ASSEMBLING THE TREE OF LIFE

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Gnathostome Fishes

Gnathostomata are a species-rich assemblage that, with the exclusion of the Petromyzontiformes (lampreys, 45 spp.), represents all living members of Vertebrata. Gnathostomes are most notably characterized by the possession of endoskeletal jaws primitively formed of dorsal palatoquadrate and ventral Meckelian cartilages articulating at a mandibular joint. Our task here is to provide a review of a large (paraphyletic) subset of gnathostome diversity—an artificial grouping often referred to as the "jawed fishes": chondrichthyans, "piscine sarcopterygians," and actinopterygians. We treat all living jawed vertebrates with the exclusion of most Sarcopterygii—the tetrapods—since they are discussed in other chapters. After a review of the chondrichthyans or cartilaginous fishes and a brief summary of the so-called "piscine sarcopterygians," we focus our contribution on the largest and most diverse of the three groups, the Actinopterygii, or rayfin fishes.

As a guide to the chapter, figure 24.1 presents, in broad summary, our understanding of the interrelationships among extant gnathostome lineages and indicates their past and present numbers (with counts of nominal families indicated by column width through time). Much of the stratigraphic information for osteichthyans is from Patterson (1993, 1994), and that for chondrichthyans is mostly from Cappetta et al. (1993).

Chondrichthyes (Cartilaginous Fishes)

Chondrichthyans (sharks, rays, and chimaeras) include approximately 1000 living species (Compagno 1999), several dozen of which remain undescribed. Recent sharks and rays are further united in the subclass Elasmobranchii (975+ spp.), whereas the chimaeras form the subclass Holocephali (35+ spp.). All chimaeras are marine; as are most sharks and rays, but about 15 living elasmobranch species are euryhaline, and some 30 are permanently restricted to freshwater (Compagno and Cook 1995).

Chondrichthyans are characterized by perichondral prismatic calcification; the prisms form a honeycomb-like mosaic that covers most of the cartilaginous endoskeleton (Schaeffer 1981, Janvier 1996). Paired male intromittent organs derived from pelvic radials (claspers) are probably another chondrichthyan synapomorphy, although they are unknown in some early fossil forms (e.g., the Devonian *Cladoselache* and Carboniferous *Caseodus*), but all recent chondrichthyans and most articulated fossil taxa have them (Zangerl 1981). Earlier notions that sharks, rays, and chimaeras evolved independently from placoderm ancestors (Stensiö 1925, Holmgren 1942, Ørvig 1960, 1962; Patterson 1965), culminating in the Elasmobranchiomorphi (placoderms + chondrichthyans) of Stensiö (e.g., 1958, 1963, 1969) and Jarvik (e.g., 1960, 1977, 1980), have not survived close inspection (e.g., Compagno 1973, Miles and Young 1977); chondrichthyan monophyly is no longer seriously challenged (Schaeffer 1981, Maisey 1984).

Sharks, rays, and chimaeras form an ancient lineage. The earliest putative remains are dermal denticles from the Late Ordovician of Colorado [some 450 million years ago (Mya)]; the first braincase is from the Early Devonian of South Af-

