 7–10; lateral scales 30–36; vertebrae 32–37.



Three species, *U. limi* in east-central North America, *U. pygmaea* in eastern United States, and *U. krameri* in southeastern Europe.

NEOTELEOSTEI (NEOTELEOSTS). The eight superorders Stenopterygii, Ateleopodomorpha, Cyclosquamata, Scopelomorpha, Lampriomorpha, Polymixiomorpha, Paracanthopterygii, and Acanthopterygii comprise the Neoteleostei, a monophyletic group not given formal rank here. Support for monophyly for many of these superorders is not as strong as for the Neoteleostei itself. Rosen (1973a) recognized the taxon in its present form on the basis of three synapomorphies, one of which, the retractor dorsalis muscle (= Rosen's retractor arcuum branchialium—RAB), is still regarded as valid. The four synapomorphies Johnson (1992) found to be the best indicators for its monophyly of the neoteleosts are given in Nelson (1994). Although not a synapomorphy, most neoteleosts have ascending and articular premaxillary processes on the premaxillae.



Cladogram showing the relationships of the neoteleosts as presented here. The sequenced superorders are shown at the top with higher unranked taxa shown on the main axis. The Euacanthomorpha and Holacanthopterygii, from Johnson and Patterson (1993), are considered valid taxa, but are not incorporated in this classification.

Monophyly of the neoteleosts has been discussed and strengthened by many workers, such as Johnson (1992), Johnson and Patterson (1993), and Stiassny (1986, 1996). Much insightful anatomical information on all following major lineages is found in Springer and Johnson (2004). It is encouraging also that the detailed molecular study of Miya et al. (2003) supported neoteleostean monophyly.

Superorder STENOPTERYGII

This group is recognized for the order Stomiiformes, a group that is probably the sister group to all remaining neoteleosts as was recognized by Rosen (1973a) and continues to be accepted. Proposed relationships based on molecular studies are not given here. Members of the stomiiforms retain some of the primitive characters of the salmoniforms and were once classified with them. The order Ateleopodiformes is removed from this superorder where it was placed in Nelson (1994) and is now placed in its own superorder to better reflect the tentative conclusion of Olney et al. (1993) that it forms an unresolved trichotomy with the stomiiforms and the eurypterygians.

Order STOMIIFORMES (Stomiatiformes) (37)—dragonfishes. Luminescent organs (photophores) present; chin barbel present in some; premaxilla and maxilla in gape of mouth—both have teeth; mouth extending past eye in most; scales, if present, cycloid and easily lost; pectoral, dorsal, or adipose fins absent in some; ventral adipose fin present in some; pelvic fin rays 4–9; branchiostegal rays 5–24. Color in most is dark brown or black; some are silvery (primarily some Gonostomatoidei). Mostly tropical to temperate; many are deep-sea.

Rosen (1973a) first proposed recognition of this group at the ordinal level. Monophyly of the stomiiforms was further supported by Fink and Weitzman

(1982) and Harold and Weitzman (1996) on the basis of various synapomorphic characters; the characters involved, for example, the unique (for teleosts) histology of the photophores and the type of tooth attachment. Major contributions to this group were made by R. H. Gibbs, Jr., in the 1960s to 1980s, and by W. L. Fink and S. H. Weitzman in the 1970s and 1980s. A satisfactory classification cannot yet be established, and I generally follow the classification used in Nelson (1994), with exceptions noted.

Five families, 53 genera, and about 391 species. All species are marine. Possible fossil stomiiforms are discussed by Fink (1985) and references therein.

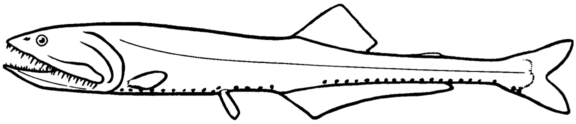
Family DIPLOPHIDAE (178). *Incertae sedis.* Adipose fin absent; anal fin rays 36–69; vertebrae 44–94.

The genera *Diplophos*, *Manducus*, and *Triplophos* were provisionally placed in the subfamily Diplophinae of the family Gonostomatidae in Nelson (1994). Harold (1998) provided phylogenetic evidence that *Diplophos* and *Manducus*, as proposed earlier by studies by W. L. Fink and S. H. Weitzman, are sister taxa and possibly sister to all other stomiiforms; the worldwide *Triplophos hemingi* may be more closely related to phosichthyids than to gonostomatids. This family is provisionally recognized in order to, as far as possible, place all extant genera in a family. Given the best evidence of relationships from Harold (1998) it may be that *Diplophos* and *Manducus* should be so placed, but not *Triplophos.*

Three genera, *Diplophos*, *Manducus*, and *Triplophos,* with eight species.

Suborder Gonostomatoidei. Four bony pectoral fin radials (except one in *Cyclothone*); serial photophores with lumen or duct; true gill rakers present; jaw teeth small, all about equal in size.

Family GONOSTOMATIDAE (179)—bristlemouths. Marine; Atlantic, Indian, and Pacific.



Body elongate, never extremely compressed; adipose fins present or absent; anal fin rays 16–31; branchiostegal rays, 12–16, 4–6 on epihyal (= posterior ceratohyal); 8–16 branchiostegal photophores; photophores on isthmus; vertebrae 29–40.

With the removal of the genera *Diplophos*, *Manducus*, and *Triplophos* (see above), a monophyletic Gonostomatidae is reduced to five genera.

Five genera, *Bonapartia, Cyclothone, Gonostoma, Margrethia,* and *Sigmops,* with 23 species (Miya, 1994; Miya and Nishida, 2000; Harold, 1998, 2003). *Cyclothone,* with 13 species, is probably a synonym of *Gonostoma,* but Harold (1998) did not change the classification pending further studies. *Cyclothone* occurs in virtually all seas including the Antarctic; it and *Vinciguerria* have the greatest abundance of individuals of any vertebrate genera in the world.

Family STERNOPTYCHIDAE (180)—marine hatchetfishes. Marine; Atlantic, Indian, and Pacific.

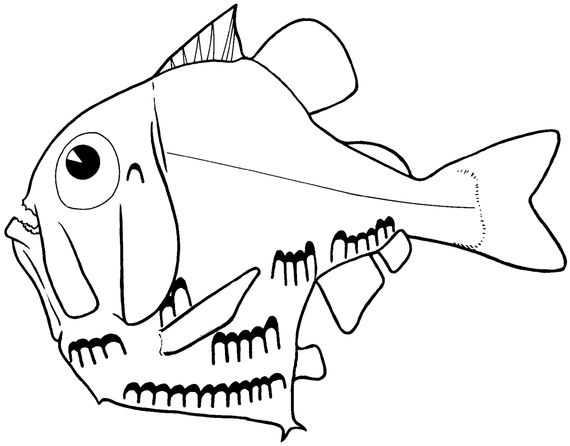
Six to 10 branchiostegal rays, three on epihyal (= posterior ceratohyal); 3–7 (usually six) branchiostegal photophores; pseudobranch present (reduced or lost in most other stomiiforms).

Ten genera and about 67 species.

SUBFAMILY MAUROLICINAE. Body elongate, never extremely compressed; adipose fin present or absent; 19–38 anal fin rays; photophores present on isthmus, six on branchiostegal membrane. This taxon is probably paraphyletic (Harold and Weitzman, 1996).

Seven genera, *Araiophos, Argyripnus, Danaphos, Maurolicus, Sonoda, Thorophos* (synonym *Neophos*), and *Valenciennellus,* with about 25 species (e.g., Parin and Kobyliansky, 1996; Harold and Lancaster, 2003; Harold, 2003).

SUBFAMILY STERNOPTYCHINAE (MARINE HATCHETFISHES). Body deep and extremely compressed; mouth nearly vertical; preopercular spine; eyes sometimes telescopic; abdominal keel-like structure; blade in front of the dorsal fin composed of specialized dorsal pterygiophores; anal fin sometimes divided, rays 11–19; dorsal fin rays 8–17; vertically orientated pelvic bones; adipose fin rarely absent (e.g., in *Polyipnus latirastrus*).



Three genera, *Argyropelecus* (seven species, broadly worldwide, high-sea pelagic, usually 100–600 m), *Sternoptyx* (four species, broadly worldwide, high-sea pelagic, 500–1,500 m), and *Polyipnus* (31 species, usually coastal, 50–400 m; most species in the western Pacific), with 42 species (e.g., Harold, 1994, 2003).

Suborder Phosichthyoidei. Three bony pectoral fin radials (rarely 0–2 in some genera with reduced pectoral fins); branchiostegal rays 10 (*Bathophilus*) to 28 (*Heterophotus*).

Family PHOSICHTHYIDAE (Photichthyidae) (181)—lightfishes. Marine; Atlantic, Indian, and Pacific.

General body shape similar to the gonostomatids; serial photophores having a lumen and a duct; gill rakers well developed in young and adults; usually two supramaxillaries; adipose fin present except in *Yarrella*; 10–16 dorsal fin rays; 12–33 anal fin rays; 11–22 branchiostegal rays, 4–7 on epihyal; barbel on lower jaw absent. This taxon is probably paraphyletic. Reasons for now accepting Phosichthyidae as the spelling of the family name are given in Nelson et al. (2004:211).

Seven genera, *Ichthyococcus*, *Phosichthys* (synonym *Photichthys*), *Pollichthys*, *Polymetme*, *Vinciguerria*, *Woodsia*, and *Yarrella*, with about 20 species (e.g., Parin and Borodulina, 1990; Harold, 2003).

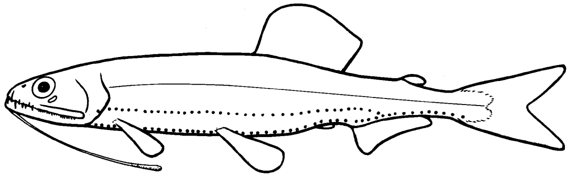
Family STOMIIDAE (182)—barbeled dragonfishes. Marine; Atlantic, Indian, and Pacific.

No true gill rakers in adults; one infraorbital bone (other stomiiforms have 2–6); one or no supramaxillaries; mesopterygoid reduced in size or absent; photophores without ducts or lumen; mental barbel in most, associated with hyoid apparatus; pectoral fin rays absent in *Tactostoma*, *Idiacanthus*, *Photostomias*, and some species of *Eustomias*; most are darkish in color.

Fink (1985) combined six “barbeled” families formerly recognized in the superfamilies Stomioidea and Astronethoidea into the one family, Stomiidae, as recognized here. The following sequence of taxa reflects Fink’s (1985) cladogram. However, as in Nelson (1994), I have not given a classification that reflects the proposed sister-group relationships so as to retain well-recognized taxa until questions recognized in Fink (1985) and in the other works on stomiiformes cited above are better resolved. Harold (2003) recognized all six higher level taxa given below as separate families.

About 28 genera and about 273 species (e.g., Parin and Borodulina, 1998, 2003; Clark, 2001; Harold, 2003; Sutton and Hartel, 2004).

SUBFAMILY ASTRONESTHINAE (SNAGGLETOOTHS)

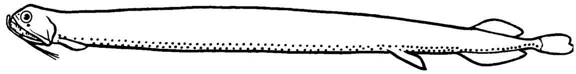


Scales absent; dorsal fin origin over or behind pelvic fin insertion but well ahead of anal fin origin; dorsal adipose fin present except in *Rhadinesthes* *decimus*; ventral adipose fin present in many, in front of anal fin; barbel on chin; dorsal fin rays 9–21; anal fin rays 12–28. Maximum length about 30 cm. Parin and Borodulina (2003) recognized 47 species in the deep-sea oceanic genus *Astronesthes* and regarded *Eupogonesthes* as a sister genus.

Six genera, *Astronesthes*, *Borostomias*, *Eupogonesthes*, *Heterophotus*, *Neonesthes*, and *Rhadinesthes*, with about 55 species.

SUBFAMILY STOMIINAE. Scales present (or body marked with scalelike hexagonal pattern).

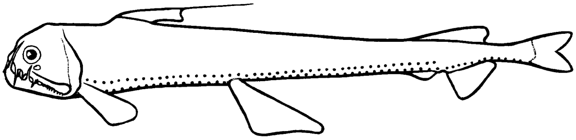
TRIBE STOMIINI (SCALY DRAGONFISHES)



Body elongate; dorsal fin origin far behind pelvics, above anal fin; long barbel on chin; no adipose fin.

One genus, *Stomias* (synonym *Macrostomias*), with 11 species (Fink and Fink, 1986).

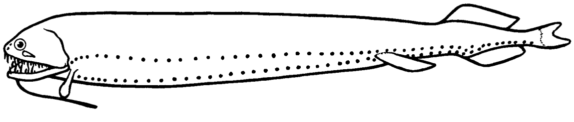
TRIBE CHAULIODONTINI (VIPERFISHES)



Dorsal fin well in advance of pelvics, shortly behind head; first dorsal fin ray greatly elongated; fanglike teeth on premaxilla and lower jaw; short chin barbel present in some; adipose fins present behind dorsal fin and in front of anal fin; dorsal fin rays 5–7; anal fin rays 10–13.

One genus, *Chauliodus*, with eight species.

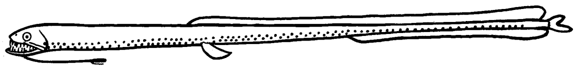
SUBFAMILY MELANOSTOMIINAE (SCALELESS BLACK DRAGONFISHES)



Scales absent; dorsal fin origin far behind pelvic fin, over anal fin; dorsal adipose fin absent except in *Chirostomias*; most with barbel on chin; supracleithrum absent in *Eustomias*.

Sixteen genera, *Bathophilus*, *Chirostomias*, *Echiostoma*, *Eustomias*, *Flagellostomias*, *Grammatostomias*, *Leptostomias*, *Melanostomias*, *Odontostomias*, *Opostomias, Pachystomias, Parabathophilus, Photonectes, Tactostoma, Thysanactis,* and *Trigonolampa,* with about 180 species. More than one-half of the species are contained in *Eustomias* (Sutton and Hartel, 2004, give 115 species for this genus, noting that most species can only be identified by the mental barbels). Fink (1985) recognized a clade comprising the genera *Bathophilus, Grammatostomias,* and *Eustomias,* which is the sister group to the remaining stomiids, comprising the herein recognized malacosteines and *Pachystomias.*

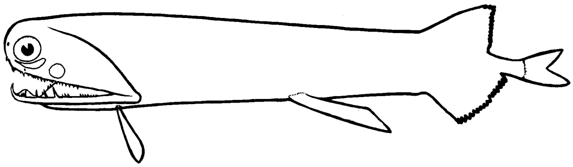
SUBFAMILY IDIACANTHINAE (BLACK DRAGONFISHES)



Body eel-like; dorsal fin extremely elongate, more than one-half the body length and with 54–74 rays; anal fin rays 29–49; each dorsal and anal fin ray flanked by a spur; scales absent; pectoral fins absent in adult; chin barbel only in females; adult males retain some larval characters; eyes on very elongate stalks in larvae allowing for an increase in field of vision.

One genus, *Idiacanthus,* with about four species. According to Fink (1985), the sister group of this genus is *Tactostoma.*

SUBFAMILY MALACOSTEINAE (LOOSEJAWS)



Jaws elongated, longer than skull; floor of mouth absent; dorsal fin origin far behind pelvic fin, over anal fin; adipose fin and scales absent; chin barbel in most; pectoral fins absent in some; dorsal fin rays 14–28; anal fin rays 17–32.

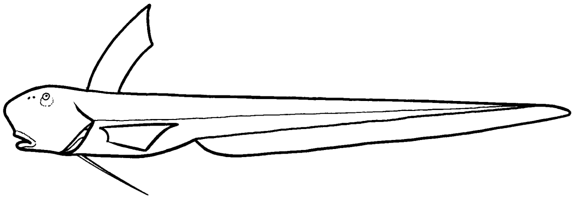
Three genera, *Aristostomias, Malacosteus,* and *Photostomias* (synonym *Ultimostomias*), with 15 species. Fink (1985) includes *Pachystomias* in a clade with these three genera.

Superorder ATELEOPODOMORPHA

Order ATELEOPODIFORMES (38)—jellynose fishes. The phylogenetic placement of this order was discussed in Olney et al. (1993). They concluded that it forms an unresolved trichotomy with the stomiiforms and eurypterygians.

The one family was once placed in the Lampriformes (e.g., Nelson, 1976, 1984), and interestingly, the molecular work of Miya et al. (2003) found support for it being the sister group of the Lampriformes with both being sister to the Myctophiformes. More work is needed to test these hypotheses of relationships.

Family ATELEOPODIDAE (183)—jellynose fishes. Marine; Caribbean Sea, eastern Atlantic, Indo-West Pacific, and eastern Pacific off Panama and Costa Rica.



Caudal fin reduced, united, except in *Guentherus,* with the long anal fin; anal fin rays 70 or more; pelvic fin of adults with single elongate ray on throat (young specimens have up to 10 rays); dorsal fin short-based with 3–13 rays (usually 9–13); skeleton largely cartilaginous; snout bulbous; branchiostegal rays 7. Maximum length about 2 m.

Four genera, *Ateleopus, Ijimaia, Parateleopus,* and *Guentherus,* with about 12 species (e.g., Smith and Heemstra, 1986; Moore, 2003). As noted by Moore (2003), the family is in great need of revision.

EURYPTERYGII (EURYPTERYGIANS). The remaining six superorders of neoteleosts compose Rosen's (1973a) Eurypterygii. Rosen recognized two subsections, the Cyclosquamata for the Aulopiformes and the Ctenosquamata for the higher eurypterygians. The sister-group relationships of the Cyclosquamata and Ctenosquamata were accepted by Fink and Weitzman (1982) and by Lauder and Liem (1983), and Stiassny (1986) and Johnson (1992) supported a monophyletic Eurypterygii as viewed by Rosen (1973a). However, many of Rosen's (1973a) synapomorphies for the Eurypterygii seem not to be valid for recognizing monophyly, and Johnson (1992) gave three synapomorphies that he considered valid (the most convincing being the fusion of the base of the ventral hemitrich of the medial pelvic fin ray to the medial pelvic radial). Miya et al. (2003), in their study using mitochondrial sequences, supported eurypterygian monophyly. The term "inioms" in the past has been used to include species of the two orders Aulopiformes and Mytophiformes; this term is no longer used as it does not reflect a monophyletic group (see Nelson, 1994, for further details).

A fossil taxon not otherwise mentioned, included as *incertae sedis,* is the Cheirotricidae (Patterson, 1993).

Superorder CYCLOSQUAMATA

Order AULOPIFORMES (39)—lizardfishes. Second pharyngobranchial greatly elongated posterolaterally, extending away from third pharyngobranchial, with elongated uncinate process of second epibranchial contacting third pharyngobranchial, and (as noted by Johnson, 1992) third pharyngobranchial lacking cartilaginous condyle for articulation of second epibranchial; swim bladder absent; medial processes of pelvic girdle fused. The specialization in the gill arches is apparently not known in any other teleost (Rosen, 1973a; Johnson, 1992).

The classification of the extant families of aulopiforms follows two major phylogenetic studies, Baldwin and Johnson (1996) with the modifications of Sato and Nakabo (2002a). The major differences between these two studies is that Sato and Nakabo (2002a) i) recognized the two clades formerly in *Chlorophthalmus* as being unrelated to one another (Baldwin and Johnson, 1996, had not included species of the clade now recognized as *Paraulopus*), ii) differed in the phylogenetic position of *Bathysauroides,* iii) assigned family status to *Bathysauroides* and *Bathysauropsis* (Baldwin and Johnson, 1996, while placing them in separate suborders, did not assign them to any family), and iv) recognized a different sequence for the alepisauroid families. Baldwin and Johnson (1996), considered Aulopidae to be the most primitive family, while Sato and Nakabo (2002a) found that position to belong to their new family, Paraulopidae. There are many differences from Nelson (1994), where the sequence of suborders was given as Giganturoidei (position uncertain), Aulopoidei (with only the one family), Chlorophthalmoidei, and Alepisauroidei (= Synodontoidei).

A review of past classifications and phylogenetic studies is given by Baldwin and Johnson (1996). Major contributions to our present understanding of the systematics of this order leading up to the above studies in the previous 25 years were made by K. E. Hartel, G. D. Johnson, R. K. Johnson, M. Okiyama, D. E. Rosen, M. L. J. Stiassny, and K. J. Sulak.

The families Aulopidae, Chlorophthalmidae, Ipnopidae and Synodontidae are benthic. Species in the remaining nine families tend to be pelagic to bathypelagic. Many aulopiforms are synchronous hermaphrodites.

Fifteen families with 44 genera and about 236 species.

The next two listed suborders and the families Cimolichthyidae and Enchodontidae, which are placed here in the suborder Alepisauroidei following Fielitz (2004), containing marine Cretaceous fishes, were placed in the †suborder Enchodontoidei in Nelson (1994). They are recognized here following Patterson (1993) and Fielitz (2004). Members have the maxilla as a long, narrow strut in gape (maxilla excluded from gape in the other members of this order). Goody (1969) recognized the members of this taxon in four suborders and placed them in the order Salmoniformes. Rosen (1973a) demonstrated their relationship to the alepisauroids. However, with the notable exception of the enchodontoids, their monophyly is yet to be established and relationships to living taxa are uncertain. Genera of uncertain relations include *Serrilepis* and *Yabrudichthys* (Taverne, 1985). In addition, Taverne (2004) described *Nardorex* (placing it in his new family Nardorexidae) from the marine Upper Cretaceous of Italy, noting it to show some resemblance with the Eurypholidae (placed here in the family Enchodontidae). There is need to have more studies similar to that of Fielitz (2004) that also involve a broad range of extant taxa.

†Suborder Ichthyotringoidei. Monophyly of the suborder with the families is doubtful.

Ichthyotringidae (including Apateopholidae)—e.g., *Apateodus* and *Ichthyotringa.*

Dercetidae—Seven genera of Cretaceous fishes with a very long snout and elongate and shallow body: *Benthesikyme, Cyranichthys, Dercetis, Dercetoides, Hastichthys, Pelargorhynchus, Rhynchodercetis,* and *Stratodus* (Taverne, 1990; Chalifa, 1989).

Prionolepididae—One genus, *Prionolepis.*

†Suborder Halecoidei. One family, Halecidae, with *Halec, Hemisaurida,* and *Phylactocephalus* (Goody, 1969).

Suborder Synodontoidei. The limits and relationships of this clade were revised by Johnson et al. (1996) and Baldwin and Johnson (1996); they altered our understanding of relationships of this group in finding characters supporting synodontoids as the most primitive aulopiform and *Aulopus* as cladistically the most primitive member of the suborder. Sato and Nakabo (2002a) supported these conclusions, but in examining species currently placed in *Paulopus* (but previously placed in *Chlorophthalmus* and not examined in the first two studies), recognized, as accepted here, *Paraulopus* as the most primitive aulopiform and sister to the remaining synodontoids. Four families.

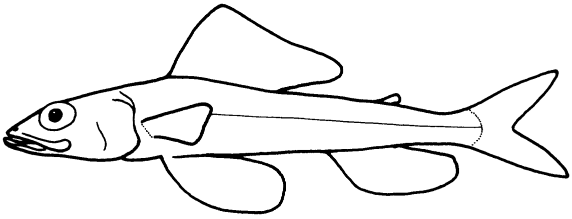
Family PARAULOPIDAE (184)—cucumber fishes. Marine; tropical to temperate, benthic, outer continental shelf and upper continental slopes, Indian and western Pacific (southern Japan and Emperor Seamounts south to Australia and New Zealand).

Dorsal fin rays 10 or 11; anal fin rays 8–11; pectoral fin rays 13–20; pelvic fin rays 9; pored lateral line scales 40–52; vertebrae usually 39–46; in addition, Sato and Nakabo (2002a) recognized this clade based on six apomorphies, primarily characters in the branchial arches, intermuscular bones, caudal skeleton, and pelvic girdle. Maximum length 35 cm.

Sato and Nakabo (2002a) showed in a cladistic analysis that two species groups formerly recognized in *Chlorophthalmus,* the *C. agassizi* species group and the *C. oblongatus* species group, were unrelated, with the latter belonging to the synodontoid clade. Within the latter clade, consisting of species of *Paraulopus,* Sato and Nakabo (2003) recognized two species groups, the *P. oblongus* group with seven species of small body size (up to 15 cm SL) and the *P. nigripinnis* group with three species endemic to southwest Australia and New Zealand of body size up to 35 cm SL.

One genus, *Paraulopus,* with 10 species (Sato and Nakabo, 2002a,b; 2003).

Family AULOPIDAE (185)—flagfins. Marine; tropical and subtropical waters, Atlantic (including the Mediterranean) and Pacific.



Two supramaxillae; body slender; fulcral scales on caudal peduncle; dorsal fin origin in front third of body, fin with 14–22 rays; anal fin rays 9–13; pelvic fin thoracic, nine rays; pectoral fin lateral, 11–14 rays; scales on head and body, cycloid or ctenoid; orbitosphenoid present; vertebrae 36–53.

This family was placed in monotypic suborder Aulopoidei in Nelson (1994), with the family name orthography being Aulopodidae.

Two genera, *Aulopus* (4) for the Atlantic species and *Hime* (6) for the Pacific species, with about 10 species (e.g., Parin and Kotlyar, 1989; Thompson, 1998). Baldwin and Johnson (1996) found no evidence supporting recognition of *Hime* as a valid genus, and in the past it was often regarded as a junior synonym of *Aulopus*. Its recognition here follows Thompson's (1998) study of additional characters, although he does note that further study of variation of these characters is required in order to better support this conclusion.

Family PSEUDOTRICHONOTIDAE (186)—sandiving lizardfishes. Marine; Izu Peninsula, Japan, and Saya de Malha Bank, Indian Ocean.

Body slender and cylindrical; mouth relatively small, upper jaw bordered only by premaxillaries and slightly protrusible; lateral line complete, midlateral; cycloid scales, 46–48 in lateral line; dorsal fin single, with about 33 soft rays; anal fin rays 13–15; pectoral fin with 11 rays; pelvic fin beneath origin of dorsal, with seven long rays; caudal fin with 19 principal rays; adipose fin absent; photophores absent; no swim bladder; orbitosphenoid and mesocoracoid absent; six branchiostegal rays; 23 or 24 abdominal vertebrae and 25 or 26 caudal vertebrae. Maximum length about 9 cm SL. Individuals of the one species have been observed to dive into the sand.

Previous systematic treatment of this family is given in Nelson (1994) and Johnson et al. (1996). The latter authors described the osteology of the Japanese form known from 30–50 m over sand bottom and confirm the placement of the species in the Aulopiformes. Parin (1992), in reporting one specimen from the Indian Ocean at 110 m as a new species (*Pseudotrichonotus xanthotaenia*), corrects in his Addendum some errors in the original description of the species. He found minor differences with the specimens from Japan, and all should probably be regarded as conspecific, at least until more information is available showing otherwise, despite the geographic distance separating them.

Probably one species, *Pseudotrichonotus altivelis.*

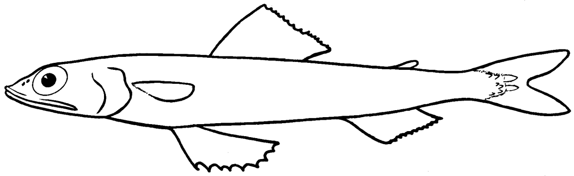
Family SYNODONTIDAE (187)—lizardfishes. Marine (rarely brackish); Atlantic, Indian, and Pacific.

Supramaxilla small (two in *Saurida* and one in *Harpadon*) or absent; branchiostegal rays 8–26; vertebrae 39–67; dioecious mode of reproduction.

The subfamily Bathysaurinae with *Bathysaurus,* formerly recognized in this family, is now placed in its own family below.

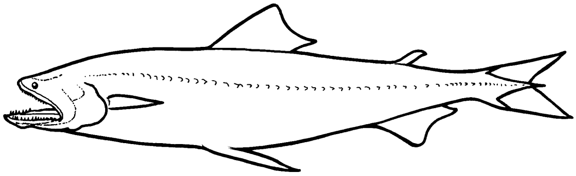
Four genera with about 57 species.

SUBFAMILY SYNODONTINAE (LIZARDFISHES). Scales along lateral line not enlarged; dorsal fin rays 10–15; anal fin rays 8–16; adipose fin usually present. Maximum length about 60 cm.



Two genera, *Synodus* (synonym *Xystodus*) and *Trachinocephalus,* with about 37 species (e.g., Waples and Randall, 1988; Russell, 1999, 2003).

SUBFAMILY HARPADONTINAE (BOMBAY DUCKS). Nine pelvic fin rays (eight in other members of family); dorsal and anal fin rays 9–15.



Two genera, *Harpadon* (shown in figure) and *Saurida,* with about 20 species (e.g., Okiyama, 1984; Russell, 1999, 2003). *Harpadon* is secondarily pelagic and has a naked head and body except for scales along the lateral line and on part of the posterior half of the body. This subfamily is Indo-Pacific; some species of *Harpadon* enter brackish water.

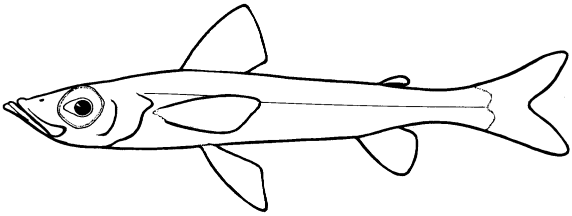
Suborder Chlorophthalmoidei. The composition of this taxon and sequence of families follows Sato and Nakabo (2002a). Five families.

Family BATHYSAUROIDIDAE (188)—bathysauroidids. Marine; Western Pacific.

Baldwin and Johnson (1996:399) noted similarities with *Bathysaurus,* and, acknowledging the evidence was weak, placed both in the Giganturoidei. The placement of *Bathysauroides* here is uncertain.

One species, *Bathysauroides gigas* (e.g ., Nakabo 2002:364; Sato and Nakabo, 2002a).

Family CHLOROPHTHALMIDAE (189)—greeneyes. Marine; tropical to temperate, deep-sea benthic, Atlantic, Indian, and Pacific.



Single elongate supramaxilla; monoecious mode of reproduction; eyes large, normal; pseudobranch present; tip of upper jaw not extending beyond orbit; pyloric caeca present; dorsal fin rays 9–13; anal fin rays 7–11; pectoral fin rays 15–19; branchiostegal rays 8; vertebrae 38–50.

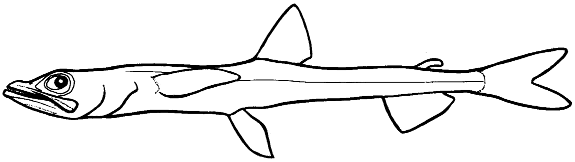
Two genera, *Chlorophthalmus* (17) and *Parasudis* (2), with about 19 species (e.g., Sato and Nakabo, 2002a; Thompson, 2003a). See under Paraulopidae above concerning the removal of some species previously placed in *Chlorophthalmus.*

Family BATHYSAUROPSIDAE (190)—bathysauropsids. Marine; mesobenthic, widespread.

Bathysauropsis gracilis is circumglobal, subtropical, and the other two are Indo-West Pacific, tropical (Shcherbachev and Pakhorukov, 2002). This genus was formerly recognized in Ipnopidae (e.g., K. J. Sulak in Smith and Heemstra,1986; Nelson, 1994); its placement in its own family follows Sato and Nakabo (2002a).

Three species, *Bathysauropsis gigas, B. gracilis,* and *B. malayanus* (Shcherbachev and Pakhorukov, 2002).

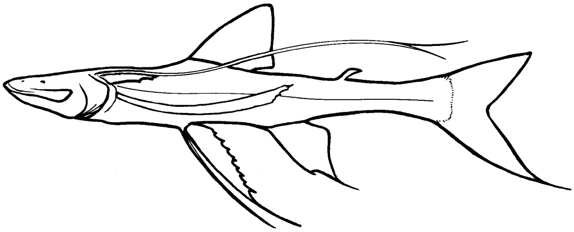
Family NOTOSUDIDAE (Scopelosauridae) (191)—waryfishes. Marine; Subarctic to Subantarctic.

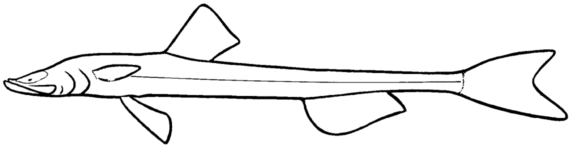


Dorsal fin rays 9–14; anal fin rays 16–21; pectoral fin rays 10–15; lateral line scales 44–65; no swim bladder; no photophores; larvae with maxillary teeth (all other larvae of the order lack teeth); vertebrae 42–66.

Three genera, *Ahliesaurus, Luciosudis,* and *Scopelosaurus* (synonym *Notosudis*), with 19 species (Bertelsen et al., 1976; Paxton and Niem, 1999; Thompson, 2003a).

Family IPNOPIDAE (192)—deepsea tripod fishes. Marine; Atlantic, Indian, and Pacific.





Eyes minute (first four genera listed here) or plate-like, directed dorsally, and lensless (*Ipnops*); pseudobranch absent in adult; tip of upper jaw extending past orbit; pyloric caeca absent; dorsal fin rays 8–16; anal fin rays 7–19; pectoral rays 9–24; branchiostegal rays 8–17; vertebrae 44–80; the 18 species of *Bathypterois* (spiderfishes) have elongated pectoral, pelvic, and caudal rays. *Bathysauropsis,* formerly recognized in this family, is now in its own family (see above).

Five genera, *Bathymicrops, Bathypterois* (synonym *Benthosaurus*) (upper figure), *Bathytyphlops* (synonym *Macristiella*), *Discoverichthys,* and *Ipnops* (lower figure), with 29 species (e.g., Nielsen and Merrett, 1992; Paxton and Niem, 1999; Sato and Nakabo, 2002a; Thompson, 2003).

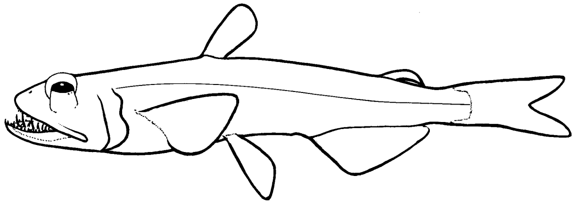
Suborder Alepisauroidei. Four extant families.

†Superfamily Enchodontoidea. Fielitz (2004) showed that the following Late Cretaceous fossil taxa form a monophyletic group that is regarded as the sister group to the Alepisauridae (*Alepisaurus* and *Omosudis*). His cladogram suggests that *Cimolichthys* is sister to the remaining taxa. He placed the enchodontid genera in four subfamilies (not shown here).

†Family CIMOLICHTHYIDAE. One genus, *Cimolichthys.*

†Family ENCHODONTIDAE. Five genera, *Enchodus, Eurypholis, Palaeolycus, Parenchodus, Rharbichthys,* and *Saurorhamphus.* Chalifa (1996) gave anatomical details on a large *Enchodus.*

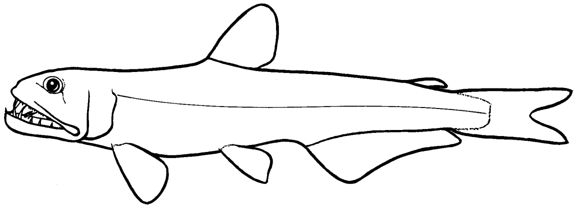
Family SCOPELARCHIDAE (193)—pearleyes. Marine; Antarctic, Atlantic, Indian, and Pacific (absent from Arctic Ocean and Mediterranean Sea).



Cycloid scales present on entire body and postorbital region, 40–65 along lateral line; strong teeth on tongue, usually hooked; large tubular eyes, directed upward or slightly dorso-anteriad; dorsal fin rays 5–10; anal fin rays usually 17–27 (up to 39); pectoral fin rays 18–28; two postcleithra; no swim bladder; vertebrae 40–65. Adults usually occur at depths between 500–1,000 m, larvae of most species usually between 100–200 m. Maximum length about 23 cm, attained in two species of *Benthalbella.*

Four genera, *Benthalbella* , *Rosenblattichthys, Scopelarchoides,* and *Scopelarchus,* with 17 species (e.g., Johnson, 1982; Paxton and Niem, 1999; Thompson, 2003a).

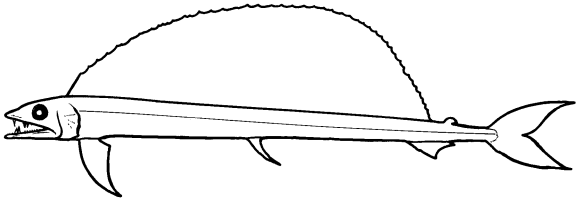
Family EVERMANNELLIDAE (194)—sabertooth fishes. Marine; Atlantic, Indian, and Pacific.

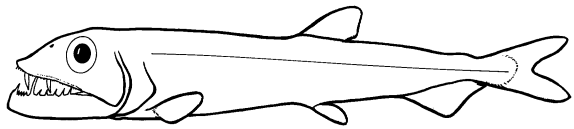


Normal scales lacking on head and body; three distinct bands of muscle tissue—epaxial, midlateral, and hypaxial—externally visible on the tail; teeth absent on tongue; anteriormost palatine tooth very elongate; eyes small to large, tubular in most species; dorsal fin rays 10–13; anal fin rays 26–37; pectoral fin rays 11–13; no swim bladder; vertebrae 45–54. The sabertooth fishes are mesopelagic predators, occurring primarily in tropical and subtropical waters and absent from cold water areas. Maximum length about 18 cm.

Three genera, *Coccorella*, *Evermannella*, and *Odontostomops*, with seven species (Johnson, 1982; Paxton and Niem, 1999; Thompson, 2003a).

Family ALEPISAURIDAE (195)—lancetfishes. Marine; Atlantic, Indian, and Pacific.



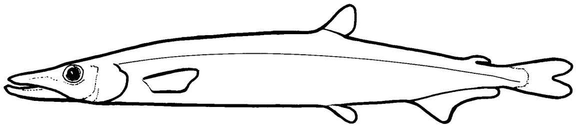


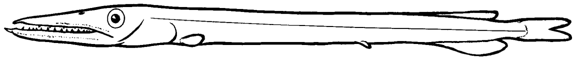
Body slender (covered with pores in *Alepisaurus*); scales and light organs absent; dorsal fin in *Alepisaurus* high and extending along most of body (originating over opercle and with 29–48 rays), in *Omosudis* only 9–12; anal fin low with 12–18 rays; pelvics abdominal with 8–10 rays; mouth large; teeth well developed, palatines especially long; vertebrae in *Alepisaurus* 47–51, 39–41 in the shorter *Omosudis*; swim bladder absent. Length up to 2 m in *Alepisaurus*, 20 cm in *Omosudis*.

Omosudis was recognized in its own family, Omosudidae, in Nelson (1994).

Two genera, *Alepisaurus* (2, upper figure) and *Omosudis* (*O. lowei*, lower figure), with three species (e.g., Paxton and Niem, 1999; Thompson, 2003a).

Family PARALEPIDIDAE (196)—barracudinas. Marine; all oceans, Arctic to Antarctic.





Dorsal fin origin in middle of trunk, fin rays 7–16 (fin absent in *Anotopterus*, but adipose fin well developed); anal fin base long, with 20–50 rays (14–16 in *Anotopterus*); pectoral fin rays 11–17; body scales present or absent; no swim bladder; vertebrae 53–121. Superfically resemble sphyraenids. Maximum length about 1 m.

Anotopterus pharao (Daggertooth) (lower figure), recognized in its own family, Anotopteridae, in Nelson (1994), as sister to the paralepidids, is placed in this family. Genera were previously assigned to subfamilies, based in part on whether the pectoral fins were small and short and vertebrae 60–121 or whether the pectoral fins were large and elongate (about head length or longer) and vertebrae 53–60 (for *Sudis* only). Subfamilies are not recognized here pending a complete cladistic study. Much of the earlier systematic work of this family was from the research of R. K. Johnson, A. Post, and R. R. Rofen.

Thirteen genera, *Anotopterus, Arctozenus, Dolichosudis, Lestidiops, Lestidium, Lestrolepis, Macroparalepis, Magnisudis, Notolepis, Paralepis, Stemonosudis, Sudis,* and *Uncisudis* (synonym *Pontosudis*), and about 56 species (Sato and Nakabo, 2002a; Thompson, 2003a; Fukui and Ozawa, 2004).

Suborder Giganturoidei. Two families.

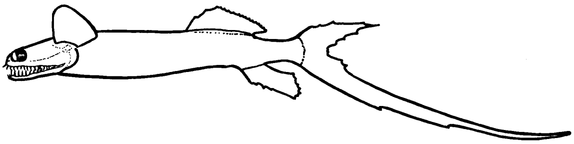
Family BATHYSAURIDAE (197)—deepsea lizardfishes. Marine; circumglobal, generally deeper than 1000 m, tropical to temperate latitudes.

Head very depressed; upper jaw long, extending well past rear of eye; scales along lateral line enlarged; dorsal fin rays 15–18; anal fin rays 11–14; pectoral fin rays 15–17; pelvic fin rays 8; dorsal adipose fin present or absent; branchiostegal rays 8–13. These bottom-dwelling deepsea fishes are hermaphrodites. Maximum length 78 cm SL.

The one genus was previously recognized in the Synodontidae. Johnson et al. (1996), in a detailed analysis of synapomorphies, showed that its relationships were outside the Synodontoidei; Baldwin and Johnson (1996) placed it in it own family in the the suborder Giganturoidei. Although the cladistic results of Sato and Nakabo (2002a) differ from those of Baldwin and Johnson (1996), there is agreement on the placement given here.

One genus, *Bathysaurus* (synonym *Macristium*), with two species (e.g., Russell, 2003).

Family GIGANTURIDAE (198)—telescopefishes. Marine; Atlantic, Indian, and Pacific.



Eyes large, tubular, and directed forward; mouth large, extending well behind eyes; sharp depressible teeth in mouth; greatly expandable stomach; pectoral fins high on body, above gill opening, with 30–43 rays; skin loose; body scaleless; pelvic fin, adipose fin, and branchiostegal rays in larvae but lost during transformation; caudal fin forked with some rays in lower lobe greatly elongated; no premaxilla, orbitosphenoid, parietal, symplectic, gill rakers, posttemporal, supratemporal, or cleithrum; no swim bladder. Color silvery. The loss of many characters that generally appear late in fish morphogenesis suggests a neotenous condition for these fish. The transformation from larvae to juveniles, commencing about 25–34 mm, is exceptionally striking among teleosts (R. K. Johnson, 1984; Johnson and Bertelsen, 1991). Maximum length 22 cm SL.

One genus with two species, *Gigantura chuni* and *G. indica* (synonyms *Rosaura rotunda* and *Bathyleptus lisae*) (Johnson and Bertelsen, 1991; Paxton and Niem, 1999; Thompson, 2003a).

CTENOSQUAMATA (CTENOSQUAMATES). Rosen (1973a) recognized two taxa ranked as septs for his subsection Ctenosquamata—the Scopelomorpha for the myctophiforms and the Acanthomorpha for the remaining taxa of teleosts. Johnson (1992) concluded that the only synapomorphy that is unique to and unreversed in the ctenosquamates is the absence of the fifth upper pharyngeal toothplate and the associated third internal levator muscle. The molecular study of Miya et al. (2003) also supported ctenosquamate monophyly.

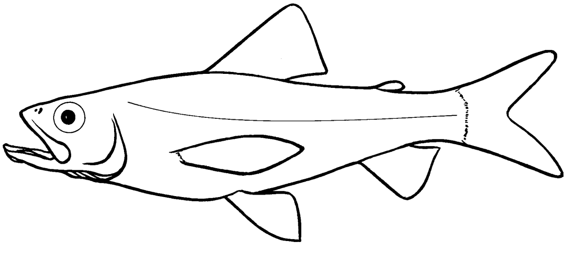
Superorder SCOPELOMORPHA

Order MYCTOPHIFORMES (40)—lanternfishes. Differs from the Aulopiformes in having the upper pharnygobranchials and retractor muscles like those of generalized paracanthopterygians (Rosen, 1973a:452). Other characteristics of the group are as follows: head and body compressed; eye lateral (dorsolateral in the myctophid *Hierops*); mouth usually large and terminal; adipose fin present; usually 8 pelvic fin rays; usually 7–11 branchiostegal rays. All are deep-sea pelagic and benthopelagic fishes.

Stiassny (1996), in addition to giving synapomorphies supporting monophyly of this order, gives synapomorphies supporting monophyly of the two families and presents a phylogenetic diagram of the genera.

Two families, 35 genera, and about 246 species.

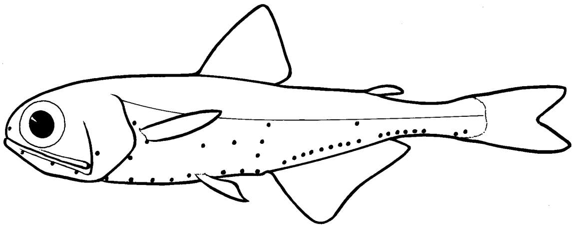
Family NEOSCOPELIDAE (199)—blackchins. Marine; Atlantic, Indian, and Pacific.



Trilobate rostral cartilage; enlarged bony protuberance on median process of maxilla; head and body compressed; long slender supramaxilla present; subocular shelf absent; origin of anal fin far behind dorsal fin base; photophores present in *Neoscopelus*; scales cycloid except in *Solivomer*, which has ctenoid scales on body; swim bladder absent only in *Scopelengys*; vertebrae 29–35. Maximum length about 30 cm.

Three genera, *Neoscopelus, Scopelengys,* and *Solivomer* (with one species known only from the Philippine Islands), with six species (Nafpaktitis, 1977; Paxton and Hulley,1999; Hartel and Craddock, 2003).

Family MYCTOPHIDAE (200)—lanternfishes. Marine; all oceans, Arctic to Antarctic.



Cartilaginous supporting plate below the adipose fin; small supramaxilla present in some genera; subocular shelf present; origin of anal fin under or short distance behind dorsal fin base; small photophores arranged in groups and rows on head and body (except in one species); scales usually cycloid (ctenoid in four species); swim bladder present (except in adults of a few species); vertebrae 28–45.

Myctophids are heavily consumed by numerous marine fishes and mammals. Most undergo a diurnal migration of several hundred meters. During the daytime the peak abundance of most species is between 300 and 1,200 m, while at night it is between 10 and 100 m.

About 32 genera with at least 240 species (Paxton et al., 1984; Paxton and Hulley, 1999; Zahuranec, 2000; Craddock and Hartel, 2003).

SUBFAMILY MYCTOPHINAE. About 14 genera (e.g., *Benthosema, Centrobranchus, Diogenichthys, Electrona, Gonichthys, Hygophum, Myctophum, Protomyctophum, Symbolophorus,* and *Tarletonbeania*).

SUBFAMILY LAMPANYCTINAE. About 18 genera (e.g., *Bolinichthys, Ceratoscopelus, Diaphus, Gymnoscopelus, Lampadena, Lampanyctus, Nannobrachium, Notolychnus, Notoscopelus, Scopelopsis, Stenobrachius,* and *Triphoturus*).

ACANTHOMORPHA (ACANTHOMORPHS)—SPINY-RAYED FISHES. Rosen (1973a) recognized this taxon for all remaining teleosts, where many members throughout the taxon have true fin spines in the dorsal, anal, and pelvic fins. Stiassny (1986) and Johnson and Patterson (1993) gave further evidence of the monophyly of the acanthomorphs. The molecular studies of, for example, Wiley et al. (2000) and Miya et al. (2003) also supported acanthomorph monophyly. The molecular study of Chen et al. (2003) found several differences with what is presented here; interestingly, some of their results agree better with earlier morphological studies where the classification was based on overall similarity. Some of their results placed Gadiformes with zeioids; blennioids with Gobiesocoidei; Channoidei with Anabantoidei; Mastacembeloidei with Synbranchioidei and these two taxa grouping with Syngnathoidei + Dactylopteridae; Ammodytidae with Cheimarrhichthyidae; Zoarcoidei with Cottoidei; Percidae with

Notothenioidei; and a clade grouping many perciform groups and Pleuronectiformes. Their results, many of which agreed with that of other molecular studies, e.g., Wiley et al. (2000), Miya et al., 2003), and Smith and Wheeler (2004), will require detailed testing. Dettai and Lecointre (2005) also supported many of the above hypothesized clades and provided new hypotheses for certain acanthomorph clades. The next few years may see growing support for differing relationships than those presented here.

Johnson and Patterson (1993) presented arguments for regarding the lampriforms as the primitive sister group to the remaining acanthomorphs. This is accepted here. In naming a higher monophyletic grouping, they introduced the new names Euacanthomorpha for the polymixiids and higher taxa and Holacanthopterygii for the Paracanthopterygians and higher taxa.

Patterson and Johnson (1995) presented a major study on the homologies of the intermuscular bones and ligaments of teleostean fishes. This study will not be reviewed here, but their conclusions must be considered in phylogenetic studies of bony fishes. However, follow-up studies will be mentioned, dealing with acanthomorphs. In a wide selection of acanthomorph taxa, Gemballa and Britz (1998) tested Patterson and Johnson's (1995) hypothesis that the single bony series of intermusculars in higher acanthomorphs is the homologue of epineurals of lower teleosts. They concluded, in contrast to Patterson and Johnson, that the first intermuscular bone of *Polymixia* is an epicentral, the single series of intermuscular bones of Holacanthopterygii are epicentrals, and the neoneurals of some percomorphs are normal epineurals. In response, Johnson and Patterson (2001) argued that their identification of epineural ligaments above the intermuscular bones in many acanthomorphs is mistaken, that the structures in question are fanlike arrays of collagen fibers, not true intermuscular ligaments. Students of ichthyology should study these works as examples of how researchers can arrive at different conclusions. For related studies see also Chanet et al. (2004).

There is a rich fossil record of acanthomorphs (beginning in the Cretaceous). The Asineopidae is an acanthomorph fossil family of uncertain affinity. It contains one species, *Asineops squamifrons* of Eocene age from the Green River formation (Grande, 1984). It has a dorsal fin of 7–10 spines and 11 or 12 soft rays; the anal fin has two or three spines and 8–11 soft rays. Other fossil acanthomorph taxa of uncertain placement include the Blochiidae and Palaeorhynchidae (these two are often put with the Scombroidei), and the Cretaceous Aipichthyidae, Aipichthyoididae, Dinopterygiidae, Pharmacichthyidae, Pycnosteroididae, and Stichocentridae (e.g., Patterson, 1993). The first Cretaceous acanthomorph recorded from a freshwater deposit is *Spinocaudichthys oumtkoutensis*, described from the Cretaceous (Cenomanian) of Morocco (referenced in Filleul and Dutheil, 2004, and described by these authors in 2001). Wilson and Murray (1996) described *Xenyllion zonensis* (a paracanthopterygian placed in the family Sphenocephalidae), the oldest North American acanthomorph fossil and among the oldest anywhere, found in the Fish Scale Zone of the Albian/Cenomanian boundary (middle Cretaceous, about 99,000,000 years old). Stewart (1996) documented various fossil occurrences in North America, such as the sphenocephalid *Neogastroplites* from the middle Cretaceous, the polymixiid *Omosoma* and various holocentrids from the middle Late Cretraceous, and notes the Cretaceous diversity to be less than in other parts of the world.

Superorder LAMPRIOMORPHA

Order LAMPRIFORMES (Lampridiformes, Allotriognathi) (41)—opahs. No true spines in fins; premaxilla excludes maxilla from gape; unique type of protrusible upper jaw (maxilla, instead of being ligamentously attached to the ethmoid and palatine, slides in and out with the highly protractile premaxilla); pelvic fins with 0–17 rays; swim bladder, whe present, physoclistous; orbitosphenoid present in some.

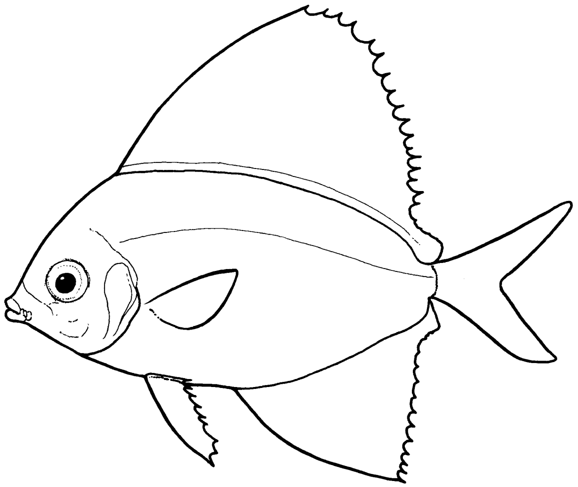
Monophyly for this group is established by Olney et al. (1993), and their study should be consulted for a listing of diagnostic characters. The deep-bodied members with symmetrical caudal fins and well-developed skeletons—the lamprids and veliferids—are referred to as the bathysomes. The other five families, with long ribbonlike bodies with dorsal fins extending from the head to the tail and asymmetrical caudal fins and weak skeletons, are referred to as the taeniosomes. These two groups were formally recognized in C. T. Regan's 1907 classification as the Bathysomi and the Taeniosomi. According to the cladogram of Olney et al. (1993), the former is paraphyletic while the latter is monophyletic. The study of Wiley et al. (1998), based on morphological and molecular evidence, confirmed monophyly of the order and, for the five lampriform species studied, agreed with the phylogenetic results of Olney et al. (1993).

Fossil lampriforms include *Bajaichthys* (family not assigned), *Palaeocentrotus, Veronavelifer,* and the lampridlike Turkmenidae (with long pelvic fins with 7–10 rays), with *Turkmene* and *Danatinia* of the Upper Paleocene and *Analectis* of the Lower Oligocene (see Nelson, 1994, for references). Olney et al. (1993) and Patterson (1993) discussed and listed the fossils.

Rosen (1973a) established that lampriforms are not percomorphs, as previously believed, but instead are basal acanthomorphs. Strong evidence that they are prepercomorphs and the sister group to all other acanthomorphs (euacanthomorphs) was presented by Olney et al. (1993) and Johnson and Patterson (1993). Positioning them as basal acanthomorphs was also supported by the molecular evidence of Wiley et al. (2000), perhaps Chen et al. (2003), and some others, but not strictly by Miya et al. (2003).

For orthography of ordinal name, see Lampridae below. Seven families with 12 genera and about 21 species. There are no freshwater species in this order. The families are sequenced to reflect the sister-group relations recognized by Olney et al. (1993).

Family VELIFERIDAE (201)—velifers. Marine, usually near-shore; Indian and western part of mid-Pacific.

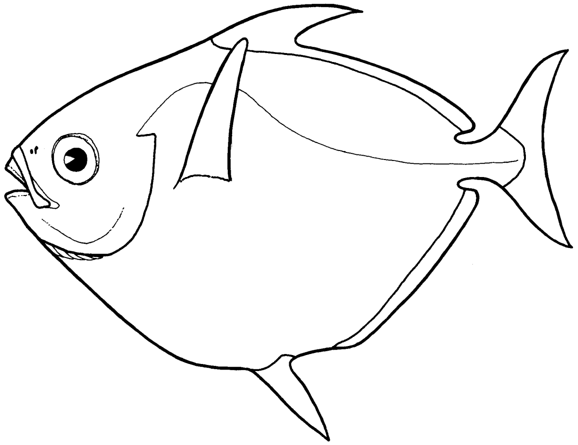


Body deep and compressed; pelvic fins with seven to nine rays (no spine); dorsal and anal fins long, total number of spines plus soft rays in dorsal fin 32–44, and in anal fin 25–35; teeth absent; swim bladder bifurcate posteriorly, the two horns extending far beyond anus; six branchiostegal rays; vertebrae 33 or 34 (16 abdominal and 17 or 18 caudal). Maximum length about 40 cm.

Veronavelifer is an Eocene fossil found in northern Italy that is relatively similar to the extant *Metavelifer multiradiatus*; the only other fossil veliferoid is *Palaeocentrotus* (family Palaeocentrotidae) of the Eocene in Denmark.

Two monotypic genera, *Velifer* and *Metavelifer* (e.g., Smith and Heemstra, 1986).

Family LAMPRIDAE (Lamprididae) (202)—opahs. Marine pelagic; Atlantic, Indian, and Pacific.

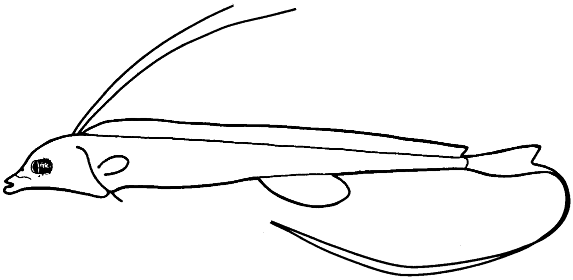


Body oval-shaped and compressed; lateral line arched high in front; dorsal and anal fins long (dorsal with 48–56 rays and anal with 33–42 rays); pelvic fin rays 12–17; minute cycloid scales; vertebrae 43–46. Its food consists primarily of squids, octopuses, and crustaceans. Maximum length up to 1.8 m.

The orthography of the family has been changed from Lamprididae to Lampridae, and some comment is required. There is a desire to have stability in the orthography of family names, while following provisions of the code of the International Commission of Zoological Nomenclature as given in the fourth edition of the "International Code of Zoological Nomenclature" (published in 1999). There is currently much disagreement in some families as to whether the suffix should be "ididae" or "idae." For the present case, Lampridiformes and Lamprididae have been the forms used in most recent literature by specialists and were used in Nelson (1994) in the belief, based on the careful work of C. Patterson in Olney et al. (1993), that this form was grammatically correct. However, the latter seems not to be correct, and Eschmeyer (1998, Online) employed the forms Lampriformes and Lampridae, as also used in Nelson (1984). Although this is open to further study, I now revert back to this form. Instability in name orthography is disturbing to all users, and through the cooperative efforts of many, it is hoped that agreement will eventually be reached on such spellings (see also discussion of this subject in the Preface).

Two species, *Lampris guttatus* (worldwide) and *L. immaculata* (cold and temperate waters of Southern Hemisphere) (Parin and Kukuyev, 1983; Collette, 2003a).

Family STYLEPHORIDAE (203)—tube-eyes or thread-tails. Marine abyssal; most oceans.

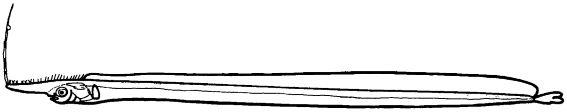


Body ribbonlike; dorsal fin extending from nape to tail, with 115–124 rays; anal fin short, 15–17 rays; pectoral fin rays 10 or 11, base horizontal; pelvic fin with only one ray; caudal fin in two parts, upper with five rays and lower with two extremely elongate rays; eyes large, telescopic, may be directed forward or upward; mouth small and protractile; teeth small; no swim bladder; about 50 vertebrae. This fish swims in a vertical position, head uppermost. It occurs at depths of about 300–800 m. Maximum length 31 cm.

Probably only one species, *Stylephorus chordatus* (e.g., Olney, 2003).

The remaining four families form a monophyletic group and share the following features: body very thin and ribbonlike; anal fin short or absent; pelvic fin rays 0–10; six or seven branchiostegal rays; swim bladder, when present, does not extend past the anus; each dorsal fin ray has more than one lateral spine at its base; suborbital series absent except for the lachrymal and second suborbital (jugal); frontal bones separated by a groove; vertebrae 62–200. According to Olney et al. (1993), the lophotids and radiicephalids are sister groups, and the trachipterids and regalecids are sister groups.

Family LOPHOTIDAE (204)—crestfishes. Marine; most oceans.



Body with small deciduous cycloid scales (sometimes appearing naked); anal fin small, near caudal and with 5–20 rays; caudal fin normal; pelvic fin, absent or with 2–6 rays; dorsal fin very long with about 220–392 rays and originating above or before tip of snout; swim bladder present; ink sac present, which discharges into cloaca; vertebrae 124–200. The extinct *Protolophotus* is known from Oligocene deposits in Iran. Maximum length about 200 cm.

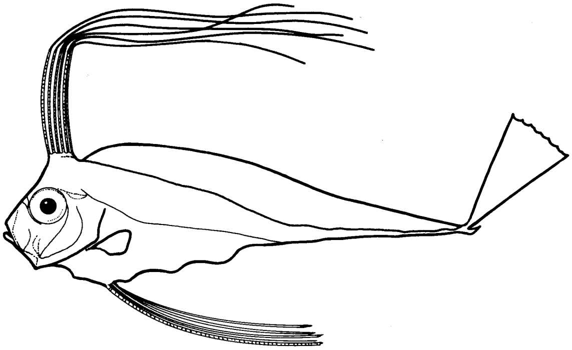
Two genera, *Lophotus* and *Eumecichthys* (e.g., Olney, 2003), and probably three species (Craig et al., 2004, as noted in Nelson et al., 2004:212, gave evidence that both *Lophotus lacepede* and *L. capellei* are valid).

Family RADIICEPHALIDAE (205)—tapertails. Marine; central and eastern Atlantic and off New Guinea.

Body elongate and laterally compressed, tapering to a thin caudal filament (caudal fin with small upper lobe of four rays and long, slender lower lobe of seven rays); dorsal fin with 152–159 rays; anal fin vestigial, with seven rays; pectorals and pelvics each with up to nine rays (pelvic rays tend to be lost with development); scales along lateral line but absent on rest of body; ribs present; swim bladder well developed; brown ink sac, which discharges into the cloaca (the ink, like that of *Lophotus*, may serve to blind would-be predators); cloaca about one-third along total length from snout; vertebrae 114–121 (36–39 + 77–82), of equal length. Maximum length about 70 cm.

One species, *Radiicephalus elongatus*, known from only a few specimens (e.g., Olney, 2003).

Family TRACHIPTERIDAE (206)—ribbonfishes. Marine; Arctic, Atlantic (including Mediterranean), Indian, and Pacific.



Body naked, with deciduous cycloid scales, or with deciduous modified ctenoid scales (tubercles may also be present); no anal fin; caudal fin long and at a right angle to the body, consisting of upper lobe only (*Desmodema* has the few caudal rays parallel to the caudal peduncle); pelvic fins with 1–10 rays; dorsal fin very long, originating distinctly behind tip of snout; eyes large; teeth present; ribs absent; swim bladder rudimentary or absent; vertebrae 62–111. Allometric growth results in various body shapes during growth (including the loss of the pelvic fins during metamorphosis in *Desmodema*). Maximum length about 1.7 m, attained in *Trachipterus altivelis.*

Three genera, *Desmodema* (2 species), *Trachipterus* (about 6—including King-of-the-Salmon), and *Zu* (2), with about 10 species (e.g., Olney, 2003).

Family REGALECIDAE (207)—oarfishes. Marine; all oceans.

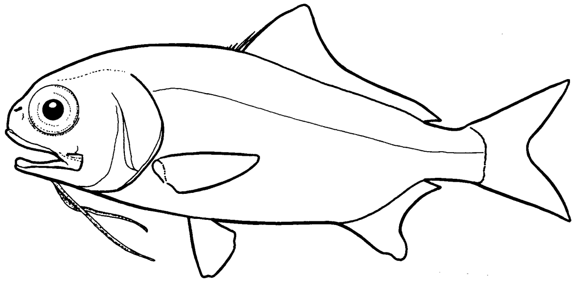
Scales absent; no anal fin; pelvic fin very elongate, slender, with one ray; dorsal fin very long, originating distinctly behind tip of snout, with 260–412 rays, the first few rays being elongate and bright red; eye small; no teeth; swim bladder absent; vertebrae about 143–170. *Regalecus glesne* (Oarfish or King-of-the-Herring) has 40–58 gill rakers; *Agrostichthys parkeri* (Streamer Fish) has 8–10 gill rakers. This group is probably responsible for many sea-serpent stories. Maximum length up to about 8 m, attained in *R. glesne,* longest of the bony fishes.

Two monotypic genera, *Regalecus* and *Agrostichthys* (e.g., Olney, 2003).

Superorder POLYMIXIOMORPHA. Position uncertain.

Order POLYMIXIIFORMES (42)—beardfishes. Few groups have been shifted back and forth as frequently as this one, while still being considered of uncertain affinity. The one family is placed within the Beryciformes by many workers employing differing methods. Several works such as Stiassny (1986) and Johnson and Patterson (1993) provided evidence that it is or could be the sister group to all other Acanthomorphs. As noted by Stiassny (1986), *Polymixia* is unique in having a palato-premaxillary ligament passing between maxillary lateral processes, rather than between contralateral palatines.

Family POLYMIXIIDAE (208)—beardfishes. Marine; tropical and subtropical Atlantic, Indian (primarily off Natal), and western Pacific.



Body moderately elongate and compressed; pair of hyoid barbels; dorsal fin continuous, with 4–6 spines and 26–38 soft rays; anal fin with four short spines and 13–17 soft rays; pelvic fins subabdominal, with one spinelike ray and six soft rays; 16 branched caudal rays; about 33–38 lateral line scales; four branchiostegal rays; 11–21 gill rakers; two supramaxillae; subocular shelf, orbitosphenoid, and basisphenoid present; three epurals; usually 29 or 30 vertebrae. This is the only acanthomorph retaining two sets of intermuscular bones, epipleurals (what are generally termed epipleurals in acanthomorphs are now thought to be homologous with the epineurals of lower teleosts—Johnson and Patterson, 1993). Maximum length 38 cm. Beardfishes usually occur between 180 and 640 m.

One genus, *Polymixia*, with 10 species (e.g., Moore, 2003). Fossils include such Upper Cretaceous genera as *Berycopsis*, *Dalmatichthys*, *Omosoma*, and *Omosomopsis*.

†Order CTENOTHRISSIFORMES. Position uncertain. Contains the marine Upper Cretaceous genera *Aulolepis* and *Ctenothrissa*. Rosen (1973a) considered it possible that the ctenothrissiforms are the "primitive sister group of the paracanthopterygian-acanthopterygian assemblage" and classified them with that assemblage under the category of Sept Acanthomorpha. *Pattersonichthys* may bear some distant relationship to *Aulolepis* and *Ctenothrissa*.

Superorder PARACANTHOPTERYGII

Doubt has existed about the monophyly of the Paracanthopterygii ever since its erection by Greenwood et al. (1966) and subsequent redefinitions. Nelson (1994) followed the then most recent analysis of the group by Patterson and Rosen (1989), but it was also concluded by Nelson (1994) that "There is still no rigorous definition of the group; in other words, there is no firm basis to believe it is monophyletic." Many subsequent studies suggested that the paracanthopterygians are probably not monophyletic and indeed possibly polyphyletic (e.g., Gill, 1996; Wiley et al., 2000; Miya et al., 2003, 2005).

The molecular evidence of Wiley et al. (2000) and Miya et al. (2001, 2003, 2005) suggested that Gadiformes and Zeiformes (as herein recognized) are sister taxa. Miya et al. (2005), in their molecular study using mitochondrial genome sequence, included the Polymixiidae in their Paracanthopterygii lineage (with Polymixiidae and Percopsiformes being sister groups) and otherwise included (as did Miya et al., 2003) only the Percopsiformes, Gadiformes, and (in adding) Zeioidei (Zeiformes as herein recognized). The Ophidiiformes, Batrachoidiformes, and Lophiiformes were excluded and found to have distant affinities even from one another. The Ophidiiformes in their phylogeny are primitive Percomorpha, with Lophiiformes coming out as highly advanced percomorphs, sister to *Antigonia* and two balistoids. For the Batrachoidiformes, Miya et al. (2005) found strong molecular evidence that they are not primitive acanthomorphs nor related to any group considered paracanthopterygian, but rather they are percomorphs showing closest affinity to *Mastacembelus, Indostomus,* and synbranchids. This suggestion of batrachoid relationships disagrees with morphological evidence, and further research is needed to determine the reasons for this conflict.

The phylogenetic arrangement given in Miya et al. (2005) may be summarized as follows:

Acanthomorpha
  Paracanthopterygii
    Unnamed lineage
      Polymixiidae
      Percopsiformes
    Unnamed lineage
      Gadiformes
      Zeioidei
  Acanthopterygii
    Berycomorpha
    Percomorpha
      Unnamed lineage
        Ophidiiformes
      Unnamed lineage
        Batrachoidiformes, etc.
        Lophiiformes, etc.

Although some of the new finds in molecular biology agree with some work in morphological analysis, there is a great need for continued studies using more representative groups before we can be confident in making major changes other than in a piecemeal fashion to the classification. Until more analytical studies are conducted using molecular and morphological characters from many more representative taxa, I prefer to not make major changes and consider it beyond the scope of the present work to suggest an alternative but comprehensive classification to better reflect our views on the relationships of its members. I therefore retain the same orders as in Nelson (1994), but in the sequence of: Percopsiformes, Gadiformes, Ophidiiformes, Batrachoidiformes, and Lophiiformes.

The papers noted above suggest major changes, and certainly, as they are followed up, there will be a complete reorganization of members in future revisions. The valuable work being done is laying the foundation for major changes to come in the future.

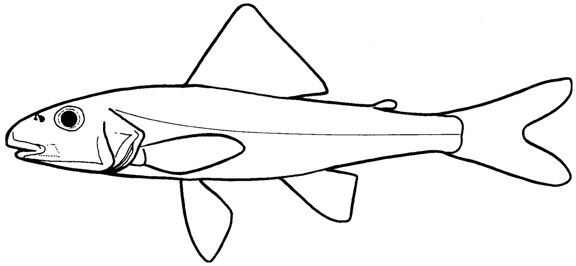
The 1,340 or so living species are placed in about 270 genera, 36 families, and five orders. About 20 species are confined to freshwater.

Order PERCOPSIFORMES (43)—trout-perches. Premaxilla nonprotractile; ectopterygoid and palatine with teeth; pelvic fins, if present, behind pectorals and with 3–8 soft rays; spines (normally weak) usually present in dorsal fin; many species with ctenoid scales; six branchiostegal rays; 16 branched caudal rays; orbitosphenoid, basisphenoid, and suborbital shelf absent; vertebrae 28–35.

Monophyly of this order has been questioned by several authors (see Nelson, 1994) with suggestions that amblyopsids may be more closely related to anacanthines (see Nelson et al., 2004:212 and Springer and Johnson, 2004: 83 for references to the 1999 A. M. Murray and M. V. H. Wilson study) or to gobioids (Poly and Proudlove, 2004); no changes are made pending confirmation of relationships.

Three families, seven genera, and nine species. All are confined to freshwater.

Family PERCOPSIDAE (209)—trout-perches. Freshwater; northern North America, primarily Alaska to Quebec and southward to Missouri and Kentucky.

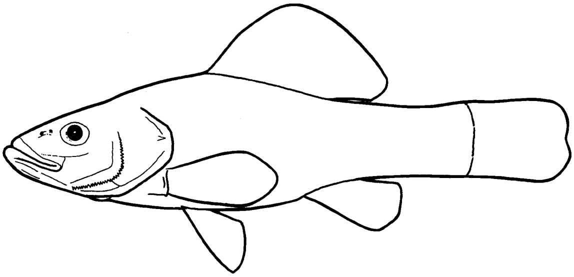


Alveolar premaxillary process broadly arched; vomer toothless; ctenoid and cycloid scales; head naked; adipose fin present; dorsal fin with one or two spines and 9–12 soft rays; anal fin with one or two spines and six or seven soft rays; pelvic fin subthoracic, with eight rays; lateral line complete or nearly so, scales 43–60; anus in front of anal fin; vertebrae 33–36. Maximum length 20 cm, attained in *Percopsis omiscomaycus.*

Two species, the widespread *Percopsis omiscomaycus* and *P.* (synonym *Columbia*) *transmontana* of Columbia River drainage in Washington, Oregon, and Idaho.

The family was well represented in Eocene times with *Amphiplaga, Erismatopterus, Lateopisciculus,* and *Massamorichthyss* (Poly, 2004a).

Family APHREDODERIDAE (210)—pirate perch. Freshwater; eastern United States, primarily lowlands of Atlantic drainage from Long Island southward, Gulf of Mexico slope, Mississippi Valley, and part of Great Lakes drainage.

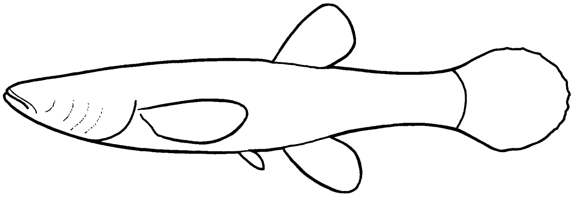


Ctenoid scales; sides of head scaly; eyes normal; dorsal fin with three or four spines and 10 or 11 soft rays; anal fin with two or three spines and 5–7 soft rays; pelvic fin subthoracic, with seven rays; anus between gill membranes in adults; adipose fin absent; lateral line absent or incomplete; vomer toothed; premaxilla segmented.

The anus is in the normal position in juveniles, just ahead of the anal fin, and moves forward during the growth of the fish. Also, in young pirate perch, the third anal ray becomes transformed from a soft ray to a spine during growth. Young individuals thus appear to have two spines and eight soft rays; adults have three spines and seven soft rays. Maximum length about 13 cm.

One species, *Aphredoderus sayanus* (Poly, 2004b).

Family AMBLYOPSIDAE (211)—cavefishes. Freshwater; southern and eastern United States.



Cycloid scales; head naked; eyes small to rudimentary; dorsal fin with 0–2 spines and 7–12 soft rays; anal fin with 0–2 spines and 7–11 soft rays; pelvic fins usually absent (present only in *Amblyopsis spelaea,* where they are small, abdominal, and with 0–6 rays); sensory papillae in rows on the head, body, and tail; myodome lost; anus between gill membranes in adults; adipose fin absent; lateral line absent or incomplete; vomer toothed; premaxilla segmented; vertebrae 27–35.

All the species, except *Chologaster cornuta* of the Atlantic coastal plains, usually live in caves in limestone formations. *Chologaster cornuta* and *Forbesichthys agassizii* are the only species with functional eyes. The other four species are blind. Maximum length about 9 cm, attained in *Amblyopsis spelaea.*

Five genera, *Amblyopsis* (2), *Chologaster* (1), *Forbesichthys* (1), *Speoplatyrhinus* (1), and *Typhlichthys* (1), with six species (Nelson et al., 2004; Poly and Proudlove, 2004; Proudlove, 2005).

†Order SPHENOCEPHALIFORMES. The one family, Sphenocephalidae, with the marine *Sphenocephalus* known from the Upper Cretaceous of Europe, was once thought to be ancestral to the living North American freshwater percopsiforms and was placed within that order as the suborder Sphenocephaloidei. Patterson and Rosen (1989) consider it to be the sister group for the remaining paracanthopterygians, termed the anacanthines, on the basis of both taxa sharing the following characters: "gadoid notch" present—a cavity behind the high postmaxillary process of the premaxilla (not present in all anacanthines, however); first vertebra with a pair of high facets off the centrum that articulate with the forwardly displaced exoccipital condyles; second and third vertebrae foreshortened (sometimes only the second centrum is foreshortened in anacanthines). *Sphenocephalus* has a small supramaxilla and lacks an adipose fin.

ANACANTHINES. The remaining paracanthopterygians are put together in a group termed the Anacanthini by Patterson and Rosen (1989). This lineage is characterized by the following characters: myodome absent (it is also absent in amblyopsids); parapophyses absent on at least the first three vertebrae and the first few pairs of ribs inserting in cavities of the centra, not on parapophyses (see Patterson and Rosen, 1989, for further details).

The monophyly of this lineage is in serious doubt (see above under Paracanthopterygii). I place the Gadiformes as the most basal lineage based on suggestive evidence from Wiley et al. (2000) and Miya et al. (2003).

Grande (1988) described a freshwater Lower Paleocene fish from northeastern Montana, *Mcconichthys longipinnis* (placed in its own family, Mcconichthyidae), which is considered to form a trichotomy with the gadiforms and the pediculates (lophiiforms and batrachoidiforms). This represents the earliest known paracanthopterygian from North America.

Order GADIFORMES (44)—cods. Pelvic fins, when present, inserted below or in front of pectorals (thoracic or jugular, rarely behind in Macrouridae) with up to 11 rays; no true spines in the fins; most with long dorsal and anal fins; scales usually cycloid, rarely ctenoid; premaxilla forms the entire margin of upper jaw, protractile in some; ectopterygoid toothless; orbitosphenoid and basisphenoid absent; branchiostegal rays 6–8; posterior vertebral reduction results in posterior dorsal and anal pterygiophores exceeding the number of caudal vertebrae; swim bladder without pneumatic duct (the swim bladder is absent in *Melanonus* and *Squalogadus*). Gadiforms have a relatively unique otolith, although the otolith in Phycidae is different and more specialized (D. Nolf and E. Steurbaut, in Cohen, 1989). Additional apomorphic features are given by D. F. Markle in Cohen, 1989).

Different concepts of the composition of Gadiformes have existed as a result of various hypotheses of relationships and philosophy of classification. For example, Berg (1940) recognized it as a relatively compact group, containing only four families: Muraenolepididae, Moridae, Bregmacerotidae, and Gadidae (a much larger family than is currently recognized, which included *Gaidropsarus* and its relatives, and *Merluccius*) (the Macruridae and Macrouroididae were placed in a separate order). At the opposite extreme, it was recognized in Nelson (1976), following Greenwood et al. (1966) and Rosen and Patterson (1969), as including two additional suborders that are now excluded—the Ophidioidei (= Ophidiiformes) and Zoarcoidei. Although there is general agreement on the monophyly of Gadiformes with its present composition, there is much disagreement on its classification as revealed in the various papers in Cohen (1989).

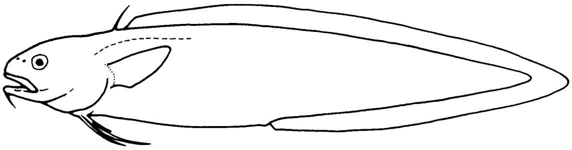
This order consists of many important commercial fishes that constitute over one quarter of the world's marine fish catch. Much information on various members is found in Cohen (1989), while keys to many of the species and much distributional and other data are provided by Cohen et al. (1990). The term "anacanthine fishes" has sometimes been restricted to apply to members of this order, but the broader use of it, with historical precedent and as used by Patterson and Rosen (1989), is followed here. See under Paracanthopterygii for studies suggesting that Gadiformes and Zeiformes (as herein defined) form a monophyletic group.

The fossil record of gadiforms and their relatives is discussed in several papers in Cohen (1989).

Many changes have been made to the classification, such as reducing the number of families recognized and changing the position of others. The changes are made, unfortunately, not because of progress in our understanding of phylogenetic relationships, but because the arrangement in Cohen et al. (1990) in many cases seems to better suit our current knowledge. However, I retain recognition of the family Phycidae, not given in Cohen et al. (1990). I, like Cohen et al. (1990) and Endo (2002) but unlike some others, continue to not recognize Lotinae at the family level. I have not recognized suborders of gadiforms because many aspects of their classification are very weakly established and because of differences of opinion concerning the phylogenetic relationships of the various families (e.g., see papers by D. F. Markle and G. J. Howes, in Cohen, 1989). The classification of Endo (2002) represented a major advance in gadiform systematics and classification, and that work should be consulted for a new cladistic approach.

Nine families, 75 genera, and about 555 species. Only one species is confined to freshwater, while a second species has some populations that are confined to freshwater.

Family MURAENOLEPIDIDAE (212)—eel cods. Marine; Southern Hemisphere, cold temperate, primarily Antarctic, continental shelf.

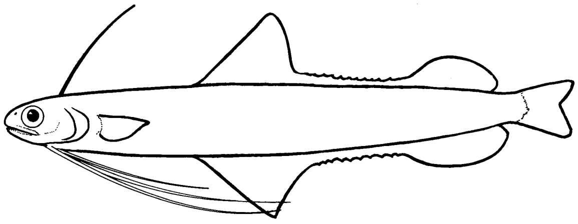


Caudal fin connected with anal and second dorsal fins; two dorsal fins, the first with only one or two rays and the second with 127–141 rays, and one anal fin with 98–112 rays; gill openings narrow, extending upward only to level of pectoral bases; pectoral radials 10–13 (usually four in other gadiforms); pectoral fin rays 37 or 38; chin barbel present; head of vomer toothless; no pyloric caeca; vertebrae 67–69. Maximum length 40 cm.

Most workers on gadiform systematics have considered the muraenolepidids to be a primitive member of the order.

One genus, *Muraenolepis*, with four species.

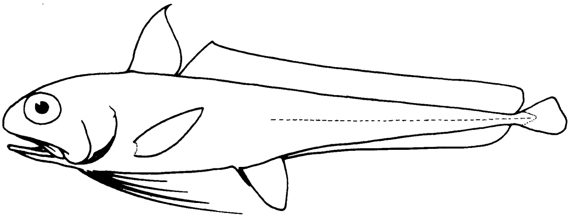
Family BREGMACEROTIDAE (213)—codlets. Marine, rarely in estuaries; tropical and subtropical seas.



Two dorsal fins and one long anal fin (first dorsal fin on nape and consisting of one elongate ray, second dorsal and anal fins with large notch in middle); no chin barbel; relatively large scales, 40–89 along side; head of vomer toothed; pelvic fins under head and with five rays, outer three are elongate free filaments; lateral line for most of its length extending along dorsal margin of body; a few pyloric caeca; swim bladder not in contact with auditory capsules; 43–59 vertebrae. Maximum length about 12 cm.

One genus, *Bregmaceros*, and at least 15 species (Harold et al., 2003; Torii et al., 2003, 2004).

Family EUCLICHTHYIDAE (214)—eucla cod. Marine; benthopelagic off New Zealand and Australia.



Two dorsal fins, nearly contiguous, the first high and with a short base of 12–15 rays and the second extending to base of the caudal fin with 74–77 rays; anal fin long, with large anterior lobe of about 15 rays and the remainder with about 77 rays; no chin barbel; pelvic fins under head and with four long rays, the longest reaching the anus; pelvic girdle inserted between the cleithra (it is farther back in almost all other gadiforms); caudal fin small but distinct, externally asymmetrical with rays of lower lobe extended; about 70 vertebrae. Maximum length about 35 cm.

The relationships of *Euclichthys* remain uncertain and its ranking as a family is very provisional.

One species, *Euclichthys polynemus* (Cohen et al., 1990).

Family MACROURIDAE (Coryphaenoididae) (215)—grenadiers (rattails). Marine; deepwater, Arctic to Antarctic.

Second dorsal and anal fins continuous with tail, which tapers to a sharp point; no true fin spines (first dorsal fin ray may be spinous); chin barbel usually present; pelvic fins more or less thoracic (under, behind, or in front of pectoral fin base), with 5–17 rays (absent in *Macrouroides*); caudal fin and usually most of the skeleton absent (fin present in one species of *Trachyrincus*); scales small; light organ, if present, subdermal along midline of abdomen with opening just before anus; 6–8 branchiostegal rays; 10–16 abdominal vertebrae. Length normally up to 0.8 m.

Four subfamilies, about 27 genera, and about 350 species. Some workers recognized the Bathygadinae at the family level. Most species are benthopelagic, occur in tropical and subtropical latitudes, and live at depths between 200 and 2,000 m.

SUBFAMILY BATHYGADINAE. Second dorsal fin rays longer than those of anal fin, starting close behind first dorsal fin; mouth wide and terminal; snout rounded. Basically worldwide in tropical to subtropical seas, but absent from the eastern Pacific, primarily 200–2,700 m. Maximum length 65 cm.

Two genera, *Bathygadus*, with the chin barbel small to absent (10 species), and *Gadomus*, with a distinct barbel (12 species).

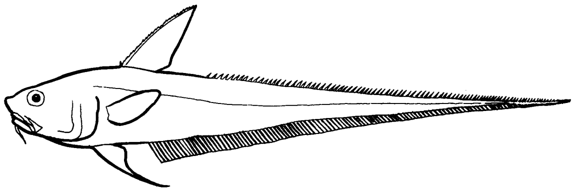
SUBFAMILY MACROUROIDINAE. Single low dorsal fin; mouth subterminal; head enlarged; chin barbel absent. Basically worldwide in tropical to temperate waters, bentho- to bathypelagic. Maximum length 40 cm.

Two monotypic genera, *Macrouroides* (pelvic fin absent) and *Squalogadus* (small pelvic fin of five rays).

SUBFAMILY TRACHYRINCINAE. Second dorsal fin rays usually somewhat longer than those of anal fin, starting close behind first dorsal fin; mouth wide and subterminal; snout long and pointed; body scales spinous. Almost worldwide in temperate waters. Maximum length 60 cm.

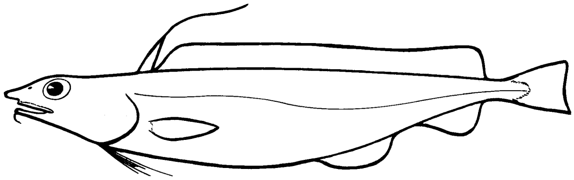
Two genera, the monotypic *Idiolophorhynchus*, lacking a chin barbel, and *Trachyrincus*, with five species with a small barbel.

SUBFAMILY MACROURINAE. Second dorsal fin rays much shorter than those of anal fin, a gap between its origin and that of first dorsal fin; mouth terminal to subterminal; ventral light organ in many species; barbel present or absent. Basically worldwide except absent in high Arctic. Maximum length 150 cm, attained in *Albatrossia pectoralis*.



About 21 genera (e.g., *Albatrossia, Cetonurus, Caelorinchus* (synonym *Coelorhynchus*), *Coryphaenoides, Hymenocephalus, Lepidorhynchus, Macrourus, Malacocephalus, Mesobius, Nezumia, Pseudonezumia* (synonym *Paracetonurus*), *Sphagemacrurus,* and *Ventrifossa*) and about 320 species (e.g., Cohen et al., 1990; Iwamoto and Williams, 1999; Merrett and Iwamoto, 2000; Iwamoto, 2003). Many new species continue to be described.

Family MORIDAE (216)—deepsea cods. Marine, deep water; all seas (rarely in brackish water).

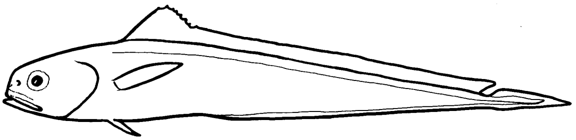


One or two, rarely three, dorsal fins; one or two anal fins; chin barbel present or absent; head of vomer toothless or with minute teeth; swim bladder in contact with auditory capsules (otophysic connection); light organ in some; vertebrae 41–72.

What appears to be a remarkable case of disjunct distribution occurs in *Halargyreus johnsonii,* a species with an antitropical distribution in the Atlantic and Pacific Oceans (Cohen et al., 1990).

About 18 genera (e.g., *Antimora, Auchenoceros, Gadella, Halargyreus, Laemonema, Lepidion, Lotella, Mora, Paralaemonema, Physiculus, Pseudophycis, Salilota,* and *Tripterophycis*) with about 105 species (e.g., Cohen et al., 1990; Long and McCosker, 1998).

