

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 *Mylokunmingia* 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 *Mylokunmingia*. In further clarification, Xian-guang et al. (2002) described details of a new specimen co-occurring with the nominal *Mylokunmingia fengjiao* and *Haikouichthys ercaicunensis* and concluded that all are conspecific; the oldest name *Mylokunmingia fengjiao* 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 *Mylokunmingia* 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 Myxiniomorphi (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 Conodonts

†Superclass Pteraspidiomorphi

†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 coelacanth, 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 (Asymmetronidae). 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

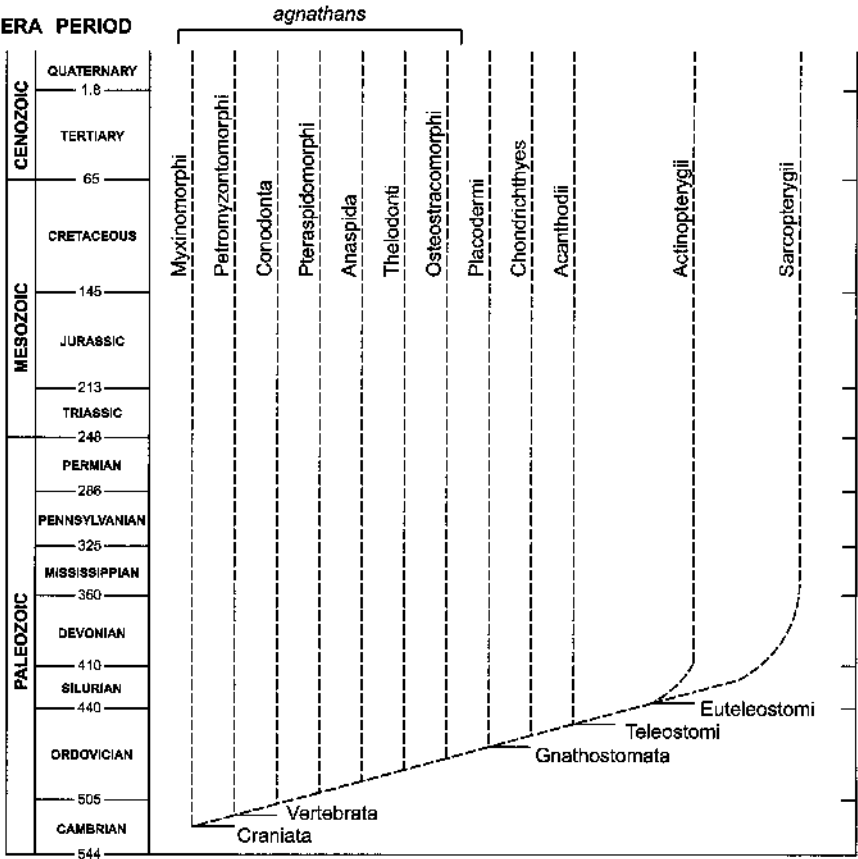
Notochord never extends in front of brain; cranium present; vertebrae usually present; cartilage or bone or both present; heart chambered; red blood

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 (ammonoetes) 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), Conodonts, Pteraspidomorphi (with *Astraspis*, Arandaspid, 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, Conodonts, 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), Arandaspid, *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.

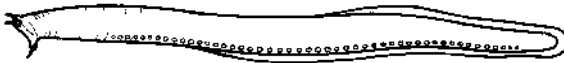
Class MYXINI

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, *Myxiniakela 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 *Myxiniakela*, 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, Paramyxiniinae (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 semi-circular 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 diphyercal (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.

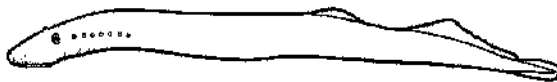
Lampreys are either parasitic or nonparasitic, and both life-history types characterize individuals of closely related species. It is believed that nonparasitic species have been independently derived from a parasitic species. The parasitic phase, after metamorphosis from the ammocoete larvae but before 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 myxiniids, *Jamoytius kerwoodi*, or anaspidiiforms, 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 *Myxiniakela* (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 semi-circular canals.

Monophyly of this group was recognized by Blicek 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).

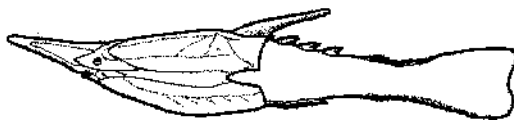
†Subclass ARANDASPIDA

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 pteraspidiiforms or heterostracans. Maximum length is 1.5 m, usually much smaller. Pteraspidiiforms 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*)

Traquairaspidiiformes (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 *Astraspidis*.

Karatajute-Talimaa and Smith (2004) established a new order of tessellate pteraspidiomorph 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 astraspidids 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 Galeaspidia, 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).

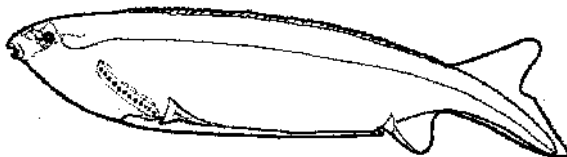
The term Myopterygii is used to include the following taxa, all forming an hypothesized monophyletic taxon.

†SUPERCLASS ANASPIDA

†Class ANASPIDA

†**Order ANASPIDIFORMES (Birkeniaae).** 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 *Shieliia 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 galeaspid, 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*, *Praetirlogania*, 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 (*Canonina*, *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 -idae or -ididae, 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); myelinated 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 PLACODERMIMORPHI

†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 diphyccercal 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 arthrodireforms, 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*).

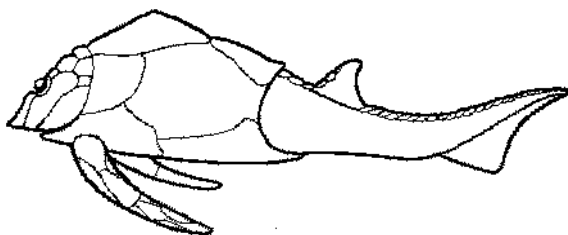
Yunnanolepidae—e.g., *Phymolepis*, *Yunnanolepis*.

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.

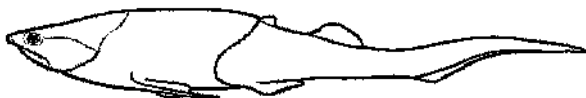
Order PTYCTODONTIFORMES. Large sexually dimorphic pelvic fins with claspers in males (fertilization was probably internal); many resemblances with living holocephalans. One family, Ptyctodontidae (e.g., *Ctenurella* and *Rhamphodopsis*), from Lower Devonian to possibly Lower Mississippian (primarily 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 jaw-bones 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 Wuttagoonaspididae.

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 myxoptergia) 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 sub-class Subterbranchialia into two clades, the Iniopterygia 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 autodiastyletic 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 (autodiastyle but a derived form of autodiastyle) (Grogan and Lund, 2000).

†**Order EUGENEODONTIFORMES.** Position uncertain. Four families, Agassizodontidae (including Helicoprionidae), Caseodontidae (e.g., *Fadenia* and *Ornithoprion*), Edestidae (e.g., *Lestroodus*), 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 (holostyle); 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 *Platyxystrodon*) (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*, *Pocilodus*, 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.