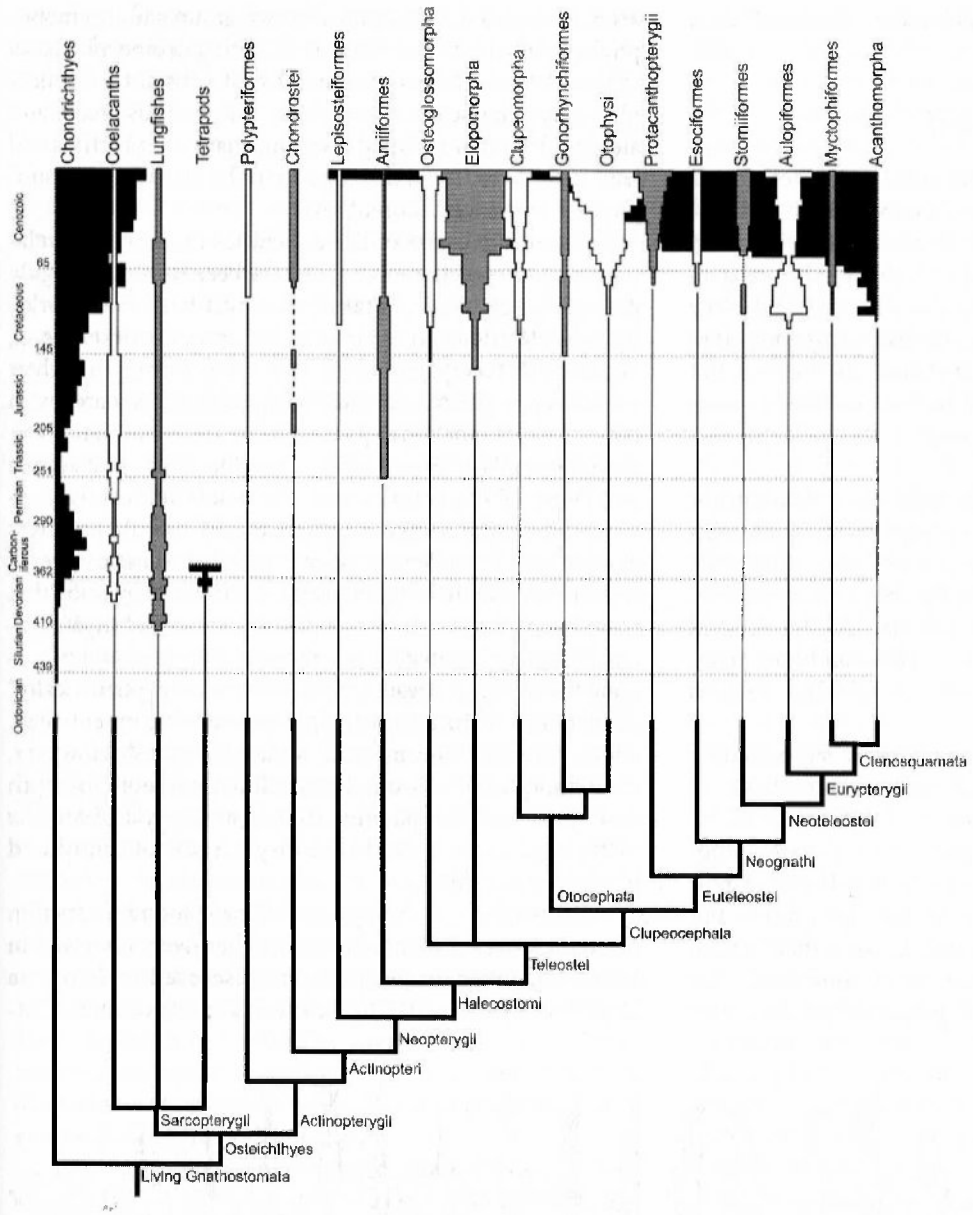

Figure 24.1. Current estimate of relationships among extant gnathostome lineages. Past and present counts of nominal families are indicated by column width through time (tetrapod diversity truncated, chondrichthyan diversity truncated to the left, and acanthomorph diversity truncated to the right). Stratigraphic information for Osteichthyes is taken from Patterson (1993, 1994) but with new data for Polypteriformes from Dutheil (1999) and for Otophysi from Filleul and Maisey (in press). Data for Chondrichthyes are from Cappatta et al. (1993), with complementary information from Janvier (1996) and other sources. For practical reasons, familial diversity is charted and this does not necessarily reflect known species diversity.

rica some 60 million years later (Maisey and Anderson 2001). The divergence between elasmobranchs and holocephalans is also relatively old, because isolated holocephalan tooth plates are known from the Late Devonian (Zangerl 1981, Stahl 1999), and articulated specimens from the Early Carboniferous (320 Mya; Lund 1990, Janvier 1996). A few of the earliest known fossil sharks may be basal to the elasmobranch–holocephalan dichotomy, such as *Pucapampella* from the Devonian of Bolivia (Maisey 2001), but much work remains to be done in early chondrichthyan phylogeny (Coates and Sequeira 1998). Sharks were remarkably diverse morphologically and ecologically during much of the Paleozoic, considerably more so than early bony fishes. Some 32 families existed during the Carboniferous, but many of these went extinct before the end of the Permian (Cappetta et al. 1993; fig. 24.1).

The entrenched notion that sharks are primitive or ancestral vertebrates because of their antiquity, "generalized design," and lack of endochondral (cellular) bone (e.g., Dean 1895, Woodward 1898) is contradicted by the theory that bone may have been lost in sharks, because it is widely distributed among stem gnathostomes (Stensiö 1925, Maisey 1986). Furthermore, acellular bone is present in the dorsal spine-brush complex of an early shark (*Stethacanthus*; Coates et al. 1999) and also in the teeth, denticles, and vertebrae of extant chondrichthyans (Kemp and Westrin 1979, Hall 1982, Janvier 1996), supporting the assertion that sharks evolved from bony ancestors. Highly complex, derived attributes of elasmobranchs, such as their semicircular canal arrangement (Schaeffer 1981), internal fertilization, and formation of maternal–fetal connections ("placentas" of some living forms; Hamlett and Koob 1999),

reveal, in fact, that sharks are much more "advanced" than previously thought.

Elasmobranchs (Sharks and Rays)

Modern sharks and rays share with certain Mesozoic fossils (e.g., *Palaeospinax*, *Synechodus*) calcified vertebrae and specialized enameloid in their teeth (both secondarily lost in some living forms) and are united with them in Neoselachii (Schaeffer 1967, 1981, Schaeffer and Williams 1977, Maisey 1984). Most of modern elasmobranch diversity originated in the Late Cretaceous to Early Tertiary (some 55–90 Mya), but several extant lineages have fossil members, usually represented by isolated teeth, dating back to the Early Jurassic (some 200 Mya).

Recent phylogenetic studies have recognized two major lineages of living elasmobranchs, Galeomorphi (galeomorph sharks) and Squalomorphi (squalomorphs or squaleans; Shirai 1992, 1996, Carvalho 1996; fig. 24.2). These studies, however, differ in the composition of Hexanchiformes and Squaliformes, and in relation to the coding and interpretation of many features; the tree adopted here (fig. 24.2) is modified from Carvalho (1996).

The phylogeny in figure 24.2 is the most supported by morphological characters, but an alternative scheme has been proposed on the basis of the nuclear *RAG-1* gene (J. G. Maisey, pers. comm.), in which modern sharks are monophyletic without the rays (an "all-shark" hypothesis). Stratigraphic data are slightly at odds with both hypotheses, but more so with the morphological one, because there are no Early Jurassic squaloids, pristiophoroids, or squatinoids. But lack of stratigraphic harmony will persist unless these taxa are demonstrated to comprise a crown group within a monophyletic "all-shark" collective (i.e., with galeomorphs basal to them). Nonetheless, dozens of well-substantiated morphological characters successively link various shark and all batoid groups in Squalomorphi, many of which would have to be overturned if sharks are to be considered monophyletic to the exclusion of rays.