Family MELANONIDAE (217)—pelagic cods. Marine, bathypelagic; Atlantic, Indian, Pacific, and subantarctic.



Single long-based dorsal fin with 72–78 rays; anal fin with 50–58 rays; barbel absent; moridlike in most features but lacks otophysic connection, vertebrae 58–62. Maximum length 15 cm.

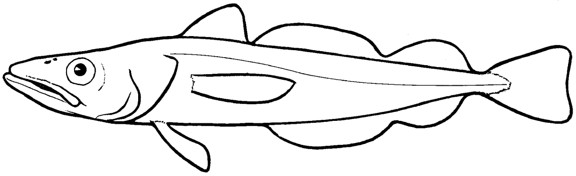
As with many gadiform families, the position of this group is uncertain. Divergent views on its relationships range from that of D. F. Markle in Cohen (1989), who considered it to be the sister group to all gadiforms except *Raniceps*, to that of G. J. Howes in Cohen (1989), who considered it to be the sister group of *Steindachneria.*

One genus, *Melanonus*, with two species.

Family MERLUCCIIDAE (218)—merluccid hakes. Marine; Atlantic (both sides and including the Mediterranean Sea and parts of the Black Sea), southwesternmost Indian, eastern Pacific (from British Columbia to tip of South America), and New Zealand.

Lloris et al. (2003) gave a catalog of the species placed here in the first two subfamilies.

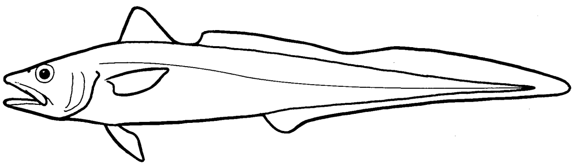
SUBFAMILY MERLUCCIINAE. Two dorsal fins, first with 8–13 rays (first principal dorsal ray is spinous—a pseudospine) and second notched and with 34–46 rays; anal fin with 35–46 rays, notched; caudal fin separate from dorsal and anal fins; no chin barbel; mouth terminal, large, and with long teeth; teeth on head of vomer, none on palatines; seven pelvic rays; seven branchiostegal rays; no pyloric caeca; anus and urogenital pore close together; lateral line scales 101–171; vertebrae 48–58.



The common names usually applied to various species of *Merluccius* throughout the world are hake and whiting (the latter name is also used for some other gadiforms and for sillaginids). However, as is often the case with common names, they are also variously applied to species of other families (e.g., hake for the phycid *Urophycis*).

One genus, *Merluccius*, with 13 species (Cohen et al., 1990). Fossils include the Eocene *Rhinocephalus.*

SUBFAMILY MACRURONIDAE (SOUTHERN HAKES). Body elongate, strongly compressed. Pectoral fin high on body, level with eye. Marine; Atlantic and Southern Hemisphere (primarily off southern South Africa, southern South America, southern New Zealand, and southern Australia).



Cohen et al. (1990) and O. Okamura in Cohen (1989) recognized the species, as have most authors, as a member of the Merlucciidae. Reasons for recognizing it at the family level in Nelson (1994) seem less warranted.

Three genera, *Lyconus, Macruronus,* and *Lyconodes,* with about eight species. *Lyconodes argenteus* is perhaps extinct.

SUBFAMILY STEINDACHNERIIDAE (LUMINOUS HAKES). Anus between pelvic fins and far forward of urogenital pore, which is immediately anterior to the anal fin (in larvae the anus is near the origin of the anal fin); elaborate light organ system on head and body; caudal fin and skeleton extremely reduced or absent, tail tapering to a fine point. Marine; Gulf of Mexico, Caribbean, and Guianan shelf off northeastern South America.

Recognized in Nelson (1994) at the family level.

One species, *Steindachneria argentea.*

Family PHYCIDAE (219)—phycid hakes. Marine; primarily Atlantic but also off South Africa, New Zealand, and Japan.

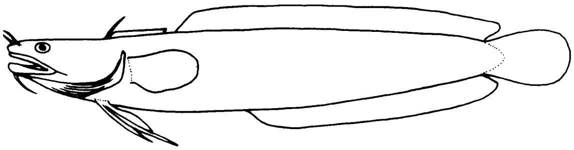
One anal fin; vertebrae 44–55; highly specialized otoliths with a completely fused ostium and cauda (D. Nolf and E. Steurbaut, in Cohen, 1989); egg diameter small, less than 1 mm (eggs with oil globules).

The monophyly and phylogenetic position of the family are uncertain. Reasons for recognizing this family are given in Nelson (1994).

Five genera with 25 species.

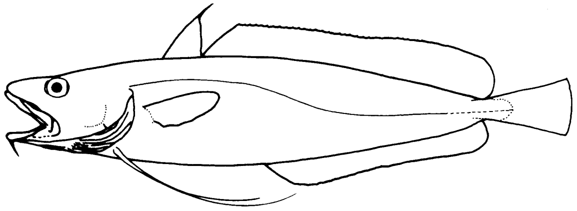
SUBFAMILY GAIDROPSARINAE. Three dorsal fins barely separated from each other (the first with a single thickened unsegmented ray; the second with small, unsegmented rays in a fleshy ridge that rises within a groove; and the third with segmented rays in an elongate fin); 2–4 prominent individual barbels on snout (rudimentary barbels may also be present), in addition to the one at the tip of the lower jaw.

Known as rocklings, they occur primarily from the northern Atlantic, including the Mediterranean Sea, but they also occur in the Southern Hemisphere (e.g., off New Zealand and Tasmania).



Three genera, *Gaidropsarus, Ciliata,* and *Enchelyopus,* with 15 species.

SUBFAMILY PHYCINAE. Two dorsal fins, first with 8–13 rays and second with 43–68 rays; pelvic fin with two highly elongated rays; no barbels on snout (but chin barbel present).



Two genera, *Phycis* with three species and *Urophycis* with 10 species. All are confined to the Atlantic (including the Gulf of Mexico and Mediterranean).

Family GADIDAE (220)—cods. Marine with one Holarctic freshwater species; Arctic, Atlantic, and Pacific.

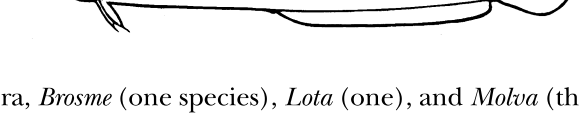
First dorsal fin posterior to head; head of vomer toothed; swim bladder not connected with auditory capsules. Maximum length about 1.8 m, attained by the Atlantic *Gadus morhua.*

Sixteen genera and about 31 species. The area of greatest diversity is the Atlantic.

The first two subfamilies recognized here are ranked as families by many workers. Whether these two taxa are each other's closest relatives is uncertain. The classification I present is consistent with the cladogram of D. F. Markle in Cohen (1989:85), in which Merlucciidae is recognized as the primitive sister group to his Lotidae and Gadidae. However, a change in the classification will be required if the cladogram presented in 1991 by G. J. Howes is supported, where the Lotidae and some phycids are considered to be the primitive sister group to his Gadidae and Merlucciidae. Endo (2002) recognized four subfamilies in Gadidae as follows: Gaidropsarinae, Phycinae, Lotinae, and Gadinae. There is general agreement that the subfamily Gadinae, as recognized here, is the most advanced taxon in the order.

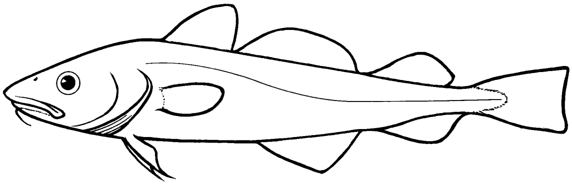
SUBFAMILY LOTINAE (CUSKFISHES). One or two dorsal fins and one anal fin; chin barbel always present but no barbels on snout; caudal fin rounded; egg with oil globule.

Recognition of this taxon is based on reasons given in Nelson (1994).



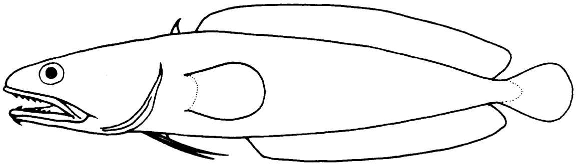
Three genera, *Brosme* (one species), *Lota* (one), and *Molva* (three), with five species. *Lota lota,* the Burbot, found in the northern parts of Eurasia and North America, is the only completely freshwater member of the order; another gadid, *Microgadus tomcod* of the Atlantic coast of North America, can spawn in freshwater, and some freshwater populations are known. The marine members of the Lotinae occur in the northern Atlantic, including the Mediterranean, and the Arctic.

SUBFAMILY GADINAE (CODS AND HADDOCK). Three dorsal fins and two anal fins; chin barbel usually present; caudal fin truncate or slightly forked; egg without an oil globule. J. R. Dunn in Cohen (1989) ranked this group at the family level and provisionally recognized four subfamilies—the Gadiculinae (monotypic), Microgadinae (monotypic), Eleginae (five genera), and Gadinae (five genera).



Twelve genera, *Arctogadus, Boreogadus, Eleginus, Gadiculus, Gadus, Melanogrammus, Merlangius, Microgadus, Micromesistius, Pollachius, Theragra,* and *Trisopterus,* with about 25 species.

SUBFAMILY RANICIPITINAE (TADPOLE CODS). Two dorsal fins, the first with three short rays; one anal fin, base long and fin not indented; head without pores or lateral line; upper jaw protruding past lower; chin barbel present. Maximum length about 30 cm. Marine, shallow coastal waters; northeastern Atlantic, Norwegian coast to British Isles and Bay of Biscay.



Recognition of *Raniceps* at the family level in Nelson (1994) and as the primitive sister group to the remaining gadiforms followed D. F. Markle in Cohen (1989). On the other hand, G. J. Howes in Cohen (1989) considered it to be a relatively advanced gadiform. Most other authors placed it in the Gadidae.

One species, *Raniceps raninus.*

Order OPHIDIIFORMES (45)—cusk-eels. Pelvic fins, when present, inserted at level of preopercle or farther anterior (mental or jugular), one or two soft rays in each, and occasionally with a spine; base of dorsal and anal fins long, extending to and usually joined with caudal fin; nostrils paired on each side; dorsal and anal fin pterygiophores more numerous than adjacent vertebrae (the ratio being about 1.8:1).

Some of the past disagreement about the phyletic relationships and taxonomic rank of this group is reviewed in Nelson (1994) (also, see above under Paracanthopterygii). The following classification is based on Nielsen et al. (1999), except that the family Parabrotulidae was excluded by them.

Five families, 100 genera, and about 385 species (in addition, many undescribed species are known). The fifth family, Parabrotulidae, is only provisionally retained here. About five species, all bythitids, are limited to freshwater or weak brackish water.

Suborder Ophidioidei. Anterior nostril well above upper lip in most species; oviparous, males lack an external intromittent organ; caudal fin usually present and connected with dorsal and anal fins (appearing as one continuous fin and tapering to a point).

Family CARAPIDAE (221)—pearlfishes. Marine; Atlantic, Indian, and Pacific.

Larvae (planktonic vexillifer stage) with a vexillum (long, deciduous, thread-like first dorsal fin ray); anal fin rays longer than opposing dorsal fin rays; anus of adults and anal fin origin far forward, behind head and usually beneath pectoral fin (which is rarely absent); scales absent; gill openings wide and extending far forward; teeth on jaws, vomer, and palatines; no spines on opercular bones; branchiostegal rays 6 or 7; supramaxillary absent; about 85–145 vertebrae.

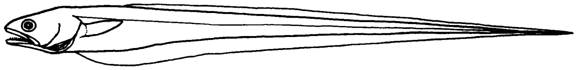
Although subfamilies were not recognized in Nielsen et al. (1999), I retain them here as given in Nelson (1994), based on the 1990 cladistic classification of D. F. Markle and J. E. Olney (1990).

Seven genera and 31 species (Nielsen et al., 1999; Olney, 2003).

SUBFAMILY PYRAMODONTINAE. Pectoral fin nearly as long as head, rays 24–30; upper jaw protractile; anal fin pterygiophores modified into a visceral cradle consisting of alternately bending pterygiophores; some pleural ribs present; precaudal vertebrae 12–15. Basically circumtropical, north to Japan and Gulf of Mexico and south to New Zealand and Chile.

Two genera, *Pyramodon* (4, pelvics present) and *Snyderidia* (1, pelvics absent), with five species (Nielsen et al., 1999).

SUBFAMILY CARAPINAE (FIERASFERIDAE)



Pectoral fin usually much shorter than head length and with 23 or fewer rays (absent in the three species of the subgenus *Encheliophis* of the genus *Encheliophis*); interarcual element ossified (also ossified in synbranchids); pelvic fins and girdle absent (the girdle is present in at least most larvae); upper jaw nonprotractile; no pleural ribs; precaudal vertebrae 17–35. Occur in tropical and temperate seas (south to New Zealand, South Georgia Island, and southern Chile).

Many species of pearlfishes (also known as fierasfers) have the interesting habit of hiding in living animals. Some live in sea cucumbers, but apparently there is no evidence as reported that they may eat the cucumber's internal organs in a parasitic fashion. Others are commensal with starfish, sea cucumbers, clams, and tunicates (known as inquiline behavior, "living as a tenant"). In paracanthopterygians, molluscan inquiline behavior, with scallops, is also known in the red hake, *Urophycis chuss.* Pearlfishes, whether free-living, commensal, or parasitic, pass through two distinct larval stages. The vexillifer, or first, larval stage is pelagic; the tenuis, or second, larval stage, perhaps absent or abbreviated in the free-living species, is demersal. In this stage the vexillum is gone, the head is relatively small, and total length is reduced. Except in the free-living species, individuals can enter the host in the tenuis stage. References for which most of the above is based were given in Nelson (1994).

Maximum length about 30 cm, attained by *Echiodon drummondii* and *Carapus bermudensis.*

Five genera, the free-living *Echiodon* (11) and *Eurypleuron* (1), the commensal *Carapus* (synonym *Disparichthys*, erected for one specimen that was collected from a brook in New Guinea and described in 1935 as an eel in its own family; a second species was added in 1938 from a specimen collected off Cuba) (4) and *Onuxodon* (3), and the parasiticlike *Encheliophis* (7), with a total of 26 species (Nielsen et al., 1999). Parmentier et al., (2000) proposed some changes to the generic diagnoses and species composition of *Carapus* and *Encheliophis* that are not yet incorporated in the above.

Family OPHIDIIDAE (222)—cusk-eels. Marine; Atlantic, Indian, and Pacific.

Dorsal fin rays usually equal to or longer than opposing anal fin rays; anus and anal fin origin usually behind tip of pectoral fin; scales present; some with one or more spines on opercle; supramaxillary present; larvae without a vexillum; pelvics rarely absent. Maximum lengths about 1.6 m, attained by *Genypterus capensis*, and 2.0 m, attained in *Lamprogrammus shcherbachevi.*

Four subfamilies with 48 genera and about 222 species (Nielsen et al., 1999; Lea and Robins, 2003). Fossils include the Tertiary *Ampheristus* and *Hoplobrotula.*

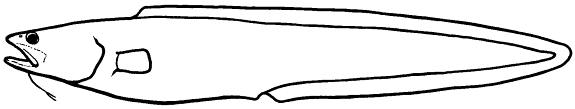
SUBFAMILY BROTULINAE. Barbels present on chin and snout.

One circumtropical genus, *Brotula* (brotulas), with at least five species.

SUBFAMILY BROTULOTAENIINAE. No barbels on chin or snout; scales in the form of small prickles.

One circumtropical genus, *Brotulotaenia*, with four species. *Lamprogrammus* may be better placed in this subfamily rather than in the non-monophyletic Neobythitinae (Fahay and Nielsen, 2003).

SUBFAMILY OPHIDIINAE. No barbels on snout or chin; pelvic fins far forward; cycloid scales present (in regular rows or at oblique angles to each other); slender, elongate filament of bone extending anteriorly from junction of ventral arms of cleithra. Considered monophyletic by Nielsen et al. (1999).



Eight genera, one tribe, Lepophidiini (21 species), with *Cherublemma, Genypterus,* and *Lepophidium,* and the other, Ophidiini (33 species), with *Chilara, Ophidion, Otophidium, Parophidion,* and *Raneya,* with about 54 species.

SUBFAMILY NEOBYTHITINAE. No barbels on snout or chin; cycloid scales present; no filament of bone extending anteriorly from junction of ventral arms of cleithra; pelvic fins absent in at least adults of the five species of the virtually circumtropical *Lamprogrammus*; eye lens minute or absent in *Leucicorus* and eye minute in *Typhlonus.* Members of this group range from the littoral to the greatest depths at which fish have been obtained (the deep-sea record being for *Abyssobrotula galatheae* obtained at 8,370 m in the Puerto Rico Trench). This subfamily is not monophyletic.

About 38 genera (e.g., *Abyssobrotula, Acanthonus, Bassogigas, Bassozetus, Dicrolene, Eretmichthys, Glyptophidium, Homostolus, Lamprogrammus, Monomitopus, Neobythites, Petrotyx, Porogadus, Sirembo,* and *Spectrunculus*) with about 159 species.

Suborder Bythitoidei. Anterior nostril immediately above upper lip in most species; viviparous, males with an external intromittent organ; caudal fin connected with dorsal and anal fins or separate.

Family BYTHITIDAE (223)—viviparous brotulas. Marine (rarely in brackish and freshwaters); Atlantic, Indian, and Pacific.

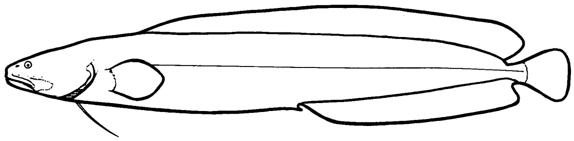
Scales usually present; swim bladder present; opercular spine usually present and strong; pyloric caeca present; precaudal vertebrae 9–22. One species of *Bythites* is known from a thermal vent in the Galapagos Rift Zone. In contrast to ophidiids, several species of bythitids extend into shallow water. About five species are confined to freshwater or weak brackish water.

About 37 genera with 107 species (Nielsen et al., 1999; Møller et al., 2004a,b).

SUBFAMILY BYTHITINAE. Caudal fin united with dorsal and anal fins; pelvic fins absent in *Bellottia* and *Hephthocara.* The six blind to partially blind species of *Lucifuga* (placed in Brosmophycinae in Nielsen et al., 1999) live in limestone caves and sinkholes in waters ranging in salin-ity from fresh to highly saline; four species occur in Cuba, one in the Bahamas, and one in the Pacific in the Galapagos (Nielsen et al., 1999; Proudlove, 2005).

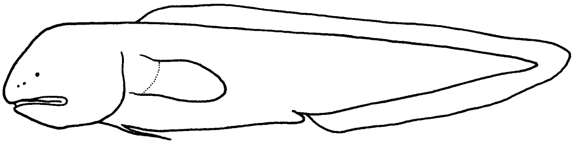
About 16 genera (e.g., *Bellottia, Bythites, Calamopteryx, Cataetyx, Diplacanthopoma, Gerhardia, Grammonus, Lucifuga, Saccogaster, Stygnobrotula, and Tuamotuichthys*) with about 62 species (e.g., Møller et al., 2004a).

SUBFAMILY BROSMOPHYCINAE. Caudal fin separate from dorsal and anal fins. One species of *Ogilbia* lives in brackishwater caves and crevices in the Galapagos, and one species of *Typhliasina* (*T. pearsei,* placed in *Ogilbia* in Nielsen et al., 1999, and Nelson et al., 2004) lives in freshwater caves in the Yucatan. Two tribes were recognized by Nielsen et al. (1999), Brosmophycinini and Dinematichthyini (with most of the genera).



About 21 genera (e.g., *Bidenichthys, Brosmophycis, Dermatopsis, Dinematichthys, Gunterichthys, Melodichthys, Ogilbia, Ogilbichthys,* and *Typhliasina*) with at least 45 species (e.g., Møller et al., 2004b).

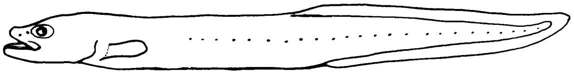
Family APHYONIDAE (224)—aphyonids. Marine; Atlantic, Indian, and Pacific.



Scales absent; swim bladder absent; dorsal and anal fins confluent; dorsal fin origin posterior, well behind pectoral fin; eyes poorly developed; opercular spine weak or absent; no sensory pores on head; pyloric caeca absent; pelvics jugular, one ray in each (absent in a few species); ovaries bilobed; precaudal vertebrae 26–48 (total of 68–86 vertebrae). A number of neotenic characters are present. Most species occur in depths exceeding 700 m.

Six genera, *Aphyonus, Barathronus, Meteoria, Nybelinella, Parasciadonus,* and *Sciadonus,* with 22 species (Nielsen et al., 1999).

Family PARABROTULIDAE (225)—false brotulas. Marine; scattered parts of Atlantic, Indian, and Pacific.



Scales absent; body eel-like; mouth small, lower jaw protruding in front of upper; dorsal and anal fins confluent with caudal fin, dorsal fin with 37–50 rays, caudal fin with 4–6 rays, and anal fin with 34–43 rays; dorsal fin origin posterior, well behind pectoral fin; two nostrils on each side of head; no sensory pores on head (neuromasts free); pelvic fins absent; pectoral fin small, with 6–8 rays; ovaries bilobed; vertebrae 54–73. Maximum length about 6 cm.

Nelson (1994) noted reasons for placing and for not placing this family near the zoarcids or, as here, the aphyonids. Nielsen et al. (1999) did not regard it as an ophidiiform. Clearly, it is a family without a home. For purposes of this classification, I leave it where placed in Nelson (1994). Just as then, more research is desirable to determine if parabrotulids are aphyonid derivatives, related to the zoarcids, or related to some other taxa.

Two genera, *Parabrotula* and *Leucobrotula,* with three species (Miya and Nielsen, 1991).

PEDICULATI. Patterson and Rosen (1989) considered the batrachoidiforms and lophiiforms to be sister groups and applied the term Pediculati to include both orders. There is doubt, based on molecular biology, that this group is monophyletic (see above under Paracanthopterygii).

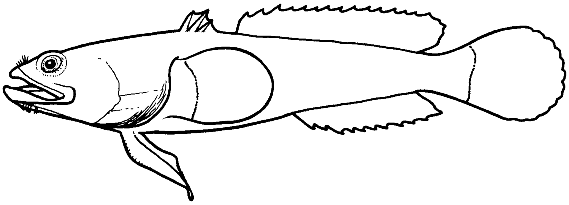
Order BATRACHOIDIFORMES (Haplodoci) (46)—toadfishes. Body usually scaleless (small cycloid scales in some); head large with eyes more dorsal than lateral; mouth large and bordered by premaxilla and maxilla; pore (foramen) in axil of pectoral fin in some; pelvic fins jugular (in front of pectorals), with one spine and two or three soft rays; three pairs of gills; gill membrane broadly joined to isthmus; branchiostegal rays six; four or five pectoral radials; swim bladder present; upper hypurals with peculiar intervertebral-like basal articulation with rest of caudal skeleton; no ribs, epiotics, or intercalars; no pyloric caeca.

Some members can produce audible sounds with the swim bladder and can live out of water for several hours. Most are drab colored.

Family BATRACHOIDIDAE (226)—toadfishes. Marine (primarily coastal benthic; rarely entering brackish water, a few species confined to freshwater); Atlantic, Indian, and Pacific.

Three subfamilies with 22 genera and 78 species.

SUBFAMILY BATRACHOIDINAE. Off coasts of the Americas, Africa, Europe, southern Asia, and Australia.

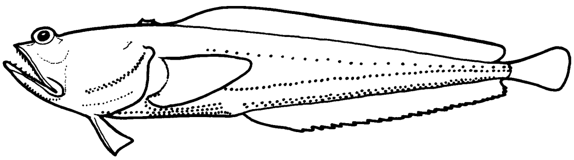


Three solid dorsal spines and solid opercular spine, no venom glands; subopercular spines present; body with or without scales (cycloid); no photophores; axillary gland at pectoral base present or absent; canine teeth absent; usually one or three lateral lines.

Toadfishes generally occur on sand and mud bottoms, although species of *Sanopus* occur in coral reefs.

Eighteen genera, *Allenbatrachus, Amphichthys, Austrobatrachus, Barchatus, Batrachoides, Batrachomoeus, Batrichthys, Bifax, Chatrabus, Halobatrachus, Halophryne, Opsanus, Perulibatrachus* (a replacement name for the fossil *Parabatrachus*), *Potamobatrachus, Riekertia, Sanopus, Tharbacus,* and *Triathalassothia,* with about 52 species (e.g., Collette, 1995a, 2001, 2003a; Greenfield, 1996, 1998; Greenfield et al., 1994; Greenfield and Smith, 2004).

SUBFAMILY PORICHTHYINAE. Eastern Pacific and western Atlantic.



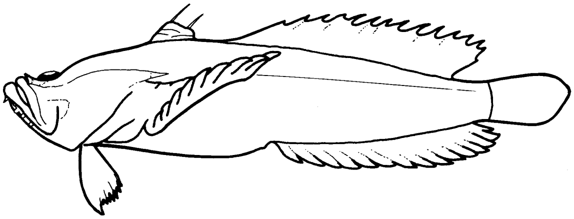
Two solid dorsal spines and solid opercular spine, no venom glands; no subopercular spines; body scaleless; photophores present or absent; axillary gland absent; canine teeth present; several lateral lines.

Two genera with 15 species.

Aphos. Lacks photophores; one southeastern Pacific (Peru and Chile) species (Walker and Rosenblatt, 1988).

Porichthys (midshipmen). Numerous photophores (this is one of the few shallow-water fishes that possess photophores); four lateral lines. Fourteen species, eight along the eastern Pacific (British Columbia to northern Peru and Galapagos Islands) and six along the western Atlantic (Virginia to Argentina, but generally absent from the West Indies) (Walker and Rosenblatt, 1988). Maximum length 43 cm, in *P. myriaster*.

SUBFAMILY THALASSOPHRYNINAE. Eastern Pacific and western Atlantic.



Two hollow dorsal spines and hollow opercular spine (serving as a venom-injecting apparatus capable of producing extremely painful wounds, connecting with venom glands; no subopercular spines; body scaleless; no photophores; no canine teeth; lateral line single or absent; pectoral fin rays 13–18.

Two genera with 11 species (e.g., Collette, 1973).

Daector. Second dorsal fin rays 22–33; anal fin rays 21–30; distinct glands with pores between bases of upper 3–7 pectoral fin rays on inner surface of fin (similar to *Opsanus*); vertebrae 31–40. Four tropical eastern Pacific marine species and *D. quadrizonatus* from freshwater, Columbia (Atrato basin, Atlantic drainage).

Thalassophryne. Second dorsal fin rays 17–22; anal fin rays 16–20; indistinct glandular tissue lacking pores scattered along upper rays of pectoral fin;

vertebrae 26–30. Five western Atlantic marine species (Panama and South America) and T. amazonica, known only from the Amazon River.

Order LOPHIIFORMES (47)—anglerfishes. First ray of spinous dorsal, if present, on head and transformed into illicium (line) and esca (bait), a device for attracting prey to mouth; pelvic fins, if present, in front of pectorals, with one spine and four (rarely) or five soft rays; gill opening small, tubelike, at or behind (rarely partly in front of) pectoral fin base; five or six branchiostegal rays; no ribs; pectoral radials 2–5, narrow and elongate; first vertebra fused to skull; swim bladder, when present, physoclistous.

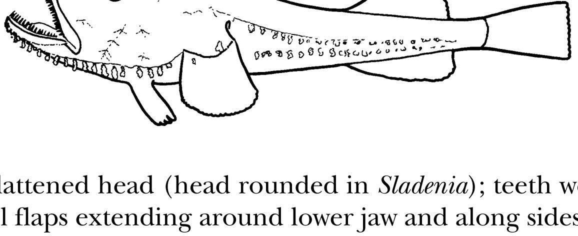
The following classification is based on the phylogenetic conclusions of Pietsch and Grobecker (1987). However, in contrast to the three suborders I present, these two workers recognized five suborders comprising the following postulated monophyletic groups.

1. Ogcocephaloidei and Ceratioidei—united by, e.g., second dorsal spine reduced to a small remnant (except well developed in the Diceratiidae), third dorsal spine and pterygiophore absent, and posttemporal fused to cranium.
2. Chaunacoidei—the sister group of the above by sharing second dorsal spine (elongate in the Chaunacidae) embedded beneath the skin of the head, and gill filaments of the first gill arch absent. The three suborders in 1 and 2 are included here in the suborder Ogcocephaloidei.
3. Antennarioidei—the sister group of the above by sharing, e.g., eggs and larvae much smaller than those of lophiids; dorsal fin spines reduced to three or less.
4. The Lophioidei—considered to be the primitive sister group of the above.

Eighteen families with about 66 genera and 313 species. All are marine. Most species occur in deep water.

Suborder Lophioidei. Pelvic fins present; spinous dorsal fin behind head with one to three spines; fourth pharyngobranchial present and toothed; pseudobranch large; body scaleless; frontals united.

Family LOPHIIDAE (227)—goosefishes. Marine; Arctic, Atlantic (including the Mediterranean Sea), Indian, and Pacific.



Huge, wide, flattened head (head rounded in *Sladenia*); teeth well developed; fringe of small flaps extending around lower jaw and along sides of head onto body; pectoral fin rays 13–28; second dorsal fin with 8–12 soft rays; anal fin with 6–10 rays; vertebrae 18 or 19 and, in *Lophius*, 26–31.

The mobile fishing apparatus has a flap of flesh at its tip that acts like a lure, attracting prey within reach of its large mouth. Size up to 1.2 m.

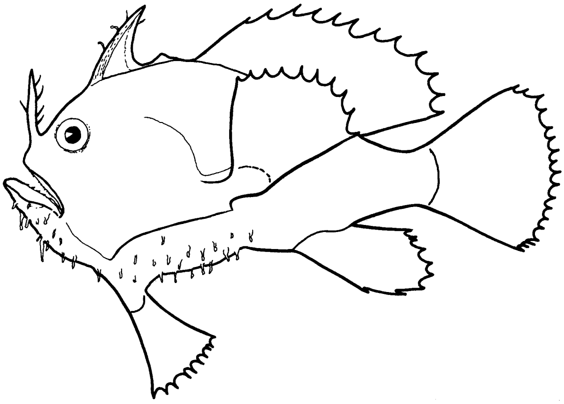
Four genera, *Lophiodes* (13), *Lophiomus* (1), *Lophius* (8), and *Sladenia* (3), with 25 species (Caruso, 1985). Fossils of Eocene age (e.g., *Eosladenia*) are known (Bannikov, 2004a).

Suborder Antennarioidei. Spinous dorsal fin consisting of three separate cephalic spines (the first is the modified illicium; the second dorsal spine may be short, but it is never embedded beneath the skin); pterygiophores of illicium and third spine of dorsal fin with highly compressed dorsal expansions.

In contrast to those taxa placed in the superfamily Ceratioidea, members of the two families of this suborder and of the Chaunacidae and Ogcocephalidae share the following features: pelvic fins present; pectorals usually armlike; pseudobranch (small) present; swim bladder present (most Antennariinae only) or absent; body usually covered with small, closely set dermal spines; frontals united posteriorly, but usually separated from each other anteriorly. Most species are benthic; only *Histrio* is epipelagic, occurring in sargassum.

Four families with 15 genera and 48 species. Unlike in Nelson (1994), *Tetrabrachium* and *Lophichthys* are placed in separate families following Pietsch and Grobecker (1987).

Family ANTENNARIIDAE (228)—frogfishes. Marine; all tropical and subtropical seas (absent from the Mediterranean), occasionally temperate (e.g., western Atlantic and southern Australia).



Deep-bodied (globose); nape not conspicuously humped; mouth large; eyes lateral; body covered with loose skin, naked or with denticles; gill opening below or behind base of pectoral fin; pelvic fin of one spine and five soft rays; parietals separated by supraoccipital; pectoral radials 3; swim bladder usually present (absent in *Kuiterichthys* and *Tathicarpus*); soft dorsal fin rays 10–16; soft anal fin rays 6–10;

pectoral fin rays 6–14; vertebrae 18–23; palatine teeth present. The fishing pole (illicium) of frogfishes, a modification of the first dorsal spine, is pronounced and highly variable between species. Maximum length 36 cm, some only 3 cm.

Frogfishes are benthic except for the widespread and pelagic *Histrio histrio*, which uses its prehensile pectoral fin for "clasping" or moving on floating sargassum. The Indo-Australian species *Antennarius biocellatus* is the only frogfish known to occur in brackish and freshwater. Pietsch and Grobecker (1987) give distributional information on the various species. The feeding dynamics of frogfishes are described by Pietsch and Grobecker (1987); they note cases of aggressive mimicry in which the lures of different species resemble a polychaete, an amphipod, and a small fish. In addition, there are a few species with parental care in which the eggs may also be acting as a lure.

Twelve genera, *Allenichthys*, *Antennarius*, *Antennatus*, *Echinophryne*, *Histiophryne*, *Histrio*, *Kuiterichthys*, *Lophiocharon*, *Nudiantennarius*, *Phyllophryne*, *Rhycherus*, and *Tathicarpus*, with 42 species (e.g., Pietsch and Grobecker, 1987; Ohnishi et al., 1997; Randall and Holcom, 2001). Over half the species are placed in the genus *Antennarius*; this genus appears to be the most primitive for the group, but unlike the other genera, its monophyly has not been established.

Family TETRABRACHIIDAE (229)—tetrabrachiid frogfishes. Marine; western and northern coasts of Australia, southern coast of New Guinea, and the south Molucca Islands of Indonesia.

Body elongate and strongly compressed; mouth small; eyes small and dorsal; swim bladder absent; nape humped; soft dorsal fin rays 16 or 17; anal fin rays 11 or 12; pectoral fin rays 9, fin divided into two portions; palatine teeth absent. Maximum length about 7 cm.

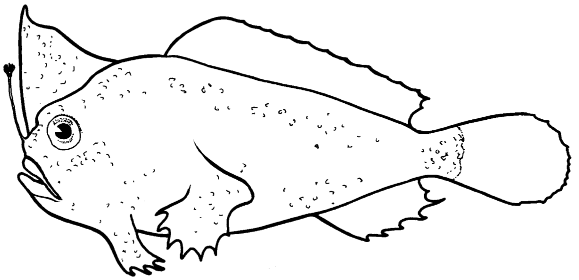
One species, *Tetrabrachium ocellatum* (Pietsch and Grobecker, 1987).

Family LOPHICHTHYIDAE (230)—lophichthyid frogfishes. Marine; Arafura Sea, western New Guinea.

Nape not humped; soft dorsal fin rays 12 or 13; anal fin rays nine; pectoral fin rays seven; palatine teeth present.

One species, *Lophichthys boschmai* (Pietsch and Grobecker, 1987).

Family BRACHIONICHTHYIDAE (231)—handfishes (warty anglers). Marine; southern Australia, primarily off Tasmania.



Body deep; skin naked or covered with denticles; second and third dorsal spines united by a membrane; gill opening small, behind base of pectoral fin; soft dorsal fin rays 15–18, unbranched; anal fin rays 7–10; pelvic fin with one spine and four soft rays; parietals meeting on midline; pectoral radials 2. Maximum length 15 cm. They are benthic, occurring in inshore waters at depths up to 60 m.

One genus, *Brachionichthys*, with about four species; there are three additional undescribed species (e.g., Paxton et al., 1989). A fossil, *Histionotophorus bassani*, very similar to the extant species, is known from the Eocene of Italy.

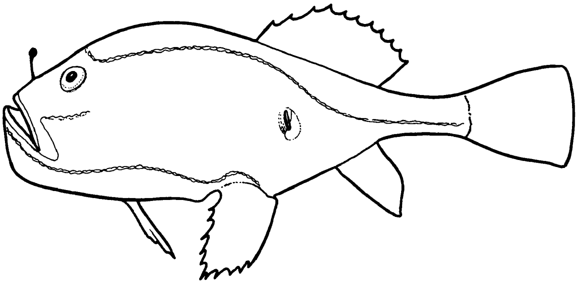
Suborder Ogcocephalioidei. Second dorsal spine reduced and embedded beneath skin of head; gill filaments of first gill arch absent (present in reduced form in some ceratioids); pterygiophore of illicium and third spine of dorsal fin without compressed dorsal expansions; pelvic fins present or absent.

The taxon Ogcocephalioidei, employed in Nelson (1994), recognized the monophyly of the lineage comprising the Chaunacidae, Ogcocephalidae, and the ceratioid families as given in Pietsch and Grobecker (1987) (and recognized as three suborders, Chaunacioidei, Ogcocephaloidei, and Ceratioidei). The Antennarioidei is the primitive sister group to the Ogcocephalioidei (as herein recognized); the Chaunacidae is the primitive sister group to the Ogcocephalidae and the ceratioids; and the Ogcocephalidae is the primitive sister group to the 11 ceratioid families.

Thirteen families, 47 genera, and 240 species.

Superfamily Chaunacioidea

Family CHAUNACIDAE (232)—coffinfishes or sea toads. Marine; Atlantic, Indian, and Pacific.

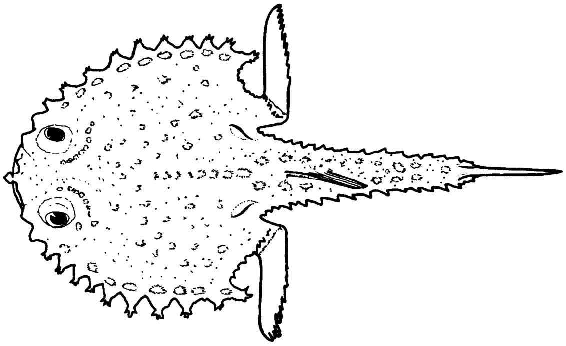


Body globose; skin covered with denticles; illicium, but no other spinous dorsal rays; mouth oblique; gill opening behind base of pectoral fin; anal fin rays 5–7; body color pink to deep reddish-orange. Maximum size about 35 cm.

Two genera, *Bathychaunax* (2, and two undescribed) and *Chaunax* (12), with 14 species (Caruso, 1989). The species occur between depths of 90 m to more than 2,000 m.

Superfamily Ogcocephalioidea

Family OGCOCEPHALIDAE (233)—batfishes. Marine; all tropical and many subtropical seas (absent from the Mediterranean Sea).



Body usually much depressed and flattened ventrally (somewhat box shaped in *Coelophrys* of the Indo-West Pacific); illicium relatively short (composed primarily of the modified pterygiophore of the first fin spine) but remnant of second dorsal spine present; illicial cavity, opening anteriorly, housing the esca when illicium is retracted; mouth nearly horizontal; gill opening in or above pectoral fin base; two or two and one-half gills (first arch reduced and lacking filaments); soft dorsal fin small, usually present, 1–6 rays; anal fin short, with 3 or 4 rays; well-developed tuberclelike scales. Species have either conical tubercles or multispined structures called "bucklers" (spines arranged in a radiating pattern) in addition to having very small tubercles. All have a modified type of scale associated with the lateral line organs.

Batfishes walk about on the bottom on their large armlike pectoral fins and smaller pelvic fins. They are awkward swimmers. Size normally 20 cm; up to 40 cm in *Ogcocephalus nasutus.* They are known primarily from outer continental shelves and continental slopes to 1,500–3,000 m with one species known from 4,000 m; a few species occur inshore, and rarely known upstream in rivers.

Ten genera, *Coelophrys, Halieutopsis, Dibranchus, Halieutaea, Halicmetus, Malthopsis, Halieutichthys, Ogcocephalus, Solocisquama,* and *Zalieutes,* with 68 species (Bradbury, 1999, 2003).

Superfamily Ceratioidea. Pelvic fins absent; pseudobranch absent; body usually scaleless (prickles, spines, or plates may be present); supraoccipitals immediately behind frontals and between the parietals; frontals not united; lower pharyngeals reduced and toothless; pectoral fin rays 12–28 (except *Ctenochirichthys* with 28–30); 8 or 9 caudal fin rays; only females with illicium, the tip of which usually has a light organ (undoubtedly increasing its function in attracting prey; light organs may also be present elsewhere); vertebrae 19–24.

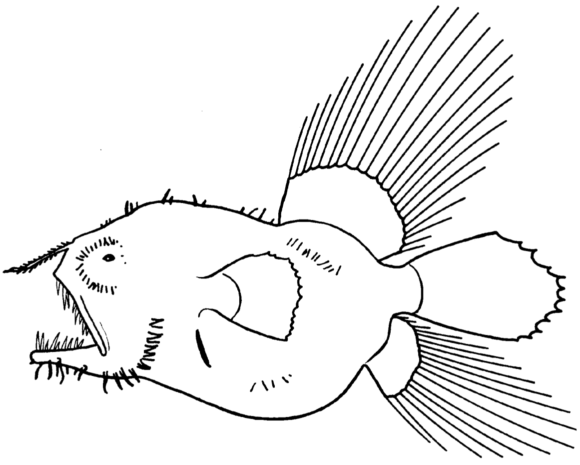
Marked sexual dimorphism is characteristic of the ceratioids. The longest female known in each family is 3 to 13 times longer than the longest male known (within species the difference can be much greater). The adult males of all species in at least four families feed in a parasitic fashion on the larger females. After metamorphosis into the parasiticlike stage, these males actively seek out females (probably through a female-emitted, species-specific pheromone), attach to their bodies, and feed on their blood (a vascular connection may exist in all such parasiticlike relationships). Males are generally different in appearance from females (females are pictured and used for the family descriptions herein), although dorsal and anal fin ray counts are the same. The sexually mature males of the Ceratiidae, Linophrynidae, and perhaps the Neoceratiidae are obligatory sexual parasites (nonparasitized females never have developed ovaries, and free-living males never have developed testes or undergo postmetamorphic growth), while parasitism in the Caulophrynidae and one oneirodid genus may be facultative (most other taxa are thought to be nonparasitic). In some families the males are nonparasitic; in these cases it appears that they do not feed after metamorphosis and survive until spawning on nutrients stored during larval life. In the past, males, females, and larva of the same species have been described as different species. Some species are still known only from males, females, or larva and often from only a few specimens. Most of what we know is based on the researches of E. Bertelsen and T. W. Pietsch.

Larval life is spent in the upper, food-rich oceanic layer; most adults are meso- or bathypelagic (usually occurring between 1,500 and 2,500 m; adult thaumatichthyids are benthic between 1,000 and 3,600 m). Ceratioids extend from the subarctic to the subantarctic but are absent from the Mediterranean Sea.

Maximum size in most species is seldom longer than 8 cm; however, *Ceratias holboelli* reaches at least 1.2 m.

Eleven families, 35 genera, and about 158 species. Most of what is presented below is from the works of E. Bertelsen and T. W. Pietsch, with the sequence of families following the 1984 work of E. Bertelsen (references given in Nelson, 1994).

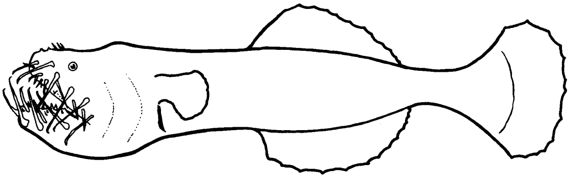
Family CAULOPHRYNIDAE (234)—fanfins. Marine; Atlantic, Indian, and Pacific.



No distal bulb with light organ on illicium; mature males feed in parasitic fashion on females; pelvic fins in larvae (only ceratioid with pelvics at some stage); two pectoral radials (all other ceratioids have 3–5); dorsal fin with six (in *Robia*) or 14–22 normal rays, and anal fin with 5 (in *Robia*) or 12–19 rays (other ceratioids have 13 or fewer anal fin rays); extremely elongate dorsal and anal rays; eight caudal fin rays.

Two genera, *Robia*, monotypic, and *Caulophryne* (4), with five species (e.g., Balushkin and Fedorov, 1986).

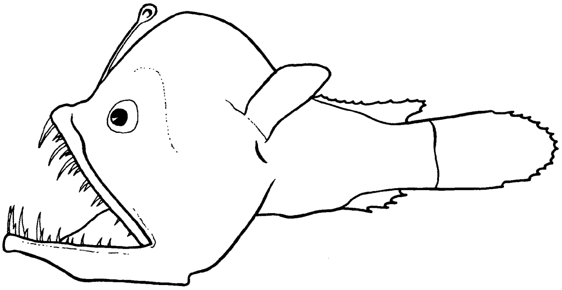
Family NEOCERATIIDAE (235)—toothed seadevils. Marine; Atlantic, Indian, and Pacific.



Illicium absent; long movable teeth outside jaws in females; mature males feed in parasitic fashion on females; dorsal fin with 11–13 rays and anal fin with 10–13 rays.

One species, *Neoceratias spinifer.*

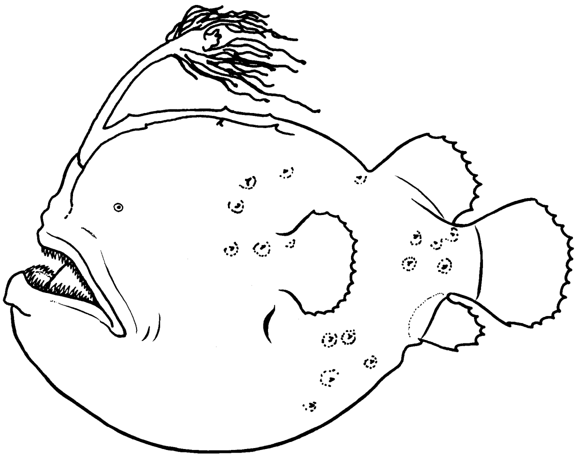
Family MELANOCETIDAE (236)—black seadevils. Marine; Atlantic, Indian, and Pacific.



Dorsal fin with 12–17 rays and anal fin with three or four rays.

One genus, *Melanocetus*, with five species.

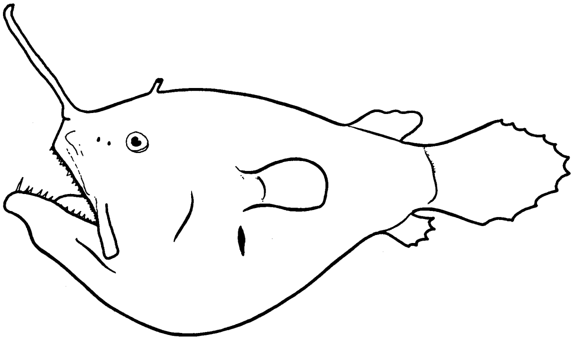
Family HIMANTOLOPHIDAE (237)—footballfishes. Marine; Atlantic, Indian, and Pacific.



Both sexes lack the parietals throughout life (present in other ceratioids except lost in adult females of *Rhynchactis*); triradiate pelvic bone; six branchiostegal rays; no epurals; bony plates, each with a median spine, over body; dorsal fin with five or six rays and anal fin with four rays; caudal fin with nine rays; pectoral fin rays 14–18; vertebrae about 19. Females differ from other ceratioids in having a blunt and short snout; papillae on snout and chin. Maximum length 46 cm (maximum length of males 3.9 cm, the largest of free-living ceratioid males) (Bertelsen and Krefft, 1988).

One genus, *Himantolophus*, with 18 species (Bertelsen and Krefft, 1988).

Family DICERATIIDAE (238)—double anglers. Marine; continental shelf or slope of tropical and subtropical seas, Atlantic and Indo-West Pacific.

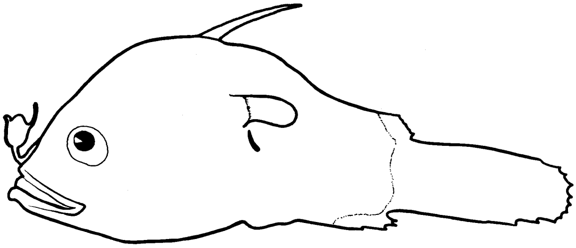


Females distinguished from all other ceratioids in having second cephalic ray externally exposed in young specimens, club shaped, with distal light organ, and emerging from head directly behind base of illicium; skin spines present;

dorsal fin with five to seven rays and anal fin with four rays; small pelvic bone present, connected with cleithrum.

Two genera, *Diceratias* (3) and *Bufoceratias* (synonym *Phrynichthys*, 3), with six species (Pietsch et al., 2004).

Family ONEIRODIDAE (239)—dreamers. Marine; Atlantic, Indian, and Pacific.



Skin naked or with short spines in some females; dorsal fin with 4–8 rays and 4–7 anal fin rays; jaws equal anteriorly.

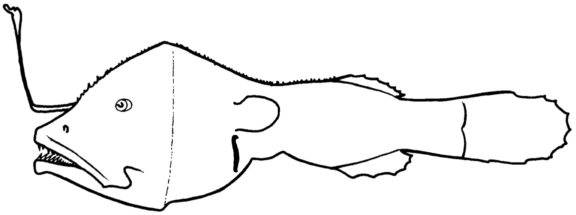
Sixteen genera (e.g., *Bertella*, *Chaenophryne*, *Ctenochirichthys*, *Danaphryne*, *Dermatius*, *Dolopichthys*, *Lophodolos*, *Microlophichthys*, *Oneirodes*, *Pietschichthys*, and *Puck*) with about 62 species (e.g., Ho and Shao, 2004; Pietsch and Kharin, 2004). The genus *Oneirodes*, with 38 species, contains over half the species.

Family THAUMATICHTHYIDAE (240)—wolftrap anglers. Marine; Atlantic and Pacific.

Similar to Oneirodidae, but differing from it and all other ceratioid families in having upper jaw (i.e., the premaxillaries) extending far beyond lower jaw and upper arm of operculum divided into two or more branches.

Two genera, *Lasiognathus* (4) and *Thaumatichthys* (3), with seven species (Bertelsen and Pietsch, 1996).

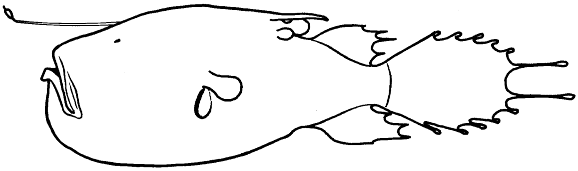
Family CENTROPHRYNIDAE (241)—deepsea anglerfishes. Marine; Atlantic, Indian, and Pacific.



Small hyoid barbel present in young; skin with numerous small spines; dorsal fin with 5–7 rays and five or six anal fin rays.

One species, *Centrophryne spinulosa.*

Family CERATIIDAE (242)—seadevils. Marine; Atlantic, Indian, and Pacific.

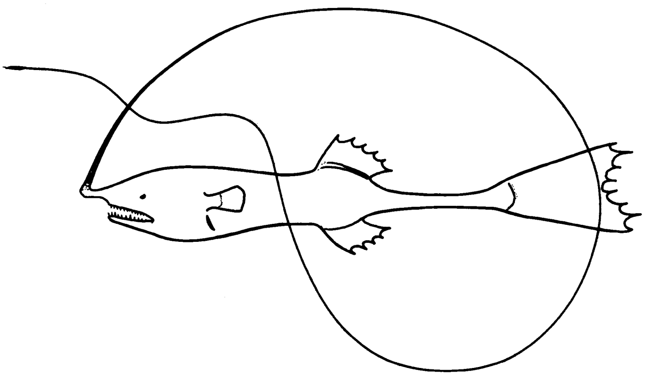


Females with two or three rays modified into caruncles (low fleshy appendages) in front of soft dorsal fin; cleft of mouth vertical to strongly oblique; parietals large; mature males feed in parasitic fashion on females; dorsal fin soft rays usually four, rarely five; anal fin rays four; larvae "humpbacked."

Maximum length at least 77 cm, up to 1.2 m (*Ceratias holboelli*).

Two genera, *Ceratias* (3) and the monotypic *Cryptopsaras*, with four species.

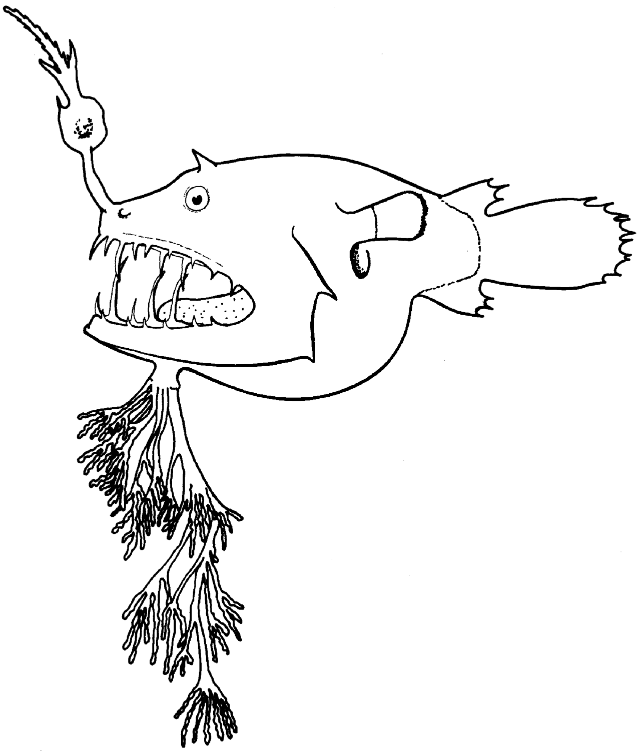
Family GIGANTACTINIDAE (243)—whipnose anglers. Marine; Atlantic, Indian, and Pacific.



Body elongate in females; illicium almost as long as or longer than body; upper jaw extending slightly beyond lower jaw; five pectoral radials; dorsal fin with 3–10 rays and anal fin with 3–8 rays; nine caudal fin rays.

Two genera, *Gigantactis* (19) and *Rhynchactis* (3), with 22 species (Bertelsen and Pietsch, 1998, 2002).

Family LINOPHRYNIDAE (244)—leftvents. Marine; Atlantic, Indian, and Gulf of Panama.



Mature males feed in parasitic fashion on females; dorsal and anal fin soft rays usually three; anus sinistral; hyoid barbel in female *Linophryne.*

Five genera, *Linophryne,* with 23 species, and the monotypic *Acentrophryne, Borophryne, Haplophryne,* and *Photocorynus,* with 27 species (e.g., Gon, 1992).

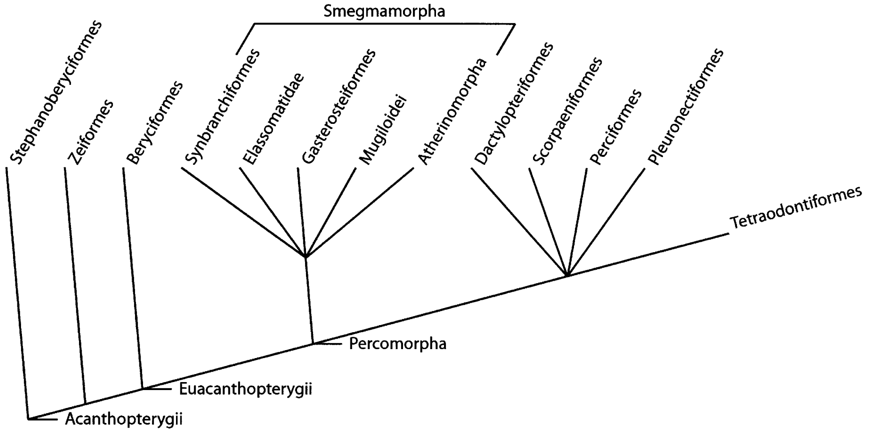
Superorder ACANTHOPTERYGII

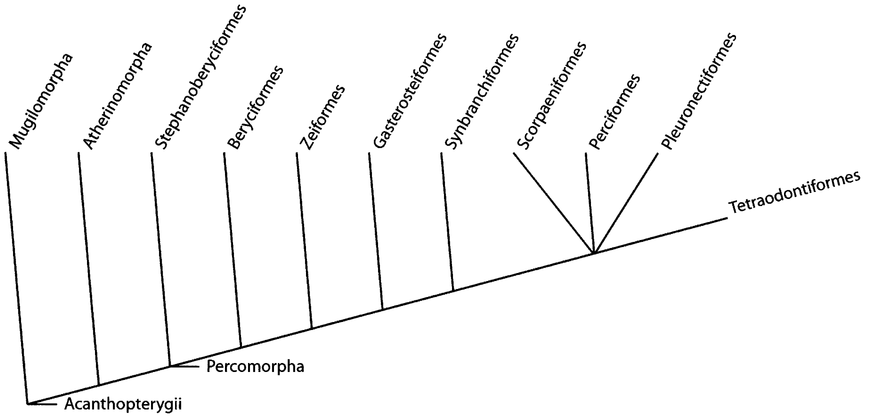
Greenwood et al. (1966) gave equal rank to the Atherinomorpha and their Acanthopterygii (= present Percomorpha). In 1969 D. E. Rosen and C. Patterson combined them under the category Acanthopterygii, and Rosen (1973a) defined the group. As described in Lauder and Liem (1983), acanthopterygians have a more mobile upper jaw than the teleosts below this level (except for the Lampriformes). This is due largely to the presence of a well-developed ascending process on the premaxilla. There is a secondary loss of the forward movement of the jaw (protrusibility) in several acanthopterygian lines. In addition, in most members of this taxon Baudelot's ligament, the ligamentous support of the pectoral skeleton (via attaching to the supracleithrum), originates on the basioccipital; in most lower teleosts, the Stephanoberyciformes, and—where it may be considered a secondary modification—some other acanthopterygian taxa, Baudelot's ligament originates on the first vertebra (Johnson and Patterson, 1993).

Johnson and Patterson (1993) recognized a new sequence and different interrelationships of some of the following major taxa. They regarded the Stephanoberyciformes as the most primitive acanthopterygian, followed by the Zeiformes and Beryciformes. In addition, they recognized the first two series given here—the Mugilomorpha and Atherinomorpha—the orders Gasterosteiformes and Synbranchiformes, and the family Elassomatidae in an unresolved polychotomy. The resulting taxon, thought to be monophyletic, is termed by them the Smegmamorpha, a term derived from the first letters of the six components (recognizing the Mastacembeloidei as one component) and meaning "cleansing agent" in Greek and Latin. The smegmamorphs are diagnosed primarily by the first epineural originating at the tip of a transverse process on the first vertebra. The Smegmamorpha and Scorpaeniformes and higher taxa compose the Percomorpha of Johnson and Patterson (1993), a considerably different use of the term than recognized herein (for further comment, see under Percomorpha). However, it is important to note that the taxon Acanthopterygii as used here has the same composition as Johnson and Patterson's (1993) Acanthopterygii. Are Smegmamorpha as defined by Johnson and Patterson (1993) monophyletic? Some components probably are, but the molecular studies of Wiley et al. (2000), Roe et al. (2002), Miya et al. (2003), and Chen et al. (2003) failed to support it. The detailed work of Springer and Johnson (2004) should be studied for more information on this group. On page 117 of that publication, V. G. Springer did not believe the group to be monophyletic and broke it into three groups, Gasterosteomorpha, Atherinomorpha, and Mugilomorpha (with the last two groups being closely related but not closely related to the Gasterosteomorpha). Coauthor Johnson disagrees with this conclusion and with Springer's feeling that the name Smegmamorpha is marginally offensive (G. D. Johnson, pers. comm., 2005).

There can be little doubt that, with all the work done since 1994, changes are required in our classification. We know a lot more now. Some of the new, exciting molecular work is being done in the laboratories of Guillaume Lecointre in Paris, France; Masaki Miya in Chiba, Japan; and Mutsumi Nishida in Tokyo, Japan. These workers and their colleagues as well as many others are finding support for new clades that must be taken seriously, especially in those areas where agreement is found when different approaches are taken. However, I faced a dilemma in how to deal with so much conflicting information, and no comprehensive synthesis seemed possible. I therefore have decided to simply refer to some of the areas where we face exciting new understandings while making very few changes from Nelson (1994).There are so many such studies now available that a review here would be impossible. However, it is my hope that within a few years an attempt at a comprehensive classification can be undertaken.

Thirteen orders, 267 families, 2,422 genera, and 14,797 species (24% limited to freshwater).





Cladograms contrasting the relationships of the Acanthopterygii as presented by Johnson and Patterson (1993) (top) and as presented here (bottom). Note the different use of the term Percomorpha (see discussion under Percomorpha).

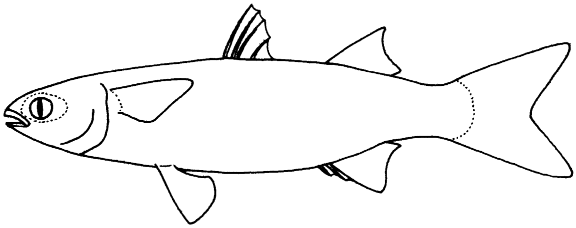
Series MUGILOMORPHA

Order MUGILIFORMES (48)—mullets. There has been much disagreement concerning the relationships of the one family placed in this order. Berg (1940) placed the three families Atherinidae, Mugilidae, and Sphyraenidae in the order Mugiliformes at the subperciform level. Gosline (1971) considered the suborder Mugiloidei as a perciform and included the families Polynemidae, Sphyraenidae, Mugilidae, Melanotaeniidae, Atherinidae, Isonidae, Neostethidae, and Phallostethidae. Gosline considered his suborder

Mugiloidei to be one of the most primitive perciform groups and listed it first in his perciform classification. He did this largely on the basis that all mugiloids lack any direct articulation between the pelvic girdle and the cleithra (whereas in most other perciforms they are attached). Greenwood et al. (1966) and Nelson (1984) gave subordinal status to the first three families and placed them in the order Perciformes.

Although reasons exist for regarding mugilids as perciform, rather than being related to the Atherinomorpha, there seems insufficient reason to change the classification from that given in Nelson (1994), based on Stiassny (1993) and Johnson and Patterson (1993). Johnson and Patterson (1993) felt that the most accurate way to show our present knowledge of relationships is to place the atherinomorphs, mugilomorphs, gasterosteiforms, synbranchiforms, and *Elassoma* in an unresolved polychotomy.

Family MUGILIDAE (245)—mullets. Coastal marine and brackish water (some are freshwater); all tropical and temperate seas.



Widely separated spiny-rayed (with four spines) and soft-rayed (8-10 rays) dorsal fins; anal fin with two or three spines and 7-11 soft rays; pectoral fins high on body; pelvic fins subabdominal, with one spine and five branched soft rays; lateral line absent or very faint; ctenoid scales in adults except *Myxus,* which has cycloid scales throughout life; mouth moderate in size; teeth small or absent; gill rakers long; stomach usually muscular and intestine exceedingly long; vertebrae 24–26. Oral and branchial filter-feeding mechanism involving gill rakers and a pharyngeal apparatus. Maximum length about 1.2 m SL. Members are also known as grey mullets.

Liza abu is known only from freshwater and estuaries in southeastern Asia. The juveniles of many otherwise marine species extend into estuaries.

About 17 genera, *Agonostomus, Aldrichetta, Cestraeus, Chaenomugil, Chelon, Crenimugil, Joturus, Liza, Mugil* (synonym *Mugiloides*), *Myxus, Neomyxus, Oedalechilus, Plicomugil, Rhinomugil, Sicamugil, Valamugil,* and *Xenomugil,* with about 72 species (e.g., Harrison, 2003).

Series ATHERINOMORPHA

Opercular and preopercular margin without spines or serrations; ctenoid scales rare; branchiostegal rays 4–15; no orbitosphenoid; four cuboidal pectoral actinosts; caudal skeleton usually with two large triangular hypural plates, never more than four; swim bladder physoclistous. The protrusible upper jaw differs from that of other acanthopterygians in lacking a ball-and-socket joint between the palatine and maxilla (a feature that prevents the premaxillaries from being locked in the protruded position) and in lacking crossed rostral ligaments extending between the palatines and the heads of the premaxillaries (however, *Odontesthes* species have a different form of crossed ligaments, Dyer, 1997). A list of synapomorphic characters is given by Parenti (1993, 2005).

Most species of this group are surface-feeding fishes, and about 75% are confined to fresh or brackish water. This taxon contains the only naturally occurring populations of unisexual (all-female) fishes; these occur in the New World—the atherinid *Menidia clarkhubbsi* and members of the poeciliid genera *Poecilia* and *Poeciliopsis* (shown by A. A. Echelle and co-authors in 1983). The diversity of adaptation for internal fertilization is not found in any other higher taxon of fishes; some freshwater members of several families have independently evolved methods for internal fertilization and may lay fertilized eggs or be viviparous (e.g., Grier and Collette, 1987). The eggs of most oviparous members have one or more long chorionic filaments that adhere to the spawning substrate and, except in most exocoetoids, have conspicuous oil droplets that coalesce at the vegetal pole. Atherinomorphs have other unusual reproductive features such as the male testis is unique in being of the restricted lobular type where spermatogonia are restricted to the distal termini of the lobules (Parenti and Grier, 2004). Delayed hatching is a common occurrence and this may be a synapomorphy (Parenti, 2005).

The concept of a monophyletic taxon Atherinomorpha containing the present assemblage of Atheriniformes, Beloniformes, (including the Adrianichthyoidei), and Cyprinodontiformes goes back to Rosen (1964), Greenwood et al. (1966), and Rosen and Patterson (1969). Few taxa have such strong evidence for monophyly as the Atherinomorpha, and the unity of this group continues to gain support and its constituent members have remained unchanged over the last 40 years, but our understanding of its relationship to other higher taxa remains uncertain while our understanding of relationships within each of the orders continues to change. A detailed review of our understanding of the phylogeny of the Atherinomorpha with emphasis to the evolution of the unusual reproductive modifications is given by Parenti (2005). The sister group of this taxon is accepted to be the Mugilidae following evidence presented by Stiassny (1990, 1993). Some support for this is given by Johnson and Patterson (1993) and Wiley et al. (2000). This and other proposals are given in Parenti (2005) and Parenti and Grier (2004); as advised by Parenti (2005), broader surveys are required to be confident in identifying its sister group.

Some changes to our understanding of atherinomorph systematics is seen by comparing the classifications used in the last three editions. The research of the above authors on systematic relationships was expressed in Nelson (1976). The higher classification in the 1976 edition was as follows:

Series Atherinomorpha (with all members placed in one order)
  Order Atheriniformes
    Suborder Exocoetoidei (present Beloniformes)
    Suborder Cyprinodontoidei (present Adrianichthyoidei + Cyprinodontiformes)
    Suborder Atherinoidei (present Atheriniformes)

Rosen (1981) and Rosen and Parenti (1981) made a major contribution in recognizing Atheriniformes (in their Division I) as sister to the Cyprinodontiformes and the Beloniformes (in their Division II). They argued that the spined atherinids were primitive, with spines being lost in the cyprinodontiforms. Their conclusions were not fully followed in the 1984 edition, where higher relationships were presented as follows:

Series Atherinomorpha (with all members placed in two orders)
  Order Cyprinodontiformes
    Suborder Exocoetoidei (present Beloniformes)
    Suborder Adrianichthyoidei (present Adrianichthyoidei)
    Suborder Cyprinodontoidei (present Cyprinodontiformes)
  Order Atheriniformes (present Atheriniformes)

The classification presented in 1994 was largely based on a reanalysis of the above and works cited in 1994 and was as follows:

Series Atherinomorpha (with all members placed in three orders)
  Order Atheriniformes (present Atheriniformes)
  Order Beloniformes (present Beloniformes)
  Order Cyprinodontiformes (present Cyprinodontiformes)

The current classification has many changes within the orders based on the extensive works cited but no change in the composition at the higher level from the previous edition (Nelson, 1994).

The Atheriniformes are thought to be sister to the remaining members (Dyer and Chernoff, 1996; Dyer, 1998); therefore, the Atheriniformes are now recognized in the superorder Atherinea, with the Beloniformes and Cyprinodontiformes, being in the superorder Cyprinodontea (the ordinal sequence is as expressed in Nelson, 1994).

Series Atherinomorpha
  Superorder Atherinea
    Order Atheriniformes (two suborders, Atherinopsoidei with one family and Atherinoidei with five families)
  Superorder Cyprinodontea
    Order Beloniformes (two suborders, Adrianichthyoidei with one family and Belonoidei with two superfamilies, each with two families)
    Order Cyprinodontiformes (10 families)

Three orders, 21 families, 193 genera, and about 1,552 species (about 1,304 are primarily freshwater).

Superorder ATHERINEA

Order ATHERINIFORMES (49)—silversides.

Usually two separated dorsal fins, the first, if present, with flexible spines, and the second preceded by a single flexible spine in most species (Parenti, 1993, suggested that the second dorsal fin is homologous with the single dorsal fin of Cyprinodontiformes); anal fin usually preceded by a spine; lateral line absent or very weak; branchiostegal rays 4–7; narial openings paired; pectoral fins inserted high on body in most; pelvic fins abdominal (most species), subabdominal, or thoracic in position (essentially absent in female phallostethids and highly modified in male phallostethids); parietals absent in infraorder Atherinoida, present in other taxa. Two derived larval features are preanal length of larvae between hatching and flexion less than 40% of body length (longer in members of most other eurypterygians); larvae with single mid-dorsal row of melanophores on dorsal margin (most other atherinomorphs have two or more mid-dorsal rows). In addition, the fin rays are not evident at hatching as they are in beloniforms and cyprinodontiforms. Most species are silvery in color (and have a silvery lateral stripe), except male melanotaenioids can be very colorful. Maximum length about 52 cm, in the atherinopsid *Odontesthes bonariensis* (Dyer and Chernoff, 1996:44). See "Series Atherinomorpha" above for further comments on this order.

The following sequenced classification follows Dyer and Chernoff (1996) and Dyer (1998, 2000). Dyer and Chernoff (1996) and Dyer (1998) give synapomorphies (most not listed here), which are primarily osteological characters not useful in field identification, supporting monophyly of the various clades, including that of the order. In the different classification given by Saeed et al. (1994), the atheriniforms are divided into two superfamilies, Atherinopsoidea (parietals present, with Atherinopsidae, Notocheiridae, and Isonidae) and Atherinoidea (parietals absent, containing all other atheriniform taxa, Bedotiidae and higher); their cladogram (p 44) renders the Atheriniformes paraphyletic, with their Atherinoidea forming a clade with Beloniformes and Cyprinodontiformes, and their families Atherinopsidae, Isonidae (herein placed in the Notocheiridae), and Notocheiridae forming the sister group to the above. Changes in the 1994 classification include the breakup of the family Atherinidae with i) the Atherinopsinae and Menidiinae recognized in the Atherinopsidae and sister to all other Atheriniformes, ii) *Atherion* recognized in its own family, and iii) the remaining members of the former Atherinidae recognized as sister to Phallostethidae.

Six families with 48 genera and about 312 species (about 210 are primarily freshwater, many also occur in brackish water, with 58 species in North American continental waters). Most atheriniforms are tropical or warm temperate and live in shallow, inshore marine or fresh waters.

Suborder Atherinopsoidei. The recognition of two suborders in the Atheriniformes reflects the cladistic results of Dyer and Chernoff (1996) showing that the Atherinopsidae is sister to the remaining families. One of the major needs in atheriniform systematics is to resolve the very different conclusions of Dyer and Chernoff (1996) from those of Aarn et al. (1998) and Aarn and Ivantsoff (1997).

Family ATHERINOPSIDAE (246)—New World silversides. Marine (pelagic coastal) and freshwater; temperate to tropical North, Central, and South America.

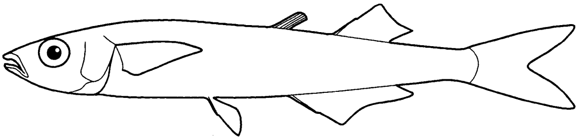
Two widely separated dorsal fins, the first with 2–9 spines; pectoral fins inserted high on body. Body often translucent, with silvery lateral stripe. Diagnostic features include sphenotic postorbital process wide at base, premaxilla with narrow anterior joint. Other characters supporting monophyly of this group and as the sister group to all other atheriniforms are given in Dyer (1997, 1998) and Dyer and Chernoff (1996). Atherinopsids are most easily separated from the atherinids in having the premaxilla protractile (usually highly protractile), distal end of the premaxilla expanded, premaxilla lacking postmaxillary process, and preopercular sensory canal connecting to mandibular canal (Chernoff, 2003) (see Atherindae for opposing characters).

Maximum length in most adults 15 cm. Some eastern Pacific species over 1 m.

This taxon, restricted to the New World, has generally been recognized as a subfamily of the Atherinidae. It was formerly removed from the Atherinidae and recognized at the family level by Saeed et al. (1994), but regarded as sister to the notocheirids, rather than as sister to all remaining atheriniforms as proposed by Dyer and Chernoff (1996).

Eleven genera and about 108 species in two subfamilies (about 58 species are primarily marine or brackish water, as defined by spawning habitat, and about 50 are confined to fresh water). These are the only atheriniforms in the New World except for *Notocheirus* and a few atherinids (see also below under Notocheiridae).

SUBFAMILY ATHERINOPSINAE

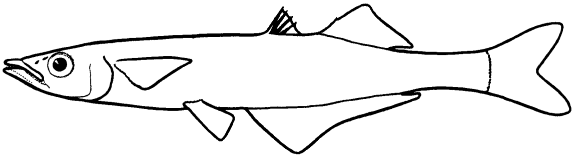


Two tribes with six genera and 34 species (Dyer, 1997, 1998; Dyer and Gosztonyi, 1999; Malabarba and Dyer, 2002).

TRIBE ATHERINOPSINI. *Atherinops, Atherinopsis, Colpichthys,* and *Leuresthes* with a total of six marine species, occasionally brackish water, temperate Pacific coast North America from British Columbia to Gulf of California).

TRIBE SORGENTININI. *Basilichthys* (five species, freshwater, Peru, and Chile) and *Odontesthes* (subgenera *Odontesthes* [paraphyletic at this time], *Austromenidia, and Cauque*) (23 species, of these about eight primarily coastal marine Peru and southern Brazil south to Tierra del Fuego and 15 primarily freshwater, Chile and southern Brazil to Patagonia, with many of the 23 also in brackish water).

SUBFAMILY MENIDIINAE. Some temperate species but primarily in the tropics with many freshwater members in Mexico and Central America.



Two tribes with five genera, and 74 species.

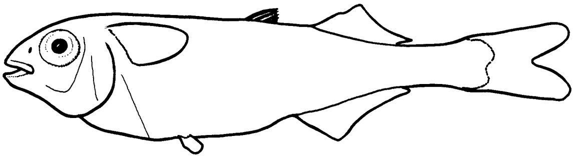
TRIBE MENIDIINI. *Labidesthes* (1, shown in the figure) and *Menidia* (29, synonyms *Chirostoma* and *Poblana*) with about 30 species (Barbour, 2002; C. D. Barbour, pers. comm., January 2003). Echelle and Echelle (1984) showed that *Chirostoma* and *Poblana* are synonyms of *Menidia* (*Labidesthes* would be the primitive sister group of *Menidia*); the synonymy of this clade of 29 species was not accepted by Dyer (2003) but was by Miller et al. (2005).

TRIBE MEMBRADINI. *Atherinella* (about 35 species in fresh, brackish, and coastal marine waters, with about 15 primarily marine and 20 primarily freshwater, Mexico to South America, Chernoff, 1986a,b; Dyer, 2003; Nelson et al., 2004), *Membras* (six marine species), and *Melanorhinus* (three marine species, Dyer, 2003); each of the three genera has Atlantic and Pacific members.

Suborder Atherinoidei. According to Dyer and Chernoff (1996), the remaining taxa form a monophyletic group, sister to the above Atherinopsidae. In their cladogram, the Notocheiridae are sister to the remaining atheriniforms (the Atherinoida) as reflected in the following classification.

Infraorder Notocheiroida

Family NOTOCHEIRIDAE (Isonidae) (247)—surf sardines. Marine, coastal; Indo-West-Pacific (South Africa to southern Japan and Australia, American Samoa, Taiwan, Hawaii, etc.) and southern South America.



Body depth greatest very anteriorly, at pectoral fin origin (due to elongated cleithrum and coracoids); body highly compressed; pectoral fins inserted exceptionally high on body, above lateral line and near dorsal surface; ventral abdominal edge keel-shaped, formed by ventral expansion of cleithra, postcleithra, and pelvic girdle; upper jaw teeth confined to symphyseal portion of premaxilla; supracleithrum absent; postcleithrum and cleithrum elongated and about equal in length. Maximum length about 5 cm.

Two genera with six species: *Iso* with five (possibly a sixth undescribed species) Indo-West Pacific species (Saeed et al., 1993, 1994; Ivantsoff, 1999), and *Notocheirus hubbsi* (known from Chile and Argentina). The two genera are recognized in separate families, Isonidae and Notocheiridae, by Saeed and Ivantsoff (1991) and Saeed et al. (1994). While there are substantial differences between the two genera (e.g., *Notocheirus* lacks the first dorsal fin and lacks epurals), they are regarded here as sister groups. The conclusions of Dyer and Chernoff (1996) are reflected here in placing the family in a monophyletic group with largely Old World atheriniforms; however, Saeed et al., (1994) and Aarn and Ivantsoff (1997) considered the New World *Notocheirus* to be closer to the New World Atherinopsidae. Known as surf silversides by Allen (1995).

Infraorder Atherinoida (Atherines of Dyer and Chernoff, 1996). Dyer and Chernoff (1996) and Dyer (2000) recognized this taxon, with the composition given here. On the basis of characters they considered apomorphic in a global analysis, they placed the members in four sequenced families, Melanotaeniidae, with three subfamilies, Bedotiinae, Melanotaeniinae, and Pseudomugilinae (but, unlike here, with two tribes, Pseudomugilini and Telmatherinini), Atherionidae, Phallostethidae, and Atherinidae (the latter two families are sister taxa and were placed in the superfamily Atherinoidea). The relationships expressed by Aarn and Ivantsoff (1997) and Aarn et al. (1998), on the basis of other characters, are quite different, in part with the recognition of Telmatherinidae as a family and the inclusion of the bedotiine genera *Bedotia* and *Rheocles* in a clade comprising what is recognized here as the Melanotaeiinae. Aarn and Ivantsoff (1997) recognized the following families in an unresolved polytomy (sequenced here from their Figure 30 from bottom up): Melanotaeniidae, Pseudomugilidae, Telmatherinidae, Atherinidae, Phallostethidae (including *Dentatherina*), and Atherionidae. They recognized their members of the Melanotaeniidae in two subfamilies, Iriatherininae (with one genus, *Iriatherina)* and Melanotaeniinae (with the two bedotiine genera being sister to *Cairnsichthys* and *Rhadinocentrus,* and these four genera being sister to the remaining three melanotaeiine genera. A similar arrangement was given in a revision of the Telmatherinidae by Aarn et al. (1998) but without the explicit subfamily relations expressed; they recognized three families in an unresolved trichotomy, Telmatherinidae, Melantaeniidae, and Pseudomugilidae, and these being sister to Atherinidae. Further studies will be needed to resolve the difference between Dyer and Chernoff (1996) and that of Aarn and Ivantsoff (1997) and Aarn et al. (1998). While the authors of the latter two studies had more species of the included families than Dyer and Chernoff (1966), they did not have as broad a taxonomic coverage, which is considered important here. I have attempted to recognize monophyletic groups based on the strengths of these works while, when there is reasonable uncertainty, maintaining generally recognized groups. Recognition of the subfamily Telmatherininae, as opposed to the action of Dyer and Chernoff (1996) in considering it a tribe of the Pseudomugilinae, is based on the study of Aarn et al. (1998). Recognition of Atherionidae, previously considered a subfamily of Atherinidae, seems well founded by Dyer and Chernoff (1996) and Aarn and Ivantsoff (1997).

Comparison of the classifications of Aarn and Ivantsoff (1997) (Aarn et al., 1998, present details of the last three families), Dyer and Chernoff (1996), and the one presented here, of the infraorder Atherinoida.

Aarn and Ivantsoff (1997)	**Dyer and Chernoff (1996)**	**Herein**
Melanotaeniidae (including *Bedotia* and *Rheocles*)	Melanotaeniidae	Melanotaeniidae
Pseudomugilidae	Bedotiinae	Bedotiinae
Telmatherinidae	Melanotaeniinae	Melanotaeniinae
Atherinidae	Pseudomugilinae	Pseudomugilinae
Phallostethidae (including *Dentatherina)*	Pseudomugilini	Telmathernininae
Atherionidae	Telmatherinini	Atherionidae
	Atherionidae	Phallostethidae
	Phallostethidae	Dentatherinae
	Dentatherinae	Phallostethinae
	Phallostethinae	Atherinidae
	Atherinidae	

Family MELANOTAENIIDAE (248)—rainbowfishes and blue eyes. Freshwater, some in brackish water, rarely in marine water; Madagascar, New Guinea and adjacent islands, northern and eastern Australia, and parts of eastern Indonesia.

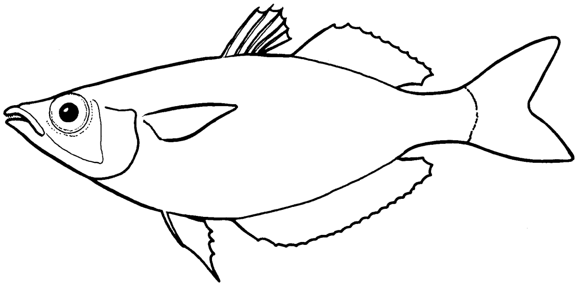
Distal premaxillary teeth enlarged (shared with telmatherinids); body compressed; dorsal fins narrowly separated, the first with 3–7 spines and the second with 6–22 rays (the first being a stout spine in some species); anal fin with 10–30 rays, the first ray a stout spine in some species; lateral line absent or weakly developed; scales relatively large, 28–60 in lateral series; innermost pelvic ray attached to abdomen by membrane along its entire length. (This is a useful character in separating rainbowfishes from silversides, but the membrane is easily broken.) Vertebrae 27–38. Most members of this family exhibit some sexual dimorphism with, for example, males usually being more colorful than females and having the median fin-ray extended (other atheriniforms except for *Quirichthys*, are monomorphic).

Seventeen genera with 113 species (some occur in marine waters but all are primarily freshwater). The four subfamilies of rainbowfishes and blue eyes have been variously recognized as separate families (e.g., Allen, 1995, Ivantsoff et al., 1997) or subfamilies of the same family (e.g., Dyer and Chernoff, 1996). They are herein placed in the same family to indicate their monophyletic relationship. The two terminal groups of the Melanotaeniidae of Dyer and Chenoff (1996), ranked as tribes, are ranked here equally as subfamilies, to better follow conventional practice while still maintaining phylogenetic relations, giving four subfamilies of Melanotaeniidae.

SUBFAMILY BEDOTIINAE (MADAGASCAR RAINBOWFISHES). Anal fin spine weak or absent; pterotic canal absent. Recognized as a family by Stiassny et al. (2002) but recognized as a subfamily of Melanotaeniidae, as done here, by Dyer and Chernoff (1996), who regarded this taxon as the primitive sister group of their Melanotaeniinae and Pseudomugilinae. Freshwater; Madagascar (primarily forested rivers, streams, and swamps, in central and eastern parts).

Two genera, *Bedotia* (6) (Stiassny and Harrison, 2000; Sparks, 2001) and *Rheocles* (7) (Stiassny and Rodriguez, 2001; Stiassny et al., 2002), with at least 13 species.

SUBFAMILY MELANOTAENIINAE (RAINBOWFISHES). Posttemporoal canal present; strong spine preceding second dorsal fin (this spine is absent in *Cairnsichthys* and *Rhadinocentrus*). Maximum length about 12 cm. Freshwater, some in brackish water. New Guinea and small nearby islands and in Australia.



Seven genera with about 68 species (Allen, 1991a; Allen and Renyaan, 1996a,b; Allen, 1997; Price, 1997; Allen, 1998; Allen and Renyaan, 1998). Most of the species are in New Guinea and a few are in common with Australia and New Guinea (*Melanotaenia* and the monotypic *Iriatherina*).

The generic relationships expressed here in three unnamed tribes are based on Aarn and Ivantsoff (1997).

Tribe—*Chilatherina* (about 10), *Glossolepis* (about 8), and *Melanotaenia* (about 45).

Tribe—*Cairnsichthys* and *Rhadinocentrus*, each being monotypic. The sister group of this taxon, unlike that given here, was considered by Aarn and Ivantsoff (1997) to be a clade of the bedotiine genera *Bedotia* and *Rheocles*.

Tribe—*Iriatherina werneri*. This clade was considered by Aarn and Ivantsoff (1997) to be sister to the above five genera and *Bedotia* and *Rheocles*.

Relationship uncertain: *Pelangia mbutaensis* (Allen, 1998).

SUBFAMILY PSEUDOMUGILINAE (BLUE EYES). Mesethmoid absent; fin spines tend not to be as rigid as in rainbowfishes and the second dorsal fin lacks a spine. These colorful fishes are generally much smaller than rainbowfishes with a maximum length of about 6.5 cm SL. Brackish and freshwater, generally at elevations under 100 m, rarely in marine water in mangrove swamps. New Guinea and small nearby islands and in Australia.

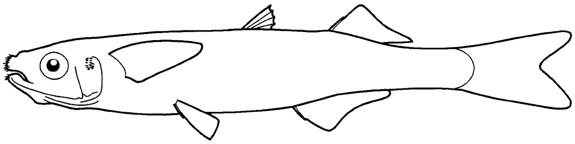
Three genera, *Kiunga, Pseudomugil* (13 species in New Guinea and Australia), and *Scaturiginichthys,* with 15 species (Allen, 1995; Allen and Renyaan, 1999; Ivantsoff et al., 1997; Ivantsoff, 1999).

SUBFAMILY TELMATHERININAE (CELEBES RAINBOWFISHES). Freshwater; Indonesia on Sulawesi and Misool Island off Irian Jaya (West Papua).

Aarn et al. (1998) rediagnosed this taxon on the basis of 26 characters and considered it a family phylogenetically separate from the Melanotaeniidae (subfamily Psuedomugilinae) whereas Dyer and Chernoff (1996) and Dyer (1998:522) place it as a sister group to their tribe Pseudomugilini (i.e., as one of two tribes of the Psuedomugilinae). The monophyly and distinctiveness of this group are not in dispute, and although Aarn et al. (1998) studied more representatives than did Dyer and Chernoff (1996), I prefer, on the basis of the larger study, to follow the main cladistic analysis of Dyer and Chernoff (1996).

Five genera, *Kalyptatherina, Marosatherina, Paratherina, Telmatherina,* and *Tominanga,* with 17 species (Aarn et al., 1998). *Kalyptatherina* and *Marosatherina* are considered to be in one clade with the last three genera in another clade (Aarn et al., 1998). Most species are from the Malili lakes and area, of Sulawesi (e.g., Kottelat et al., 1993; Aarn et al., 1998).