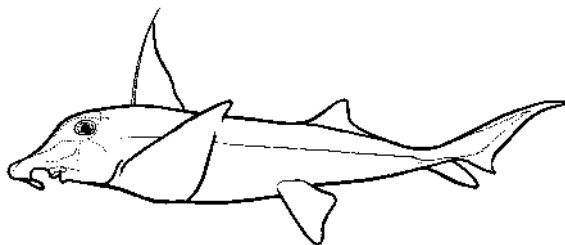
Suborder Chimaeroidei (chimaeras). Two dorsal fins, the first erectile, with short base, and preceded by an erectile spine, the second nonerectile, low, and with long base; mouth inferior. In living forms, at least, fertilization is internal; the deposited egg is encased in a brown horny capsule. Water 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 Callorhynchidae (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 *Callorhynchus* are known from the Eocene of Antarctica (Kriwet and Gaździcki, 2003).

One genus, *Callorhynchus*, 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.

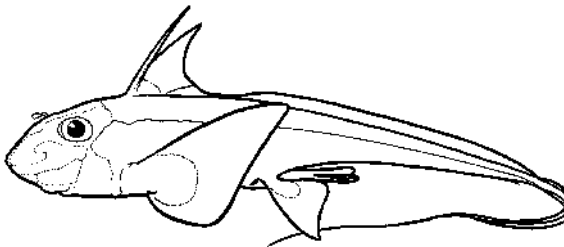


Snout long, fleshy, and pointed, not hooklike; lateral line canals are open grooves; tail diphycercal; anal fin separated from caudal in *Neoharriotta* and joined with it in the other genera. Egg capsule ovoid (pear-like) (typically 15 cm × 6 cm), with ribbed lateral web.

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 semi-circular 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).

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

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

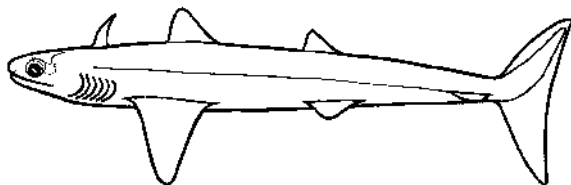
†Infraclass CLADOSELACHIMORPHA

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*), Falcataidae (*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.



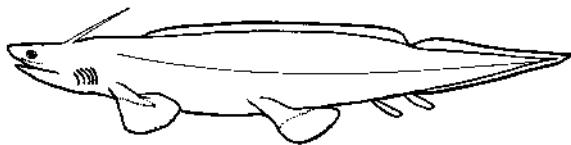
Maximum length about 2 m. Includes the well-known *Cladoselache*.

†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; diphyccercal 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 Phoeodontiformes, 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 pristiphoriforms 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 Squalia, 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 Squalia (= superorder Squalomorphi + subdivision Batoidea)	Superorder Squalia (= 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 strata-graphic 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*, *Pseudodolatias*, *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).

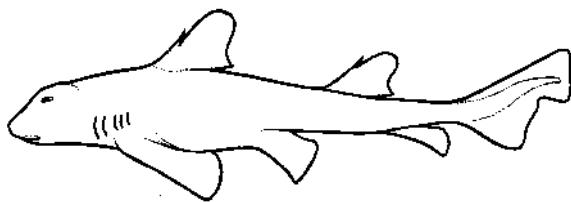
Four orders, 23 families, 74 genera, and 279 species.

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 PARASYLLIIDAE (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 expositum*, most under 0.9 m.

Two genera, *Cirrhoscyllium* (3, South China Sea to Japan) and *Parascyllum* (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 *Hemiscyllum ocellatum*, most under 70 cm.

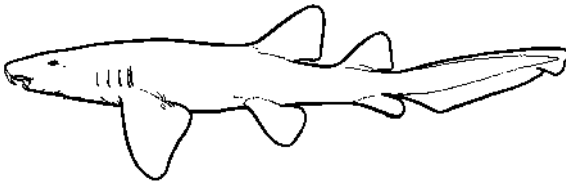
Two genera, *Chiloscyllium* (7) and *Hemiscyllum* (5, primarily western Pacific, the long-tailed carpet sharks), with 12 species (Compagno, 2001, 2005).

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).

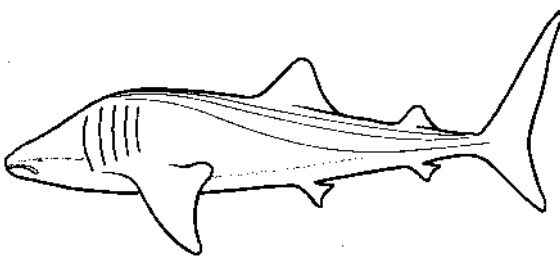


Spiracles small (smaller than the eyes), behind the eyes; eyes lateral on head in *Nebrius*; nostrils with short to moderately long barbels; no lobe and groove around outer edges of nostrils; fourth and fifth gill slits almost overlapping. Vertebrae 135–195.

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).

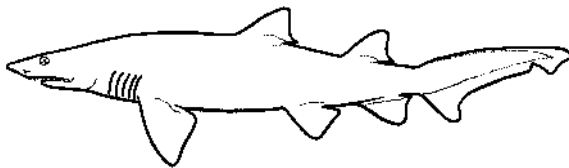
The following fossil taxa, known primarily from teeth, are recognized in Lamniformes by Cappetta (1987).

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

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

Anacoracidae. Lower to Upper Cretaceous. Includes *Pseudocorax* and *Squalicorax*.

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).

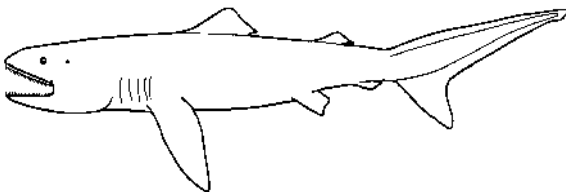
Family PSEUDOCARCHARIIDAE (18)—crocodile sharks. Marine, tropical to subtropical, inshore (rarely) to oceanic and circumglobal (surface to at least 590 m); scattered localities, western Atlantic (Brazil), eastern Atlantic (Cape Verde Islands to South Africa), western Indian (primarily southern Africa), 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 kamoharui*, 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).

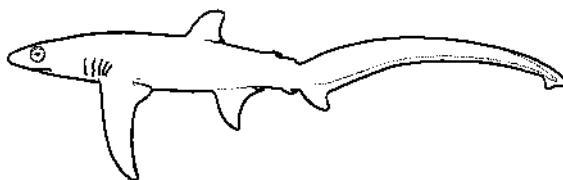


Head elongated, about length of trunk; mouth exceptionally large, terminal; snout short and broadly rounded; gill openings moderately long but not

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 semi-parasitic shark *Isistius brasiliensis*.

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

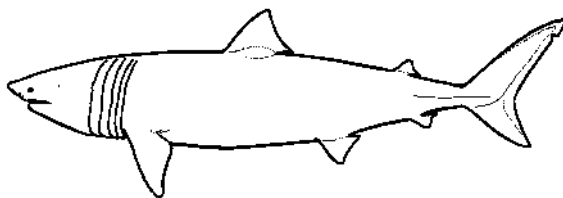
Family ALOPIIDAE (20)—thresher sharks. Marine, tropical to cold temperate, coastal and oceanic (surface—at least 500 m); scattered across Atlantic, Indian, and Pacific.



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).

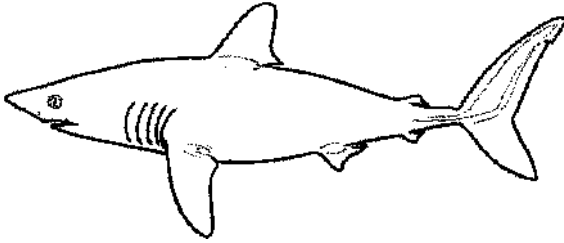
Family CETORHINIDAE (21)—basking sharks. Marine, warm temperate (rarely subtropical) to cool temperate, continental and insular shelves, possibly oceanic (usually in shallow water); Atlantic (including the Mediterranean and western Barents Sea), Indian (only off western Australia), and Pacific.