Historically, some of the difficulties in discerning relationships among elasmobranchs have been due to the highly derived design of certain taxa (e.g., angelsharks, sawsharks, batoids, electric rays), which has led several workers (e.g., Regan 1906, Compagno 1973, 1977) to isolate them in their own lineages, ignoring their homologous features shared with other elasmobranch groups (Carvalho 1996). Elevated levels of homoplasy (Shirai 1992, Carvalho 1996, McEachran and Dunn 1998), coupled with the lack of dermal ossifications (a plentiful source of systematically useful characters in bony fishes), hinders the recovery of phylogenetic patterns within elasmobranchs. Moreover, the (erroneous) notion that there is nothing left to accomplish in chondrichthyan systematics is unfortunately common. In fact, the situation is quite the contrary, because many taxa are only "phenetically" defined and require rigorous phylogenetic treatment (e.g., within Carcharhiniformes and Myliobatiformes). However, many morphological complexes still require more in-depth descriptive and comparative study (in the style of Miyake 1988, Miyake et al. 1992) before they can be confidently used in phylogenetic analyses.

The general morphology, physiology, and reproduction of extant sharks and rays are comprehensively reviewed in Hamlett (1999). Fossil forms are discussed in Cappetta (1987) and Janvier (1996). Below is a brief account of ex-

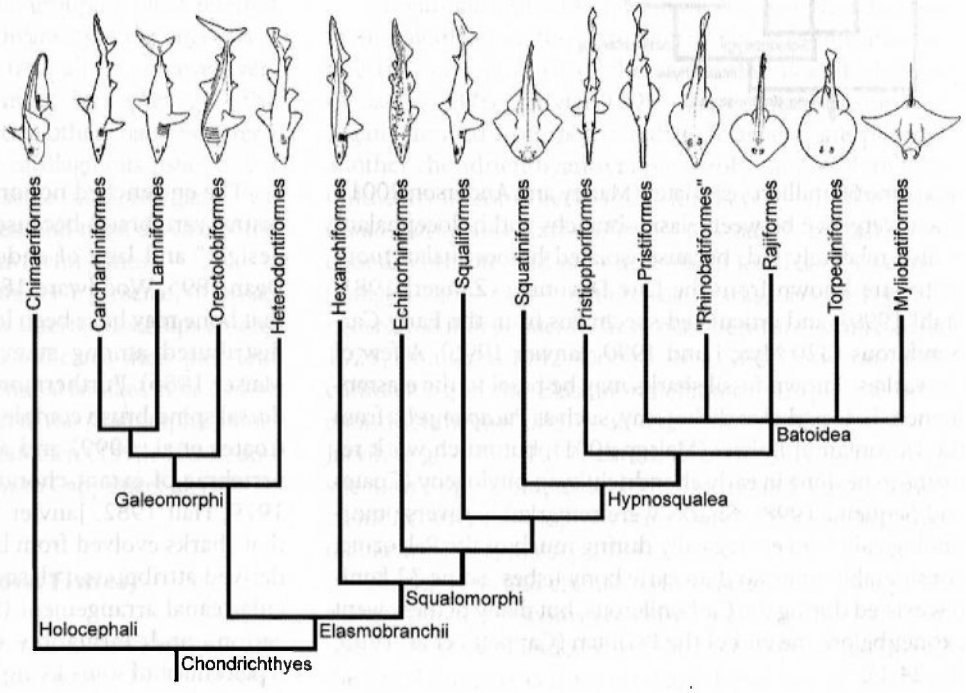

Figure 24.2. Intrarelationships of extant chondrichthyan lineages based mostly on Carvalho (1996). Relationships among rays (Batoidea) are left unresolved, with guitarfishes (Rhinobatiformes) in quotation marks because the group is probably not monophyletic (see McEachran et al. 1996).

tant elasmobranch orders; their monophyly ranges from the relatively well established (Orectolobiformes) to the poorly defined (Squaliformes; Compagno 1973, 1977, Shirai 1996, Carvalho 1996).

Galeomorph sharks encompass four orders (fig. 24.2): Heterodontiformes (bullhead sharks), Orectolobiformes (carpet sharks), Lamniformes (mackerel sharks), and Carcharhiniformes (ground sharks). Galeomorphs have various specializations (Compagno 1973, 1977), such as the proximity between the hyomandibular fossa and the orbit on the neurocranium, and are the dominant sharks of shallow and epipelagic waters worldwide (Compagno 1984b, 1988, 2001).

The two most basal galeomorph orders are primarily benthic, inshore sharks. Bullheads (*Heterodontus*, eight spp.) are distributed in tropical and warm-temperate seas of the western and eastern Pacific Ocean and western Indian Ocean (Compagno 2001). *Heterodontus* has a unique dentition, composed of both clutching and grinding teeth, and is oviparous. It was once believed to be closely related to more primitive Mesozoic hybodont sharks (which also had dorsal fin spines) and therefore regarded as a living relic (e.g., Woodward 1889, Smith 1942), but its ancestry with modern (galeomorph) sharks is strongly corroborated (Maisey 1982). Orectolobiforms (14 genera, 32+ spp.) are among the most colorful elasmobranchs, occurring in tropical to warm-temperate shallow waters; they are most diverse in the Indo-West Pacific region but occur worldwide. Species are aplacentally viviparous or oviparous. One orectolobiform, the planktophagous whale shark (*Rhincodon typus*), is the largest known fish species, reaching 15 m in length. Derived characters of carpet sharks include their complete oronasal grooves and arrangement of cranial muscles (Dingerkus 1986, Goto 2001). Their taxonomy is reviewed in Compagno (2001), and their intrarelationships in Dingerkus (1986) and Goto (2001). An alternative view recognizes bullheads and carpet sharks as sister groups (Compagno 1973; fig. 24.2).