Family ATHERIONIDAE (249)—pricklenose silversides. Marine (tropical and subtropical); Indian (South Africa to India) and western Pacific (southern Japan to Fiji and Australia).



Shagreen denticles present on outside of mouth area and parts of head; origin of first dorsal fin behind tip of pelvic fins; first dorsal fin with 3–6 spines, second with 1 spine and 8–13 soft rays; anal fin with 1 spine and 13–17 soft rays; midlateral scales about 40–44. Maximum length about 5.5 cm.

Previously considered a subfamily of Atherinidae; the studies of Dyer and Chernoff (1996) and Aarn and Ivantsoff (1997) strongly support its separation.

One genus, *Atherion,* with three species.

Family PHALLOSTETHIDAE (250)—tusked silversides and priapiumfishes. Freshwater and marine, Southeast Asia.

All members are compressed and nearly transparent.

Dentatherina was recognized in Atherinidae before L. R. Parenti's 1984 study in which she considered it and the phallostethines to be sister taxa; this hypothesis was strengthened by Dyer and Chernoff (1996) and the clade is recognized on the basis of several osteological features. Dentatherinines and phallostethines are frequently recognized in separate families (e.g., Ivantsoff, 1999; Parenti and Louie, 1998) but are placed in the same family by Dyer and Chernoff (1996) and Aarn and Ivantsoff (1997) as is done here. Since these are sister taxa, ranking them as separate families (of the same superfamily) or as separate subfamilies of Phallostethidae is a subjective decision, and the latter choice is made here. However, the distinctiveness of *Dentatherina* could be used in favor of separate family recognition.

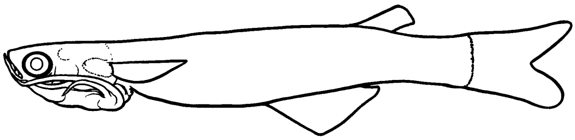
The two sister taxa have a relatively small area of overlap in Borneo and the Philippines, with the coastal marine *Dentatherina* extending much further east than the largely coastal and freshwater phallostethines, which are in the western part of the Indo-Australian archipelago. The only phallostethine to occur east of Borneo and across Wallace's Line is a species of *Neostethus* found in Sulawesi (Parenti and Louie, 1998).

Two subfamilies with five genera and 22 species.

SUBFAMILY DENTATHERININAE (TUSKED SILVERSIDES). Large lateral wings of parasphenoid beneath orbits; maxilla with large spatulate process from anterior edge; one epural; elongate ventral postcleithrum (dorsal postcleithrum absent); ectopterygoid and quadrate fused; branchiostegal rays usually 5; first dorsal fin with 5–8 spines; midlateral scales 40–43. Called "pygmy silversides" in Allen (1995). Marine; tropical western Pacific (Philippines to northern Java, New Guinea, northeastern Australia, and Fiji).

One species, *Dentatherina merceri* (Patten and Ivantsoff, 1983; Parenti and Louie, 1998; Ivantsoff, 1999).

SUBFAMILY PHALLOSTETHINAE (PRIAPIUMFISHES). Brackish and freshwater (rarely coastal marine); Southeast Asia, from the Philippines to Thailand and Sumatra.



Males with unique bilaterally asymmetric, subcephalic copulatory organ under the throat termed the priapium (see below for description), modified primarily from pelvic skeleton; pelvic skeleton absent in females, except, primarily, in *Gulaphallus falcifer* (see Parenti, 1986a, 1989); fertilization internal but development oviparous with females laying fertilized eggs; eggs with a filamentous process; anus and urogenital openings anterior, below pectoral fin in both sexes; fleshy keel extending on abdomen from urogenital opening to origin of anal fin; body compressed and transparent to translucent in life; usually two dorsal fins, the first, if present, with one or two short spines or thickened rays and second with 5–10 rays; anal fin with 13–28 rays; pectoral fin high, with 9–13 rays; two pectoral radials; scales cycloid, 28–58 in lateral series; branchiostegal rays 4–6; vertebrae 31–40.

The priapium is used to hold the female during mating. This complex muscular and bony organ contains ducts from the kidney and gonads as well as terminal parts of the intestine. Parenti (1989), in identifying homologies, gives a detailed description of the priapium and its three components:

i) suspensory components,
ii) holding or clasping component consisting of elongate parts of the ctenactinium (or toxactinium), and
iii) papillary component.

The male's body is asymmetrical with the anus and priapium being on opposite sides. In what are termed sinistral males, the anal opening is on the right side (proctal side) with the priapium being on the left side (aproctal side). In dextral males the anal opening is on the left side (proctal side) with the priapium being on the right side (aproctal side). Females have the anal opening on the mid-line. In most species the sinistral and dextral males are about in equal numbers, but a few species are predominantly sinistral or dextral (Parenti, 1986b). Unique features in the gonad structure are discussed in Grier and Parenti (1994).

Maximum length 3.7 cm SL, attained in *Gulaphallus eximus* of Luzon, Philippines.

Four genera with 21 species (Parenti, 1989, 1996, 1999; Parenti and Louie, 1998). The relationships of the member groups were well established by Parenti (1989, 1996); however, the category of subfamily employed in her studies has been altered to tribe to accommodate recognizing the dentatherinines as a subfamily of the phallosthethids.

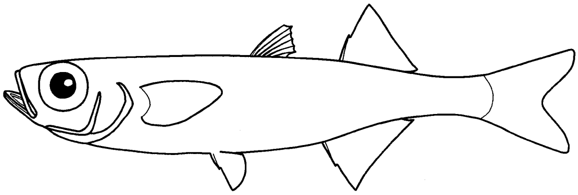
TRIBE PHALLOSTETHINI. Jaws highly protrusible with elongate premaxillary ascending processes, priapium with a reduced second ctenactinium; shield-like pulvinulus present, covering articulation of toxactinium and proctal axial bone; skin of gular flap not perforated. *Neostethus,* which is coastal marine, brackish, and freshwater in Thailand, Malayasia, and Philippines, is thought to be sister to the clade of the other two genera, found in brackish and freshwater in Malayasia (Malay Peninsula and northern Borneo) and Thailand.

Three genera, *Neostethus* (11 species), *Phallostethus* (2), and *Phenacostethus* (3), with 16 species.

TRIBE GULAPHALLINI. Jaws only slightly protrusible; priapium lacking a second ctenactinium; pulvinulus absent; adult males with a perforated gular skin flap through which anterior end of first ctenactinium projects.

One genus, *Gulaphallus,* with five species. Four species in streams on Luzon and one in brackish to coastal marine areas of Panay, Philippines.

Family ATHERINIDAE (251)—Old World silversides. Marine (pelagic coastal) and freshwater; Atlantic and Indo-West Pacific.



Two widely separated dorsal fins, the first with 2–5 spines; pectoral fins inserted high on body. Body often translucent, with silvery lateral stripe. Diagnostic features include lacrimal notch present on posterior margin (where it articulates with the condyle of the lateral ethmoid), ventral postcleithrum between first and second pleural ribs (as in atherinopsids), and ventral pelvic spine on pelvic bone (separating the abductor muscles of the pelvic spine and pelvic soft rays) (Dyer and Chernoff, 1996). Formerly included members now placed in Atherinopsidae (see Atheriniformes for reasons for separation). Most easily separated from the atherinopsids in having the premaxilla not protractile, distal end of the premaxilla narrow, premaxilla with a postmaxillary process, and preopercular sensory canal connecting to anterior infraorbital canal (Chernoff, 2002) (see Atherinopsidae for opposing characters).

Maximum length about 10 cm.

Three subfamilies, 12 genera, and about 60 species. Species of this family occur primarily in the Old World, in the Indo-West Pacific, in contrast to the New World silversides of the family Atherinopsidae; however, three species of the subfamily Atherinomorinae are in the subtropical/tropical western Atlantic (southern Florida to Argentina), *Alepidomus evermanni* (endemic to Cuba where it is primarily freshwater), *Atherinomorus stipes,* and *Hypoatherina harringtonensis* (Chernoff, 2003). According to Dyer and Chernoff (1996), the Craterocephalinae and Atherininae are sister groups, and the resulting clade is sister of the Atherinomorinae.

SUBFAMILY ATHERINOMORINAE. Five genera, *Alepidomus* (1), *Atherinomorus* (11), *Hypoatherina* (7), *Stenatherina* (1), and *Teramulus* (2), with about 22 species (e.g., Ivantsoff and Crowley, 1999; Kimura et al., 2002; S. Kimura, pers. comm., January 2003). Mainly Indo-West Pacific and tropical western Atlantic (see family for listing of western Atlantic species).

SUBFAMILY CRATEROCEPHALINAE (HARDYHEADS). Two genera, *Craterocephalus* (*Allanetta*) (25, Crowley et al., 1995; Ivantsoff and Crowley 1999) and *Quirichthys* (1), with 26 species. Most species freshwater, some brackish and coastal marine; mainly New Guinea and Australia.

SUBFAMILY ATHERININAE. Five genera, *Atherina, Atherinason, Atherinosoma, Kestratherina,* and *Leptatherina,* with about 12 species. Freshwater and marine; primarily eastern Atlantic (including Mediterranean Sea) for the five species of *Atherina* and Australia for species of the other four genera.

Superorder CYPRINODONTEA

Order BELONIFORMES (50)—needlefishes. Interarcual cartilage (connects the epibranchial of the first gill arch with the infrapharyngobranchial of the second gill arch) small or absent; small second and third epibranchials; interhyal absent; lower caudal fin lobe with more principal rays than the upper lobe. In addition, all species of this order have a fixed or nonprotrusible upper jaw. The loss of premaxillae movement is associated with the above noted loss of the interhyal and, in at least the medaka, in the secondary loss of long ascending processes of the premaxillae; it is inferred that the entire branchial apparatus has limited movement (Parenti, 1987).

Ordinal status for the Beloniformes is recognized here for reasons given in Nelson (1994:264). See discussion below under Adrianichthyoidei.

Five families, 36 genera, and 227 species. About 98 species are confined to freshwater or weak brackish water. Beloniforms dominate the epipelagic region of the tropics and subtropics.

Suborder Adrianichthyoidei. Prior to the 1980s, this taxon was classified with the Cyprinodontiformes (as herein defined). Rosen and Parenti (1981) provided evidence, primarily based on characters of the gill arch skeleton and hyoid apparatus, indicating monophyly of a taxon comprising the Adrianichthyidae within the Beloniformes, and the adrianichthyids were placed within Beloniformes in the 1994 edition, in one of two suborders recognized. Li (2001) considered only the interhyal absence in both suborders of beloniforms to be valid and, on the basis of several assumed synapomorphies, placed the adrianichthyoids within the Cyprinodontiformes. However, pending further work in evaluating these and other characters, this taxon is still regarded as having a closer affinity to belonoids than to cyprinodontiforms. If the characters of Li (2001) were considered as valid indicators of relationships, then the group could be treated as a separate order, sister to the Cyprinodontiformes, and placed between the Beloniformes and Cyprinodontiformes.

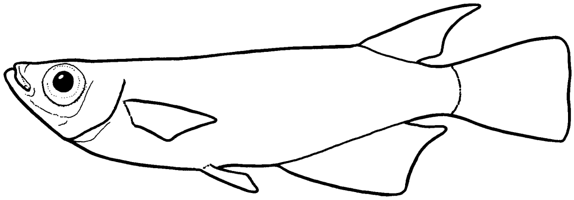
Family ADRIANICHTHYIDAE (252)—adrianichthyids. Freshwater and brackish water; India to Japan and to Indo-Australian archipelago.

Lateral line absent on body; narial opening paired; branchiostegal rays 4–7; vomer, supracleithrum, metapterygoid, and ectopterygoid absent; rostral cartilage absent.

Three subfamilies with four genera and 28 species.

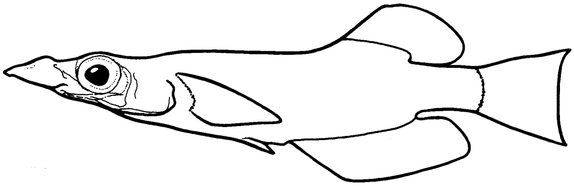
Prior to Rosen and Parenti (1981), the three subfamilies recognized here were given family status (Oryziidae, Horaichthyidae, and Adrianichthyidae), as in Nelson (1976, 1984).

SUBFAMILY ORYZIINAE (MEDAKAS OR RICEFISHES). Jaws not tremendously enlarged; dorsal and anal fins of male (shown in figure) usually more pronounced than in female; most species with 5–7 dorsal fin rays and 18–25 anal fin rays; almost always egg layers. Maximum length about 9 cm. Freshwater and brackish water; India to Japan and to Indo-Australian archipelago.



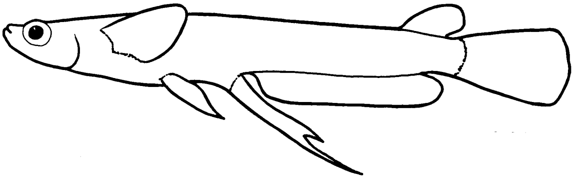
One genus, *Oryzias*, with about 22 species (Parenti, 1987; Kottelat, 1990b, 2001a; Roberts, 1998a; Parenti and Soeroto, 2004).

SUBFAMILY ADRIANICHTHYINAE (DUCKBILLED FISHES). Jaws tremendously enlarged; scoop-shovel-type mouth; almost always egg layers, eggs held in place against belly by pelvic fins. Maximum size up to 20 cm. Freshwater; Sulawesi (= Celebes Island).



Two genera, *Adrianichthys* (2) and *Xenopoecilus* (3), with five species (Kottelat, 1990b, Kottelat et al., 1993; Parenti and Soeroto, 2004).

SUBFAMILY HORAICHTHYINAE. Body thin and translucent; dorsal fin small, near caudal fin; anal fin elongate; right pelvic fin absent in females; maxilla absent. Superficially similar to the poeciliid *Tomeurus*. *Horaichthys* is the only atherinomorph known to produce spermatophores or encapsulated sperm bundles (Grier, 1984). Numerous other atherinomorphs form naked sperm bundles, spermatozeugmata, such as halfbeaks of the genus *Zenarchopterus* (Grier and Collette, 1987). Maximum length about 3 cm. Freshwater and brackish water; coastal western India. Females are inseminated and lay fertilized eggs (Burns et al., 1997).



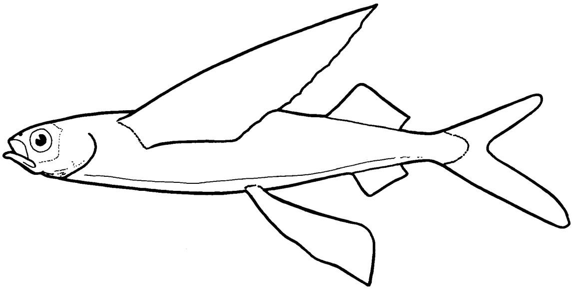
One species, *Horaichthys setnai*, found in 1937, occurs along coastal India from near the Gulf of Kutch (northwestern India) to Trivandrum near the southern tip (Hubbs, 1941; Silas, 1959).

Suborder Belonoidei (= Exocoetoidei). Lateral line low on body, along ventral margin of body behind pectoral fin (absent in some freshwater hemiramphids and in *Cololabis adocetus*); narial opening single; branchiostegal rays 6–15; elongate lower jaw at least in some stage of life history; no spines in fins; dorsal and anal fins placed far back on body; pectoral fin with 5–20 rays, fin inserted high on body in most species; pelvic fin with six rays, abdominal; caudal fin usually with 13 branched rays; oil droplets in egg minute or absent.

The suggestion of Lovejoy (2000) and Lovejoy et al. (2004) that halfbeaks and the related flyingfishes are basal to needlefishes is followed here. However, their suggestion i) that flyingfishes are nested within halfbeaks (with a clad comprising *Hemiramphus*, *Oxyporhamphus*, and *Euleptorhamphus* as the sister group of the monophyleteic flyingfishes), ii) that sauries appear to be nested within the needlefishes (with *Belone* being sister to the monophyletic sauries), and iii) that the Indo-West Pacific freshwater halfbeaks appear to be most closely related to the needlefish/saury clade (see also family Hemiramphidae below, is not reflected in the classification pending further analysis, preferably with morphological evidence.

Superfamily Exocoetoidea. Scales large, usually 38–60 in lateral line; mouth opening small, upper jaw never elongate; no isolated finlets; dorsal and anal fins usually with 8–18 rays each, up to 25 in *Euleptorhamphus*; teeth small; premaxillary canal absent; third pair of upper pharyngeal bones united into a palate.

Family EXOCOETIDAE (253)—flyingfishes. Marine; tropical to warm temperate, epipelagic oceanic to coastal, Atlantic, Indian, and Pacific.



Jaws relatively short and equal in length (lower jaw produced in some juveniles); exceptionally large pectoral fins, except in *Oxyporhamphus*, (gliding flights can be made out of water with the pectorals spread like wings) inserted high on body; pelvic fins exceptionally large in some species (thus two-winged and four-winged types can be recognized); lower lobe of caudal fin longer than dorsal lobe (fin deeply forked); juveniles of many have a pair of long, flaplike barbels (see below); swim bladder extends into haemal canal; 39–51 vertebrae. Maximum length 45 cm (attained in *Cheilopogon pinnatibarbatus californicus*); most species are less than 30 cm. This is one of the few fish groups to actively glide in the air. There is a stepwise increase in gliding capability, with sequential changes in the caudal, pectoral, and pelvic fins, in proceeding through the cladogram of Dasilao and Sasaki (1998).

Five subfamilies (based on Collette et al., 1984, and Dasilao and Sasaki, 1998), eight genera, and about 52 species. In North America there are 27 species (12 Atlantic, 19 Pacific).

SUBFAMILY OXYPORHAMPHINAE. One genus, *Oxyporhamphus*, with two species. This group, showing many intermediate characters between flyingfishes and halfbeaks and formerly placed in the Hemiramphidae in earlier works and in the 1994 edition, is regarded as the sister group of all other exocoetids (Dasilao et al., 1997; Dasilao and Sasaki, 1998), based on 10 synapomorphies. Collette (1999, 2002, 2004a) retained *Oxyporhamphus* in the Hemiramphidae. Lovejoy et al. (2004) included *Oxyporhamphus* in a clade with *Hemiramphus* (type genus of the family Hemiramphidae) and *Euleptorhamphus*, and sister to the flying fishes.

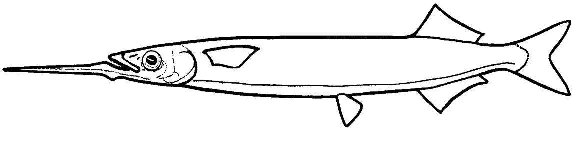
SUBFAMILY FODIATORINAE. One genus, *Fodiator*, with two species. This forms a monophyletic group to the remaining subfamilies, to which it is the sister group, based on 10 synapomorphies (Dasilao and Sasaki, 1998). The remaining taxa, except for *Hirundichthys* and *Prognichthys*, have barbels in the lower jaw in juveniles.

SUBFAMILY PAREXOCOETINAE. One genus, *Parexocoetus*, with three species. Unique in having strongly protrusible jaws and in having a process on the exoccipital directly articulating with the cleithrum (this joint between the cranium and shoulder girdle gives increased head maneuverability) (Dasilao and Sasaki, 1998).

SUBFAMILY EXOCOETINAE. One genus, *Exocoetus*, with three species.

SUBFAMILY CYPSELURINAE. Four genera, *Cheilopogon* (considered a synonym of *Cypselurus* in some works but N.V. Parin regarded them as separate in a major 1961 study and continues to do so in Parin, 1999a, 2003), *Cypselurus*, *Hirundichthys* (including *Danichthys*, a valid subgenus, and *Exonautes*), and *Prognichthys*, with about 48 species (e.g., Parin 1996; 1999a,b; 2003).

Family HEMIRAMPHIDAE (254)—halfbeaks. Marine and freshwater; tropical to warm temperate; epipelagic coastal and offshore, Atlantic, Indian, and Pacific.



Upper jaw much shorter than lower (lower jaw elongate in juveniles and in most adults), premaxillae pointed anteriorly; pectoral and pelvic fins short; some species with lower lobe of caudal fin longer than upper lobe (fin rounded, truncate, or forked); vertebrae 38–75 (except 18–25 in *Arrhamphus*). Maximum length about 40 cm SL, attained in *Euleptorhampus viridis*.

Hemiramphids, which are herbivorous, are one of 15 families of stomachless fish, all of which posses a pharyngeal jaw apparatus (pharyngeal mill) (Tibbetts and Carseldine, 2003). They share many pharyngeal features with cichlids (e.g., Stiassny and Jensen, 1987), but there are also many differences and at least in *Arrhamphus sclerolepis* there are departures from general euteleostean pharyngeal anatomy (Tibbetts and Carseldine, 2003).

Most of the freshwater species are in the Indo-Australian region, whereas most of the freshwater needlefishes are in the Neotropical region. There is molecular evidence that this family is paraphyletic. Lovejoy (2000) and Lovejoy et al. (2004) suggested that i) the clade of marine *Hemiramphus* may be phylogenetically most closely related to flyingfishes, ii) the clade of freshwater/estuarine Zenarchopterinae are more closely related to needlefishes and sauries than they are to marine *Hemiramphus* halfbeaks and the flyingfishes (i.e., the main exocoetoid lineage) (support for this may be provided by Tibbetts and Carseldine, 2004, finding major differences in the pharyngeal jaw apparatus between *Arrhamphus* and *Zenarchopterus,* although more comparative work is needed), and iii) the clade of marine *Chriodorus* and *Hyporhamphus* may be sister to most other belonoids (flyingfishes, other halfbeaks, needlefishes, and sauries).

Two subfamilies, 12 genera, and about 109 species. In North America there are 13 species (6 Atlantic, 1 freshwater Mexico, 6 Pacific).

SUBFAMILY HEMIRAMPHINAE. Species are marine except for four freshwater species of *Hyporhamphus* (Berra, 2001). Most species are coastal continental but some extend into the western and central Pacific (one species is endemic to New Zealand). This group of halfbeaks, with external fertilization, do not necessarily form a monophyletic assemblage.

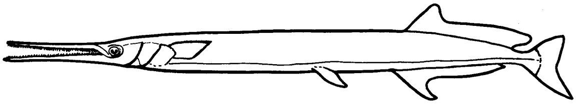
Seven genera, *Arrhamphus* (1), *Chriodorus* (1), *Euleptorhamphus* (with 20–25 dorsal and anal fin rays and 105–125 lateral line scales) (2), *Hemiramphus* (10), *Hyporhamphus* (including *Reporhamphus*) (36), *Melapedalion* (1), and *Rhynchorhamphus* (4), with about 55 species (e.g., Collette et al., 1984; Collette and Su, 1986; Collette, 1995, 2004a; Banford and Collette, 2001). The most species-rich genus is *Hyporhamphus* with 36 species. Species of *Oxyporhamphus,* formerly placed in this family, are now considered to be exocoetids.

SUBFAMILY ZENARCHOPTERINAE. All occur in freshwater or estuaries in the Indo-West Pacific, and have a modified anal fin (termed an andropodium and analogous to the gonopodium found in some cyprinodontiforms) for internal fertilization. The spermatozeugmata in the testes of species of *Zenarchopterus* provide a unique method of sperm packaging (Grier and Collette, 1987). Contains all the species of halfbeaks with internal fertilization; all are viviparous live-bearing except as noted below. Lovejoy et al. (2004) gave family status (Zenarchopteridae) to this clade (as done by some other authors, and a move that probably should be accepted), providing strong molecular evidence that it is sister to a clade of needlefishes and sauries.

Five genera, *Dermogenys* (13), *Hemirhamphodon* (6), and *Nomorhamphus* (16), and the oviparous (lay fertilized eggs) *Tondanichthys* (1, Collette, 1995b) and *Zenarchopterus* (20 species), with about 54 species (Anderson and Collette, 1991; Meisner and Burns, 1997; Meisner and Collette, 1999; Meisner and Louie, 2000; Meisner, 2001; Collette, 2004a).

Superfamily Scomberesocoidea. Scales small, 70 to over 350 in lateral line; mouth opening usually relatively large, at least upper jaw slightly elongate (i.e., both jaws usually elongate); premaxillary canal present. Lovejoy (2000) concluded that the sister group of sauries is *Belone*, thus Belonidae is only monophyletic if sauries are included.

Family BELONIDAE (255)—needlefishes. Marine and freshwater (e.g., South America, Pakistan, India, and Southeast Asia); tropical to warm temperate, epipelagic in coastal and oceanic tropical and temperate waters, Atlantic, Indian, and Pacific.



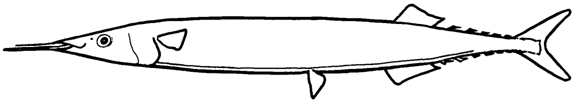
Both upper and lower jaws extend into long beaks with numerous needlelike teeth (two South American freshwater species of *Belonion* have a short upper jaw, similar to halfbeaks); mouth opening large; scales small (usually 130–350 in lateral line and easily detached); no isolated finlets behind the dorsal and anal fins; dorsal fin rays usually 11–26, up to 43; anal fin rays 12–39; posttemporal forked; interruptions in the cephalic lateralis system; vertebrae 52–97; general body shape superficially resembling *Lepisosteus.* One species, *Belonion apodion,* unlike the only other species in the genus, lacks the pelvic fin and girdle. Some species are capable of high jumps out of water. Maximum length about 1.5 m (reported to 2 m); several species of *Tylosurus* reach over 1 m.

At hatching, belonids have short jaws of equal length. During growth, the lower jaw first elongates forming the "halfbeak" stage; then the upper jaw elongates forming the "needlenose" stage. Lovejoy (2000) gave phylogenetic evidence that this pattern in ontogeny of passing through the flyingfish and halfbeak states is a good example of recapitulation. See above under Belonoidei for evidence that this family is not monophyletic without the inclusion of the Scomberesocidae.

Ten genera, *Ablennes* (1), *Belone* (2), *Belonion* (2), *Petalichthys* (1), *Platybelone* (1), *Potamorrhaphis* (3), *Pseudotylosurus* (2), *Strongylura* (14), *Tylosurus* (6), and *Xenentodon* (2), with 34 species (Collette, 1999, 2003a,b; Collette and Banford, 2001; Collette et al., 1984; Lovejoy and Collette, 2001). About 12 species are restricted to freshwater. The seven species of *Belonion, Potamorrhaphis,* and *Pseudotylosurus,* the New World clade, are South American river endemics (Lovejoy, 2000; Lovejoy and Collette, 2001), while the two species of *Xenentodon* are Southeast Asian river endemics, and the widespread but polyphyletic *Strongylura,* with some species belonging to the New World needlefish clade, includes both freshwater (two in Central and South America and one in Asia) and marine species (Lovejoy and Collette, 2001; Collette, 2003b). Lovejoy and Collette (2001) demonstrated multiple independent invasions into freshwater by marine taxa. Over half the species are in *Strongylura* and

Tylosurus. In North America there are 10 species (7 in Atlantic, 2 in freshwater, 5 in Pacific).

Family SCOMBERESOCIDAE (256)—sauries. Marine; epipelagic tropical to temperate seas.



Four to seven finlets after both dorsal and anal fins; scales small (70–91 along midline in two dwarf species and 107–148 in two large species); mouth opening relatively small, jaw length varies from long slender beaks with both jaws produced (as in *Scomberesox* and shown in figure) to relatively short beaks with lower jaw only slightly produced (small juveniles of all species have short jaws); teeth relatively small; dorsal fin rays 14–18; anal fin rays 16–21; swim bladder absent and ovary single in two dwarf species; vertebrae 54–70 (32–43 precaudal). Maximum length about 45 cm SL, attained in *Scomberesox saurus.*

See above under Belonoidei for molecular evidence that members of this family should be placed in Belonidae.

Two genera, *Scomberesox* and *Cololabis,* each with two species. Each genus, representing an evolutionary lineage, has one relatively large species and one dwarf which is more tropical than the large paired species. The classification of Collette et al. (1984) and Collette (2003a, 2004b) is followed here, but C. L. Hubbs and R. L. Wisner in a 1980 publication recognized all four species in monotypic genera, as was followed in the 1994 edition. The species are found as follows:

Scomberesox—the large species in the North Atlantic and Southern Hemisphere and the dwarf one, placed by some in *Nanichthys,* in the Atlantic and small portion of Indian.
Cololabis—the large species in the North Pacific and the dwarf and more tropical relative, placed by some in *Elassichthys,* in the eastern central Pacific.
In North America there are 2 species (1 Atlantic, 1 Pacific).

Order CYPRINODONTIFORMES (Microcyprini) (51)—killifishes. Monophyly of this order is recognized on the basis of several derived characters: e.g., caudal fin truncate or rounded; caudal fin skeleton symmetrical, with one epural; first pleural rib on second vertebra rather than third; pectoral fin insertion ventrolateral (primitively, low-set pectoral girdle); scalellike first postcleithrum; an alveolar arm of the premaxillae; extended developmental period (Parenti, 1981; Rosen and Parenti, 1981; Costa, 1998a). In addition, they possess the following characters: lateral line canal and pores chiefly on head, lateral line represented on body only by pitted scales; narial opening paired; branchiostegal rays 3–7; pelvic fins and girdle present or absent; upper jaw bordered by premaxilla only, protrusible; vomer usually present and supracleithrum always present; metapterygoid usually absent and ectopterygoid always absent; parietals present or absent; vertebrae 24–54. Marked sexual dimorphism with the males often brightly colored.

Members of this suborder are popular aquarium and experimental fishes. Rosen (1973b) presented a key to the salt-tolerant species, and Parenti (1981) gave a key to genera of most of the families. Scheel (1990) discussed the biology of the world rivulines and of some other cyprinodontiform taxa and has numerous color photographs. Lazara (2001) presented an annotated checklist, synonymy, and bibliography of the oviparous members of this order (once placed in the family Cyprinodontidae). Egg diameter varies from less than 0.3 mm to about 3 mm, and embryonic development may be less than one week to over one year (Able, 1984).

Classifications of the late 1960s, 1970s, and early 1980s, and followed by some authors even later, generally adopted Greenwood et al. (1966), who recognized the following families together (in their suborder Cyprinodontoidei): Oryziatidae, Adrianichthyidae, Horaichthyidae, Cyprinodontidae (including the herein recognized Aplocheiloidei, Profundulidae, Fundulidae, and two viviparous goodeid genera, *Crenichthys* and *Empetrichthys*), Goodeidae, Anablepidae, Jenynsiidae, and Poeciliidae. In a detailed anatomical study and cladistic analysis, Parenti (1981) gave good evidence that this view of relationships was not correct. A major result of Parenti's (1981) valuable work was the breaking up to the Cyprinodontidae and recognizing that the viviparous families did not form a monophyletic group. Her study was largely followed by Nelson (1994). While the monophyly of Parenti's (1981) nine families and recognition of two lineages, the Aplocheiloidei and Cyprinodontoidei, has been confirmed by most subsequent studies, there are changes in our understanding of the relationships of the families, based primarily on the works of Parker (1997), Costa (1998a), and Ghedotti (2000), which are given in Parenti's (2005) classification and accepted here. These works should be consulted for a listing of synapomorphies. The largest change is that of the Goodeidae, now considered sister to Profundulidae and not to the Cyprinodontidae (Costa, 1998a). Further changes are made within families as noted.

Ten families with 109 genera and about 1,013 species (about 996 being primarily freshwater).

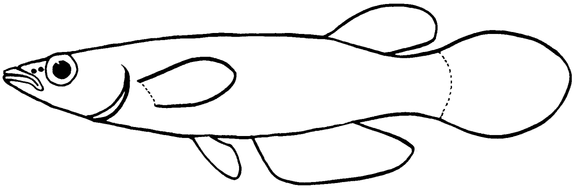
Suborder Aplocheiloidei. Pelvic fin bases inserted close together; metapterygoid present; three basibranchials; a dorsal ray on each of the first two dorsal radials; dorsal-fin origin posterior or anterior to anal fin origin. In all other members of the order the pelvic fin bases are not inserted close together, and they possess two basibranchials, lack the metapterygoid, and have one dorsal ray articulating with the first two radials.

Some members are termed "annuals." In these, adults spawn during the rainy season in temporary waters and the drought resistant eggs with a thickened chorion may survive dry periods in diapause buried in the substrate. Hatching normally occurs during the next rainy season but may be delayed for over one year. According to Parenti (1981), the true annuals do not form a monophyletic group, and independent origins of diapause has been identified in the rivulids (Costa, 1998b; Hrbek and Larson, 1999). Many species are particularly colorful and are popular aquarium fishes.

Nelson (1994) placed all members of this clade in one family, Aplocheilidae, with two subfamilies, Aplocheilinae (Old World rivulines) and the Rivulinae (New World rivulines), whereas many workers preferred to recognize these at the family level (either arrangement recognized the larger group as monophyletic). It has been suggested that the Old World rivulines are not a monophyletic group (with the primitive defining characters including supracleithrum fused to posttemporal, premaxillary ascending processes tapered posteriorly, and first postcleithrum present). Costa (2004) gave cladistic evidence identifying three clades of aplocheiloids, i) members occurring off continental Africa (Aplocheilidae), ii) members occurring on continental Africa (the resurrected Nothobranchiidae), and iii) New World members (Rivulidae). He furthermore found the continental African members to be more closely related to the New World members than to the others and proposed the superfamilies Aplocheilidea (for Aplocheilidae) and Nothobranchiidea (for Nothobranchiidae and Rivulidae)(this conclusion is only provisionally recognized here). Not all species have been studied in arriving at these phylogenetic conclusions, and more work may further refine our views of relationships. Costa (1998a, 2004) gave the synapomorphies used to define the various lineages. Despite Parenti's (1981) work showing otherwise, some recent authors have placed members of this group in a paraphyletic Cyprinodontidae.

Three families with about 36 genera, and at least 493 species.

Family APLOCHEILIDAE (257)—Asian rivulines. Freshwater (rarely brackish); Madagascar, Seychelles, Indian subcontinent, Sri Lanka, and Indo-Malaysian archipelago to Java.



Black blotch on the dorsal fin of females.

Two genera, *Aplocheilus* and *Pachypanchax*, with at least seven species.

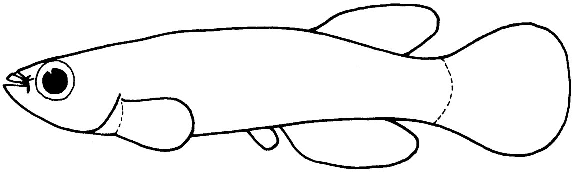
Family NOTHOBRANCHIIDAE (258)—African rivulines. Freshwater (rarely brackish); continental Africa (south of Sahara Desert to South Africa).

Three oblique red stripes on postorbital region of males.

At least *Aphyosemion* (includes *Callopanchax*, *Diapteron.* and *Scriptaphyosemion*), *Epiplatys* (includes *Aphyoplatys*), *Fundulopanchax*, *Nothobranchius*, and probably

Adamas and *Foerschichthys*, with perhaps at least 250 species. Aarn and Shephard (2001) examine some members of the lineage Epiplatina but with differing results from Costa (2004).

Family RIVULIDAE (259)—New World rivulines. Freshwater (rarely brackish); southern Florida through much of Middle America to Uruguay and northeastern Argentina.



Supracleithrum not fused to posttemporal; first postcleithrum absent; opercular and branchiostegal membrane united and often covered with scales; pelvic fins and skeleton absent in *Rivulus nudiventris* (Costa and Brasil, 1991), and in *Simpsonichthys boitonei*, *S. parallelus*, and *S. cholopteryx* (Wilson Costa, personal communication, 2004). Maximum length 20 cm TL, most less than 8 cm, and some miniature species under 3 cm TL.

Kryptolebias marmoratus (formerly placed in *Rivulus*, Costa, 2004a), which occurs in freshwater and strong brackish water in southern Florida and the West Indies, and one or more other species of the genus, are unique among fishes and indeed all vertebrates, in consisting of individuals with simultaneously functional ovary and testis (self-fertilizing hermaphrodites). Fertilization is internal and then eggs are laid; however, internal fertilization occurs in species of *Campellolebias* and *Cynopoecilus*, in which the anal fin is modified in males.

Twenty-eight genera, *Aphyolebias*, *Austrofundulus*, *Austrolebias*, *Campellolebias*, *Cynolebias*, *Cynopoecilus*, *Gnatholebias*, *Kryptolebias* (proposed by Costa 2004a for the preoccupied *Cryptolebias*, used earlier by Costa, 2004b), *Leptolebias*, *Maratecoara*, *Megalebias*, *Micromoema*, *Millerichthys*, *Moema*, *Nematolebias*, *Neofundulus*, *Papiliolebias*, *Pituana*, *Plesiolebias*, *Pterolebias*, *Rachovia*, *Renova*, *Rivulus*, *Simpsonichthys*, *Spectrolebias*, *Stenolebias*, *Terranatos*, and *Trigonectes*, with about 236 species and many undescribed species are known to exist (e.g., Costa, 1998b, 2003, 2004; Hrbek et al., 2004). The most species-rich genera are *Rivulus* and *Simpsonichthys*. Two subfamilies are established by Costa (2004a,b), Kryptolebiatinae for *Kryptolebias* and Rivulinae for all other genera. In North America there are 4 species (1 Atlantic and 4 freshwater).

Suborder Cyprinodontoidei. The superfamily classification follows Costa (1998a) and Parenti (2004).

Superfamily Funduloidea. The Profundulidae and Goodeidae are sister taxa in the analysis of Costa (1998a), and support for this was found in the molecular study of Webb et al. (2003).

Family PROFUNDULIDAE (260)—Middle American killifishes. Freshwater; Atlantic and Pacific slopes of Middle America in Mexico, Guatemala, and Honduras.

Gillrakers on anterior arm of first arch 14–23; dorsal fin with 1–3 rudimentary rays and 10–16 principal rays; scales in lateral series 31–39. Fertilization external.

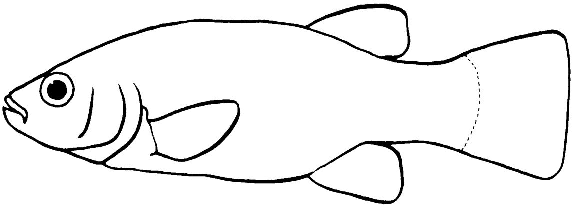
One genus, *Profundulus*, with five species. All five occur in North America (Mexico).

Family GOODEIDAE (261)—goodeids. Freshwater; Nevada and west central Mexico.

First two to seven middle anal radials fused to the proximal radials; dorsal processes of the maxillaries greatly reduced; distal arm of the premaxilla straight; articular reduced.

The Empetrichthyinae, formerly placed in the large and polyphyletic Cyprinodontidae, are regarded as a sister group to what was formerly regarded as the goodeids following Parenti (1981). The molecular study of Webb et al. (2003) also supported the monophyly of Goodeidae and the sister-group relationship of the Empetrichthyinae and Goodeinae.

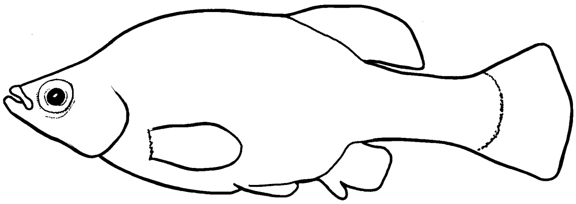
SUBFAMILY EMPETRICHTHYINAE. Pelvic skeleton and pelvic fins absent; epibranchial Y-shaped; anal rays of males not shortened; pseudophallus not present; scales in lateral series 26–30; dorsal fin with one rudimentary ray and 11 soft rays; pectoral fin with 16 or 17 rays; vertebrae 28 or 31. Fertilization external. Southern Nevada.



Two genera, *Crenichthys* (springfishes, two species) and *Empetrichthys* (poolfishes, two species from Nye County, Nevada, one of which is probably extinct).

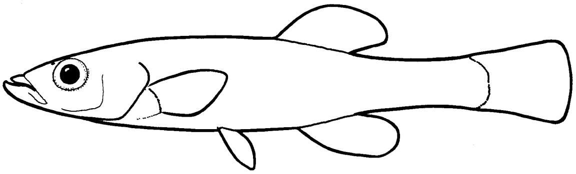
SUBFAMILY GOODEINAE. Viviparous with internal fertilization; anterior rays of anal fin in males crowded, shortened, and slightly separated by a notch from the rest of the fin (gonopodium-like structure termed a pseudophallus or andropodium; scales in lateral series 30–35; dorsal fin with one rudimentary ray and 14 or 15 soft rays; pectoral fin with 15 or 16 rays; vertebrae 37; ovaries partly united into a single median organ, eggs small and with little yolk; embryos and newborn young usually have a placentalike trophotaeniae (ribbonlike extensions from anal region associated with nutrition and respiration). Mesa Central, Mexico.

This subfamily, centered in the Rio Lerma basin, has species of many diverse body forms (deep bodied to long bodied) and feeding habits (carnivores to herbivores). Maximum length up to 20 cm. Many species are known as splitfins.



Sixteen genera, *Allodontichthys, Alloophorus, Allotoca* (synonym *Neoophorus*), *Ameca, Ataeniobius, Chapalichthys, Characodon, Girardinichthys* (synonym *Lermichthys*), *Goodea, Hubbsina, Ilyodon, Skiffia* (synonyms *Neotoca* and *Ollentodon*), *Xenoophorus, Xenotaenia, Xenotoca,* and *Zoogoneticus,* with about 36 species (Webb, 2002; Nelson et al., 2004).

Family FUNDULIDAE (262)—topminnows. Freshwater, brackish water, and coastal marine (rarely hypersaline); lowlands of North America from southeastern Canada to the Yucatan (Mexico), including Mississippi River drainage, Bermuda, and Cuba.



Interior (ventral) arms of maxillaries directed anteriorly, often with pronounced hooks; maxilla twisted, not straight. Dorsal fin (7–16 soft rays) in mid-body, origin in front of or near anal fin (9–15 soft rays) origin. Maximum length 30 cm.

Many species are remarkably euryhaline. *Adinia xenica* occurs in freshwater and salt marshes, as do several species of *Fundulus* such as the Mummichog, *F. heteroclitus,* which lives primarily in coastal seawater (marshes and estuaries) but also occurs in freshwater. Common names often reflect former views of relationships or otherwise cut across present family boundaries for other reasons; the accepted common name used for this family, topminnow, is also used for a poeciliid and the name killifishes is used for species in this family as well as for some cyprinodontids.

Four genera, *Adinia, Fundulus* (including *Plancterus* and *Xenisma*), *Leptolucania,* and *Lucania,* with about 50 species (e.g., Bernardi, 1997; Nelson et al., 2004). In North America there are 40 species (12 Atlantic and 37 freshwater).

Superfamily Valencioidea

Family VALENCIIDAE (263)—Valencia toothcarps. Freshwater; southeastern Spain, Italy, and western Greece.

Elongate and attenuate dorsal process of the maxilla; rostral cartilage minute or absent; total number of rays in dorsal fin 8–11; scales in lateral series 28–34. Fertilization external.

One genus, *Valencia*, with two species (Bianco and Miller, 1989).

Superfamily Cyprinodontoidea. The superfamilies Cyprinodontoidea and Poecilioidea are thought to be sister taxa (Costa, 1998a).

Family CYPRINODONTIDAE (264)—pupfishes. Freshwater, brackish water, and coastal marine; United States, Middle America, West Indies, parts of northern South America, North Africa, and Mediterranean Anatolian region.

Dorsal processes of maxillaries expanded medially, nearly meeting in the midline; lateral arm of maxilla expanded. Origin of dorsal fin (10–18 soft rays) anterior to origin of anal fin (8–13 soft rays). Fertilization external. Maximum length 8 cm SL.

Nine genera and 104 species.

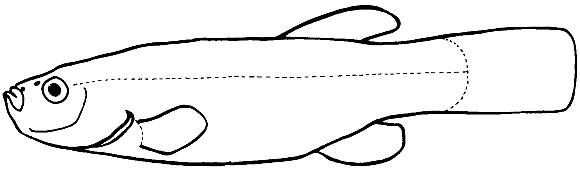
SUBFAMILY CUBANICHTHYINAE. Enlarged supraoccipital crest; elongate process of the autopalatine; parietals present; dorsal fin with 2 rudimentary rays and 9 principal rays, fin enlarged in males; pectoral fin with 18 rays; scales in lateral series 24–26; vertebrae 27. Cuba and Jamaica.

One genus, *Cubanichthys*, with two species (Costa, 2003).

SUBFAMILY CYPRINODONTINAE. Second pharyngobranchial offset relative to the third; Meckel's cartilage expanded posteriorly; parietals absent; outer jaw teeth uniserial.

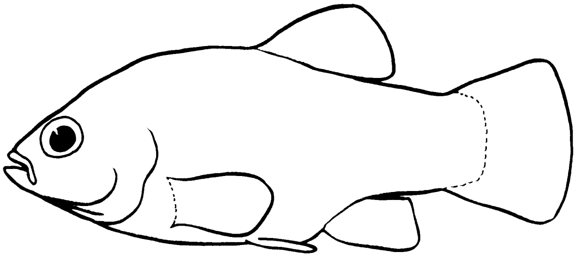
TRIBE ORESTIINI. Lower jaw robust due to medial extension of dentary; pelvic fin and pelvic skeleton, vomer, and first postcleithrum absent in species of *Orestias* (pelvic fin also absent in *Aphanius apodus*, as well as in a Miocene fossil species of *Aphanius*, Gaudant, 1993); scales absent or present, 0–60 in lateral series; 26–37 vertebrae. Maximum length about 22 cm, attained in *O. cuvieri.*

The 10 or so species of *Aphanius* (probably not a monophyletic group) occur in the Mediterranean region in brackish and freshwater (e.g., North Africa, Spain, Italy, Turkey, Greece, Arabian Peninsula, and Iran); the four species of *Kosswigichthys* occur in freshwater lakes of Turkey; and the 43 species of *Orestias* occur in high-altitude lakes in Peru, western Bolivia, and northernmost Chile along the Continental Divide (especially common in Lake Titicaca). Although the Eurasian and American cyprinodontiforms do not form monophyletic groups, the highly disjunct occurrence of the freshwater members of this tribe has been a serious biogeographic challenge to Parenti's (1981) hypothesis of relationships (addressed by Parenti, 1981:535–38). It is certainly one of the more notable cases of disjunct distributions in postulated monophyletic freshwater taxa, similar to that seen in polyodontids and *Umbra.*



Three genera, *Aphanius, Kosswigichthys* (synonym *Anatolichthys*), and *Orestias,* with about 57 species (Parenti, 1981; Costa, 2003).

TRIBE CYPRINODONTINI. Lower jaw without an anteriorly directed medial extension; first vertebrae lacking neural spine, its neural arches applied to supraoccipital of skull; exoccipital condyles absent; pelvic fin and skeleton absent in *Cyprinodon diabolis* of Devil's Hole, Nevada, and in *Megupsilon aporus* of Nuevo Leon, Mexico, present or absent in *C. nevadensis* of Nevada and California; scales in lateral series 23–29; vertebrae 23–29. Southern and eastern United States, Middle America, and West Indies to Venezuela. Some species occur in marine and brackish water such as *Floridichthys carpio* and *Cyprinodon variegatus* (also in freshwater). Information on the biology of the species of *Cyprinodon* is given in a 1981 book edited by R. J.Naiman and D. L. Soltz.



Five genera, *Cualac* (one species), *Cyprinodon* (about 40), *Floridichthys* (one), *Jordanella* (perhaps valid as *Garmanella*) (two), and *Megupsilon* (one), with about 45 species (e.g., Costa, 2003; Nelson et al., 2004).

Superfamily Poecilioidea. Ghedotti (2000) gave a detailed morphological analysis of this taxon and reviewed past taxonomic treatment. His proposed phylogeny supported the monophyly of the Anablepidae and Poeciliidae of Parenti (1981), but many changes are made to the classification of the Poeciliidae in order to present monophyletic groups as we now understand them. Although three subfamilies are recognized as previously in Nelson (1994), their composition is very different.

Family ANABLEPIDAE (265)—four-eyed fishes. Freshwater and brackish water, rarely coastal marine; southern Mexico to southern South America.

Epiotic and supraoccipital robust; pelvic fins distinctly behind tip of pectoral fin; pectoral girdle set low on side, radials situated ventrally or posteriorly; dorsal fin posteriorly placed, origin well behind anal fin. Maximum length 32 cm.

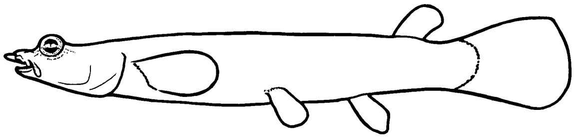
The recognition of the two subfamilies and their composition following Parenti (1981) has been supported by Ghedotti (1998, 2000). The Miocene fossil *Carrionellus* of Ecuador may be an anablepid (Ghedotti, 1998).

Three genera and 15 species (Ghedotti, 2003).

SUBFAMILY ANABLEPINAE. Tubular gonopodium formed from anal fin rays and associated with sperm duct. In some males the gonopodium can move only to the left (sinistral); in others, only to the right (dextral). In females the genital aperture is open to the right or to the left. Perhaps, in mating, a left-handed (sinistral) male copulates only with a right-handed (dextral) female and vice versa. Dextral and sinistral mating types are known in both sexes of all species. Fertilization internal, bear young alive (viviparous).

Two genera and 14 species.

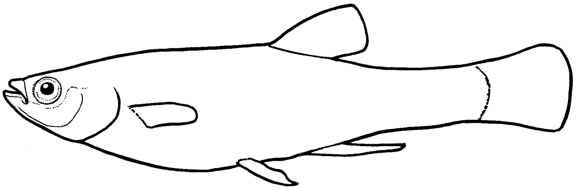
Anableps (four-eyed fishes)



Eyes elevated above top of head and divided longitudinally (horizontally) into upper and lower portions giving two pupils on each side (water line in surface-swimming individuals in center of eye, and they can focus on images simultaneously from above and below water with their unusual double vision); gonopodium formed primarily from anal rays 3–6; first three anal fin rays (excluding anteriormost, rudimentary ray of males) unbranched (as in Poeciliidae); dorsal fin with 7–10 rays and lying well behind anal fin; pectoral fin rays 20–26; scales in lateral series 50–96; vertebrae 45–54 (more than in other Cyprinodontiformes). Maximum length up to 32 cm TL, usually somewhat less (females much larger than males), the largest of any cyprinodontiform.

Anableps has three species (Zahl et al., 1977; Miller, 1979; Ghedotti, 2003). Freshwater and brackish water, rarely coastal marine; lowlands in southern Mexico to Honduras (Pacific slope) and northern South America (Atlantic slope).

Jenynsia (one-sided livebearers)



Eyes normal; gonopodium unscaled and formed primarily from anal rays 3, 6, and 7; pectoral fin rays 15; scales in lateral series 25–28; vertebrae 29–31. Maximum length up to 12 cm in females, about 4 cm in males.

Jenynsia contains about 11 species (Ghedotti, 2003). Freshwater; southern South America in lowlands from Brazil, Paraguay, Uruguay, and Argentina.

SUBFAMILY OXYZYGONECTINAE. No gonopodium; inner jaw teeth tricuspidate; head in lateral view pointed anteriorly; dorsal and anal fins posteriorly placed, just before caudal peduncle and well behind midbody; scales in lateral series 29 or 30; vertebrae 28. Maximum length about 15 cm TL. Fertilization external. Pacific drainages in Nicaragua, Costa Rica, and Panama (occurs in estuaries but breeds in freshwater).

One species, *Oxyzygonectes dovii*, the White Eye (Ghedotti, 2003).

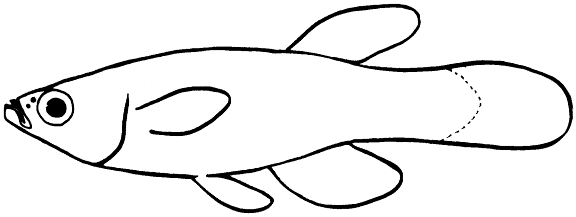
Family POECILIIDAE (266)—livebearers. Freshwater and brackish water; low elevations, eastern United States to South America and in Africa (including Madagascar).

Pectoral fins placed high on side of body due to radials placed in a dorsal position on the scapulocoracoid; anterior placement of pelvic fins; pleural ribs on the first several haemal arches; ventral hypohyal forms a bony cap over the anterior facet of the anterior ceratohyal; supraorbital pores modified such that neuromasts are found embedded in fleshy grooves. Gonopodium present or absent. Maximum length 20 cm attained in *Belonesox belizanus*, most species much smaller.

The subfamily classification of this family has been changed based on the work of Ghedotti (2000). Previously, in Nelson (1994) the three subfamilies recognized after Parenti (1981) were i) Poeciliinae with the same composition as here but with differing tribes recognized, ii) Fluviphylacinae with the one species of *Fluviphylax* then recognized, and iii) Aplocheilichthyinae with the present members of Aplocheilichthyinae and Procatopodinae.

Thirty-seven genera with about 304 species.

SUBFAMILY APLOCHEILICHTHYINAE (BANDED LAMPEYES). Western coastal Africa from mouth of the Senegal River to the mouth of the Congo River. This subfamily was previously recognized with six genera, including a nonmonophyletic *Aplocheilichthys* (some earlier works also recognized that a larger *Aplocheilichthys* was not monophyletic, and Huber, 1999, reviewed the African members). Now, following Ghedotti (2000), all but *Aplocheilichthys spilauchen* are placed in the Tribe Procatopodini. The one included species is regarded by Ghedotti (2000) as sister to all remaining poeciliids.



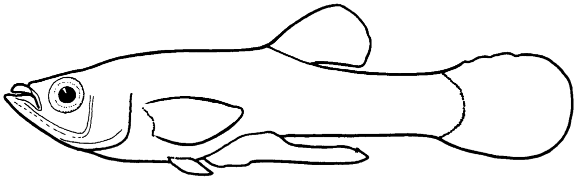
One species, *Aplocheilichthys spilauchen* (Banded Lampeye).

SUBFAMILY PROCATOPODINAE. Contains some 78 species (Lucinda, 2003).

TRIBE FLUVIPHYLACINI—*Fluviphylax* (5) (Lucinda, 2003). South America (Brazil, Colombia, and Venezuela). Maximum length 2 cm SL, these are the smallest of the cyprinodontiforms. Considered a subfamily in Nelson (1994).

TRIBE PROCATOPODINI (LAMPEYES)—Eight genera, *Micropanchax* (four species of which should be placed in a new genus) (with the subgenera *Micropanchax, Lacustricola,* and *Poropanchax* and possible synonym *Laciris*), *Platypanchax, Lamprichthys, Pantanodon, Hypsopanchax, Procatopus* (including synonym *Hylopanchax*), *Cynopanchax, Plataplochilus,* with 73 species (Huber, 1999, comments on some members). This group is known from Africa.

SUBFAMILY POECILIINAE (LIVEBEARERS). Male with elongated anterior anal fin rays (gonopodium, primarily formed from the third, fourth, and fifth rays) with internal fertilization; eggs with large yolks, have live birth (ovoviparous) (except in *Tomeurus,* which is egg-laying); exoccipital condyles absent; neural arches of the first vertebra open, not meeting to form a neural spine; metapterygoid absent; parietals present or absent; dorsal fin rays 4–14; first three anal fin rays unbranched; scales in lateral series 30–34; vertebrae usually 37. North, Central, and South America from southeastern Canada through to northeastern Argentina and Uruguay, including the Caribbean. This group includes many popular aquarium fishes such as the guppy, livebearers, mollies (molly in singular when used as the suffix in the common name), mosquitofishes, platyfishes (or the platys), and the swordtails. Several species, such as the Western Mosquitofish *Gambusia affinis* and the Sailfin Molly *Poecilia latipinna,* in addition to occurring in freshwater, can occur in brackish water and coastal marine waters. The many species of limias (*Limia*) are limited in their distribution to freshwater and coastal brackish water of several Caribbean islands, comprising a significant part of the freshwater fishes of these islands.



Nine tribes (following Ghedotti, 2000), 27 genera, and 225 species. Six of the tribes with 93 species occur in North America, ranging north from Mexico to southeastern Canada. The number of species given below is based on Ghedotti (2000) with updates for Central and South American species from Lucinda (2003); genera are largely recognized after Lucinda (2003). Lucinda and Reis (2005) revised this subfamily but changes could not be incorporated here; they resurrected the tribe Tomeurini and described the new tribes Brachyrhaphini and Priapichthyini as well as the supertribe Poeciliini.

TRIBE ALFARINI—*Alfaro* (2).

TRIBE PRIAPELLINI—*Priapella* (4).

TRIBE GAMBUSINI—Three genera, *Belonesox* (1), *Brachyrhaphis* (11), and *Gambusia* (45), with 57 species.

TRIBE HETERANDRINI—Six genera, *Heterandria* (with *H. formosa* in the subgenus *Heterandria* and eight other species in the subgenus *Pseudoxiphophorus* – Ghedotti, 2000, recognized *Pseudoxiphophorus* as a valid genus), *Neoheterandria* (4), *Poeciliopsis* (21), *Priapichthys* (7), *Pseudopoecilia* (3), and *Xenophallus* (1), with 45 species.

TRIBE GIRARDINI—Three genera, *Carlhubbsia* (2), *Girardinus* (8), and *Quintana* (1), with 11 species.

TRIBE POECILIINI—Six genera, *Limia* (21), *Micropoecilia* (considered a synonym of *Poecilia* by some, e.g., Rodriguez, 1997) (5), *Pamphorichthys* (6), *Phallichthys* (4), *Poecilia* (27), and *Xiphophorus* (25), with 88 species.

TRIBE CNESTERODONTINI—Five genera, *Cnesterodon* (7), *Phalloceros* (1), *Phalloptychus* (3), *Phallotorynus* (3), and *Tomeurus* (1), with 15 species. *Tomeurus* was placed alone in the tribe Tomeurini in Nelson (1994).

TRIBE SCOLICHTHYINI—*Scolichthys* (2).

TRIBE XENODEXINI—*Xenodexia* (1).

Series PERCOMORPHA

The Percomorpha, the most derived euteleostean clade, was recognized by Rosen (1973a). Problems and changes in its classification are reviewed by Johnson (1993). In this taxon the pelvic girdle is directly or ligamentously attached to the cleithrum or coracoid of the pectoral girdle, and there is a ventrally displaced anterior pelvic process (Stiassny and Moore, 1992). However, its monophyly was challenged by Johnson and Patterson (1993) who recognized a monophyletic group comprising their smegmamorphs (the mugilomorphs, atherinomorphs, gasterosteiforms, synbranchiforms, and elassomatids) and, as herein recognized, the scorpaeniforms, perciforms, pleuronectiforms, and tetraodontiforms, as the Percomorpha. Of the groups recognized here in the Percomorpha, they thus excluded the stephanoberciforms, beryciforms, and most zeiforms (but included mugilomorphs and atherinomorphs). While identifying this major difference, and although the Johnson and Patterson (1993) definition of Percomorpha is widely used and supported from much recent research, I retain a similar composition to that recognized in Nelson (1994) until questions of the monophyly of Smegmamorpha and the phylogenetic position of other nominal taxa given ordinal status are better resolved, as expected in the near future. See above discussion under superorder Acanthopterygii.

Some nine orders with 245 families, 2,212 genera, and 13,173 species are placed in this series.

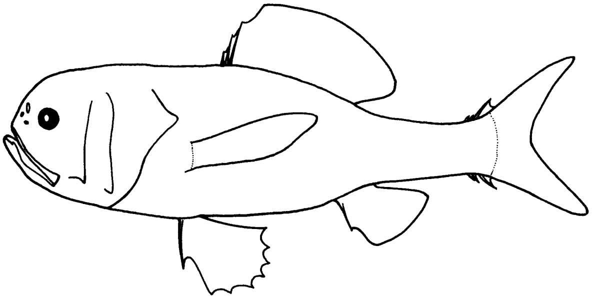
Order STEPHANOBERYCIFORMES (Xenoberyces, in part) (52)—prickle-fishes. Body usually roundish; palate toothless; skull bones, in general, exceptionally thin; orbitosphenoid absent (except present in *Hispidoberyx*); subocular shelf absent; supramaxilla absent or reduced. Johnson and Patterson (1993) discussed the uniquely modified extrascapular.

Recognition of this order follows Johnson and Patterson (1993). However, Moore (1993) had a different view of the interrelationships of the taxa placed in the orders Stephanoberyciformes and Beryciformes that warrants consideration. He included all the stephanoberyciforms and most of the beryciforms in his order Trachichthyiformes (including the former lampridiform taxa Mirapinnatoidei and Megalomycteroidei, which are given here in the stephanoberyciforms) on the basis of the following characters: ocular sclera absent (most other acanthomorphs have two ossified sclera circling the eyeball); neural arch of first vertebrae fused to underlying centrum; one (the posterior) supramaxilla. In an examination of the characters of this proposed order and of the Holocentridae and Berycidae, Johnson and Patterson (1993) concluded that the Trachichthyiformes as recognized by Moore (1993) are paraphyletic. They gave arguments for recognizing the present Stephanoberyciformes as the sister group to all remaining acanthomorphs. They placed the Trachichthyoidei of Moore (1993) with the Berycidae and Holocentridae, recognizing the resulting group as the Beryciformes (provisionally accepted here), which in turn is thought to be the sister group to the remaining acanthomorphs (but excluding the Zeiformes). Colgan et al. (2000) questioned the monophyly of the Stephanoberyciformes based on DNA sequences, and more studies are needed.

Nine families with 28 genera and 75 species (with many undescribed species). All species are marine

Superfamily Stephanoberycoidea. According to Moore (1993) the Melamphaidae are the sister group to the remaining stephanoberycoids with the three families, given here after the melamphaids, forming one clade and the last four forming another. See below under superfamily Cetomimoidea for transfer of Gibberichthyidae from the superfamily Stephanoberycoidea.

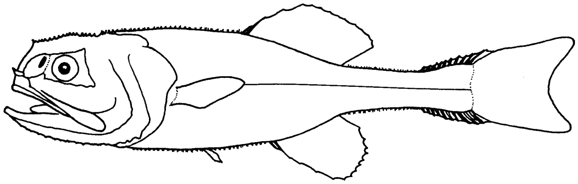
Family MELAMPHAIDAE (267)—bigscale fishes. Marine, bathypelagic; most oceans (absent from Arctic and Mediterranean).



Dorsal fin single, 1–3 weak spines preceding the soft rays; pelvic fin thoracic or subthoracic, with one spine and 6–8 soft rays; caudal fin with three or four procurrent spines; scales usually large, cycloid, and deciduous; no lateral line (one or two pored scales at most); 24–31 vertebrae.

Five genera, *Melamphaes*, *Poromitra*, *Scopeloberyx*, *Scopelogadus*, and *Sio*, with 36 species (Moore, 2003; Kotlyar, 1996, 2004a).

Family STEPHANOBERYCIDAE (268)—pricklefishes. Marine; tropical and subtropical western parts of Atlantic, Indian (off South Africa), and Pacific.



Spines, if any, in dorsal and anal fins, weak; each fin with about 10–14 soft rays; pelvic fin abdominal or subabdominal, with five soft rays, no spine; caudal fin with 8–11 procurrent spines (these precede the principal rays dorsally and ventrally); scales smooth or spiny; lateral line faint; 30–33 vertebrae.

Three monotypic genera: *Acanthochaenus* (Atlantic and off Durban, South Africa), *Malacosarcus* (Pacific), and *Stephanoberyx* (Atlantic) (Moore, 2003; Kotlyar, 1996, 2004c). All are known from relatively few specimens.

Family HISPIDOBERYCIDAE (269)—hispidoberycids. Marine; northeastern Indian Ocean and South China Sea.

Spinulose scales; operculum with a long, stout spine; palatine and vomerine teeth present; dorsal fin with four or five spines and 10 soft rays; anal fin with three spines and nine soft rays; pelvic fin with one spine and six or seven soft rays; lateral line scales 32–34; vertebrae 34.

One species, *Hispidoberyx ambagiosus* (Kotlyar, 1996, 2004d).

Superfamily Cetomimoidea (Cetunculi, Xenoberyces, in part). Complete loss of fin spines.

The taxonomic history of this group is reviewed in Nelson (1984) and Moore (1993) and references therein. The current classification follows the conclusions of Moore (1993), some of which were expressed by Rosen (1973a). In Nelson (1984) only the whalefish families Rondeletiidae, Barbourisiidae, and Cetomimidae were included in this taxon (as the suborder Cetomimoidei of Beryciformes). The added families Mirapinnidae and Megalomycteridae were placed in separate suborders of the Lampridiformes. The first three families, the whalefishes, have the following features: body whale-shaped; mouth very large and stomach highly distensible; eyes well developed to degenerate; lateral line made up of enormous hollow tubes; luminous tissue on body; dorsal and anal fins far back on body and opposite one another; no swim bladder; orbitosphenoid absent; supramaxilla absent or reduced; color usually orange and red on a black body. Bathypelagic. Length up to 39 cm.

Paxton et al. (2001) found that *Rondeletia* and *Gibberichthys* are sister taxa, based on the presence of Tominaga's organ (below the nasal rosette), and concluded that "the whalefishes," Barbourisiidae, Rondeletiidae, and Cetomimidae, as a group are, at best, paraphyletic. For this reason, *Gibberichthys* has been transferred from the superfamily Stephanoberycoidea and placed here, but a cladistic study employing more characters is desirable.

Six families (three families of whalefishes). Paxton (1989), Paxton et al. (2001), and Moore (1993) discuss the families.

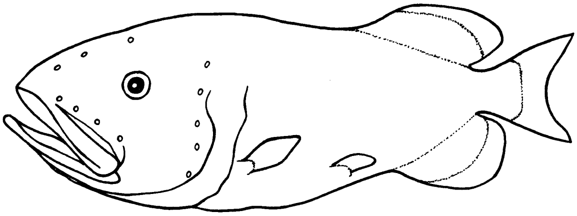
Family GIBBERICHTHYIDAE (270)—gibberfishes. Marine; tropical western Atlantic, western Indian, and western and southwestern Pacific.

Pelvic fin subabdominal, with one spine and five or six soft rays (prejuvenile with elongate appendage off third pelvic ray); adults with semi-isolated series of 5–8 short spinous rays before soft dorsal fin and four or five before anal fin (about 7–9 soft rays in each fin); scales cycloid, about 28–34 in lateral line; vertical rows of papillae on sides of body over the vertical lateral line tubes; swim bladder present and partially filled with fat; 28–31 vertebrae. Maximum length about 12 cm. Prejuveniles have been found between near-surface waters and 50 m, while adults have been captured primarily between 400 and 1,000 m.

Kasidoron, once given family status (Kasidoridae), is the larva of *Gibberichthys pumilus.*

One genus, *Gibberichthys,* with two species known from relatively few specimens (Moore, 2003; Kotlyar, 1996, 2004b).

Family RONDELETIIDAE (271)—redmouth whalefishes. Marine; oceanic.



Box-shaped head; skin smooth; lateral line system composed of a number of pores in each of a series of 14–26 vertical rows; pelvics subabdominal with five or six rays; three epurals and six hypurals; vertebrae 24–27. Maximum length about 11 cm.

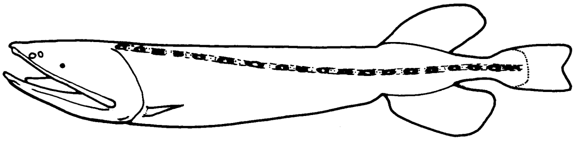
Two species, *Rondeletia bicolor* and *R. loricata* (e.g., Kotlyar, 1996; Paxton and Trnski, 2003).

Family BARBOURISIIDAE (272)—red whalefishes. Marine; parts of Atlantic (including Gulf of Mexico where first found), Indian, and Pacific.

Pelvic fins present, subabdominal, with six rays; skin spiny; dorsal fin rays 19–22; anal fin rays 15–18; vertebrae 40–43. Color reddish-orange. Maximum length 39 cm SL.

One species, *Barbourisia rufa* (J. R. Paxton and D. J. Bray in Smith and Heemstra, 1986; Paxton et al., 2001; Paxton, 2003).

Family CETOMIMIDAE (273)—flabby whalefishes. Marine; oceanic.



Pelvic fins absent; skin loose and scaleless; eyes reduced or rudimentary; three or four gills; no photophores present, but luminous organ often present around anus and dorsal and anal fin bases; pleural ribs absent; vertebrae 38–59. Live color brown or orange with brilliant orange or red jaws and fins. Maximum length 39 cm, attained in a species of *Gyrinomimus.*

Members of this family are second only to the anglerfish family Oneirodidae in being the most species-rich family in the bathypelagic zone (1,000 m–4,000 m) and may be the most abundant one below 1,800 m (Paxton, 1989). Only recently have males been found in this group; they are small, the five known ones are 3–5 cm and previously had been classified as immature juveniles.

Nine genera, *Cetichthys*, *Cetomimus*, *Cetostoma*, *Danacetichthys*, *Ditropichthys*, *Gyrinomimus*, *Notocetichthys*, *Procetichthys*, and *Rhamphocetichthys*, with about 20 species (15 more undescribed), most known from only a few specimens (e.g., Paxton, 1989, 2003). The monotypic *Procetichthys*, with a large nasal organ and the eye with a lens in specimens over 10 cm (vs. small nasal organ and eye without lens in specimens over 10 cm) is placed in one subfamily and the other eight genera in another.

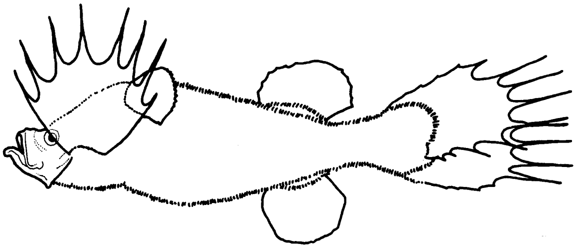
Family MIRAPINNIDAE (274)—tapertails. Marine; Atlantic, Indian, and western Pacific.

No scales; gill membranes separate and free from isthmus; dorsal and anal fins opposite one another; pelvic fins jugular, 4–10 rays; 3–5 branchiostegal rays; vertebrae 42–55.

The first specimen of this group was collected in 1911. At one time they were placed in order, Mirapinnati. All specimens are immature and 6 cm or less.

Three genera and five species (one undescribed) (e.g., Paxton, 2003).

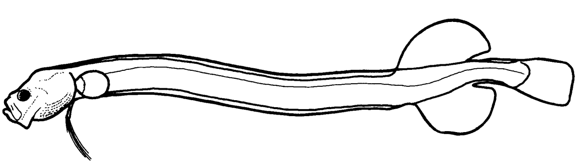
SUBFAMILY MIRAPINNINAE—HAIRYFISH



Body moderately elongate, covered with short hairlike pile; two halves of caudal fin overlapping; large, winglike pelvic fins; pectoral fins relatively small and placed high on body.

One species, *Mirapinna esau.* Atlantic.

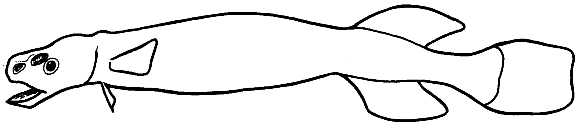
SUBFAMILY EUTAENIOPHORINAE—TAPERTAILS OR RIBBONBEARERS



Body very elongate, smooth; caudal fin in juveniles with extremely long tapelike streamer (several times body length); dorsal and anal fins near caudal fin; dorsal and anal fins each with 15–31 rays.

Two genera, *Eutaeniophorus* and *Parataeniophorus*, with four species. Atlantic, Indian, and western Pacific.

Family MEGALOMYCTERIDAE (275)—largenose fishes. Marine, deep-sea; Atlantic and Pacific.



Olfactory organs exceptionally large; pelvic fin usually absent, although present and inserted slightly ahead of the pectorals in *Megalomycter* (three rays) and *Ataxolepis henactic* (one ray); dorsal and anal fins near caudal fin; pleural ribs absent; vertebrae 45–52.

Perhaps four genera, *Ataxolepis*, with two species (one in the Atlantic and one in the tropical eastern Pacific), and the monotypic *Cetomimoides*, *Megalomycter*, and *Vitiaziella* (about five species with three undescribed) (e.g., Paxton and Trnski, 2003).

Order BERYCIFORMES (53)—alfonso squirrelfishes. Orbitosphenoid present; two supramaxillae in Berycidae and Holocentridae; subocular shelf present (may be reduced); pelvic fins usually with more than five soft rays; 16 or 17 branched caudal fin rays (or 18 or 19 principal rays); maxillae partially included in gape in some. As noted by Johnson and Patterson (1993), all share a modification of the anterior part of the supraorbital and infraorbital sensory canals, termed by them "Jakubowski's organ."

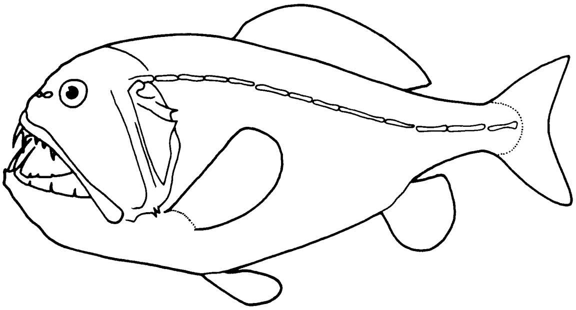
Johnson and Patterson (1993) recognized the Beryciformes as the sister group to their Percomorpha, a taxon excluding the Zeiformes but including the Smegmamorpha (e.g., Atherinomorpha, Gasterosteiformes, and Synbranchiformes), Scorpaeniformes, and higher taxa. The beryciforms and Johnson and Patterson's (1993) percomorphs comprise their taxon Euacanthopterygii, which is diagnosed by such characters as a complex pelvic spine and a "myoseptal" ligament from the postcleithrum to the posterolateral corner of the pelvic girdle. The Euacanthopterygii and the Zeiformes are recognized by Johnson and Patterson (1993) as an unnamed taxon diagnosed in part in having Baudelot's ligament originating on the basioccipital. Johnson and Patterson (1993) argued that the Berycidae and Holocentridae and what is given herein as the suborder Trachichthyoidei form a monophyletic group, and this is retained here. Kotlyar (1996) gave extensive information on the beryciforms.

Seven families with 29 genera and 144 species. All species are marine.

Suborder Trachichthyoidei. The recognition of this clade and the superfamilies given below is based on the cladogram of Moore (1993). Baldwin and Johnson (1995) and Konishi and Okiyama (1997), based on larval characters, corroborated the relationships and supported the monophyly of this group. Five families, 18 genera, and 45 species.

Superfamily Anoplogastroidea. Spines present on parietals, frontals, and preoperculum of larva.

Family ANOPLOGASTRIDAE (276)—fangtooths. Marine, bathypelagic; Atlantic, Indian, and Pacific.



Body short, deep, and compressed; numerous long fanglike teeth on jaws in adults; eye small, diameter less than snout length; scales small or minute; lateral line an open groove (partly covered by scales); fins without spines, dorsal with 16–20 rays and anal usually with 7–9 rays; pelvic fin with seven soft rays, the first unbranched; Baudelot's ligament absent; subocular shelf absent; neural spines steeply slanted; vertebrae 25–28. Maximum length about 16 cm.

Two species, *Anoplogaster cornuta* and *A. brachycera* (Kotlyar, 1996, 2003; Moore, 2003).

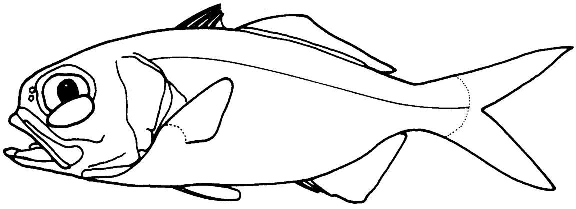
Family DIRETMIDAE (277)—spinyfins. Marine; Atlantic, Indian, and Pacific.

No lateral line; dorsal and anal fins without spines, dorsal rays 24–30 and anal rays 19–22; pelvic fin with laminar spine and six soft rays; sharp edge to abdomen formed by ventral scutes; branchiostegal rays seven or eight; vertebrae 20–32. Maximum length 37 cm.

Three genera, *Diretmichthys*, *Diretmoides*, and *Diretmus*, with four species (Kotlyar, 1996; Moore, 2003).

Superfamily Trachichthyoidea (changed from Anomalopoidea). Neural arch of second preural centrum unfused.

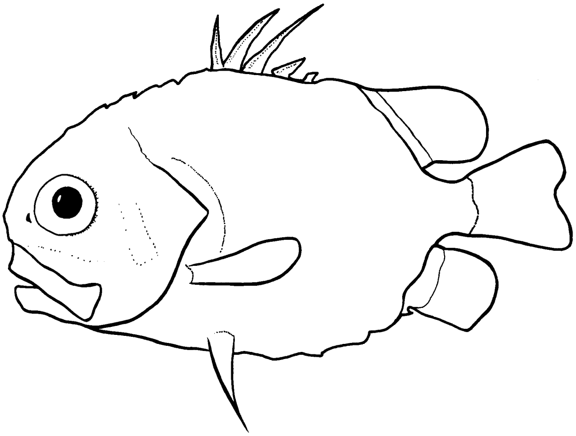
Family ANOMALOPIDAE (278)—flashlight fishes. Marine; scattered warm-water localities, primarily Indo-Pacific.



Luminous organ beneath eye with rotational and shutter mechanism for controlling light emission (hence the common name, lanterneye or flashlight fishes); pelvic fin with one spine and five or six soft rays; dorsal fin with 2–6 spines and 14–19 soft rays, spinous and soft portions continuous (*Photoblepharon* only) or with notch; anal fin spines two or three and soft rays 10–13; short subocular shelf; vertebrae 25–30. Johnson and Rosenblatt (1988) described the mechanical means of controlling light emission from the subocular organ with symbiotic luminous bacteria that glow continuously, by rotation of its luminous organ downward or by the erection of a black membrane over it or by both mechanisms, and the advantage of the blinking action in avoiding predation. Maximum length about 27 cm, attained by the planktivore, *Anomalops katoptron.* Also known as lanterneye fishes. Baldwin et al. (1997) presented a cladogram of the six genera, giving the sister group of this family the Monocentridae.

Six genera—the western Pacific *Anomalops* (1), Indo-West Pacific *Photoblepharon* (2), the Caribbean *Kryptophanaron* (1), the Pacific *Parmops* (2, known from Fiji and Tahiti), and the eastern Pacific *Phthanophaneron* (1, the Gulf of California), and the South Pacific *Protoblepharon* (1, from off Rarotonga, Cook Islands)—with eight species (Kotlyar, 1996; Baldwin et al., 1997; Johnson and Rosenblatt, 1988; Johnson et al., 2001; Moore, 2003).

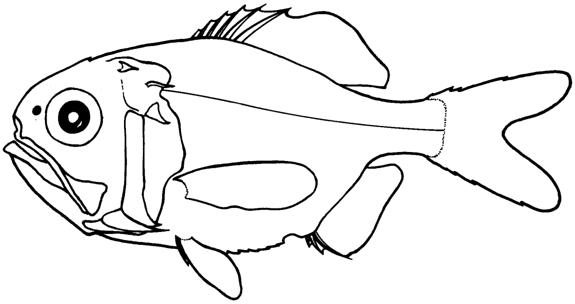
Family MONOCENTRIDAE (Monocentrididae) (279)—pinecone fishes. Marine; tropical and subtropical, Indian and Pacific.



Body covered with large, heavy platelike scales; phosphorescent (luminous bacteria) light organs on lower jaw; pelvic fin with one large spine and two to four small soft rays; two dorsal fins, the first with 4–7 strong spines alternating from side to side and the second with 9–12 soft rays; anal fin with 10–12 soft rays (no spines); pectoral fin with 13–15 rays; branchiostegal rays eight. Maximum length about 21 cm.

Two genera, *Cleidopus* and *Monocentris*, with four species (Kotlyar, 1996). They occur primarily at depths of 30–300 m.

Family TRACHICHTHYIDAE (280)—roughies. Marine; Atlantic, Indian, and Pacific.



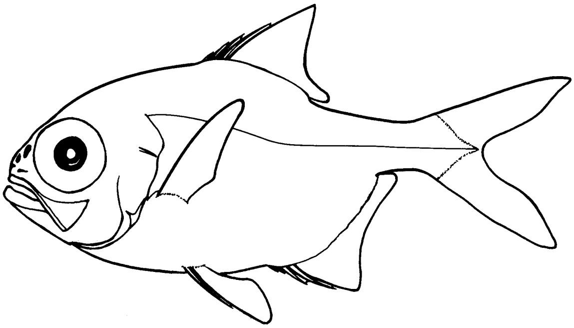
Distinct spine at angle of preopercle; posteriorly pointing spine on posttemporal bone (also found in *Centroberyx*); pelvic fin with one normal spine and six or seven soft rays; dorsal fin with 3–8 spines and 10–19 soft rays; anal fin with two or three spines and 8–12 soft rays; caudal fin usually with 4–7 procurrent spines on each lobe; abdomen with median ridge of scutes; scales variable between species (e.g., thick and spiny to thin and cycloid); body very deep in the Australian *Trachichthys* and the widespread *Gephyroberyx* and *Hoplostethus* (shown in figure) to only moderately deep; some species with luminescence. Maximum length about 55 cm.

Some members of this family are called roughies, such as the widespread Orange Roughy, *Hoplostethus atlanticus*, which has been important in the commercial fisheries in many areas but because recruitment is slow, stock depletion can easily occur. Depth distribution for the family is about 100–1,500 m; most species occur in deep water. Also known as slimeheads. Fossils include the Late Cretaceous *Antarctiberyx* from Antarctica described by L. Grande and S. Chatterjee in 1987, the Late Cretaceous *Lissoberyx* from Italy described by L. Taverne in 2003, and *Hoplopteryx*.

Seven genera, *Aulotrachichthys*, *Gephyroberyx*, *Hoplostethus*, *Optivus*, *Paratrachichthys*, *Sorosichthys*, and *Trachichthys*, with about 39 species (e.g., Kotlyar, 1995, 1996; Moore, 1993, 2003). About half of the species are placed in *Hoplostethus*.

Suborder Berycoidei

Family BERYCIDAE (281)—alfonsinos. Marine; Atlantic, Indian, and western and central Pacific.



Pelvic fin with one spine and 7–13 soft rays; dorsal fin without notch, with 4–7 spines increasing in length from first to last, and 12–20 soft rays; anal fin with four spines and 12–17 (*Centroberyx*) or 25–30 (*Beryx*) soft rays; lateral line scales 39–51 (*Centroberyx*) or 66–82 (*Beryx*); 24 vertebrae. Most species occur between 200–600 m.

Two genera, *Beryx* and *Centroberyx*, with about nine species (e.g., Kotlyar, 1996; Moore, 2003).

Suborder Holocentroidei. Fossil genera include the Upper Cretaceous *Alloberyx*, *Caproberyx*, *Paracentrus*, and *Trachichthyoides*. Tertiary fossils include *Africentrum*, *Berybolcensis*, *Eoholocentrum*, *Holocentrites*, and *Tenuicentrum*. Gallo-Da-Silva and De Figueiredo (1999) included the Cretaceous *Pelotius hesselae* in the Holocentroidei because of the presence of four spines in the anal fin, and concluded that the presence of seven rays in the pelvic fin excluded it from the Trachichthyoidei, Stichocentridae and Pycnosteroididae but suggested its inclusion in the Holocentridae; it shared the presence of two predorsals with the clade *Erygocentrus* + Tenuicentrinae + Myripristinae + Holocentrinae.

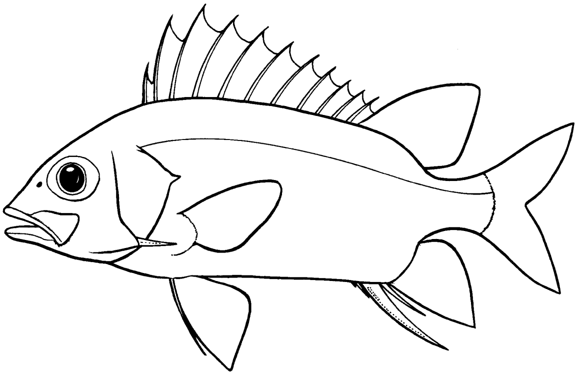
Family HOLOCENTRIDAE (282)—squirrelfishes. Tropical marine; Atlantic, Indian, and Pacific.

Pelvic fin with one spine and 5–8 (usually seven) soft rays; long dorsal fin with spiny portion (10–13 spines) and soft-rayed portion (11–17 rays) divided by a notch; anal fin with four spines and 7–16 soft rays; caudal fin forked, with 18 or 19 principal rays; scales large and ctenoid (extremely rough); eyes large; opercle with spiny edge; vertebrae 26 or 27; color usually reddish.

Squirrelfishes are mostly nocturnal, usually hiding in crevices or beneath ledges of reefs in the daytime (along with cardinalfishes, bigeyes, and sweepers). Most species occur between the shoreline and 100 m, rarely over 200 m. Adults tend to remain close to the bottom. Maximum length about 61 cm, attained in *Sargocentron spinifer*.

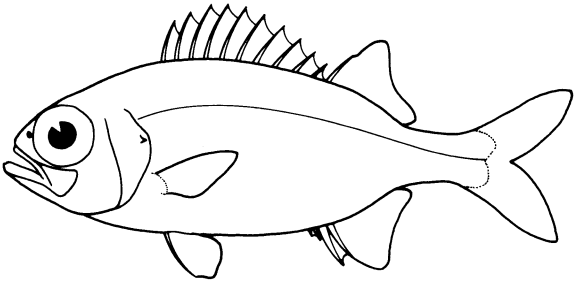
Eight genera with about 78 species (e.g., Kotlyar, 1996; Randall, 1998; Randall and Greenfield, 1996; Randall and Yamakawa, 1996; Greenfield, 2003).

SUBFAMILY HOLOCENTRINAE (SQUIRRELFISHES). A strong spine present at angle of preoperculum (sometimes a toxin is associated with this spine); longest anal spine usually longer than or equal to longest dorsal spine; anal fin soft rays 7–10; swim bladder tubular, extending entire length of body (contacting the skull in a few species).



Three genera—*Holocentrus*, *Neoniphon*, and *Sargocentron*.

SUBFAMILY MYRIPRISTINAE (SOLDIERFISHES). No enlarged preopercular spine (except in the Atlantic *Corniger spinosus*, which has two enlarged spines at the corner of the preopercle); longest anal spine usually shorter than longest dorsal spine; anal fin soft rays 10–16; swim bladder constricted in anterior third to form two more or less separate chambers (anterior section with two anterolateral projections).



Five genera, *Myripristis*, *Ostichthys*, *Plectrypops*, *Corniger*, and *Pristilepis*.