Gill openings exceptionally large, extending almost to the top of the head; teeth small and numerous; mouth large; eyes small; gill rakers elongate (hair-like), 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.



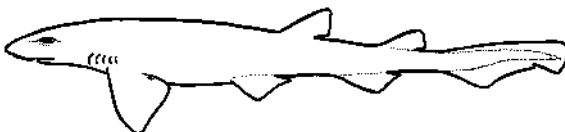
Gill openings large, barely extending onto dorsal surface of head; teeth relatively few and enlarged; gill rakers absent; caudal fin nearly symmetrical and caudal peduncle with strong lateral keel and precaudal pits. Vertebrae 153–197. Maximum length at least 6.0 m, attained in *Carcharodon carcharias* (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), *Atelomyxerus* (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.

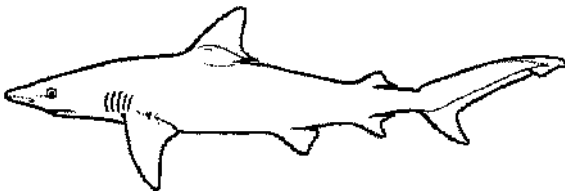
SUBFAMILY GALEORHININAE. Small or barbel-like nasal flaps. *Furgaleus* (1), *Galeorhinus* (1), *Gogolia* (1), *Hemitriakis* (4), *Hypogaleus* (1), and *Iago* (2), with 10 species.

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.



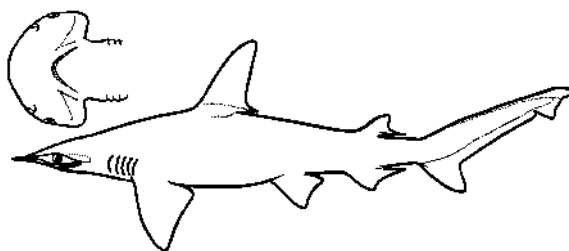
Dorsal fin margin undulated; precaudal pit present; spiracles usually absent; nictitating eyelids internal; intestine with scroll valve, lacking spiral valve. Maximum length at least 7.4 m, attained in *Galeocerdo cuvier*.

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, sphyrnids (hammerhead sharks) were placed in this family because independent evidence based on morphological and molecular data suggested that the Carcharhinidae were not monophyletic unless sphyrnids 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 sphyrnids. Carcharinids and sphyrnids 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 sphyrnids 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.

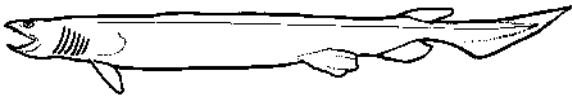
de Carvalho (1996)	Shirai (1996)	Herein
Superorder Notidanoidea	Order Chlamydoselachiformes	Order Hexanchiformes (2)
Order Hexanchiformes (2)	Order Hexanchiformes	
Superorder Echinorhinoidea		
Order Echinorhiniformes	Order Echinorhiniformes	Order Echinorhiniformes
Superorder Squaloidea	Order Dalatiiformes (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 *Notidanoidea* (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).

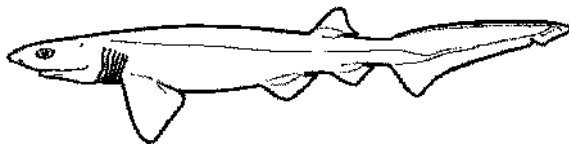
Family CHLAMYDOSELACHIDAE (31)—frill sharks. Marine, continental and insular slopes, occasionally on shelves; scattered in western North Atlantic, eastern Atlantic (Norway to around South Africa), southwestern Indian, western Pacific (Japan to New Zealand), and eastern Pacific (California and Chile).



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.



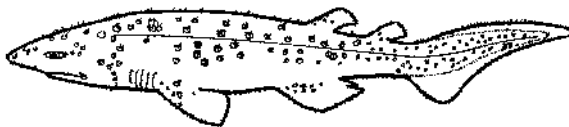
Six or seven gill openings, margin of first gill not continuous across throat; mouth ventral; teeth in upper jaw different from those in lower jaw; lateral-line canal open in *Notorynchus*. Maximum length about 4.7 m, attained in *Hexanchus griseus*.

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.

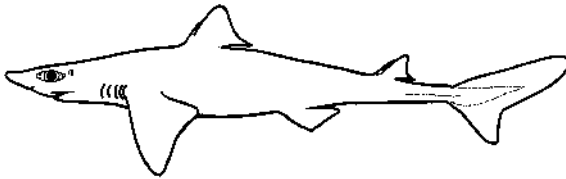
Order SQUALIFORMES (10)—dogfish sharks.

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 undescribed 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, *Centroscyrnus* (2), *Centroselachus* (1), *Proscymnodon* (2), *Scymnodalatias* (4), *Scymnodon* (1), *Somniosus* (including *Rhinoscyrnus*, 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).

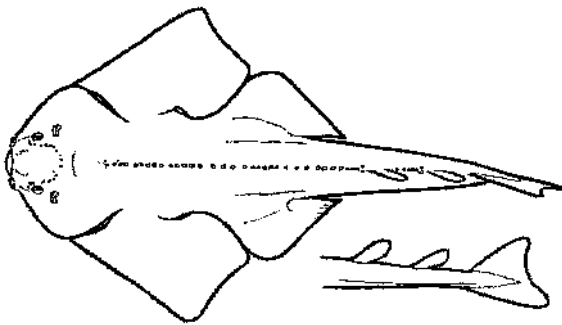
In Nelson (1994), the Etmopteridae, Somniosidae, and Oxynotidae were recognized as subfamilies of the Dalatiidae.

Seven genera, *Dalatias* (1), *Euprotomicroides* (1), *Euprotomiscrus* (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 remaining neoselachians in the present classification). Although this phylogeny is not followed here, *Protospinax* is regarded as sister to the remaining squalomorphs, the squatinids and pristiphorids.

Order SQUATINIFORMES (11)—angel sharks.

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



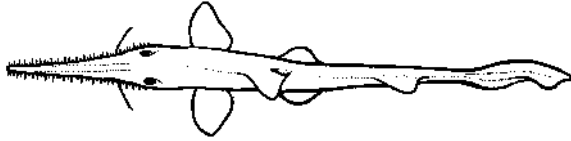
Body raylike; eyes dorsal; two spineless dorsal fins; no anal fin; five gill openings; spiracle large; mouth almost terminal; nostrils terminal with barbels on anterior margin. Maximum length up to 2 m.

Squatina and the remaining euselachians (the pristiphorids 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 pristiphorids and pristids including *Ankistrohynchus*, *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	Platyrrhinidae	Rhinobatidae	Rhinidae
Rhinobatidae	Zanobatidae	Rajidae	Rhynchobatidae
Rajidae	Torpediniformes	Myliobatiformes	Rhinobatidae
Myliobatoidei	Narcinidae	Platyrrhinoidei	Rajidae
Plesiobatidae	Narkidae	Platyrrhinidae	Myliobatiformes
Hexatrygonidae	Hypnidae	Zanobatoidei	Platyrrhinoidei
Dasyatidae	Torpedinidae	Zanobatidae	Platyrrhinidae
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).