From a systematic perspective, Lamniformes (10 genera, 15 spp.) contain some of the best-known sharks, characterized by their "lamniform tooth pattern" (Compagno 1990, 2001). Although their low modern-day diversity pales compared with the numerous Cretaceous and Tertiary species described from isolated teeth (Cappetta 1987), this order contains some of the most notorious sharks, such as the great white (Klimley and Ainley 1997), its gigantic fossil cousin *Carcharodon megalodon* (Gottfried et al. 1996), the megamouth (now known from some 15 occurrences worldwide; Yano et al. 1997), and the filter-feeding basking shark. Lamniforms are yolk-sac viviparous, and adelphophagy (embryos consuming each other in utero) and oophagy (embryos eating uterine eggs) have been documented in some species (Gilmore 1993). Molecular data sets (Naylor et al. 1997, Morrissey et al. 1997) are at odds with morphological ones (and with each other), indicating that the jury is still out in relation to the evolutionary history of lamniform genera.

Carcharhiniformes (48 genera, 216+ spp.) are by far the largest order of sharks, containing more than half of all living species, and about half of all shark genera (Compagno 1984b). Carcharhiniforms have specialized secondary lower eyelids (nictitating eyelids), as well as unique clasper skeletons (Compagno 1988). Species are oviparous (Scyliorhinidae) or viviparous, with or without the development of a yolk-sac placenta (Hamlett and Koob 1999). Ground sharks range from sluggish, bottom-dwelling catsharks (Scyliorhinidae, the largest shark family) to epipelagic, streamlined, and active requiem sharks (Carcharhinidae), which includes some of the most common and economically important species (e.g., blue and tiger sharks, *Carcharhinus* spp.). Hammerhead sharks (Sphyrnidae) are morphologically very distinctive (Nakaya 1995) and capable of complex behavioral patterns (e.g., Myrberg and Gruber 1974). Some ground sharks may be restricted to freshwater (*Glyphis* spp.), and the bull shark, *Carcharhinus leucas*, penetrates more than 4000 km up the Amazon River, reaching Peru. New species have been described in recent years, particularly of catsharks (e.g., Nakaya and Séret 1999, Last 1999), and additional new species await formal description (Last and Stevens 1994). Phylogenetic relationships among ground sharks requires further study (Naylor 1992), which may eventually result in the merging of several currently monotypic genera and some of the families. Compagno (1988) presents a comprehensive review of the classification and morphology of Carcharhiniformes.

Squalomorphs (equivalent to the Squalea of Shirai 1992) are a very diverse and morphologically heterogeneous group that includes the six- and seven-gill sharks (Hexanchiformes), bramble sharks (Echinorhiniformes), dogfishes and allies (Squaliformes), angelsharks (Squatiniformes), sawsharks (Pristiophoriformes), and rays (Batoidea; fig. 24.2). These taxa share complete precaudal hemal arches in the tail region, among many other features (Shirai, 1992, 1996, Carvalho 1996). Many previous authors defended similar arrangements for the squalomorphs, but usually excluded one group or another (e.g., Woodward 1889, White 1937, Glickman 1967, Maisey 1980). The most dramatic evolutionary transition among elasmobranchs has taken place within the squalomorphs—the evolution of rays from sharklike ancestors, which probably took place in the Early Jurassic (some 200 Mya). *Protospinax*, from the Late Jurassic (150 Mya) Solnhofen limestones of Germany, is an early descendent of the shark–ray transition because it is the most basal hypnosqualean (fig. 24.2), sister group to the node uniting angelsharks, sawsharks, and batoids, and has features intermediate between sharks and rays (Carvalho and Maisey 1996).

Basal squalomorph lineages are relatively depauperate; hexanchiforms (four genera, five spp.) and bramble sharks (*Echinorhinus*, two spp.) are mostly deep-water inhabitants of the continental slopes but occasionally venture into shallow water. All species are aplacentally viviparous. Hexanchiforms have a remarkable longevity; fossil skeletons date from

the Late Jurassic. They are united by several derived characters, such as an extra gill arch and pectoral propterygium separated from its corresponding radials (Compagno 1977, Carvalho 1996; compare Shirai 1992, 1996, which do not support hexanchiform monophyly). The frilled shark, *Chlamydoselachus anguineus*, is one of the strangest living sharks, with an enormous gape, triple-cusped teeth, and eel-like body. Some researchers even thought it was a relic of Paleozoic "cladodont" sharks (reviewed in Gudger and Smith 1933). *Echinorhinus* has traditionally been classified with the Squaliformes (Bigelow and Schroeder 1948, Compagno 1984a) but was given ordinal status by Shirai (1992, 1996, Carvalho 1996); studies of its dentition further support this conclusion (Pfeil 1983, Herman et al. 1989).