Order ZEIFORMES (54)—dories. Dorsal, anal, and pectoral fin rays unbranched; three and one-half gills (seven hemibranchs); no open gill slit between fourth and fifth branchial arches; palatine teeth absent; vomerine teeth present; caudal fin usually with 11 branched rays (13 in grammicolepidids); dorsal fin with 5–10 spines and 22–36 soft rays; body usually thin and deep; jaws usually greatly distensible; no orbitosphenoid; simple posttemporal fused to skull; swim bladder present; vertebrae usually 30–44.

The classification of this order, changed from that given in Nelson (1994), follows Tyler et al. (2003). They presented strong arguments with detailed anatomical evidence for the relationships presented here. In all, nine synapomorphies and 17 other characters were used to establish monophyly for this order (with the removal of the caproids). As stated in Nelson (1994), "Two major questions on zeiform systematics exist: Is it a monophyletic group with the inclusion of the caproids? What are the relationships of the zeiforms"? It was noted that Rosen (1973a) presented evidence that caproids might be better placed in Perciformes than in Zeiformes. In 1980, P. C. Heemstra removed the Caproidae and he (in Smith and Heemstra, 1986) placed them in the perciforms. Johnson and Patterson (1993) excluded the caproids to establish monophyly for the Zeiformes (recognized in Nelson, 1994, as the Zeioidei). Tyler et al. (2003) firmly established monophyly for the group without the caproids, and the latter are now placed as a suborder of Perciformes. They also presented reasons, accepted here, for not considering zeiforms as related to the tetraodontiforms as has been suggested (see comments in Nelson, 1994, and below under Caproidei, the last suborder of Perciformes). See above under Paracanthopterygii for studies suggesting that Gadiformes and Zeiformes (as herein defined) form a monophyletic group. Meristic counts for species were given in Tyler et al. (2003). Heemstra (2003a) also gave much information. The family Macrurocyttidae is no longer recognized.

Most zeiform species are deep-sea; some, however, tend to occur 100–300 m.

The earliest fossil zeiform is *Cretazeus* (family Cretazeidae) from the Upper Cretaceous, about 72,000,000 million years old, described in 2000 by J. C. Tyler and colleagues.

Six families with about 16 genera and 32 species. There are no freshwater species.

Suborder Cyttoidei. Recognized after Tyler et al. (2003).

Family CYTTIDAE (283)—lookdown dories. Marine; southeast Atlantic and Indo-West Pacific (e.g., from South Africa to off Australia and New Zealand).

No large buckler scales present along bases of dorsal and anal fins or along ventral midline; dorsal fin with 8–10 spines and 28–36 soft rays. Placed in Zeidae in Nelson (1994).

One genus, *Cyttus*, with 3 species.

Suborder Zeioidei. This subordinal name was used in Nelson (1994) but also included *Cyttus*. Present use follows Tyler et al. (2003).

Family OREOSOMATIDAE (284)—oreos. Marine; Antarctic, Atlantic, Indian, and Pacific. Known primarily from off South Africa and southern Australia.

Body very deep and compressed; mouth upturned, protractile; eyes large; scales small, cycloid or ctenoid; young with conical scutes on parts of body;

pelvic fin with one spine and 5–7 soft rays; dorsal fin with 5–8 spines and 28–36 soft rays; anal fin with 2–4 spines and 26–33 soft rays; pectoral fin rays 17–22; vertebrae 34–43. Maximum length about 50 cm.

Most species occur between 400–1,800 m.

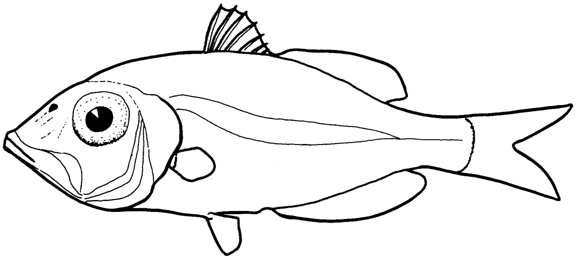
Tyler et al. (2003) recognized two subfamilies, Pseudocyttinae for *Pseudocyttus maculates,* and Oreosomatinae for the other three genera.

Four genera, *Allocyttus, Neocyttus, Pseudocyttus,* and *Oreosoma,* with about nine or 10 species (C. Karrer in Smith and Heemstra, 1986; Heemstra, 2003a; Tyler et al., 2003).

Family PARAZENIDAE (285)—smooth dories. Marine; scattered localities in the western Atlantic and the Indo-Pacific.

Pelvic fin with no spine and 7–9 soft rays.

SUBFAMILY PARAZENINAE. Body compressed and elongate; premaxillaries extremely protractile; two dorsal fins, the first with eight spines, second with 26–30 soft rays; anal fin with one spine and 31 soft rays; pectoral fin with 15 or 16 rays; pelvic fins thoracic (origin behind pectoral fin origin), with one unbranched ray and six branched rays; 34 vertebrae. The species has only one lateral line, rather than two as previously thought (Kotlyar, 2001).



One species, *Parazen pacificus,* and perhaps an undescribed species in the western Atlantic (Kotlyar, 2001).

SUBFAMILY CYTTOPSINAE. Dorsal fin with six or seven spines (rarely eight); pectoral fin with 13–15 rays; pelvic fin base under or slightly in front of pectoral fin base, fins with nine rays.

Two genera, *Cyttopsis* and *Stethopristes,* with about three species (placed in Zeidae in Nelson, 1994).

Family ZENIONTIDAE (Zenionidae) (286)—armoreye dories. Marine; Atlantic, Indian, and Pacific.

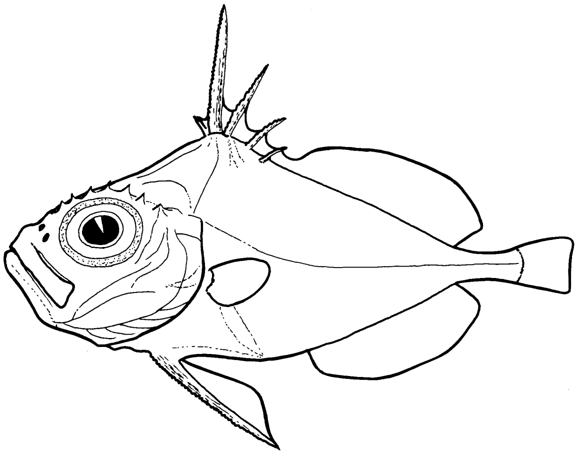
Pectoral fin rays 12–18; scales on most of body rounded to squarish.

Three genera, *Capromimus, Cyttomimus,* and *Zenion* (synonym *Cyttula*), with about seven species (e.g., Heemstra, 2003a) (the first two genera were placed in Zeidae and the latter in Macrurocyttidae in Nelson, 1994).

Family GRAMMICOLEPIDIDAE (287)—tinselfishes. Marine; scattered parts of Atlantic and Pacific.

Scales narrow and greatly elongate vertically.

SUBFAMILY MACRUROCYTTINAE. Pelvic fin, in addition to the spine, with two inconspicuous soft rays; spinous dorsal elevated, with five spines (strong, all but one relatively short); soft dorsal rays 27, and anal fin with 22 soft rays; pectoral rays 15. Luzon (Philippines).

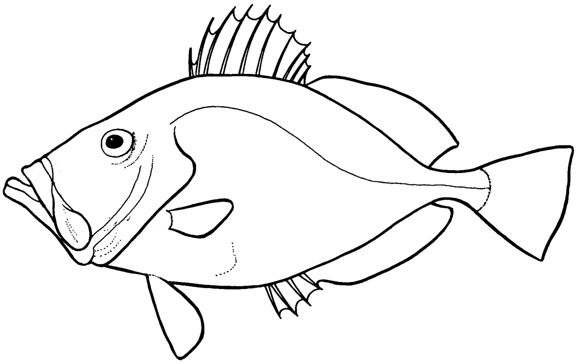


One species, *Macrurocyttus acanthopodus.*

SUBFAMILY GRAMMICOLEPIDINAE. Mouth small, nearly vertical; dorsal fin with 5–7 spines and 27–34 soft rays; anal fin with two spines and 27–35 soft rays; row of spines along each side of dorsal and anal fin bases; pelvic fin with one spine and six soft rays; caudal fin with 13 branched rays; vertebrae 37–46.

Two monotypic genera, *Grammicolepis* (synonym *Daramattus*) and *Xenolepidichthys.*

Family ZEIDAE (288)—dories. Marine; Atlantic, Indian, and Pacific.



Large buckler scales with posteriorly directed processes present along bases of dorsal and anal fins. Also known as John dory and St. Peter fish.

Two genera, *Zenopsis* and *Zeus*, with about five species.

Order GASTEROSTEIFORMES (55)—sticklebacks. Pelvic girdle never attached directly to the cleithra; supramaxillary, orbitosphenoid, and basisphenoid absent; postcleithrum a single bone or absent; branchiostegal rays 1–5; body often with armor of dermal plates; mouth usually small.

As noted in greater detail in Nelson (1994), some authors have recognized the Gasterosteoidei and Syngnathoidei in separate but related orders (either under the ordinal name Gasterosteiformes or Syngnathiformes), while McAllister (1968) felt that they belonged to separate lineages. Although evidence for the monophyly is not strong, I accept the view of Johnson and Patterson (1993) and earlier studies by T. W. Pietsch and R. A. Fritzsche that they are probably each other's closest relatives. Bowne (1994) reviews the systematics and morphology of Gasterosteiformes. The Indostomidae is moved from Syngnathoidei to Gasterosteoidei following the conclusions of Britz and Johnson (2002).

Two suborders with 11 families, 71 genera, and 278 species. About 21 species are restricted to freshwater and another 42 species are found in brackish water (some being variously diadromous or at least able to commonly enter freshwater and marine water).

Suborder Gasterosteoidei. Upper jaw protractile, ascending process of premaxilla well developed; postcleithrum absent; circumorbital bones, in addition to lachrymal, present; nasals and parietals present; anterior vertebrae not elongate; kidneys produce a gluelike substance used by males to construct a nest of plant material (condition in some species unknown); supracleithrum absent in *Aulorhynchus*, *Spinachia*, and *Gasterosteus wheatlandi.*

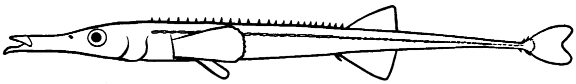
Four families, nine genera, and about 14 species (see comment on number of species under Gasterosteidae).

Family HYPOPTYCHIDAE (289)—sand eel. Marine; Japan and Korea to Sea of Okhotsk.

Body elongate, scutes and scales absent; spines absent; dorsal and anal fins posteriorly placed, each with about 20 soft rays; pelvic girdle and fins absent; pectoral fin rays nine; caudal fin with 13 principal rays (11 branched); four branchiostegal rays; circumorbital ring incomplete; premaxillary teeth present in males but absent in females; about 29 pairs of pleural ribs, epipleurals absent; vertebrae about 55–57; hypural plate divided into upper and lower halves (all other gasterosteioids have a fused hypural plate except *Gasterosteus*, which also has a split hypural). Maximum length about 8.5 cm.

One species, *Hypoptychus dybowskii.*

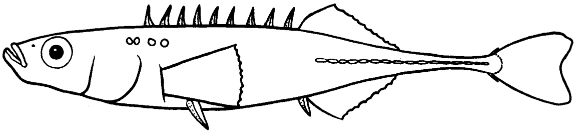
Family AULORHYNCHIDAE (290)—tubesnouts. Coastal marine; North Pacific.



Body elongate, with lateral bony scutes; series of 24–26 very short isolated dorsal spines, followed by a normal dorsal fin with about 10 soft rays; pelvic fin with one spine and four soft rays; caudal fin with 13 rays; four branchiostegal rays; circumorbital ring complete posteriorly; epineurals 0–3 (Johnson and Patterson, 1993, note that the epipleurals of acanthomorphs, except for *Polymixia,* are epineurals); vertebrae 52–56. Adult males of *Aulichthys* have a well-developed urogenital papilla. Maximum length 17 cm, attained in *Aulorhynchus flavidus.*

Two species, *Aulichthys japonicus* from Japan and Korea and *Aulorhynchus flavidus* from Alaska to California.

Family GASTEROSTEIDAE (291)—sticklebacks. Marine, brackish, and freshwater; Northern Hemisphere.



Body elongate or not, with lateral bony scutes (plates) or naked; series of 3–16 well–developed isolated dorsal spines (very rarely fewer than three) followed by a normal dorsal fin with 6–14 rays; pelvic fin (rarely absent) with one spine and one or two soft rays; caudal fin usually with 12 rays; three branchiostegal rays; circumorbital ring incomplete posteriorly; epineurals present; vertebrae 28–42. Maximum length about 18 cm, attained in *Spinachia spinachia.* Parental care is given by the males of all species. A high proportion of individuals of three species in certain localities fail to develop the pelvic skeleton.

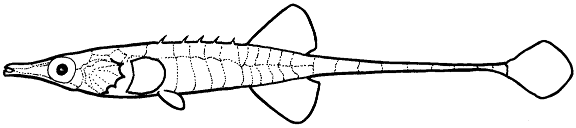
This family is famous for the numerous studies made of its species, especially in the fields of evolution, genetics, ethology, and physiology.

Five genera with, as a conservative figure (including species complexes), about eight species: *Spinachia spinachia* (Fifteenspine Stickleback), marine, Atlantic of northern Europe; *Apeltes quadracus* (Fourspine Stickleback), usually marine and brackish water, Atlantic coast of central North America; *Gasterosteus wheatlandi* (Blackspotted Stickleback), usually marine, Atlantic coast of central North America; *Gasterosteus aculeatus* complex (Threespine Stickleback), marine, anadromous, and freshwater, Atlantic and Pacific coastal areas of North America (specimens have been taken in the open North Pacific) and Eurasia and part of Arctic, seldom above 100 m elevation; *Pungitius pungitius* complex (Ninespine Stickleback), diadromous and freshwater, Atlantic, Pacific, and Arctic coastal areas of North America and Eurasia and across much of above continental areas up to about 600 m; *Pungitius platygaster,* primarily in the Black Sea to Aral Sea area; *Pungitius hellenicus* in Greece; *Culaea inconstans* (Brook Stickleback), freshwater, North America. Miocene *Gasterosteus* are known from eastern Siberia and California. Recent taxonomic studies include those by Keivany and Nelson (2000) and McLennan and Mattern (2001).

The recognition of only eight species in this family fails to account for the enormous diversity that exists. There are many taxonomic problems in the *Gasterosteus aculeatus* complex and the *Pungitius pungitius* complex. In the

Gasterosteus aculeatus complex, the taxonomic problems exist partly because of the extensive phenotypic variation that is present. Some very exciting problems deal with sympatric pairs of *Gasterosteus* in British Columbia, first studied in detail by J. D. McPhail (see Nelson et al., 2004:220, for references), diversity in forms in nearby localities studied over many years by T. E. Reimchen and M. A. Bell, and evolutionary studies on plate variation (e.g., cyclical variation), also by T. E. Reimchen. Three species have forms with and without the pelvic girdle occurring in sympatry (e.g., *Culaea* in Alberta documented by J. S. Nelson in 1969).

Family INDOSTOMIDAE (292)—armored sticklebacks. Freshwater; parts of Southeast Asia.



Body slender and covered with bony scutes; upper jaw not protrusible; opercle with five to seven spines; dorsal and anal fins each with six rays, usually five isolated spines preceding the dorsal fin; three pectoral radials; 22–24 pectoral fin rays; pelvic fin with four soft rays, no spine; gill filaments lobate; subopercle minute and interopercle present; parietals absent; six branchiostegal rays; no ribs; usually 21 vertebrae; swim bladder physoclistic. Maximum known length about 3.3 cm SL.

The systematic placement of the family in the Gasterosteoidei follows the conclusions of Britz and Johnson (2002) in their detailed anatomical study.

The first species, *Indostomus paradoxus,* was described in 1929 from Lake Indawgyi in Upper Myanmar.

One genus, *Indostomus,* and three species (Britz and Kottelat, 1999b).

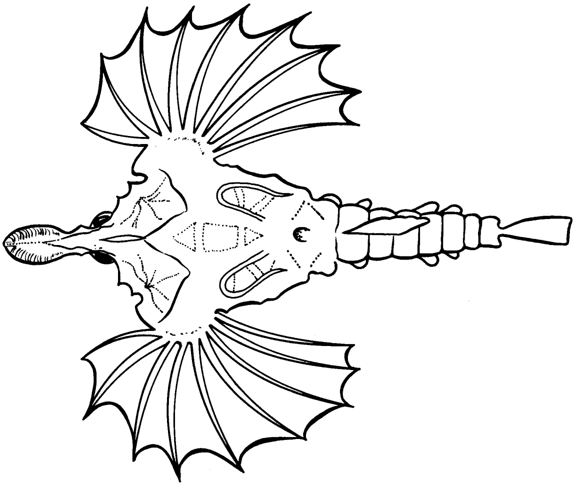
Suborder Syngnathoidei. Mouth small, at end of tube-shaped snout (except in the "finless" pipefish *Bulbonaricus,* whose adults lack even a short tubiform snout); pelvic fins, when present, abdominal; upper jaw not protractile; lachrymal usually present, other circumorbital bones usually absent; ribs absent; anterior 3–6 vertebrae elongate; aglomerular kidney in at least some. Members of the first infraorder—the pegasids, syngnathids, and solenostomids—share a similar-shaped gill filament, a unique lobate gill filament termed the lophobranch pattern (described by Johnson and Patterson, 1993). In these taxa and *Indostomus,* the gill filaments have fewer lamellae than in other teleosts, such as members of the infraorder Aulostomoida with the normal elongate gill filaments (described as comblike). These three families, which share a complete body armor of bony plates, may form a monophyletic group (see Johnson and Patterson, 1993, and modifications by Britz and Johnson, 2002, for a description of various characters shared in these groups).

Seven families with 62 genera and about 264 species.

Infraorder Syngnatha. Head and trunk encased in bony plates and tail encircled by bony rings; metapterygoid and postcleithrum absent; gill openings each a small hole on dorsolateral surface behind head; lachrymal large; gill filaments tufted or lobate; posttemporal co-ossified with cranium; hyoid apparatus short, with elongate branchiostegal rays; common feeding mechanism (with interopercle widely separated from reduced subopercle); articular processes of mobile vertebral centra absent (Pietsch, 1978c). In addition, all members have a small toothless mouth.

Superfamily Pegasoidea. T. W. Pietsch in a 1978 study concluded that pegasids are most closely related to the solenostomid-syngnathid lineage. He also believed them to be closely related to the lower Eocene *Ramphosus* of Italy and Denmark (and recognized the fossil family Ramphosidae in the same superfamily).

Family PEGASIDAE (293)—seamoths. Marine, rarely brackish water; tropical to temperate, Indo-West Pacific.

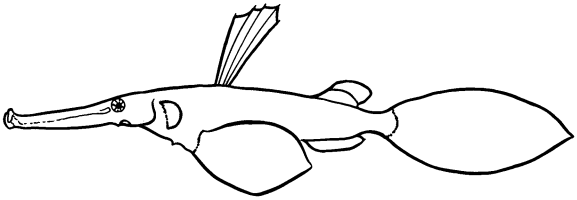


Body oddly shaped (broad and depressed), encased in bony plates; mouth beneath a long flattened rostrum (formed by fused elongate nasals), with an unusual mechanism for protrusion of the jaws; opercle and subopercle minute (widely separated from the interopercle), preopercle greatly enlarged; dorsal and anal fins short, opposite one another, each with five unbranched soft rays (spinous dorsal fin represented only by a horizontal pterygiophore); pectoral fins relatively large, horizontal, with 9–19 unbranched rays; pelvics abdominal, with one spine and two or three soft rays; caudal fin with eight unbranched rays; caudal peduncle quadrangular; five filamentous branchiostegal rays; supracleithrum absent; three circumorbital bones, lachrymal largest; no swim bladder; 19–22 vertebrae (anterior six of the seven abdominal ones elongate). Maximum length 14 cm, perhaps up to 18 cm, attained in *Pegasus volitans.* Seamoths occur in coastal waters, up to 150 m in depth.

Two genera, *Eurypegasus* (two species, with eight or nine tail rings and eyes visible in ventral view) and *Pegasus* (three species, with 11 or more tail rings and eyes not visible in ventral view), with five species (documented in a 1989 study by W. A. Palsson and T. W. Pietsch).

Superfamily Syngnathoidea. Branchiostegal rays 1–3; no lateral line; anterior three vertebrae elongate.

Family SOLENOSTOMIDAE (294)—ghost pipefishes. Marine; tropical Indo-West Pacific (from South Africa and the Red Sea to Fiji).



Body short, compressed and with large stellate bony plates; two separate dorsal fins, the first with five long feeble spines and the second with 17–22 unbranched soft rays on an elevated base; anal fin with 17–22 unbranched rays; pelvic fins relatively large, with one spine and six soft rays, opposite spinous dorsal; gill openings moderately large; females with brood pouch formed by the pelvics (the females brood the eggs, not the males as in syngnathids); circumorbital bones absent; vertebrae 32–34. Maximum length up to 16 cm.

One genus, *Solenostomus*, with four or five species (Orr et al., 2002).

Family SYNGNATHIDAE (295)—pipefishes and seahorses. Marine and brackish water, some species in freshwater; Atlantic, Indian, and Pacific.

Body elongate and encased in a series of bony rings; one dorsal fin, usually with 15–60 soft rays, anal fin very small and usually with 2–6 rays, and pectoral fin usually with 10–23 rays (the dorsal, anal, and pectoral fins may be absent in adults of some species, and all three are absent in adults of *Bulbonaricus*); no pelvic fins; caudal fin absent in some; tail (caudal peduncle) may be prehensile and employed for holding on to objects when caudal fin is absent; gill openings very small; supracleithrum absent; kidney present only on right side, aglomerular. Some species are very colorful. Maximum length about 65 cm.

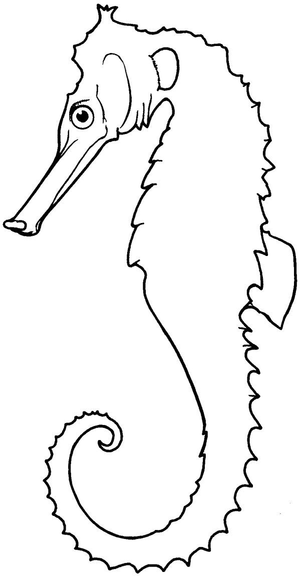
Syngnathids are usually confined to shallow water. Most species occur in warm temperate to tropical waters but some pipefishes range into relatively cool water, occurring from southwestern Alaska to Tierra del Fuego in the Americas. At least 18 species are known only from freshwater (streams and lakes, most in the genus *Microphis*), about 37 are euryhaline (entering brackish water from either the oceans or rivers or both), and the rest are marine. Males care for the eggs, which are attached to them by the female in a special area in the undersurface of the trunk or tail, which may or may not be developed into a pouch. Two groups, once given taxonomic rank, may be recognized based on whether the brood organ is on the tail (the Urophori or syngnathines), as in most genera and including seahorses and the ghost pipefishes, or on the trunk (the Gastrophori or doryrhamphines). Some genera such as *Acentronura* are, to a certain extent, morphological intermediates, if not evolutionary links, between pipefishes and seahorses. The intermediate forms and the various genera of seadragons of Australia, which resemble seahorses but reach a larger size and have leaflike appendages, are placed in the pipefish subfamily.

Two subfamilies with 52 genera and about 232 species.

SUBFAMILY SYNGNATHINAE (PIPEFISHES). Marine and brackish water, some in freshwater.

Fifty-one genera—e.g., *Acentronura, Anarchopterus, Bhanotia, Bryx, Bulbonaricus, Campichthys, Choeroichthys, Corythoichthys, Cosmocampus, Doryichthys, Doryrhamphus, Enneacampus, Festucalex, Halicampus, Heraldia, Hippichthys, Leptonotus, Lissocampus, Micrognathus, Microphis, Nerophis, Nannocampus, Penetopteryx, Phyllopteryx, Siokunichthys, Solegnathus, Syngnathoides,* and *Syngnathus*—with about 196 species (Fritzsche, 2003; Fritzsche and Vincent, 2003; Kottelat, 2000a).

SUBFAMILY HIPPOCAMPINAE (SEAHORSES). Marine.

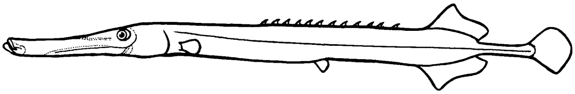


One genus, *Hippocampus,* with about 36 species (e.g., Kuiter 2001, 2003; Lourie et al., 1999; Lourie and Randall, 2003).

Infraorder Aulostomoida. Teeth small or absent; lateral line well developed to absent; usually four or five (rarely three) branchiostegal rays; gills comblike (not lobate); postcleithrum present.

Superfamily Aulostomoidea. Anterior four vertebrae elongate; three median, well-developed bones dorsally behind head (nuchal plates); usually six (rarely five) soft pelvic rays.

Family AULOSTOMIDAE (296)—trumpetfishes. Tropical marine; Atlantic and Indo-Pacific.

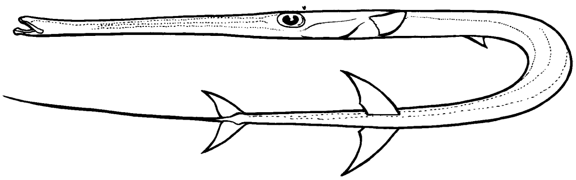


Body compressed, elongate, and scaly; fleshy barbel at tip of lower jaw; series of 8–12 isolated dorsal spines followed by a normal dorsal fin of 22–27 soft rays; anal rays 23–28; caudal fin rounded; anus far behind pelvics; lateral line well developed; abdominal vertebrae with two transverse processes of equal size (or a divided process); body musculature with a network of bony struts that forms an interwoven pattern (observed in *Aulostomus chinensis*); vertebrae 59–64 (24–26 + 35–38).

Trumpetfishes are predators and are usually seen on reefs. They often swim alongside larger fish or lie with their bodies at odd angles such as vertical with the head downward. Maximum length up to 80 cm.

One genus, *Aulostomus,* probably with three species (e.g., Fritzsche, 2003).

Family FISTULARIIDAE (297)—cornetfishes. Tropical marine; Atlantic, Indian, and Pacific.



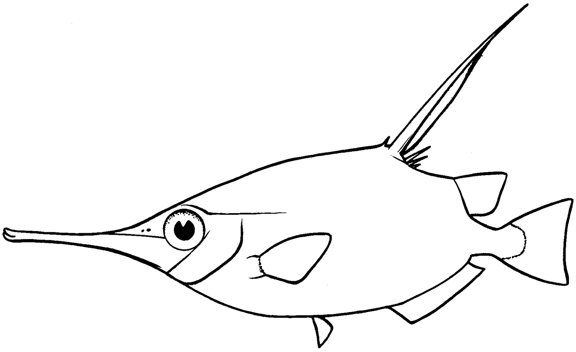
Body depressed, elongate, and naked or with minute prickles, and linear series of scutes (no scales); no barbel on jaw; no dorsal spines; anal and dorsal fins each with 13–20 soft rays; caudal fin forked with elongate filament produced by middle two caudal rays; anus short distance behind pelvic fins; lateral line well developed, arched anteriorly almost to middle of back and continuing onto caudal filament; abdominal vertebrae with two transverse processes but the posterior ones reduced; vertebrae 76–87.

Cornetfishes usually inhabit shallow waters of tropical and subtropical seas. They are predatory on other fishes, feeding both in open water and in coral reefs. Their long tubular snout, which functions as a pipette, is an excellent adaptation for feeding among reefs. Maximum length up to 1.8 m, attained in *Fistularia tabacaria,* usually less than 1 m.

One genus, *Fistularia,* with four species (e.g., Fritzsche, 2003).

Superfamily Centriscoidea. Anterior five or six vertebrae elongate; pelvic fins with one spine and four soft rays. The two included families are recognized as subfamilies of Centriscidae by some (e.g., Eschmeyer, 1998).

Family MACRORAMPHOSIDAE (298)—snipefishes. Tropical and subtropical marine; Atlantic, Indian, and Pacific.

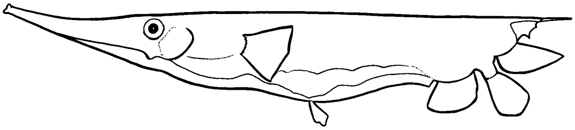


Body compressed, deep, and usually with bony plates on each side of back; no barbel on jaw; 4–8 dorsal spines, second spine very long, all joined by a membrane; second dorsal fin has about 11–19 soft rays; lateral line present or absent. Maximum length up to 30 cm.

First known in the fossil record from the Upper Cretaceous, the earliest record of any syngnathiform. The species involved, *Gasterorhamphosus zuppichinii,* resembles *Macroramphosus* in body shape but, among various differences, has some characters suggesting an affinity with the Gasterosteoidei.

Three genera, *Centriscops* (1), *Macroramphosus* (about 5), and *Notopogon* (5), with about 11 species (e.g., Duhamel, 1995; Fritzsche, 2003).

Family CENTRISCIDAE (299)—shrimpfishes. Marine; Indo-Pacific.



Extremely compressed, razorlike body with sharp ventral edge; body almost entirely encased by thin bony plates that are expansions of the vertebral column; first dorsal spine long and sharp at extreme end of body, followed by two shorter spines; soft dorsal fin and caudal fin displaced ventrally; no lateral line; mouth toothless. Swimming is in a vertical position, snout down. Maximum length up to 15 cm.

As with many of the other gasterosteiform families, there are many Tertiary fossils known. Fossil centriscids are known from the Eocene to Pliocene and fossil *Aeoliscus* are known from Oligocene-Miocene deposits of Europe (Parin and Micklich, 1996).

Two genera, *Aeoliscus* and *Centriscus*, with about four species.

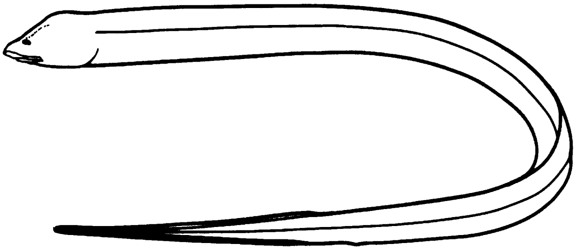
Order SYNBRANCHIFORMES (56)—swamp eels. Body elongate; pelvic fins absent; gill openings confined to lower half of body; ectopterygoid enlarged; endopterygoid reduced or absent; premaxillae nonprotrusible and without ascending process.

The family composition of this order and its placement follows Johnson and Patterson (1993), Britz et al. (2003), and work by W. A. Gosline in 1983 and R. A. Travers in 1984. The synbranchiforms are thought to form a monophyletic group with the mugilomorphs, atherinomorphs, gasterosteiforms, and elassomatids (the smegmamorphs) by Johnson and Patterson (1993).

Three families, 15 genera, and about 99 species. All except about three species occur in freshwater.

Suborder Synbranchoidei

Family SYNBRANCHIDAE (300)—swamp eels. Tropical and subtropical freshwater, some species occasionally in brackish water (rarely marine); western Africa, Liberia, Asia, Indo-Australian Archipelago, Mexico, and Central and South America.



Body eel-like; pectoral and pelvic fins absent (pectorals present in early development of some species); dorsal and anal fins vestigial (reduced to a rayless ridge); caudal fin small (in *Macrotrema caligans*) or vestigial to absent; scales absent except in the species of the subgenus *Amphipnous* of *Monopterus*; eyes small (some species functionally blind with eyes sunken below skin); anterior and posterior nostrils widely separated; fourth aortic arch complete; palatoquadrate articulating in two places, making these the only teleosts with an "amphistylic" jaw suspension; gill membranes united; small gill opening as slit or pore under head or throat (*Macrotrema* has normal size gill openings continuous with each other under throat); branchiostegal rays 4–6; swim bladder absent; ribs absent; vertebrae 98–188 (51–135 abdominal). Most species are protogynous hermaphrodites. As noted by Lauder and Liem (1983), these are among the most highly specialized teleosts in a large number of features.

Most species are capable of air breathing. The cuchias of the genus *Monopterus* have paired lunglike suprabranchial pouches (with respiratory function) and the partially scaled body. These species are highly evolved as airbreathing fishes. Many have burrowing habits, while some live in caves. *Ophisternon*, as studied by D. E. Rosen in 1975, has a highly disjunct distribution in the pantropics (e.g., one species is found in isolated centers in northern South America, northern Central America and southern Mexico, and Cuba). Maximum length almost 1 m, attained in *Ophisternon aenigmaticum* of the New World.

The major revision of this family by D. E Rosen and P. H. Greenwood in 1976 forms the basis of the information here. They recognized two subfamilies of synbranchids—Macrotreminae (for *Macrotrema caligans*) and Synbranchinae (for the other species).

Four genera, *Macrotrema* (1, fresh and brackish water, in Thailand and Malay Peninsula), *Ophisternon* (6, two Americas and four Eurasia), *Synbranchus* (2, Mexico and Central and South America), *Monopterus* (8, Liberia and Pakistan to Japan), with 17 species (e.g., Bailey and Gans, 1998).

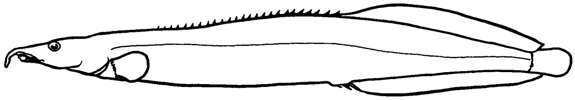
Suborder Mastacembeloidei. Body elongate (eel-like); no pelvic fins; dorsal and anal fins continuous to or continuous with the small caudal fin; posttemporal absent, pectoral girdle (supracleithrum) attached to the vertebral column by a ligament; no air duct to swim bladder (physoclistic); no posttemporal bone.

Family CHAUDHURIIDAE (301)—earthworm eels. Freshwater; northeastern India through Thailand to Korea (including parts of Malaysia and Borneo).

No dorsal or anal fin spines; body naked (*Chendol* has scales); no lateral line (except in *Chendol*); rostral appendage lost and dorsal, anal, and caudal fins fused in *Nagaichthys* (pectoral fin with only one ray) and *Pillaia*; endopterygoid and epineurals absent; basisphenoid present. Maximum length about 8 cm.

Six genera, *Bihunichthys* (1), *Chaudhuria* (2), *Chendol* (2), *Garo* (1), *Nagaichthys* (1), and *Pillaia* (2), with nine species (e.g., Kottelat and Lim, 1994; Kottelat, 2000a; Kullander et al., 2000; Britz and Kottelat, 2003).

Family MASTACEMBELIDAE (302)—spiny eels. Freshwater; tropical Africa and through Syria to Malay Archipelago, China, and Korea.



Series of 9–42 isolated spines preceding the dorsal fin of 52–131 soft rays; anal fin usually with two or three spines and 30–130 soft rays; fleshy rostral appendage present; body covered with small scales (naked in about three species); no basisphenoid; vertebrae about 66–110. Maximum length up to 0.9 m. In some places mastacembelids are regarded as an excellent food fish; they are occasionally kept as an aquarium fish. They are found in a wide variety of habitats. Some species burrow in the substrate during the day or for certain months and have been found buried in soil in drying ponds.

Two subfamilies, not given here, were established by R. A. Travers in 1984 (see also Kottelat and Lim, 1994; Britz, 1996; Vreven and Teugels, 1996) as follows: Mastacembelinae (caudal fin distinct, rays either not confluent with dorsal and anal fin membranes or they extend posterior to and remain distinct from these fins, for *Macrognathus*, *Mastacembelus*, and *Sinobdella*, in southern Asia) and Afromastacembelinae (caudal fin rays confluent with posterior rays of dorsal and anal fins, for *Aethiomastacembelus* and *Caecomastacembelus*, in Africa).

Five genera, *Aethiomastacembelus*, *Caecomastacembelus*, *Macrognathus*, *Mastacembelus*, and *Sinobdella* (1, synonym *Rhynchobdella*) (Kottelat and Lim, 1994; Britz, 1996), with about 73 species (e.g., Britz, 1996; Arunkumar and Singh, 2000; Vreven, 2004; Vreven and Teugels, 1996, 1997).

Order SCORPAENIFORMES (57)—mail-cheeked fishes. This order contains the "mail-cheeked" fishes, distinguished by the suborbital stay, a posterior extension of the third infraorbital bone (counting the lachrymal), which extends across the cheek to the preoperculum and is usually firmly attached to that bone (it is variously developed and absent in the Pataecidae). Head and body tend to be spiny or have bony plates; pectoral fin usually rounded, membranes between lower rays often incised; caudal fin usually rounded (occasionally truncate, rarely forked).

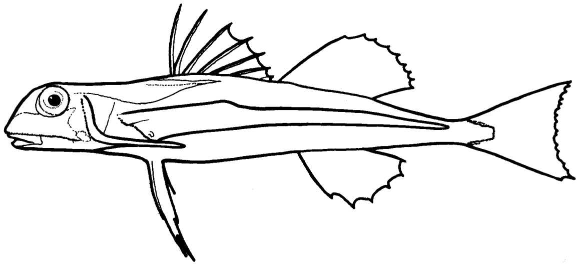
Twenty-six families with 279 genera and about 1,477 species. About 60 species, all cottoids, are confined to freshwater. The classification and placement of this order is very provisional. As noted by Johnson and Patterson (1993), there is no basis for considering it as either i) a preperciform sister group to the remaining three orders or ii) a part of the perciform assemblage, perhaps still as a monophyletic derivative of a paraphyletic Perciformes (it is listed after the perciforms by some authors). In regarding the Scorpaeniformes as a perciform derivation, Mooi and Gill (1995) and Mooi and Johnson (1997) gave it subordinal status with the Perciformes. Imamura and Yabe (2002) also presented reasons for regarding this order as a suborder of perciforms. While I agree that such a placement seems sound, I make no formal change here pending, perhaps in the near future, a more comprehensive review of other changes that should also be made (i.e., also including two other perciform derivatives, currently treated as orders, the Pleuronectiformes and Tetraodontiformes).

Of the suborders, the Dactylopteroidei is sequenced first. Johnson and Patterson (1993), in their detailed and critical analysis of percomorphs, recognized the Dactylopteridae in a separate order and forming a monophyletic group with, in an unresolved polychotomy, the Scorpaeniformes, Perciformes, Pleuronectiformes, and Tetraodontiformes. The suborders are undefined in terms of postulated shared derived characters, and their recognition serves only to group families thought to bear a closer relationship with one another than with those placed in other suborders based on overall similarities. The arrangement of families and family boundaries is subject to much disagreement.

The classification of the Scorpaeniformes is complex and controversial. Many detailed studies show that the scorpaeniforms are probably not monophyletic and that our present classification (at least that given here) does not reflect the phylogeny. However, there is no comprehensive and convincing classification to replace it. Suggestions for some needed changes are given in Ishida (1994), Imamura and Shinohara (1998), Mandrytsa (2001), Imamura and Yabe (2002), Imamura (1996, 2004), and Smith and Wheeler (2004). Imamura and Yabe (2002) and Smith and Wheeler (2004) proposed major changes to a polyphyletic Scorpaeniformes. For example, Imamura and Yabe (2002) supported placing a new suborder Scorpaenoidei aligned with Serranidae in the Perciformes and aligning the suborder Cottoidei with the Zoarcoidei. Mandrytsa (2001) added many new taxa and placed the family Pataecidae in the Perciformes, in its own suborder Pataecoidei. Mooi and Johnson (1997) suggested that the trachinoid family Champsodontidae is a scorpeaniform (which they rank as the perciform suborder Scorpaenoidei); this was not supported in the molecular study of Smith and Wheeler (2004). It should be clear, and let me repeat, the classification of the Scorpaeniformes is complex and controversial. Even without the conflicts, a synthesis of all proposals is beyond the scope of this edition.

Suborder Dactylopteroidei. The placement of this taxon is controversial. Johnson and Patterson (1993), in not finding any evidence of scorpaeniform relationship, placed it in its own order next to the Scorpaeniformes. See also the detailed study of Imamura (2000), who found 20 synapomorphies showing a monophyletic relationship with the perciform family Malacanthidae (the subsequent redefined percoid family Dactylopteridae was divided into four subfamilies, of which the dactylopterids are one). However, this realignment was not supported in the molecular study of Smith and Wheeler (2004). Until additional confirmatory studies are done, I prefer to retain it where placed in Nelson (1994).

Family DACTYLOPTERIDAE (Cephalacanthidae) (303)—flying gurnards. Marine tropical; Indo-Pacific and Atlantic.



Large, blunt, bony head (with spines and keels); body covered with scutelike scales; tremendously enlarged and colorful pectoral fins with inner rays free, total of 28–37 rays; two free spines (the first may be on the nape) before the two dorsal fins; pelvic fins thoracic, each with one spine and four soft rays; no lateral line; 22 vertebrae. Maximum length about 50 cm.

These benthic fishes, which superficially resemble triglids, produce sounds by stridulation by using the hyomandibular bone and "walk" on the sea floor by alternately moving the pelvic fins. The common name arose in the belief that because of their large pectoral fin they could fly or at least glide for short distances. However, they seldom, if ever, leave the substrate and there is no evidence that they ever leave the water and glide.

Two genera, *Dactyloptena* (Indian and western and central Pacific) and *Dactylopterus* (Atlantic), with about seven species (e.g., W. N. Eschmeyer in Smith and Heemstra, 1986; Eschmeyer, 1997).

Suborder Scorpaenoidei. Contains the world's most venomous fishes. Usually brightly colored.

In splitting the present family Scorpaenidae, Ishida (1994) recognized the following families in the suborder Scorpaenoidei (also listed in Imamura and Shinohara, 1996): Sebastidae, Setarchidae, Neosebastidae (the latter two being sister taxa), Scorpaenidae, Apistidae, Tetrarogidae (the latter two being sister taxa), Synanceiidae, Congiopodidae (the latter two being sister taxa), Gnathanacanthidae, Aploactinidae, and Pataecidae (the latter two being sister taxa), with the Caracanthidae, of unknown relationships, not being included. Imamura (2004), in his new classification of his superfamily Scorpaenoidea, included the following 20 families (and suggested more might be recognized): Sebastidae (paraphyletic), Sebastolobidae (includes only *Sebastolobus*), Scorpaenidae (included the Pteroini, Setarchidae, and *Trachyscorpia* but did not recognize subfamilies or tribes), Apistidae, Tetrarogidae, Synanceiidae (with four subfamilies), Aploactinidae (with three subfamilies), Congiopodidae, Gnathanacanthidae, Pataecidae, Caracanthidae, Eschmeyeridae, Neosebastidae, Plectrogenidae, Parabembridae, Bembridae, Triglidae, Peristediidae, Hoplichthyidae, and Platycephalidae. It should be noted that this includes families placed in the suborder Platycephaloidei. He compared his cladistic results with those of others (e.g., Mandrytsa, 2001), but did not have all families given above included in his study and therefore could provide no independent confirmation of the conclusions of others (this is one reason why I do not split the present family Scorpaenidae).

While I fully acknowledge that the present arrangement, somewhat changed from Nelson (1994), is not satisfactory, I prefer not to recognize numerous additional families (by, for example, raising existing subfamilies to family status), where workers disagree on relationships, until other broad-based studies are done using all genera. The studies noted, in making important contributions, show just how poorly we understand relationships. Users intent on recognizing additional families (as, for example, in splitting the Scorpaenidae) are free to choose between alternative proposals; I prefer to await more research. While systematic researchers should present the implications of their phylogenetic conclusions to classification, my general advice is that for general use, such as for field guides, when conflicting information exists, it is better to not follow some system that may prove unstable and soon change. On the other hand, all workers in comparative biology will want to be aware of various phylogenetic hypotheses and consult the original research.

Six families with about 82 genera and 473 species.

Family SCORPAENIDAE (304)—scorpionfishes (rockfishes). Marine (rarely in freshwater); all tropical and temperate seas.

Body compressed; head usually with ridges and spines, one or two opercular spines (usually two divergent) and three to five preopercular spines (usually five); suborbital stay usually securely fastened to preopercle (no attachment in some); scales, when present, usually ctenoid; dorsal fin usually single (often with a notch), usually with 11–17 spines and 8–17 soft rays; anal fin with 1–3 spines (usually three) and 3–9 soft rays (usually five); pelvic fin with one spine and 2–5 soft rays (usually five); pectoral fin well developed (11–25 rays), rarely with one to three free lower rays; gill membranes free from isthmus; swim bladder absent in some (e.g., *Plectrogenium* and *Sebastolobus*); vertebrae 24–31. Venom gland in dorsal, anal, and pelvic spines. Most have internal fertilization, and some give birth to live young (e.g., *Sebastes*). Some lay eggs on a gelatinous balloon, and *Scorpaena guttata* is reported to have an egg balloon that may be as much as 20 cm in diameter. Many species are commercially important.

At least 56 genera with about 418 species (e.g., Poss and Eschmeyer, 2003). Most species are in the Indian and Pacific oceans. For comments on the classification see above under suborder Scorpaenoidei. The sequencing of the following subfamilies, recognized as families from some workers as noted above, is based, in part, on conclusions in some of the works listed above. Extensive work over many decades has been done on this family by W. N. Eschmeyer, with much work also by S. G. Poss and more recently by H. Motomura.

SUBFAMILY SEBASTINAE. Imamura (2004) recognized *Trachyscorpia* with the Scorpaenini (as here used) and placed *Adelosebastes* in his paraphyletic Sebastidae (as he states, it would be cladistically reasonable to have each genus treated as a separate family, something he and certainly not I were prepared to do), leaving only *Sebastolobus* in his Sebastolobidae.

Seven genera and about 133 species. Extensive information is given on the members of this subfamily, known as rockfishes, in the northeast Pacific by Love et al. (2002).

TRIBE SEBASTINAE. Four genera, *Helicolenus*, *Hozukius*, *Sebastes*, and *Sebastiscus*, with about 128 species. *Helicolenus* and *Sebastes* occur in all oceans, whereas *Sebastiscus* and *Hozukius* occur only in the western Pacific. Kai et al. (2003)

suggested that *Helicolenus*, *Hozukius* are more closely related to *Sebastes* than to *Sebastiscus*. The live-bearing genus *Sebastes* is the largest in the family with about 110 species (almost all of them occurring in the North Pacific).

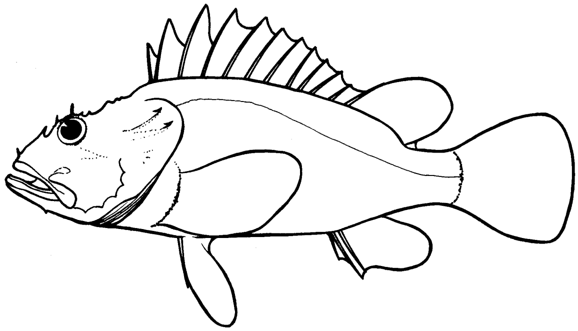
TRIBE SEBASTOLOBINAE. Three genera, *Adelosebastes*, *Sebastolobus* (with 15–17 dorsal spines, highest for the family), and *Trachyscorpia*, with five species.

SUBFAMILY SETARCHINAE. Three genera, *Ectreposebastes*, *Lioscorpius*, and *Setarches*, with five species. Imamura (2004) recognized this subfamily with the Scorpaenini (as here used).

SUBFAMILY NEOSEBASTINAE. Two genera, *Maxillicosta* (5) and *Neosebastes* (12), with 17 species (Motomura, 2004a). As noted by Motomura (2004a), Ishida (1994) inferred that his families Neosebastidae and Setarchidae had a sister relationship and were secondarily divided from other scorpaenids. Imamura (1996), how-ever, suggested that *Setarches* was more closely related to *Pontinus* and *Scorpaena* (tribe Scorpaenini herein), *Neosebastes* being sister to a clade comprising a species of Tetraroginae, two genera of Synanceiinae, an Aploactinidae, and an Apistinae. Smith and Wheeler (2004), in a molecular analysis, showed that *Maxillicosta* and *Congiopodus* had a sister relationship. As Motomura (2004a) concluded, the systematic position and relationships of the family Neosebastidae (as he recognized it), still lacks an established basis. Imamura (2004) regarded this subfamily (at the family level) as sister to the Platycephaloidei (as given here) and further studies await with interest.

SUBFAMILY SCORPAENINAE. At least 20 genera and about 185 species.

TRIBE SCORPAENINI



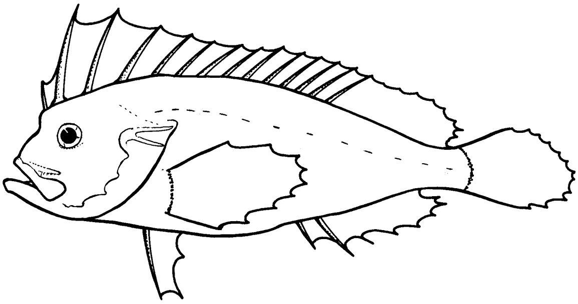
At least 15 genera (e.g., *Idiastion*, *Iracundus*, *Neomerinthe*, *Parascorpaena*, *Phenacoscorpius*, *Pontinus*, *Pteroidichthys*, *Pteropelor*, *Rhinopias*, *Scorpaena*, *Scorpaenodes*, *Scorpaenopsis*, *Sebastapistes*, and *Taenianotus*) with about 165 species (e.g., Randall and Eschmeyer, 2002; Randall and Greenfield, 2004).

TRIBE PTEROINI. Five genera, *Brachypterois, Dendrochirus, Ebosia, Parapterois,* and *Pterois* (highly venomous lionfishes and turkeyfishes), with about 20 species.

SUBFAMILY APISTINAE.

Three monotypic genera, *Apistops, Apistus,* and *Cheroscorpaena.* Members of this taxon have one or three free lower pectoral rays and a bilobed swim bladder.

SUBFAMILY TETRAROGINAE (SAILBACK SCORPIONFISHES OR WASP FISHES)



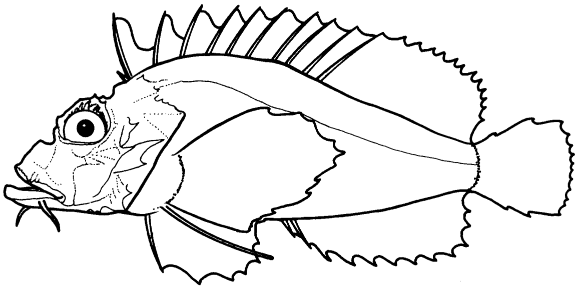
At least 11 genera (e.g., *Ablabys, Amblyapistus, Centropogon, Cottapistus, Neocentropogon, Notesthes, Ocosia, Paracentropogon, Tetraroge,* and *Vespicula*) with about 38 species. Tetrarogines are extremely venomous. They show some resemblance to the Aploactinidae. *Notesthes robusta* of coastal eastern Australia is primarily a freshwater fish.

SUBFAMILY SYNANCEINAE.

Body scaleless (except for buried scales along the lateral line and other parts of the body), usually covered with skin glands; head large; swim bladder usually absent; venom glands present near base of hypodermiclike dorsal fin spines. The neurotoxin of these fishes is the most deadly of the fish venoms and can be fatal to humans. The fish is particularly dangerous because it usually rests in a half-buried position, looking much like a rock.

About nine genera and about 35 species.

TRIBE MINOINI. Lowermost ray of pectoral fin separated from the other 11 rays, fitted at its tip with a peculiar "cap"; body smooth; dorsal fin with 8–12 spines and 10–14 soft rays (4 spines and 18 soft rays in one species); anal fin with two spines and 7–11 soft rays; pelvic fin with one spine and five soft rays; soft fin rays unbranched; swim bladder present or absent; vertebrae 24–27. Maximum length usually 15 cm. Members of this group occur on mud and sand bottoms from about 10–420 m in the western Pacific and Indian oceans. They are thought to use the free pectoral ray for "walking" on the bottom.



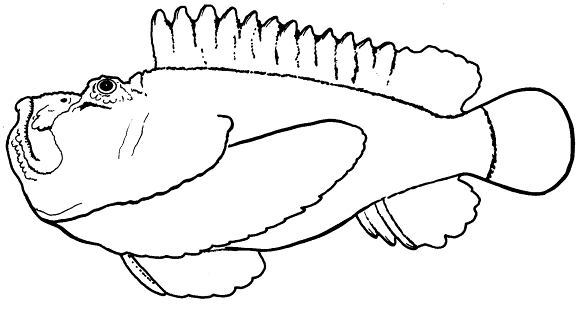
One genus, *Minous,* with 11 species.

TRIBE CHORIDACTYLINI. Two (*Inimicus*) or three (*Choridactylus*) lowermost pectoral rays separated from rest; body often with warts or lumps (caused by buried scales); dorsal fin with 12–18 spines and 5–10 soft rays; anal fin with two spines and 8–13 soft rays; pelvic fin with one spine and five soft rays; most soft fin rays branched; vertebrae 26–30. Members of this group occur on sand and silty bottoms from near shore to about 90 m in the western Pacific and Indian oceans. Imamura (2004) placed the two genera in separate subfamilies.

Two genera, *Inimicus* with 10 species and *Choridactylus* with four species (e.g., Poss and Mee, 1995).

TRIBE SYNANCEINI (STONEFISHES). No free pectoral rays; skin glands present (appearing as "warts" in most species) and usually scattered over the body; dorsal fin with 11–17 spines and 4–14 soft rays; anal fin with 2–4 spines and 4–14 soft rays; pelvic fin with one spine and 3–5 soft rays; pectoral fin rays 11–19; vertebrae 23–30.

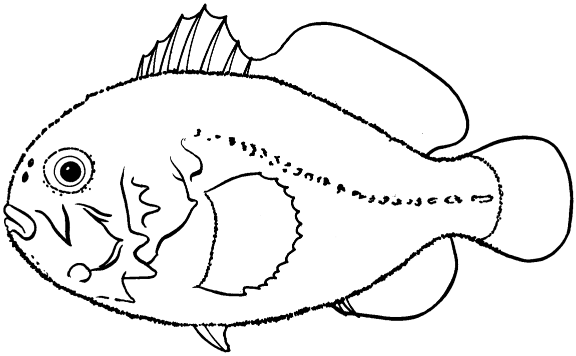
Two species, *Erosa erosa* (Japan to Australia) and *Dampierosa daruma* (northwestern Australia), have a terminal mouth that is slightly oblique and lateral eyes that are directed outward. The remaining species have a vertical or superior mouth and dorsal eyes that are directed outward and upward or only upward. Some species are known from rivers.



Six genera, the monotypic *Erosa*, *Dampierosa*, *Pseudosynanceia*, *Leptosynanceia*, and *Trachicephalus* and *Synanceia* (with five species), with a total of 10 species.

SUBFAMILY PLECTROGENINAE. One genus, *Plectrogenium*, with two species. There is good evidence showing a relationship with the Platycephaloidei (Imamura, 1996, 2004).

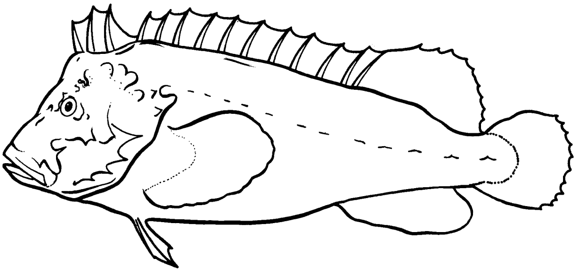
Family CARACANTHIDAE (305)—orbicular velvetfishes. Marine; Indian and Pacific.



Body oval, extremely compressed, and covered with small rough papillae; mouth small and terminal; one dorsal fin with a notch, origin on nape, with 6–8 spines and 11–14 soft rays; anal fin with two spines and 11–14 soft rays; pectoral fins with 12–15 rays; pelvic fins inconspicuous, with one spine and two or three small soft rays; gill openings restricted to sides; scales below the dorsal fin base and on the dorsal surface of the head (the latter are minute and bear a single spine) and tubelike scales on the lateral line; vertebrae 24. Maximum length only 7 cm.

One genus, *Caracanthus*, with about four species.

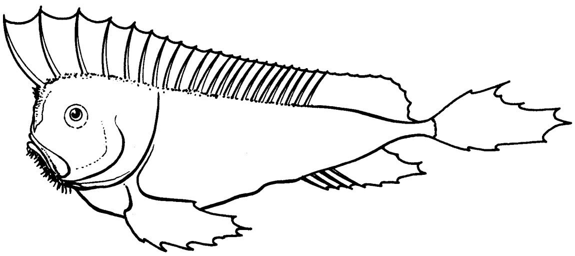
Family APLOACTINIDAE (306)—velvetfishes. Marine; primarily coastal parts of western Pacific and Indian oceans.



Body usually covered with modified, prickly scales giving a velvety appearance (some species lack the prickles and have a smooth skin); head armed with knoblike lumps (rarely with pungent spines); all fin rays unbranched; anal fin spines usually indistinct (rarely pungent) or absent; origin of dorsal fin far forward, above eye or almost so (except in *Adventor* and *Peristrominous*); anterior 3–5 dorsal fin spines usually divergent, either elevated or largely devoid of connecting membrane; four species with three or four anterior spines forming a separate fin; pelvic fin with one spine and two or three soft rays; most species with fleshy extension on the anterior isthmus; palatine teeth absent; no gill slit behind the last arch; vertebrae 24–33. A species of the South China Sea, *Prosoproctus pataecus* is unique among scorpaenoid fishes in having the anus far forward, immediately behind the pelvic fin base. Most species occur in the Indonesian and Australian regions.

About 17 genera (e.g., *Acanthosphex, Adventor, Aploactis, Aploactisoma, Bathyaploactis, Cocotropus, Erisphex, Kanekonia, Karumba, Matsubarichthys, Paraploactis, Peristrominous, Prosoproctus, Ptarmus, Sthenopus,* and *Xenoploactis*) with about 38 species (e.g., Imamura and Shinohara, 2003). Three subfamilies are recognized by Mandrytsa (2001) and Imamura (2004), Aploactininae, Bathyaploactininae, and Matsubarichthyinae.

Family PATAECIDAE (307)—Australian prowfishes. Marine; Australia.

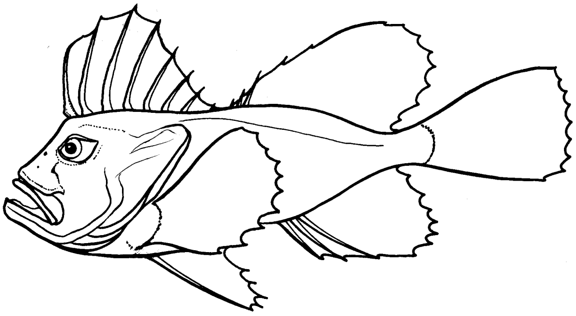


No pelvic fins; very long continuous dorsal fin extending from head to tail (connected with or free from caudal fin), with 19–25 spines and 7–17 soft rays; anal fin with 5–11 spines and 3–7 soft rays; pectoral fin with eight rays; all fin rays unbranched; body scaleless (smooth or with tubercles or papillae); fleshy extension on the anterior isthmus; suborbital stay absent; vertebrae 34–44. Maximum length 30 cm. The modifier "Australian" has been added to the common name of the family in order to avoid confusion with the northern prowfish, a zaprorid.

Mandrytsa (2001) placed this family in the Perciformes, in its own suborder Pataecoidei.

Three genera, each probably monotypic, *Aetapcus, Neopataecus,* and *Pataecus,* with three species.

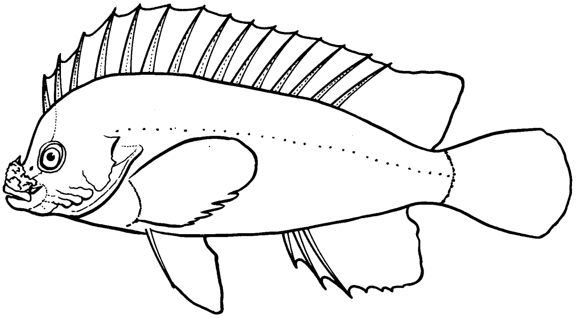
Family GNATHANACANTHIDAE (308)—red velvetfishes. Marine; southern Western Australia, South Australia, Victoria, and Tasmania.



Subrectangular fleshy pad in intermandibular area; pelvic fins present, with one spine and five soft rays; two separate dorsal fins of about equal length, the first with seven spines, the second with three spines and 8–10 soft rays; anal fin with three spines and eight or nine soft rays; pectoral fin with 10–12 rays; body scaleless, with soft skin; two large spines on opercle, may be concealed by skin; vertebrae 28–30. The spines can inflict painful wounds. Maximum length 30 cm.

One species, *Gnathanacanthus goetzeei.*

Family CONGIOPODIDAE (309)—racehorses (pigfishes or horsefishes). Marine; Southern Hemisphere.



Snout relatively long; body without scales, skin sometimes granular; only one nostril on each side; gill opening reduced, above pectoral base; lateral line usually well developed; dorsal fins joined (separate in *Zanclorhynchus*), with 8–21 spines and 8–14 soft rays; anal fin with 0–3 spines and 5–10 soft rays; pectoral fin with 8–12 rays; vertebrae 28–39. Maximum length about 80 cm.

Species of this family tend to be benthic and occur up to 500 m in depth.

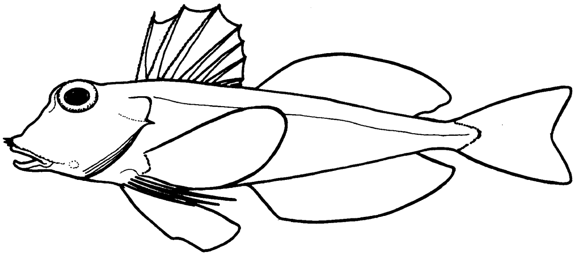
Mandrytsa (2001) placed *Alertichthys* and *Zanclorhynchus* in their own family, Zanclorhynchidae (placing Congiopodidae and Zanclorhynchidae in their own suborder Congiopodoidei). *Perryena* was placed in a new group (his Neocentropogoninae) in the Tetraroginae.

Four genera, *Congiopodus* with six species and the monotypic *Alertichthys*, *Perryena*, and *Zanclorhynchus*, with nine species.

Suborder Platycephaloidei. Body elongate; head depressed, usually with ridges and spines; two separate dorsal fins; pelvic fins widely separated, with one spine and usually five soft rays (as few as three in *Hoplichthys*); anal fin with 0, 1, or 3 spines and 5–18 soft rays; swim bladder present or absent; vertebrae 26 or 27. Imamura (1996) revised this taxon, but all suggestions have not yet been adapted.

Five families with 38 genera and about 226 species. The families Triglidae and Peristediidae are included in this lineage following Imamura (1996). See below under Bembridae for the possible recognition of two additional families, Parabemdridae and Plectrogenidae. This suborder is not recognized by Imurara (2004) and that study should be consulted for an alternative classification (see above under suborder Scorpaenoidei).

Family TRIGLIDAE (310)—searobins (gurnards). Marine; all tropical and temperate seas.



Mouth terminal or slightly inferior; head without barbels; preorbitals usually projecting forward; pectoral fin with lower three rays free and enlarged; barbels absent on lower jaw; two separate dorsal fins, the first with 7–11 spines and the second with 10–23 soft rays; anal fin with 0–1 spines and 11–23 soft rays; casquelike, bony head; lower two or three pectoral rays enlarged and free, used for detecting food; caudal fin with 9 or 10 branched rays; tip of snout usually with paired rostral (preorbital) projections, often bearing spines, giving the snout a bilobed appearance in dorsal view (especially pronounced in most peristediines); branchiostegal rays seven. Benthic habitat. Triglids are good sound producers. Maximum length up to 1 m.

Ten genera in three tribes with about 105 species (e.g., del Cerro and Lloris, 1997a, b; Richards and Jones, 2002; Richards and Miller, 2003; Richards et al., 2003).

TRIBE PRIONOTINI. Lateral line not bifurcate on caudal fin; Baudelot's ligament originates on skull; 26 vertebrae. Western Atlantic and eastern Pacific oceans (i.e., off Americas); most species in Atlantic.

Two genera, *Bellator* and *Prionotus.*

TRIBE PTERYGOTRIGLINI. One genus, *Pterygotrigla.*

TRIBE TRIGLINI. Seven genera, *Aspitrigla, Chelidonichthys, Eutrigla, Lepidotrigla, Parapterygotrigla, Trigla,* and *Trigloporus.*

Family PERISTEDIIDAE (311)—armored searobins. Marine; found in deep water in the tropics of all oceans.

Body entirely encased by four rows of heavy spine-bearing plates on each side; mouth inferior; preorbitals each with a forward projection; pectoral fin with lower two rays free and enlarged; barbels on lower jaw.

About four genera, *Gargariscus, Heminodus, Peristedion,* and *Satyrichthys,* with about 36 species (e.g., Miller and Richards, 2003).

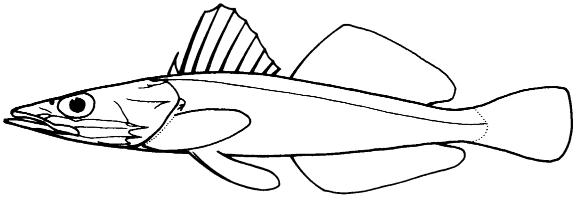
Family BEMBRIDAE (312)—deepwater flatheads. Marine; Indian and Pacific.

Head moderately to strongly depressed; pelvics below pectoral base; first dorsal fin with 6–12 spines and second dorsal fin with 8–12 soft rays; pectoral fin with 21–27 rays. Most are small, red, benthic fishes occurring from about 150–650 m.

The Indo-West Pacific *Parabembras,* with two species, is placed in its own family, Parabemdridae, by Imamura (1996, 2004). *Bembradium* is aligned with *Plectrogenium* and placed in its own platycephaloid family Plectrogenidae by Imamura (1996). Both *Parabembra* and *Bembradium* are provisionally retained here.

Five genera, *Bembradium, Bembradon, Bembras, Brachybembras,* and *Parabembras,* with about 10 species (e.g., Imamura and Knapp, 1998).

Family PLATYCEPHALIDAE (313)—flatheads. Marine (some brackish); primarily Indo-Pacific.

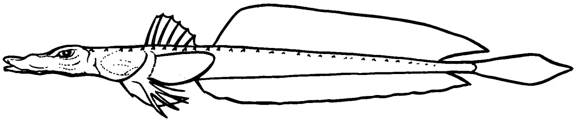


Head moderately to strongly depressed; pelvics behind pectoral base; first dorsal fin with 6–10 spines, first dorsal spine short and barely connected with rest of fin, and second dorsal fin with 11–15 soft rays; pectoral fin with 16–22 rays. Benthic habitat, often burying in the bottom, occurring from about 10–300 m. Maximum length about 1.1 m.

Solitas gruveli is the only species outside the Indo-Pacific, and it is in the eastern Atlantic off Africa. Two subfamilies are recognized by Imamura (1996), Platycephalalinae (for two genera) and Onigociinae.

About 18 genera (e.g., *Ambiserrula, Cociella, Elates, Eurycephalus, Grammoplites, Inegocia, Leviprora, Onigocia, Papilloculiceps, Platycephalus, Rogadius, Solitas, Sorsogona, Suggrundus,* and *Thysanophrys*) with about 65 species (e.g., Knapp, 1996; Imamura, 1996; Imamura and Knapp, 1999).

Family HOPLICHTHYIDAE (314)—ghost flatheads. Marine; Indo-Pacific.

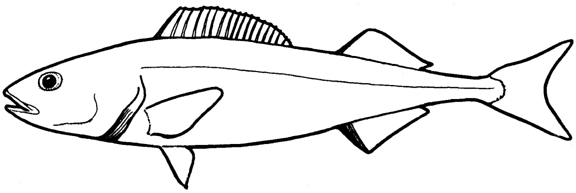


Body elongate; head extremely depressed and very wide, with spines and ridges; no scales, row of spiny scutes along side; lower pectoral rays (three or four) free; no anal spines; 26 vertebrae (8 + 18). Benthic, from about 10–1,500 m. Maximum length 43 cm. Winterbottom (1993a) provides evidence of a possible (and unexpected) sister-group relationship of hoplichthyids to gobioids due to their sharing more apparently unique derived characters with that group than with any other taxon; this warrants further investigation.

One genus, *Hoplichthys*, with about 10 species.

Suborder Anoplopomatoidei

Family ANOPLOPOMATIDAE (315)—sablefishes. Marine; North Pacific.



Head without spines, ridges, or cirri; two dorsal fins, the second with 16–21 soft rays; anal fin with three weak spines and 11–19 soft rays; pelvic fins with one spine and five soft rays; two well-developed nostrils on each side; gill membranes attached to isthmus; lateral line single. Maximum length about 1.8 m, attained in *Erilepis zonifer* (the Skilfish).

Two genera and species (Mecklenburg, 2003), *Anoplopoma fimbria* (with well-separated dorsal fins and 17–30 spines in first dorsal) and *Erilepis zonifer* (with closely spaced dorsal fins and 12–14 spines in first dorsal). Both species range from Japan through the Bering Sea to California, although *E. zonifer* does not extend quite as far north or south as *A. fimbria.*

Suborder Hexagrammoidei

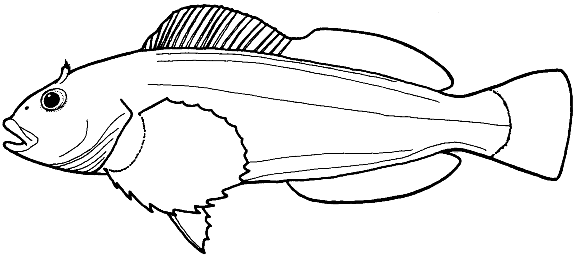
Family HEXAGRAMMIDAE (316)—greenlings. Marine; North Pacific.

Head with cirri but without ridges or spines; lateral lines one or five; scales cycloid or ctenoid; one dorsal fin (but with a notch) with 16–28 spines and 11–30 soft rays; pelvic fin with one spine and five soft rays; well-developed anterior nostril on each side, posterior nostril (if present) reduced to a small pore; anal fin with 0–3 spines followed by soft rays; six or seven branchiostegal rays; swim bladder absent; vertebrae 36–63. Maximum length up to 1.5 m, attained in *Ophiodon elongatus*; most other species less than 45 cm.

Although small, this is the most speciose family endemic to the North Pacific. Most species are primarily littoral.

Five subfamilies, five genera, and 12 species (Mecklenburg and Eschmeyer, 2003). Nelson (1994) gave references for the basis of this classification. Shinohara (1994) should be consulted for its study of comparative morphology and phylogeny.

SUBFAMILY HEXAGRAMMINAE (GREENLINGS). Dorsal fin divided approximately in the middle by a notch into an anterior spinous portion and a posterior soft portion; anal fin without spines; head covered with scales; caudal fin rounded, truncate, or slightly emarginate; no large ridges on skull; single lateral line (in the one species of the subgenus *Agrammus*, *H. agrammus* of Japan, Korea, and North China) or five (some may be short); vertebrae 47–57.



One genus, *Hexagrammos*, with six species, from western and eastern coasts of the North Pacific (south to Japan and northern Mexico).

SUBFAMILY PLEUROGRAMMINAE. Dorsal fin without a notch but with 21–24 spines and 24–30 soft rays; anal fin usually without a spine and with 23–32 soft rays; scales partly covering head; caudal fin forked; strongly developed ridges on upper surface of skull; five lateral lines on body; vertebrae 59–62. Primarily pelagic.

Two species of *Pleurogrammus* (Atka mackerels) in the northern Pacific from northern Japan to Alaska (rarely south to California).

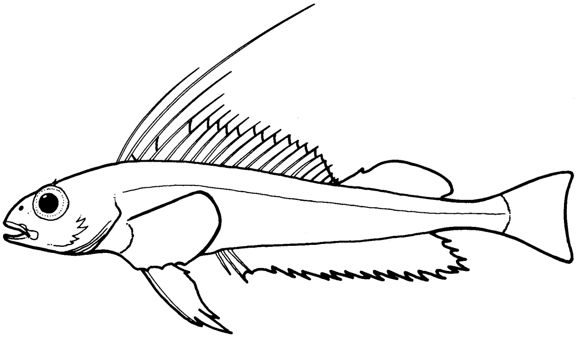
SUBFAMILY OPHIODONTINAE. Dorsal fin divided into two parts by a deep notch, first portion with 24–28 spines and second portion with 20–24 soft rays; anal fin with three nonsegmented rays and 21–25 soft rays; head not covered with scales; only member with cycloid scales on body, others may have cycloid scales on head; caudal fin truncate or slightly emarginate; single lateral line; mouth large; jaws with small teeth interspersed with large fanglike teeth; feeds primarily on fishes, crustaceans, and squids and is extremely voracious; 57–59 vertebrae.

One species, *Ophiodon elongatus* (Lingcod), of eastern Pacific from southern Alaska to northern Mexico.

SUBFAMILY OXYLEBIINAE. Dorsal fin divided by a shallow notch; anal fin usually with three large spines, of which the second is longest; scales covering the head; caudal fin rounded; one lateral line.

One species, *Oxylebius pictus* (painted greenlings), of eastern Pacific from British Columbia to California.

SUBFAMILY ZANIOLEPIDINAE (COMBFISHES). Dorsal fin with deep notch in posterior third of fin; first three dorsal fin spines elongate, the second greatly prolonged in *Zaniolepis latipinnis*; ctenoid scales; first two pelvic fin rays thickened and extending past origin of anal fin; one lateral line. Primarily benthic. Maximum length about 30 cm.



Two species, *Zaniolepis frenata* and *Z. latipinnis*, found in eastern North Pacific from British Columbia to California.

Suborder Normanichthyoidei. The relationships of the one included species, described by H. W. Clark in 1937, are very uncertain. It was previously excluded from the Cottoidei, and this is supported by recent work (e.g., Yabe and Uyeno, 1996; Smith and Wheeler, 2004); but its relationships remain uncertain. Further comments are given in Nelson (1994).

Family NORMANICHTHYIDAE (317)—normanichthyids. Marine; off Peru and Chile.

Body covered with ctenoid scales; head unarmed; pelvic fin with one spine and five soft rays; no ribs.

One species, *Normanichthys crockeri.*

Suborder Cottoidei. The recognition of two monophyletic lineages, ranked as superfamilies, follows the conclusions of M. Yabe in his 1985 study. However, monophyly of the suborder itself is not certain. We have a great deal of evidence that our present understanding of relationships is not only weak, but it is wrong. However, it is as yet impossible to erect a sound cladistic classification. Some of the problems are as follows: Smith and Wheeler (2004) in their molecular study found that the Hexagrammidae, Liparidae, Cyclopteridae, and Psychrolutidae are monophyletic, but they did not corroborate the monophyly of the Cottidae, Hemitripteridae, or Agonidae. Based on the studies of

Kontula et al. (2003), Sideleva (2003), Smith and Wheeler (2004), and Kinziger et al. (2005), it seems that all Lake Baikal sculpins are nested within *Cottus*. For example, Kontula et al. (2003) found strong support for the monophyly of the whole endemic Baikalian cottoid diversity, and found it to be nested within the Holarctic freshwater genus *Cottus*. The implications of this for cladistic classification are straightforward. Yet, I am reluctant to make the obvious step to show relationships.

Bugutskaya and Naseka (2004) recognized the subfamilies Cottinae, Cottocomephorinae (with three species in *Cottocomephorus* and *Paracottus*), Comephorinae, and Abyssocottinae (including *Batrachocottus* and *Cyphocottus*) in Cottidae (the latter two subfamilies are recognized here as families). In the next few years there is expected to be sound evidence published for recognizing several of the following families in an expanded Cottidae.

The relationships of this suborder are also in doubt. Imamura and Yabe (2002) supported aligning the suborder Cottoidei with the Zoarcoidei. A relationship between the cottoids, gasterosteoids, and zoarcoids was suggested in the molecular studies of Chen et al. (2003), Miya et al. (2003), and Smith and Wheeler (2004). Interestingly, my former PhD student P. S. Bowne found evidence for a relationship between cottoids and gasterosteiforms (e.g., Bowne, 1994).

Eleven families with about 149 genera and 756 species.

Superfamily Cottoidea. Basisphenoid absent; intercalar present, small and not contacting the prootic; scapula not attached to coracoid; hypurapophysis absent.

The higher classification of this taxon as in Nelson (1994) was based on the 1985 work of M. Yabe and the 1984 work of B. B. Washington and colleagues. In addition to comments given above, ongoing work of my former PhD student K. L. Jackson suggests changes to the classification.

Family RHAMPHOCOTTIDAE (318)—grunt sculpins. Marine; North Pacific, Japan through Alaska to southern California.

Basioccipital-parasphenoid fossa present; pelvis highly modified, with an elongate subpelvic keel projecting forward and an anterodorsally projecting suprapelvic keel; four infraorbitals; palatine without teeth; six branchiostegal rays; all fin rays unbranched; first dorsal fin with 7–9 spines and second with 12–14 soft rays; anal fin with 6–8 soft rays; vertebrae 26–28. This is a very distinctive sculpin with its long head (head length is about half the standard length) and its elongate snout. Maximum length about 8 cm.

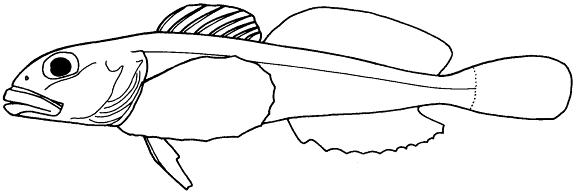
One species, *Rhamphocottus richardsonii* (Mecklenburg, 2003).

Family EREUNIIDAE (319)—deepwater sculpins. Marine; deep water, western and western central North Pacific.

Four lower pectoral fin rays free (similar to triglids); basihyal absent; body with spinous ctenoid scales; preopercle with simple spines (uppermost never antlerlike); six branchiostegal rays; first dorsal fin with 9–11 spines and second with 12–16 soft rays; anal fin with 11–14 soft rays; pectoral fin with 14 or 15 rays; two slender postcleithra; completely fused hypural complex; vertebrae 35–39 (13 precaudal vertebrae). Maximum length 30 cm.

Two genera, the monotypic *Ereunias* (without the pelvic fin but with underlying pelvis and one vestigial spine present or absent; five rows of bony scales on body) from off south Japan and *Marukawichthys* with two species (pelvic fin present and with one spine and four soft rays; six rows on bony scales on body) from the Japan Sea and the Emperor Seamount Chain.

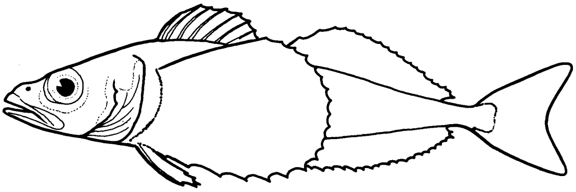
Family COTTIDAE (320)—sculpins. Marine and freshwater; Northern Hemisphere and eastern Australia, near New Guinea, and New Zealand.



Body often appearing naked, commonly with scales or prickles (never completely encased in heavy bony armor); eye usually large and placed high on the head; lateral line present, single; pelvic fins (absent in one species) with one spine and 2–5 soft rays (usually 2 or 3 soft rays); no spines in anal fin; adults without swim bladder. Maximum length about 78 cm (e.g., *Scorpaenichthys marmoratus*).

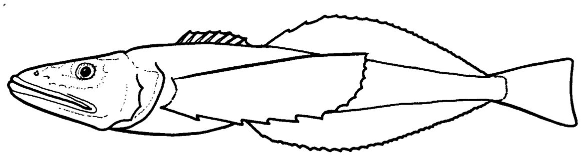
Most species are marine with the greatest diversity occurring along the North Pacific coastline. The only Southern Hemisphere cottids are four deepwater species of the genus *Antipodocottus* known from Australia, Kai Islands west of New Guinea, and New Zealand.

For comments on the placement of all Lake Baikal sculpins in Cottidae see above under suborder Cottoidei.



About 70 genera (e.g., *Alcichthys, Artediellus, Artedius, Ascelichthys* (lacks pelvics), *Asemichthys, Bero, Chitonotus, Clinocottus, Cottiusculus, Cottocomephorus* (lower figure, above), *Cottus, Enophrys, Furcina, Gymnocanthus, Hemilepidotus, Icelinus, Icelus, Jordania, Leptocottus, Micrenophrys, Myoxocephalus, Oligocottus, Pseudoblennius, Radulinus, Rastrinus, Ruscarius, Scorpaenichthys, Sigmistes, Synchirus, Taurulus, Trachidermis, Trichocottus, Triglops,* and *Vellitor*) with about 275 species (e.g., Kinziger et al., 2000; Yabe and Pietsch, 2003; Sideleva, 2003).

Family COMEPHORIDAE (321)—Baikal oilfishes. Freshwater pelagic; Lake Baikal, Siberia.

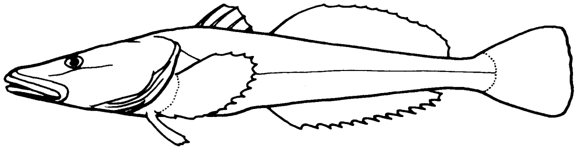


Body naked; pectoral fins very long; no pelvic fins (pelvic bones present); postcleithra absent; body glassy-dull and translucent in living fish; body usually high in fat content; vertebrae 48–50; ovoviviparous. The lateral-line system on the head on these pelagic fishes consists of large cavities linked by narrow bony bridges with small external pores; the bone is porous. These adaptations that reduce the weight of the skeleton seem similar to that found in some psychrolutids. Maximum length about 20 cm.

For comments on the placement of all Lake Baikal sculpins in Cottidae see above under suborder Cottoidei. Although not done here, given the phylogenetic evidence, all members should be included within Cottidae, and such a move will be made should further studies support current views.

One genus, *Comephorus,* with two species (e.g., Sideleva, 2003).

Family ABYSSOCOTTIDAE (322)—deepwater Baikal sculpins. Freshwater; primarily Lake Baikal, Siberia.



Postcleithra reduced or absent; dorsal fin with 3–10 spines and 10–21 soft rays; anal fin with 8–16 soft rays; pelvic fin with one spine and 2–4 soft rays; vertebrae 30–37 (see Sideleva, 1982:52–55, for a description of this family).

In the present classification, the sculpins in Lake Baikal are placed in this family, in the Comephoridae, and in the Cottidae (genus *Cottus* and subfamily Cottocomephorinae); they account for slightly over half of its 50 known species. The species generally occur below 170 m. For comments on the placement of all Lake Baikal sculpins in Cottidae see above under suborder Cottoidei. Although not done here, my preference, given the phylogenetic evidence, is to include all members within Cottidae.

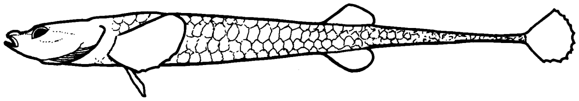
Six genera, *Abyssocottus, Asprocottus, Cottinella, Limnocottus, Neocottus,* and *Procottus,* with about 22 species (e.g., Sideleva, 2003).

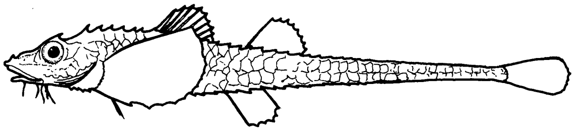
Family HEMITRIPTERIDAE (323)—searavens. Marine; northwestern Atlantic (one species) and North Pacific.

Minute spines covering the body; basihyal absent; six branchiostegal rays; vertebrae 35–41.

Three genera, *Blepsias* (two species), *Hemitripterus* (three, with one, the Sea Raven, in the Atlantic), and *Nautichthys* (three), with eight species (Mecklenburg, 2003).

Family AGONIDAE (324)—poachers. Marine; Arctic, northern North Atlantic, North Pacific, and southern South America.





Body covered with bony plates and usually elongate; pelvic fins thoracic, with one spine and two soft rays; all fin rays unbranched; one or (usually) two dorsal fins, the first, when present, with 2–21 spines and second with 4–14 soft rays; anal fin with 4–28 soft rays; principal caudal fin rays 10–12; five or six branchiostegal rays; basihyal rudimentary or absent; one or no tabular bones; predorsal bone absent; swim bladder absent; vertebrae 34–47. Maximum length about 30 cm.

Agonids range in depth from inshore shallow water to over 1,000 m. Most species occur in the North Pacific (extending south to Japan and northern Mexico). The following four species occur elsewhere: *Agonopsis chiloensis*—southern Chile and Argentina, including the Straits of Magellan and the Falkland Islands (the closest congeneric member of this remarkably disjunct species is in northern Mexico); *Agonus cataphractus*—Iceland, northeastern Atlantic, and adjacent Arctic; *Aspidophoroides monopterygius*—Arctic, northwestern Atlantic south to New York, and North Pacific south to Japan; *Leptagonus decagonus*—Arctic, northern Bering Sea, and northeastern and northwestern Atlantic; and *Ulcina olriki*—Arctic, northern Bering Sea, and northern northwestern Atlantic.

Six subfamilies, 22 genera with 47 species (Sheiko and Mecklenburg, 2004).

SUBFAMILY HYPSAGONINAE. Three genera, *Agonomalus*, *Hypsagonus*, and *Percis*, with seven species.

SUBFAMILY BATHYAGONINAE. Three genera, *Bathyagonus, Odontopyxis,* and *Xeneretmus,* with nine species.

SUBFAMILY BOTHRAGONINAE. One genus, *Bothragonus,* with two species.

SUBFAMILY ANOPLAGONINAE. Three genera, *Anoplagonus* (in upper figure), *Aspidophoroides,* and *Ulcina,* with four or five species.

SUBFAMILY AGONINAE. Six genera, *Agonopsis, Agonus* (in lower figure), *Freemanichthys, Leptagonus, Podothecus,* and *Sarritor,* with 13–15 species.

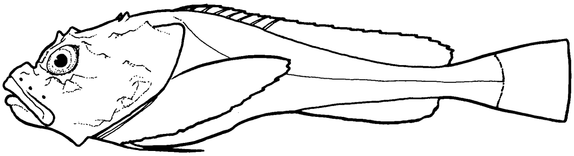
SUBFAMILY BRACHYOPSINAE. Six genera, *Brachyopsis, Chesnonia Occella, Pallasina, Stellerina,* and *Tilesina,* with nine species.

Family PSYCHROLUTIDAE (325)—fathead sculpins. Marine; Atlantic, Indian, and Pacific.

Body naked or with plates bearing prickles; interorbital space usually greater than exposed eye diameter (much smaller in *Malacocottus*); lateral line reduced, with 20 or fewer pores; pelvic fin with one spine and three soft rays; dorsal fins usually continuous with spinous dorsal, often partially hidden by skin (bases separate or nearly so in *Malacocottus* and *Dasycottus*); branchiostegal rays seven; prevomerine teeth present or absent, palatine teeth always absent; one or two postorbitals (if two, they are usually ringlike; cottids have two or three elongate postorbitals); system of well-developed bony arches, which may bear spines, on the cranium over the lateral line system with wide intervening space; vertebrae 28–38. Maximum length about 65 cm, attained in *Psychrolutes paradoxus.* Psychrolutids range in depth from inshore shallow water (*P. sigalutes*) to up to about 2,800 m (*P. phrictus*).