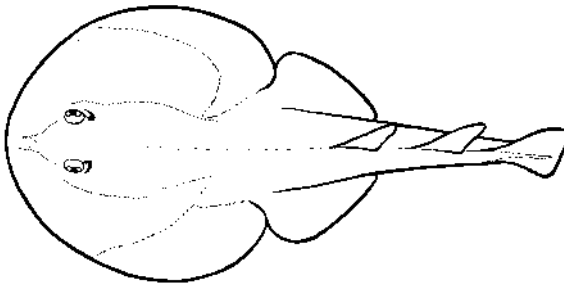
One species, *Hypnos monopterygius* (Compagno, 1999, 2005).

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 shark-like, 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 mid-line 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).

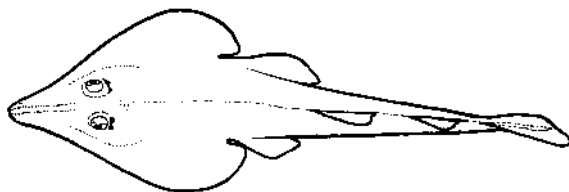
One monotypic genus, *Rhina* (Compagno, 2005; Compagno and Last, 1999).

Family RHYNCHOBATIDAE (46)—wedgfishes. 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.

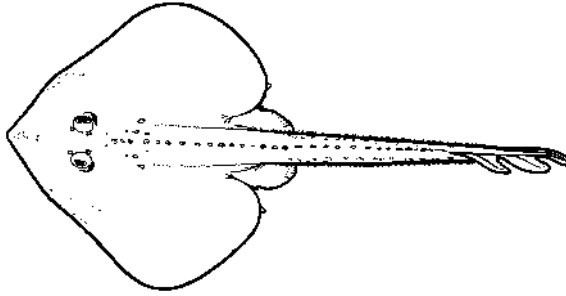


Body intermediate between sharklike and skatelike; tail stout, not definitely marked off from body; two distinct dorsal fins and a caudal fin, the latter not bilobed; origin of first dorsal behind pelvics; denticles over body form a row on midline of back; tail without spine.

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 undescribed 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). Platyrrhinids 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 Platyrrhinoidei

Family PLATYRRHINIDAE (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, *Platyrrhina* (2, the fanrays) and *Platyrrhinoidis* (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 Platyrrhinidae.

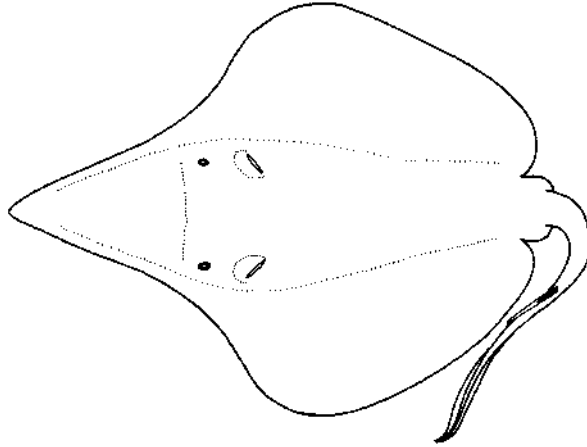
One genus, *Zanobatus*, with possibly two species (Compagno, 1999, 2005).

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 *Trygonopectera* 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

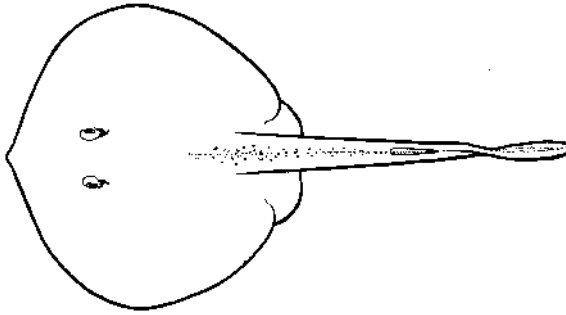
Family PLESIOBATIDAE (52)—deepwater stingrays. Marine; continental and insular slopes, Indo-West Pacific (South Africa to Hawaii).

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.

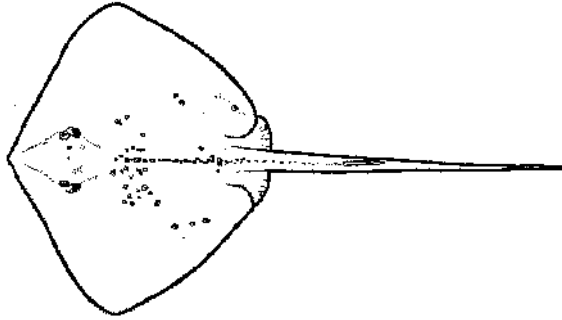
Disc not more than 1.3 times as broad as long; tail slender and about as long as disc length, without dorsal fin but with one or more long, poisonous spines; caudal fin distinct.

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 ampho-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).

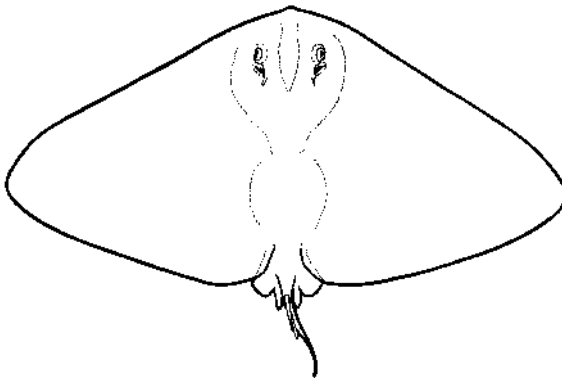
Long, median, anteriorly directed process from the pelvic girdle; angular cartilages present (except *Paratrygon*), within hyomandibular-Meckelian ligament;

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 Cretaceous 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).

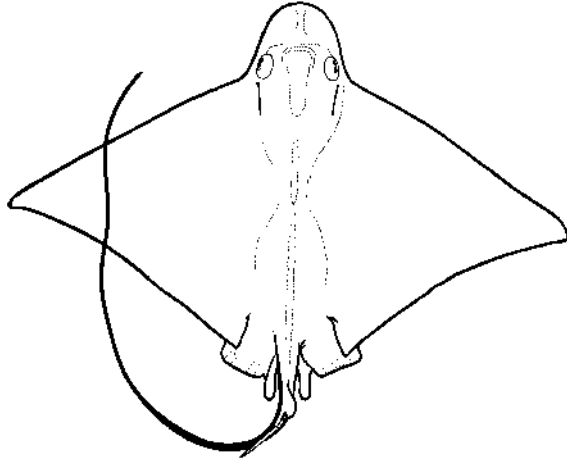
Family GYMNURIDAE (57)—butterfly rays. Marine; tropical to temperate, continental shelves, Atlantic, Indian, and Pacific.



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.

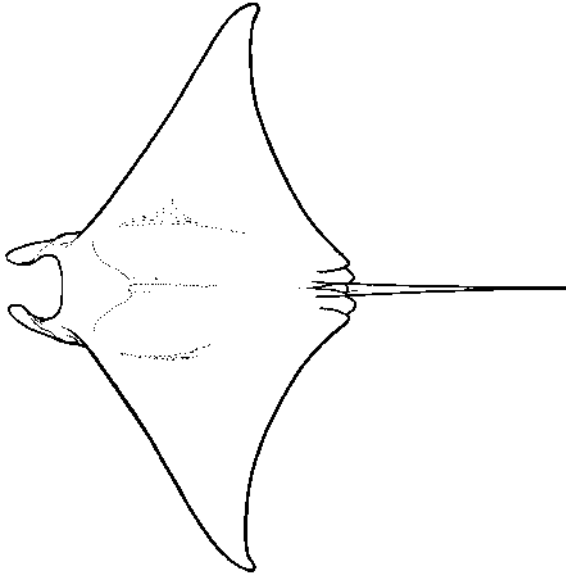
Four genera, *Aetobatus* (3), *Aetomylaeus* (4), *Myliobatis* (at least 11), and *Pteromylaeus* (2), with at least 20 species (Compagno, 1999).