Squaliformes (20 genera, 121+ spp.), Squatiniformes (*Squatina*, 15+ spp.), and Pristiophoriformes (two genera, five or more spp.) form successive sister groups to the rays (Batoidea, 73+ genera, 555+ spp.). The squaliform dogfishes are mesopelagic, demersal, and deep-water species that vary greatly in size (from 25 cm *Euprotomicrus* to 6 m *Somniosus*). Many species are economically important, and new species continue to be described (Last et al. 2002). They are aplacentally viviparous, and some have the longest gestation periods of all vertebrates (*Squalus*, some 24 months). Shirai (1992, 1996) and Carvalho (1996) disagree in relation to the composition of this order, which is recognized as monophyletic by Carvalho, but broken into several lineages by Shirai. Squatiniforms (angelsharks) are morphologically unique, benthic sharks that resemble rays in being dorsoventrally flattened with expanded pectoral fins. They are distributed worldwide, but most species are geographically restricted (Compagno 1984a). Pristiophoriforms (sawsharks) are poorly known benthic inhabitants of the outer continental shelves (Compagno 1984a). They first appear in the fossil record during the Late Cretaceous of Lebanon (some 90 Mya) and have an elongated rostral blade ("saw") with acute lateral rostral spines that are replaced continuously through life; the saw is used to stun and kill fishes by slashing it from side to side. Similar to angelsharks, sawsharks are yolk-sac viviparous.

Rays (batoids), once thought to represent a gargantuan evolutionary leap from sharklike ancestors (e.g., Regan 1906), are best understood as having evolved through stepwise anatomical transformations from within squalomorphs. Sawsharks are their sister group, sharing with rays various characters (Shirai 1992), such as enlarged supraneurals extending forward to the abdominal area. But at least one feature traditionally considered unique to rays (the antorbital cartilage) can be traced down the tree to basal squalomorphs, in the form of the ectethmoid process (Carvalho and Maisey 1996) of hexanchiforms, *Echinorhinus*, and squaliforms, or as an unchondrified "antorbital" in pristiophoriforms (Holmgren 1941, Carvalho 1996). Even though "advanced" rays are very modified (e.g., *Manta*), basal rays retain various sharklike traits such as elongated, muscular tails with dorsal fins.

In precladistic days, Batoidea were traditionally divided into five orders (e.g., Compagno 1977): Pristiformes (sawfishes, two genera, five or more spp.), "Rhinobatiformes" (guitarfishes, nine genera, 50+ spp.), Rajiformes (skates, 28 genera, 260+ spp.), Torpediniformes (electric rays, 10 genera, 55+ spp.), and Myliobatiformes (stingrays, 24 genera, 185+ spp.). Phylogenetic analyses have revealed that Rhinobatiformes is not monophyletic (Nishida 1990, McEachran et al. 1996), but all other groups are morphologically well defined (Compagno 1977, McEachran et al. 1996). There is conflict as to which batoid order is the most basal, whether it is sawfishes (Compagno 1973, Heemstra and Smith 1980, Nishida 1990, Shirai 1996) or electric rays (Compagno 1977, McEachran et al. 1996). The most comprehensive phylogenetic study to date is that of McEachran et al. (1996); molecular analyses have hitherto contributed very little to the resolution of this problem (e.g., Chang et al. 1995). Rays are clearly monophyletic, with ventral gill openings, synarcual cartilages, and an anteriorly expanded propterygium, among other characters (e.g., Compagno 1973, 1977). There is as much morphological distinctiveness among the different groups of rays as there is among the orders of sharks. The oldest ray skeletons are from the Late Jurassic of Europe and are morphologically reminiscent of modern guitarfishes (Saint-Seine 1949, Cavin et al. 1995), but their relationships require further study (see Carvalho, in press).

Sawfishes are large batoids (up to 6 m long), present in inshore seas and bays, but also in freshwaters. The precise number of species is difficult to determine because of the paucity of specimens but is between four and seven; some are critically endangered because of overfishing and habitat degradation (Compagno and Cook 1995). They differ from sawsharks in the arrangement of canals for vessels and nerves within the rostral saw and in the mode of attachment of rostral spines. Guitarfishes are widespread in tropical and warm temperate waters, and are economically important. Much work is needed on their species level taxonomy; the last comprehensive revision was by Norman (1926). Characters supporting their monophyly are known, but they are undoubtedly a heterogeneous assemblage that requires subdivision (as in McEachran et al. 1996); for simplicity they are treated as a single taxon in figure 24.2. Electric rays are notorious for their electrogenic abilities. Although known since antiquity, they have been neglected taxonomically until very recently (e.g., Carvalho 1999, 2001). Their electric organs are derived from pectoral muscles and can produce strong shocks that are actively used to hunt prey (Bigelow and Schroeder 1953, Lowe et al. 1994). All electric ray species are marine, in tropical to temperate waters, and some occur in deep water. Skates are oviparous (all other rays are viviparous), marine, mostly deep water and more abundant in temperate areas. They also produce weak discharges from caudal electric organs (Jacob et al. 1994). Even though skates are the most species-rich chondrichthyan assemblage, they are

rather conservative morphologically. Rajiform intrarelationships have been studied by McEachran (1984), McEachran and Miyake (1990), and McEachran and Dunn (1998). Many new species still await description (J. D. McEachran, pers. comm.). Stingrays are also highly diverse (Last and Stevens 1994) and are found in both marine and freshwaters (the 20+ species of South American potamotrygonid stingrays are the only supraspecific chondrichthyan group restricted to freshwater). Stingrays can be very colorful and range from 15 cm (*Urotrygon microphthalmum*) to 5 m (*Manta*) across the disk. Stingray intrarelationships have been recently investigated by Nishida (1990), Lovejoy (1996), and McEachran et al. (1996). Stingray embryos are nourished in utero by milk-like secretions from trophonemata (Hamlett and Koob 1999); there are at least 10 undescribed species.