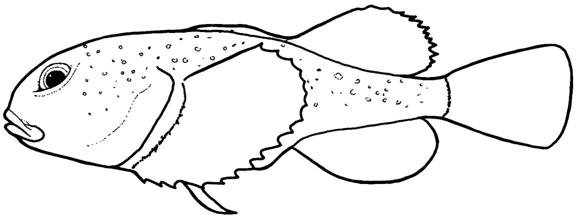
Two subfamilies (paraphyletic according to Jackson and Nelson, 1998) with eight genera and about 35 species (e.g., Nelson, 1995; Jackson and Nelson, 1998, 1999, 2000). Both subfamilies have members in the Northern and Southern Hemispheres.

SUBFAMILY COTTUNCULINAE. Head well ossified, interorbital margins hard, and head spines often present; relatively narrow interorbital area, width less than two times diameter of exposed eye; body and fins usually not of uniform color.



Five genera, *Ambophthalmos, Cottunculus, Dasycottus, Eurymen,* and *Malacocottus.*

SUBFAMILY PSYCHROLUTINAE. Head poorly ossified, interorbital margins soft, and head spines absent; wide interorbital area, width more than two times diameter of exposed eye; body and fins usually of uniform color.



Three genera, *Ebinania*, *Neophrynichthys*, and *Psychrolutes* (synonym *Gilbertidia*).

Family BATHYLUTICHTHYIDAE (326)—Antarctic sculpins. Marine; Antarctic Ocean (south Georgia Island).

Body naked; wide interorbital; one pair of long barbels on lower jaw at corner of mouth; single dorsal with anterior portion submerged under the skin, with 13 spines and 28 soft rays; anal fin with 36 rays; pelvic fin with 3 soft rays; all fin rays unbranched; teeth absent on vomer and palatines; branchiostegal rays seven; radials two; postcleithrum and pleural ribs absent; vertebrae 49.

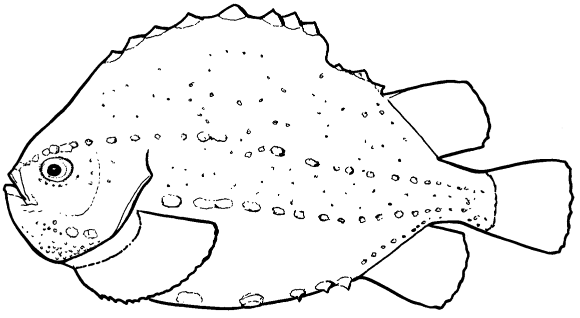
Except for the elongate barbels and the caudal fin being joined with the dorsal and anal fins, the one known specimen (from 1,650 m) superficially looks like a *Psychrolutes.* The family was established with the description of the one species. Its phylogenetic position within the Cottoidei is uncertain.

One species, *Bathylutichthys taranetzi.*

Superfamily Cyclopteroidea. Pelvic fins, when present, modified into a sucking disc, thoracic; lateral line usually absent; gill opening small. Able et al. (1984) describe larval characters and present comparative information on the two included taxa, the lumpfishes and the snailfishes.

Lumpfishes and snailfishes are thought to form a monophyletic group, and I previously (Nelson, 1984) expressed this view by recognizing both in the one family, Cyclopteridae. However, most workers have recognized snailfishes in their own family, and this is followed here with monophyly of the group being expressed by the recognition of the superfamily Cyclopteroidea.

Family CYCLOPTERIDAE (327)—lumpfishes (lumpsuckers). Marine; cooler regions of the Northern Hemisphere.

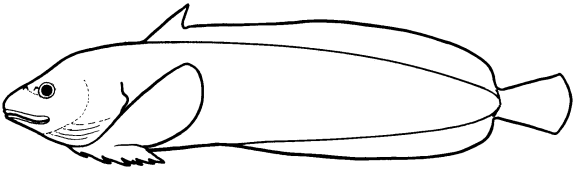


Body globose, usually covered with tubercles; usually two short dorsal fins, the first with 4–8 spines (the spinous fin is beneath the skin in some species and not externally visible), the second with 8–13 soft rays, never confluent with caudal; anal fin short, with 7–13 soft rays; vertebrae about 23–29. Maximum length up to 60 cm.

About six genera, *Aptocyclus* (synonym *Pelagocyclus*), *Cyclopterus*, *Cyclopteropsis*, *Cyclopsis*, *Eumicrotremus*, and *Lethotremus*, and 28 species (Mecklenburg and Sheiko, 2003). In Nelson (1994) I followed the 1970 classification of T. Ueno and recognized two subfamilies, Aptocyclinae with two species in monotypic *Aptocyclus* and *Pelagocyclus* and Cyclopterinae.

Family LIPARIDAE (Liparididae) (328)—snailfishes.

Marine; Arctic to Antarctic.



Body elongate, scaleless (small prickles in some) and skin jellylike; dorsal fin (28–82 soft rays) and anal fin (24–76 soft rays) long, confluent, or nearly so, with caudal fin; pelvic fin (disc) absent in the 45 or more species of *Paraliparis* and in the monotypic *Nectoliparis*; nostrils single or paired (usually in *Liparis*); vertebrae 38–86. Maximum length about 80 cm.

Snailfishes have an unusually wide geographic and habitat range. They occur from tide pools to depths of over 7,000 m. They are one of the most species-rich families of fishes in the Southern Ocean, the North Pacific, and the Arctic: they occur in the deep Indian Ocean, but only a few species are known from there (Chernova et al., 2004). They have also been found in the Galapagos Islands (Stein and Chernova, 2002). As noted by Chernova et al. (2004), various subfamilies have been proposed (Paralipariidinae, Careproctinae, Rhodichthyinae, Nectolipariidinae), they believe there is not enough information to support their use.

About 29 genera (e.g., *Acantholiparis, Careproctus, Crystallichthys, Elassodiscus, Liparis, Lopholiparis, Nectoliparis, Notoliparis, Paraliparis, Polypera, Psednos,* and *Rhodichthys*) with about 334 species (Andriashev, 2003; Stein and Chernova, 2002; Stein et al., 2001, 2003; Chernova et al., 2004; Orr, 2004). Chernova et al. (2004) noted that much work remains to be done on the taxonomy and these numbers will continue to change.

Order PERCIFORMES (58)—perches. The order Perciformes is the most diversified of all fish orders. Indeed, it is the largest order of vertebrates. Perciforms dominate in vertebrate ocean life and are the dominant fish group in many tropical and subtropical freshwaters.

The classification of this order is unsettled and will certainly be subject to changes that will better reflect the evolutionary history of the higher percomorphs. As noted in Nelson (1994), Johnson and Patterson (1993) presented evidence that the perciforms may be part of a monophyletic group only if we include members of the orders Scorpaeniformes (including the Dactylopteridae), Pleuronectiformes, and Tetraodontiformes. There is evidence that the last three ordinal taxa are probably derivatives of perciform lineages, although there is also evidence that the Tetraodontiformes (and Caproidae) are pre-perciforms (Springer and Johnson, 2004). I have not made changes to the classification until we better understand just how these groups are related. It is unfortunate that a monophyletic order Perciformes cannot be recognized. In addition, most families in many suborders are not currently definable in terms of common shared derived characters and thus may not be monophyletic.

Perciformes contains 20 suborders, 160 families, about 1,539 genera, and about 10,033 species. Some 52 families have a single genus, 23 have a single species (i.e., are monotypic), and 21 have 100 or more species. Three suborders, the Percoidei, Labroidei, and Gobioidei, account for over three-quarters of the species. The eight largest families are Gobiidae, Cichlidae, Serranidae, Labridae, Blenniidae, Pomacentridae, Apogonidae, and Sciaenidae. Together, with 5,479 species, they constitute about 55% of the species. Most perciforms are marine shore fishes, while about 2,040 species normally occur only in freshwater, and at least some individuals of about 2,335 species occur in freshwater for at least part of their life history. Unlike in Nelson (1994), Johnson and Patterson (1993) excluded the family Elassomatidae from the Perciformes but included the family Caproidae. I now include the Caproidae, but continue to include the Elassomatidae.

Fossil groups were covered in Patterson (1993). Some perciform or perciformlike fossils covered in recent literature and not otherwise mentioned below are: i) *Priscacara* (Priscacaridae) and *Mioplosus,* freshwater middle Eocene and early percoid fish from North America, (e.g., Grande, 2001); ii) *Eoserranus, Indiaichthys, Nardoichthys, and Saldenioichthys* (e.g., Arratia et al., 2004); iii) Asianthidae (*Asianthus, Eosasia,* and *Pauranthus*) from the Upper Paleocene of Turkmenistan that may form a monophyletic assemblage together with the families Priacanthidae and Caproidae (Sytchevskaya and Prokofiev, 2003); iv) *Tungtingichthys* (Chang and Huanzhang, 1998); v) and Sorbinipercidae (*Sorbiniperca scheuchzeri*) (Tyler, 1999); vi) *Synagropoides,* a possible acropomatid from the Eocene of the Northern Caucasus (Bannikov, 2002); and vii) Eocottidae (*Eocottus* and *Bassania*) from the Eocene of Monte Bolca, Italy (Bannikov, 2004b). Many other important studies have been done on perciform fossils not given in the Bibliography, such as: i) a 1996 paper by N. Micklich on middle Eocene *Amphiperca, Palaeoperca,* and *Rhenanoperca,* ii) a 1999 paper by O. Otero and M. Gayet on the Plio-pleistocene *Semlikiichthys,* and iii) a 1999 paper by P. F. Chen and coauthors on *Coreoperca* and *Siniperca.* The latter two genera, the related *Coreoperca* and *Siniperca* with cycloid scales, have extant species in eastern Asia, but family placement is uncertain; they have been placed in Centropomidae, Percichthyidae, or, as is more appropriate and done in 1993 by C. D. Roberts, in their own family Sinipercidae (e.g., see Nelson, 1994) and they are not further classified here. All species of Sinipercidae, both extant and fossil, are known from fresh water, except for the probably marine Miocene *Inabaperca taniurai* (Yabumoto and Uyeno, 2000).

Suborder Percoidei. This suborder, the largest of the Perciformes, contains 79 families, 549 genera, and about 3,176 species. Of the 79 families, 26 have a single genus, 10 have a single species, and 10 have 100 or more species. The ten largest families (each with over 100 species)—Serranidae, Apogonidae, Sciaenidae, Percidae, Haemulidae, Carangidae, Chaetodontidae, Pseudochromidae, Sparidae, and Lutjanidae—with 1,965 species, contain about 62% of the species. About 380 or 12% of the species normally occur only in freshwater (over half of these are percids). This suborder contains many highly colorful fishes.

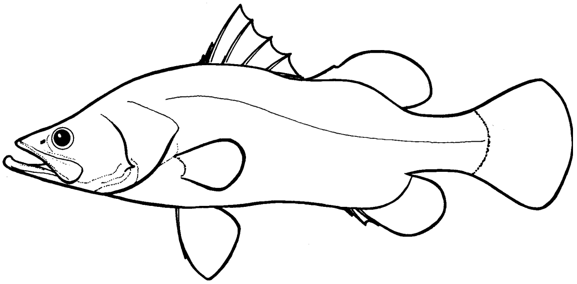
This may be the basal evolutionary group from which the other perciform groups and the remaining two orders have been derived. Even if this were not so, it is probably not a monophyletic group, being recognized solely on primitive characters.

	Lower teleosts	Percoidei
Spines in fins	Absent	Present in dorsal, anal, and pelvic fins
Dorsal fin number	One, adipose fin may also be present	Two, never an adipose fin
Scales	Cycloid	Ctenoid
Pelvic fin position	Abdominal	Thoracic
Pelvic fin rays	Six or more soft rays	One spine and five soft rays
Pectoral fin base	Ventral and horizontal	Lateral and vertical
Upper jaw bordered by	Short premaxilla and long maxilla	Premaxilla
Swim bladder	Duct present (physostomes)	Duct absent (physoclists)
Orbitosphenoid	Present	Absent
Mesocoracoid	Present	Absent
Epipleural and epicentral bones	Present	Absent
Bone cells in bone of adult	Present	Not apparent
Principal caudal fin ray number	Often 18 or 19	Never more than 17, often fewer

Although they are a morphologically and ecologically diverse group with secondary losses and gains, we can generalize, as I have done in the table, the level of evolution reached, as contrasted with “typical” lower teleosts (Protacanthopterygii and Ostariophysi). Many exceptions to these generalizations occur; for example, the bodies of many percoids are covered mainly by cycloid scales. Many of the features of the Percoidei are also present in many acanthomorphs; the table is not intended to show features originating in the Percoidei, but merely serves to contrast the lower teleosts with the percoids.

Superfamily Percoidea. Many of the 73 families are very similar and poorly separated from one another; some are very distinctive and have been allied with other orders or placed in their own order. As with the order and suborder in which this taxon is placed, there is no evidence that it represents a monophyletic group. However, although this taxon is probably not monophyletic, several groups of families form distinct lineages. For example, based on several works by G. D. Johnson (e.g., Johnson, 1993 and references therein) and others, the following are thought to form monophyletic groups and could be given superfamily rank as done in some works: i) the carangoid lineage—Nematistiidae, Coryphaenidae, Rachycentridae, Echeneidae, and Carangidae and ii) the sparoid lineage—Nemipteridae, Lethrinidae, Sparidae, and Centracanthidae. I retain all in the one superfamily. Many changes have been made since Nelson (1994) in the families recognized and the species composition.

Family CENTROPOMIDAE (329)—snooks. Marine (often brackish) and freshwater; tropical and subtropical waters North and Central America.



Lower jaw extending forward beyond upper jaw; lateral line extending onto tail, reaching posterior margin of fin; scaly process usually in pelvic axis; caudal fin deeply forked; dorsal fin in two portions (separated by a small gap), the first with eight spines and the second with one spine and 8–11 soft rays; anal fin with three spines and 5–8 soft rays; pelvic fin with one spine and five soft rays; seven branchiostegal rays; 24 vertebrae. Maximum length about 2.0 m.

In a cladistic analysis using 29 characters Otero (2004) demonstrated that the family Centropomidae, as previously defined, is paraphyletic, and the previously recognized subfamily Latinae is now recognized as a separate family.

One genus, *Centropomus*, with 12 species (e.g., Nelson et al., 2004).

Family AMBASSIDAE (Chandidae) (330)—Asiatic glassfishes. Marine, brackish, and freshwater; Indo-West Pacific (freshwater in Madagascar and India to the Australian region).

Many species with semitransparent body; scales entirely absent in the transparent *Gymnochanda filamentosa*; dorsal fin usually with seven or eight spines and 7–11 soft rays; anal fin with three spines and 7–11 soft rays; vertebrae usually 24 or 25. *Paradoxodacna piratica* is a scale-eater. Maximum length about 26 cm.

Centropomidae appears to be sister to the Ambassidae (Otero, 2004). The family name Chandidae was used in Nelson (1994). The family names

Ambassidae, Chandidae, and Bogodidae were discussed by Anderson and Heemstra (2003) and Kottelat (2003).

Eight genera, *Ambassis, Chanda, Denariusa, Gymnochanda, Paradoxodacna, Parambassis, Priopis,* and *Tetracentrum,* with about 46 species (e.g., Roberts, 1994; Kottelat, 1995, 2003; Anderson and Heemstra, 2003).

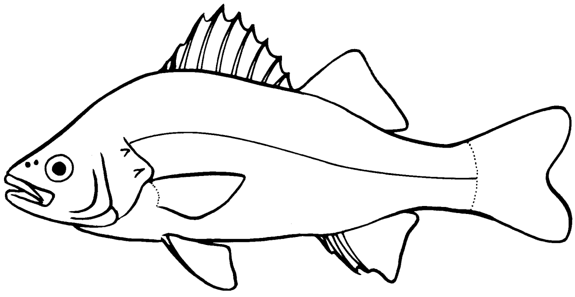
Family LATIDAE (331)—lates. Marine, brackish, and freshwater; Indo-West Pacific and Africa.

Dorsal fins not completely separated or, if separated, with one or two isolated spines between them; caudal fin usually rounded; 25 vertebrae. This family includes the large Nile Perch, *Lates niloticus.* The marginally catadromous Indo-West Pacific *Lates calcarifer* in Australia is known as the barramundi, a term rarely also used for species of *Scleropages.*

Mooi and Gill (1995) gave family status to the former Latinae, a subfamily of Centropomidae. In a cladistic analysis using 29 characters Otero (2004) demonstrated that the family Centropomidae, as previously defined, is paraphyletic. The new family Latidae is monophyletic and includes *Lates, Psammoperca* and the fossil *Eolates* (Eocene and Oligocene). Centropomidae appears to be sister to the Ambassidae with Latidae being sister to the one serranid examined; therefore, recognition of Latidae as a valid family is warranted (Otero, 2004, defined it on the basis of six apomorphies).

Two genera, *Lates* (8, seven live in freshwater, four are endemic to Lake Tanganyika, to brackish habitat of tropical Africa and one is in the coastal marine and estuarine waters of the Indo-Pacific, fossils are well known in Africa and Europe) and *Psammoperca* (1, coastal Indo-Pacific waters), with nine species (Otero, 2004).

Family MORONIDAE (332)—temperate basses. Brackish and freshwater and marine coastal areas; North America (Atlantic and Gulf of Mexico drainages, introduced elsewhere), Europe, and northern Africa.



Two dorsal fins, the first with 8–10 spines and the second with one spine and 10–13 soft rays; anal fin with three spines and 9–12 soft rays; opercle with two spines; lateral line extends almost to posterior margin of caudal fin; auxiliary row of lateral line scales on the caudal fin above and below the main row; seven branchiostegal rays; 25 vertebrae.

Three genera, *Morone* (synonym *Roccus*) with four species from North America (two are confined to freshwater) (e.g., Heemstra, 2003a; Nelson et al., 2004), the closely related *Dicentrarchus* with two species from off Europe and North Africa, including the Mediterranean and Black seas and in coastal rivers, and provisionally the Asian *Lateolabrax*, the Asian seaperches, with two species, that may have affinities with this family, but put in its own family, Lateolabracidae, in Eschmeyer (1998) and Springer and Johnson (2004), with eight species.

Family PERCICHTHYIDAE (333)—temperate perches. Freshwater (rarely brackish); Australia and South America (primarily Argentina and Chile).

Dorsal fins continuous, with or without a notch (may be deep); 7–12 spines (except 1–3 in *Gadopsis bispinosus*) and 8–38 soft rays; anal fin with three spines and 7–13 soft rays (16–20 in *Gadopsis*); scales ctenoid (with simple needlelike ctenii on posterior field) or secondarily cycloid, vertebrae 25–36 (40–50 in *Gadopsis*).

Eleven genera with about 34 species: in South America—*Percichthys;* in Australia—*Gadopsis, Guyu, Maccullochella, Macquaria, Percalates,* and *Plectroplites,* and the relatively derived *Bostockia, Edelia, Nannatherina,* and *Nannoperca*; the marine *Howella* is provisionally placed here (e.g., Pusey and Kennard, 2001; Arratia, 2003; López-Arbarello, 2004).

Family PERCILIIDAE (334)—southern basses. Freshwater; Chile.

Maximum length about 9 cm. Changes in family composition will be required if, as Arratia (2003) suggests, *Percilia* forms a clade with the Australian *Bostockia, Edelia,* and *Nannoperca.* This genus is usually placed in the Percichthyidae.

Two species, *Percilia gillissi* and *P. irwini* (Arratia, 2003).

Family ACROPOMATIDAE (335)—lanternbellies. Marine; Atlantic, Indian, and Pacific.

Two dorsal fins, the first with 7–10 spines and the second with or without a spine and 8–10 soft rays; anal fin with two or three spines and 7–9 soft rays; seven branchiostegal rays; 25 vertebrae. The three species of *Acropoma* have light organs and the anus near the pelvic fin base—the only other perciforms with such an anterior anus is the serranid *Bullisichthys caribbaeus* and the apogonid *Apogon gularis.*

The family common name used in Nelson (1994) was temperate ocean-basses.

Eight genera, *Acropoma, Apogonops, Doederleinia, Malakichthys, Neoscombrops, Pseudohowella, Synagrops,* and *Verilus,* with about 31 species (e.g., Okamoto and Ida, 2002; Yamanoue and Matsuura, 2002; Heemstra, 2003a). Several genera provisionally placed here in Nelson (1994) are now recognized in other families (Polyprionidae and Symphysanodontidae). See Perciformes for possible fossils.

Family SYMPHYSANODONTIDAE (336)—slopefishes. Marine; Atlantic, Indian, and Pacific.

Two opercular spines; dorsal fin usually with nine spines and 10 soft rays.

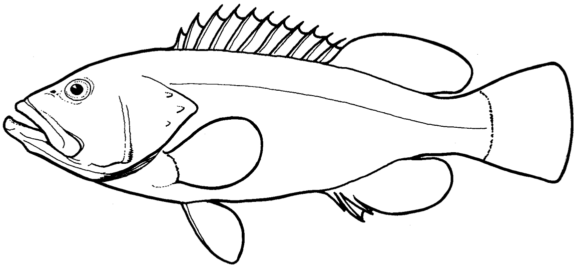
One genus, *Symphysanodon*, with six species (e.g., Anderson, 1999, 2003a) (additional species are being described by W. D. Anderson, Jr., and V. G. Springer).

Family POLYPRIONIDAE (337)—wreckfishes. Marine; Atlantic, Indian, and Pacific.

Opercle with a horizontal ridge on dorsal aspect ending in a short spine; dorsal fin with 11 or 12 strong spines and 11 or 12 soft rays.

Two genera, *Polyprion* and *Stereolepis*, with about five species (e.g., Sedberry, 2003).

Family SERRANIDAE (338)—sea basses. Marine (a few freshwater); tropical and temperate seas.



Opercle with three spines—the main spine with one above it and one below it. Scales usually ctenoid, cycloid in some; lateral line complete and continuous (absent in one species), not extending onto caudal fin (running close to dorsal fin base in some Anthiinae); dorsal fin generally continuous, may be notched, with 7–13 spines—most have 10 or fewer and only *Acanthistius* and *Niphon* have 13; three anal fin spines; caudal fin usually rounded, truncate, or lunate (rarely forked); tip of maxilla exposed, not slipping beneath lachrymal when mouth closed; no scaly axillary pelvic process; pelvic fin with one spine and five soft rays; usually seven branchiostegal rays; usually 24 vertebrae (25–28 in Anthiinae and some grammistins and 30 in *Niphon*); hermaphroditic, although the two sexes usually do not develop at the same time (most *Serranus* and their immediate relatives are functional hermaphrodites). Maximum length up to about 3 m (and weight up to about 400 kg); many species, however, grow no longer than 10 cm, and some anthiines such as *Plectranthias longimanus* reach only 3 cm.

The family in its present composition is thought to be monophyletic based on the apomorphic features of three opercular spines and the reductive specializations of absence of the posterior uroneural, procurrent spur, and third preural radial cartilages. The composition and recognition of monophyly is based on the 1983 study of G. D. Johnson and his study in 1984. Some of the additional studies, cited in Nelson (1994), that provide the basis for the classification were done by Randall and McCosker in 1992 and by C. C. Baldwin and G. D. Johnson in 1993.

Three subfamilies recognized (following the 1984 study of A. W. Kendall, Jr.), with about 64 genera and 475 species (e.g., Heemstra et al., 2003). Various other subfamily classifications have been proposed in the past, with up to 15 subfamilies given in some classifications employing noncladistic methods. Some workers have recognized the anthiine genus *Giganthias* in its own subfamily and epinepheline genus *Liopropoma* in the Liopropominae. *Caesioscorpis* is placed *incertae sedis.*

SUBFAMILY SERRANINAE. About 13 genera (e.g., *Bullisichthys, Centropristis, Chelidoperca, Cratinus, Diplectrum, Hypoplectrus* (the synchronous hermaphroditic hamlets), *Paralabrax, Parasphyraenops, Schultzea, Serraniculus,* and *Serranus*).

SUBFAMILY ANTHIINAE. At least 21 genera, *Acanthistius, Anthias, Caesioperca, Caprodon,* perhaps *Epinephelides, Giganthias, Hemanthias, Holanthias, Hypoplectrodes, Lepidoperca, Luzonichthys, Plectranthias, Pronotogrammus, Pseudanthias, Rabaulichthys, Sacura, Serranocirrhitus, Stigmatonotus, Tosana, Tosanoides,* and *Trachypoma,* with about 170 species, most being Indo-West Pacific.

SUBFAMILY EPINEPHELINAE. Larvae with one or more elongate anterior dorsal fin spines (usually the second) and, in the tribe Epinephelini, an elongate pelvic fin spine. The five tribes recognized here for the subfamily Epinephelinae, defined on the basis of larval and adult characters, following several studies by C. C. Baldwin, G. D. Johnson, and A. W. Kendall, Jr. However, Heemstra and Randall (1993) restrict the composition of the subfamily to the groupers (the tribe Epinephelini given here) as classically viewed. The species of "soapfishes" (with the skin toxin grammistin in four genera) are placed in the epinepheline tribes Diploprionini and Grammistini.

TRIBE NIPHONINI. One species, *Niphon spinosus.*

TRIBE EPINEPHELINI (GROUPERS). Fifteen genera, *Aethaloperca, Alphestes, Anyperodon, Cephalopholis, Cromileptes, Dermatolepis, Epinephelus* (about 100 species, some extending into estuaries), *Gonioplectrus, Gracilia, Mycteroperca, Paranthias, Plectropomus, Saloptia, Triso,* and *Variola* (e.g., Heemstra and Randall. 1993).

TRIBE DIPLOPRIONINI. Three genera, *Aulacocephalus, Belonoperca,* and *Diploprion,* with five species (Baldwin and Smith, 1998).

TRIBE LIOPROPOMINI. Three genera, *Bathyanthias, Liopropoma,* and *Rainfordia.*

TRIBE GRAMMISTINI. Eight genera, *Aporops*, *Grammistes*, *Grammistops*, *Jeboehlkia*, *Pogonopera*, *Pseudogramma*, *Rypticus*, and *Suttonia*, with about 21 species (e.g., Randall and Baldwin, 1997).

Family CENTROGENIIDAE (339)—false scorpionfishes. Marine (rarely brackish); east Indian and western Pacific.

Posterior rim of anterior nostril with large fringed flap; ventral margin of preopercle with three or four large forward pointing spines; dorsal fin with 13 or 14 spines and 9–11 branched soft rays, origin of fin over posterior margin of preopercle. Maximum length about 25 cm TL. This family was not classified in Nelson (1994), but mentioned under Percoidea.

One species, *Centrogenys vaigiensis* (e.g., Gill, 1999; Leis and Trnski, 1999).

Family OSTRACOBERYCIDAE (340)—ostracoberycids. Marine; eastern and northern Indian and western Pacific.

Prominent spine extending back from lower limb of preopercle; two separate dorsal fins, first with nine spines and second with 9–10 soft rays; 25 vertebrae.

One genus, *Ostracoberyx*, with three species (Quéro and Ozouf-Costaz, 1991).

Family CALLANTHIIDAE (341)—groppos. Marine; eastern Atlantic (including the Mediterranean), Indian, and Pacific.

Flat nasal organ devoid of lamellae; lateral line running along base of dorsal fin and terminating near end of dorsal fin or on caudal peduncle; dorsal fin with 11 spines and 9–11 soft rays; midlateral row of modified scales that have a series of pits and/or grooves; vertebrae 24. Maximum length about 25 cm. Magnificently colored.

Two genera, *Callanthias* (8) and *Grammatonotus* (4), with about 12 species (e.g., Anderson, 1999; Mundy and Parrish, 2004).

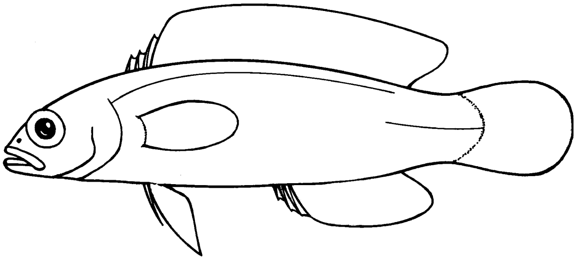
Family PSEUDOCHROMIDAE (342)—dottybacks. Marine; tropical Indo-Pacific.

Dorsal and anal fins each with one to three spines (often inconspicuous, no anal spine in congrogadines), in addition, except for congrogadines, dorsal with 21–37 soft rays and anal usually with 13–21 soft rays; pelvic fin (absent in some) with one spine and three to five soft rays, inserted below or in front of pectoral fin base; lateral line variable; six branchiostegal rays; no interarcual cartilage between uncinate process of the first epibranchial and the second infrapharyngobranchial; ligamentous attachment between lower jaw and hyoid arch, unlike in most percoids; vertebrae, except in congrogadines, 26–35 (10–13 + 16–25); eggs with filaments attached to the chorion. Maximum length about 45 cm, most less than 11 cm.

This and the next four families—the Grammatidae, Plesiopidae, Notograptidae, and Opistognathidae—are probably related, but whether or not they form a monophyletic group is uncertain.

About 20 genera and at least 119 species (e.g., Gill, 1999 and references below).

SUBFAMILY PSEUDOCHROMINAE



Pelvic fin with one spine and five branched soft rays; head scaled; teeth on palatine; pectoral fin rays 16–20; lateral line interrupted, two parts (one dorsoanteriorly, one midlateral posteriorly). Maximum length about 19 cm (obtained in *Labracinus*).

About six genera, *Assiculoides, Assiculus, Cypho, Labracinus, Ogilbyina,* and *Pseudochromis,* with at least 68 species (e.g., Gill and Hutchins, 1997; Gill and Randall, 1998), with several new species soon to be described.

SUBFAMILY PSEUDOPLESIOPINAE. Pelvic fin with one spine and three or four simple (unbranched) soft rays; head scaled; most dorsal fin rays simple; teeth on palatine; pectoral fin rays 17–19; lateral line with one anterior-pored scale.

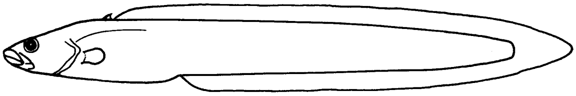
A solid foundation for monophyly of this subfamily and its genera has been laid by Gill and Edwards (1999, 2004).

Five genera, *Amsichthys* (1), *Chlidichthys* (13), *Lubbockichthys* (1), *Pectinochromis* (1), and *Pseudoplesiops* (about 10), with about 26 species (e.g., Gill and Edwards, 1999, 2002, 2003, 2004).

SUBFAMILY ANISOCHROMINAE. Pelvic fin with one spine and four soft rays (three branched and one simple), inserted distinctly in front of pectoral base; head naked; teeth absent on palatine; pectoral fin rays 13–15; single lateral line along base of dorsal fin; dorsal fin with one weak spine.

One genus, *Anisochromis,* with three species in the western Indian Ocean (Gill and Fricke, 2001).

SUBFAMILY CONGROGADINAE (EELBLENNIES). Body elongate to eel-like; body with small cycloid scales; dorsal fin with 32–79 rays, one spine before dorsal fin (absent in *Congrogadus subducens*); anal fin with 26–66 rays, no anal spines; dorsal and anal fins long; pelvic fin present (in eight species) (jugular and with one small spine and two to four soft rays) or absent (in 11 species); caudal fin confluent with dorsal and anal fins in a few species, slightly separated in most; mouth protractile; gill membranes united; opercle with strong, posteriorly directed spine on upper margin; one to three lateral lines, fully or partly complete (only *Halidesmus* has three and auxiliary lines may be present); palatine teeth absent, vomerine teeth present or absent; cordlike ligament extending from ceratohyal to dentary symphysis; egg surface with cruciform hooks. Maximum length about 40 cm. Eelblennies occur on coral reefs and on gravel and mud bottoms from the intertidal zone to about 140 m. One species is known to inhabit the insides of sponges in the Gulf of Carpentaria.



Eight genera, *Blennodesmus*, *Congrogadus*, *Halidesmus*, *Halimuraena*, *Halimuraenoides*, *Haliophis*, *Natalichthys*, and *Rusichthys*, with about 22 species (e.g., Winterbottom, 1996; Winterbottom and Randall, 1994). Indo-West Pacific.

Family GRAMMATIDAE (Grammidae) (343)—basslets. Marine; tropical western Atlantic.

Lateral line on body interrupted or absent; pelvic fin with one spine and five soft rays; spines in dorsal fin 11–13; eggs with filaments. Maximum length about 10 cm.

Species of this family and some members of the above few families (e.g., *Pseudochromis* and *Liopropoma*) are especially colorful and are popular as marine aquarium fishes.

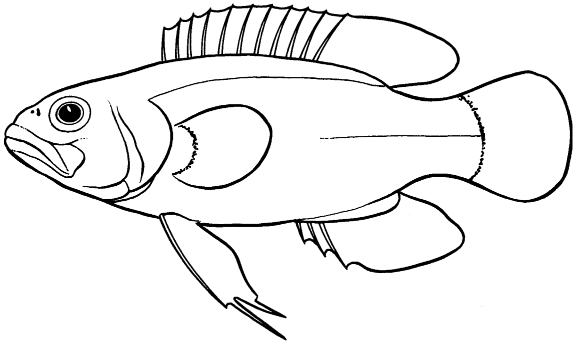
Two genera, *Gramma* (4, West Indies) and *Liopogramma* (8, tropical western Atlantic), with 12 species (e.g., Gilmore, 1997; Sazima et al., 1998).

Family PLESIOPIDAE (344)—roundheads. Marine; Indo-West Pacific.

Third branchiostegal ray extending farther posteriorly than adjacent rays resulting in a projection on the margin of the branchiostegal membrane (except in *Calloplesiops*); lateral line incomplete or disjunct. Maximum length about 20 cm.

Two subfamilies, 11 genera, and about 46 species (e.g., Mooi, 1995, 1999).

SUBFAMILY PLESIOPINAE (ROUNDHEADS OR LONGFINS)

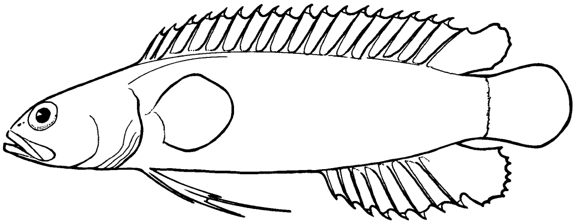


Scales on gill cover and often on top of head; dorsal fin with 11–15 spines and 6–21 soft rays; anal fin with three spines and 7–23 soft rays; pelvic fin with one spine and four soft rays. Maximum length about 20 cm.

Nelson (1994) gave the sequenced subfamily classification suggested in the 1993 cladistic study of R. D. Mooi.

Seven genera, *Assessor, Calloplesiops, Fraudella, Paraplesiops, Plesiops, Steeneichthys,* and *Trachinops.* Indo-Pacific, south to Tasmania.

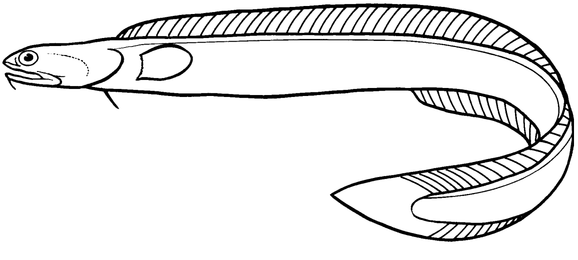
SUBFAMILY ACANTHOCLININAE (SPINY BASSLETS)



Head lacking scales or almost so; dorsal fin with 17–26 spines and 2–6 soft rays; anal fin with 7–16 spines and 2–6 soft rays; pelvic fin with one spine and two soft rays; 1–4 lateral lines; vertebrae 26–35. Maximum length about 21 cm, attained in *Acanthoclinus fuscus.*

Four genera, *Acanthoclinus, Acanthoplesiops, Beliops,* and *Belonepterygion.* Indo-West Pacific (Africa to Japan and Marshall Islands and south to New Zealand). Generally less than 70 m in depth.

Family NOTOGRAPTIDAE (345)—bearded eelblennies. Marine; southern New Guinea and northern Australia (south to northern Queensland).

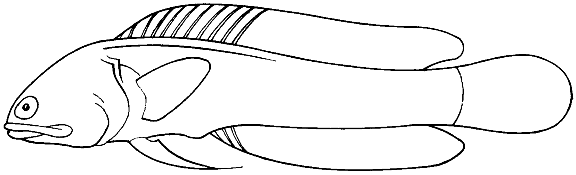


Dorsal, caudal, and anal fins confluent; dorsal fin with 62–69 spines and one or two soft rays; anal fin with 37–43 spines and one or two soft rays; caudal fin with 11 rays and a few rudimentary ones; pectoral fin rays 16–20; pelvic fin with one small, slender spine and two soft rays; median barbel on lower jaw (mental); interarcual cartilage absent; reduced gill arch skeleton; lateral line along dorsal fin base; bone of opercle deeply incised, as with many other groups such as creediids (observed in a specimen in the Academy of Natural

Sciences of Philadelphia, catalogue number ANSP 109653); vertebrae 71–75. Maximum length about 20 cm TL.

One genus, *Notograptus*, with perhaps three valid species, but the validity of the five nominal species is uncertain (e.g., Mooi, 1999).

Family OPISTOGNATHIDAE (346)—jawfishes. Marine; western and central Atlantic, Indian, and western and eastern Pacific (Gulf of California to Panama).



Mouth large; body with cycloid scales; eyes relatively large and high on head; head naked; pelvic fins ahead of pectorals, with one spine and five soft rays (inner three weak and branched and outer two stout and unbranched, unlike any other perciform); dorsal fin continuous, with 9–12 dorsal spines and usually 12–22 soft rays; anal fin with two or three spines and 10–21 soft rays; lateral line high, ending near middle of dorsal fin (one species has both a ventral and a dorsal lateral line); palate without teeth. The species of *Stalix* are probably unique among fishes in having the first 5–9 dorsal fin spines transversely forked distally (Smith-Vaniz, 1989). The males practice oral incubation. The eggs have filaments arranged around the micropyle. All jawfishes are burrow dwellers (usually having only their heads exposed) and use their large mouth to excavate their burrows. Maximum length about 40 cm; some species under 3 cm.

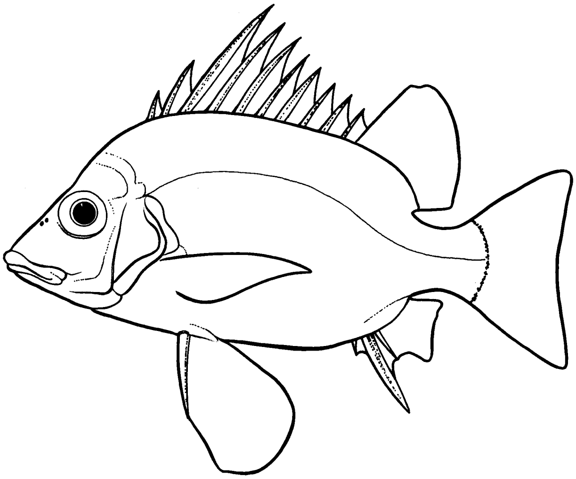
Three genera, *Opistognathus*, *Lonchopisthus*, and *Stalix*, with about 78 species (and many species remain to be described) (e.g., Bussing and Lavenberg, 2003; W.F. Smith-Vaniz in Smith and Heemstra, 1986; Smith-Vaniz, 1989, 1999, 2003, 2004).

Family DINOPERCIDAE (347)—cavebasses. Marine; Indian Ocean and eastern Atlantic Ocean off Angola.

Dorsal fin continuous but notched, with 9–11 spines and 18–20 soft rays; anal fin with three spines and 12–14 soft rays; caudal fin truncate; protruding lower jaw; exposed maxillae; large supramaxillae; preopercle serrate; frontal bones with high median crest; two opercular spines; seven branchiostegal rays; large swim bladder with three pairs of intrinsic muscles; 26 vertebrae.

Two species, *Centrarchops chapini* and *Dinoperca petersi* (Heemstra and Hecht, 1986).

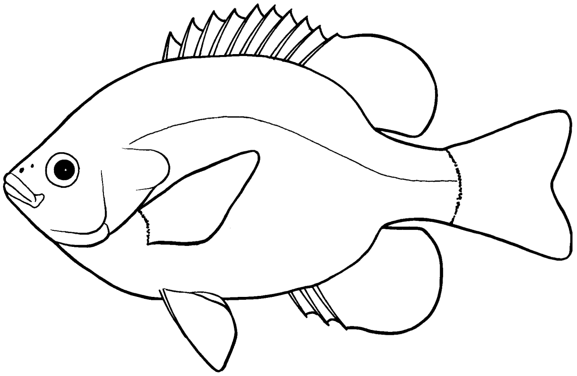
Family BANJOSIDAE (348)—banjofishes. Marine; western Pacific, primarily coasts of China, southern Japan, and Korea.

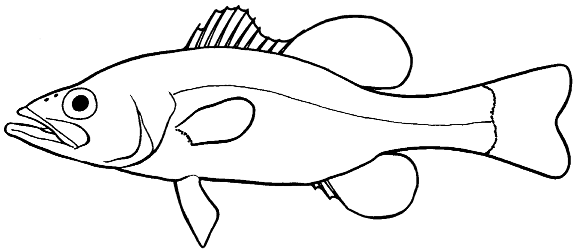


Body deep, strongly compressed; head with steep, nearly straight profile; opercle spineless; dorsal fin with 10 flattened spines and 12 soft rays; anal fin with three spines, the second much longer than the other anal rays, and seven soft rays; pelvics inserted behind base of pectorals; caudal fin slightly emarginate; lateral line continuous and complete; color brownish or olive with eight faint longitudinal darkish bands. This fish closely resembles the pomadasyids. Maximum length about 30 cm.

One species, *Banjos banjos* (e.g., Nakabo, 2002).

Family CENTRARCHIDAE (349)—sunfishes. Freshwater; North America.





Suborbital bones present in addition to the lachrymal; dentary and angular penetrated by lateral line; lateral line present on body, sometimes incomplete; anal fin spines usually three (or fewer, typically in species of *Enneacanthus, Lepomis,* and *Micropterus*) or five (or more, typically in species of *Acantharchus, Ambloplites, Archoplites, Centrarchus,* and *Pomoxis*); dorsal fin usually with 5–13 spines (most with 10–12); pseudobranch small and concealed; branchiostegal rays 6 or 7; gill membranes separate; vertebrae 28–33.

Most sunfishes are nest builders. The male hollows out a small depression with his tail and then guards the eggs. Centrarchids are an important sports fish and have been introduced into many areas beyond their native range. Some, such as *Lepomis macrochirus,* the Bluegill, have been used in physiological and ecological experimental work. Maximum length about 83 cm, attained in *Micropterus salmoides* (Largemouth Bass).

Centrarchids were widespread west of the Rocky Mountains by the Late Miocene; the fossil record includes *Plioplarchus* and species of extant genera.

Eight genera with 31 species. The classification with genera recognized is based on Roe et al. (2002) and the species numbers are from Nelson et al. (2004). Gilbert (1998) gives a type catalogue of recent and fossil taxa.

SUBFAMILY CENTRARCHINAE. Five genera, *Ambloplites* (4), *Archoplites* (1, the Sacramento Perch, is the only living centrarchid native west of the Rocky Mountains), *Centrarchus* (1), *Enneacanthus* (3), and *Pomoxis* (2, crappies), with 11 species.

SUBFAMILY LEPOMINAE. One genus, *Lepomis* (12, upper figure, synonym *Chaenobryttus*).

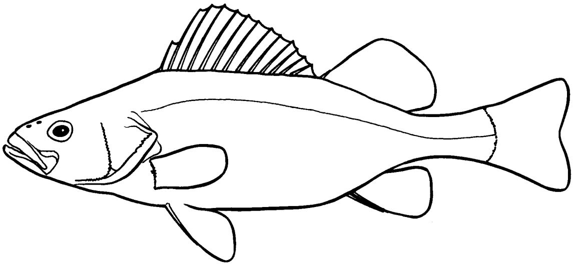
SUBFAMILY uncertain. The genera *Acantharchus* (1) and *Micropterus* (7, basses) (lower figure) are of uncertain relationships and not placed in either subfamily until their relationships are better known.

Family PERCIDAE (350)—perches. Freshwater; Northern Hemisphere.

Two dorsal fins, separate or narrowly joined (broadly joined in *Zingel*); one or, usually, two anal spines (the second is usually weak); pelvic fins thoracic, with one spine and five soft rays; premaxilla protractile or nonprotractile; branchiostegal rays 5–8; branchiostegal membrane not joined to isthmus (may be united to each other or not); pseudobranchiae well developed to rudimentary; no subocular shelf; supramaxilla absent; one or no predorsal bones (rarely two) (interneural before first pterygiophore); vertebrae 32–50. Maximum size up to 90 cm, attained in *Sander vitreus* (Walleye); most species much smaller.

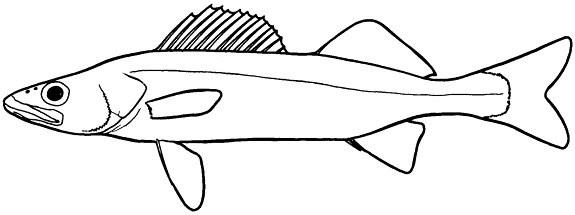
Ten genera with 201 species (187 in North America and 14 in Eurasia). The number of species in the genera endemic to North America is from Nelson et al. (2004), which is based on a series of continuing studies describing new species. The classification of Song et al. (1998) is followed below where three monophyletic groups are each recognized as subfamilies. The two tribes of the subfamily Percinae in Nelson (1994) are now recognized as subfamilies (i.e., Percinae and Etheostomatinae). *Mioplosus,* an Eocene Green River Formation percoid, may have its closest affinity with the percids (Grande, 1984), but more work is needed before we can understand its relationships (Grande, 2001).

Subfamily Percinae. Anteriormost interhaemal bone greatly enlarged; anal spines usually well developed; preopercle strongly serrate; usually seven or eight branchiostegal rays; body compressed; anal spines prominent; swim bladder well developed.



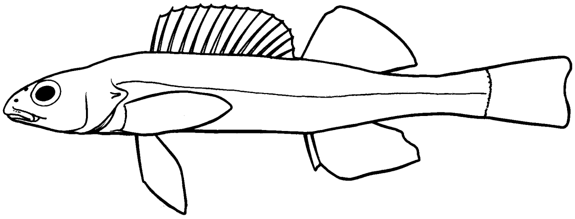
Three genera with eight species: the circumpolar *Perca* (3, the Eurasian *P. fluviatilis* which has been introduced into South Africa, Australia, and New Zealand, the almost identical North American *P. flavescens,* and *P. schrenki* of the Balkhash and Alakul' lakes area of Asia); the European and western Asian *Gymnocephalus* (4); and *Percarina demidoffi* of the northern Black Sea area. The biology of various species, especially of *Perca,* is given by Craig (2000).

Subfamily Luciopercinae. Anteriormost interhaemal no larger than posterior ones; anal spines weak; lateral line extending onto tail.



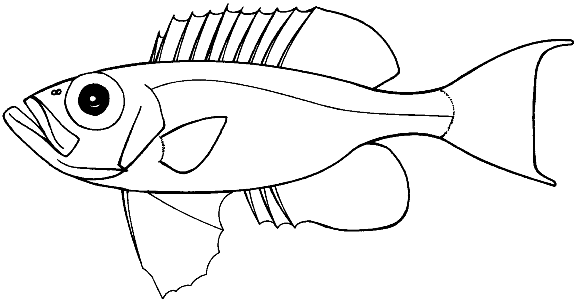
Three genera and nine species. Contains the genus of predaceous pikeperches, *Sander* (synonym *Stizostedion*), possessing a well-developed swim bladder, with three species in Europe (including the Caspian and Aral seas) and two species (Sauger and Walleye) in North America. It also contains two genera of European darterlike fishes lacking a swim bladder, *Zingel,* with three species, of the Danube, Rhone, and Vardar systems and the very restricted *Romanichthys valsanicola* of Romania.

Subfamily Etheostomatinae. Anteriormost interhaemal bone greatly enlarged; anal spines usually well developed; preopercle margin smooth or partly serrated; usually five or six branchiostegal rays; body slightly compressed or fusiform; anal spines moderately prominent; swim bladder reduced or absent. Seldom over 11 cm.



Four genera of North American darters: *Ammocrypta* (6), *Crystallaria* (with one species, *C. asprella*), *Etheostoma* (136), and *Percina* (41), giving a total of 184 described species (species listed in Nelson et al., 2004). There are many studies on North American darters, with many new species described in the last few decades (as noted in Nelson et al., 2004); much of this work has been done by L. M. Page and his students (e.g., Burr and Page, 1993; Page et al., 2003).

Family PRIACANTHIDAE (351)—bigeyes (catalufas). Marine; tropical and subtropical, Atlantic, Indian, and Pacific.

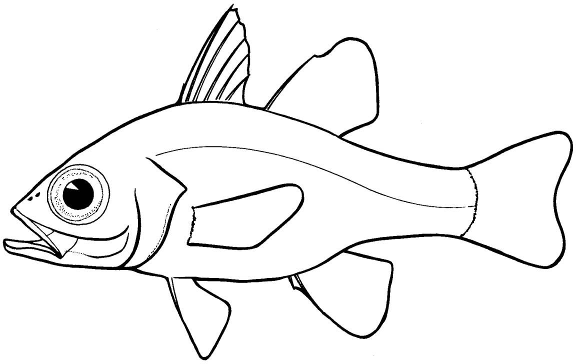


Eyes very large; mouth large, strongly oblique; dorsal fin continuous, usually with 10 spines and 11–15 soft rays; anal fin with three spines and 10–16 soft rays; caudal fin with 16 principal rays (14 branched), slightly emarginate to rounded; membrane present connecting the inner rays of the pelvic fin to the body; scales modified spinous cycloid (with strong spines but not ctenoid); scales on the branchiostegal membrane; color usually bright red; vertebrae 23 (very few other percoids have so few vertebrae).

Bigeyes are usually carnivorous and nocturnal. The tapetum lucidum, a brilliant reflective layer producing "eyeshine," may be of a unique form among teleosts. Maximum length about 65 cm TL.

Four genera, *Cookeolus*, *Heteropriacanthus*, *Priacanthus*, and *Pristigenys*, with about 18 species (e.g., Starnes, 2003). The fossil record is discussed in the 1988 revision of W. C. Starnes.

Family APOGONIDAE (352)—cardinalfishes. Marine, some brackish water, a few in streams in the tropical Pacific; Atlantic, Indian, and Pacific.



Two separated dorsal fins, the first with 6–8 spines and the second with one spine and 8–14 soft rays (*Paxton* has a continuous dorsal fin); anal fin with two spines and 8–18 soft rays; scales usually ctenoid, but cycloid in several groups and absent in *Gymnapogon*; seven branchiostegal rays; usually 24 vertebrae (10 + 14). Several other families have widely separated dorsal fins, but this is the only one in which the distal radial of the last spine is short (vs elongate) (Johnson, 1993). Species of *Siphamia* have a ventral luminous organ. Many of the species are mouthbreeders; it is suspected that in some only the males incubate the eggs, whereas in others it is only the females. Most species nocturnal. Maximum length usually about 20 cm, and most are less than 10 cm.

The nine species of *Glossamia* are found only in freshwater; they occur primarily in New Guinea but also in Australia. A few species of *Apogon* occur in estuaries and the lower reaches of rivers. The relatively deep dwelling (60–290 m) *Apogon gularis* is unique among apogonids in having the anus located just behind the origin of the pelvic fins. Baldwin and Johnson (1999) supported the recognition of the following two subfamilies.

About 23 genera and roughly 273 species.

SUBFAMILY APOGONINAE. Oral incubation of eggs in at least many species. About 19 genera (e.g., *Apogon, Apogonichthys, Archamia, Astrapogon, Cercamia, Cheilodipterus, Coranthus, Foa, Fowleria, Glossamia, Neamia, Phaeoptyx, Rhabdamia, Siphamia,* and *Vincentia*), with about 260 species (Fraser, 2000, 2005; Allen, 2001; Greenfield, 2001; Gon, 2003; Gon and Randall, 2003a, b).

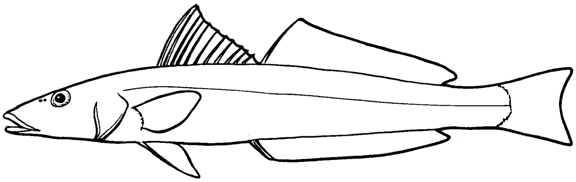
SUBFAMILY PSEUDAMINAE. Large canine teeth always present on dentary and premaxillae; lateral line incomplete or absent; scales cycloid or absent. Four genera, *Gymnapogon, Paxton, Pseudamia,* and *Pseudamiops*, with roughly 13 species (e.g., Baldwin and Johnson, 1999).

Family EPIGONIDAE (353)—deepwater cardinalfishes. Marine; Atlantic, Indian, and Pacific.

Differ from apogonids in having vertebrae usually 25; infraorbitals more than six; ascending processes of premaxillaries reduced or absent; rostral cartilage greatly enlarged; soft dorsal and anal fins covered with scales. *Sphyraenops* has three opercular spines as do serranids. Maximum length about 58 cm.

Six genera, *Brinkmannella, Epigonus, Florenciella, Microichthys, Rosenblattia,* and *Sphyraenops,* with roughly 25 species (e.g., McCosker and Long, 1997; Gon, 2003).

Family SILLAGINIDAE (354)—sillagos (whitings, smelt-whitings). Marine (coastal) and brackish water, rarely into freshwater; Indo-West Pacific.



Body elongate; mouth small; two dorsal fins (little or no interspace), first with 10–13 spines (second spine elongate in *Sillaginopsis*) and second with one slender spine and 16–27 soft rays; anal fin with two small spines and 14–26 soft rays; three predorsal bones; swim bladder absent or vestigial (in *Sillaginopsis*) to highly complex with various extensions; vertebrae 32–44 (their number is highly variable for a small percoid family). Maximum length usually about 45 cm, up to about 70 cm.

The juveniles of several species commonly enter estuaries; a few species extend into freshwater, and then only rarely. Members occur in relatively shallow water and extend from South Africa to Japan and Australia. The common name "whitings" is used in Australia, but it is used elsewhere for some gadiforms.

Three genera (the first two monotypic), *Sillaginodes, Sillaginopsis,* and *Sillago,* with a total of about 31 species (McKay, 1992).

Family MALACANTHIDAE (355)—tilefishes. Marine; Atlantic, Indian, and Pacific.

Dorsal fin relatively long, continuous, and with spines and soft rays (total of 22–84 elements); anal fin relatively long, with one or two weak spines and 11–55 soft rays; pelvic fin with one spine and five soft rays; single opercular spine, sharp and strong in Malacanthinae and *Caulolatilus*; six branchiostegal rays; caudal fin truncate to variously forked; 24, 25, or 27 vertebrae (10 or 11 precaudal vertebrae); larvae with elaborate head and scale spination.

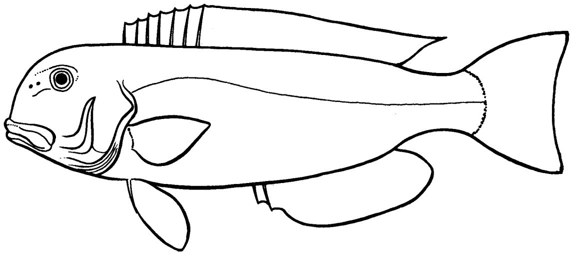
Reasons for recognizing the tilefishes in one family, instead of two, were given in Nelson (1984) and a 1984 paper of G. D. Johnson. For a proposal by Imamura (2000) to combine this family with the Dactylopteridae see above under suborder Dactylopteroidei (order of Scorpaeniformes). Imamura (2000) gave reasons for recognizing this new group, under the family name Dactylopteridae, with four subfamilies, Branchiosteginae, Malacanthinae, Hoplolatilinae, and Dactylopterinae. Springer and Johnson (2004) felt Imamura's conclusions needed further study, but Springer maintained the association of Dactylopteridae and Malacanthidae by recognizing the two families in the suborder, Dactylopteroidei, placed after the Nothenthioidei (Johnson does not agree with this placement or that of Imamura, 2000, G.D. Johnson, pers. comm., 2005).

Five genera and about 40 species.

SUBFAMILY MALACANTHINAE (SAND TILEFISHES). Predorsal ridge absent; enlarged spine at angle of preoperculum in some; body usually more enlongate than in Latilinae, head rounded in profile; dorsal fin with 1–4 spines and 43–60 soft rays (*Malacanthus*) or 3–10 spines and 13–34 soft rays (*Hoplolatilus*); anal fin with 12–55 soft rays in addition to the spines. Sand tilefishes, unlike members of Latilinae, are known to construct or inhabit mounds or borrows. They are usually found in depths less than 50 m, whereas latilines are usually found at depths more than 50 m.

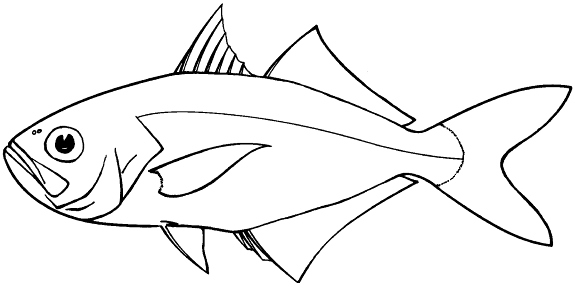
Two genera, *Malacanthus* (3) and *Hoplolatilus* (9), with 12 species (e.g., Earle and Pyle, 1997).

SUBFAMILY LATILINAE (= BRANCHIOSTEGINAE) (TILEFISHES). Predorsal ridge present; never an enlarged spine at angle of preopercle; body depth usually greater than in malacanthines; head rounded to squarish in profile; dorsal fin with 6–10 spines and 14–27 soft rays; anal fin with 11–26 soft rays in addition to the spines. Species are found at depths of 20–600 m.



Three genera, *Caulolatilus*, *Lopholatilus*, and *Branchiostegus*, with about 28 species (e.g., Dooley, 2003).

Family LACTARIIDAE (356)—false trevallies. Marine; Indo-West Pacific.



Dorsal fins separate; soft-rayed portion of dorsal and anal fins covered with scales (all scales easily shed); each jaw with two small canine teeth at front; 24 vertebrae. Maximum length 40 cm TL.

One species, *Lactarius lactarius.*

Family DINOLESTIDAE (357)—long-finned pikes. Marine; southern Australia.

Body shape much like *Sphyraena*; lower jaw extending beyond upper jaw; vomer and palatine with teeth, some teeth in mouth caninelike; head, including maxilla, snout, and occiput covered with scales; axillary scale at pelvic base; dorsal fins widely separated, first with four or five visible spines, second with one short spine and 17–19 soft rays; anal fin with one short spine and 25–28 soft rays; lateral line scales about 63–70, cycloid; lateral line continuing onto caudal fin; vertebrae 27 (10 + 17). Maximum length about 80 cm TL.

One species, *Dinolestes lewini* (Last et al., 1983; Paxton et al., 1989).

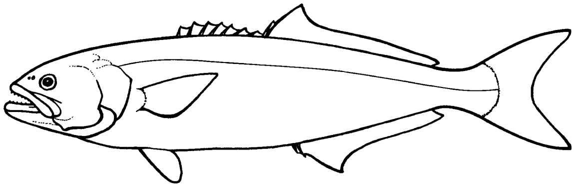
Family SCOMBROPIDAE (358)—gnomefishes. Marine; Indo-West Pacific and western Atlantic.

Eyes relatively large; two moderately high dorsal fins, first with 7–10 spines.

This genus was placed in the family Pomatomidae in Nelson (1994). There, I noted the research of G. D. Johnson published in 1984 and 1986, placing this genus in its own family. I now follow this placement. Johnson in 1986 (see Johnson, 1993:12) also concluded that *Scombrops* and *Pomatomus*, along with some acropomatids and *Scombrolabrax*, may be related to the scombroids (this possible relationship should be studied further). Heemstra (2003a) placed the genus in Acropomatidae. At least two species are Indo-West Pacific with *Scombrops oculatus* being widespread (it being the only one in the Atlantic, e.g., Bahamas and Caribbean Sea area).

One genus, *Scombrops*, with about three species (Smith-Vaniz et al., 1999; Heemstra, 2003a).

Family POMATOMIDAE (359)—bluefishes. Marine; Atlantic, Indian, and Pacific.



Dorsal fins separate, the first with seven or eight short spines and the second with one spine and 23–28 soft rays; anal fin with two or three spines and 23–27 soft rays; soft dorsal and anal fins covered with scales; jaw teeth prominent, ankylosed; preoperculum with a membrane flap over the suboperculum; black blotch at base of pectoral; 26 vertebrae. Maximum length 1.1 m.

The cosmopolitan *Pomatomus saltatrix* (Bluefish) is described as being a voracious predator, killing more fish than it can consume. See note above under family Scombropidae.

One species, *Pomatomus saltatrix* (e.g., Collette and Klein-MacPhee, 2002; Collette, 2003c).

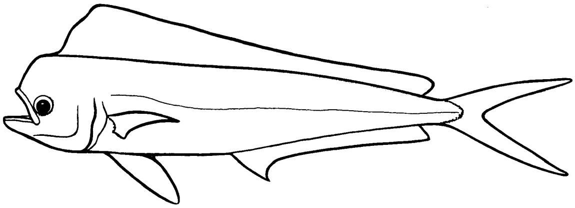
Carangoid lineage—consists of the next five families, Nematistiidae, Coryphaenidae, Rachycentridae, Echeneidae, and Carangidae. The 1984 works of G. D. Johnson and of W. F. Smith-Vaniz found Coryphaenidae, Rachycentridae, and Echeneidae to comprise a monophyletic group, with this clade being sister to Carangidae (these two studies differ in some details of relationships from that of O'Toole, 2002, see below under Coryphaenidae, and further analysis is desired).

Family NEMATISTIIDAE (360)—roosterfishes. Marine; tropical eastern Pacific.

Body compressed; small cycloid scales, about 120–130 in irregular series along lateral line (no scutes along lateral line); first dorsal with seven very elongate spines (which normally rest in a groove), second with one spine and 25–28 soft rays; anal fin with three spines (none detached from rest of fin) and about 15–17 soft rays; unique otophysic connection, swim bladder enters skull through large foramina in basioccipital and contacts inner ear (presumably increasing hearing sensitivity); 24 vertebrae (10 abdominal and 14 caudal).

One species, *Nematistius pectoralis* (Roosterfish), which is a popular gamefish ranging from southernmost California to Peru.

Family CORYPHAENIDAE (361)—dolphinfishes. Marine; Atlantic, Indian, and Pacific.



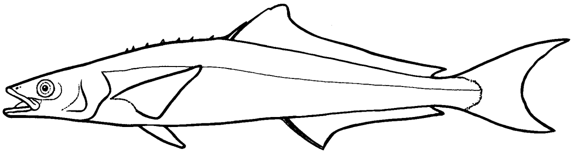
Dorsal fin originating on head, with 48–65 rays; no spines in dorsal and anal fins; caudal fin deeply forked; forehead prominent (steep and high) in adult males of the largest of the two species; color in life exceedingly beautiful; vertebrae 30–34. Maximum length 1.5 m, attained in *Coryphaena hippurus*. The term dolphinfish for the common name is preferred to the commonly used term dolphin to avoid confusion with the cetacean mammals known as dolphins. In parts of the Pacific, dolphinfishes are also known as mahimahi (and this is the name commonly used on restaurant menus). The common names for the two species are Pompano Dolphinfish (Spanish dorado enano) and Dolphinfish (Spanish dorado) (Nelson et al., 2004).

This family and the Rachycentridae and Echeneidae are thought by O'Toole (2002) to form a monophyletic group, with Coryphaenidae being the sister group to the clade of Rachycentridae + Echeneidae (O'Toole, 2002).

Nematistiidae and Carangidae are also hypothesized by O'Toole (2002) to be part of a clade with these three families, perhaps forming a trichotomy (see also above under Carangoid lineage).

One genus, *Coryphaena*, with two species (e.g., Smith-Vaniz et al., 1999; Collette, 2003c).

Family RACHYCENTRIDAE (362)—cobias. Marine; Atlantic and Indo-Pacific.

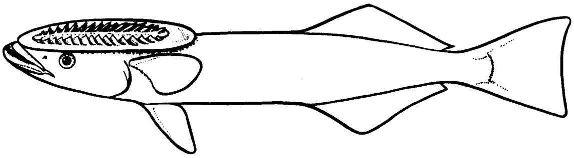


Body elongate, head depressed; 6–9 short free spines ahead of the long dorsal fin (1–3 spines and 26–33 soft rays); anal fin long, with two or three spines and 22–28 soft rays; three dark stripes on side of body; 25 vertebrae. Maximum length up to 1.5 m.

See note on sister-group relationships above under family Coryphaenidae.

One species, *Rachycentron canadum* (e.g., Smith-Vaniz et al., 1999; Collette, 2003c).

Family ECHENEIDAE (Echeneididae) (363)—remoras (sharksuckers). Marine; Atlantic, Indian, and Pacific.

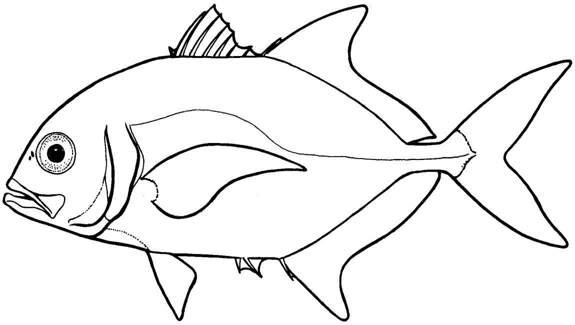


Body elongate, head flattened, and lower jaw projecting past upper jaw; scales small, cycloid; dorsal and anal fins lacking spines, each with about 18–45 soft rays; swim bladder absent; branchiostegal rays 8–11; 26–41 vertebrae; sucking disc on head (developed from a transformed spinous dorsal fin, the spines of which are split to form 10–28 transverse movable lamina inside a fleshy margin). The remora presses the disc against other fishes and creates a partial vacuum by operating the movable disc ridges like the slats in a Venetian blind, thereby causing the sucking action that permits it to obtain rides on larger animals. Remoras are found on sharks, bony fishes, sea turtles, and marine mammals; some species show considerable host specificity. A fully formed disc is present in specimens as small as 27 mm. Maximum length about 1.0 m, attained in *Echeneis naucrates*. The smallest species is 17 cm.

See note on sister-group relationships above under family Coryphaenidae. A Lower Oligocene fossil was described by N. Micklich in 1998.

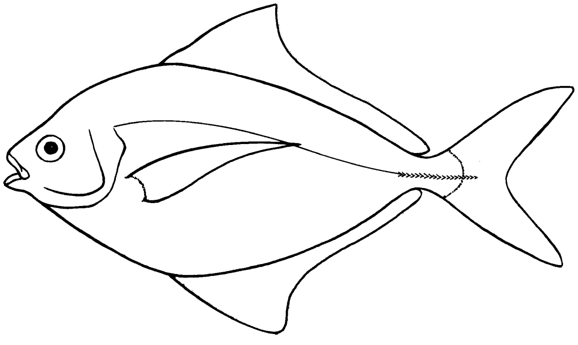
Four genera, *Echeneis*, *Phtheirichthys*, *Remora*, and *Remorina*, with eight widespread species (Smith-Vaniz et al., 1999; O'Toole, 2002; Collette, 2003c).

Family CARANGIDAE (364)—jacks and pompanos. Marine (rarely brackish); Atlantic, Indian, and Pacific.



Body generally compressed (but ranging from very deep to fusiform); only small cycloid scales in most species, ctenoid in a few (some scales on the lateral line are modified into spiny scutes in many species), naked areas variously developed; up to nine detached finlets sometimes present behind dorsal and anal fins (counts for these rays are included in following ray counts); two dorsal fins in large juveniles and adults, the first with 4–8 spines (which in a few species are very short and lack a continuous membrane) and the second with one spine and 17–44 soft rays; usually three anal spines with the first two (rarely only one) detached from the rest of the anal fin and usually 15–39 soft rays; caudal fin widely forked; caudal peduncle slender; vertebrae 24–27 (usually 24).

Carangids are extremely variable in body shape, ranging from the shallow-bodied *Decapterus* and *Elagatis* to the extremely thin and deep-bodied *Selene*. The family contains some very important food species. The juveniles of some species extend into estuaries.



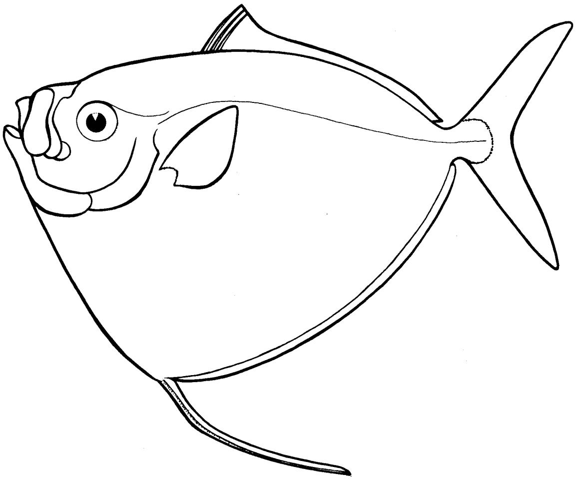
Two carangid species lack the pelvic fins, the surf inhabiting *Parona signata* from off southern Brazil and Argentina, and the epipelagic *Parastromateus niger* (in above figure), from the Indo-West Pacific. The latter species, which has a small pelvic fin in juveniles under 9 cm, was placed in its own family, Apolectidae (Formionidae), in Nelson (1984); placement in Carangidae follows the 1984 study of W. F. Smith-Vaniz. Both species have a deep and extremely compressed body, but what the selective forces are that are causing an independent loss of the pelvic fins in the only percoids to lack these fins is unknown; their ecology and swimming behavior are very dissimilar. Paleocene-Eocene species of the genus *Trachincaranx*, which have the pelvic fins, may be relatively closely related to *Parastromateus*.

Some of the common names used for carangids are amberjacks, jacks, moonfishes, pilotfish, rudderfishes, pompanos, scads, and trevallies (singular trevally = crevally).

About 32 genera and 140 species (e.g., Smith-Vaniz et al., 1999; Smith-Vaniz, 2003). Four subfamilies are provisionally recognized following the major 1984 study of W. F. Smith-Vaniz (he ranked them as tribes). S. Gushiken published a phylogenetic study in 1988.

Trachinotinae—Two genera, *Lichia* and *Trachinotus*, with 21 species.
Scomberoidinae—Three genera, *Oligoplites*, *Parona*, and *Scomberoides*, with 10 species.
Naucratinae—Five genera, *Campogramma*, *Elagatis*, *Naucrates*, *Seriola*, and *Seriolina*, with 13 species.
Caranginae—only subfamily with scutes present. Twenty-two genera (e.g., *Alectis*, *Atropus*, *Carangoides*, *Caranx*, *Chloroscombrus*, *Decapterus*, *Gnathanodon*, *Hemicaranx*, *Megalaspis*, *Parastromateus*, *Pseudocaranx*, *Selar*, *Selene*, *Trachurus*, and *Uraspis*) with about 96 species (the status of *Citula* is uncertain).

Family MENIDAE (365)—moonfishes. Marine; Indo-West Pacific.

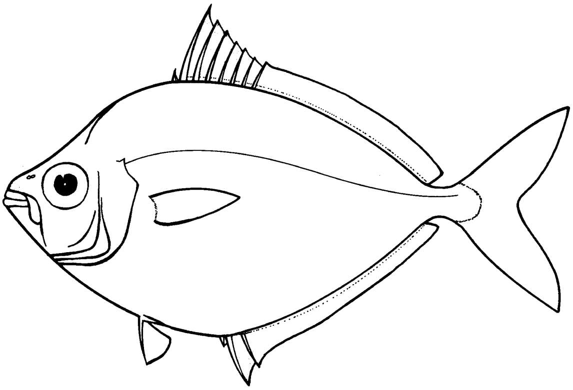


Body compressed, disclike, with sharp breast; dorsal contour nearly horizontal; mouth highly protrusible; dorsal fin with 43–45 soft rays, no spines; anal fin with 30–33 soft rays, no spines; first pelvic ray in adult prolonged.

V. G. Springer in Springer and Johnson (2004) placed Menidae in its own order, Meniformes, between Tetraodontiformes (which he regarded as pre-perciform) and Beryciformes, and suggested it might be more closely related to pre-percomorphs than to percomorphs. Coauthor Johnson strongly disagrees with this placement (G. D. Johnson, pers. comm., 2005), as detailed in a study by M. Friedman and G.D. Johnson (in press). I await publication of ongoing studies before making any changes and maintain it in the percoids near the carangids.

One species, *Mene maculata.*

Family LEIOGNATHIDAE (366)—ponyfishes, slimys, or slipmouths. Marine and brackish water; Indo-West Pacific.



Body greatly compressed and slimy, with small scales; head usually naked, upper surface with bony ridges; gill membranes united with isthmus; mouth small and highly protrusible; teeth absent on palate; no pseudobranchiae; dorsal fin continuous, the anterior portion usually with eight or nine spines that are more or less elevated and the posterior portion with 14–16 soft rays; anal fin with three spines and 14 soft rays; both dorsal and anal fins fold into a basal scaly sheath; branchiostegal rays four or five; vertebrae 22–24. Ventral portion of body very silvery. The dorsal and anal fin spines have a locking mechanism. Leiognathids have a circumesophageal light organ with bacterial luminescence.

Three genera, *Gazza, Leiognathus* (synonym *Equula*), and *Secutor,* with about 30 species (e.g., Yamashita and Kimura, 2001; Kimura et al., 2003).

Family BRAMIDAE (367)—pomfrets. Marine; oceanic, Atlantic, Indian, and Pacific.

Single dorsal fin (extending length of body in some) with unbranched anterior spines; anal spines lost; 36–54 vertebrae. *Eumegistus* is thought to be the most primitive genus. Maximum length 85 cm, attained in *Taractichthys longipinnis.*

Seven genera with about 22 species (Yatsu and Nakamura, 1989; Moteki et al., 1995; Thompson and Russell, 1996; Hartel and Triant, 1998; Thompson, 2003).

SUBFAMILY BRAMINAE. Dorsal and anal fins of adults with scales and not wholly depressible; pelvic fins thoracic. Oligocene fossils of *Paucaichthys* are known from Romania (Baciu and Bannikov, 2003).

Five genera, *Brama, Eumegistus, Taractes, Taractichthys,* and *Xenobrama.*

SUBFAMILY PTERACLINAE. Dorsal and anal fins high, scaleless, and completely depressible; pelvic fins often jugular or nearly so.

Two genera, *Pteraclis* and *Pterycombus.*

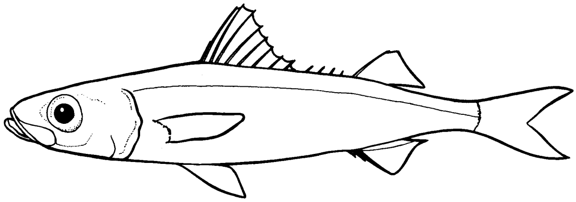
Family CARISTIIDAE (368)—manefishes. Marine; oceanic.

Body deep; dorsal fin high and with long base (origin on head); anal spines lost; pelvic fins elongate, in advance or behind pectoral fin base, with one spine and five soft rays; 15 branched caudal rays; seven branchiostegal rays; 35–40 vertebrae.

These fishes have an association with siphonophores, including feeding on them. As noted by Hartel and Triant (1998) this small family is badly in need of revision.

Two genera, *Caristius* (4) and *Platyberyx* (1), with about five species (e.g., Hartel and Triant, 1998).

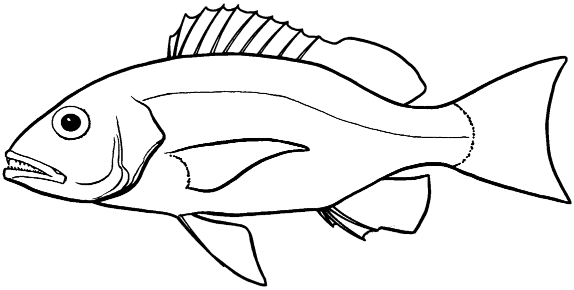
Family EMMELICHTHYIDAE (369)—rovers. Marine; primarily tropical to warm temperate regions of Indo-Pacific, southern Pacific, eastern Atlantic, and Caribbean Sea.



Jaws toothless or nearly so, very protractile; maxilla expanded distally, scaled, and not covered by preorbital bone when mouth closed; supramaxilla well developed; rostral cartilage large; dorsal fin continuous but with slight notch (*Plagiogeneion*), divided to base (*Erythrocles*), or with an apparent gap with intervening isolated short spines visible or not (*Emmelichthys*, as shown in figure); dorsal fin with 11–14 spines and 9–12 soft rays; anal fin with three spines and 9–11 soft rays; caudal fin forked with the two lobes folding in scissorlike fashion; seven branchiostegal rays; 24 vertebrae (10 + 14). Maximum length up to 50 cm. Adults are usually near the bottom in depths of 100–400 m.

Three genera, *Plagiogeneion* (5), *Emmelichthys* (4), and *Erythrocles* (6), with 15 species (Miyahara and Okamura. 1998; Heemstra, 2003b).

Family LUTJANIDAE (370)—snappers. Marine (rarely in freshwater and estuaries); tropical and subtropical, Atlantic, Indian, and Pacific.



Dorsal fin continuous or with a shallow notch, with 9–12 spines and 9–18 soft rays; anal fin with three spines and 7–11 soft rays; pelvic fins inserted just behind pectoral base; mouth terminal, moderate to large; most with enlarged canine teeth on jaws, small teeth on palatines and usually on vomer; maxilla slips beneath preorbital when mouth closed; supramaxilla absent; seven branchiostegal rays; caudal fin truncate to deeply forked; 24 vertebrae (10 + 14). Maximum length about 1.0 m.

Nelson (1994) gave reasons for treating the Caesionidae as a subfamily. I now change back to the classification followed in Nelson (1984) until there is more original research clearly showing the cladistic relationships of all taxa involved.

Snappers are important food fishes but are sometimes responsible for ciguatera, the tropical fish-poisoning disease. They generally occur near the bottom in tropical and subtropical seas from shallow water to depths of about 550 m. Three species of *Lutjanus*, *L. fuscescens*, *L. goldiei*, and perhaps *L. maxweberi* of the Philippine-New Guinea region, are known only from freshwater and estuaries (not from purely marine waters). The juveniles of several otherwise marine species of *Lutjanus* are known to enter brackish and freshwater.

Seventeen genera with about 105 species recognized in four subfamilies (e.g., Anderson, W. D., Jr. 2003a).

SUBFAMILY ETELINAE. Five genera, *Aphareus*, *Aprion*, *Etelis*, *Pristipomoides*, and *Randallichthys*, with 19 species.

SUBFAMILY APSILINAE. Four genera, *Apsilus*, *Lipocheilus*, *Paracaesio*, and *Parapristipomoides*, with 12 species.

SUBFAMILY PARADICHTHYINAE. Two monotypic genera, *Symphorichthys* and *Symphorus*.

SUBFAMILY LUTJANINAE. Six genera, *Hoplopagrus*, *Lutjanus*, *Macolor*, *Ocyurus*, *Pinjalo*, and *Rhomboplites*, with about 72 species (the genus *Lutjanus*, has about 64 species).

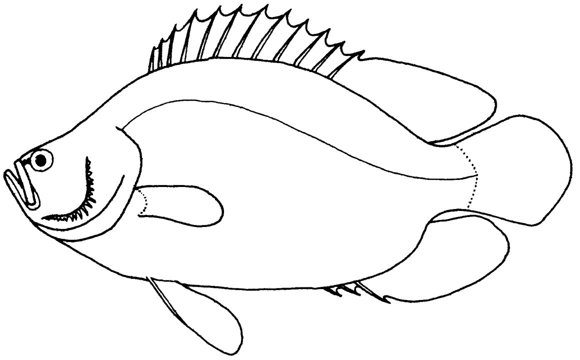
Family CAESIONIDAE (371)—fusiliers. Marine; Indo-West Pacific.

Ascending premaxillary process as a separate ossification from premaxilla; dorsal fin continuous with 10–15 slender spines and 8–22 soft rays; anal fin with three spines and 9–13 soft rays; mouth slightly upturned, small, and highly protrusible; jaw teeth small (absent in two species); caudal fin deeply forked; lateral line scales 45–88; seven branchiostegal rays; 24 vertebrae. Fusiliers are planktivorous in contrast to the snappers, which tend to be benthic carnivores. Maximum length about 60 cm.

For comments on change in family recognition, see above under Lutjanidae.

Four genera, *Caesio, Dipterygonotus, Gymnocaesio,* and *Pterocaesio,* with 20 species (Carpenter, 1990, 2001). *Dipterygonotus* and *Gymnocaesio* are monotypic.

Family LOBOTIDAE (372)—tripletails. Marine, brackish, and freshwater; most warm seas.



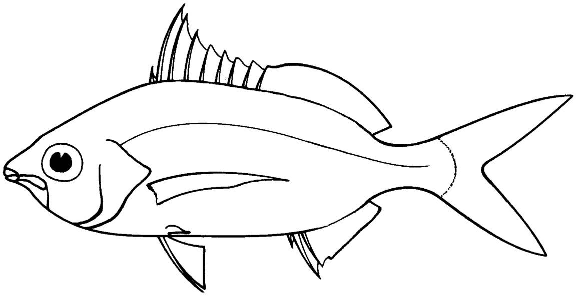
Palatine and vomer toothless; caudal fin rounded, profile similar to centrarchids; rounded lobes on anal and second dorsal fins giving fish the appearance of having three tails; dorsal fin with 12 spines and 15 or 16 soft rays; 24 vertebrae.

The very young can camouflage themselves by turning sideways and floating like leaves. Maximum length about 1.0 m.

The inclusion of the species of *Datnioides* (tigerperches) in this family is provisional; some works place it in its own family or have aligned it with other families. If recognized in its own family, Kottelat (2000b) argued that the valid family-group name is Datnioididae. Species of *Datnioides* have been recognized under the generic name *Coius* (family Coiidae) (e.g., Kottelat, 1998:111); but Kottelat (2000b) regarded *Coius* as a synonym of *Anabas,* thus Datnioididae can no longer be considered a synonym of Coiidae. Although there is no firm evidence that *Labotes* and *Datnioides* form a monophyletic group, I retain them in the same family as a conservative measure until a phylogenetic study demonstrates other relationships.

Two genera, *Datnioides* (with about three species that are freshwater and brackish water from India to Borneo and New Guinea) and *Lobotes* (at least two species, marine), with about five species.

Family GERREIDAE (373)—mojarras. Marine (occasionally brackish and rarely in freshwater); most warm seas.

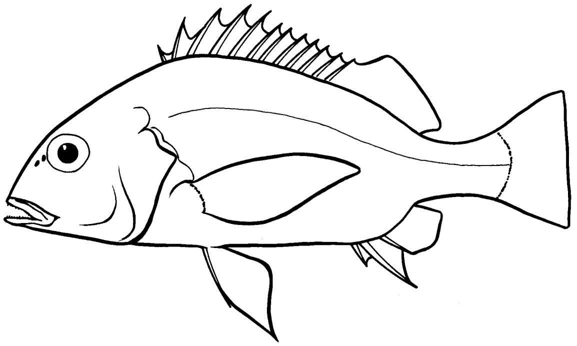


Mouth highly protrusible; head scaly, upper surface smooth; scaly sheath along bases of dorsal and anal fins; dorsal fin with 9 or 10 spines and 9–17 soft rays; scales usually cycloid and often partially deciduous; gill membranes free from isthmus; tail deeply forked; 24 vertebrae. Maximum length 41 cm SL.

Eugerres mexicanus, of southern Mexico and northern Guatemala, is confined to freshwater. In addition, several species that are otherwise marine enter rivers (for example, *Eucinostomus melanopterus* and five species of *Gerres* in Africa, with *G. filamentosus* also in the Australian region, and species of *Diapterus*, *Eugerres*, and *Eucinostomus* in the New World).

Eight genera, *Diapterus*, *Eucinostomus*, *Eugerres*, *Gerres*, *Parequula*, *Pentaprion* (with five or six spines in anal fin), *Ulaema*, and *Xystaema*, with about 44 species (e.g., Iwatsuki et al., 2002; Ruiz-Carus and Uribe-Alcocer, 2003; Gilmore and Greenfield, 2003).

Family HAEMULIDAE (Pomadasyidae) (374)—grunts. Marine (many in brackish water, rarely in freshwater); Atlantic, Indian, and Pacific.



Dorsal fin continuous, with 9–14 spines and 11–26 soft rays; anal fin with three spines and 6–18 soft rays; mouth small; teeth on jaws usually cardiform, generally absent on vomer; enlarged chin pores usually present; seven branchiostegal rays; 26 or 27 vertebrae (10 or 11 + 16). Maximum length about 60 cm.

In a 1980 study, G. D. Johnson recognized two subfamilies: the Haemulinae, primarily of the New World with a short dorsal fin of 13–16 soft rays, and the Plectorhynchinae, of the Indo-West Pacific and eastern Atlantic with a long dorsal fin of 17–26 soft rays (comprises the last three genera listed below). Fishes in the last subfamily often have thick fleshy lips as adults (these are called the rubberlips or sweetlips) and are brightly colored. The eastern tropical Atlantic *Parakuhlia macrophthalmus* may belong in this family, but it has been placed in the Kuhliidae by many. Springer and Raasch (1995) established the family name Hapalogeniidae (Haplogeniidae) for *Hapalogenys*, a genus of uncertain relationships.

Seventeen genera—e.g., *Anisotremus*, *Conodon*, *Haemulon*, *Microlepidotus*, *Orthopristis*, *Pomadasys*, *Xenichthys*, and *Xenistius* in Haemulinae, and *Diagramma*, *Parapristipoma*, and *Plectorhinchus* in Plectorhynchinae—with about 145 species (e.g., Iwatsuki et al., 2000; Lindeman and Toxey, 2003).

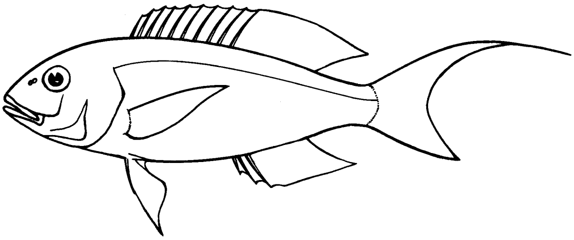
Family INERMIIDAE (375)—bonnetmouths. Marine; western tropical Atlantic.