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 lagenae; 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.

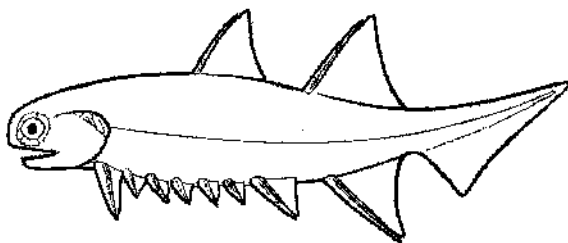
The acanthodians, with their large eyes, terminal or near terminal mouth, and small nasal capsules, mostly were mid- and surface-water feeders. Many were microphagous while others, especially the ischnacanthiforms, ate fishes and invertebrates. Acanthodians are known from both freshwater and marine environments; 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 *Lupopsyrroides*, 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

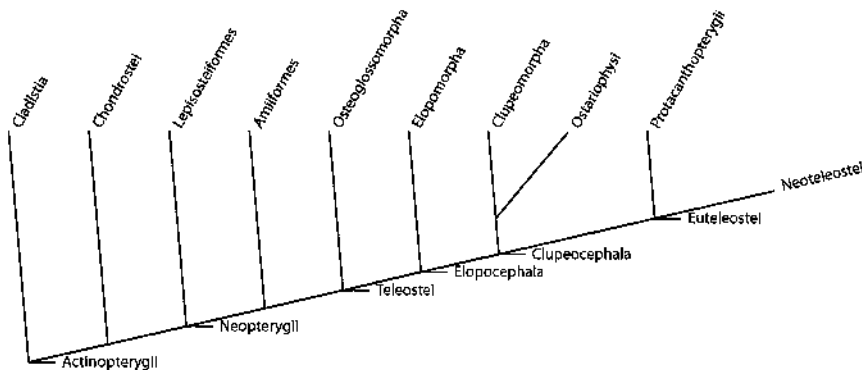
Subclass Osteolepimorpha

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 *Ligulalepis*, 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 chondrosteian 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 *Polliia*, *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

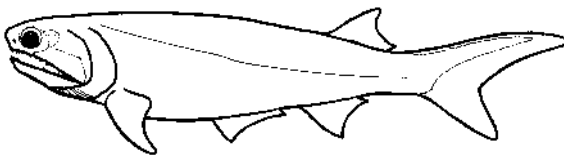
Interopercle absent; premaxilla and maxilla rigidly attached to the ectopterygoid and dermopalatine; spiracle usually present; myodome absent in the most primitive taxa.

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 remaining taxa, by perhaps i) Cheirolepididae, ii) *Mimia* and *Moythomasia*, iii) *Osoioichthys* 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 chondrosteian family not otherwise classified here is Haplolepididae (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 chondrosteian level of organization to the holostean level.

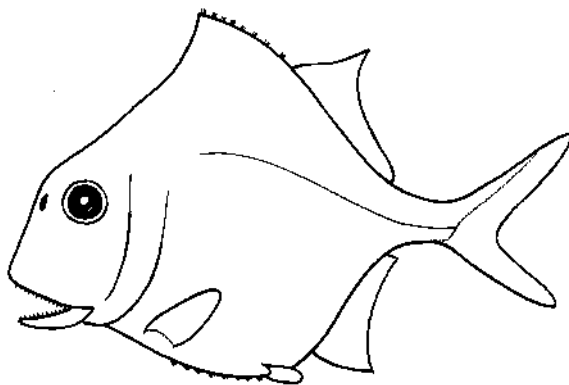
Coccolepis. incertae sedis. The morphology of *Coccolepis bucklandi* was described by Hilton et al. (2004).

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 plate-like bones; single external naris surrounded by a distinctive “premaxilla,” rostral, nasal, and adnasal bones. Triassic and Lower Jurassic, freshwater.

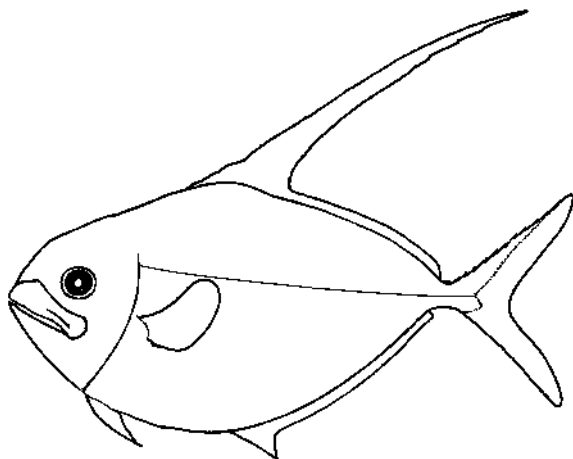
About 15 genera, herein treated as belonging to one family, Redfieldiidae (e.g., *Brookvalia*, *Dictyopyge*, *Helichthys*, *Redfieldius*, and *Schizurichthys*).

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 diphyccercal 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., *Acidorrhynchus* (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.

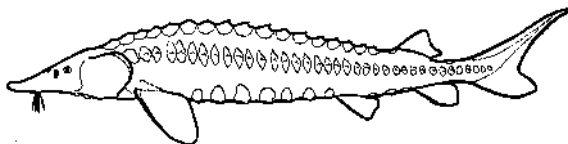
Extant representatives in two families with six genera and 27 species (Grande and Bemis, 1996; Bemis et al., 1997).

†**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 *Protoscapirhynchus*, 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.

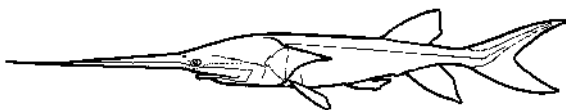
Pseudoscaphirhynchus. Aral Sea basin. Caudal peduncle short, slightly depressed, and not completely armored. Three species.

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.

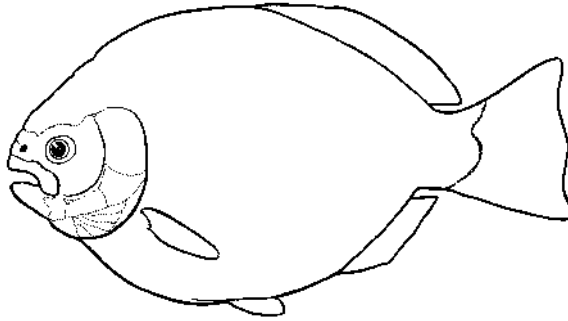
There are many neopterygian taxa of uncertain position. For example, Nursall and Capasso (2004) described a fascinating fossil from the upper Middle Cretaceous of Lebanon (*Gebrayelichthys uyenoi*, the Archangelfish). It is a highly compressed fish placed in its own family, Gebrayelichthyidae.

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).