Holocephalans (Chimaeras)

Living holocephalans represent only a fraction of their previous (mostly Carboniferous) diversity. As a result, fossil holocephalans (summarized in Stahl 1999) have received more attention from systematists than have extant forms. The single surviving holocephalan order (Chimaeriformes) contains three extant families: Chimaeridae (2 genera, 24+ spp.), Callorhynchidae (*Callorhinchus*, three spp.), and Rhinochimaeridae (three genera, eight spp.). Chimaeras are easily distinguished from elasmobranchs, with opercular gill covers, open lateral-line canals, three pairs of crushing tooth plates with hypermineralized pads (tritors), and frontal tenacula on their foreheads (Didier 1995). Most species are poorly known, deep-water forms of relatively little economic significance. All chimaeras are oviparous, and some of their egg capsules are highly sculptured (Dean 1906). Relationships among living holocephalans is summarized by Didier (1995). New species are still being described (e.g., Didier and Séret 2002), but relationships among chimaeriform species are unknown.

Osteichthyes (Bony Fishes)

Before the advent of *Phylogenetic Systematics* (Hennig 1950, 1966, and numerous subsequent authors), Osteichthyes constituted only bony fishes; tetrapod vertebrates were classified apart as coordinate groups (usually ranked as classes). With the recognition that vertebrate classifications should strictly reflect evolutionary relationships, it has become apparent that Osteichthyes cannot include only the bony fishes, but must also include the tetrapods. Thus, there are two great osteichthyan groups of approximately equal size: Sarcopterygii (lobefins and tetrapods) and Actinopterygii (rayfins). Here, we briefly review the so-called "piscine sarcopterygians," or lobefins, before considering the largest, and most diverse radiation of the jawed fishes, the actinopterygians or rayfins.

Sarcopterygii (Lobefin Fishes and Tetrapods)

The lobefin fishes and tetrapods comprise some 24,000+ living species of fishes, amphibians, and amniote vertebrates (mammals; birds, crocodiles; turtles; snakes, lizards, and kin) with a fossil record extending to the Upper Silurian. All sarcopterygians are characterized by the evolutionary innovation of having the pectoral fins articulating with the shoulder girdle by a single element, known as the humerus in tetrapods. In contrast, actinopterygian fishes retain a primitive condition similar to that seen in sharks, in which numerous elements connect the fin with the girdle. A rich record of fossil lobefin fishes provides numerous "transitional forms" leading to Tetrapoda (Cloutier and Ahlberg 1996, Zhu and Schultze 1997, Zhu et al. 1999, Clack 2002). Two living groups survive, lungfishes and coelacanths.

Lungfishes

There are six living species of lungfishes, one in Australia (*Neoceratodus forsteri*), one in South America (*Lepidosiren paradoxa*), and four in Africa (*Protopterus* spp.). All are freshwater, but there are more than 60 described fossil genera dating back to the Devonian, almost all of which were marine. Of the living lungfishes all except the Australian species share an ability to survive desiccation by aestivating in burrows. This lifestyle is ancient; Permian lungfishes are commonly found preserved in their burrows. Considerable controversy surrounds the interrelationship of lungfishes. Most recent studies place them at (Zhu and Schultze 1997) or near (Cloutier and Ahlberg 1996) the base of the sarcopterygian tree, although some ichthyologists have claimed that they are the closest relatives of Tetrapoda (Rosen et al. 1981), a view recently supported with molecular evidence by Venkatesh et al. (2001).

Coelacanths

Coelacanths were once thought to have become extinct in the Cretaceous. The discovery of a living coelacanth off the coast of South Africa in 1938 caused a sensation in the zoological community [Weinberg (2000) presents a very readable history; see also Forey (1998)]. Between the 1950s and the 1990s, extant coelacanths were thought to be endemic to the Comoro Islands. But in 1997 Arnaz and Mark Erdmann photographed a specimen in a fish market in Indonesia (Sulawesi) and eventually obtained a specimen through local fishermen (Erdmann 1999). Since that time, coelacanths have been discovered off South Africa, Kenya, and Madagascar [see Third Wave Media Inc. (2003) for accounts of these discoveries and other coelacanth news]. Like lungfishes, the phylogenetic position of coelacanths has been subject to some dispute. Cloutier and Ahlberg (1996) placed them at the base of Sarcopterygii; Zhu and Schultze (1997) placed them near the clade containing Tetrapoda.

Actinopterygii (Rayfin Fishes)

The actinopterygian fossil record is rich, but unlike that of most other vertebrate groups, there are far more living forms than known fossils. The exact number of rayfin fishes remains to be determined, but most authors agree that the group minimally consists of some 23,600–26,500 living species, with approximately 200–250 new species being described each year (Eschmeyer 1998). Early actinopterygian fishes are characterized by several evolutionary innovations (synapomorphies) still found in extant relatives (Schultze and Cumbaa 2001). These include several technical features of the skull and paired fins, and the composition and morphology of the scales [see Janvier (1996) for an excellent overview of actinopterygian anatomy]. The earliest well-preserved actinopterygian, *Dialipina*, from the lower Devonian of Canada and Siberia, retains several primitive features of their osteichthyian and gnathostome ancestors, such as two dorsal fins (Schultze and Cumbaa 2001).