Dorsal fins separated by a deep notch, first fin with 10 (first genus below) or 17 spines (second genus) and second fin with two spines and 10 soft rays or 9 soft rays, respectively; anal fin with three spines and 8 or 10 soft rays; teeth absent on jaws, vomer, and palatine; two enlarged chin pores; caudal fin deeply forked; 26 vertebrae (12 or 13 abdominal). These fishes are planktivorous and have a highly protrusible upper jaw. Maximum length about 25 cm. This family is probably a haemulid derivative.

Two monotypic genera, *Emmelichthyops* (Bonnetmouth) and *Inermia* (Boga) (Smith-Vaniz et al., 1999).

Sparoid lineage—consists of the next four families Nemipteridae, Lethrinidae, Sparidae, and Centracanthidae.

Family NEMIPTERIDAE (376)—threadfin breams. Marine; tropical and subtropical, Indo-West Pacific.

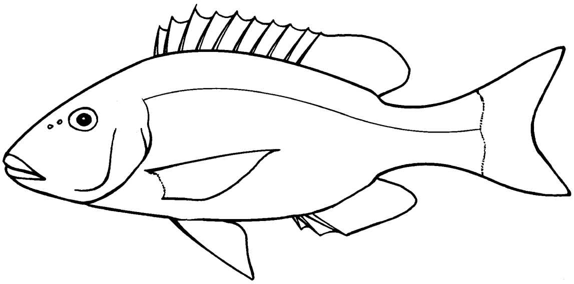


Dorsal fin continuous, with 10 spines and nine soft rays; anal fin with three spines and seven or eight soft rays; caudal fin in some with filament off upper lobe; six branchiostegal rays; gill membranes free from isthmus; subocular shelf and accessory subpelvic keel well developed; opisthotic (= intercalar) well developed (lost or fused in the three related families); 24 vertebrae. Nemipterids, part of the sparoid assemblage, appear to be most closely related to lethrinids.

As proposed in a 1980 study by G. D. Johnson and confirmed by Carpenter and Johnson (2002), the families Nemipteridae, Lethrinidae, Sparidae, and Centracanthidae (with the centracanthids being unresolved with respect to sparid genera), in phyletic sequence as given, form a monophyletic clade and could be placed in the superfamily Sparoidea. The study of Orrell et al. (2002) found Lethrinidae are sister to Sparidae and generally gave support to the monophyly of the Sparoidea. I do not recognize a formal superfamily Sparoidea in classification pending more study of other percoid families in hopes of presenting a comprehensive and monophyletic classification of the entire group.

Five genera, *Nemipterus, Parascolopsis, Pentapodus, Scaevius,* and *Scolopsis,* with about 64 species (e.g., Russell, 2001).

Family LETHRINIDAE (377)—emperors or emperor breams. Marine coastal; tropical, west Africa and Indo-West Pacific.

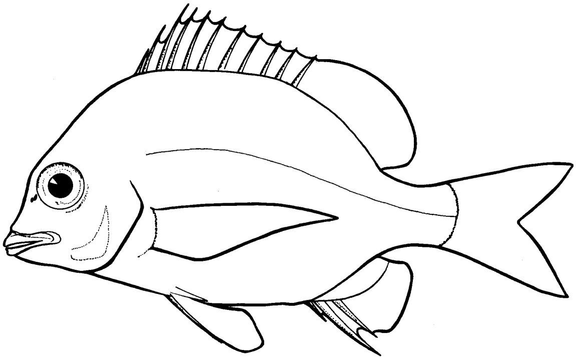


Dorsal fin continuous, with 10 spines and 9 or 10 soft rays; anal fin with three spines and 8–10 soft rays; six branchiostegal rays; no accessory subpelvic keel; reduced subocular shelf; 24 vertebrae.

Only one species occurs in the Atlantic Ocean—*Lethrinus atlanticus.* Some authors recognize the subfamily Lethrininae (the emperors—cheek scaleless, nine soft dorsal fin rays, subocular shelf absent) for *Lethrinus* and the subfamily Monotaxinae (the large-eye breams—cheeks each with at least three transverse rows of scales, 10 soft dorsal fin rays, subocular shelf present) for the other four genera; the phylogenetic validity of this arrangement, however, is uncertain. See above under family Nemipteridae, for comment on phylogenetic relationships of this family.

Five genera, *Gnathodentex* (1), *Gymnocranius* (8), *Lethrinus* (28), *Monotaxis* (1), and *Wattsia* (1), with about 39 species (e.g., Carpenter and Randall, 2003).

Family SPARIDAE (378)—porgies. Marine (very rarely brackish and freshwater); Atlantic, Indian, and Pacific.



Dorsal fin continuous, usually with 10–13 spines and 10–15 soft rays; anal fin with three spines and 8–14 soft rays; maxilla covered by a sheath when mouth closed; six branchiostegal rays; 24 vertebrae (10 + 14). Maximum length about 1.2 m.

The continental western Atlantic Sheepshead, *Archosargus probatocephalus*, which occasionally occurs in brackish water, is known to enter freshwater rarely in Florida. Four species of sparids occur in brackish water in Australia and one species of *Acanthopagrus*, which enters freshwater, is known to spawn in brackish water.

As noted in Orrell et al. (2002), six sparid subfamilies have been recognized (Boopsinae, Denticinae, Diplodinae, Pagellinae, Pagrinae, and Sparinae); they were not monophyletic in all their analyses. Their analysis supported a monophyletic Sparidae only with the inclusion of *Spicara* (included here, as traditionally, in Centracanthidae). See above under family Nemipteridae for comment on phylogenetic relationships of this family.

Thirty-three genera (e.g., *Archosargus*, *Boops*, *Calamus*, *Chrysophrys*, *Dentex*, *Diplodus*, *Lagodon*, *Pagellus*, *Pagrus*, *Pimelepterus*, *Rhabdosargus*, *Sparus*, and *Stenotomus*) with about 115 species (e.g., Orrell et al., 2002; Carpenter, 2003:1554–1577).

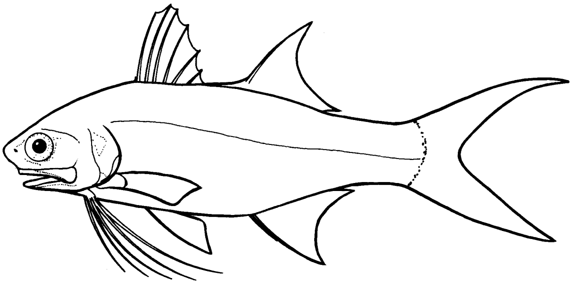
Family CENTRACANTHIDAE (Maenidae) (379)—picarel porgies. Marine; eastern Atlantic (including Mediterranean) and off South Africa.

Dorsal fin continuous, with 11–13 spines and 9–17 soft rays; anal fin with three spines and 9–16 soft rays; six branchiostegal rays; 24 vertebrae. The species of this group of planktivorous fishes have a highly protrusible upper jaw. Maximum length about 38 cm.

See above under family Nemipteridae, for comment on phylogenetic relationships of this family.

Two genera, *Centracanthus* (1) and *Spicara* (7), with eight species (references in Nelson, 1994).

Family POLYNEMIDAE (380)—threadfins. Marine and brackish water (some in rivers, especially in Borneo); all tropical and subtropical seas.

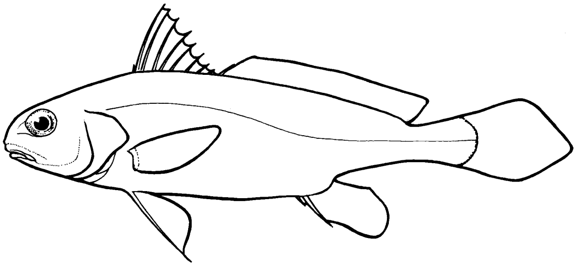


Pectoral fin divided into two sections, the upper with rays attached and the lower with 3–7 long unattached rays (but usually 14 or 15 in *Polynemus* (= *Polistonemus multifilis*)); two widely separated dorsal fins (one spiny and one soft rayed); pelvics subabdominal, with one spine and five branched rays; caudal fin deeply forked; mouth subterminal; 24 or 25 vertebrae. Maximum length 1.8 m, attained in *Eleutheronema tetradactylum*. About four species are known only from freshwater.

The previously assumed relationship of this family to the mugilids and sphyraenids (Nelson, 1984), all of which have widely separated dorsal fins, is no longer considered probable. It may be the sister group of sciaenids (Johnson, 1993). Much work on this group has been done since 1994 by R. M. Feltes and by H. Motomura and his coauthors.

Eight genera, *Eleutheronema, Filimanus, Galeoides, Leptomelanosoma, Parapolynemus, Pentanemus, Polydactylus,* and *Polynemus,* with 41 species (Motomura, 2004b, c).

Family SCIAENIDAE (381)—drums (croakers). Marine, brackish, and freshwater (particularly in South America); Atlantic, Indian, and Pacific.



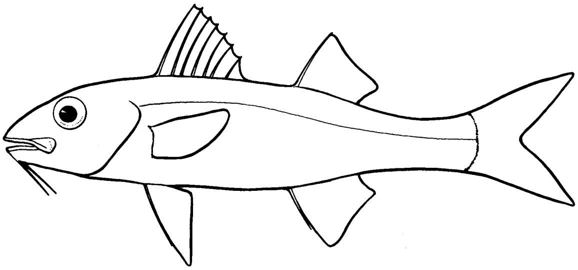
Dorsal fin long, with a deep notch separating spinous from soft portion (rarely separate), first with 6–13 spines and second with one spine and usually 20–35 soft rays; anal fin with one or two spines (both are usually weak but the second may be large) and 6–13 soft rays; lateral line scales extending to the end of caudal fin; caudal fin slightly emarginate to rounded; upper bony edge of opercle forked, bony flap present above gill opening; single barbel or a patch of small barbels on chin of some species; head with large cavernous canals (part of the lateral-line system); conspicuous pores on snout and lower jaw; vomer and palatine without teeth; swim bladder (rarely rudimentary in adults) usually with many branches; otoliths (sagitta at least) exceptionally large; vertebrae 24–30.

Sciaenids can produce sound by using the swim bladder as a resonating chamber. Some are important food fishes. They occur in shallow water, usually near continental regions, and are absent from islands in the mid-Indian and Pacific oceans. Several marine species enter estuaries, and about 28 species are restricted to freshwater (Atlantic drainages) in the Americas. The freshwater members are *Aplodinotus grunniens*, extending from southern Saskatchewan and Quebec to Guatemala, and species of *Pachypops*, *Pachyurus*, and *Plagioscion* (enters estuaries), in South America. K. Sasaki in 1989 revised the family, recognizing 10 subfamilies.

Bortone (2002) gives much information on various members of *Cynoscion*, especially *C. nebulosus*.

About 70 genera (e.g., *Aplodinotus, Atractoscion, Atrobucca, Bairdiella, Cheilotrema, Cynoscion, Equetus, Genyonemus, Johnius, Larimus, Leiostomus, Menticirrhus, Micropogon, Micropogonias, Ophioscion, Otolithes, Otolithoides, Paranebris, Pogonias, Protosciaena, Roncador, Sciaena, Sciaenops, Seriphus, Stellifer,* and *Umbrina*) with about 270 species (e.g., Schwarzhans, 1993; Chao et al., 2001; Chao, 2003).

Family MULLIDAE (382)—goatfishes. Marine (rarely brackish water); Atlantic, Indian, and Pacific.

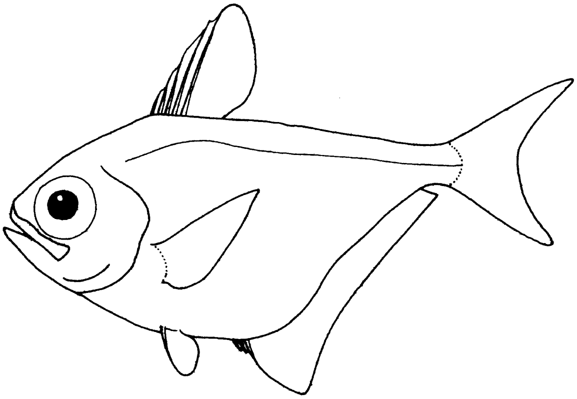


Two long independently movable hyoid barbels (used in detecting food); body elongate; two widely separated dorsal fins, the first with 6–8 spines and second with one spine and 8 or 9 soft rays; soft dorsal fin shorter than anal fin; anal fin with one or two small spines and 5–8 soft rays; caudal fin forked; 24 vertebrae.

Goatfishes are important as a food fish. Many are brightly colored. Maximum length up to 60 cm.

Six genera, *Mulloidichthys*, *Mullus*, *Parupeneus*, *Pseudupeneus*, *Upeneichthys*, and *Upeneus*, with about 62 species (Golani, 2001; Kim and Nakaya, 2002; Randall and Myers, 2002; Randall, 2003).

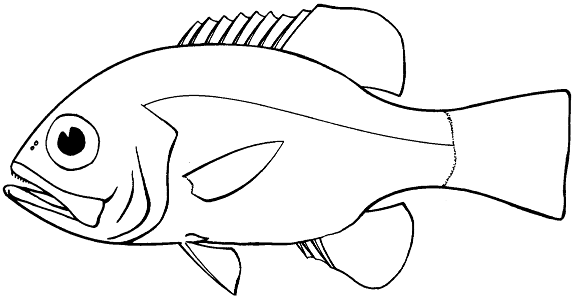
Family PEMPHERIDAE (383)—sweepers. Marine and brackish water; western Atlantic, Indian, and Pacific.



Body compressed and deep; maxillae not reaching beyond center of eye; preorbital smooth; eye large, without adipose lid; one short dorsal fin, originating before middle of body, with 4–7 graduated spines and 7–12 soft rays; anal fin with two (very rarely) or three spines and 17–45 soft rays; lateral line scales usually 40–82; lateral line extending onto caudal fin; tubes of lateral line usually short and wide; gill rakers long and usually 25–31; luminescent organs in a few species; pyloric caeca 9 or 10; swim bladder absent in one species (*Pempheris poeyi*); 25 vertebrae (10 + 15). Maximum length about 30 cm.

Two genera, *Parapriacanthus* (about 5) and *Pempheris* (about 21), with about 26 species (e.g., Mooi, 1998).

Family GLAUCOSOMATIDAE (384)—pearl perches. Marine; eastern Indian and western Pacific (Japan to Australia).



Dorsal fin with eight graduated spines and 11–14 soft rays; anal fin with three spines and 12 soft rays; maxillae scaled; lateral line nearly straight and extending to tail; caudal fin lunate or truncate; vertebrae 25. Maximum length at about 1.2 m. This taxon, which shares similarities in the complex swim bladder/vertebral association and dorsal gill-arch elements with *Pempheris,* is thought to be closely related to the pempherids.

One genus, *Glaucosoma,* with four species (McKay, 1997).

Family LEPTOBRAMIDAE (385)—beachsalmon. Marine and brackish water (occasionally entering rivers); coasts of southern New Guinea, Queensland, and Western Australia.

Body compressed and deep; maxillae reaching far behind eye; preorbital serrate; eye relatively small, with adipose lid; one short dorsal fin behind middle of body (above anal fin), with four spines and 16–18 soft rays; anal fin with three spines and 26–30 soft rays; lateral line scales about 75–77; tubes in lateral line long and narrow; gill rakers short, usually 10. Maximum length about 35 cm.

One species, *Leptobrama muelleri.*

Family BATHYCLUPEIDAE (386)—bathyclupeids. Marine oceanic; Indian, western Pacific, and Gulf of Mexico.

One dorsal fin in posterior half of body, without spines; anal fin long, with one spine; dorsal and anal fins covered with scales; premaxillae and maxillae bordering mouth; usually 31 vertebrae (10 + 21).

One genus, *Bathyclupea,* with about five species.

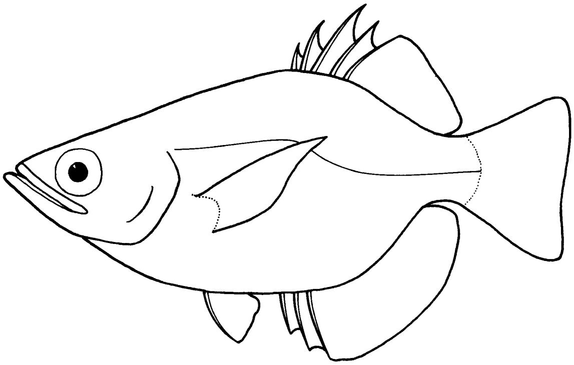
Family MONODACTYLIDAE (387)—moonfishes (fingerfishes). Marine and brackish water (sometimes entering freshwater); western Africa and Indo-Pacific.

Body strongly compressed and deep (deeper than long in some); pelvic fins present in juveniles but absent or vestigial in adults of *Monodactylus*; dorsal fin single and with a long base, covered with scales and 5–8 short graduated spines; anal fin with three spines, long base; scales cycloid or ctenoid.

Moonfishes are occasionally sold as aquarium fishes. They are often of a silvery color. The three species of *Monodactylus* often ascend rivers, and some populations may live in freshwater. For the possible relationships of this and the next several families see the comment on Squamipennes under Chaetodontidae.

Two genera, *Monodactylus* and *Schuettea,* with about five species. Some authors place *Schuettea* (with two species in New South Wales and Western Australia) in the Monodactylidae, but Y. Tominaga in 1968 recommended placement in a family of its own. It differs from other monodactylids in a few characters (e.g., normally developed pelvic fins, cycloid scales, teeth absent from endopterygoid and ectopterygoid) and is provisionally retained in the family as a conservative measure.

Family TOXOTIDAE (388)—archerfishes. Marine coastal, brackish, and freshwater; from India to Philippines and Australia and Polynesia.



Body deep and compressed, greatest body depth 1.8–2.5 times in standard length; eye large; dorsal fin with 4–6 strong spines and 11–14 soft rays; anal fin with three spines and 15–18 soft rays; length of soft dorsal much shorter than soft portion of anal; mouth large, terminal (lower jaw protruding), and highly protractile; lateral line scales about 25–47; seven branchiostegal rays; 24 vertebrae (10+14).

Archerfishes are capable of forcefully ejecting squirts of water from their mouths and downing insects. The widespread *Toxotes jaculator*, extending from India to New Hebrides, is normally found in brackish water near mangroves, while the others frequently occur in freshwater (often well inland). Maximum length 40 cm, attained in *T. chatereus*; usually under 16 cm.

One genus, *Toxotes*, with six species (reviewed by G. R. Allen in 1978).

Family ARRIPIDAE (389)—Australasian salmon (kahawai). Marine; South Pacific (southern Australia to New Zealand region).

Dorsal fin with 9 spines and 13–19 soft rays; anal fin with three spines and 9 or 10 soft rays; gill membranes free from isthmus; anal fin much shorter than the soft dorsal; caudal fin forked; 25 vertebrae. Maximum length about 90 cm.

One genus, *Arripis*, with four species (Paulin, 1993).

Family DICHISTIIDAE (Coracinidae) (390)—galjoen fishes. Marine coastal and brackish water; South Africa and Madagascar.

Body relatively deep; mouth small; dorsal fin with 10 spines and usually 18–23 soft rays; anal fin with three spines and usually 13 or 14 soft rays; gill membranes fused with isthmus; some teeth incisiform.

This inshore fish is a highly sought after sports fish in South Africa (Smith and Heemstra, 1986).

This family was recognized under the name Coracinidae in Nelson (1994), with the generic name *Coracinus*; Eschmeyer (1998) noted that *Coracinus* was published in a rejected work and is not available (the family name should be after the next available synonym).

Although monophyly of this family could not be confirmed, Leis and van der Lingen (1997) found larval evidence to support the historical linking of species of Microcanthinae, Scorpidinae, Girellinae, and Kyphosinae (recognized by them at the family level; a grouping in the earlier study of G. D. Johnson) with possibly some affinity to the Arripidae (but not to the Ephippidae or Drepaneidae).

One genus, *Dichistius*, with about two species (e.g., Leis and van der Lingen, 1997).

Family KYPHOSIDAE (391)—sea chubs. Marine; Atlantic, Indian, and Pacific.

Three spines and 10–28 soft rays; dorsal fin with 9–16 spines and 11–28 soft rays; 24–28 vertebrae (34 in *Graus*). Members of the first two subfamilies, except for *Graus*, are herbivorous, primarily consuming algae, while the others are primarily carnivorous. All are usually found near shore.

Monophyly for the group has not been established, and the following subfamilies, or combinations thereof, are often recognized as separate families (it may be desirable to recognize the subfamily Parascorpidinae at the family level). G. D. Johnson and R. A. Fritzsche in a 1989 study provided evidence for the monophyly of a taxon including the first three subfamilies (which they rank as families, as did the 1984 study of G. D. Johnson). Yagishita et al. (2002) made a valuable start in determining whether or not this family is monophyletic, but as they stated, many more taxa need to be included in an analysis. Their results suggested that *Scorpis, Labracoglossa* (these two being sister taxa), *Girella, Microcanthus,* and *Kyphosus* are part of a monophyletic group but one shared with *Kuhlia* and *Oplegnathus.* Much of the basis for the generic composition of these taxa is based on the G. D. Johnson studies. See comments above under family Dichistiidae.

Sixteen genera with about 45 species.

SUBFAMILY GIRELLINAE (NIBBLERS). Some incisiform teeth present; maxilla concealed beneath suborbital bone. Pacific (primarily Philippines to Australia but extending to California where the Opaleye, *Girella nigricans*, is a common inshore species) with *G. zonata* in the Atlantic. *Graus* occurs off Chile.

Two genera, *Girella* and *Graus*, with about 17 species (e.g., Yagishita and Nakabo, 2000).

SUBFAMILY KYPHOSINAE (RUDDERFISHES). Some incisiform teeth; maxilla exposed. Atlantic, Indian, and Pacific.

Four genera, *Hermosilla, Kyphosus, Neoscorpis,* and *Sectator* (e.g., Sakai and Nakabo, 2004) with 13 species.

SUBFAMILY SCORPIDINAE (HALFMOONS). No incisiform teeth; pelvics well behind pectorals. Indo-Pacific (to California).

Four genera *Bathystethus, Labracoglossa, Medialuna,* and *Scorpis*, with about seven species.

SUBFAMILY MICROCANTHINAE. Recognized as a family by Johnson (1984:469).

Five genera, *Atypichthys*, *Microcanthus*, *Neatypus*, and *Tilodon*; *Vinculum* may also belong here. About seven species.

SUBFAMILY PARASCORPIDINAE (JUTJAWS). Mouth large with lower jaw projecting forward; upper jaw not protractile; 27 vertebrae. Maximum length 60 cm.

It may be desirable to recognize this subfamily at the family level; its affinities are uncertain.

One species, *Parascorpis typus*, known only from South Africa (e.g., Smith and Heemstra, 1986).

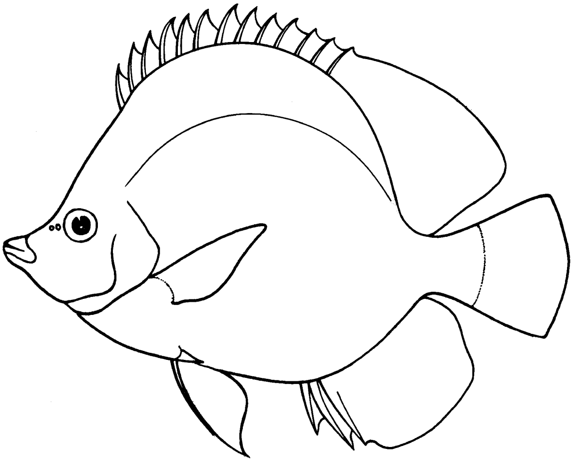
Family DREPANEIDAE (392)—sicklefishes. Marine; Indo-West Pacific and West Africa.

Dorsal fin with 13 or 14 spines and 19–22 soft rays; anal fin with three spines and 17–19 soft rays; mouth markedly protractile; pectoral fins longer than head, falcate; maxilla distally exposed; subocular shelf absent; 24 vertebrae. The recognition of this family for *Drepene* follows the 1984 study of G. D. Johnson, who placed it next to the Dichistiidae (= Coracinidae).

The spelling of this family name in previous editions was Drepanidae. As noted in Eschmeyer, 1998, Vol 3:2889, Opinion 1046 of the ICZN required that it be Drepaneidae. See below under the suborder Acanthuroidei for evidence from Tang et al. (1999) that it belongs within that suborder.

One genus, *Drepane*, with two or three species.

Family CHAETODONTIDAE (393)—butterflyfishes. Marine; tropical to temperate Atlantic, Indian, and Pacific (primarily tropical Indo-West Pacific).



Body strongly compressed; no spine at angle of preopercle (small serrations may be present on the preopercle); well-developed pelvic axillary process; head region in larval (tholichthys) stage of most species covered with bony plates; dorsal fin continuous or with slight notch, with 6–16 spines and 15–30 soft rays, no procumbent spine; anal fin with 3–5 (usually 3) spines and 14–23 soft rays; caudal fin with 15 branched rays (17 principal), margin rounded to emarginate; scales extending onto the dorsal and anal fins; mouth small, terminal, protractile (the two species of the Indo-Pacific *Forcipiger* have a very elongate snout); gut coiled many times; swim bladder with two anteriorly directed processes; 24 vertebrae (11 + 13).

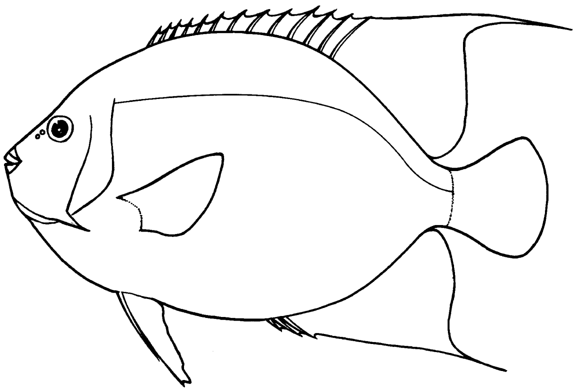
Most species of butterflyfish have brightly colored patterns. Also, most have a dark band running across the eye, and many have an "eyespot" on the dorsal or posterior part of the body—both patterns may serve to confuse predators. Butterflyfishes generally occur near coral reefs and at depths of less than 20 m, but a few go to at least 200 m. A few species occur in brackish water. Most species are in the Australian to Taiwan region. Only 13 species occur in the Atlantic and 4 in the eastern Pacific. Butterflyfishes are known to feed on coral polyps (but are not known to break off coral) and on other invertebrates.

G. Cuvier included chaetodontids and all other fishes with the proximal portion of the dorsal and anal fins covered with scales in the family Squamipinnes (= Squamipennes). Various authors subsequently employed this taxon, usually at the subordinal level following Jordan and Evermann's 1898 work, with varying membership. Nelson (1994) noted the families forming the squamipinnes group and referred to the 1983 study of H.-K. Mok and S.-C. Shen, who provided evidence that the squamipinnes, the acanthuroids, and the tetraodontiforms form a monophyletic taxon.

Butterflyfishes and angelfishes were, until the mid-1970s, combined in the same family; however, W. E. Burgess in a 1974 study gave reasons for recognizing them in separate families (and noted many morphological differences, including those in osteology, between the two groups), and Bellwood et al. (2004) confirmed that the families are monophyletic (but not necessarily each other's closest relatives).

Eleven genera (e.g., *Chaetodon, Chelmon, Coradion, Forcipiger, Hemitaurichthys, Heniochus, Johnrandallia,* and *Prognathodes*) with about 122 species (Allen et al., 1998; Kuiter and Debelius, 1999; Burgess, 2001; W. L. Smith et al., 2003; Burgess, 2003).

Family POMACANTHIDAE (394)—angelfishes. Marine; tropical Atlantic, Indian, and Pacific (primarily in western Pacific).

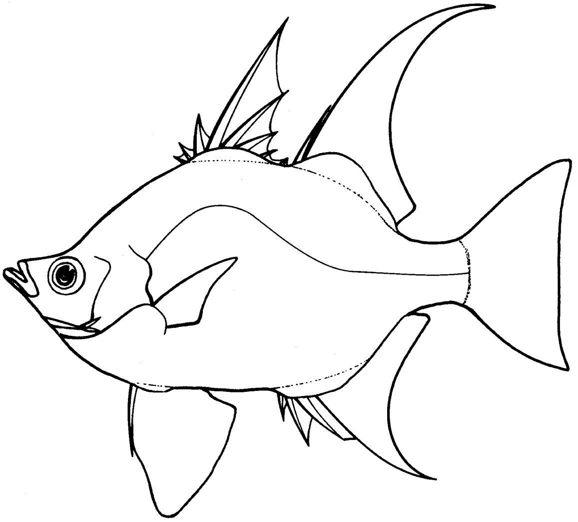


Body strongly compressed; strong spine at angle of preopercle; no well-developed pelvic axillary process; larval stage lacking bony head plates but having spiny scales; dorsal fin continuous, with 9–15 spines and 15–37 soft rays, no procumbent spine; anal fin with three spines and 14–25 soft rays; dorsal and anal fins with elongate extension on hind margin in many species (shown in figure); caudal fin with 15 branched rays, margin rounded to lunate (strongly lunate, often with produced lobes, in some species of *Genicanthus*); swim bladder lacking anteriorly directed processes; 24 vertebrae (10 + 14).

Angelfishes have striking color patterns and in many species the pattern in juveniles differs markedly from that of adults. They generally occur near coral reefs at depths of less than 20 m (very seldom below 50 m).

Eight genera, *Apolemichthys*, *Centropyge* (synonym *Sumireyakko*), *Chaetodontoplus*, *Genicanthus*, *Holacanthus*, *Paracentropyge*, *Pomacanthus*, and *Pygoplites*, with about 82 species (e.g., Pyle, 1997; Allen et al., 1998; Allen and Steene, 2004; Randall and Carlson, 2000; Burgess, 2003; Bellwood et al., 2004).

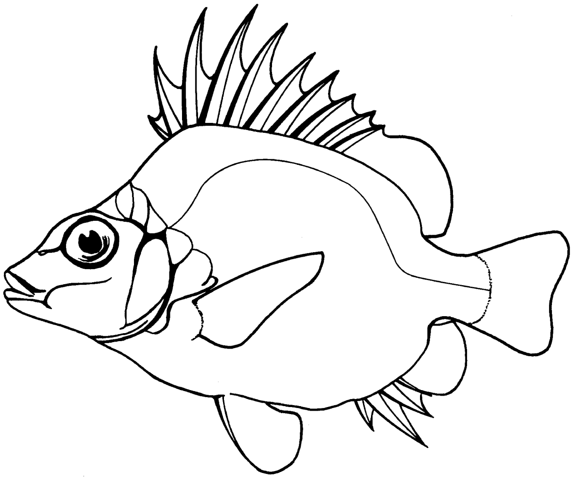
Family ENOPLOSIDAE (395)—oldwives. Marine; southern half of Australia.



Pelvic fins unusually large, each with a strong spine; external bones of head not rough; supramaxilla present; two sharp spines on lower angle of preoperculum. The fish has black vertical bands on a silvery body.

One species, *Enoplosus armatus* (Oldwife).

Family PENTACEROTIDAE (396)—armorheads. Marine; Indo-Pacific and southwestern Atlantic.



Body strongly compressed, ranging from very deep in *Pentaceros* (shown in figure) to only moderately deep in adult *Pentaceropsis*; head encased in exposed, rough, striated bone; no supramaxilla; single dorsal fin with 4–15 strong spines and 8–29 soft rays; anal fin with 2–5 strong spines and 6–17 soft rays; pelvic fins large, with one long, strong spine and five soft rays; scales small; 24–27 vertebrae. These fishes are commonly called boarfishes in Australia.

Seven genera in three subfamilies: *Evistias*, *Histiopterus*, and *Zanclistius* in Histiopterinae (spinous dorsal fin base shorter than soft dorsal fin and vomer toothless); *Paristiopterus* and *Pentaceropsis* in Paristiopterinae (spinous dorsal fin base longer than or equal to soft dorsal base and vomer toothless), and *Pentaceros* and *Pseudopentaceros* in Pentacerotinae (spinous dorsal base much longer than soft dorsal base and vomer with teeth), with a total of about 12 species (Parin and Kotlyar, 1988; Humphreys et al., 1989).

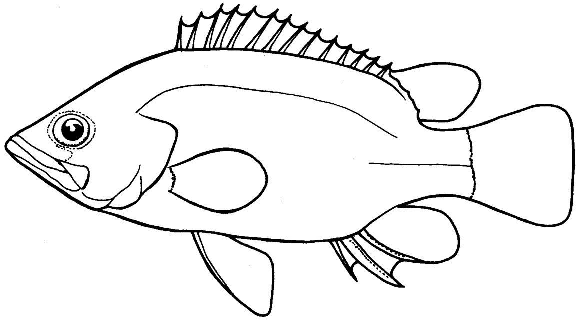
Family NANDIDAE (397)—Asian leaffishes. Freshwater (occasionally brackish water); southern Asia.

Head usually large; mouth usually large and highly protrusible; dorsal fin continuous; caudal fin rounded; lateral line incomplete or absent; pelvic fin usually scaly axillary process. Many are vicious predators. At rest, most look deceptively like drifting leaves. Maximum length about 21 cm, attained in *Pristolepis fasciata.*

As with many families, this one has been split in various ways by past authors. G. Barlow and coauthors in a 1968 study erected a new family for *Badis badis* and concluded that it descended from a proto-anabantoid stock. Gosline (1971) recognized three families, Badidae, Nandidae, and Pristolepidae, and placed them at the start of his Percoidei. K. F. Liem in a 1970 study argued that nandids (Nandinae here) resembled relatively advanced Percoidei. He also placed *Badis* and *Pristolepis* in separate families and did not believe that they bear a close affinity to his Nandidae. Although acknowledging the diversity of the group, Nelson (1994) placed the following taxa and the Polycentridae in one family, Nandidae. I now recognize Polycentridae in its own family based on Britz (1997), Berra (2001), Springer and Johnson (2004), and the statement in Britz and Kullander (2003) that "There is no evidence of a close relationship between the Polycentridae and the Nandidae + Badidae." The classification is provisional and further studies are needed to show what the sister-group relationships are before a cladistic classification can be established.

Four genera with about 21 species.

SUBFAMILY NANDINAE. Pakistan, India, and southeastern Asia (to Borneo).



Anal fin with three spines.

One genus, *Nandus* (Pakistan to Borneo), with possible three species.

SUBFAMILY BADINAE. Pakistan and Burma.
Mouth relatively small and only slightly protrusible; no subocular shelf; dorsal fin with six or seven spines and 6–10 soft rays; anal fin with three spines and 6–8 soft rays; lateral line scales 23–33.

These are colorful fishes that can change its color quite rapidly. Maximum length about 8 cm. This taxon was recognized with only one species in Nelson (1994), *Badis badis.*

Kullander and Britz (2002) provided evidence that *Nandus* and *Badis* form a monophyletic group, and I keep them in the same family (although they recognized Badinae at the family level).

Two genera, *Badis* (12) and *Dario* (3), with 15 species, more may be described (Kullander and Britz, 2002).

SUBFAMILY PRISTOLEPIDINAE. Small area of peninsular India and Sri Lanka, southeastern Asia, and parts of Malay Archipelago (e.g., Sumatra, Java, and Borneo).
Mouth relatively small and only slightly protrusible; subocular shelf present. The most widespread species, *Pristolepis fasciata,* has dorsal fin with 13–16

spines and 14–16 soft rays; anal fin with three spines and eight or nine soft rays; lateral line scales 26–28.

One genus, *Pristolepis*, with about three species.

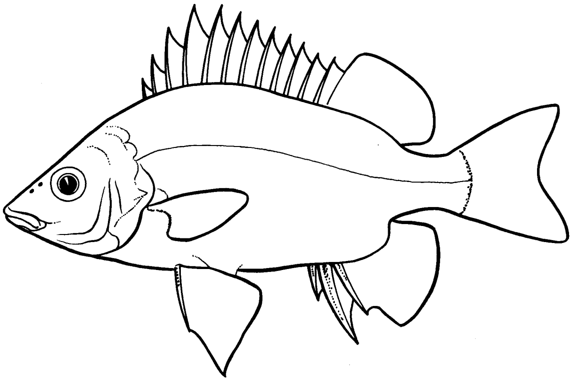
Family POLYCENTRIDAE (398) —Afro-American leaffishes. Freshwater; tropical western Africa and northeast South America.

Characters suggesting monophyly are given in Britz (1997), based on egg morphology, and Springer and Johnson (2004). Anal fin with four spines in *Afronandus sheljuzhkoi*, 9–12 in *Polycentropsis abbreviata*, and 12 or 13 in the South American species. Parental care is given to eggs and larvae.

See comments above under family Nandidae.

Four genera with four species. In Africa there are two monotypic genera, *Afronandus* (streams in Ivory Coast and Ghana) and *Polycentropsis* (West Africa). In South America there are at least two species in separate genera, *Monocirrhus polyacanthus* (Guiana and the Amazon lowlands) and *Polycentrus schomburgkii* (synonym *punctatus*) (Trinidad to Guiana) (Britz, 1997; Berra, 2001; Britz and Kullander, 2003; Springer and Johnson, 2004).

Family TERAPONTIDAE (Teraponidae, Theraponidae) (399)—grunters or tigerperches. Marine coastal, brackish, and freshwater, Indo-West Pacific (Africa to Japan, Fiji, and Samoa).

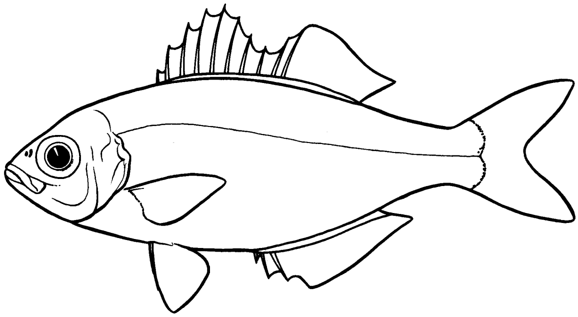


Body oblong to oblong-ovate, somewhat compressed; opercle with two spines, lower spine longer; dorsal fin with notch, 11–14 spines and 8–14 soft rays, spinous portion depressible into a groove formed by a sheath of scales; anal fin with three spines and 7–12 soft rays; pelvic fins inserted distinctly behind base of pectoral fins, with one spine and five soft rays; caudal fin rounded, truncate, or emarginate; lateral line continuous and extending onto caudal fin; vomer and palatines of most species lacking teeth; six branchiostegal rays; paired extrinsic swim-bladder muscles arising from rear of skull or posttemporal and inserting on anterodorsal surface of the anterior chamber of the swim bladder (employed for sound production—a few other perciforms have sonic muscles, but they differ in position); swim bladder transversely divided (Vari, 1978, gives details on these features of the swim bladder which are unique within the perciforms); 25–27 vertebrae. Maximum length about 80 cm.

Much work on this family has been done by R. P Vari. Nelson (1984, 1994) used the family name spelling Teraponidae; I now follow Eschmeyer (1998) in using spelling Terapontidae. Most of the freshwater species occur in Australia and in New Guinea.

Sixteen genera (e.g., *Amniataba, Bidyanus, Hephaestus, Leiopotherapon, Mesopristes, Pelates* (synonym *Helotes*), *Pingalla, Scortum, Syncomistes, Terapon,* and *Variichthys* (a replacement name for *Varia*) with about 48 species (e.g., Yoshino et al., 2002).

Family KUHLIIDAE (400)—flagtails. Marine, brackish, and freshwater; Indo-Pacific.



Dorsal and anal fins each with a well-developed scaly sheath; dorsal fin deeply notched, with 10 spines and 9–13 soft rays; anal fin with three spines and 9–13 soft rays; no scaly pelvic axillary process; opercle with two spines; 25 vertebrae. Color generally silvery, often with dark markings on the caudal fin. Maximum length up to 50 cm. The three nannopercine genera formerly placed in this family are now placed in the Percichthyidae. The most wide-ranging species and the only one to occur in the Americas is the coastal *Kuhlia mugil* (synonym *taeniura*), which extends from Africa to the tropical eastern Pacific, sometimes occurring in freshwater. The common name for the family in Hawaii, aholeholes, is also used elsewhere.

One genus, *Kuhlia,* with about 10 species; most of the species are marine and brackish water but one, *K. rupestris,* occurs primarily in freshwater, and several others extend up rivers in continental areas and on oceanic islands (e.g., Tahiti) (e.g., Randall and Randall, 2001.

Family OPLEGNATHIDAE (401)—knifejaws. Marine; Indo-Pacific (South Africa, Japan, southern half of Australia including Tasmania, Hawaiian archipelago, Galapagos, and Peru).

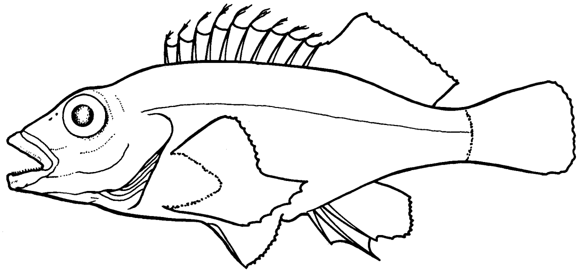
Teeth in adult united to form a parrotlike beak (as in Scaridae, but with usual percoid type of pharyngeal dentition, capable of crushing barnacle shells and sea urchins); spinous dorsal fin low in adults, basically as high as soft dorsal and continuous with it in juveniles; dorsal fin with 11 or 12 spines and 11–22 soft rays; anal fin with three spines and 11–16 soft rays; scales very small (unlike in scarids where they are large). Maximum length about 0.9 m.

One genus, *Oplegnathus*, with about seven species.

Superfamily Cirrhitoidea. Pelvics rather far behind pectorals; lower 5–8 rays of pectorals unbranched, usually thickened, and sometimes separate from one another; anal fin usually with three spines. In the provisional arrangement of cirrhitoid family relationships, Greenwood (1995) showed that the Cirrhitidae was most plesiomorphic, followed by the Chironemidae, with the Aplodactylidae, Cheilodactylidae, and Latridae forming an unresolved trichotomy. Changes in the family classification as shown here and the need for further study are also suggested in the study of Burridge and Smolenski (2004). Their molecular study suggested that the Latridae should be expanded to encompass some cheilodactylids, and further studies are desirable to understand the cladistic relationships of all genera in this superfamily.

Five families, 23 genera, and about 73 species.

Family CIRRHITIDAE (402)—hawkfishes. Marine; tropical western and eastern Atlantic, Indian, and Pacific (majority are Indo-Pacific).



Dorsal fin continuous with 10 spines and 11–17 soft rays; pectoral rays 14, the lower five to seven unbranched and membrane incised; cirri on interspinous membrane; anal fin soft rays 5–7; scales cycloid or ctenoid; swim bladder absent; vertebrae 26. Maximum length about 55 cm.

Hawkfishes are usually small and richly colored fishes that live in rocky and coral habitats. They have many features in common with the scorpaenids.

Twelve genera (e.g., *Amblycirrhitus, Cirrhitichthys, Cirrhitops, Cirrhitus, Isocirrhitus, Notocirrhitus, Oxycirrhites,* and *Paracirrhites*) with about 33 species (Randall, 2001a).

Family CHIRONEMIDAE (403)—kelpfishes. Marine; coastal Australia and New Zealand.

Dorsal fin with 14–16 spines and 15–21 soft rays; anal fin soft rays 6–8; vomer with teeth, palatines without teeth; jaw teeth conical or villiform. Maximum length about 40 cm.

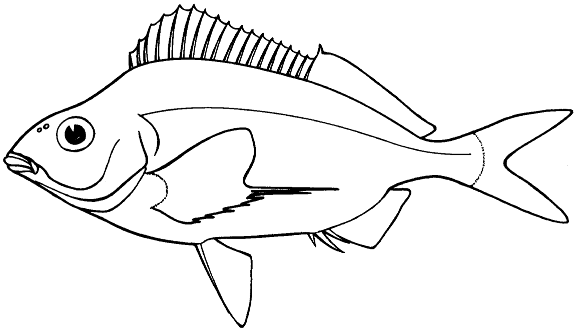
Two genera, *Chironemus* (about 4) and *Threpterius* (1), with about five species.

Family APLODACTYLIDAE (Haplodactylidae) (404)—marblefishes. Coastal marine; southern Australia, New Zealand, Peru, and Chile.

Dorsal fin with 14–23 spines and 16–21 soft rays; anal fin soft rays 6–8; vomer with teeth; jaw teeth incisiform, lanceolate, or tricuspid.

One genus, *Aplodactylus* (synonyms *Crinodus* and *Dactylosargus*), and about five species (Russell, 2000; Burridge, 2000).

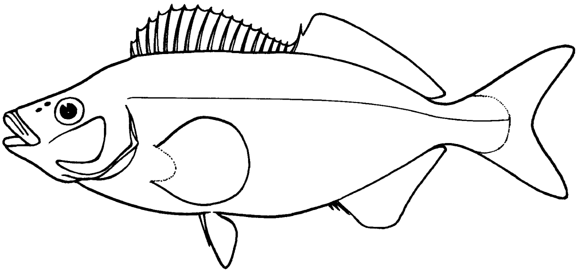
Family CHEILODACTYLIDAE (405)—morwongs. Marine; parts of the Southern Hemisphere in Atlantic, Indian, and Pacific, and in the Northern Hemisphere off coasts of China and Japan and the Hawaiian Islands.



Dorsal fin continuous, may be almost separated, with 14–22 spines and 19–39 soft rays; anal fin with three spines (third may be difficult to detect) and 7–19 soft rays; vomer and palatines toothless; lower four to seven pectoral rays in adults usually thickened, elongated, and detached (free of rest of fin); usually 24 vertebrae. Maximum length about 1.0 m. The only species in the Northern Hemisphere belongs to the subgenus *Goniistius* of the genus *Cheilodactylus*, a taxon with an antitropical distribution. The last major revision was by J. E. Randall in 1983.

Five genera, *Acantholatris*, *Cheilodactylus* (synonym *Goniistius*), *Chirodactylus*, *Nemadactylus*, and *Sciaenoides*, with about 22 species (e.g., Burridge, 2004).

Family LATRIDAE (406)—trumpeters. Marine; coastal southern Australia, New Zealand, Chile, and in the southern Atlantic.

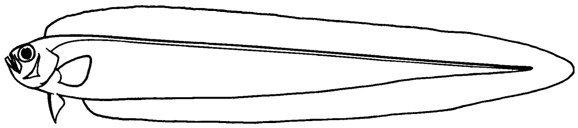


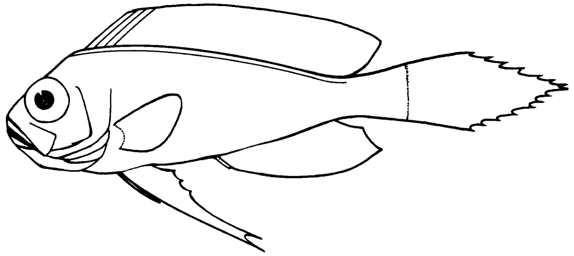
Dorsal fin with 14–24 spines and 23–40 soft rays; anal fin with 18–35 soft rays; vomer with or without teeth. Trumpeters form an important sport fishery and are known for their fine taste.

Three genera, *Latridopsis*, *Latris*, and *Mendosoma*, with about eight species.

Superfamily Cepoloidea. It would be desirable to demonstrate in a phylogenetic study whether or not the formerly recognized Owstoniidae and Cepolidae (e.g., Nelson, 1984) represent monophyletic lineages within the Cepoloidea and, if so, to evaluate whether or not they appear as distinct from one another as do other percoid families.

Family CEPOLIDAE (407)—bandfishes. Marine; eastern Atlantic (off Europe and in Mediterranean) and Indo-West Pacific (including New Zealand).





Dorsal fin continuous, with 0–4 spines (usually three); anal fin with 0–2 spines; vomer and palatine toothless; single postcleithrum; six branchiostegal rays; lateral line along base of dorsal fin; epipleural ribs in some trunk vertebrae fused proximally to corresponding pleural ribs; body color generally red or pink. Maximum length 70 cm, attained in *Cepola rubescens* of the northeastern Atlantic and Mediterranean.

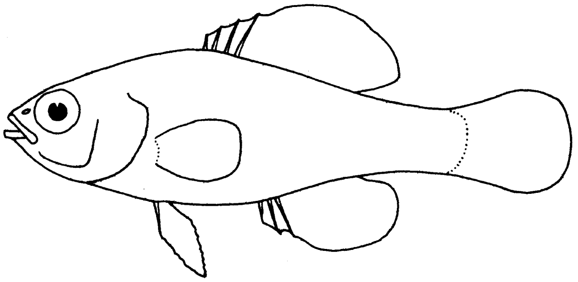
Four genera with 19 species (e.g., Smith-Vaniz in Smith and Heemstra, 1986). Two subfamilies are provisionally recognized.

SUBFAMILY CEPOLINAE. Highly compressed elongate body gradually tapering to the tail; dorsal and anal fins very long, each with over 65 rays, and connected with caudal fin; minute scales; about 65–80 vertebrae. Two genera, *Acanthocepola* (4) and *Cepola* (3), with about seven species. Shown in upper figure. *Cepola haastii* is the only cepolid from New Zealand.

SUBFAMILY OWSTONIINAE. Elongate caudal fin; dorsal and anal fins each with fewer than 32 rays; 28–30 vertebrae. Deepwater. Two genera, *Owstonia* (11) and *Pseudocepola* (one), with 12 species. Shown in lower figure.

Suborder Elassomatoidei

Family ELASSOMATIDAE (ELASSOMIDAE) (408)—pygmy sunfishes. Freshwater; eastern United States (including the Mississippi River Valley).



Infraorbitals (except lachrymal), basisphenoid, and endopterygoid absent; branchiostegal rays five; gill membranes broadly united across isthmus; dentary and angular not penetrated by lateral line; no lateral line on body; caudal fin rounded; cycloid scales; dorsal fin with 2–5 spines and 8–13 soft rays; anal fin with three spines and 4–8 soft rays. Maximum length 4.5 cm.

Pygmy sunfishes were often included in the Centrarchidae in literature of the 1980's and earlier (e.g., Nelson, 1976, 1984) or placed in their own family but regarded as related to the Centrarchidae. Evidence published by G. D. Johnson in 1984 showed that they are probably not neotenic centrarchids, and that their affinities may even lie outside the Percoidei (supported in Johnson, 1993). Furthermore, Johnson and Patterson (1993) found that they share some derived features with the mugilomorphs, atherinomorphs, gasterosteiforms, and synbranchiforms, and they included the elassomatids within a group comprising these taxa and termed by them the Smegmamorpha. G. D. Johnson and V. G. Springer in a 1997 conference talk presented evidence that they are closely related to the Gasterosteidae, but they later concluded that the matter remains unresolved (Spinger and Johnson, 2004:117) and placed them in their own order, Elassomatiformes, between Synbranchiformes and Mugilomorpha (Spinger and Johnson, 2004:124). The limited molecular evidence of Jones and Quattro (1999) is more consistent with a relationship between *Elassoma* and Centrarchidae plus Moronidae than between *Elassoma* and atherinomorphs or cichlids. Roe et al. (2002) did not find support for a relationship to either centrarchids or gasterosteids, but stated that a sister relationship with Centrarchidae could not be rejected. While I have removed pygmy sunfishes from the Percoidei here, I have retained them in the Perciformes, as in Nelson (1994), pending a clearer resolution of their relationships.

Gilbert (1998) gave a type catalogue of recent and fossil taxa.

One genus, *Elassoma,* with six species (e.g., Nelson et al., 2004; Gilbert, 2004).

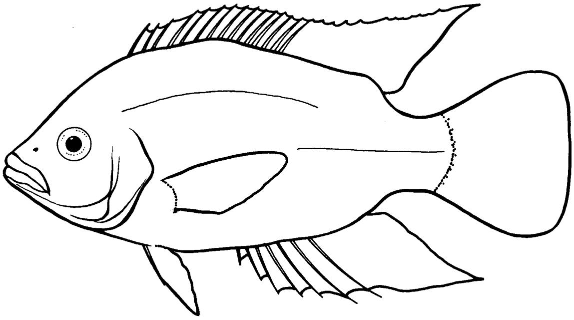
Suborder Labroidei. The recognition of monophyly for this clade is based on characters in the pharyngeal region, particularly in the pharyngeal jaws, which are specialized for food processing. For example, i) the fifth ceratobranchials are united or fused to form a single lower pharyngeal jaw, suspended in a muscle sling (single or double), and ii) the upper pharyngeal jaw articulates by means of a diarthroses with the basicranium (see Stiassny and Jensen, 1987, for a detailed and critical discussion). However, as noted by Stiassny and Jensen (1987) and Johnson (1993), there is a high degree of homoplasy involved, and corroborative evidence from characters independent of the pharyngeal area is lacking. I echo the advice of Johnson (1993), considered especially relevant for this group given the nature of the synapomorphies and the great interest by nonsystematists in the families, that workers seeking to understand the historical origins of various traits (e.g., behavioral) not regard the monophyly of this taxon, with cichlids being the postulated sister-group of the remaining families, as dogma.

The last three families labrids, odacids, and scarids form a monophyletic group and are combined into one family, the Labridae, by some past workers. However, while not necessarily arguing that each family might be monophyletic, I prefer, as in Nelson (1994) and most specialists, to recognize each until phylogenetic information is available to suggest otherwise (however, a cladistic analysis is needed of all genera to follow up on the statement in Bellwood, 1994:54, supporting the 1979 finding in the PhD dissertation of M. F. Gomon, that the Scaridae, the labrid *Pseudodax,* and the labrid hypsigenyine genera may form a monophyletic assemblage. Springer and Johnson (2004) recognize these three families in the superfamily Labroidea: while this is quite appropriate, I do not do so because of the uncertainty in how to rank the other three families (e.g., in three separate superfamilies).

Most species of labrids and scarids are protogynous, that is, they can change their sex from female to male; there is a wide diversity of color patterns associated with sex and size. Males may be primary (not capable of sex change) or secondary (resulting from a sex change of a female). Various populations may consist of only secondary males (monandry) or primary and secondary males (diandry). In coloration, individuals with a color pattern characteristic of small adults are said to be in the initial phase, while those having a color pattern characteristic of the largest males are in the terminal phase. Sexual dichromatism is common and refers to the situation where terminal-phase males have a different color pattern from females.

Six families with about 235 genera and roughly 2,274 species. About 1,330 species, all being cichlids, are confined to freshwater (an embiotocid is also virtually confined to freshwater). Fossils include the Eocene *Tortonesia* (Tortonesidae), thought to be related to the Pomacentridae, with the uppermost branched principal ray of the caudal fin greatly elongated and 25 or 26 vertebrae (described by L. Sorbini and coauthors in 1990), and the Eocene labrids *Eocoris* and *Phyllopharyngodon.* The African cichlid fossil record, known as early as the Eocene, was discussed in Murray (2000) and Stewart (2001).

Family CICHLIDAE (409)—cichlids. Freshwater and occasionally brackish water; Central and South America (one species extending north to Texas), West Indies, Africa, Madagascar, Israel, Syria, coastal India, and Sri Lanka.



Single nostril on each side; lateral line interrupted, generally 20–50 scales in lateral lines but number may exceed 100; generally 7–25 spines and 5–30 soft rays in dorsal fin and 3–15 spines (3 in the majority of species) and 4–15 soft rays in the anal fin. (*Etroplus* has about 12–15 anal spines, but most other species exceeding three spines have 4–9; a few cichlids may have more than 30 soft rays in the anal fin.) No subocular shelf. Maximum length about 80 cm, attained in *Boulengerochromis microlepis* of Lake Tanganyika.

As in many families, there is much variability in body shape between some species. Most cichlids have a moderately deep and compressed body similar to *Cichlasoma* shown in the figure. However, the body can be disc shaped and have extremely high, saillike fins, as in *Pterophyllum* (angelfishes), or low fins, as in *Symphysodon* (discus fishes); it can also be elongate, as in *Crenicichla* (pike cichlids).

Cichlids form an important group of relatively large and often colorful aquarium fishes. Many color patterns have been developed through selective breeding in some of the species for the aquarium trade. Keep in mind that the common names for the species of *Pterophyllum*, the angelfishes, can be confused with the pomacanthids, which are also known as angelfishes; the first group is freshwater and the latter is marine, and, where confusion could arise, refer to them as either the freshwater angelfishes or the marine angelfishes. There is an extensive aquaculture for several species of tilapia, especially for *Oreochromis niloticus.*

Species of the family have highly organized breeding activities (see Keenleyside, 1991). Two general forms of parental care may be recognized: i) mouthbrooders, which are usually polygamous and usually only the female carries the fertilized eggs and newly hatched eggs in the mouth; and ii) substratebrooders, which are usually monogamous and both sexes may care for the eggs. A few species combine both methods, e.g., eggs are laid and cared for on the substrate, but the newly hatched young are carried in the parent's mouth. Mouthbrooding or oral incubation is common and appears to have arisen independently in several groups of African cichlids but is known from only a relatively few species in Central and South America. Female discus fish secrete a whitish milklike substance from the skin to “nurse” their young.

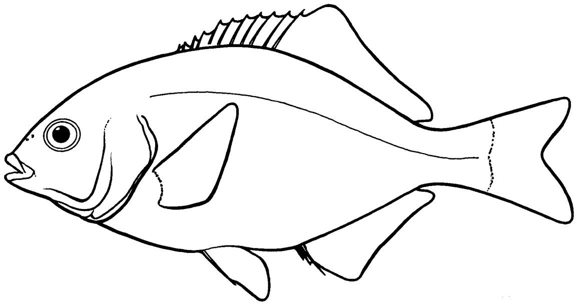
Cichlids have attracted much attention in evolutionary biology because of the existence of species flocks in Africa. A wealth of information on the biology, adaptive radiation, and speciation of African cichlids exists. Endemic cichlids make up most of the fish fauna in the three African lakes that contain the most species of fish of any lake in the world, namely, Lake Malawi, Lake Victoria, and Lake Tanganyika. These cichlids exhibit a vast diversity of feeding habits, including species specialized to eat the scales of other fishes. Berra (2001) summarized much of what is known on the above subjects (see also Keenleyside,1991). Much of the recent major contributions to the systematics and taxonomy of cichlids in Central and South America has been made by S. O. Kullander, and in Africa by M. L. J. Stiassny and by T. Takahashi. Their works should be consulted for details and only a few references are given here.

Cichlids are the most species-rich non-Ostariophysan family in freshwaters worldwide (Kullander, 2003). Several species of tilapias (species of *Tilapia, Sarotherodon,* and *Oreochromis*) are euryhaline and can disperse along some brackish coastlines between rivers. In Africa there are at least 900 species (with an estimated total of 1,300 when all are discovered and described) (see also Turner et al., 2001), four species in the Jordan Valley in the Middle East, one in Iran, three in India and Sri Lanka (also in brackish water), 17 on Madagascar (some also in brackish water), four in Cuba and Hispaniola (some in brackish water), 111 in North and Central America, and 291 in South America (Kullander, 2003, with figures updated from Kullander, 1998). There are thus at least an estimated 1,300 valid species of cichlids (a figure also given in Nelson, 1994), with several hundred more probably existing (a number of recent species described primarily in Africa gives an estimated 1,350). Several authors have discussed whether or not the cichlids in various continental areas form a monophyletic group and this will not be explored here (but for a discussion of cichlid biogeography, see Chakrabarty, 2004).

There is much active work on the taxonomy and systematics of cichlids (e.g., Kullander, 1998; Stauffer et al., 1997; Takahashi, 2002, 2003, 2004; Koblmüller et al., 2004). While progress is being made, there are many areas of disagreement and agreement, but we still lack a comprehensive system of assigning species to monophyletic genera. We are by no means at a point where a classification of the genera can be given despite attempts by Kullander (1998) and others. There is not complete agreement on the genera that should be recognized in this family. Because of this, in the list of common and scientific names of fishes from the United States, Canada, and Mexico, Nelson et al. (2004), pending a phylogenetic study of all species involved, recognized many species that probably belong in other genera, in a broad genus *Cichlasoma.* They also gave the genera into which they are placed in Kullander (2003).

Roughly about 112 genera: for example, the phylogenetically primitive *Paratilapia* and *Ptychochromis* of Madagascar; *Acaronia, Aequidens, Amphilophus, Apistogramma, Astronotus, Cichla, Cichlasoma, Crenicichla, Geophagus, Gymnogeophagus, Herichthys, Heros, Parachromis, Pterophyllum, Retroculus,* *Symphysodon, Theraps, Thorichthys, Uaru,* and *Vieja* from Central and South America*; Alcolapia, Chromidotilapia, Haplochromis, Hemichromis, Heterochromis, Julidochromis, Lamprologus, Oreochromis, Pelmatochromis, Pelvicachromis, Pseudocrenilabrus, Pseudotropheus, Sarotherodon* (ranges to Syria), *Teleogramma, Tilapia, Trematocara,* and *Tylochromis* from Africa; *Tristramella,* endemic to Sea of Galilee, Israel; *Iranocichla,* endemic to southern Iran; and *Etroplus,* from India and Sri Lanka. As stated in Nelson (1994), it is almost meaningless to attempt to give a number of recognized valid species because estimates vary widely due to differing definitions of a species (with special problems in the species flocks of Africa, not to mention the possible loss of undescribed species from the introduction of a species of *Lates* in Lake Victoria). In addition, there undoubtedly are many species yet to be described and perhaps many yet to be placed in synonymy with others. However, because an objective of this book is to provide the number of species currently recognized as valid in each family, I give the figure of 1,350. Nelson (1994) and Kullander (2003) estimated at least 1,300; the slight increase estimated here is based largely on species described recently from Africa.

Family EMBIOTOCIDAE (410)—surfperches. Coastal marine (rarely in freshwater); North Pacific.



Dorsal fin continuous, with 6–11 spines (except 15–19 in *Hysterocarpus traski*) and 9–28 soft rays; anal fin with three spines and 15–35 soft rays; lateral line high on body, complete (but not on caudal fin); scales cycloid, generally 35–75 in lateral line; caudal fin forked. Viviparous (impregnation by the male is aided by the thickened forward end of the anal fin, and embryos may rely on connections to maternal tissue for developmental requirements). Maximum length about 45 cm, attained in *Rhacochilus toxotes.*

Eighteen species occur in the Pacific off western North America with one in freshwater (Nelson et al., 2004), and three or four occur off Japan and Korea. *Hysterocarpus traski* is in freshwater in California (but reduced from its former range and rarely extending into brackish-water estuaries). *Cymatogaster aggregata,* an otherwise marine species, extends into estuaries and the lower portions of coastal rivers in North America.

Thirteen genera, *Amphistichus, Brachyistius, Cymatogaster, Ditrema, Embiotoca, Hyperprosopon, Hypsurus, Hysterocarpus, Micrometrus, Neoditrema, Phanerodon,* *Rhacochilus,* and *Zalembius,* with about 23 species (based, in part, on references given in Nelson, 1994).

Family POMACENTRIDAE (411)—damselfishes. Marine (rarely brackish); all tropical seas (primarily Indo-Pacific).

Nostril usually single on each side (*Chromis* and *Dascyllus* have species with double nostrils, a condition that may be difficult to see); body usually high (generally terete in the plankton-pickers) and compressed; mouth small; lateral line incomplete or interrupted; anal fin with two spines (very rarely three); subocular shelf present; palate toothless; single continuous dorsal fin with 8–17 and usually 11–18 soft rays (but base of spinous portion longer than soft). Maximum length about 35 cm. Parental care of eggs by males.

Damselfishes present many problems to the taxonomist because of the many species complexes and color patterns that vary with individuals and between localities in a species. Considerable morphological diversity exists in many of the genera. The classification of this family is based primarily on Allen (1991). Tang (2001) confirmed a monophyletic Pomacentridae and subfamily Amphiprioninae (but *Premnas* was recovered within *Amphiprion,* and is thus considered a junior synonym); Chrominae and Pomacentrinae were not found to be monophyletic but no changes are made to these subfamilies.

Twenty-eight genera with about 348 species. Many new species have been described since Nelson (1994), primarily by G. R. Allen and by J. E. Randall. The region from the Philippines to Australia has the most species. The fossil record was reviewed in a paper by D. R. Bellwood and L. Sorbini in 1996.

SUBFAMILY AMPHIPRIONINAE (ANEMONEFISHES). Transverse scale rows 50–78 (most members of the following subfamilies have fewer than 40); all the opercles usually serrate (all the opercles not serrate in the other subfamilies); dorsal fin with 10 spines, rarely nine or 11 (most members of the following subfamilies have 12–14 spines) and usually 14–20 soft rays; color variable, 0–3 white transverse bands.

These fish live in coral reefs and show a commensal relationship with large sea anemones, living about and within them for protection (nematocyst discharge is inhibited).

One genus, *Amphiprion* (synonym *Premnas*) (Tang, 2001), found in coastal tropical Indo-West Pacific waters, with about 27 species.

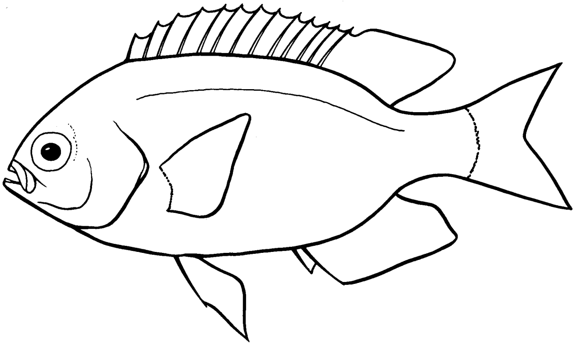
SUBFAMILY CHROMINAE. Upper and lower edges of caudal peduncle usually with two or three short spiny procurrent caudal rays. *Dascyllus* appears to have a commensal relationship with coral.

Five genera, *Acanthochromis, Altrichthys, Azurina, Chromis,* and *Dascyllus.*

SUBFAMILY LEPIDOZYGINAE. Body elongate; upper and lower edges of caudal peduncle without projecting spiny caudal rays; small papillalike structures on inner edge of posterior circumorbitals.

One species, *Lepidozygus tapeinosoma,* a plankton-picker found throughout much of the tropical Indo-West Pacific.

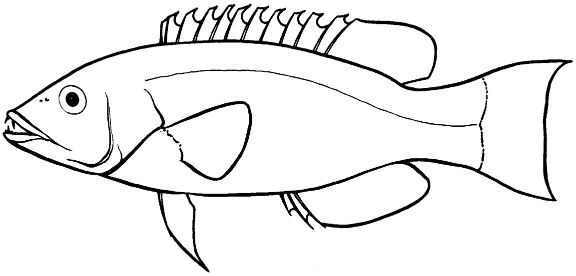
Subfamily Pomacentrinae. Body orbiculate to moderately elongate; upper and lower edges of caudal peduncle without projecting spiny caudal rays.



In the Indian Ocean and western Pacific, one of the species of *Neopomacentrus*, *N. taeniurus*, the Freshwater Demoiselle, enters estuaries and penetrates the lower reaches of streams. In the western tropical Atlantic, a species of *Stegastes*, *S. otophorus*, the Freshwater Gregory, also occurs in estuaries and the lowermost reaches of streams.

Twenty-one genera, *Abudefduf* (sergeant-majors), *Amblyglyphidodon, Amblypomacentrus, Cheiloprion, Chrysiptera, Dischistodus, Hemiglyphidodon, Hypsypops, Mecaenichthys, Microspathodon, Neoglyphidodon, Neopomacentrus, Nexilosus, Parma, Plectroglyphidodon, Pomacentrus, Pomachromis, Pristotis, Similiparma, Stegastes* (synonym *Eupomacentrus*), and *Teixeirichthys.*

Family LABRIDAE (412)—wrasses. Marine; Atlantic, Indian, and Pacific.



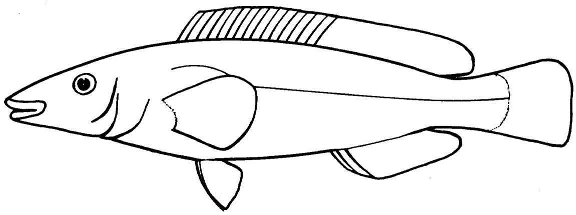
Mouth protractile; jaw teeth mostly separate, usually projecting outward; dorsal fin with 8–21 spines (usually fewer than 15) and 6–21 soft rays; anal fin with 2–6 spines (usually three) and 7–18 soft rays; scales cycloid, generally large to moderate with 25–80 along side (but may be small and exceed 100); lateral line continuous or interrupted; vertebrae usually 23–42. *Gomphosus* has an elongate snout.

This family is one of the most diversified of all fish families in shape, color, and size. Many species are highly colorful, and several color patterns may exist within a species. Most species bury themselves in sand at night. Some small species clean larger fishes of their ectoparasites. Wrasses are popular aquarium fishes, particularly species of the genus *Coris*. Maximum length about 2.3 m (e.g., *Cheilinus undulatus*), although many species are under 15 cm, and the shortest may be the 4.5 cm (*Minilabrus striatus* of the Red Sea). One labrid, *Conniella apterygia*, lacks the pelvic fins and supporting skeleton; it is part of the *Cirrhilabrus* group.

This is the second largest family of marine fishes and the third largest perciform family. Various subfamilies and tribes have been recognized, but monophyly has been established in only one subfamily, the Bodianinae (Gomon, 1997); recognized tribes include Cheilinini and Hypsigenyini (e.g., *Bodianus* and *Choerodon*) (Gomon, 1997). Many species have been described recently by G. R. Allen and, in a series of generic revisions, by J. E. Randall (e.g., Randall, 1999a,b, 2000). Ongoing systematic work is being done, for example, by M. W. Westneat. J. E. Randall and R. H. Kuiter in 1989 noted examples of partially piscivorous wrasses mimicking harmless fishes and in turn a harmless wrasse being mimicked by a piscivorous grouper.

About 68 genera, e.g., *Acantholabrus, Anampses, Bodianus* (one of the genera of hogfishes), *Cheilinus, Cheilio, Choerodon* (synonym *Hypsigenys), Cirrhilabrus, Clepticus, Coris, Ctenolabrus, Cymolutes, Decodon, Doratonotus, Epibulus, Gomphosus, Halichoeres* (the most species-rich genus), *Hemipteronotus, Hologymnosus, Julichthys, Labroides, Labrus, Lachnolaimus, Macropharyngodon, Neolabrus, Oxyjulis, Paracheilinus, Pseudodax, Pseudojulis, Pteragogus, Semicossyphus, Stethojulis, Tautoga, Tautogolabrus, Thalassoma, and Xyrichtys* (one of the genera of razorfishes), with about 453 species (Parenti and Randall, 2000; Westneat, 2003).

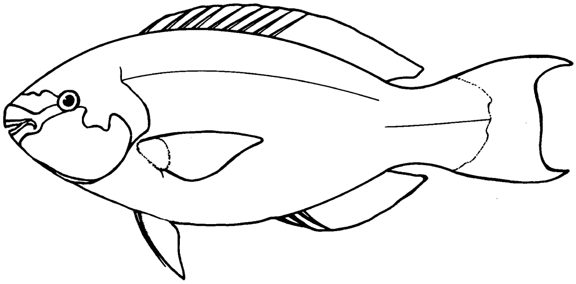
Family ODACIDAE (413)—cales. Coastal temperate marine; Australia and New Zealand.



Mouth nonprotractile; jaw teeth coalesced (parrotlike teeth); dorsal fin with 14–27 spines and 9–22 soft rays; pelvic fins each with one spine and four soft rays (pelvic fins absent in *Siphonognathus argyrophanes*, an extremely elongate odacid that is unique in several other features such as not exhibiting sexual dichromatism and having high meristic values); scales cycloid, usually small to moderate in size (about 30–108 in lateral line); vertebrae 31–54. Maximum length about 40 cm. The body shape is variable, some species are similar to scarids, and others are elongate with an elongated snout. Also known as weed-whitings.

Four genera, *Haletta* (1), *Neoodax* (1), *Odax* (4), and *Siphonognathus* (6), with a total of 12 species (Gomon and Paxton, 1985). Two of the four species of *Odax* are endemic to New Zealand, while the other odacids are confined to southern Australia.

Family SCARIDAE (Callyodontidae) (414)—parrotfishes. Marine (mainly tropical); Atlantic, Indian, and Pacific.



Mouth nonprotractile; jaw teeth usually coalesced (parrotlike teeth); dorsal fin with nine spines and 10 soft rays; anal fin with three spines and nine soft rays; pelvics each with one spine and five soft rays; branched caudal rays 11; scales large and cycloid, usually 22–24 in lateral line; 24–26 vertebrae.

Parrotfishes are herbivorous, usually grazing on dead coral substrates; they rarely feed on live coral (and rarely on seagrasses). Individuals of some species are known to secrete an envelope of mucus at night in which they rest. As with wrasses, sex change appears to be common in species of this family, and males in most species that have been studied may be either primary or secondary. Unlike the wrasses, parrotfishes are remarkably uniform in most meristic characters. The living color pattern, of which there is a wide diversity, is important in identifying many species; however, in addition to fading quickly in preservation, the color pattern can vary greatly with growth and sex change.

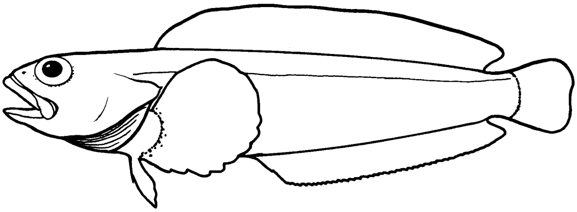
Previously the subfamilies Scarinae and Sparisomatinae were recognized, but Bellwood (1994) showed in a cladistic analysis that they were not justified.

Ten genera, *Bolbometopon, Calotomus, Cetoscarus, Chlorurus, Cryptotomus, Hipposcarus, Leptoscarus, Nicholsina, Scarus* (synonym *Callyodon*), and *Sparisoma,* with 88 species (Bellwood, 2004; Parenti and Randall, 2000; Westneat, 2003).

Suborder Zoarcoidei. All have a single nostril, but there is no known diagnostic character or simple combination of characters that distinguishes this group from the other blennylike perciforms. The monophyly of this taxon and most of its families is uncertain. The bathymasterids are still recognized as the most primitive family, and the suborder is thought to be most closely related to the notothenoids.

The nine included families with about 95 genera and 340 species occur primarily in the North Pacific. All species are marine.

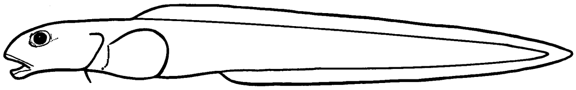
Family BATHYMASTERIDAE (415)—ronquils. Marine coastal; North Pacific.



Dorsal fins continuous, usually with 41–48 rays, unbranched and branched; anal fin usually with 30–36 rays; pectoral fin base vertical; lateral line high, ending near end of dorsal fin; palate with teeth; vertebrae 46–55. Maximum length about 38 cm.

Three genera, *Bathymaster, Rathbunella,* and *Ronquilus,* and seven species (Mecklenburg, 2003).

Family ZOARCIDAE (416)—eelpouts. Marine, usually benthic; Arctic to Antarctic.



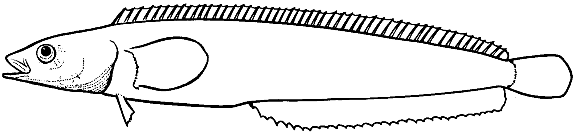
Body elongate; dorsal and anal fins long and confluent with caudal fin; mouth subterminal to terminal; pelvics, when present, small and in front of pectorals, jugular (in *Derepodichthys* the erectile pelvic fins are beneath the eyes); scales very small and embedded or absent; gill membranes joined to isthmus; swim bladder absent; vertebrae 58–150. The three species of *Zoarces* are ovoviviparous (not truly viviparous), and the other zoarcids are oviparous, some showing parental care. Length up to about 1.1 m, in *Macrozoarces americanus.*

The pelvic fins have been lost independently in many zoarcid genera. The genera *Parabrotula* and *Leucobrotula,* placed in this family in Nelson (1984) and thought by some workers to be at least related to the zoarcids (but in their own family, Parabrotulidae), are placed in the order Ophidiiformes. Extensive work on this family has been done by M. E. Anderson.

Four subfamilies are recognized in Anderson (1994) and Anderson and Fedorov (2004): Lycozoarcinae (with *Lycozoarces regaini,* western North Pacific), Zoarcinae (*Zoarces* with 4 species, 2 in North Atlantic and 2 in western North Pacific), Gymnelinae (12 genera and 35 species, most in the North Pacific), and Lycodinae (32 genera and 120 species, in all oceans).

About 46 genera (e.g., *Aprodon, Bothrocara, Crossostomus, Davidijordania, Derepodichthys, Dieidolycus, Gymnelopsis, Gymnelus, Hadropareia, Iluocoetes, Lycenchelys, Lycodapus, Lycodes, Lycodonus, Lycodopsis, Lycozoarces, Macrozoarces, Maynea, Melanostigma, Oidiphorus, Ophthalmolycus, Pachycara, Phucocoetes, Rhigophila,* and *Zoarces*) and about 230 species (Anderson, 1994; Anderson and Fedorov, 2004). The majority of species are in the North Pacific and North Atlantic; about 15 species are known from Arctic Canada, and at least 21 are known from the Antarctic and subantarctic. They are also known from temperate and tropical latitudes.

Family STICHAEIDAE (417)—pricklebacks. Marine, intertidal zone to 250 m; primarily North Pacific, a few in North Atlantic.



At least some spinous rays in long dorsal fin (entirely spinous in most species), 22–127 spines and 0–82 soft rays; anal fin with 1–5 spines at origin followed by 20–102 soft rays; pelvic fin absent or with up to one spine and four branched rays; pectoral fin small to large; ribs present; distance from snout to anal origin usually equal to or less than distance from anal origin to caudal fin; lateral line absent or up to four per side.

Mecklenburg and Sheiko (2004) placed the 37 genera in six subfamilies, based on several studies of others, but stated that more work is needed to resolve monophyly within the family and its subfamilies and to better define some genera. The subfamilies are Stichaeinae (6 genera), Opisthocentrinae (6), Lumpeninae (8), Chirolophinae (3), Xiphisterinae (9), and Neozoarcinae (4). I have not placed the genera in subfamilies pending a comprehensive published study of the monophyly of these taxa.

About 37 genera, *Acantholumpenus, Alectrias, Alectridium, Anisarchus, Anoplarchus, Askoldia* (synonym *Ascoldia*), *Azygopterus, Bryozoichthys, Cebidichthys, Chirolophis, Dictyosoma, Ernogrammus, Esselenia, Eulophias, Eumesogrammus, Gymnoclinus, Kasatkia, Leptoclinus, Leptostichaeus, Lumpenella, Lumpenopsis* (synonym *Allolumpenus*), *Lumpenus, Neolumpenus, Neozoarces, Opisthocentrus, Pholidapus, Phytichthys, Plagiogrammus, Plectobranchus, Poroclinus, Pseudalectrias, Soldatovia, Stichaeopsis, Stichaeus, Ulvaria, Xiphister,* and *Zoarchias,* with about 76 species (e.g. Mecklenburg and Sheiko, 2004).

Family CRYPTACANTHODIDAE (418)—wrymouths. Marine; northwest Atlantic and northern Pacific.

Pelvic fins absent (pelvic girdle present); mouth very oblique; dorsal and anal fins extending to caudal fin base or confluent with caudal fin, dorsal fin with 60–80 spines and anal fin with 0–3 spines and 43–52 soft rays; lateral line obsolete; vertebrae 71–88.

One genus, *Cryptacanthodes* (synonyms *Cryptacanthoides, Delolepis,* and *Lyconectes*), with four species (Mecklenburg, 2003).

Family PHOLIDAE (419)—gunnels. Marine; North Atlantic and North Pacific.

Dorsal fin with 75 to 100 spines, about twice as long as the anal fin; pectoral fins small or rudimentary, with 7–17 rays; pelvic fins rudimentary (one spine and one soft ray) in most species or absent, along with pelvic girdle, in species of *Apodichthys* and some specimens of *Pholis fasciata*; vertebrae 80–107, centra asymmetrical; ribs absent; distance from snout to anal origin usually more than distance from anal origin to caudal fin; lateral line short or absent.

Gunnels are small littoral fishes that, like some pricklebacks, are often found under rocks or in tide pools at low tide.

Three genera with about 15 species (Mecklenburg, 2003).

SUBFAMILY PHOLINAE. Body with pigmented patterns (bars, blotches, or spots). Most are North Pacific, a few North Atlantic.

One genus, *Pholis* (synonym *Allopholis*), with about 11 species.

SUBFAMILY APODICHTHYINAE. Body color relatively uniform (e.g., dark brown, green, or red). North Pacific.

Two genera, *Apodichthys* with three species off the North American coast and the monotypic *Rhodymenichthys* from Japan.

Family ANARHICHADIDAE (420)—wolffishes. Marine; North Atlantic and North Pacific.

Body naked or with minute cycloid scales; lateral line faint, with one or two branches anteriorly or absent; gill membranes attached to isthmus; dorsal fin with spines only; pectoral fins large; pelvic fins absent (rudiments of girdle retained); caudal fin small or pointed; jaws with strong conical canines anteriorly and with large molariform teeth laterally; vertebrae 72–89 to more than 250. Maximum length about 2.5 m.

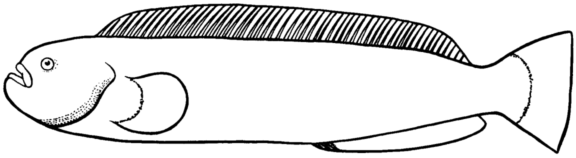
Two genera, *Anarhichas* with about four species (North Atlantic and Pacific) and *Anarrhichthys ocellatus* (Alaska to California) (Mecklenburg, 2003), with five species.

Family PTILICHTHYIDAE (421)—quillfishes. Marine; Pacific North America (Puget Sound to northwestern Alaska).

Body extremely elongate and slender; caudal fin absent; pelvics absent; body naked; dorsal fin with 90 isolated low spines and 137–145 high soft rays; anal fin with 185–196 high soft rays; no lateral line; vertebrae about 222–240. Maximum length 33 cm.

One species, *Ptilichthys goodie* (Mecklenburg, 2003).

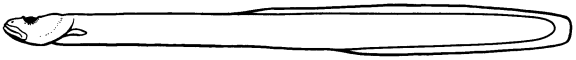
Family ZAPRORIDAE (422)—prowfishes. Marine; North Pacific (California to Alaska and Hokkaido).



No pelvic fins; gill membranes united; small cycloid scales on body; no lateral line; pectoral rays 24 or 25; dorsal fin long, with 54–57 spines; anal fin short, with three weak spines and 24–27 soft rays; large pores on head; vertebrae 61 or 62 (24–26 abdominal); pyloric caeca about 36—77; vertebrae 61–64. Maximum length 88 cm.

One species, *Zaprora silenus* (Mecklenburg, 2003).

Family SCYTALINIDAE (423)—graveldivers. Marine; Pacific coast North America (southern California to northwestern Alaska).



No pelvic fins; gill membranes united; eyes very small and placed high on head; no scales; no lateral line; dorsal and anal fins on posterior half of back and confluent with caudal fin; vertebrae 69–71. Maximum length 15 cm.

One species, *Scytalina cerdale* (Mecklenburg, 2003).

Suborder Notothenioidei. Pelvic fins each with one spine and five (rarely four) branched rays, jugular; one nostril on each side; three platelike pectoral fin radials (actinosts); dorsal fin spines usually nonpungent; principal caudal fin rays 10–19, usually fewer than 15; usually two or three lateral lines, occasionally one (as in all bovichthyids); body with ctenoid or cycloid scales or naked (except for lateral line scales); ribs poorly developed, floating or absent (the epineurals are usually well developed); palatine teeth absent and vomerine teeth usually absent except in bovichthyids, which have both; branchiostegal rays 5–9; swim bladder absent; primarily Antarctic in distribution.

Most of the species of coastal fishes in the Antarctic region belong to this suborder. Some species live at an average temperature of —1.9 degrees C and have a glycoprotein in their blood that lowers the freezing point. Most of the species in subzero water are aglomerular. Some species lack red blood cells and hemoglobin. Most species are benthic; however, despite lacking a swim bladder, there are several species that have developed means of becoming buoyant, and some are pelagic.

Eight families with about 44 genera and 125 species. Three additional families are recognized from the five given in Nelson (1994), Pseudaphritidae, Eleginopidae, and Artedidraconidae. Eocene fossils are known (Balushkin, 1994). The Antarctic and subantarctic species were keyed and descriptive material given in Gon and Heemstra (1990) and Antarctic species given in Miller (1993). The interrelationships of the notothenoid families were discussed in Balushkin (1992, 2000), Lecointre et al. (1997), Eastman and Eakin (2000), Last et al. (2002), and the references therein. Much of the following is based on these works and much additional information can be found in publications by, for example, J. T. Eastman and R. R. Eakin. Many workers, apart from those mentioned, have contributed to our knowledge of these southern fishes (e.g., A. P. Andriashev). There is general agreement on the sequencing of the families. Notothenioids and zoarcoids may be closely related, with both having some affinity with the trachinoids, and all three being derived from some percoid group.

Family BOVICHTIDAE (Bovichthyidae) (424)—temperate icefishes. Marine; southern Australia, New Zealand, and southern South America regions.

Gill membranes free from isthmus, extending far forward; teeth on palatine and vomer; mouth protractile; spinous dorsal fin present (i.e., two dorsal fins present); one lateral line; snout not produced.

The spelling of the family name, changed from Bovichthyidae in Nelson (1994), follows Eschmeyer (1998). *Pseudaphritis urvilli*, formally recognized in this family, is now placed in its own family (see below). Also known as thornfishes.

Three genera, *Bovichtus* (9, synonym *Bovichthys*), *Cottoperca* (1), and *Halaphritis* (1), with about 11 species (e.g., Eastman and Eakin, 2000; Last et al., 2002).

Family PSEUDAPHRITIDAE (425)—catadromous icefishes. Freshwater, brackish, and marine; southeastern Australia (including Tasmania).

The one species was formerly placed in the Bovichtidae. It is recognized in its own family following Balushkin (1992) and Lecointre et al. (1997), and this has also been accepted in Last et al. (2002) and Eastman and Eakin (2000). Last et al. (2002) summarize that there two opposing schools of thought on the relationships of *Pseudaphritis*: that it belongs to a monotypic family considered to be the sister group of other notothenioids including the bovichtid genera *Bovichtus* and *Cottoperca* (Balushkin), or that it is the sister group of the rest of the notothenioids excluding *Bovichtus* and *Cottoperca* (e.g., Lecointre et al. 1997); either way, assigning family status is appropriate. *Pseudaphritis urvillii* occurs primarily in freshwater in coastal areas with spawning appearing to occur in estuaries (e.g., Berra, 2001).