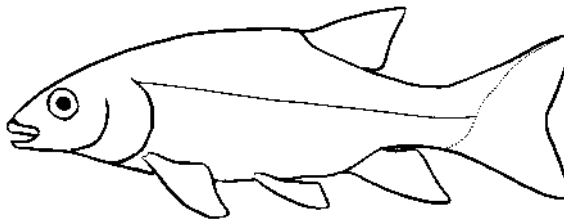
†**Order SEMIONOTIFORMES.** Extant gar and the fossil Semionotidae are often recognized in the same order, either under the ordinal name Lepisosteiformes or Semionotiformes (e.g., Nelson, 1976, 1994). In contrast, I placed them in separate orders in Nelson (1984) and do so now following the scholarly 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 LEPISTOSTEIFORMES (19)—gars.

Family LEPISTOSTEIDAE (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*.

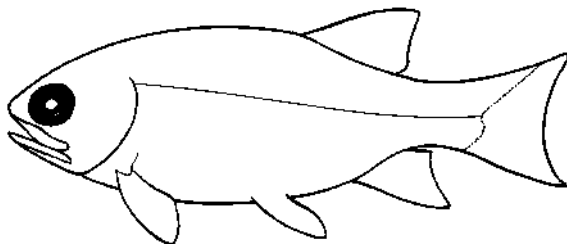
The northernmost limit is reached by *Lepisosteus osseus* in southern Quebec; the southernmost limit is reached by *A. tropicus* in Costa Rica. This is also the only species that ranges to Pacific slope drainages (from southern Mexico to Honduras). *Atractosteus tristoechus* is known to enter marine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

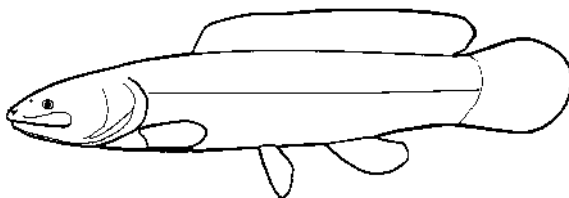
The families recognized in recent literature are Gibbodontidae, Gyrodontidae (e.g., *Gyrodus*), Mesturidae, Brembodontidae, Pycnodontidae (with several subfamilies such as Nursalliinae and Proscinetinae), Coccodontidae (with *Coccodus* the only benthic member of the order), Hadrodontidae, and Trewavasiidae (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.

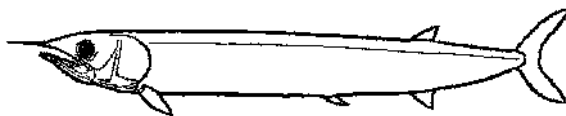


Caudal fin abbreviate heterocercal; dorsal fin base long, with about 48 rays; large median gular plate and 10–13 branchiostegal rays; swim bladder can function as a lung; no pyloric caeca. Maximum length about 90 cm.

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*.

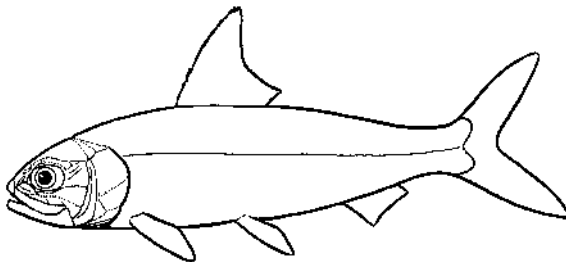
In the following classification, I will give several groups of primitive fossil teleosts first. These are followed by the four lineages, including all living teleosts (collectively termed the Teleocephala by de Pinna, 1996a), given as subdivisions, the Osteoglossomorpha, Elopomorpha, Ostarioclupeomorpha

(= 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.

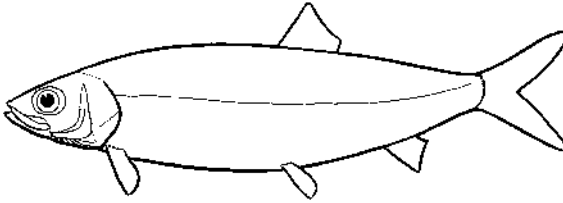
†**Order PHOLIDOPHORIFORMES.** Position uncertain. Probably not monophyletic, possibly polyphyletic (e.g., Arratia, 2004, and reference to her 2000 study). Some members of this group may have shared a common ancestry with the leptolepidiforms in the Triassic and, independently, the elopomorph and osteoglossomorph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

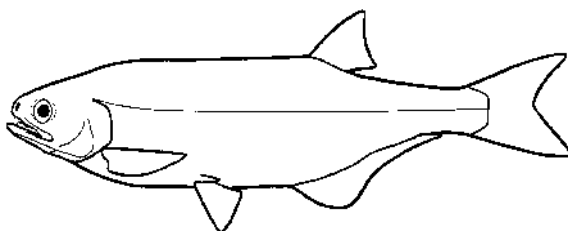
†**Order LYCOPERIFORMES.** *Incertae sedis*.

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

Includes the well-known genus *Lycopera*. Li and Wilson (1996), on the basis of four synapomorphies, regarded the Lycoperidae 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 *Plesioleptera* 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 urodormals, 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 Osteoglossoidi, 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.

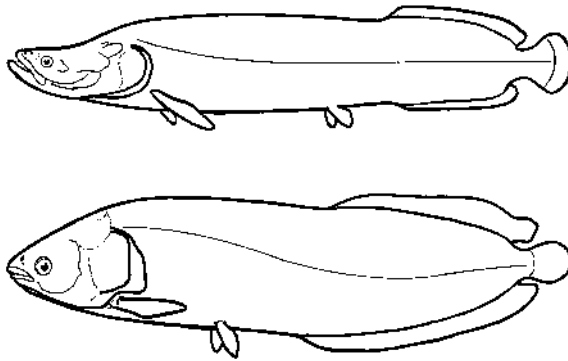
Family OSTEOGLOSSIDAE (65)—osteoglossids or bonytongues. Freshwater; circumtropical, South America, Africa, and Southeast Asia to northern Australia.

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.

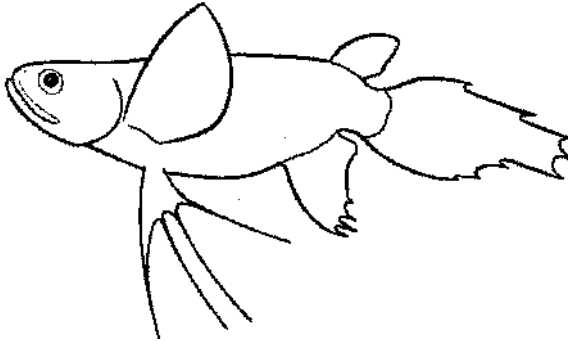
SUBFAMILY OSTEOGLOSSINAE. *Osteoglossum* and *Scleropages* have mandibular barbels present; 10–17 branchiostegal rays.

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



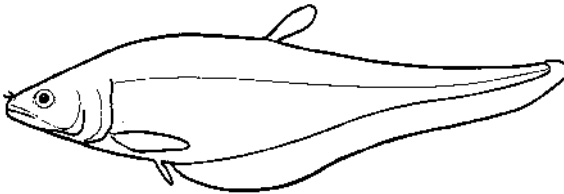
Scleropages jardinii of northern Australia and New Guinea, *S. leichardti* of the Fitzroy River in Queensland, Australia, and *S. formosus* of Southeast Asia

(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).

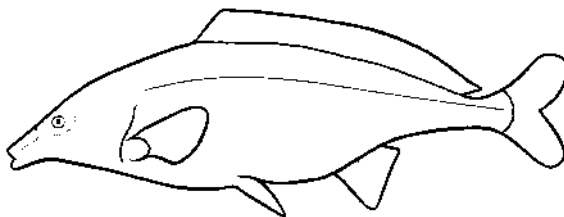
Chitala. Craniodorsal profile concave (vs. convex, straight, or slightly concave). Formerly ranked as a subgenus of *Notopterus*. Four species, Pakistan and India to Sumatra and Borneo.