Living actinopterygian diversity resides mostly in the crown group Teleostei (see below), but between the species-rich teleosts and the base of Actinopterygii are a number of small but interesting living groups allied with a much more diverse but extinct fauna. For example, an actinopterygian thought to represent the closest living relative of teleost fishes is the North American bowfin, *Amia calva* (Patterson 1973, Wiley 1976, Grande and Bemis 1998). The bowfin is the last remaining survivor of a much larger group of fishes (the Halecomorphi) that radiated extensively in the Mesozoic and whose fossil representatives have been found in marine and freshwater sediments worldwide. As another example, between and below the branches leading to the living bichirs and the living sturgeons and paddlefishes are a whole series of Paleozoic fishes generally termed "palaeoniscoids." They display a dazzling array of morphologies, many paralleling the body forms now observed among teleost fishes and probably reflecting similar life styles. A review of this fossil diversity is beyond the scope of this chapter, but the reader can refer to Grande (1998) and Gardiner and Schaeffer (1989). However, fossil diversity has important consequences for our study of the evolution of characters. When we only consider living groups on the Tree of Life, we might get the impression that the appearance of some groups was accompanied by massive morphological change. This is usually not the case. When the fossils are included, we gain a very different impression: most of the evolutionary innovations we associate with major groups are gained over many speciation events, and the distinctive nature of the living members of the group is largely due to the extinction of its more basal members. Thus, it is true that the living teleost fishes are distinguished from their closest relatives by a large number of evolutionary innovations (DePinna 1996). Yet, when we include all the fossil diversity, this impressive number is, according to Arratia (1999), significantly reduced. Of course, this is to be expected; evolution by large saltatory steps is more the exception than the rule, because derived characters were acquired gradually. Another example is that gnathostomes, today remarkably diverse and divergent in anatomy, appear to have been very similar to each other shortly after their initial separation, because many features were primitively retained in now extinct stem gnathostome lineages (Basden et al. 2000, Maisey and Anderson 2001, Zhu et al. 2001, Zhu and Schultze 2001).

Living Actinopterygian Diversity and Basal Relationships

Wiley (1998) and Stiassny (2002) provide nontechnical overviews of basal actinopterygian diversity, and the review of Lauder and Liem (1983) remains a valuable and highly readable summary of actinopterygian relationships. The most basal of living actinopterygians are the bichirs (Polypteridae), a small group (11 spp.) of African fishes previously thought to be related to the lobefin fishes (sarcopterygians), or to form a third group. Despite past controversy, two recent molecular studies provide additional support for the birchirs as the basal living actinopterygian lineage (Venkatesh et al. 2001, Inoue et al. 2002), and this placement now seems well established. Compared with other rayfin fishes, birchirs are distinctive in having a rather broad fin base (even giving the external appearance of a lobe fin), a dorsal fin composed of a series of finlets running atop an elongate body, and only four gill arches. Although the analysis by Schultze and Cumbaa (2001) places them one branch above the basal *Dialipina*, their fossil record only just extends to the Lower Cretaceous (Dutheil 1999), a geologic enigma, but such a disparity between the phylogenetic age of a taxon and its first known fossil occurrence is not uncommon among rayfin fishes (fig. 24.1).

The living chondrostean fishes include the sturgeons of the Holarctic and the North American and Chinese paddlefishes. The comprehensive morphological analyses of Grande and Bemis (1991, 1996) have established a hypothesis of relationships among the living and fossils members of this group, which originated in the Paleozoic. The diversification of the living chondrosteans may go back to the Jurassic (Zhu 1992), when paddlefishes and sturgeons were already diversified. Paddlefishes and sturgeons retain many primitive characters, such as a strongly heterocercal tail that led some 19th century ichthyologists to believe that they are related to sharks. Sturgeons are among the most endangered, sought after, and largest of freshwater fishes. The Asian beluga *Huso huso* reaches at least 4 m in length, and a large female may yield 180 kg of highly prized caviar. Paddlefish caviar is also prized, and the highly endangered Chinese paddlefish grows to twice the size of its American cousins, reaching 3 m.

The remaining rayfin fishes belong to the clade Neopterygii. Garfishes (Lepisosteidae) are considered by most to be the

basal group (Patterson 1973, Wiley 1976). They form an exception among rayfin fishes in that there are as many living gars (a mere seven species) as fossil forms. Although fossils are known from many regions of the world and their record extends to the Lower Cretaceous, living gars are now confined to North and Middle America and Cuba.

Amia calva, the North American bowfin, is the sole living representative of Halecomorphi, a group that radiated in the Mesozoic. It shares a number of evolutionary innovations with teleost fishes (first detailed by Patterson 1973) but also displays a number of teleost characters that are now considered convergent, such as having cycloid rather than ganoid scales. Although most workers have followed Patterson (1973) in the recognition of *Amia* as the closest living relative of the Teleostei, there remains some controversy about their systematic position (Patterson 1994); alternative schemes of basal neopterygian relationships and the proximate relatives of the Teleostei are reviewed in Arratia (2001).

Teleostei

Among vertebrates, without doubt, Teleostei dominate the waters of the planet. The earliest representatives of living teleost lineages (the Teleocephala of DePinna 1996) date to the Late Jurassic some 150 Mya, but as noted by Arratia (2001), if definitions of the group are to include related fossil lineages, this date is pushed back into the Late Triassic–Early Jurassic (~200–210 Mya). Regardless of how fossil lineages are incorporated into definitions of the group, today's teleosts occupy almost every conceivable aquatic habitat from high-elevation mountain springs more than 5000 m above sea level to the ocean abyss almost 8500 m below. Estimates of the number of living species vary, but most authors agree that a figure of around 26,000 is reasonable. Although discovery rates are more or less constant at around 200–250 new species a year, for some groups, particularly those in little explored or inaccessible habitats, new species are being described in extraordinary numbers, for example, 30 new snailfishes from deep water off Australia (Stein et al. 2001) with some 70 more to be described from polar seas, or an estimated 200 new rock-dwelling cichlids from Lake Victoria, Africa (Seehausen 1996). There are more teleost species than all other vertebrates combined, and their number contrasts starkly with the low species diversity in their immediate amiiform relatives, or indeed of all basal actinopterygian lineages. Among actinopterygians the extraordinary species richness of the teleostean lineage is noteworthy, and although "adaptationist" explanations are not readily testable, it seems probable that much of their success may be attributed to the evolution of the teleost caudal skeleton, permitting increased efficiency and flexibility in movement (Lauder 2000), and to the evolution of powerful suction feeding capabilities that have facilitated a wide range of feeding adaptations (Liem 1990).