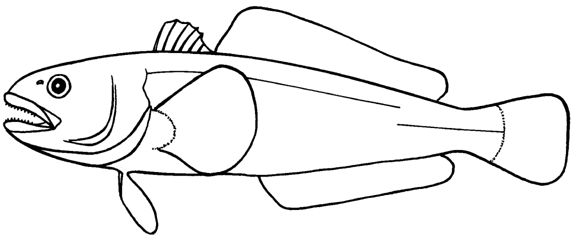
At least one species, *Pseudaphritis urvillii.*

Family ELEGINOPIDAE (426)—Patagonian blennies. Marine; off Chile and Argentina to Tierra del Fuego.

Dorsal fin with seven or eight spines and 23–27 soft rays. The one species was formerly placed in the Nototheniidae. It is recognized in its own family following Balushkin (1992) and this has also been accepted in Eastman and Eakin (2000).

One species, *Eleginops maclovinus.*

Family NOTOTHENIIDAE (427)—cod icefishes. Marine (rarely brackish); coastal Antarctic and southern Southern Hemisphere.



Body scaled; gill membranes forming a fold across the isthmus; mouth protractile; spinous dorsal fin present, with 3–11 spines (the second with 25–42 soft rays); one to three lateral lines; ribs present; three radials in pectoral skeleton, all with some connection to coracoid; 45–59 vertebrae. Nototheniids show a certain similarity to hexagrammids.

The majority of notothenioids are benthic. However, several species of this family, such as the abundant and circumpolar plankton feeder *Pleuragramma antarcticum,* are pelagic. They utilize lipid deposits and reduced skeletal mineralization to attain near neutral buoyancy in the absence of a swim bladder. Some species are cryopelagic, living beneath the sea ice.

About 12 genera, *Aethotaxis, Cryothenia, Dissostichus, Gobionotothen, Gvozdarus, Lepidonotothen* (synonym *Lindbergichthys* and perhaps *Nototheniops*), *Notothenia* (synonym *Indonotothenia*), *Pagothenia, Paranotothenia, Patagonotothen, Pleuragramma,* and *Trematomus* (synonym *Pseudotrematomus*), and about 50 species (e.g., Eastman and Eakin, 2000). Some species range northward to such regions as New Zealand, Macquarie Island, Chile, and Argentina. Most species of the family, however, occur in Antarctica.

Family HARPAGIFERIDAE (428)—spiny plunderfishes. Marine; littoral, extending north to subantarctic and to, for example, southern part of South America and Kerquelen and Macquarie islands.

Body naked; gill membranes broadly united to isthmus; spinous dorsal fin present, with 1–7 flexible spines; mouth protractile; chin barbel absent; strong spine on opercle and on subopercle; three hypurals; vertebrae 34–37.

Family content changed from Nelson (1994); see below under Artedidraconidae.

One genus, *Harpagifer,* with about six species (Eastman and Eakin, 2000).

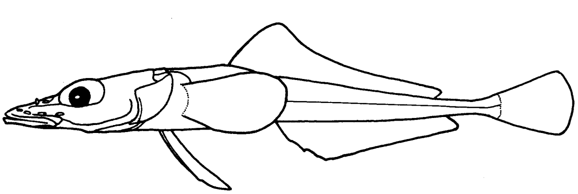
Family ARTEDIDRACONIDAE (429)—barbeled plunderfishes. Marine; deepwater Antarctic.

Body naked; gill membranes broadly united to isthmus; spinous dorsal fin present, with 1–7 flexible spines; mouth protractile; chin barbel present; opercle with hook-shaped spine; four or five hypurals; vertebrae 33–41.

Nelson recognized this as a subfamily of Harpagiferidae (although the two lineages are distinct, they also form a monophyletic group). It is recognized now following earlier studies by R. R. Eakin and, subsequently, by J. C. Hureau in 1986; its recognition is generally accepted (e.g., Eastman and Eakin, 2000).

Four genera, *Artedidraco, Dolloidraco, Histiodraco,* and *Pogonophryne,* with about 25 species (e.g., Eastman and Eakin, 2000).

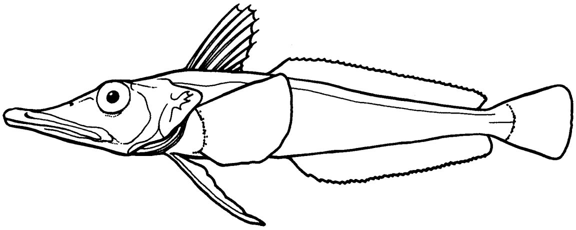
Family BATHYDRACONIDAE (430)—Antarctic dragonfishes. Marine; Antarctic.



Gill membranes united; mouth usually nonprotractile; no spinous dorsal fin; connection between nasal tube and buccal cavity (internal choana) in *Gymnodraco* and *Psilodraco* (Gon and Heemstra, 1990; Eastman, 1991); one or more lateral lines; 45–79 vertebrae.

Eleven genera, *Acanthodraco, Akarotaxis, Bathydraco, Cygnodraco, Gerlachea, Gymnodraco, Parachaenichthys, Prionodraco, Psilodraco, Racovitzia,* and *Vomeridens,* with 16 species (Eastman and Eakin, 2000).

Family CHANNICHTHYIDAE (Chaenichthyidae) (431)—crocodile icefishes. Marine; Antarctic and southern South America.



Gill membranes united; mouth nonprotractile; snout produced and depressed; spinous dorsal fin present; pelvic fins broad or elongate; vertebrae 22–31. Maximum length 75 cm.

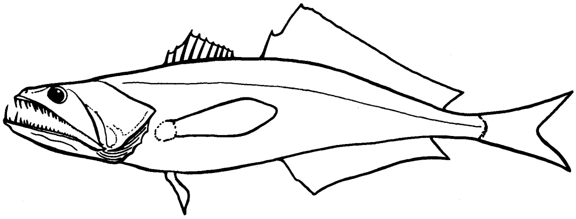
Most or all species are without red blood cells, and their blood is nearly colorless. The muscles lack myoglobin. Survival is probably permitted by the fish living in extremely cold, well-oxygenated water and having skin respiration and a large volume of blood that is efficiently circulated.

Eleven genera, *Chaenocephalus, Chaenodraco, Champsocephalus, Channichthys, Chionobathyscus, Chionodraco, Cryodraco, Dacodraco, Neopagetopsis, Pagetopsis,* and *Pseudochaenichthys,* with about 15 species (Eastman and Eakin, 2000).

Suborder Trachinoidei. The placement of several families in this suborder is very provisional. T. W. Pietsch, in a 1989 paper on the relationships of uranoscopids, excluded *Pholidichthys* and the trichodontids from his cladogram of a hypothesized monophyletic group of core trachinoids. Springer and Johnson (2004) placed *Pholidichthys* (Pholidichthyidae) in its own suborder, and this is followed here. Mooi and Johnson (1997) suggested that the trachinoid family Champsodontidae is a scorpaeniform (which they ranked as the perciform suborder Scorpaenoidei). They demonstrated that the placement of several additional families (Cheimarrhichthyidae, Pinguipedidae, Percophidae, Creediidae, and Chiasmodontidae) in this suborder is questionable and that their relationships require further investigation. I fully agree but do not make changes pending such a comprehensive study and retain this suborder for the families given for convenience only.

Twelve families with a total of 53 genera and 237 species, the majority of which are tropical marine fishes, are recognized in this suborder.

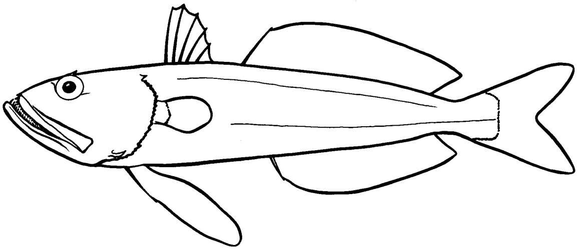
Family CHIASMODONTIDAE (432)—swallowers. Marine; oceanic.



Premaxilla and maxilla long and slender, firmly united posteriorly; anterior tip of premaxilla expanded dorsally and diverging laterally; highly distensible mouth and stomach. Placed in the Percoidei in Gosline (1971).

Four genera, *Chiasmodon*, *Dysalotus*, *Kali* (synonym *Gargaropteron*), and *Pseudoscopelus*, with about 15 species (e.g., Johnson and Cohen, 1974; McEachran and Sutton, 2003). The last genus bears photophores.

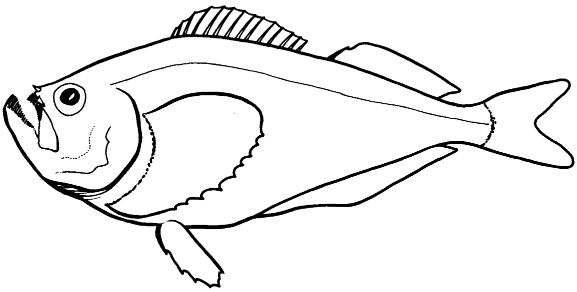
Family CHAMPSODONTIDAE (433)—gapers. Marine; Indo-Pacific.



Pelvic fins elongate, in front of pectorals; pectoral fins small, base oblique; spinous dorsal short, with five spines, soft dorsal, with 17–20 rays; anal fin with one spine and 17–20 soft rays. There is no evidence that *Champsodon* is related to chiasmodontids or to other trachinoids, and Johnson (1993) and Mooi and Johnson (1997) noted that it may be related to the scorpaeniforms. Eocene fossils of *Eochampsodon* are known from the Northern Caucasus (Bannikov, 2004c).

One genus, *Champsodon*, with about 13 species (Nemeth, 1994).

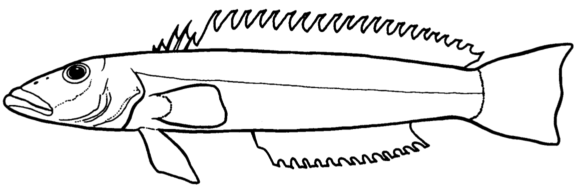
Family TRICHODONTIDAE (434)—sandfishes. Marine; North Pacific.



Mouth nearly vertical, with fringed lips; preopercle with five sharp spines; body scaleless; two dorsal fins, separated, the first with 8–16 spines and the second with 0–1 spine and 12–20 soft rays; anal fin with 0–1 spine and 28–32 soft rays; vertebrae 44–52. Normal habitat is lying partly buried in the bottom. Maximum length about 30 cm.

Two species, *Arctoscopus japonicus* (Alaska to Korea) and *Trichodon trichodon* (northern California to Alaska) (Mecklenburg, 2003).

Family PINGUIPEDIDAE (435)—sandperches. Marine; Atlantic coast of South America and Africa, Indo-Pacific (to New Zealand and Hawaii), and off Chile.

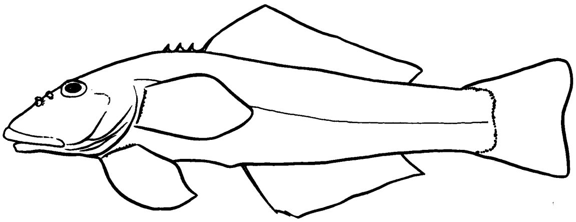


Pelvic fins below or slightly in front of pectorals, with one spine and five soft rays; mouth protractile and terminal; caudal fin truncate to deeply crescentic, with 13 or 15 branched rays; dorsal fin continuous, with 4–7 short spines and 19–27 soft rays; anal fin with 17–25 rays, first one or two may be spinelike; lateral line continuous; gill membranes united, free from isthmus, vertebrae 30–37.

The genera *Pinguipes*, *Prolatilus*, and *Pseudopercis*, with five species, are endemic to South America (one species of *Parapercis* occurs in South America) (Rosa and Rosa, 1998). See comments below under Cheimarrhichthyidae.

Five genera, *Kochichthys*, *Parapercis*, *Pinguipes*, *Prolatilus*, and *Pseudopercis*, with about 54 species (Rosa and Rosa, 1998; Randall and McCosker, 2002; Imamura and Matsuura, 2003).

Family CHEIMARRHICHTHYIDAE (436)—New Zealand torrentfishes. Freshwater (young are known from the sea); rivers of New Zealand.



Pelvic fins well in front of pectorals, wide apart, mouth nonprotractile and inferior; caudal fin with 13–15 branched rays; dorsal fin has three to five spines and 18–21 soft rays, the anterior three or four spines are short and stout and separated from the remainder of the continuous fin; anal fin with one or two spines and 15 soft rays; 15 pectoral rays; about 50 scales along lateral line; vertebrae 31–33. Maximum length about 15 cm.

The one species was placed its own family in previous editions (Nelson, 1976, 1984, and 1994); this placement, as opposed to recognition in the Pinguipedidae, was supported in the 1989 study by T. W. Pietsch, and recently by the systematic studies of Rosa and Rosa (1998) and Imamura and Matsuura (2003); the latter argued against a close relationship with *Paracercis.* However, a cladistic analysis involving all trachinoid genera is desirable to demonstrate whether or not *Cheimarrichthys* and the Pinguipedidae together form a monophyletic taxon. McDowall (2000) gave life history, ecological, and biogeographic information.

One species, *Cheimarrichthys fosteri* (McDowall, 1990).

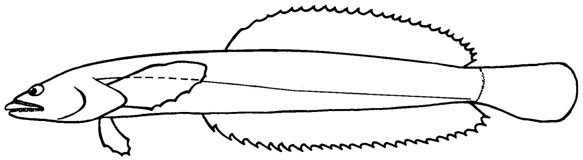
Family TRICHONOTIDAE (437)—sanddivers. Marine; Indo-West Pacific.

Eye with dorsal iris flap consisting of numerous elongate strands extending over lens; lower jaw projecting beyond upper jaw; anterior rays of dorsal fin in males of at least some species elongated; pelvic fin with one spine and five soft rays; lateral line on midside of body; predorsal bone between first two neural spines; postcleithrum present; lateral line scales with a deep V-shaped notch in the posterior margin.

The families Trichonotidae, Creediidae, and Percophidae may form a monophyletic assemblage.

One genus, *Trichonotus,* and about eight species (Randall and Tarr, 1994; Clark and Pohle, 1996; Nelson, 2001).

Family CREEDIIDAE (438)—sandburrowers. Marine; Indo-West Pacific (South Africa to Hawaii and Easter Island).



Row of cirri bordering lower jaw; dorsally projecting knob at symphysis of lower jaw; snout fleshy, projecting beyond lower jaw; lateral line descending abruptly or gradually to ventral surface; lateral line scales, except for anteriormost ones, with posterior extension, often trilobed; body largely scaleless in a few species (lateral line scales always present); dorsal fin continuous, with 12–43 unbranched soft rays; pelvis uniquely shaped, like an inverted bowl; pelvic fin with one spine and 3–5 soft rays (fins absent in the one species of *Apodocreedia*), interpelvic space very small; eye with infolding of the cornea at cornea-skin junction, and eyes slightly protruding. Bone of operculum highly splintered or fimbriated (can be revealed by passing light through the gill cover, this condition is present in some species of several other families). Maximum length about 8 cm.

I. L. Rosa revised this family in her 1993 dissertation.

Seven genera, *Apodocreedia*, *Chalixodytes*, *Creedia*, *Crystallodytes*, *Limnichthys*, *Schizochirus*, and *Tewara*, with about 16 species (Yoshino et al., 1999; Nelson, 2001).

Family PERCOPHIDAE (439)—duckbills. Marine; Atlantic, Indo-West Pacific, and southeast Pacific.

Head depressed; eyes usually large and interorbital space narrow; spinous dorsal, if present, separate from soft dorsal; anal fin with or without a single spine; pelvic fin with one spine and five soft rays, interpelvic space wide.

Eleven genera and about 44 species.

SUBFAMILY PERCOPHINAE. Tropical western Atlantic. Dorsal fins with eight or nine spines and about 31 soft rays; anal fin with one weak spine and about 38–42 soft rays; lower jaw projecting past upper; caudal fin with 13 branched rays; dorsal iris flap absent; distinct flap above pectoral fin base; scales above lateral line ctenoid but lateral line scales not serrated, trilobed, or with keel; minute scales extending along rays of caudal fin.

One species, *Percophis brasiliensis*.

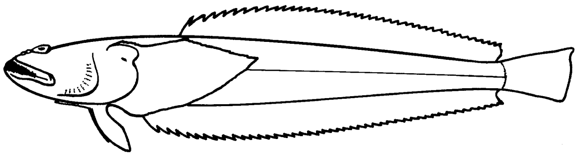
SUBFAMILY BEMBROPINAE. Dorsal fins with six spines (only first two crowded) and 13–18 soft rays; anal fin with 15–20 soft rays; lower jaw projecting past upper; caudal fin with 10 or 11 branched rays; maxillary tentacle present in *Bembrops*; scales ctenoid, with prominent keel on anterior few lateral line scales.

Two genera, *Bembrops* and *Chrionema*, with about 22 species (e.g., Nelson, 1994; Das and Nelson, 1996; Thompson and Suttkus, 2002; Thompson, 2003b).

SUBFAMILY HEMEROCOETINAE. Spines in dorsal fin, if present, 2–6 and usually very crowded at base; jaws about equal or upper jaw slightly longer than lower; caudal fin with seven or eight branched rays; dorsal iris flap present in most species; lateral line scales trilobed or serrated on posterior margin; medial barbel at tip of snout in males of some species of *Hemerocoetes*.

Eight genera and about 22 species (e.g., Nelson, 1994; Suzuki and Nakabo, 1996). *Dactylopsaron*, *Enigmapercis*, *Matsubaraea*, and *Squamicreedia* lack protruding maxillary spines. *Acanthaphritis* (synonyms *Branchiopsaron* and *Spinapsaron*), *Hemerocoetes* (a New Zealand endemic lacking the spinous dorsal fin), *Osopsaron*, and *Pteropsaron* (the latter two may be congeneric) have a spine protruding from the anterior face of the maxilla.

Family LEPTOSCOPIDAE (440)—southern sandfishes. Marine, occasionally in estuaries; Australia and New Zealand.

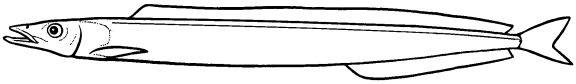


Mouth moderately oblique; lips fringed; eyes dorsal or nearly so; lateral line on middle of side; body with scales; pelvic fins widely separated; dorsal and anal fins long.

In New Zealand, *Leptoscopus macropygus* is known to occur also in the lower reaches of slow rivers (McDowall, 1990).

Three genera, *Crapatulus*, *Leptoscopus*, and *Lesueurina*, with five species (Nelson, 1994; P. R. Last et al. in Carpenter and Niem, 2001).

Family AMMODYTIDAE (441)—sand lances. Marine; cold to tropical, Arctic, Atlantic, Indian, and Pacific.

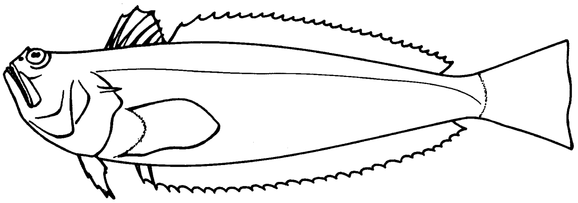


Body elongate; premaxilla protractile (except in *Hyperoplus*); caudal fin forked; dorsal and anal fin spines absent; lower jaw projecting forward beyond upper jaw with symphysial process; scales cycloid, minute, arranged in oblique rows; pelvic fins usually absent (jugular and with one spine and four or five soft rays in *Embolichthys*); lateral line high, close to dorsal fin; no teeth; single long dorsal fin usually with 40–69 soft rays; anal fin rays 14–36; seven branchiostegal rays; gill membranes separate; no swim bladder; vertebrae 52–78. Length up to 30 cm.

In a 1990 study, T. W. Pietsch and C. P. Zabetian regarded ammodytids as a possible sister group to Trachinidae plus Uranoscopidae, and gave a summary of meristic characters for many taxa of the suborder.

Eight genera, *Ammodytes*, *Ammodytoides*, *Bleekeria*, *Embolichthys*, *Gymnammodytes*, *Hyperoplus*, *Lepidammodytes*, and *Protammodytes*, and about 23 species (Collette and Randall, 2000; Ida et al., 1994).

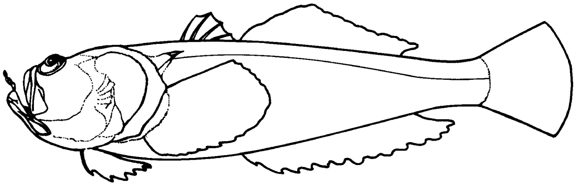
Family TRACHINIDAE (442)—weeverfishes. Marine; eastern Atlantic (most common in Mediterranean) and Black Sea.



Body elongate; dorsal fin with 5–7 spines and 21–32 soft rays; anal fin with two spines and 24–34 soft rays; pectoral fin with 15 rays; pelvic fins in front of pectorals, with one spine and five soft rays; poisonous glands associated with gill-cover spine and first dorsal spines; six infraorbitals; 34–43 vertebrae. These fish have a habit of burying in sand. They are able to inflict painful stings with their spines.

Two genera (as determined in 1983 by F. Bentivegna and G. Fiorito), the monotypic *Echiichthys* and *Trachinus* (about 5), with about six species.

Family URANOSCOPIDAE (443)—stargazers. Marine, occasionally in estuaries; Atlantic, Indian, and Pacific.



Head large and cuboid; body naked or covered with small smooth scales; mouth extremely oblique; lips fringed; eyes dorsal or nearly so; lateral line on upper part of side; pelvic fins narrowly separated, with one spine and five soft rays, located under the throat; dorsal and anal fins moderately long, spinous dorsal absent in many; anal fin with 12–18 soft rays; some with a small worm-like filament extending from floor of mouth used to lure prey fish; two large double-grooved poison spines, with a venom gland at each base, just above the pectoral fin and behind the opercle; four infraorbitals; 24–29 vertebrae. Maximum length 70 cm.

One genus, *Astroscopus,* has internal nares used during inspiration and electric organs derived from portions of eye muscle.

Xenocephalus armatus (the Armored Blenny) from New Ireland, for which the family Xenocephalidae has been recognized, once thought to be a trachinoid or blennioid and based on the missing holotype, was provisionally placed in the Dactylopteridae in Nelson (1994). Springer and Bauchot (1994) concluded that *Xenocephalus* Kaup, 1858, is a senior synonym of the currently recognized uranoscopid genus *Gnathagnus* Gill, 1861. Therefore, if the type species of *Gnathagnus, G. elongates* (Temminck & Schlegel, 1843), is regarded as congeneric with *Xenocephalus armatus* Kaup, 1858, then all species currently placed in *Gnathagnus* (e.g., *G. egregious*) should be recognized in *Xenocephalus* (e.g., *X. egregious*).

Eight genera, *Astroscopus, Genyagnus, Ichthyscopus, Kathetostoma, Pleuroscopus, Selenoscopus, Uranoscopus,* and *Xenocephalus* (synonym *Gnathagnus*), and about 50 species (e.g., Springer and Bauchot, 1994; H. Kishimoto in Carpenter and Niem, 2001:3519–3531; K. E. Carpenter in Carpenter, 2003:1746—1747).

Suborder Pholidichthyoidei

Family PHOLIDICHTHYIDAE (444)—convict blenny. Marine, southwesternmost Philippines to Solomon Islands.

Body eel shaped; one nostril on each side; scales absent; pelvics below or slightly in front of pectoral base, with one thin spine and two or three soft rays, rarely absent; caudal fin rounded and joined with dorsal and anal fins; dorsal fin with 66—98 soft rays; anal fin with 49—81 soft rays; pectoral fin with 15 rays; lower pharyngeals fused into a single bone; septal bone present in interorbital area; larvae with four adhesive attachment glands between the eyes; vertebrae 71–101.

Placed in the Trachinoidei in Nelson (1994), this fish is of very uncertain position in the Perciformes. Springer and Johnson (2004), in noting previous studies associating it also with the blennioids and labroids, placed *Pholidichthys* (Pholidichthyidae) in its own suborder, as had been previously suggested by others, and this is followed here.

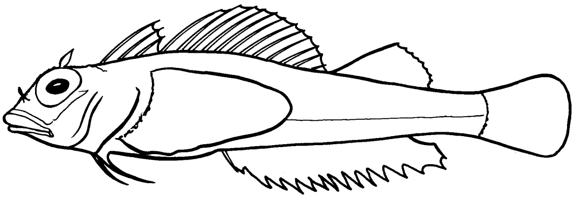
One genus, *Pholidichthys*, with two species (Springer and Larson, 1996).

Suborder Blennioidei. Monophyly for this taxon is based on the following five specialized character complexes given in a 1993 study by V. G. Springer: i) the third infrapharyngobranchial present but second and fourth absent and first absent or cartilaginous; uncinate process absent on first epibranchial and interarcual cartilage absent; ii) among other features of the caudal skeleton, the parhypural and hypurals 1 and 2 are fused to form a plate, and there is a dorsal hypural plate thought to comprise hypurals 3 and 4 fused to each other and to the urostylar complex; iii) pelvic fin usually with one embedded spine and two to four simple soft rays (fins absent in two species of *Plagiotremus*) and inserted in front of the pectoral fin base, and the pelvis forming a nutlike pod open ventrally; iv) anal fin with fewer than three (0–2) spines and all soft rays simple; and v) among other features of the pectoral complex, at least some of the pectoral radials are longer than deep. Synapomorphic characters were added by Johnson (1993), Mooi and Gill (1995), and Springer and Johnson (2004). In addition, blennioids share the following: dorsal- and anal-fin spine pterygiophores a single element; usually six branchiostegal rays; two nostrils on each side (except for some species of *Enchelyurus*); cirri often on head (variously on nape, above eye, on nostrils, or on margin of cephalic sensory pores). Monophyly of this suborder and of several of the families was reinforced by Stepien et al. (1997) in a study of the evolution of blennioid fishes based on an analysis of mitochondrial DNA. Differing analyses produced differing results, but one of their trees suggested that the Dactyloscopidae, rather than the Tripterygiidae, is the basal family and the sister group to the other blennioids, followed by the Blenniidae being sister to the remaining four families, and the Tripterygiidae being sister to the clade of Clinidae, Labrisomidae, and Chaenopsidae. Miocene fossils are known for several groups (references in Stepien et al, 1997:268).

Six families are recognized in this group following much earlier work by V. G. Springer (see Nelson, 1994, and Springer and Johnson, 2004) who considered them to be the sole members of their Blennioidei. The families Clinidae, Labrisomidae, and Chaenopsidae were treated as one family, Clinidae, in some works, an assemblage that is probably a monophyletic group (e.g., Stepien et al., 1997).

Six families, 136 genera, and at least 818 species.

Family TRIPTERYGIIDAE (445)—triplefin blennies. Marine (primarily tropical), one species occasionally in estuaries; Atlantic, Indian, and Pacific.

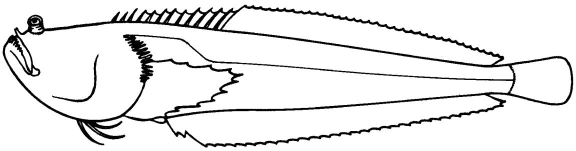


Dorsal fin divided into three distinct segments, the first two composed of spines and the third with never fewer than seven soft rays but fewer in number than the spines; no dorsal fin spine articulating with pterygiophore serially associated with first segmented dorsal fin ray; anal fin spines absent to two (usually two); no cirri on nape; scales usually ctenoid, with radii in anterior field only; gill membranes broadly attached across isthmus; premaxillae protractile. Maximum length about 25 cm, most species less than 6 cm. In New Zealand, one species is known to also occur in estuaries (McDowall, 1990).

Some of the generic changes in the important work of Fricke (1997) are in error (e.g., Smith and Williams, 2002).

About 23 genera (e.g., *Axoclinus, Crocodilichthys, Enneanectes, Enneapterygius, Forsterygion, Helcogramma, Lepidoblennius, Notoclinus, Ruanoho, Springerichthys, Trianectes,* and *Tripterygion*) with about 150 species (e.g., Shen, 1994; Fricke, 1994, 1997; J. T. Williams and R. Fricke in Carpenter and Niem, 2001:3532–3535; Smith and Williams, 2002; Williams and Howe, 2003). The area of greatest diversity is the Indo-West Pacific. There are relatively few species in the Atlantic.

Family DACTYLOSCOPIDAE (446)—sand stargazers. Marine (rarely brackish); warm temperate to tropical in North and South America.

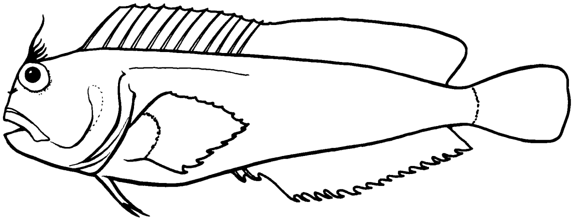


Mouth extremely oblique; lips usually fringed; upper edge of gill cover subdivided into fingerlike elements; gill membranes separate and free from isthmus; eyes dorsal, somewhat protrusive (may be on stalk); pelvic fins with one spine and three soft rays, jugular; dorsal fin long, continuous or divided, with 7–23 spines and 12–36 soft rays; anal fin with 21–41 soft rays; lateral line scales 33–73; scales cycloid; pterosphenoids absent (Springer, 1993); abdominal vertebrae 10–13 and caudal vertebrae 23–42. Maximum length about 15 cm.

Sand stargazers frequently bury themselves in sand bottoms, similar to some trachinoids. However, unlike virtually all other teleosts, which normally pump water over the gills by alternately expanding and contracting the buccal and opercular cavities, they have evolved a branchiostegal pump that replaces the opercular pump (other benthic fishes have both). Fingerlike labial and opercular fimbriae probably function to prevent particles from clogging the branchial chamber.

Nine genera, *Dactylagnus, Dactyloscopus, Gillellus, Heteristius, Leurochilus, Myxodagnus, Platygillellus, Sindoscopus,* and *Storrsia,* with 43 species (e.g., Doyle, 1998; Feitoza, 2002; Williams, 2002). Nineteen species occur in the Atlantic (United States to Brazil) and 24 in the Pacific (Gulf of California to Chile).

Family BLENNIIDAE (447)—combtooth blennies. Marine (rarely freshwater and occasionally brackish water, primarily tropical and subtropical); Atlantic, Indian, and Pacific.



Body naked (modified lateral line scales in a few species); premaxillae not protractile; head usually blunt; pelvic fins present (except in two species of *Plagiotremus*), anterior to the pectorals, and with one short embedded spine (easily overlooked) and 2–4 segmented rays; palatines toothless, vomer may have teeth; jaws with comblike teeth, fixed or freely movable (most species with at least some canine teeth); dorsal fin with 3–17 flexible spines and 9–119 segmented rays (fewer spines than soft rays in most species); pectoral rays not branched, 10–18; caudal fin rays branched or unbranched; anal fin with two spines (the first is buried beneath genital tissue in females); basisphenoid present except in Nemophini; adults without swim bladder except in *Phenablennius, Omox,* and most Nemophini where it may be minute and easily overlooked; vertebrae usually 28–44 (up to 135 in *Xiphasia*). Maximum length about 54 cm, most species under 15 cm.

Many species of blenniids are involved in mimetic associations with other fishes, being similar in external appearance to the other species (e.g., Smith-Vaniz et al. (2001).

Fifty-six genera with about 360 species. Except for combining the tribes Salariini and Parablenniini based on Bath (2001), I maintain the same tribes as recognized in Nelson (1984, 1994), based on the works of V. G. Springer and of W. F. Smith-Vaniz (see Nelson 1984, 1994, for the many references to their works and those of others that form the main basis of this classification). The study of Williams (1990) and Bath (2001) gave our current understanding of relationships; based on Williams (1990), the last four tribes may be each other's closest relatives and form a taxon sister to the new Salariini. Many recent species have been described since Nelson (1994), e.g., Smith-Vaniz et al. (2001), Springer and Allen (2004), and Bath (2004).

TRIBE SALARIINI. Marine (rarely brackish and freshwater), primarily Indo-West Pacific. Some species can spend much of their time out of water.

About 41 genera. Bath (2001) combined the formerly recognized tribes Salariini and Parablenniini because they lacked defining characters. Formerly recognized in the tribe Salariini were, for example, *Alticus, Andamia, Antennablennius, Cirripectes, Ecsenius, Entomacrodus, Istiblennius, Ophioblennius, Praealticus, Rhabdoblennius, Salarias,* and *Scartichthys,* and formerly recognized in the tribe Parablenniini were, for example, *Aidablennius, Chalaroderma, Chasmodes, Coryphoblennius, Hypleurochilus, Hypsoblennius, Lipophrys, Lupinoblennius, Parablennius, Salaria,* and *Scartella.*

TRIBE BLENNIINI. Two genera, *Blennius* (3) and *Spaniblennius* (2), with five species.

TRIBE OMOBRANCHINI. Marine (rarely brackish and freshwater). Caudal fin rays not branched; two segmented pelvic fin rays; 15–27 segmented dorsal fin rays.

Seven genera, *Enchelyurus, Haptogenys, Laiphognathus, Oman, Omobranchus, Omox,* and *Parenchelyurus.*

TRIBE PHENABLENNIINI. Brackish and freshwater; Sumatra, Cambodia, and Sarawak, northern Borneo. Body similar in appearance to Omobranchini; all fin rays unbranched; three segmented pelvic fin rays; 14 or 15 segmented dorsal fin rays (12 or 13 spines); five infraorbital pores; labial flaps on both jaws; postcleithrum single (other blenniids have two postcleithra or 1–3 fragments); vertebrae 32–34 (10 + 22–24).

One species, *Phenablennius heyligeri.*

TRIBE NEMOPHINI (SABER-TOOTHED BLENNIES). Marine (including brackish and freshwater for *Meiacanthus anema*); Indian and Pacific oceans. All fin rays unbranched; total dorsal rays 25–133; pelvic fin with one embedded spine and three segmented rays (fin absent in two species of *Plagiotremus*); swim bladder present (except in *Xiphasia*); circumorbital bones usually four, rarely three; basisphenoid absent; body eel-like in *Xiphasia* (which has the highest number of dorsal and anal fin rays and vertebrae); unique toxic buccal glands in *Meiacanthus*; vertebrae 30–135 (11–16 + 19–119).

Five genera, *Aspidontus, Meiacanthus, Petroscirtes, Plagiotremus,* and *Xiphasia.*

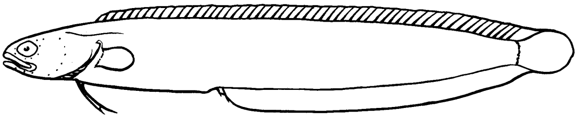
Family CLINIDAE (448)—kelp blennies. Marine, primarily temperate in both Southern and Northern hemispheres; Atlantic, Indian, and Pacific.

Scales cycloid, with radii on all fields (scales absent only in *Clinoporus biporosus* of South Africa), and usually small and embedded; nape cirri absent (cirri may be present elsewhere on head); dorsal fin with more spines than soft rays;

all fin rays simple; anal fin with two spines; cordlike ligament extending from ceratohyal to dentary symphysis. Maximum length about 60 cm, attained in *Heterostichus rostratus*, most much smaller.

Three tribes provisionally recognized with about 20 genera and 74 species. Nelson (1994) gave references to studies covering the family; since then, there appears to have only been one new species described (Zsilavecz, 2001). Unlike related families, clinids are generally absent from the tropics; there are only about four species in the tropics (in the Indo-Pacific).

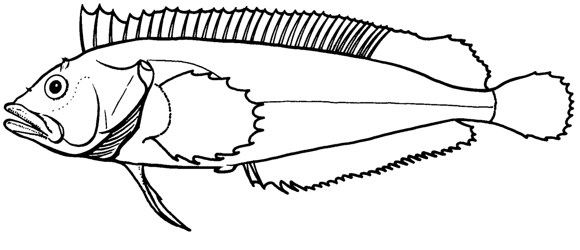
TRIBE OPHICLININI. Southern Australia.



Dorsal and anal fins united to caudal fin; dorsal fin continuous and without elongated anterior rays, with 36–84 spines and 1–4 soft rays; pectoral fins vestigial in several species, both pectoral and pelvic fins vestigial in *Peronedys*; no orbital cirri and nostril cirri usually absent; lateral line reduced; males with intromittent organ; ovoviviparous; body eel-shaped, especially in *Peronedys* and *Sticharium*; vertebrae 48–96 (18–35 precaudal). Maximum length 16 cm.

Four genera, *Ophiclinops*, *Ophiclinus*, *Peronedys*, and *Sticharium*, with 12 species.

TRIBE CLININI. Widespread in temperate Indo-West Pacific (including New Zealand) with about four species in the tropics.



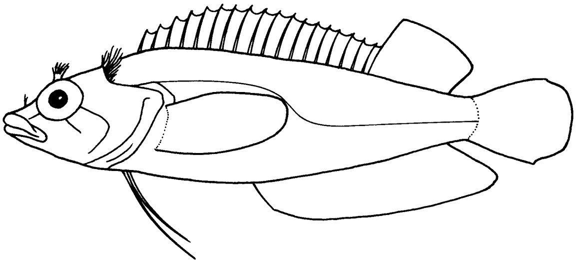
First three dorsal fin spines usually longer than remaining spines and separated from them by a small notch; anal fin rarely attached to caudal fin; orbital and nasal cirri usually present; males with intromittent organ; ovoviviparous.

About 11 genera, *Cancelloxus, Clinoporus, Clinus, Cologrammus, Ericentrus, Gynutoclinus, Heteroclinus, Neoblennius, Pavoclinus, Springeratus,* and *Xenopoclinus,* with about 53 species.

TRIBE MYXODINI. Temperate waters of Western Hemisphere and Mediterranean Sea. First three dorsal fin spines usually not separated from rest by notch (last two genera listed below have a deep notch between spines three and four); anal fin not attached to caudal fin; dorsal fin with 30–38 spines and 2–14 soft rays; anal fin with two spines and 18–36 soft rays; orbital and nasal cirri present; vomerine teeth present in first two genera listed below; males without an intromittent organ; oviparous; vertebrae 40–58 (precaudal 13–22).

Five genera, *Clinitrachus*, *Gibbonsia*, *Heterostichus*, *Myxodes*, and *Ribeiroclinus*, with about nine species. *Clinitrachus* is known only in the Mediterranean, *Ribeiroclinus* from the Atlantic coast of South America, and the others from the Pacific coast from British Columbia to the tip of Baja California and Peru to southern Chile.

Family LABRISOMIDAE (449)—labrisomid blennies. Marine, most tropical; Atlantic and Pacific.

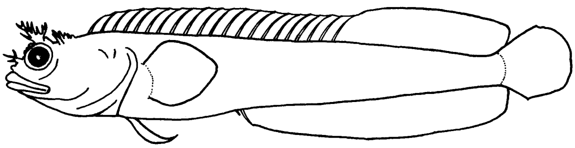


Scales cycloid, with radii only on anterior margin (scales absent in five of the six species of the New World genus *Stathmonotus* and in one species of *Neoclinus* from Taiwan) and never small and embedded; cirri often present on nape, nostril, and above eye; dorsal fin with more spines than soft rays (some species with only spines); only *Xenomedea* and eastern Pacific species of *Starksia* are viviparous, and only *Starksia* has intromittent organ in males (but of a different type than in clinids).

The monophyly of this family is uncertain; Stepien et al. (1997) found that chaenopsids form a monophyletic clade within labrisomids in their molecular analysis.

Fifteen genera, *Alloclinus, Auchenionchus, Calliclinus, Cottoclinus, Cryptotrema, Dialommus, Exerpes, Haptoclinus, Labrisomus, Malacoctenus, Mnierpes, Nemaclinus, Paraclinus, Starksia,* and *Xenomedea,* with about 105 species (e.g., Guimarães and de Bacellar, 2002; McCosker et al., 2003; Nelson et al., 2004; also see references in Nelson, 1994). Most species of this family occur in the tropics of North America (primarily in Central America) and South America: four species of *Neoclinus* are in the western Pacific (Taiwan to Japan), about 53 in the eastern Pacific, 47 in the western Atlantic, and two in the eastern Atlantic off Africa (one of which, a *Labrisomus,* is widespread in the western Atlantic).

Family CHAENOPSIDAE (450)—tube blennies. Warm seas of North and South America.

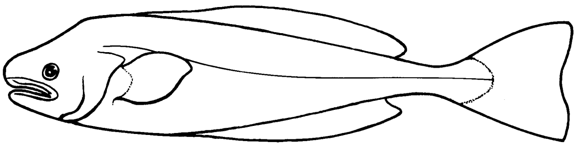


Body naked; no lateral line (three pores at most behind opercle); maxilla not visible externally; some species with anterior portion of dorsal fin much higher than rest; dorsal fin with 17–28 spines and 10–38 soft rays (total rays 29–57); anal fin with two spines and 19–38 soft rays; pectoral fin with 12–15 rays; caudal fin separate or variously united with dorsal and anal fins; orbital and nasal cirri variously present or absent (cirri on nape absent); palatines with teeth; head often spiny or rough; body usually elongate and compressed (as shown in figure), particularly slender (eel-like) in *Chaenopsis.* Maximum length about 16 cm, attained in various species of *Chaenopsis,* most much less.

Thirteen genera, *Acanthemblemaria, Chaenopsis, Coralliozetus, Ekemblemaria, Emblemaria, Emblemariopsis, Hemiemblemaria, Lucayablennius, Mccoskerichthys, Neoclinus, Protemblemaria, Stathmonotus,* and *Tanyemblemaria,* with about 86 species (e.g., Rosenblatt and McCosker, 1988; Tyler and Tyler, 1997; Hastings and Robertson, 1999; Smith-Vaniz, 2000; Hastings, 2001; Williams, 2002; Ramos et al., 2003; Nelson et al., 2004). Most of the genera are amphi-American. [*Cirriemblemaria* was inadvertently left off the list of genera]

Suborder Icosteoidei (Malacichthyes). The one included family and species was placed in its own order, Icosteiformes, by Berg (1940) and Gosline (1971). Recently, Springer and Johnson (2004) presented a detailed analysis on its systematic relationships and presented evidence that it is probably not associated with the stromateoids, as suggested by some earlier authors. First author V. G. Springer argued that it is probably a prepercomorph, and concluded that its closest relationship is probably with the Stephanoberyciformes given its many similarities with Barbourisidae. Coauthor Johnson strongly disagrees with this conclusion (G. D. Johnson, pers. comm., 2005). I prefer to maintain the group as placed in Nelson (1994), pending further morphological and/or molecular analyses that may support or refute Springer's stephanoberyciform hypothesis.

Family ICOSTEIDAE (451)—ragfishes. Marine; Pacific coast of North America.

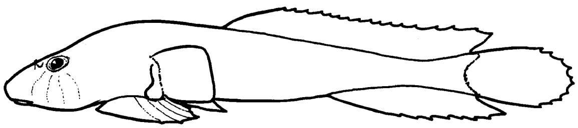


Body elliptical, highly compressed, and limp; skeleton largely cartilaginous; no spines in fins; minute prickles on fin rays; dorsal fin rays 52—58; scales imbedded or absent in adult; pelvic fins loosely attached in young, lost in adults; five hypurals; 66–72 vertebrae. Maximum length 2 m. As noted in Springer and Johnson (2004), G. H. Allen in 2001[2003] presented information on records of the one species.

One species, *Icosteus aenigmaticus* (Mecklenburg, 2003).

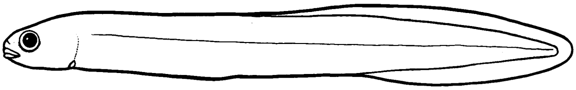
Suborder Gobiesocoidei (Xenopterygii). The relationships of the one included family are uncertain, and, as a result, its position in classifications has varied considerably. In Nelson (1976), I accepted the view of W. A. Gosline in a 1970 paper that it was related to the Callionymidae and Draconettidae, a group thought to be a notothenoid derivative. All three were placed in the order Gobiesociformes. In Nelson (1984), I removed the Gobiesocidae from the postperciform groups and included it in the Paracanthopterygii, in the order Gobiesociformes, following Greenwood et al. (1966) and a 1969 paper of D. E. Rosen and C. Patterson. Nelson (1994), while noting other papers presenting evidence to the contrary or supporting a paracanthopterygian affinity, accepted Patterson and Rosen's (1989) conclusion that there is no evidence to align the Gobiesocidae with the paracanthopterygians and accepted Gosline's (1970) evidence that it probably bears some affinity with the callionymoids and possibly with the notothenoids (and therefore cladistically belonging within the Perciformes as given here). As also noted, no osteological study has been done to demonstrate its cladistic relationships. Matters have not subsequently been clarified. A. C. Gill (1996) presented some evidence from the glossopharyngeal nerve supporting a paracanthopterygian affinity of both gobiesocids and callionymoids, but he did not propose transferring them to the paracanthopterygians and wisely advocated, similar to D. E. Rosen in 1985, the need for studies of homology of all relevant synapomorphies. Springer and Johnson (2004) placed the Gobiesocidae in the suborder Callionymoidei (placed as a perciform group next to the Blennioidei). The evidence for a close callionymoid relationship seems strong; the evidence for the relationships of the resulting group is weak and I maintain the classification presented in Nelson (1994), recognizing the suborders Gobiesocoidei and Callionymoidei next to one another and both as possible perciforms.

Family GOBIESOCIDAE (452)—clingfishes. Marine, primarily shallow water or intertidal, few in freshwater; Atlantic, Indian, and Pacific.



Pelvic fins modified into a thoracic sucking disc (permitting fish to adhere to substrate), with underlying pelvic bones specialized for supporting disc (pelvic skeleton highly reduced in *Alabes*); each pelvic fin with one small spine and four soft rays (rarely five); single dorsal fin without spines; head and body scaleless; branchiostegal rays 5–7 (three in *Alabes*); no circumorbital bones posterior to the lachrymal; articular process of premaxilla either fused with ascending process or absent; basibranchials one and two probably absent; supracleithrum with concave process that articulates with condyle on cleithrum (not known from other fishes); basisphenoid and orbitosphenoid absent; genital papilla behind anus; three or three and half gills; hypurals fused into a single plate; no swim bladder. Most species are shallow-water bottom-dwelling fishes. The following characters apply to all gobiesocids except *Alabes*: scapula and four pectoral radials and 16–31 pectoral fin rays; usually two postcleithra (rarely one); either common gill opening or separate opening on each side; ribs attached to the epineural ribs (an opposite relationship to that found in most fishes); total caudal fin rays 16–27 (8–14 articulating on hypural fan); vertebrae 25–54 (11–20 + 13–33). Maximum length normally 7 cm; two species, however, reach 30 cm or slightly more— *Chorisochismus dentex* of South Africa and *Sicyases sanguineus* of Chile. Much taxonomic work has been done on the species of this family over many decades by J. C. Briggs.

The highly modified marine *Alabes* (synonym *Cheilobranchus*) of the Australian region was once placed in its own family Alabetidae (Cheilobranchidae).



The four species of *Alabes* differ from the other members of the family in having: pelvic bones absent in three species and present in one behind the gill opening (jugular) with three reduced rays (vestigial "sucking disc" in some specimens of one species); no rays in dorsal and anal fins; scapula and pectoral fin radials and rays absent; no postcleithra; single gill opening to both gill chambers situated on midventral side of head; pleural ribs absent (epipleurals attached to vertebral centra); total caudal fin rays 8–11 (seven or eight articulating on hypural fan); vertebrae 60–78.

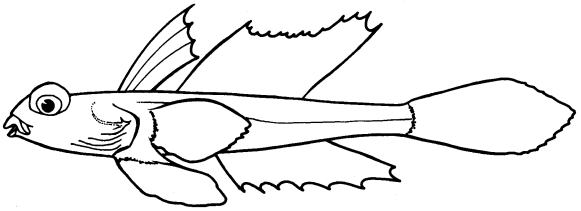
About 36 genera, e.g., *Acyrtops, Alabes, Aspasmogaster, Arcos, Aspasma, Chorisochismus, Cochleoceps, Conidens, Diademichthys* (questionably included), *Diplecogaster, Gastrocyathus, Gobiesox* (four species of which occur in freshwater streams in Central America), *Haplocylix, Lepadichthys, Lepadogaster, Parvicrepis, Rimicola, Tomicodon,* and *Trachelochismus,* with about 140 species (Briggs, 2002a,b, 2002; Williams and Tyler, 2003; Nelson et al., 2004).

Suborder Callionymoidei. Head usually broad and depressed; body scaleless; mouth small; usually two dorsal fins present and first with 1–4 flexible spines (spinous fin absent in *Draculo*); pelvic fin with one spine and five soft rays; basibranchials present; vertebrae 21–23.

See the preceding section on gobiesocoids for comments on a possible affinity between that group and the callionymoids. Much work on this family has been done by R. Fricke and by T. Nakabo; they have differing opinions on some generic compositions.

Two families, about 12 genera, and about 194 species (Fricke, 2002a).

Family CALLIONYMIDAE (453)—dragonets. Marine (two species enter rivers), benthic; all warm seas, primarily Indo-West Pacific.



Gill opening reduced to a small opening on upper side of head; preopercle with a strong spine, opercle and subopercle spineless; lateral line continued on body; three radials in pectoral skeleton; usually no basisphenoid or posttemporal; paired nasal bones; two postcleithra; hypurals fused into a single plate; dorsal fin spines usually four and soft rays 6–11; anal fin with 4–10 soft rays. Maximum length about 25 cm. Dragonets can be very colorful; sexual dimorphism is common.

About 10 genera, *Anaora, Callionymus* (synonym *Calliurichthys*), *Chalinops, Dactylopus, Diplogrammus, Draculo* (*Pogonymus*), *Eleutherochir* (synonym *Bathycallionymus), Paracallionymus, Protogrammus,* and *Synchiropus* (synonym *Foetorepus*), with about 182 species, and several undescribed species are known (e.g., Fricke, 2002a).

Family DRACONETTIDAE (454)—slope dragonets. Marine; Japan to Hawaii, Atlantic, and Indian.

Gill opening comparatively broad; opercle and subopercle each with a strong straight spine; preopercle spineless; lateral line developed on head but degenerate on body (in a groove); four radials in pectoral skeleton; basisphenoid and posttemporal present; no nasal bone; one postcleithrum; two separate hypurals; three dorsal fin spines and 12–15 soft rays; anal fin with 12 or 13 soft rays; two nostrils on each side.

Draconettids are relatively rare. They occur primarily in tropical to warm temperate waters along the edge of the continental shelf or on seamounts in widely scattered areas.

Two genera, *Centrodraco* (about 11) and *Draconetta* (1), with about 12 species (e.g., Fricke, 2002a,b).

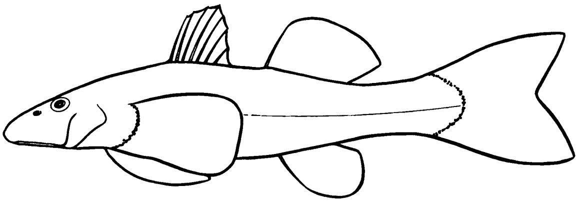
Suborder Gobioidei. Parietals absent; infraorbitals, except for the lachrymal, unossified or absent; lateral-line system reduced to variably developed cephalic canals except in the primitive *Rhyacichthys* (free neuromasts may be involved); swim bladder usually absent; gill membranes usually joined to isthmus; barbels on head in some; no pyloric caeca; spinous dorsal, when present, with 1–8 flexible spines; pelvic fins below pectorals, with one spine and usually four or five soft rays, often united; unique sperm gland present; vertebrae 25–35 (exceptions to some characters occur in Microdesmidae and *Schindleria*).

The molecular phylogeny of Thacker (2003), which did not include the hypothesized basal family Rhyacichthyidae, supported the monophyly of a clade consisting of the families Kraemeriidae, Gobiidae, Microdesmidae, Ptereleotridae, and Schindleriidae, to the exclusion of Odontobutidae, Eleotridae, and Xenisthmidae. She noted that morphological character evidence agrees with this (for example, the hypothesized derived five families have five branchiostegal rays while the Rhyacichthyidae, Odontobutidae, Eleotridae, and Xenisthmidae have six). The sequence of the families in the classification of Nelson (1994) has been changed slightly to agree with Thacker (2003) and the family Ptereleotridae is recognized following Thacker (2000, 2003) (giving nine families). However, despite much effort over the past 20 or so years, a classification of monophyletic subtaxa for this large and diverse assemblage has yet to be established. The sister group of gobioids is uncertain; there is evidence that it could be the callionymoids or trachinoids. Our knowledge of Gobioidei systematics employed in Nelson (1994) relied heavily on such workers as R. S. Birdsong, D. F. Hoese, E. O. Murdy, F. L. Pezold, V. G. Springer, and R. Winterbottom. There is an immense literature, very little of which could possibly be incorporated here, on the taxonomy and systematics by such recent workers as P. J. Miller, E. O. Murdy, F. L. Pezold, J. E. Randall, and R. E. Watson. There are many more.

The Upper Oligocene fossil *Pirskenius* from freshwater deposits of Bohemia may warrant family status.

Nine families, about 270 genera, and approximately 2211 species. Many gobioids, probably over 200, occur in freshwater (for example, in New Guinea and Africa).

Family RHYACICHTHYIDAE (455)—loach gobies. Freshwater streams; Indo-Australian Archipelago (e.g., Java, Sulawesi, and New Guinea), Philippines, China, and Solomon Islands.



Head depressed, tail compressed; mouth inferior with fleshy upper lip; eyes small; pelvic fins widely separated; pectoral fins very broad, with 21 or 22 rays; lower surface of head and anterior part of body, with the paired fins, form an adhesive disc; dorsal fins well separated, first with seven feeble spines and second with one spine and eight or nine soft rays; anal fin with one feeble spine and eight or nine soft rays; lateral line scales (ctenoid) about 27–40; lateral line system on body and head well developed (presumably a unique primitive feature to the suborder); six branchiostegal rays; caudal fin lunate. The fish superficially resembles the homalopterids in appearance and habit. Maximum length about 32 cm.

One genus, *Rhyacichthys*, with two species.

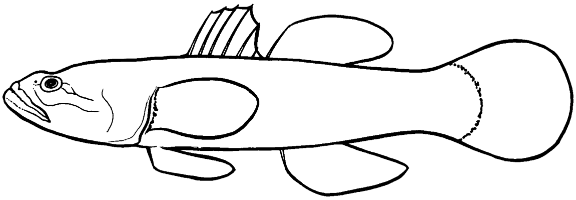
Family ODONTOBUTIDAE (456)—freshwater sleepers. Freshwater; northern Vietnam, China, Korea, Japan, and Russia.

This taxon may be distinguished from other gobioid families by the following characters: scapula large, excluding proximal radial from contact with cleithrum (as in *Rhyacichthys*); six branchiostegal rays (as in *Rhyacichthys*, eleotrids, and xenisthmids); no lateral line (*Rhyacichthys* is the only gobioid with a lateral line).

This family, once placed in the eleotrids, may not be monophyletic (e.g., Ahnelt and Göschl, 2004).

Five genera, *Micropercops, Neodontobutis, Odontobutis, Perccottus,* and *Terateleotris,* with about 15 species (Kottelat, 1998; Shibukawa et al., 2001; Chen et al., 2002).

Family ELEOTRIDAE (Eleotrididae) (457)—sleepers. Marine, brackish, and freshwater; most tropical and subtropical areas (rarely temperate areas).



Pelvic fins separate (no sucking disc), bases close together or united (there is considerable variation in the degree of union or separation of the pelvic fins, and sleepers and gobies cannot always be neatly separated on the basis of this character alone); mouth never inferior; spinous dorsal with 2–8 flexible spines; scales cycloid or ctenoid; six branchiostegal rays; vertebrae 25–28. Maximum length about 60 cm, attained in *Dormitator maculatus.*

Eleotrids extend as far north as the Atlantic coast of the United States and as far south as Stewart Island, New Zealand. Six species occur in New Zealand freshwaters in swift streams, and the larvae are thought generally to drift downstream to the ocean (McDowall, 1990).

About 35 genera with about 155 species. The monophyly of the two subfamilies is uncertain. Recent studies include Pezold and Cage (2002).

SUBFAMILY BUTINAE. Confined to freshwater and estuaries of the tropical Indo-Pacific and West Africa and perhaps paraphyletic. Thirteen genera, e.g., *Butis, Incara, Kribia,* and *Oxyeleotris.*

SUBFAMILY ELEOTRINAE. Worldwide and found mostly in freshwater and mangrove environments. Twenty-two genera, e.g., *Calumia, Dormitator, Eleotris, Erotelis, Gobiomorphus, Gobiomorus, Guavina, Hypseleotris, Mogurnda, Philypnodon,* and *Thalasseleotris.*

Family XENISTHMIDAE (458)—xenisthmids. Marine; Indo-Pacific.

Lower lip with a free ventral margin; ascending process of premaxilla absent or rudimentary; six branchiostegal rays.

About six genera, *Allomicrodesmus, Kraemericus, Paraxenisthmus, Rotuma,* and *Tyson,* and *Xenisthmus,* with about 12 species (e.g., Gill and Randall, 1994).

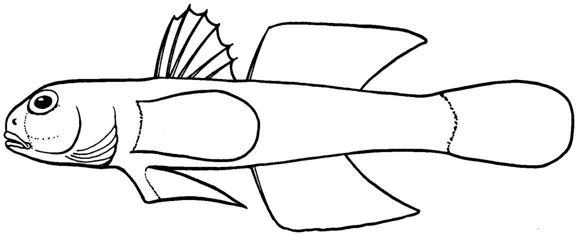
Family KRAEMERIIDAE (459)—sandfishes or sand gobies. Marine (rarely brackish or freshwater); Indo-Pacific (to Hawaii).

Body elongate; tongue bilobed at tip; lower jaw protruding forward with enlarged chin; eyes small; body naked; dorsal and anal fins free of caudal; dorsal fin usually single with 4–6 feeble spines and usually 13–18 soft rays; pelvics with one spine and five soft rays, usually separate; five branchiostegal rays.

These fishes generally inhabit sandy shallow waters. Many species burrow into the sand with only the head protruding. Maximum length about 6 cm.

Two genera, the monotypic *Gobitrichinotus* (with fused pelvics) and *Kraemeria*, with a total of about eight species.

Family GOBIIDAE (460)—gobies. Marine, brackish, and occasionally freshwater; most tropical and subtropical areas.



Pelvic fins, when well developed, united, usually forming an adhesive or sucking disc; spinous dorsal, when present, separate from soft dorsal and with 2–8 flexible spines; scales cycloid or ctenoid (rarely absent); some species with prominent head barbels; five branchiostegals rays.

Some gobies live in close association with other animals (e.g., sponges, shrimps, and sea urchins). Some species of *Gobiosoma* feed on ectoparasites of other fishes. Several gobies live on wet beaches and may spend several days out of water. Some of the land gobies, such as the mudskippers, *Boleophthalmus*, *Periophthalmus*, and *Periophthalmodon*, can move along with considerable speed. Their eyes, placed on top of the head on short stalks and capable of being elevated or retracted, are well adapted for vision in air. *Gillichthys mirabilis*, which usually remains in the water, comes to the surface when the water is low in oxygen and gulps air, which is held in the highly vascularized buccopharynx for respiratory exchange. Some gobies exhibit sequential hermaphroditism, and some also have parental care.

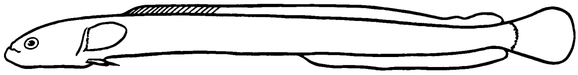
Maximum length up to 50 cm in *Glossogobius giuris* (D. F. Hoese in Smith and Heemstra, 1986), most under about 10 cm. This family contains the world's smallest fishes (and vertebrates). The scaleless *Trimmatom nanus* of the Chagos Archipelago in the Indian Ocean is the shortest species, with mature females reaching only 8–10 mm SL. Some species of the marine *Eviota* and *Mistichthys* are only slightly larger. The freshwater *Pandaka pygmaea* and *Mistichthys luzonensis* of Luzon, Philippines, are one of the shortest freshwater fishes with females maturing as short as about 10–11 mm.

This family has more marine species than any other fish family; in addition, gobiids are often the most abundant fish in freshwater on oceanic islands. A few species are known even in the headwaters of rivers in mountains. Some species that occur in freshwater spawn in the ocean and are thus catadromous like the anguillids. Together with blenniids, they form the dominant element in the small-fish fauna of benthic habit in tropical reefs. Most species occur in the tropical Indo-West Pacific, but they extend well into temperate waters of both the Northern and Southern hemispheres. The Gobiidae seem now to have fewer valid species than the Cyprinidae, and they would thus be the second most species-rich family of vertebrates. The estimate for the number of valid gobiid species is probably less accurate than is the comparable number for cyprinids; as is also true for the other groups, some nominal species may be placed into synonymy with others, but many species are undescribed.

About 210 genera and at least 1,950 species. Five provisionally recognized subfamilies are given here as in Nelson (1994). As noted above under the subordinal name, there is an immense recent literature on gobies that cannot be covered here (e.g., Parenti and Maciolek, 1996; Greenfield and Randall, 1999; Watson and Allen, 1999; Watson, 2000; Hoese and Reader, 2001; Thacker and Cole, 2002; Winterbottom, 2002; Murdy, 2002, 2003; Murdy and Shibukawa, 2003; Pezold, 2004 a,b).

Oxudercinae—Inhabit mangrove and mudflat areas from Africa eastward to Samoa. Ten genera (e.g., *Apocryptes, Boleophthalmus, Oxuderces, Periophthalmodon, Periophthalmus,* and *Zappa*) with about 34 species (based on a 1989 revision by E. O. Murdy).
Amblyopinae—A worldwide group commonly found off estuaries or in rivers. About 10 genera (e.g., *Amblyotrypauchen, Brachyamblyopus, Caragobius, Kasten, Taenioides,* and *Trypauchen*).
Sicydiinae—A worldwide group occurring primarily in freshwater with some having sea-run larvae. A few species can ascend fast-flowing rivers and even surmount waterfalls. About seven genera, *Awaous, Cotylopus, Lentipes, Sicydium, Sicyopterus, Sicyopus,* and *Stiphodon.*
Gobionellinae—Recognition of this subfamily is based on the 1993 paper of F. Pezold. Many of the species occur in freshwater. About 56 genera—e.g., *Acanthogobius, Astrabe, Brachygobius, Chasmichthys, Clevelandia, Ctenogobius, Eucyclogobius, Evorthodus, Gillichthys, Gnatholepis, Gobioides, Gobionellus, Gobiopterus, Ilypnus, Lepidogobius, Lethops, Lophiogobius, Mistichthys, Mugilogobius, Neogobius, Pandaka, Quietula, Rhinogobius, Stigmatogobius, Tridentiger,* and *Typhlogobius.*
Gobiinae—A worldwide group with about 130 genera—e.g., *Acentrogobius, Amblygobius, Anatirostum, Asterropteryx, Barbulifer, Bathygobius, Bollmannia, Coryogalops, Coryphopterus, Evermannichthys, Eviota, Gobiopsis, Gobiosoma, Gobius, Gobulus, Heterelotris, Istigobius, Knipowitschia, Lophogobius, Lythrypnus, Microgobius, Nematogobius, Nes, Palatogobius, Parkraemeria, Pomatoschistus, Priolepis, Risor, Trimma, Trimmatom, Varicus,* and *Zebrus.*

Family MICRODESMIDAE (Cerdalidae) (461)—wormfishes. Marine (rarely brackish and freshwater); tropical and subtropical waters.



Body elongate to eel-like, strongly compressed; eyes lateral; body with small embedded cycloid scales; lower jaw heavy and protruding; dorsal fin continuous and extending along most of body, with a combination of 10–28 flexible spines and 28–66 soft rays; anal fin with 23–61 soft rays; pelvic fins small, inserted below pectorals, with one spine and 2–4 soft rays; pectoral fin rays 10–16; caudal fin free or united to dorsal and anal fins, with 15 or 17 principal rays; branchiostegal rays five; vertebrae 42–76. Wormfishes often burrow in sand and mud and are known from coral reefs to muddy estuaries and from tidepools to about 40 m depth. Maximum length 30 cm.

Five genera, *Cerdale*, *Clarkichthys*, *Gunnellichthys*, *Microdesmus*, and *Paragunnellichthys*, with about 30 species (Thacker, 2000).

Family PTERELEOTRIDAE (462)—dartfishes. Marine; rarely freshwater; tropical and subtropical waters.

Mouth almost vertical; first dorsal fin with six spines and second with one spine and 9–37 soft rays; anal fin with one spine and 9–36 soft rays; pelvic fin with one spine and 4 or 5 soft rays; some are brightly colored.

Parioglossus multiradiatus is known from streams in the Seychelles Islands (Keith et al., 2004). The largest genus with 17 species is *Parioglossus*.

Five genera, *Aioliops*, *Nemateleotris*, *Oxymetopon*, *Parioglossus*, and *Ptereleotris* (synonyms *Ioglossus*, *Pogonoculius*), with about 36 species (Rennis and Hoese, 1987; Thacker, 2000; Williams and Lecchini, 2004; Keith et al., 2004).

Family SCHINDLERIIDAE (463)—infantfishes. Marine; oceanic.

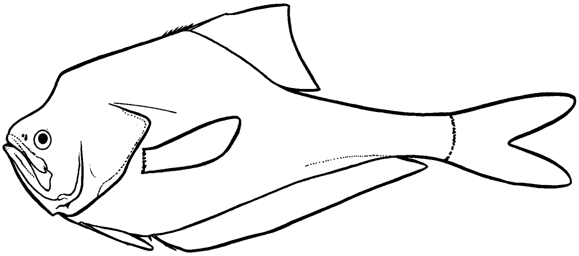
Small neotenic fishes. Some of the larval characteristics found in sexually mature individuals include functional pronephros, transparent body, and numerous cartilage and dermal bones that do not develop. Other characteristics are 15–22 unbranched dorsal fin rays, 11–17 anal fin rays, 11–18 pectoral fin rays, pelvic fins absent, 13 principal rays in caudal fin, five short branchiostegal rays, 31–44 vertebrae, and rodlike terminal section on vertebral column. Maximum length about 20 mm.

Evidence that the affinities of the highly paedomorphic *Schindleria* are with the Gobioidei is provided by a 1993 paper by G. D. Johnson and E. B. Brothers. These authors note that, although many gobioids have a truncated ontogeny, *Schindleria* is the most extreme known among all fishes. One species has the distinction of being the world's lightest and possibly shortest lived and most paedomorphic vertebrate.

One genus, *Schindleria*, with three species (Watson and Walker, 2004).

Suborder Kurtoidei

Family KURTIDAE (464)—nurseryfishes. Brackish and freshwater (rarely marine), in Indo-Malay area and parts of Australia.



Males with occipital hook, used for carrying eggs on the head; scales small and cycloid; lateral line short and rudimentary; mouth large; dorsal fin single, with spines and soft rays; anal fin with two spines and 31–47 soft rays; pelvic fins with one spine and five soft rays; caudal fin deeply forked; ribs expanded, partly enclosing the anterior portion of the swim bladder and entirely enclosing the posterior portion. Maximum length 60 cm, attained in *Kurtus gulliveri.*

Much information on these fascinating fishes with a bizarre method of parental care is contained in many works by T. M. Berra (e.g., Berra, 2001, 2003; Berra and Humphrey, 2002; Berra and Neira, 2003).

One genus, *Kurtus,* with two species. *K. gulliveri* has 44–47 soft rays in the anal fin and is found in southern New Guinea and northern Australia; *K. indicus* has 31 or 32 soft rays in the anal fin and is found in the Indo-Malay area (e.g., India, China, Borneo) (e.g., Berra, 2001, 2003).

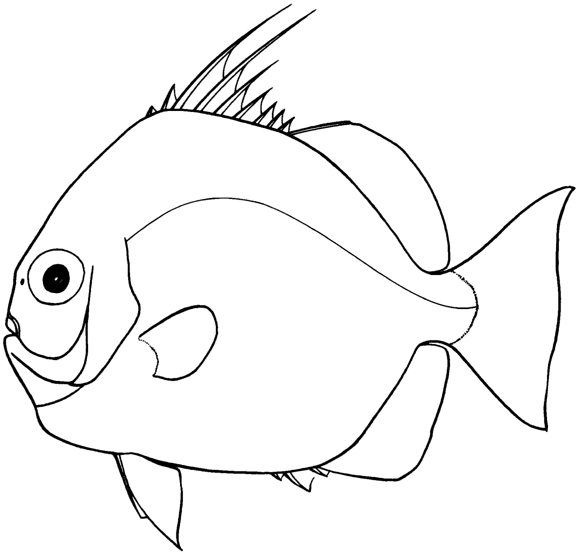
Suborder Acanthuroidei. Gill membranes broadly united at the isthmus, restricting the branchial aperture ventrally; premaxillae nonprotrusible or only slightly so; frontal and supraoccipital bones cancellous in most; interarcual cartilage absent; body deeply compressed; mouth small.

Monophyly of the suborder Acanthuroidei and sequencing of the families are recognized following the classical works of J. C. Tyler, G. D. Johnson, I. Nakamura, and B. B. Collette in 1989 and of R. Winterbottom in 1993 (Nelson, 1994), and subsequently supported by Tyler and Sorbini (1999). Tang et al. (1999), in a detailed study based on molecular and morphological evidence, largely agreed with our understanding of relationships although there was some disagreement between the molecular and morphological evidence. These authors found, contrary to the older view and that followed here, *Zanclus* to be nested within the acanthurids (versus the two being considered sister taxa) and found that *Drepane* may belong within this suborder; it is recognized here in the suborder Percoidei, in the family Drepaneidae (392). Their tree supported retaining the very different appearing *Luvarus* (family Luvaridae) in this suborder; the one species had classically been placed on the Scombroidei as in Nelson (1984). There have been many changes in the composition of this suborder over the past few decades (e.g., Nelson, 1976, recognized only two families, Acanthuridae, with *Zanclus* in its own subfamily, and Siganidae). Except for the uncertain position of *Drepane,* the monophyly of this suborder, based on synapomorphies, is stronger than most other perciform suborders and is certainly stronger than that for the order.

Almost all species of the clade comprising the last four families (as also supported by Tyler and Sorbini, 1999) are herbivorous, feeding mostly on algae. They pass through a planktonic larval stage, termed the acronurus stage, in which their bodies are transparent. In addition, members of these families usually have a large swim bladder, lunate caudal fin, usually five branchiostegal rays, and 22 or 23 vertebrae.

Six families, 19 genera, and about 129 species.

Family EPHIPPIDAE (465)—spadefishes. Marine (rarely in brackish water); Atlantic, Indian, and Pacific.



Comblike series of large blunt gill rakers on first epibranchial; basihyal reduced or absent; interarcual cartilage absent; dorsal fin with five or nine spines and 18–40 soft rays; three anal fin spines and 15–28 soft rays; gill membranes united to isthmus; body deep and laterally compressed; mouth small; no teeth on vomer or palatines; spinous portion of dorsal fin distinct from soft-rayed portion (except in *Platax*, in which the young have very elongate dorsal and anal fins); six branchiostegal rays; 24 vertebrae. Young may have black bands extending around the body that are lost with growth.

Eight genera, *Chaetodipterus*, *Ephippus*, *Parapsettus*, *Platax*, *Proteracanthus*, *Rhinoprenes*, *Tripterodon*, and *Zabidius*, with about 16 species (e.g., P. C. Heemstra in Carpenter and Niem, 2001; Burgess, 2003).

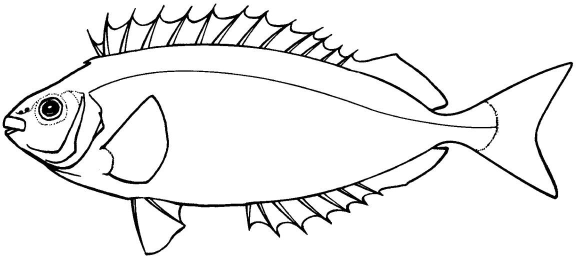
Family SCATOPHAGIDAE (466)—scats. Marine and brackish water, occasionally entering freshwater; Indo-West Pacific (primarily southeastern Asia and Indo-Australian Archipelago but extending from South Africa to the Society Islands).

Body deep and compressed, resembling that of butterflyfishes; pelvic axillary process present; dorsal fin deeply notched, with 11 or 12 spines, first dorsal spine procumbent, and 15–18 soft rays; anal fin with four spines and 14–17 soft rays; caudal fin with 16 branched rays; mouth not protractile; 23 vertebrae (11 + 12). Maximum length about 35 cm. At least one species, *Scatophagus tetracanthus*, can reproduce in freshwater.

As noted by P. Parenti (2004), the family gets its name from their habit of including human feces in the diet. Tyler and Sorbini (1999) gave a phylogeny of fossil (Eocene and Oligocene) and extant species and provided a key to all genera.

Two genera, *Scatophagus* (2) and *Selenotoca* (2), with four species (P. Parenti, 2004).

Family SIGANIDAE (467)—rabbitfishes. Marine (rarely in estuaries); tropical Indo-West Pacific and eastern Mediterranean.



Pelvic fins each with two strong spines and three soft rays between them; single dorsal fin with 13 strong spines and 10 soft rays; anal fin with seven spines and nine soft rays; spines venomous; a single row of compressed, asymmetrically bicuspid incisiform teeth in both jaws; vertebrae 23. Maximum length about 50 cm.

Most siganids are herbivorous. There is one species that is truly estuarine, *Siganus vermiculatus*; individuals of several other species may occur in estuaries for part of their life. Of the 27 species, 13 are schooling species while the remainder live among coral.

Four Eocene and Oligocene fossil genera are known, *Archaeoteuthis*, *Eosiganus*, *Ruffoichthys* (which has only one spine and three soft rays in each pelvic fin), and *Siganopygaeus* (Tyler and Bannikov, 1997).

One genus, *Siganus* (synonym *Teuthis*) with two subgenera, the subgenus *Siganus* with 22 species and the subgenus *Lo* with five species (established by D. J. Woodland in1990; Tyler and Bannikov, 1997).

Family LUVARIDAE (468)—louvar. Marine; tropical and subtropical seas.

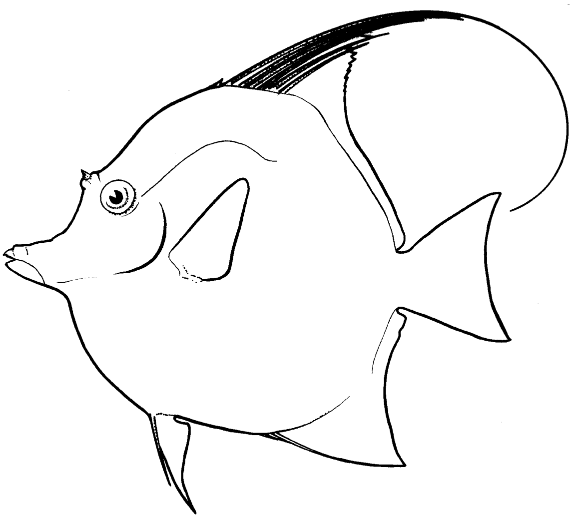
Dorsal fin origin in juvenile well forward, fin initially with two spines and 20–22 soft rays, anterior ones lost with growth; anal fin lacking spines; 22 vertebrae, last two fused.

These fish have an enormous egg production; a 1.7-m individual had an estimated 47.5 million eggs, characteristic of nonschooling oceanic fish. Length up to 1.8 m. *Luvarus imperialis* is the only pelagic member of an otherwise shorefish group.

Bannikov and Tyler (1995) revised the families Luvaridae (and described new Eocene fossils including the genus *Avitoluvarus*, see also Bannikov and Tyler, 2001) and †Kushlukiidae (with the Eocene *Kushlukia*) and found 10 synapomorphies showing that both families are sister taxa (at the node between the siganid and zanclid + acanthurid clades).

One species, *Luvarus imperialis* (Bannikov and Tyler, 1995).

Family ZANCLIDAE (469)—Moorish Idols. Marine; tropical Indo-Pacific.



Caudal peduncle unarmed; spine at corner of mouth in juveniles and protuberances in front of eyes in adults.

The Moorish Idol is most commonly found in coral-reef areas. The extended snout in the adult is well suited for foraging for invertebrates and algae in small crevices. The broad vertical black bars on a largely whitish background and elongated dorsal fin filament make it a very attractive fish. The butterflyfish, *Heniochus acuminatus*, another popular aquarium fish, and the Moorish Idol bear a marked resemblance to one another.

One species, *Zanclus cornutus* (synonym *Z. canescens*) (see Nelson et al., 2004:247, regarding advice from J. E. Randall in accepting *Z. cornutus* as the senior synonym).

Family ACANTHURIDAE (470)—surgeonfishes. Marine; all tropical and subtropical seas (absent in Mediterranean).

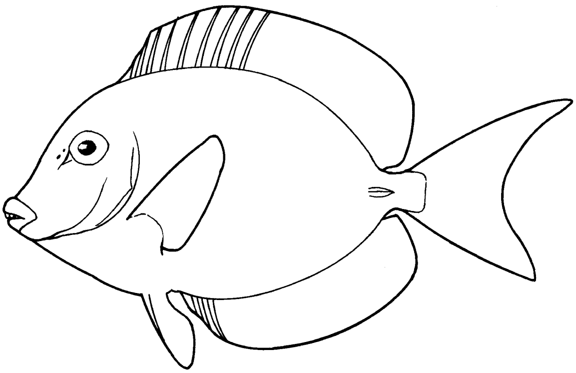
Pelvic fins with one spine and three (*Naso* and *Paracanthus*) or (usually) five soft rays; dorsal fin usually with 4–9 spines and 19–31 soft rays; anal fin with two or three spines and usually 19–36 soft rays.

Six genera and about 80 species. The subfamilies and tribes are recognized after a 1993 study of R. Winterbottom. From the rich Eocene and Oligocene fossil record, it appears that the group was as diversified then as it is now (J. C. Tyler has many papers describing the fossil record, e.g., Tyler, 2000).

SUBFAMILY NASINAE (UNICORNFISHES). Two anal spines, three soft pelvic rays rather than five in addition to the spine, one or two plates on the caudal peduncle, and some species with a protuberance on the frontal region developing with age; four branchiostegal rays. Indo-Pacific.

One genus, *Naso* (including the subgenus *Axinurus*), and about 16 species (Borden, 1998; Randall, 2001b, c).

SUBFAMILY ACANTHURINAE. Three anal spines; one or more movable spines (fixed in *Prionurus*) on caudal peduncle, which, when extended, can form a formidable weapon (in a deep groove in the Acanthurini); five branchiostegal rays; jaw teeth spatulate. Maximum length about 66 cm.



There are three recognized tribes with five genera and about 64 species (e.g., Randall, 2001c,d; Randall and Earle, 1999; Randall and Clements, 2001).

Prionurini (primarily Pacific), with *Prionurus* (three anal spines and 3–10 bony plates on the caudal peduncle).
Zebrasomini with two genera, *Paracanthus* and *Zebrasoma* (tangs).
Acanthurini with two genera, *Acanthurus* and *Ctenochaetus.*

Suborder Scombrolabracoidei

Family SCOMBROLABRACIDAE (471)—longfin escolars. Marine; deepwater Atlantic, Indian, and Pacific.

Premaxillae protractile; preopercle and opercle serrated; swim bladder with thin, elastic walls and, in adult, with bubblelike evaginations fitting into vertebral bullae; 30 vertebrae, fifth through twelfth of adults with expanded parapophyses, called the bullae, that bulge dorsolaterally and with ventral opening.

Maximum length about 30 cm. As noted in Nelson (1994), C. E. Bond and Uyeno (1981), because of the mixed percoid and scombroid characteristics of the one species (in general appearance it most closely resembles the gempylids), favor placing it in its own suborder, the Scombrolabroidei. The study of Johnson (1986) suggests, in cladistic terms, that it may be the primitive sister group of *Pomatomus* and the scombroids.

One species, *Scombrolabrax heterolepis* (Nakamura and Parin, 2003).

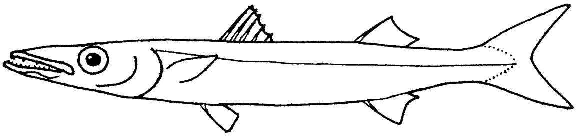
Suborder Scombroidei. Upper jaw not protrusible (premaxilla fixed, a secondary modification adapting the fish to feeding on large prey); teeth ankylosed.

This suborder includes species that are probably the world's fastest-swimming fish. Sailfish, Swordfish, and Bluefin Tuna have had short periods of speeds between 60 and 100 km per hour attributed to them. Endothermy, the ability to maintain elevated body temperature by metabolic means, has evolved in three lineages. It is achieved in tunas (tribe Thunnini) in a manner similar to that in birds and mammals, whereas cranial endothermy, in which only the brain and eyes are warmed, occurs in *Gasterochisma* and the billfishes.

As noted in Nelson (1994), in presenting a classification of the scombroids, I have been helped by G. D. Johnson's 1986 critical evaluation of a 1984 classification by B. B. Collette and coauthors (these two studies based on morphological evidence arrived at differing hypotheses of relationships). Carpenter et al. (1995) discussed problems and solutions with stable and unstable classifications, for economically important groups, arising from cladistic hypotheses.

Six families with 46 genera and about 147 species. The fossil family †Blochiidae (e.g., the Eocene *Blochius* and possibly *Aglyptorhynchus*) is related to the Xiphiidae, but the Cretaceous *Cylindracanthus* cannot be assigned to any order (Fierstine and Monsch, 2002). Other fossil scombroids include the Oligocene *Abadzekhia* (Bannikov, 2005) and †Palaeorhynchidae. H. L. Fierstine has published on many fossil scombroids.

Family SPHYRAENIDAE (472)—barracudas. Marine (young occasionally in estuaries); tropical and subtropical Atlantic, Indian, and Pacific.



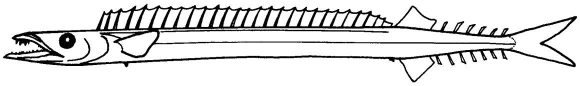
Body elongate; mouth large, jutting lower jaw with strong large teeth; lateral line well developed; gill rakers absent to vestigial; pectoral fins relatively low; two widely separated dorsal fins, the first with five spines and the second with one spine and nine soft rays; lateral line scales 80–166; vertebrae 24 (11 + 13).

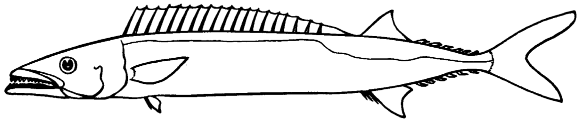
Barracudas are known to attack humans and are feared more than sharks in some areas. Maximum length normally to 1.8 m but said to reach somewhat longer lengths.

In a critical study of scombroid relationships in 1986, G. D. Johnson concluded that *Sphyraena* is the primitive sister group to the remaining scombroids and included the family Sphyraenidae within the suborder Scombroidei.

One genus, *Sphyraena,* with about 21 species (e.g., H. Senou in Carpenter and Niem, 2001).

Family GEMPYLIDAE (473)—snake mackerels. Marine, tropical and subtropical seas, often in very deep water.





Body oblong or elongate and compressed; protruding lower jaw; teeth very long; maxilla exposed; isolated finlets usually present behind dorsal and anal fins; anal fin with one to three spines and 8–35 soft rays; caudal fin present; pectoral fin low on body; pelvic fin with one spine and five soft rays or reduced to one spine; vertebrae 32–58. Several genera, such as *Tongaichthys,* have many scombrid characters. *Diplospinus,* with its unusual lateral line and which is intermediate between the gempylids and trichiurids in many characters, is placed in the Gempylidae following Parin and Bekker (1973). According to G. D. Johnson in a 1986 study, *Lepidocybium* forms the sister group to the other gempylids.

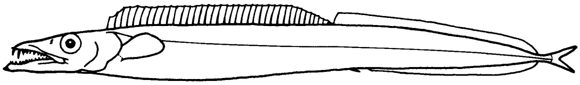
Sixteen genera, *Diplospinus, Epinnula, Gempylus* (upper figure), *Lepidocybium, Nealotus, Neoepinnula, Nesiarchus* (synonym *Escolar*), *Paradiplospinus, Promethichthys, Rexea, Rexichthys, Ruvettus, Thyrsites* (lower figure), *Thyrsitoides, Thyrsitops,* and *Tongaichthys,* with about 24 species (e.g., Nelson, 1994; Roberts and Stewart, 1997; I. Nakamura and N. V. Parin in Carpenter and Niem, 2001).

Family TRICHIURIDAE (474)—cutlassfishes. Marine: Atlantic, Indian, and Pacific.

Body very elongate and strongly compressed; protruding lower jaw; teeth very long; maxilla concealed by preorbitals; fanglike teeth usually present; single nostril on each side; gill cover splintered; dorsal fin extremely long based, with spines and soft rays (spinous portion usually shorter than soft rayed portion, notch between two portions in some species); anal fin with two spines and 56–121 soft rays; caudal fin small or absent; pectoral fin low on body; pelvic fin reduced (with a scalelike spine and one rudimentary soft ray) or absent; vertebrae 98–192 (34–53 + 55–151).

Ten genera with 39 species (e.g., Nelson, 1994; Parin, 1995; I. Nakamura and N. V. Parin in Carpenter and Niem, 2001).

SUBFAMILY APHANOPODINAE. Caudal fin small, forked; pelvic fin present, with scalelike spine and one rudimentary soft ray (external fin may be present only in juvenile); spinous dorsal fin with 38–46 rays, slight notch at division of spinous and soft portions.

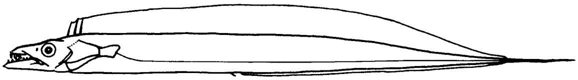


Two genera, *Aphanopus* and *Benthodesmus*, with 18 species (e.g., Parin, 1995).

SUBFAMILY LEPIDOPODINAE. Caudal fin present (small and forked) or absent; pelvic fin present, rudimentary; spinous dorsal fin usually with 3–10 rays, spinous and soft portions continuous; lateral line descending gradually behind the pectoral fin.

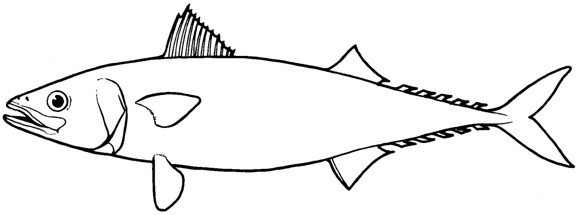
Five genera, *Assurger, Eupleurogrammus, Evoxymetopon, Lepidopus,* and *Tentoriceps,* with about 18 species.

SUBFAMILY TRICHIURINAE (HAIRTAILS). Caudal fin and hypurals absent; pelvic fin and skeleton absent; spinous dorsal fin with three or four rays, spinous and soft portions continuous; lateral line descending steeply from the pectorals and running near ventral profile of body.



Three monotypic genera, *Demissolinea, Lepturacanthus,* and *Trichiurus* (e.g., Burhanuddin and Iwatsuki, 2003).

Family SCOMBRIDAE (475)—mackerels and tunas. Marine (rarely freshwater); tropical and subtropical seas.