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.



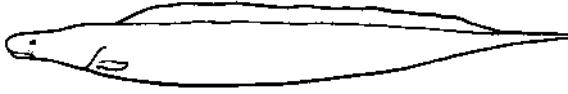
Anal, caudal, and pelvic fins present; caudal peduncle narrow; caudal fin deeply forked; teeth present on parasphenoid and tongue; 6–8 branchiostegal rays; dorsal fin rays 12–91; anal fin rays 20–70; dorsal and anal fins usually opposite and placed back on body; vertebrae 37–64.

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 Elopoccephala. 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.

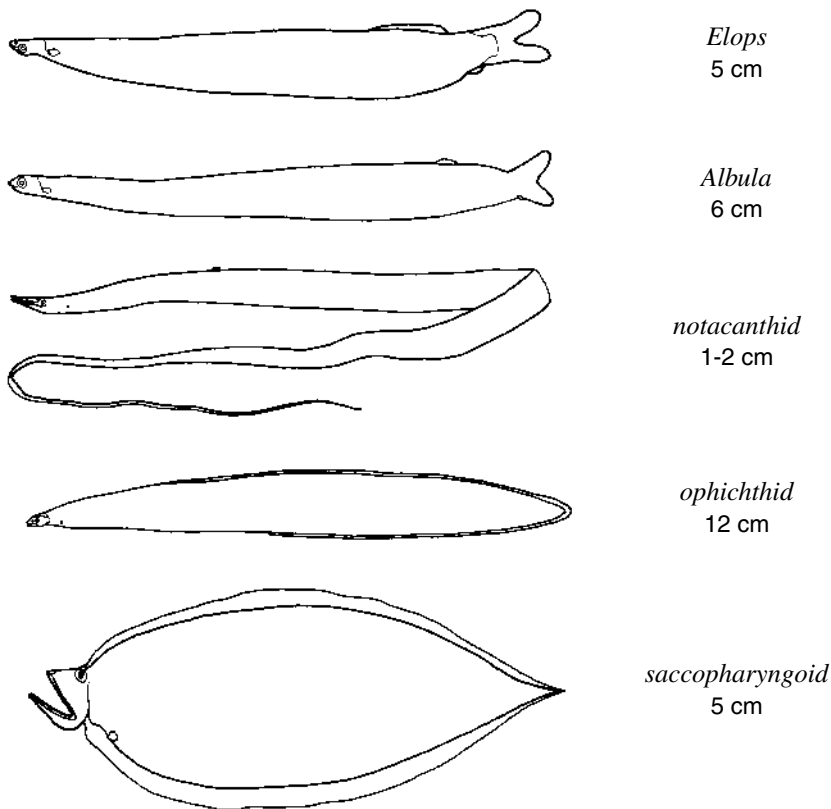
Body deep; dorsal and anal fins with long base; pelvic fins and skeleton absent; pectoral fins attached low on body; caudal fin forked; teeth in jaws absent; premaxilla protractile and forming border of upper jaw; supramaxilla present; supraorbitals absent.

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 nucleotide 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).

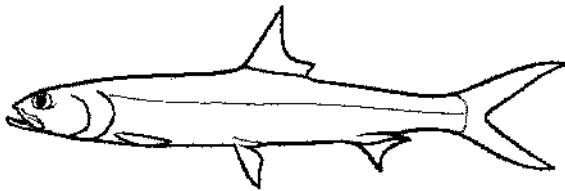
Of the fossil taxa, *Eichstaettia* and the possibly related *Leptolepides* (Arratia, 1991) may be the most primitive known elopomorph fossils. Other fossil elopomorphs not mentioned below include Anaethalionidae with *Anaethalion* (oldest record is Late Jurassic), *Davichthys*, *Lebonichthys*, and *Brannerion* 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.

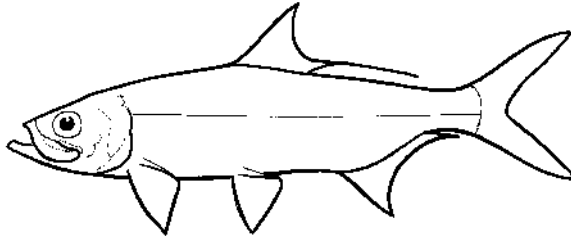


Body rounded (little compressed); mouth terminal; pseudobranchiae large; branchiostegal rays 27–35; dorsal fin rays usually 20–25, the last ray not elongate; anal fin rays usually 13–18; pelvic rays usually 12–16, no conus arteriosus;

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.

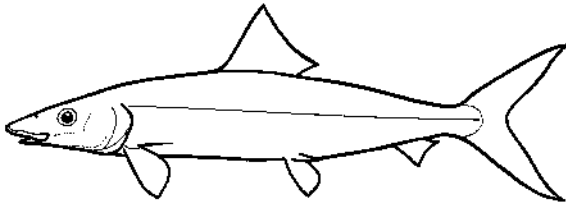
Suborder Albuloidei. Body herringlike; gular plate reduced to a thin median splint or absent; pelvic rays 10–14; mouth bordered primarily by the premaxilla (maxilla toothed only in Pterothrissinae); upper jaw not extending as far

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*.

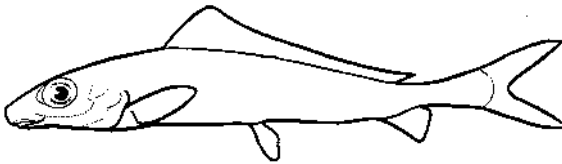
SUBFAMILY ALBULINAE. Most tropical seas (rarely brackish and freshwater).



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

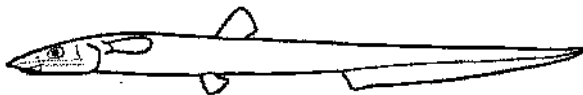
by a membrane); anal fin base long and merged with what remains of the caudal fin; caudal fin skeleton reduced or absent; tail easily regenerated when lost (analogous to loss of tail in lizards?); branchiostegal rays 5–23; swim bladder present. Some have photophores.

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.



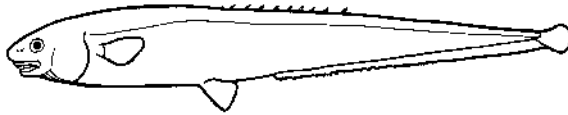
One species, *Lipogenys gilli*, deep-sea, in the western North Atlantic and off Japan (Nakabo et al., 1991).

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 Synphobranchidae); 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 Synphobranchidae) (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.

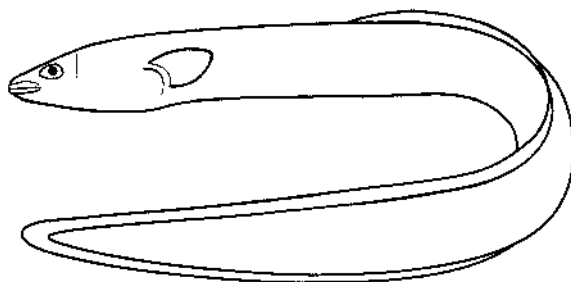
The leptocephalus larva of anguilliforms differs from that of elopiforms and notacanthiforms (but not saccopharyngiforms) in having the caudal fin small and round, continuous with the dorsal and anal fins (note: the many-rayed dorsal and anal fins are usually very inconspicuous) (as with notacanthiforms 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.