Two dorsal fins (depressible into grooves) with 5–12 finlets behind second dorsal and anal fins; first dorsal fin with 9–27 rays, origin well behind head;

pectoral fins inserted high on body; pelvic fins with six rays, placed beneath the pectorals; gill membranes free from isthmus; scales cycloid and usually small; slender caudal peduncle with two keels; specialized subcutaneous vascular system in *Thunnus* and its close relatives; vertebrae 31–64.

Some members are endothermic (see under suborder Scombroidei). These fast-swimming fish constitute popular sport and valuable commercial fisheries. Length up to 4.2 m, attained by *Thunnus thynnus.*

Fifteen genera with 51 species (about half the species belong to *Scomberomorus* and *Thunnus*) (e.g., Collette et al., 2001; Collette, 2003c,d). The following classification is based on Collette et al. (2001). An immense literature exists on this subfamily with B. B. Collette giving us our present understanding of the diversity and systematics of this commercially important group.

SUBFAMILY GASTEROCHISMATINAE. Scales moderate in size, about 80 in lateral series; pelvic fins longer than head length in juveniles, fitting into a deep ventral groove.

One species, the aberrant *Gasterochisma melampus,* primarily of the Southern Ocean.

SUBFAMILY SCOMBRINAE. Scales minute or absent.

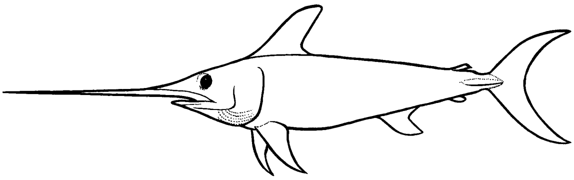
TRIBE SCOMBRINI (MACKERELS). Two genera, *Rastrelliger* and *Scomber,* with seven species. As with many common names, the name "mackerel" is used for species in many different families (e.g., Nelson et al., 2004).

TRIBE SCOMBEROMORINI (SPANISH MACKERELS). Three genera, *Acanthocybium, Grammatorcynus,* and *Scomberomorus,* with 21 species. *S. sinensis,* although normally marine, occurs in estuaries and is known from 300 km up the Mekong River.

TRIBE SARDINI (BONITOS). Four genera, *Cybiosarda, Gymnosarda, Orcynopsis,* and *Sarda,* with seven species.

TRIBE THUNNINI (TUNAS). Five genera, *Allothunnus, Auxis, Euthynnus, Katsuwonus,* and *Thunnus,* with 15 species.

Family XIPHIIDAE (476)—swordfishes. Marine; tropical and subtropical seas.



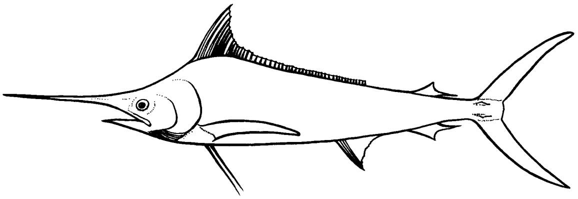
Bill depressed; scales absent in adult; pelvic fins and girdle absent; jaws toothless in adult; caudal peduncle in adult with single median keel on each side; 26 vertebrae.

Swordfish are a valuable commercial species. Length up to 4.5 m.

There is abundant evidence that the Xiphiidae and Istiophordae are sister groups. In addition to less visible characters, both groups share the following features: elongate premaxillary bill (rostrum) in adults; mouth inferior; finlets absent behind dorsal and anal fins; dorsal fin origin over back of head, first dorsal lacking true spines and with 37–55 rays; two anal fins; pectorals inserted low on body; pelvics reduced, one spine and two rays or absent; gill membranes free from isthmus; vertebrae 24 or 26. As the terminal groups of the scombroid clade, both could be recognized in the same family and were in Nelson (1994). However, such a synonymy is generally not followed (e.g., in Nelson et al., 2004) and I recognize both as separate families.

One species, *Xiphias gladius* (Swordfish).

Family ISTIOPHORIDAE (477)—billfishes. Marine; most tropical and subtropical seas.



Bill rounded; scales present in adults; pelvic fins elongate; jaws with teeth; caudal peduncle in adult with two keels on each side; dorsal fin with very long base, sometimes saillike, depressible into groove; lateral line retained throughout life; 24 vertebrae.

The bill is used to stun prey fish by slashing back and forth. Billfishes are an extremely popular sportfish. Length up to 4 m.

Three genera with about 11 species (e.g., I. Nakamura in Carpenter and Niem, 2001).

Istiophorus (sailfishes): first dorsal fin sail shaped and distinctly taller than body depth; rays of pelvic fin very long. Two species. There may be only one worldwide species, *Istiophorus platypterus* (as recognized in Nelson et al., 2004), but, following works of I. Nakamura, *I. albicans* of the Atlantic is recognized here.

Tetrapturus (synonym *Kajikia)* (spearfishes): forward portion of first dorsal fin about as high as body is deep. Six species.

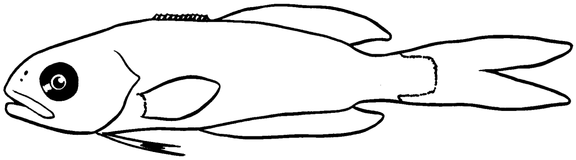
Makaira (synonym *Istiompax)* (marlins): forward portion of first dorsal fin not as high as body is deep (shown in figure). Three species.

Suborder Stromateoidei. Toothed saccular outgrowths in gullet behind last gill arch (except in amarsipids); lachrymal bone covering most of maxilla; scales usually cycloid, weakly ctenoid in some; branchiostegal rays 5–7; hypural plates 2–6; caudal fin with 15 branched rays; vertebrae 24–61. Length up to 1.2 m.

Six families, 16 genera, and about 70 species. All are marine. The classification is based primarily on the studies of R. L. Haedrich and M. H. Horn

(Nelson, 1994). Doiuchi et al. (2003) provided a needed cladistic study based on morphological characters of the stromateoids employing all genera. A major finding was that the family Centrolophidae was not monophyletic with the inclusion of *Psenopsis*, with that genus being sister to a clade comprising amarsipids, ariommatids, nomeids, tetragonurids, and stromateids. It would be justified to place *Psenopsis* in its own family; such a move is not yet made.

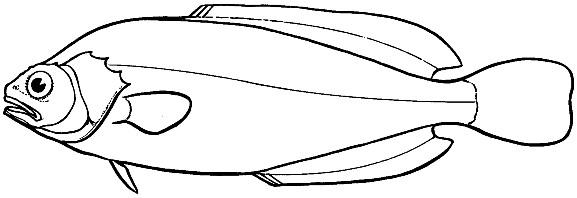
Family AMARSIPIDAE (478)—amarsipas. Marine; tropical Indian and Pacific, close to the equator.



Pelvic fins present, jugular, their origin well before the pectoral fins; body translucent, no color pattern; pharyngeal sacs absent; dorsal fin with 10–12 short spines and 22–27 longer soft rays; anal fin with 28–32 soft rays, no spines; pectoral fin with 17–19 rays; vertebrae 45–47. No adults of this pelagic fish are known.

One species, *Amarsipus carlsbergi*, described in 1969 (e.g., P. R. Last in Carpenter and Niem, 2001).

Family CENTROLOPHIDAE (479)—medusafishes. Marine; tropical to temperate, all seas except most of mid-Indian and mid-Pacific.

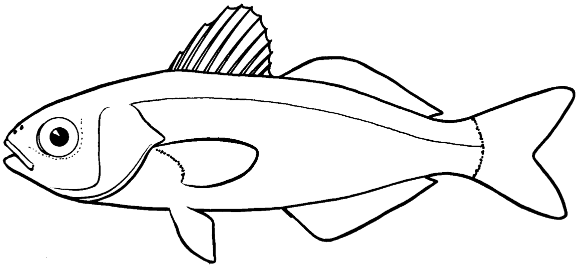


Pelvic fins present in adult; dorsal fin continuous, spines either 0–5, weakly developed and graduating into the soft rays (as in figure and in the first three genera listed) or 5–9, stout, and considerably shorter than and generally not graduating into the soft rays (in the last three genera listed); total anal fin rays 15–41 (usually three spines).

Centrolophus is the only stromateoid in the far North Atlantic (to Iceland), whereas *Icichthys* is the only stromateoid in the far North Pacific (to Alaska). Both genera are also in southern oceans. See above under suborder Stromateoidei for the study of Doiuchi et al. (2003) that showed that this family is not monophyletic with the inclusion of *Psenopsis* (with six Indo-West Pacific species).

Seven genera, *Centrolophus, Hyperoglyphe, Icichthys, Psenopsis, Schedophilus, Seriolella,* and *Tubbia,* with about 28 species (R. M. McDowall in Carpenter and Niem, 2001; Haedrich, 2003). *Schedophilus* and *Seriolella* were found to be sister taxa by Doiuchi et al. (2003).

Family NOMEIDAE (480)—driftfishes. Marine; tropical and subtropical seas.

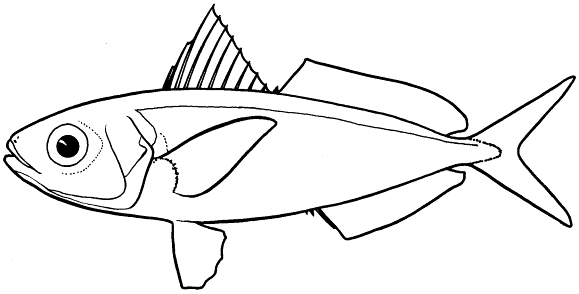


Pelvic fins present in adult; two dorsal fins, the first with 9–12 slender spines and the second with 0–3 spines and 15–32 soft rays; anal fin with 1–3 spines and 14–30 soft rays. Maximum length about 1 m.

The 10-cm *Nomeus gronovii* (Man-of-War Fish) is circumtropical and usually found with the Portuguese Man-of-War (*Physalia*). The fish swims unharmed among the stinging tentacles.

Three genera, *Cubiceps, Nomeus,* and *Psenes,* with about 16 species (P. R. Last in Carpenter and Niem, 2001; Haedrich, 2003).

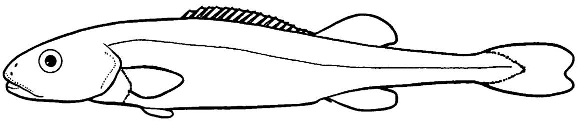
Family ARIOMMATIDAE (481)—ariommatids. Marine; deep water, tropical and subtropical coastlines of eastern North and South America, Africa, Asia, Kermadec Islands, and Hawaii.



Pelvic fins present in adult; two dorsal fins, the first with 10–12 slender spines and the second with 14–18 soft rays; anal fin with three short spines and 13–16 soft rays; pectoral fin with 20–24 rays; caudal peduncle with two low, fleshy, lateral keels on each side; vertebrae 30–32.

One genus, *Ariomma,* with about seven species (P. R. Last in Carpenter and Niem, 2001; Haedrich, 2003).

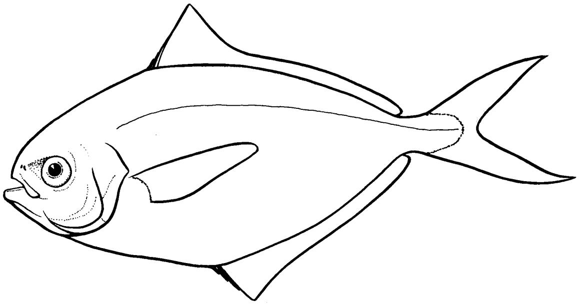
Family TETRAGONURIDAE (482)—squaretails. Marine; tropical and subtropical seas.



Body elongate; pelvic fins present in adult; two dorsal fins, the first with 10–20 short spines and the second with 10–17 soft rays; anal fin with one spine and 10–16 soft rays; caudal peduncle with a single keel on each side; lateral scales 73–114; vertebrae 40–58. Individuals are thought to feed almost exclusively on coelenterates and ctenophores.

One genus, *Tetragonurus*, with three species. This is the most widely distributed of all the stromateoid genera (P. R. Last in Carpenter and Niem, 2001; Haedrich, 2003).

Family STROMATEIDAE (483)—butterfishes. Marine; coastal North and South America, western Africa, and southern Asia (Indo-Pacific).



Body usually very deep; pelvic fins absent in adult (present in some young—pelvic bones present); dorsal fin continuous; anal fin usually with 2–6 spines and 30–50 soft rays.

Three genera, *Pampus*, *Peprilus*, and *Stromateus*, with about 15 species (Liu and Li, 1998; P. R. Last in Carpenter and Niem, 2001; Haedrich, 2003).

Suborder Anabantoidei (Labyrinthici, in part). A suprabranchial organ present, usually labyrinthine, formed by expansion of first epibranchial; dorsal and anal fins with spines except in *Luciocephalus*; gill membranes scaly and broadly united; pelvic fins thoracic, usually with one spine and five soft rays; five or six branchiostegal rays; exoccipital bone usually with foramen covered by a membrane overlying the sacculus; swim bladder divided posteriorly, extending into caudal region; vertebrae 25–31.

The suprabranchial organ is an auxiliary breathing apparatus, allowing anabantoids to respire aerially as well as in water. Air taken in through the mouth passes through the labyrinth, where capillaries absorb oxygen. As air is taken in at various intervals, old air is forced out of the labyrinth through the gill covers. This organ has enabled many species to occupy submarginal or even anoxic waters. In most anabantoids the male builds a nest of floating bubbles. Eggs are deposited in the bubbles and the male exhibits parental care.

Lauder and Liem (1983) recognized this suborder with the inclusion of the *Luciocephalus* as being monophyletic on the basis of four derived characters. The classification of the families within the suborder has been changed from Nelson (1994) based on references given below.

Three families, 19 genera, and about 120 species. All are freshwater and indigenous to Africa and southern Asia.

Family ANABANTIDAE (484)—climbing gouramies. Freshwater (rarely brackish); Africa and India to Philippines.

Jaws, prevomer, and parasphenoid with fixed conical teeth; mouth relatively large; upper jaw only weakly protrusile; one genus, *Sandelia,* only with cycloid scales, not ctenoid; gill rakers few and diet generally carnivorous.

Four genera, *Anabas, Ctenopoma, Microctenopoma,* and *Sandelia,* with about 33 species (e.g., Norris and Douglas, 1992). Most of the species, contained in the genera *Ctenopoma, Microctenopoma,* and *Sandelia,* occur in Africa; *Anabas* occurs in Asia.

Family HELOSTOMATIDAE (485)—kissing gouramies. Freshwater; Thailand to Malay Archipelago.

Premaxilla, dentaries, palatine, and pharynx devoid of teeth; two lateral lines, the lower commencing below the end of the upper; dorsal fin with 16–18 spines and 13–16 soft rays; anal fin with 13–15 spines and 17–19 soft rays; lateral line scales 43–48; scales on top of head cycloid, others ctenoid. Numerous gill rakers form an elaborate filter apparatus on the gill arches which adapts the fish to filter feeding (horny teeth on the lips also enable the fish to scrape algae off surfaces). Maximum length about 30 cm.

One species, *Helostoma temminckii* (Kissing Gourami).

Family OSPHRONEMIDAE (486)—gouramies. Freshwater; Pakistan and India to Southeast Asia.

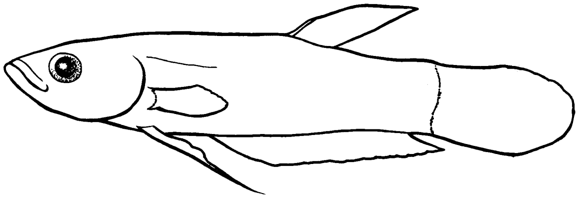
Four subfamilies, 14 genera, and about 86 species. The classification of this family is based largely on Britz et al. (1995) and Britz (2001).

SUBFAMILY OSPHRONEMINAE (GIANT GOURAMIES). Freshwater; Southeast Asia. Prevomer and palatine devoid of teeth; one lateral line, complete and continuous; all scales ctenoid; dorsal fin with 11–16 spines and 10–14 soft rays; anal fin with 9–12 spines and 16–23 soft rays; 14–16 pectoral fin rays; lateral scale rows 31–34; 30 or 31 vertebrae. Maximum length about 80 cm. *Osphronemus goramy* has been introduced around the world in the tropics.

One genus, *Osphronemus,* with four species (Britz, 2001).

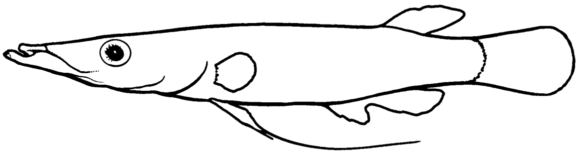
SUBFAMILY BELONTIINAE (COMBTAIL GOURAMIES). One genus, *Belontia*, with two species.

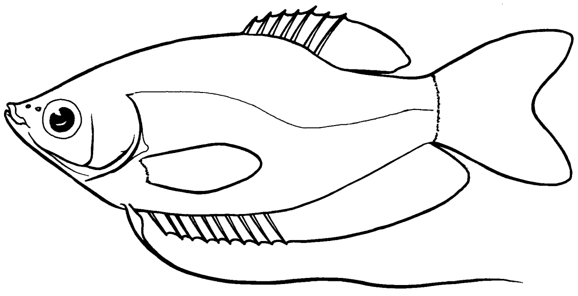
SUBFAMILY MACROPODINAE (SIAMESE FIGHTING FISHES, PARADISEFISHES)



Six genera, *Betta* (shown in figure), *Macropodus*, *Malpulutta*, *Parosphromenus*, *Pseudosphromenus*, and *Trichopsis*, with about 60 species (e.g., Tan and Kottelat, 1998; Britz, 2001; Freyhof and Herder, 2002). The genus *Betta*, with about 45 species, is the largest; some species are oral brooders and others are bubble nesters.

SUBFAMILY LUCIOCEPHALINAE. Freshwater; Malay Peninsula and Archipelago. Five branchiostegal rays (most members of this family have six, but the first has been lost in this clade (Britz, 2001)).





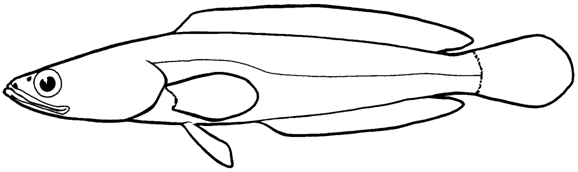
In Nelson (1994), *Luciocephalus* (Pikehead) was recognized in its own family, and the others were placed in the subfamily Trichogastrinae (gouramies) of the family Belontiidae. *Luciocephalus* is quite distinctive in having the following characters: no dorsal or anal fin spines; dorsal fin inserted posteriorly, with 9–12 rays; anal fin with a deep notch and 18 or 19 rays; pelvic fin with one spine and five soft rays (one of which is produced into a threadlike ray);

caudal fin rounded; lateral line scales about 40–42; mouth exceptionally protractile; gill membranes not united; median gular element present; no swim bladder; maximum length about 18 cm.

Six genera, *Colisa, Ctenops, Luciocephalus* (shown in upper figure), *Parasphaerichthys, Sphaerichthys,* and *Trichogaster* (shown in lower figure), with about 20 species.

Suborder Channoidei (Ophiocephaliformes)

Family CHANNIDAE (487)—snakeheads. Freshwater; tropical Africa and southern Asia.



Body elongate; long dorsal and anal fins; pelvic fins usually present (some Asian species of *Channa* lack the pelvics), with six rays; no fin spines; cycloid or ctenoid scales; lower jaw protruding beyond upper; suprabranchial organ for air breathing present. Maximum length about 1.2 m.

Distribution maps and descriptive information for the species are given in Courtenay and Williams (2004).

Two genera, *Channa* (26, synonym *Ophicephalus*) and *Parachanna* (3), with about 29 species (Courtenay and Williams, 2004; Courtenay et al., 2004). The species of *Channa* are found in Asia and those of *Parachanna* in Africa.

Suborder Caproidei. Nelson (1994) included this taxon in the zeiforms despite evidence suggesting that it showed stronger relationships elsewhere. For example, Rosen (1973a) observed that the caproid caudal skeleton is of percoid type in having three epurals and the parhypural and five hypurals articulating with a terminal half-centrum, whereas the other zeiforms have only one or two epurals and the hypurals fused together into large plates. Subsequently, in a 1984 study, D. E. Rosen suggested that caproids, zeiforms, and tetraodontiforms form a clade. However, Tyler et al. (2003) found in their analysis such a relationship to be ambiguous; it was supported in three of their four analyses but not in the one they considered most rational and best justified. Pending further clarification, I retain the Zeiformes as a preperciform taxon and place the caproids in the perciforms, as supported by Johnson and Patterson (1993), although caproids could be considered preperciform from the study of Tyler et al. (2003).

The †Sorbinipercidae, containing *Sorbinicapros* and *Sorbiniperca,* two Middle Eocene taxa found at Monte Bolca, Italy, was thought by Bannikov and Tyler (1999) to have sister-group relationships with a clade of caproids + zeiforms +

tetraodontiforms or with a larger clade also including some other percomorphs. As noted above, there are reasons for doubting a caproid, zeiform, and tetraodontiform relationship. In addition, Tyler and Bannikov (2002) described *Zorzinichthys* from the Eocene of Monte Bolca, Italy, representing a new family, the †Zorzinichthyidae, and related to the caproid and sorbinipercidlike clades.

Family CAPROIDAE (488)—boarfishes. Marine; Atlantic, Indian, and Pacific.

Body covered with small ctenoid scales; dorsal fin spines 7–9; anal fin spines two or three; pelvic fin with one spine and five soft rays; caudal fin rounded; distinct sagittal crest; pleural ribs present; vertebrae 21–23. Monophyly of this family is uncertain.

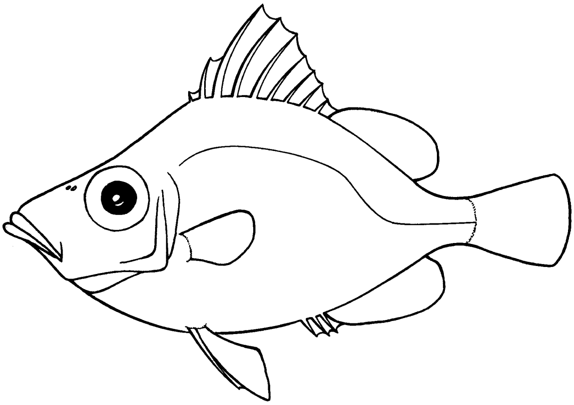
Two subfamilies, two genera, and about 11 species.

Subfamily Antigoniinae. Red-colored fishes with extremely deep and slim bodies (rhomboid shape); most body scales with large elevated ridge, curved posteriorly; dorsal fin with eight or nine spines and 26–38 soft rays; three anal spines, separate from the anal soft rays; 10 branched caudal rays (12 principal rays and total of seven or eight procurrent rays); maxillary process of palatine articulates with anterior end of nasal.

Most species occur between approximately 50–600 m.

One genus, *Antigonia*, with about 10 species. In addition, fossil species of *Antigonia* are known from the Eocene and Miocene. See Nelson (1994) and Parin (2003) for references.

Subfamily Caproinae. Caudal fin with 12 branched rays (14 principal rays and total of two procurrent rays); five distinct hypurals (not fused). Also differ from Zeidae, with which they have a very superficial external similarity, in lacking abdominal spinous plates.



One species, *Capros aper*, occurring in the Mediterranean Sea and eastern North Atlantic.

Order PLEURONECTIFORMES (Heterosomata) (59)—flatfishes. Adults not bilaterally symmetrical, with one eye migrating to the other side of the cranium; dorsal and anal fins with long bases, dorsal fin base overlapping at least the neurocranium except in *Psettodes*; body highly compressed, somewhat rounded on eyed side and flat on eyeless side; eyes can protrude above body surface, allowing fish to see when buried in the substrate; usually six or seven branchiostegal rays, rarely eight; body cavity small; adults almost always without swim bladder; scales cycloid, ctenoid, or tuberculate. Variation in caudal fin ray number was discussed by Hoshino (2001a).

This is a very distinctive group. Young flatfishes are bilaterally symmetrical and swim upright, but early in their development, between 5–120 mm but usually 10–25 mm in length, one eye migrates across the top of the skull to lie adjacent to the eye on the other side. They then lie and swim on the eyeless side. The metamorphosis involves a complex modification of skull bones, nerves, and muscles, and it leaves one side of the fish eyeless (lower side) and the other side with two eyes (upper side). The upper side is pigmented, whereas the underside is usually light colored. Asymmetry may also be reflected in other characters such as dentition, squamation, and paired fins. Most species have both eyes on the right side and lie on the left side (dextral) or have both eyes on the left side and lie on the right side (sinistral). In some species both dextral (right-eyed) and sinistral (left-eyed) individuals may occur. Among the latter species, the pleuronectid *Platichthys stellatus* (the Starry Flounder) is especially interesting because of the varying frequency of dextral to sinistral individuals over its range in the North Pacific. Other members of the family are dextral, but almost all Starry Flounder from Japanese waters are sinistral, while off California the two types are about equal in frequency. As yet there appears to be no convincing argument for a direct adaptive advantage for being sinistral or dextral.

Flatfishes are benthic and carnivorous. Sexual maturity is attained from 1 to 15 years of age. Maximum length almost 3 m in the halibuts; much smaller in most groups.

Common names for flatfishes include flounder, halibut, sole, plaice, dab, sanddab, tonguefish, and turbot; some of these names apply to species in different families. Many species are important in commercial fisheries and are valued as a food source.

Many changes have been made from Nelson (1994). The classification of this order is based largely on Chapleau (1993), Cooper and Chapleau (1998a, b), and Hoshino (2001b). In addition, much information now and in the past has been based on the research of E. H. Ahlstrom, K. Amaoka, D. A. Hensley, and their colleagues. Much taxonomic information is in Desoutter, Chapleau, et al. (2001). The order is thought to be monophyletic (Chapleau, 1993; Berendzen and Dimmick, 2002). Its sister group may be some percoid taxon, but its relationships are essentially unknown.

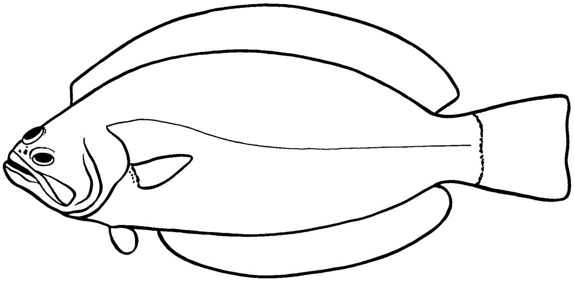
Caudal fin rays have been used in flatfish systematics, and Hoshino (2001a) established homologies between various rays and discussed the phylogenetic significance of the rays and associated structures. As an example of an earlier study involving caudal fin ray morphology, the bothoid lineage as comprising the Pleuronectinae (Pleuronectidae in this edition), most Paralichthyidae, Scophthalmidae, and most Bothidae was recognized in a 1984 paper by E. H. Ahlstrom and D. A. Hensley. Schwarzhans (1999) documents the recent and fossil otoliths of the order; it contains much useful taxonomic information but lacks a cladistic analysis. Chanet (2003) gave references, including that of his major 1997 cladistic review, to studies on the fossils of this order (in a 1995 paper he placed the Eocene *Joleaudichthys* in the suborder Pleuronectoidei).

There is general agreement that the Psettodidae are the primitive sister group to other pleuronectiforms (the Pleuronectoidei) (Cooper and Chapleau, 1998; Hoshino, 2001b; Berendzen and Dimmick, 2002) with a monophyletic Citharidae being sister to the remaining pleuronectoids (Hoshino, 2001b). Two major clades are thought to accommodate all other flatfishes, with Scophthalmidae, Paralichthyidae, Pleuronectidae, and Bothidae forming one clade and Paralichthodidae, Poecilopsettidae, Rhombosoleidae, Samaridae, Achiridae, Soleidae, and Cynoglossidae forming the other clade; *Tephrinectes* (placed here in the Paralichthyidae) was thought to be sister to these two clades by Hoshino (2001b). The Paralichthodidae and Achiropsettidae were not in the cladogram of Hoshino (2001b). The former was placed following Cooper and Chapleau (1998). The Achiropsettidae were placed between Samaridae and Achiridae in Hoshino (2001a); because the clade of Samaridae and the other three families seems strong, I place Achiropsettidae before Samaridae but after the families formerly placed in Pleuronectidae. In order to reflect our current understanding of relationships in the suborder Pleuronectoidei based on Hoshino (2001b:401) and modifications in Chanet et al. (2004:10), I recognize three superfamilies: Citharoidea, Pleuronectoidea (this is what was termed the bothoid lineage in some literature), and Soleoidea. It might be reasonable to also recognize the family Tephrinectidae for the paralichthyid *Tephrinectes sinensis* as suggested by Desoutter, Chapleau, et al. (2001) and done by Chanet (2003), but I prefer to wait for confirming studies. The molecular study of Berendzen and Dimmick (2002), while in agreement with the higher-level classification, found differences at lower levels that invite further study. Additional comments on possible higher relationships within the order are given below under family Citharidae (see also Cooper and Chapleau, 1998a); future changes are expected. Munroe (2005a,b) discussed the taxonomic and geographic diversity of flatfishes.

About 678 extant species are recognized in approximately 134 genera and 14 families. About 10 species are thought to occur only in freshwater (six achirids, one soleid, and three cynoglossids); another few that are primarily freshwater enter estuaries or marine water, and another 20 species that are normally marine occasionally enter freshwater.

Suborder Psettodoidei. Dorsal fin not extending onto head (to or past eye); anterior dorsal and anal rays spinous; palatine with teeth; basisphenoid present; supramaxilla large; 24 or 25 vertebrae.

Family PSETTODIDAE (489)—spiny turbots. Marine; western Africa and Indo-West Pacific.



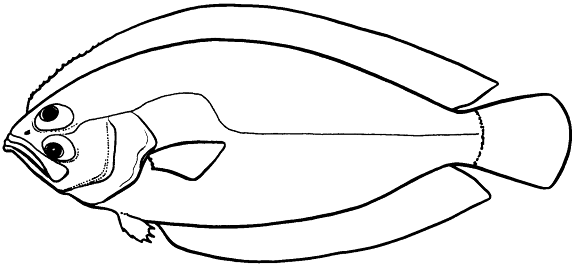
Pelvic fins nearly symmetrical, with one spine and five soft rays; mouth large; jaw teeth barbed; gill arches with groups of teeth; eyes sinistral or dextral; preopercular margin distinct, not covered with skin; 15 branched caudal fin rays. Maximum length about 60 cm.

One genus, *Psettodes*, with three species: *P. belcheri* and *P. bennetti* from tropical western Africa (eastern Atlantic) and *P. erumei* from eastern Africa and the Red Sea to the western Pacific (e.g., D. A. Hensley in Carpenter and Niem, 2001).

Suborder Pleuronectoidei. Dorsal fin extending onto head at least to eyes; dorsal and anal fins without spines; palatine without teeth; no basisphenoid; supramaxilla vestigial (in some citharids) or absent; vertebrae 26–70, 10 or more are abdominal.

Superfamily Citharoidea. One family.

Family CITHARIDAE (490)—largescale flounders. Marine; Mediterranean, Indo-West Pacific (Japan to Australia).



Pelvic fins with one spine and five soft rays; pelvic fin bases short; branchiostegal membranes basically separated from each other; posterior nostril on eyeless side enlarged.

The monophyly of this family has until recently been questioned. The cladistic analysis shown in Cooper and Chapleau (1998b) suggested that the dextral *Lepidoblepharon* is sister to all remaining pleuronectiforms, and the sinistral *Citharoides* is sister to the remaining pleuronectiforms. The sinistral *Citharus* was not shown on the cladogram, but the dextral *Brachypleura* was sister to a clade comprising the four families Scophthalmidae, Paralichthyidae, Bothidae, and Pleuronectidae; this clade along with *Brachypleura* (termed the bothoid lineage) was sister to all other pleuronectiforms, although Achiropsettidae was not placed in the Cooper and Chapleau (1998) cladogram. Hoshino (2001b) established monophyly for the family based on six synapomorphies and showed that sinistral species and those that are dextral do not form monophyletic groups.

Five genera, *Brachypleura*, *Citharoides*, *Citharus* (synonym *Eucitharus*), *Lepidoblepharon*, and *Paracitharus*, with about six species (e.g., D. A. Hensley in Carpenter and Niem, 2001; Hoshino, 2000, 2001b).

Superfamily Pleuronectoidea. Four families.

Family SCOPHTHALMIDAE (491)—turbots. Marine (occasionally in brackish water); northern Atlantic and Baltic, Mediterranean, Black seas.

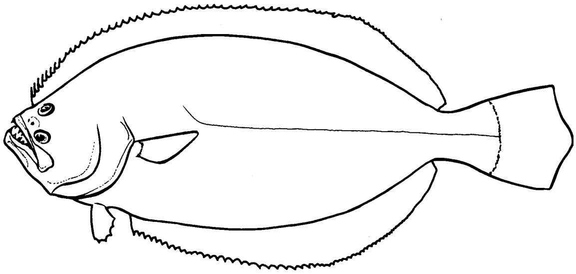
Eyes sinistral; both pelvic fin bases elongate, mouth large and lower jaw prominent. Maximum length about 100 cm.

Monophyly of this family was confirmed by Chanet (2003), who recognized two subfamilies.

The position of this family is changed from Nelson (1994). Common names for species include turbots, windowpanes, and brills. Only one species occurs in the western Atlantic; the others occur in the northeastern Atlantic area.

Four genera, *Lepidorhombus* (2), *Phrynorhombus* (2), *Scophthalmus* (3, synonym *Psetta*), and *Zeugopterus* (1), with about eight species (e.g., Chanet, 2003; Munroe, 2003b).

Family PARALICHTHYIDAE (492)—sand flounders. Marine, rarely in freshwater; Atlantic, Indian, and Pacific.



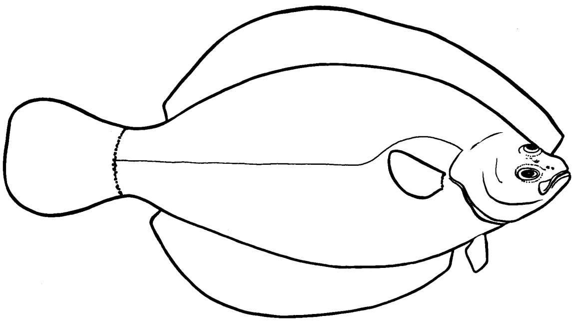
Eyes in most species sinistral; pelvic fin bases short and nearly symmetrical (but position of bases variable between species); pectoral rays branched. Maximum length about 1.5 m.

A species of *Citharichthys* and of *Pseudorhombus* ascends rivers from the ocean in Africa. Also called largetooth flounders. This family may not be monophyletic. Hoshino (2001b) found *Tephrinectes* to be sister to the remaining families (including this one) (see comments under the order concerning the recognition of a separate family for this genus); the osteology of *Tephrinectes* was given by Hoshino and Amaoka (1998).

The position of this family is changed from Nelson (1994). Paralichthyidae and Pleuronectidae are sister taxa (Hoshino, 2001b).

About 16 genera, *Ancylopsetta, Cephalopsetta, Citharichthys, Cyclopsetta, Etropus, Gastropsetta, Hippoglossina, Lioglossina, Paralichthys, Pseudorhombus, Syacium, Tarphops, Tephrinectes, Thysanopsetta, Verecundum,* and *Xystreurys*, and about 105 species (e.g., van der Heiden and Mussot-Pérez, 1995; Hoshino and Amaoka, 1998, 1999; K. Amaoka and D. A. Hensley in Carpenter and Niem, 2001; Munroe, 2003b; Khidir et al, 2004).

Family PLEURONECTIDAE (493)—righteye flounders. Marine (occasionally in brackish water, rarely in freshwater); Arctic, Atlantic, Indian, and Pacific.



Eyes almost always dextral; no oil globule in yolk of egg except for two species; origin of dorsal fin above the eyes; lateral line well developed on both sides; pelvic fins symmetrical.

Nelson (1994) and Evseenko (2004) treated this family at the subfamily level, Pleuronectinae. The subfamilies Paralichthodinae, Poecilopsettinae, and Rhombosoleinae, given in Nelson (1994), are now recognized as separate families. Paralichthyidae and Pleuronectidae are sister taxa (Hoshino, 2001b).

Twenty-three genera with about 60 species. The following five subfamilies and the four tribes in the last subfamily are based on the cladistic analysis of Cooper and Chapleau (1998). The commercially important and large halibuts belong to this family.

SUBFAMILY HIPPOGLOSSINAE. Five genera, *Atheresthes, Clidoderma, Hippoglossus, Reinhardtius,* and *Verasper*, with eight species (Cooper and Chapleau, 1998;

Nelson et al., 2004). Cooper and Chapleau (1998) placed species of *Atheresthes* within *Reinhardtius*, but Nelson et al. (2004) recognized both genera, as did Orr and Matarese (2000); Nelson et al. (2004) also noted the 2001 molecular study of N. Suzuki, M. Nishida, and K. Amaoka finding that *A. evermanni* is not closely related to *Reinhardtius* and supporting the retention of *Atheresthes* as a valid genus.

SUBFAMILY EOPSETTINAE. One genus, *Eopsetta*, with two species (Cooper and Chapleau, 1998).

SUBFAMILY LYOPSETTINAE. One monotypic genus, *Lyopsetta* (Cooper and Chapleau, 1998).

SUBFAMILY HIPPOGLOSSOIDINAE. Three genera, *Acanthopsetta*, *Cleisthenes*, and *Hippoglossoides*, with seven species (Cooper and Chapleau, 1998).

SUBFAMILY PLEURONECTINAE. Thirteen genera and 42 species.

TRIBE PSETTICHTHYINI. One monotypic genus, *Psettichthys*.

TRIBE ISOPSETTINI. One monotypic genus, *Isopsetta*.

TRIBE MICROSTOMINI. Six genera, *Dexistes*, *Embassichthys*, *Glyptocephalus* (synonyms *Errex* and *Tanakius*), *Lepidopsetta*, *Microstomus*, and *Pleuronichthys*, with 20 species (Cooper and Chapleau, 1998; Orr and Matarese, 2000). Cooper and Chapleau (1998) placed *Embassichthys bathybius* within *Microstomus*, but Nelson et al. (2004) recognized both genera, as did Orr and Matarese (2000); however, as Nelson et al. (2004) emphasized, the phylogenetic conclusions of Cooper and Chapleau (1998) in recognizing monophyly of this clade are not in question.

TRIBE PLEURONECTINI. Five genera, *Limanda*, *Parophrys*, *Platichthys*, *Pleuronectes*, and *Pseudopleuronectes*, with 20 species (Cooper and Chapleau, 1998).

Family BOTHIDAE (494)—lefteye flounders. Marine; Atlantic, Indian, and Pacific.

Eyes sinistral; pelvic fin base on eyed side longer than on eyeless side, on midventral line and origin anterior to base on eyeless side; pectoral and pelvic fin rays not branched; pelvic fins without a spine; at least two series of intermuscular bones (termed myorhabdoi); branchiostegal membranes connected; egg with a single oil globule in the yolk (true also of scophthalmids and paralichthyids). Chanet et al. (2004) demonstrated that the similarity in the ossification of ligaments in bothids and samarids is the result of convergence, not common ancestry.

Twenty genera, *Arnoglossus*, *Asterorhombus*, *Bothus*, *Chascanopsetta* (synonym *Pelecanichthys*), *Crossorhombus*, *Engyprosopon*, *Engyophrys*, *Grammatobothus*, *Japonolaeops, Kamoharaia, Laeops, Lophonectes, Monolene, Neolaeops, Parabothus, Perissias, Psettina, Taeniopsetta, Tosarhombus,* and *Trichopsetta,* with about 140 species (e.g., Hensley and Smale, 1997; Amaoka, Arai, et al., 1997; Amaoka, Mihara, et al., 1997; Amaoka and Imamura, 2000; D. A. Hensley and K. Amaoka in Carpenter and Niem, 2001; Munroe, 2003b; Hensley and Randall, 2003).

Superfamily Soleoidea. Eight families.

Family PARALICHTHODIDAE (495)—measles flounders. Marine; southern Africa.

Origin of dorsal fin before the eyes; lateral line with prominent curve over pectoral fin; vertebrae 30–31; eyed side brownish gray with small dark spots.

Considered a subfamily of Pleuronectidae in Nelson (1994) and Evseenko (2004).

One species, *Paralichthodes algoensis* of southern Africa (P. C. Heemstra in Smith and Heemstra, 1986:864; Evseenko, 2004).

Family POECILOPSETTIDAE (496)—bigeye flounders. Marine: Atlantic, Indian, and Pacific, primarily in deep water.

Origin of dorsal fin above the eyes; lateral line rudimentary on eyeless side; pelvic fins symmetrical; vertebrae 36–43.

Considered a subfamily of Pleuronectidae in Nelson (1994) and Evseenko (2004).

Three genera, *Marleyella* (2), *Nematops* (4), and *Poecilopsetta* (14), with 20 species (e.g., Guibord and Chapleau, 2001; Hoshino et al., 2001; Munroe, 2003b; Evseenko, 2004).

Family RHOMBOSOLEIDAE (497)—rhombosoleids. Marine; primarily a South Pacific group, occurring mostly around Australia and New Zealand, with one species in the southwestern Atlantic.

Pelvic fins asymmetrical (one on the eyed side may be joined to anal fin); lateral line equally developed on both sides; pectoral radials absent; vertebrae 30–46.

Only *Oncopterus darwini* occurs in the southwestern Atlantic. Two species of *Rhombosolea* enter freshwater in New Zealand (McDowall, 1990). Some of the species resemble the Soleidae.

Considered a subfamily of Pleuronectidae in Nelson (1994) and Evseenko (2004).

Nine genera, *Ammotretis, Azygopus, Colistium, Oncopterus, Pelotretis, Peltorhamphus, Psammodiscus, Rhombosolea,* and *Taratretis,* with 19 species (e.g., Evseenko, 2004).

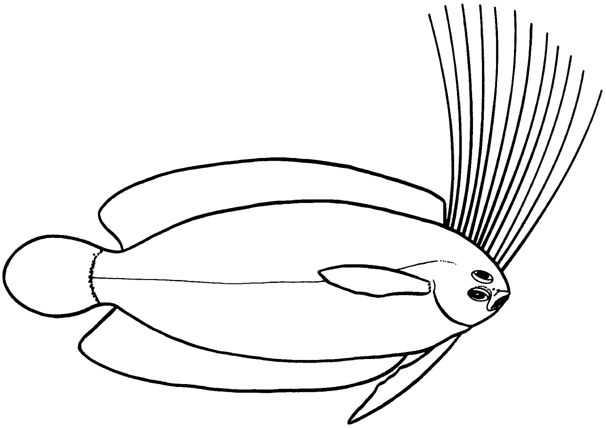
Family ACHIROPSETTIDAE (498)—southern flounders. Marine; Southern Hemisphere, Antarctic and subantarctic.

Eyes sinistral; body extremely compressed; pectoral fins rudimentary (juveniles) or absent; no fin spines; lateral line straight; branchiostegal membranes separate. Its relationships are uncertain, but it probably belongs in the clade of the following families.

This family was established by S. A. Evseenko in 1984. For placement in classification, see above under the order.

Four genera, *Achiropsetta, Mancopsetta, Neoachiropsetta,* and *Pseudomancopsetta,* with five or six species (P. C. Heemstra in Gon and Heemstra, 1990; Miller, 1993; Evseenko, 1997).

Family SAMARIDAE (499)—crested flounders. Marine, tropical and subtropical; Indo-Pacific, primarily in deep water.



Origin of dorsal fin in front of eyes; lateral line well developed or rudimentary; pelvic fins symmetrical; postcleithra absent (as is also true for the Achiridae, Soleidae, and Cynoglossidae).

Three genera, *Plagiopsetta, Samaris,* and *Samariscus,* with about 20 species (Quéro et al., 1989).

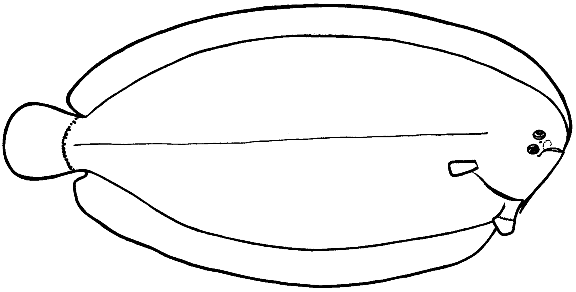
Family ACHIRIDAE (500)—American soles. Marine and freshwater; Amphi-American (United States to Argentina).

Eyes dextral; margin of preoperculum represented by a superficial groove; dorsal and anal fins free from caudal fin; right pelvic fin joined to anal fin.

The families Achiridae, Soleidae, and Cynoglossidae form a monophyletic group, with the Achiridae being the primitive sister group to the families Soleidae and Cynoglossidae. These three families have the skin of the lower jaw and interopercle continuous ventrally and covering the isthmus and branchiostegals.

About seven genera, *Achirus, Apionichthys* (synonyms *Achiropsis, Pnictes,* and *Soleonasus*), *Baiostoma, Catathyridium, Gymnachirus, Hypoclinemus,* and *Trinectes,* with about 33 species (Walker and Bollinger, 2001; Munroe, 2003b; Ramos, 2003a, b).

Family SOLEIDAE (501)—soles. Marine, tropical to temperate seas, primarily Europe to Australia and Japan, entering rivers in Africa (one species in freshwater), Asia, and Australia.



Eyes dextral; margin of preoperculum completely concealed; dorsal and anal fins free from caudal fin or united with caudal; pelvics free from anal fin. The Moses Sole or Speckled Sole, *Pardachirus marmoratus*, of the Indian Ocean, has a chemical defense against predation. Chapleau and Desoutter (1996) noted that *Dagetichthys lakdoensis* occurs 1,300 km inland from the Atlantic Ocean in Cameroon.

About 35 genera (e.g., *Achiroides, Aesopia, Aseraggodes, Bathysolea, Brachirus, Dagetichthys, Heteromycteris, Liachirus, Microchirus, Monochirus, Pardachirus, Pegusa, Solea, Synaptura,* and *Zebrias*) with about 130 species (Chapleau and Desoutter, 1996; Desoutter and Chapleau, 1997; Quéro, 1997; Desoutter, Chapleau, et al., 2001; Desoutter, Munroe, et al., 2001; T. A. Munroe in Carpenter and Niem, 2001; Randall, 2002). *Euryglossa,* formerly recognized in this family, is an invalid name (Desoutter, Munroe, et al., 2001).

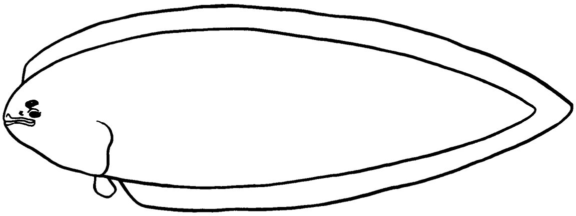
Family CYNOGLOSSIDAE (502)—tonguefishes. Marine (some entering freshwater); tropical and subtropical seas.

Eyes sinistral; margin of preoperculum concealed by skin and scales; dorsal and anal fins confluent with the pointed caudal fin; pelvic fin of eyeless side of four rays along midventral line, linked to anal fin in some, and pelvic girdle and fin on eyed side absent in some; pectoral fins absent (a fine membrane in *Symphurus*); eyes very small and usually close together; mouth asymmetrical; vertebrae 42–78 (usually 9 or 10 abdominal and 33–66 caudal). Maximum length for most species is less than 30 cm, rarely over 40 cm (up to about 48 cm).

Monophyly for this family and its two subfamilies was established by F. Chapleau in 1988.

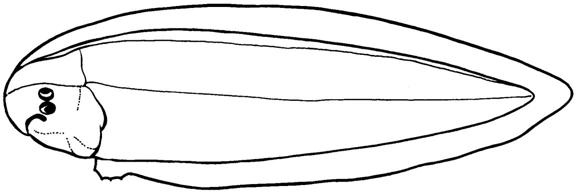
Three genera with about 127 species (e.g., Munroe, 1998).

SUBFAMILY SYMPHURINAE. Snout not hooked; mouth terminal and almost straight; lateral line absent on both sides; pelvic fin free from anal fin. Most are in deep water, occurring about 300–1,900 m.



One genus, *Symphurus,* with about 77 species, found on both sides of the Americas and in the eastern Atlantic and Indo-West Pacific (including Hawaii) (e.g., Munroe, 1998, 2003b; Munroe et al., 2000; T. A. Munroe in Carpenter and Niem, 2001; Krabbenhoft and Munroe, 2003).

SUBFAMILY CYNOGLOSSINAE. Snout hooked; mouth inferior and contorted; lateral line(s) well developed, at least on eyed side; pelvic fin confluent with anal fin. Most are shallow-water burrowing forms; about five species are known primarily from rivers, and three may occur in only freshwater, as noted by T. R. Roberts in 1989.



Two genera, *Cynoglossus* (lips without fringes) with about 50 species and *Paraplagusia* (lips on eyed side with fringes) with three species, found in the Old World from the eastern Atlantic to the western Pacific (e.g., T. A. Munroe in Carpenter and Niem, 2001).

Order TETRAODONTIFORMES (Plectognathi) (60)—plectognaths. No parietals, nasals, or infraorbitals, and usually no lower ribs; posttemporal, if present, simple and fused with pterotic of skull; hyomandibular and palatine firmly attached to skull; gill openings restricted; maxilla usually firmly united or fused with premaxilla; scales usually modified as spines, shields, or plates; lateral line present or absent, sometimes multiple; swim bladder present except in molids; 16–30 vertebrae.

Tetraodontiformes can produce sounds by grinding the jaw teeth or the pharyngeal teeth or by vibrating the swim bladder. The stomach of some tetraodontiforms is highly modified to allow inflation to an enormous size. Fishes with this ability belong to the families Tetraodontidae, Diodontidae, and, where it is less well developed, Triodontidae; they are popularly called "puffers." Inflation is caused by gulping water into a ventral diverticulum of the stomach when the fish is frightened or annoyed. Deflation occurs by expelling the water. If the fish is removed from the water, inflation can occur with air. The triodontid and most balistids have another mechanism for slightly enlarging their bodies. They do this by expanding a ventral flap supported by a large movable pelvic bone.

The present classification, changed above the family level from Nelson (1994), is based on the cladistic study of fossil and extant taxa by Santini and Tyler (2003) (extensive information on the finely preserved Monte Bloca fossils was given in Tyler and Santini, 2002). There are many changes in our understanding of relationships between families.

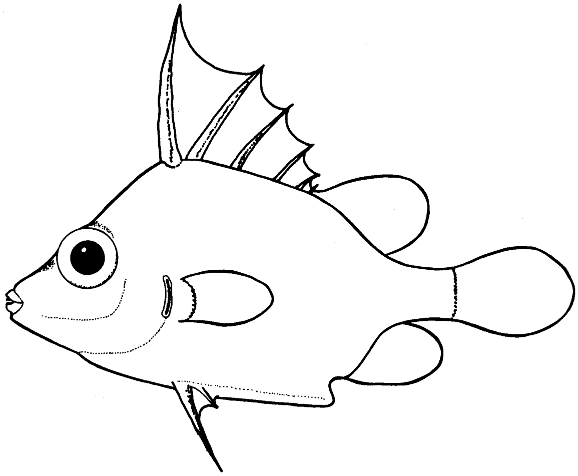
The sister group of this order is the subject of considerable uncertainty, and more studies are needed on this problem. Some studies have concluded that all or some tetraodontiforms are related to acanthuroids, zeiforms, or caproids (see above under order Perciformes, and suborder Caproidei, for brief discussion). I have retained the Tetraodontiformes in their classical postperciform position pending further studies.

Nine families with approximately 101 genera and 357 extant species. About 14 species occur only in freshwater, and another eight or so may be found in freshwater.

†Suborder Plectocretacicoidei. Three Upper Cretaceous families, Cretatriacanthidae, Plectocretacicidae, and Protriacanthidae, are recognized by Tyler and Sorbini (1996) and Santini and Tyler (2003).

Suborder Triacanthodoidei. Synapomorphies were given in Santini and Tyler (2003). The one family shares the following primitive features with the Triacanthidae, formerly placed in this suborder: pelvic fin spine large and able to be locked into position; upper jaw slightly protractile (ascending process of premaxilla well developed); pelvic fin with one large spine and up to two soft rays; dorsal fin usually with six spines; caudal fin with 12 principal rays; 2–6 separate hypurals; 20 vertebrae.

Family TRIACANTHODIDAE (503)—spikefishes. Marine; deepwater benthic; tropical and subtropical western Atlantic and Indo-Pacific.



Dorsal fin rays 12–18; anal fin rays 11–16; caudal fin rounded to truncate.

Two subfamilies, 11 genera, and about 21 species (Tyler, 1997; Matsuura in Carpenter and Niem, 2001).

SUBFAMILY HOLLARDINAE. Western Atlantic, one species in Hawaii.

Two genera, *Hollardia* and *Parahollardia*, with five species. The orthography of the subfamily name is changed from Nelson (1994) following Santini and Tyler (2003).

SUBFAMILY TRIACANTHODINAE. Indo-Pacific, one species in western Atlantic.

Nine genera, *Atrophacanthus, Bathyphylax, Halimochirurgus, Johnsonina, Macrorhamphosodes, Mephisto, Paratriacanthodes, Triacanthodes,* and *Tydemania,* with 16 species.

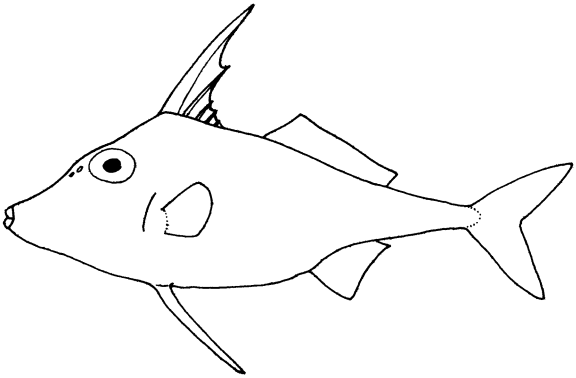
Suborder Balistoidei (Sclerodermi). Frontals extending far anterior to articulation between lateral ethmoid and ethmoid.

Five fossil families were recognized by Santini and Tyler (2003), Moclaybalistidae, Bolcabalistidae, Eospinidae, Spinacanthidae, and Protobalistidae (the last two were placed in the superfamily Ostracioidea).

Four families, 61 genera, and 182 species.

Superfamily Triacanthoidea. One family.

Family TRIACANTHIDAE (504)—triplespines. Marine; shallow benthic; Indo-Pacific.



Dorsal fin rays 19–26; anal fin rays 13–22; caudal fin deeply forked. Maximum length about 28 cm.

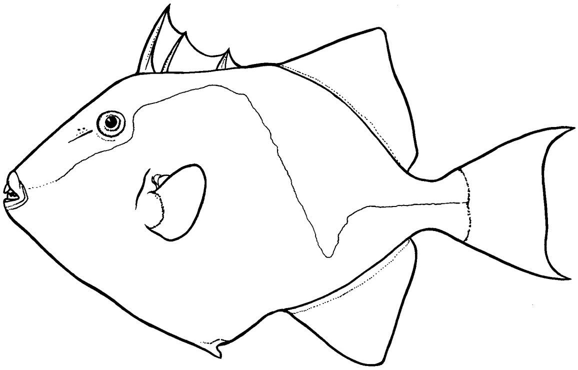
Fossils include the Eocene *Protacanthodes* (Tyler and Santini, 2002).

Four genera, *Pseudotriacanthus, Triacanthus, Tripodichthys,* and *Trixiphichthys,* with seven species (e.g., K. Matsuura in Carpenter and Niem, 2001; Santini and Tyler, 2002a).

Superfamily Balistoidea (leatherjackets). Body usually compressed; head and body covered with scales (scales may be highly modified and hidden by tissue); no pelvic fins (pelvic spine or tubercle present in balistines and some monacanthines, underlying pelvis present); first dorsal spine with locking mechanism (the small second spine, when present, forms the locking mechanism); upper jaw not protractile; upper jaw with two rows of protruding incisorlike teeth; soft dorsal fin with 23–52 rays and anal fin with 20–66 rays; caudal fin with 12 principal rays; the eyes can be rotated independently. Maximum length about 1.0 m, attained in *Aluterus scriptus.*

About 43 genera and 142 species.

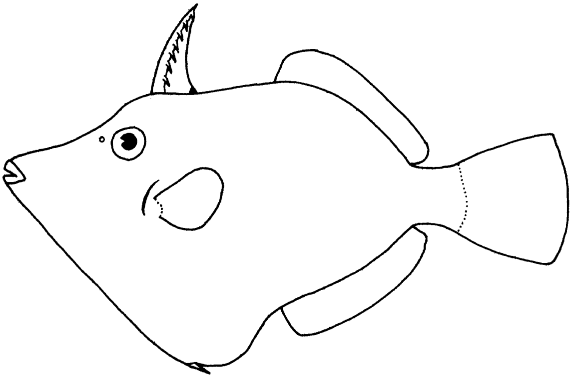
Family BALISTIDAE (505)—triggerfishes. Marine; Atlantic, Indian, and Pacific.



Three dorsal spines (third can be minute); all soft fins with branched rays; scales in regular series, platelike; upper jaw usually with four teeth in outer and three in the inner series on each premaxillary, developed more for crushing than for nibbling; 18 vertebrae.

Eleven genera, *Abalistes, Balistapus, Balistes, Balistoides, Canthidermis, Melichthys, Odonus, Rhinecanthus, Sufflamen, Xanthichthys,* and *Xenobalistes,* with about 40 species (e.g., K. Matsuura in Carpenter and Niem, 2001).

Family MONACANTHIDAE (506)—filefishes. Marine; Atlantic, Indian, and Pacific.



Usually two dorsal spines—the second is usually much smaller and it may be absent; soft dorsal, anal, and pectoral rays simple; scales small, in regular series; body prickly or furry to touch; upper jaw usually with three teeth in outer and two in the inner series on each premaxillary, developed for nibbling; 19–31 vertebrae. The greatest number of filefishes, some 54 species, occur in Australia (Hutchins, 1977). Pliocene fossils are known from Italy (Sorbini, 1988).

About 32 genera (e.g., *Aluterus, Amanses, Anacanthus, Brachaluteres, Cantherhines, Chaetoderma, Enigmacanthus, Monacanthus, Navodon, Oxymonacanthus, Paraluteres, Paramonacanthus, Pervagor, Pseudalutarius, Rudarius, Stephanolepis,* and *Thamnaconus*) with about 102 species (e.g., Hutchins, 1997, 2002; J. B. Hutchins in Carpenter and Niem, 2001).

Superfamily Ostracioidea (Ostracodermi)

Family OSTRACIIDAE (Ostraciontidae) (507)—boxfishes (cowfishes and trunkfishes). Marine, tropical; Atlantic, Indian, and Pacific.

Body encased in a bony carapace; no pelvic skeleton; no spinous dorsal; dorsal and anal fins each with 9–13 rays; upper jaw not protractile; usually 18 vertebrae. Maximum length about 60 cm.

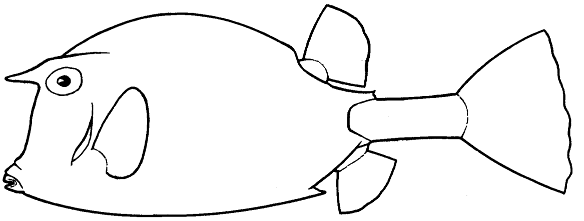
Some trunkfishes are known to discharge a toxic substance, termed "ostracitoxin," which will kill other fishes in confined quarters. The substance is also toxic to the trunkfish, but less so than to most other fishes. Fossils include the Eocene *Eolactoria* and *Proaracana* and the Oligocene *Oligolactoria* (e.g., Tyler and Santini, 2002).

Two subfamilies, 14 genera, with about 33 species (e.g., K. Matsuura in Carpenter and Niem, 2001). Many authors recognize the two subfamilies as separate families (e.g., K. Matsuura in Carpenter and Niem, 2001; Santini and Tyler, 2003); however, the two appear to form a tight clade relative to the two maintained subfamilies of the Tetraodontidae. J.M Leis in a 1984 article based on early life history characters in the *"Ontogeny and systematics of fishes"* placed this family in a clade with the Diodontidae and Molidae (i.e., it would be placed in the present suborder Tetraodontoidei), in contrast with earlier works using adult specimens aligning it with the Balistidae and Monacanthidae.

SUBFAMILY ARACANINAE. Carapace open behind the dorsal and anal fins; ventral ridge more or less developed; caudal fin usually with 11 principal rays. These fishes are found in relatively deep water in the Indo-West Pacific from Hawaii to South Africa; they are most abundant around Australia.

Seven genera, *Anoplocapros, Aracana, Caprichthys, Capropygia, Kentrocapros, Polyplacapros,* and *Strophiurichthys,* with about 13 species.

SUBFAMILY OSTRACIINAE. Carapace closed, at least behind the anal fin; no ventral ridge; caudal fin with 10 principal rays.



Seven genera, *Acanthostracion, Lactophrys, Lactoria, Ostracion, Rhinesomus, Rhynchostracion,* and *Tetrosomus,* with about 20 species.

Suborder Tetraodontoidei (Gymnodontes). Jaw "teeth" fused (true teeth are absent—the upper and lower jaws have cutting edges; a similar looking beak is found in the Scaridae); depending on the presence or absence of sutures, there may be two, three, or four such "teeth"; upper jaw not protractile; posttemporal absent; urohyal absent except in *Triodon*; pelvis absent except in *Triodon* and pelvic fin (spine and rays) absent. Fossils include the Eocene *Eoplectus* and *Zignoichthys* (Tyler and Santini, 2002).

Four families, 29 genera, and 154 species.

Family TRIODONTIDAE (508)—threetooth puffers. Marine; Indo-West Pacific.

Three fused teeth in jaws (upper jaw with a median suture, the lower without); pelvis present; dorsal and anal fins usually with 11 rays (a small spiny dorsal fin of one or two rays is present in most specimens from Indonesia to Japan); ribs and epipleurals present; caudal fin with 12 principal rays and numerous procurrent rays, deeply forked. Maximum length about 48 cm.

An Eocene fossil, *Triodon antiquus,* is very similar to the one extant species.

One species, *Triodon macropterus* (synonym *bursarius*) (e.g., K. Matsuura in Carpenter and Niem, 2001).

Family TETRAODONTIDAE (509)—puffers. Marine, with several entering and occurring in brackish and freshwater; tropical and subtropical; Atlantic, Indian, and Pacific.

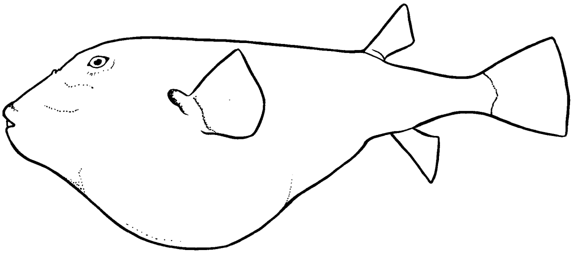
Body inflatable; body naked or with only short prickles (often confined to belly); four fused teeth in jaws (teeth in each jaw fused but separated by a median suture); premaxillae and dentaries not fused to opposite member at midline; dorsal and anal fins usually each with 7–18 soft rays (many more in *Chonerhinos* and *Xenopterus*); ribs and epineurals absent; caudal fin with 10 principal rays and no procurrent rays, moderately forked to rounded.

The "flesh" (especially the viscera) of some puffers contains the alkaloid poison tetraodotoxin, produced by the fish, which can be fatal. In at least some species, the gonads at spawning time contain the highest concentration of this poison; none occurs in the muscle.

About 12 species of *Carinotetraodon, Chonerhinos,* and *Tetraodon* occur only in freshwater, primarily in the Congo River and in southern Asia. Maximum length 90 cm; most much less.

Nineteen genera with about 130 species (e.g., K. Matsuura in Carpenter and Niem, 2001).

SUBFAMILY TETRAODONTINAE. Body broadly rounded in cross section; one or two conspicuous nostrils on each side; lateral line usually conspicuous; gill opening usually extending below midportion of pectoral fin; erectable ridge of skin on dorsal and ventral midline only in *Carinotetraodon* (which is probably related to *Canthigaster*, placed in the next subfamily); vertebrae 17–29.

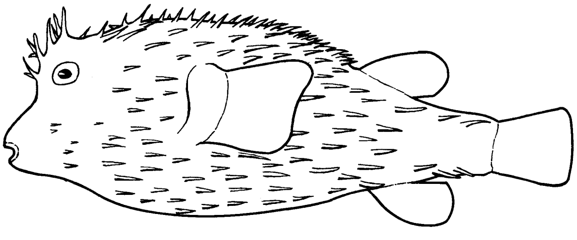


About eighteen genera (e.g., *Amblyrhynchotes*, *Arothron*, *Carinotetraodon*, *Colomesus*, *Contusus*, *Feroxodon*, *Javichthys*, *Lagocephalus*, *Omegophora*, *Sphoeroides*, *Takifugu* (synonym *Fugu*), *Tetraodon* (see Eschmeyer, 1998, for discussion of orthography of possible synonym *Monotretus*, *Monotreta*, or *Monotrete*), *Torquigener*, and *Xenopterus*) with about 98 species (e.g., Roberts, 1998b).

SUBFAMILY CANTHIGASTRINAE (SHARPNOSE PUFFERFISHES). Body laterally compressed (deeper than broad) in uninflated condition; single inconspicuous nostril on each side; lateral line inconspicuous; gill opening restricted, ending ventrally about level of midportion of pectoral fin; snout elongate and relatively pointed; erectable ridge of skin on dorsal and ventral midline; vertebrae usually 17 (8 + 9). Maximum length usually less than 12 cm. Most species of sharpnose puffers occur in shallow water, usually near coral reefs, and feed on benthic organisms. All but one species (which occurs in the Atlantic) occur in tropical Indo-Pacific waters (from the Red Sea and South Africa to Central America).

One genus, *Canthigaster*, with 32 species (e.g., Moura and Castro, 2002).

Family DIODONTIDAE (510)—porcupinefishes (burrfishes). Marine; Atlantic, Indian, and Pacific.

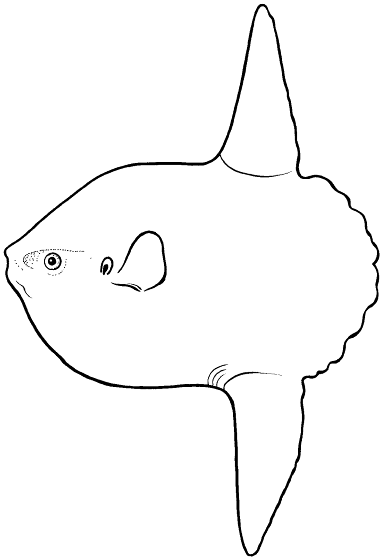


Body inflatable; body covered with well-developed sharp spines (in some species the spines erect only when body is inflated); two fused teeth in jaws (parrotlike); premaxillae and dentaries completely fused to opposite member at midline.

Adults inhabit inshore waters while the young are pelagic.

Six genera, *Allomycterus*, *Chilomycterus*, *Cyclichthys*, *Diodon*, *Lophodiodon*, and *Tragulichthys*, with 19 species (J. M. Leis in Carpenter and Niem, 2001).

Family MOLIDAE (511)—molas. Marine; tropical and subtropical; Atlantic, Indian, and Pacific.



Two fused teeth in jaws; no spines in dorsal or anal fins; no caudal peduncle; caudal fin lost, posterior end of body reduced to a leathery flap or pseudocaudal (clavus); two minute nostrils on each side; lateral line absent; no swim bladder; 16–18 vertebrae.

Johnson and Britz (2005) tested the hypothesis that the clavus is 1) a highly modified caudal fin, or 2) formed by highly modified elements of the dorsal and anal fins. Based on ontogenetic evidence, they concluded that the latter is correct, that it is formed by modified elements of the dorsal and anal fin, and that the caudal fin is lost in molids (see also Britz and Johnson, 2005).

The major locomotory thrust is provided by the powerful dorsal and anal fins. It has been estimated that up to 300 million eggs can be produced by *Mola mola* (the Ocean Sunfish), probably making it the most fecund fish species. Molas feed extensively on jellyfishes. Maximum length over 2 m with weights up to 1,000 kg. Fossils include the Eocene *Eomola*. Santini and Tyler (2002b) gave a phylogeny of this family. Also known as ocean sunfishes.

Three genera and four species: *Masturus lanceolatus* (recognized in *Mola* by some), *Mola mola, Mola ramsayi,* and *Ranzania laevis* (P. Parenti, 2003).

Class SARCOPTERYGII—lobe-finned fishes and tetrapods

The Sarcopterygii, as used here, form the monophyletic taxon that includes the remaining group of vertebrates. It includes several fish groups, both recent and fossil, and the tetrapods. All the included fishes are thus more closely related to mammals and other tetrapods than they are to other fishes. The closest sister group to the tetrapods among living fishes is probably the lungfishes (versus the coelacanths), although there are differing theories. In the past, the term Sarcopterygii has been variously used; some workers used it to include only fishes conventionally called crossopterygians and dipnoans (the lobe-finned fishes). I use the term to include also the tetrapods as have many earlier authors (e.g., see Nelson, 1994). Synapomorphies recognized by M.-M. Chang in 1991 for this group include enamel on the teeth.

In an exciting find, Zhu and Yu (2002) described a fossil sarcopterygian fish from the Lower Devonian of China, *Styloichthys*, that showed characteristics suggesting it might be close to the last common ancestor of tetrapods and lungfish. It appears to bridge the morphological gap between stem-group sarcopterygians (*Psarolepis* and *Achoania*, described in 1999 and 2001, respectively, by M. Zhu and coauthors) and basal tetrapodomorphs/basal dipnomorphs. The description of these possible links between what are recognized in classification as major breaks (e.g., with *Psarolepis* combining features of actinopterygians and sarcopterygians) provides very valuable information.

Some earlier views of relationships between crossopterygians, lungfishes, and tetrapods were given in Nelson (1994). The present classification of the nontetrapods is largely from Cloutier and Ahlberg (1996). Much information on this group is in Long (1995), Janvier (1996), Maisey (1996), Schultze and Cloutier (1996), Ahlberg (2001), and Clack (2002).

The Sarcopterygii are recognized here with two subclasses, having about 26,742 species, of which eight are fishes.

Subclass COELACANTHIMORPHA (Actinistia)

Order COELACANTHIFORMES (61)—coelacanths. Caudal fin diphycercal, consisting of three lobes; external nostrils, no choana; branchiostegals absent; lepidotrichia never branched; lepidotrichia in tail equal to number of radials or somewhat more numerous; anterior dorsal fin in front of center of body. Maximum length about 1.8 m, in *Latimeria chalumnae*.

The order is recognized with nine families (Cloutier and Ahlberg, 1996), eight with only fossil members, and one with fossil members and the living species. Much of the classification of Cloutier and Ahlberg (1996) is based on the 1993 study of H.-P. Schultze. There is a good fossil record of this group from the Upper Devonian to the Upper Cretaceous. The majority of species were marine, but some were freshwater. Forey (1998) gave extensive information on this order.

Two living species.

†Family MIGUASHAIIDAE. *Miguashaia*. Devonian.

†Family DIPLOCERCIDAE. *Diplocercides* (synonym *Nesides*). Devonian and Lower Carboniferous.

†Family HADRONECTORIDAE. *Allenypterus, Hadronector,* and *Polyosteorhynchus.*

†Family RHABDODERMATIDAE. Paraphyletic. E.g., *Caridosuctor* and *Rhabdoderma*. Primarily Carboniferous.

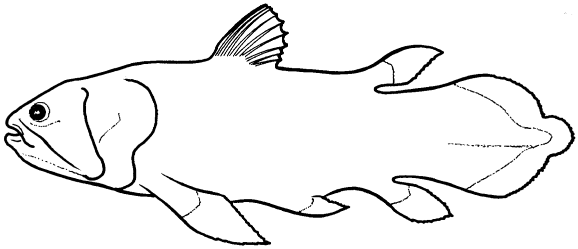
†Family LAUGIIDAE. *Coccoderma* and *Laugia*. Lower Triassic to Lower Cretaceous.

†Family WHITEIIDAE. *Whiteia*. Triassic.

†Family COELACANTHIDAE. E.g., Axelia, *Coelacanthus,* and *Wimania.*

†Family MAWSONIIDAE. E.g., *Alcoveria, Axelrodichthys, Chinlea, Diplurus, Holophagus,* and *Mawsonia*. Triassic and Jurassic.

Family LATIMERIIDAE (512)—gombessas or coelacanths. Marine; off southern Africa (Mozambique, Madagascar, and Comoros Archipelago) and Indonesia (Celebes Sea, north of Sulawesi).



The first living species, *Latimeria chalumnae* (Gombessa), a marine species known from South Africa, Comoros Archipelago, and off Mozambique, was formerly recognized as the sole extant member of the family Latimeriidae. Views that *Latimeria* is more closely related to Chondrichthyes than to bony fishes (based in part on similarities in the pituitary gland, presence of a rectal gland, and high blood levels of urea) are not considered probable.

The first specimen was trawled off East London, South Africa, in December 1938. This species is livebearing. Length of adults up to 1.8 m. There is much interest in the unusual head-standing behavior of *L. chalumnae,* filmed by Hans Fricke in his submersible at about 170–200 m depth (the species ranges between about 150–400 m). It also has an unusual mode of swimming, especially for a notochordal fish, in keeping the body rigid. It is the only living chordate with an intracranial joint, also found in other coelacanths, porolepiforms, and osteolepidiforms. As described by M.-M. Chang in a 1991 study discussing its phylogenetic importance, the intracranial joint is a plesiomorphic character of sarcopterygians with mobility reduced in porolepiforms and lost in dipnoans. This joint divides the neurocranium into an orbitosphenoid anterior half and an otico-occipital posterior half. It, with other joints, may allow the upper jaw to be elevated.

Events leading to the discovery of the second species (*Latimeria menadoensis*) began with the sighting by Mark and Arnaz Erdmann of a coelacanth in an Indonesian fish market in Manado, Sulawesi, on 18 September 1997, and the subsequent preservation of a second specimen on 30 July 1998. These events are documented in a 1999 issue of *Environmental Biology of Fishes.* The new species was described by Pouyaud et al. (1999).

Two species, *Latimeria chalumnae* and *L. menadoensis.* In addition to the two living species, there are Jurassic and Cretaceous genera, e.g., *Holophagus, Libys, Macropoma,* and *Undina.* All taxa recognized here in the family Latimeriidae were recognized in the Coelacanthidae in Nelson (1994). Reasons for splitting the two families are given in Cloutier and Ahlberg (1996).

Subclass DIPNOTETRAPODOMORPHA

This new term (Dipnotetrapodomorpha) in this edition is for the unnamed taxon of Onychodontida + Rhipidistia in Cloutier and Ahlberg (1996). The classification of the taxon has changed from that in Nelson (1994). It is now based primarily on Cloutier and Ahlberg (1996). An overview is presented below.

Subclass Dipnotetrapodomorpha, sister to subclass Coelacanthimorpha (Actinistia)
- Unranked 1a. Onychodontida
- Unranked 1b. Rhipidistia
  - Unranked 2a. Dipnomorpha
    - Superorder Porolepimorpha
      - †Order Porolepiformes
    - †Superorder Dipterimorpha—several fossil families, paraphyletic.
    - Superorder Ceratodontimorpha
      - Order Ceratodontiformes—two suborders with three extant families
  - Unranked 2b. Tetrapodomorpha
    - Unranked 3a. †Rhizodontimorpha
    - Unranked 3b. Osteolepidimorpha
      - Unranked 4a. Unnamed Osteolepidiformes + Elipistostegalia + Tetrapoda
        - Order Osteolepidiformes
      - Unranked 4b. Unnamed. Elipistostegalia + Tetrapoda
        - †Infraclass Elipistostegalia
        - Infraclass Tetrapoda

Unranked 1a. Onychodontida

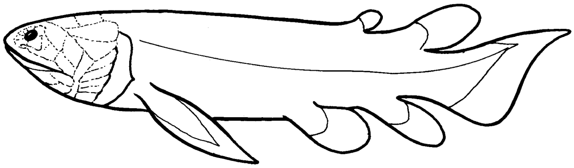
†Order ONYCHODONTIFORMES (Struniiformes). Position uncertain but hypothesized to be sister to the rhipidistians (all other vertebrates). A poorly known Middle to Upper Devonian group (e.g., *Onychodus* and *Strunius*). Long (2001), in discussing the relationships of this taxon to other sarcopterygians, suggested that *Psarolepis* may be the sister taxon to *Onychodus,* and the most basal member of the onychodontiform lineage.

Unranked 1b. Rhipidistia

Unranked 2a. Dipnomorpha

†Superorder POROLEPIMORPHA

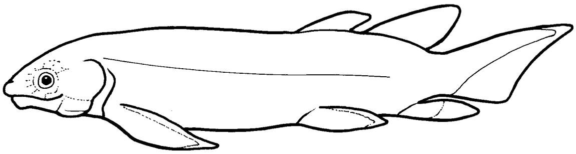
†Order POROLEPIFORMES (Holoptychiiformes). Body plump; pectorals inserted relatively high on body; thick rhombic cosmoid scales to thin round scales; no pineal foramen.



Two families, Porolepidae and Holoptychiidae. Devonian.

DIPNOI (DIPNEUSTI, DIPNOIFORMES OF CLOUTIER AND AHLBERG, 1996)—LUNGFISHES. The following two superorders comprise the lungfishes. They have platelike teeth (suited for crushing and grinding). Lungfishes probably arose in the Lower Devonian. The Lower Devonian *Powichthys* and *Youngolepis* (Youngolepididae) may belong in this clade. See Nelson (1994) for references to the older literature, especially for the major contributions of such continuing workers as M.-M. Chang and H.-P. Schultze. Much continuing work is being done (e.g., by M.-M. Chang and A. Kemp) (see also the major study of vertebral columns by Arratia et al., 2001).

†Superorder DIPTERIMORPHA



Branchiostegal rays 0–3, gular plates present; caudal fin heterocercal or diphycercal.

Devonian to Triassic.

Unfortunately, a stable cladistic classification of members of this group, which may be paraphyletic, does not exist. Campbell and Barwick (2001) critically discussed problems arising in hypothesizing, in cladistic analysis, relationships in lungfishes—in particular, whether or not *Diabolepis* is, as regarded by some, the sister group of the Dipnoi. Some of the fossil families recognized in Cloutier and Ahlberg (1996) are as follows:

†Family DIABOLEPIDIDAE. *Diabolepis*. Early Devonian.

†Family URANOLOPHIDAE. Early Devonian.

†Family DIPNORHYNCHIDAE. E.g., *Dipnorhynchus*. Early Devonian.

†Family CHIRODIPTERIDAE. E.g., *Chirodipterus*.

†Family STOMIAHYKIDAE.

†Family DIPTERIDAE. E.g., *Dipterus*.

†Family RHYNCHODIPTERIDAE. E.g., *Griphognathus*.

†Family FLEURANTIIDAE.

†Family PHANEROPLEURIDAE.

†Family CTENODONTIDAE.

Palaeospondylus—a larval lungfish, and not a jawless fish. Thomson et al. (2003) clarified the puzzle in paleontology as to the identity of *Palaeospondylus* *gunni*, a tiny (5–60 mm) and abundant vertebrate fossil from the Middle Devonian (approximately 385,000,000 years ago) from primarily Achanarras Quarry, Caithness, Scotland, first discovered in 1890. They showed that it is the larval stage of a lungfish, most probably *Dipterus valenciennesi.*

Superorder CERATODONTIMORPHA

Branchiostegals and gulars absent; caudal fin diphycercal, confluent with dorsal and anal fins; premaxilla and maxilla absent; lungs functional.

Extensive fossil record since the Lower Triassic and three extant genera and six species.

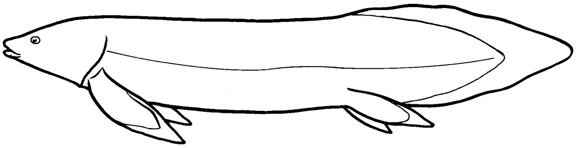
Although the three families with living species are restricted to widely separated continents, this was not always the case. *Ceratodus* and *Lepidosiren* tooth plates occur together in the lower Paleocene in Bolivia, and *Ceratodus* is also known from Africa and Madagascar. This and the fact that some fossil South American ceratodontids and lepidosirenids have their closest relatives in Africa and Australia may suggest that the species involved dispersed in freshwater on a united supercontinent; but, apparently, as also noted in 1991 by H.-P. Schultze, Cretaceous ceratodontids show marine tolerance and might, therefore, have been able to disperse without land connections.

Order CERATODONTIFORMES (62)—living lungfishes. All three extant families are placed in this order, in two suborders (each suborder was recognized at the ordinal level in Nelson, 1994). This change was made to better accommodate the changed classification based on Cloutier and Ahlberg (1996).

Three families, three genera, and six species.

Suborder Ceratodontoidei. Pectoral and pelvic fins flipperlike; scales large; air bladder (lung) unpaired; larvae without external gills; adults do not estivate.

Family CERATODONTIDAE (513)—Australian lungfishes. Freshwater; Southeast Queensland, Australia.

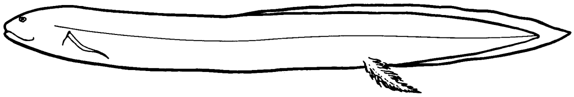


R. S. Miles in 1977 and Cloutier and Ahlberg (1996) recognized the extant *Neoceratodus* in the family Neoceratodontidae. Cloutier and Ahlberg (1996) acknowledged that their fossil family Ceratodontidae may be paraphyletic, and until relationships are resolved I prefer to continue to recognize the Triassic *Ceratodus* and the extant *Neoceratodus* in the same family.

One species, *Neoceratodus forsteri.*

Suborder Lepidosirenoidei. Pectoral and pelvic fins filamentous, without rays; scales small; air bladder (lungs) paired; larvae with external gills; adults estivate in dry season. Fossils that may belong here include the Paleozoic *Gnathorhiza.* Cloutier and Ahlberg (1996) placed both genera in the same family, Lepidosirenidae.

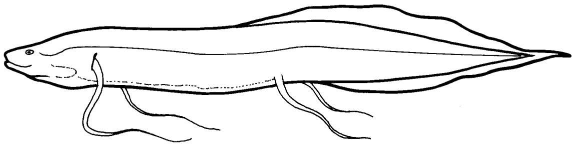
Family LEPIDOSIRENIDAE (514)—South American lungfishes. Freshwater; Brazil and Paraguay.



Five gill arches and four gill clefts; body very elongate.

One species, *Lepidosiren paradoxa.* This was the first living lungfish to be formally described, in 1837.

Family PROTOPTERIDAE (515)—African lungfishes. Freshwater; Africa.



Six gill arches and five gill clefts; body moderately elongate. Maximum length about 1.8 m.

One genus, *Protopterus,* with four species (however, a revision of all species may result in more being recognized).

Unranked 2b. Tetrapodomorpha

†Unranked 3a. RHIZODONTIMORPHA (Rhizodontida)

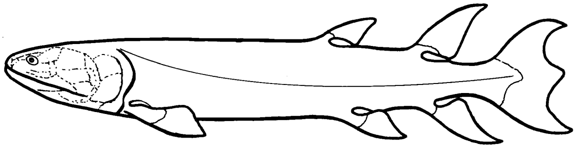
†Order RHIZODONTIFORMES. One family, Rhizodontidae, containing *Barameda, Pycnoctenion, Propycnoctenion, Rhizodus, Sauripterus, Screbinodus,* and *Strepsodus,* known from the Upper Devonian to the Pennsylvanian. Rhizodontiforms probably lacked a choana since they have two pairs of external nostrils.

†Unranked 3b. OSTEOLEPIDIMORPHA (Osteolepidida)

The term Choanata was applied to this monophyletic taxon in Nelson (1994), based on its earlier use by others. Ahlberg and Johanson (1998) discussed hypotheses concerning whether or not the Osteolepiforms and tetrapods form a monophyletic group.

Unranked 4a. Unnamed Osteolepidiformes + Elipistostegalia + Tetrapoda

†Order OSTEOLEPIDIFORMES. Body slender; pectorals usually inserted low on body; thick rhombic scales; pineal foramen present.



About five families (based on work of H.-P. Schultze in 1993 and Cloutier and Ahlberg, 1996), Canowindridae, Megalichthyidae (e.g., *Megalichthys*), Osteolepididae (e.g., *Osteolepis,* and perhaps *Thursius*), Tristichopteridae (= Eusthenopteridae) (*Eusthenopteron* is one of the best known of all fossil fishes), and Rhizodopsidae. *Gogonasus* is included within the osteolepidiforms, but it is of uncertain position as are several other genera.

Unranked 4b. Unnamed. Elipistostegalia + Tetrapoda

†Infraclass ELIPISTOSTEGALIA

One family, Elipistostegidae (= Panderichthyidae), with two genera, *Elpistostege* and *Panderichthys* (Cloutier and Ahlberg, 1996).

Infraclass TETRAPODA—tetrapods

This taxon, of about 26,734 extant species, comprises the following extant groups (not given rank here) (based, in part, on the references given in Nelson, 1994:75). The list does not accommodate all fossil groups. Cracraft and Donoghue (2004) gave details on their phylogeny and classification. The number of extant species of amphibians is from D. Cannatella and D. M. Hillis in Cracraft and Donoghue (2004), of reptiles from M. S. Y. Lee et al. in

Cracraft and Donoghue (2004) (for birds they give “more than 9,000”), and mammals from Wilson and Reeder (1993) and Wilson and Cole (2000) (raised from their 4,629 figure due to new descriptions, but an increase of several hundred is expected in the revision of the 1993 edition). The terms Synapsida and Reptilia are used with a different composition than is used by many. Clack (2000) reviewed what is known of the transition of tetrapods from water to land. Tetrapods appear in the fossil record in the Upper Devonian and probably arose by at least the Middle Devonian.

Amphibia (amphibians)—with about 5,504 extant species (165 caecillians, 502 salamanders, and 4,837 frogs, including toads)
Amniota (amniotes)—with about 21,230
  Synapsida (including Mammalia)—with about 4,830 extant species
  Reptilia—with about 16,400 extant species
    Turtles—with about 300 species
    Diapsida
Archosauromorpha (including 24 crocodiles, dinosaurs [which are paraphyletic without birds], and 9,050 birds)—with about 9,100 extant species
Lepidosauromorpha (including tuataras, 4,100 lizards, which are a paraphyletic group without snakes, and 2,900 snakes)—with about 7,000 extant species

Appendix

Checklist of the classes (numbered), extant subclasses (not numbered), extant orders (numbered), extant suborders (not numbered), and extant families (numbered). Page number given for all.

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