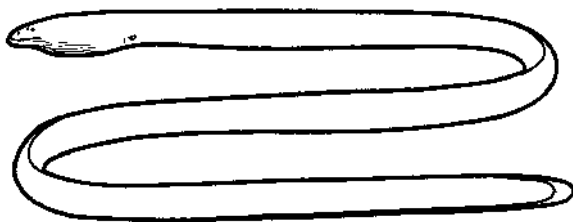
One genus, *Anguilla*, with 15 species (D. G. Smith, in Böhlke, 1989:24–47).

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.



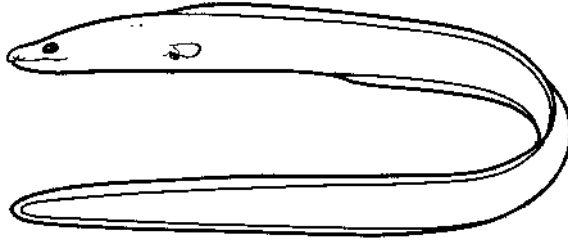
Body extremely elongate; scales absent; gill openings low on body; dorsal and anal fins reduced to low folds, posteriorly; pectoral fin small to feeble; eyes small and covered with skin; vertebrae 98–180. Many of their features are adaptations to their fossorial life (they burrow head first). *Moringua*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

Nine families, 112 genera, and about 555 species.

Family SYNAPHOBANCHIDAE (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.

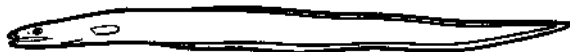
Ten genera and about 32 species (C. H. Robins and C. R. Robins in Böhlke, 1989:207–53; Chen and Mok, 1995; Sulak and Shcherbachev, 1997).

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 *Thermobiotus*; head shape depressed and relatively rounded; some teeth relatively long.



Seven genera, *Atractodenchelys*, *Dysomma*, *Dysommima*, *Ilyophis*, *Linkenchelys*, *Meadia*, and *Thermobiotus*.

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.

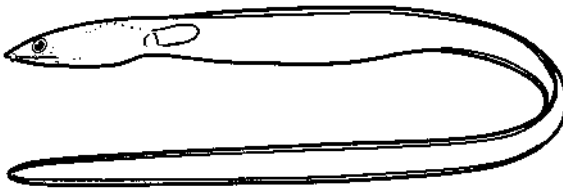
Ophichthids, with their stiffened tail, burrow tail first; they are thought to move through the sediment equally well going forward or backward (unlike the head-burrowing heterenchelyids and moringuids). Some members are especially sharp-tailed, an adaptation for rapid burrowing.

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.

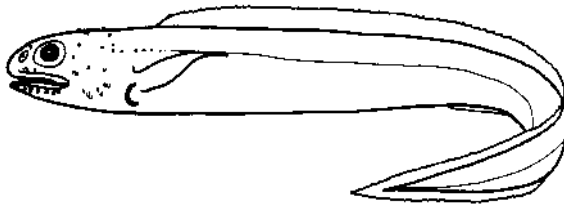


Forty-one genera—e.g., *Apterichtus* (synonym *Verma*), *Bascanichthys*, *Caecula*, *Callechelys*, *Cirrhimuraena*, *Dalophis* (freshwater in Africa), *Echelus*, *Echiophis*,

Ethadophis, *Lamnostoma* (with four western Pacific species generally found in freshwater), *Letharchus*, *Myrichthys*, *Mystriophis*, *Ophichthus*, *Phaenomonas*, *Pisodonophis*, and *Yirkala*

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.

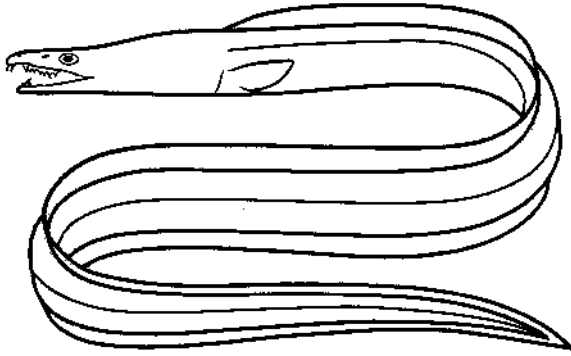
Series of parallel striations on the head forming part of a sensory system; branchial region not expanded, with body behind gill opening somewhat compressed; pectoral fins present; dorsal fin origin behind tip of pectoral fin; anus well behind midlength; lateral line virtually complete; vertebrae 125–160;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

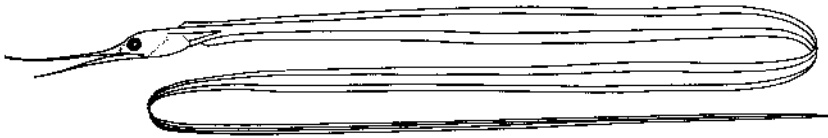
Teeth well developed, especially on the vomer; pectorals well developed; eyes large and covered with skin; dorsal fin origin over or slightly before pectoral base; lateral line conspicuous; vertebrae 120–216.

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).

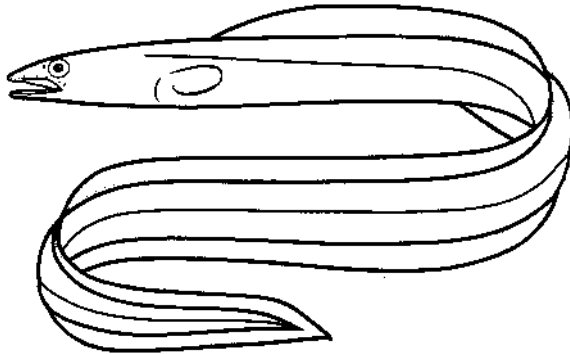
SUBFAMILY HETEROCONGRINAE (GARDEN EELS). Dorsal and anal fin rays unsegmented; pectoral fin minute or absent; body very elongate and slender; mouth short and lower jaw projecting beyond upper. Garden eels have the interesting habit of hovering above their sand burrows in large colonies (giving the appearance 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.

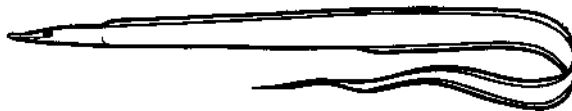
About five genera, *Ariosoma*, *Bathymyrus*, *Chiloconger*, *Parabathymyrus*, and *Paraconger*.

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 congrid.

Six genera, *Facciolella*, *Hoplunnis*, *Nettastoma*, *Nettenchelys*, *Saurenychelys*, 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.

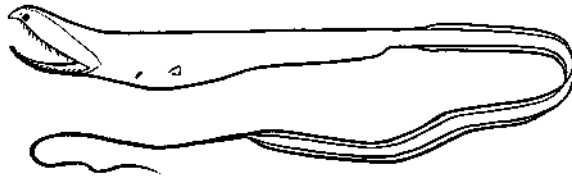
Two monotypic genera—*Cyema* (body black; long, nonocclusible upper and lower jaws) and *Neocyema* (body bright red; pectoral skeleton absent, although a rayless fin is present—probably neotenic).

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).

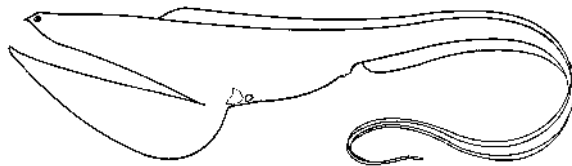
Family SACCOPHARYNGIDAE (90)—swallowers. Marine; Atlantic, Indian, and Pacific.



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 about 10 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).