Teleostean Basal Relationships

Systematic ichthyology has a rich history, and the past three centuries have seen waves of progress and revision. But in the modern era, perhaps one of the most important contributions on teleost relationships was that of Greenwood et al. (1966; fig. 24.3). In that paper, the authors presented a tentative scheme of relationships among three main lineages, Elopomorpha (tarpons and eels), Osteoglossomorpha (elephantfishes and kin), and what are now known as the Euteleostei (all "higher teleosts," including such groups as cods and basses). Greenwood et al. (1966) found placement of Clupeomorpha (herrings and allies) problematic, but most subsequent workers have placed them as the basal euteleosts. Recently, however, this alignment has been challenged (see below). As Patterson (1994) later noted, it was as if the distinction between monotremes, marsupials, and placental mammals was not recognized until the mid 1960s.

By 1989, Gareth Nelson summarized the previous 20 years of ichthyological endeavor with the by now much quoted observation that "recent work has resolved the bush at the bottom but that the bush at the top persists." He presented a summary tree that showed a fully resolved scheme of major teleostean lineages as a comb leading to the spiny rayed Acanthomorpha that contains the percomorph "bush at the top."

The outstanding problem of Percomorpha is discussed below, but it is perhaps also worth noting that some recent studies have begun to challenge the notion of a fully resolved teleostean tree and to question the monophyly of some lineages (e.g., Lê et al. 1993, Johnson and Patterson 1996, Arratia 1997, 1999, 2000, 2001, Filleul and Lavoué 2001, Inoue et al. 2001, Miya et al. 2001, 2003). This is perhaps not surprising given that Nelson (1989) was somewhat guarded in his optimism and noted that although the interrelationships of major groups of fishes were resolved no group was defined by more than a few characters. Results of more refined matrix-based analyses that incorporate broader taxon sampling than the previously more standard "exemplar " approaches, the inclusion of new high quality fossil data, and the beginnings of more sophisticated multigene molecular studies indicate that character support for many teleost nodes is weak, ambiguous, or entirely wanting. Some of these changes or uncertainties are reflected in figure 24.1, in which basal teleostean relationships are represented as unresolved. For example, in a highly influential paper, Patterson and Rosen (1977) hypothesized that osteoglossomorphs are the sister group of elopomorphs and other living teleosts, whereas Shen (1996) and Arratia (e.g., 1997, 1999) have proposed that elopomorphs occupy that basal position.

We turn now to a brief review of diversity within extant non-acanthomorph teleost groups. Osteoglossomorpha consist of two freshwater orders: the North American Hiodonti-

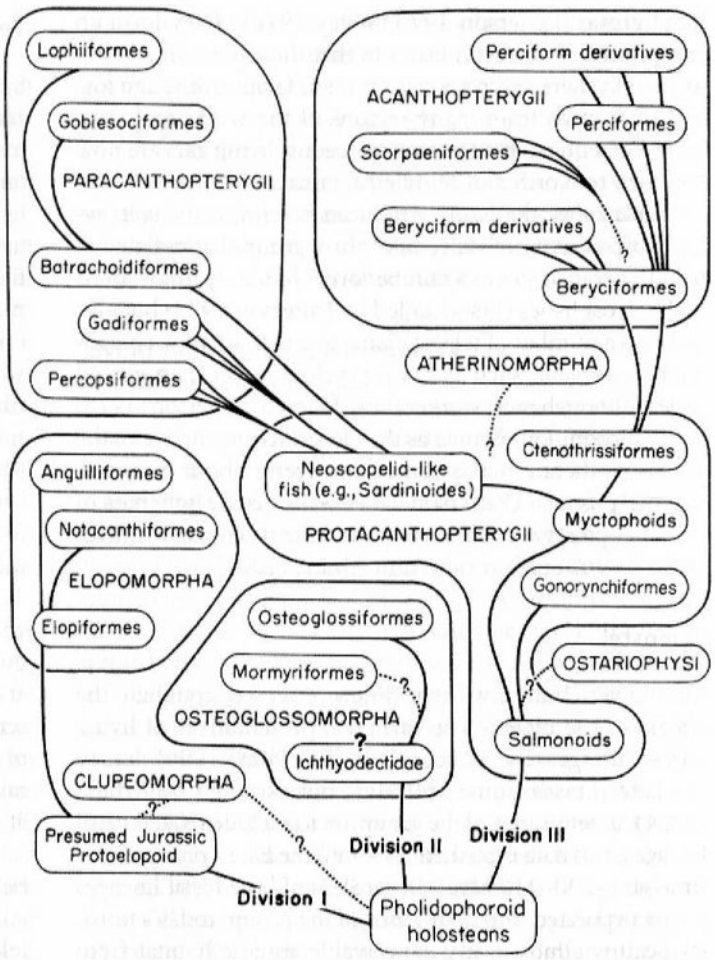

Figure 24.3. Diagram of teleostean relationships from Greenwood et al. (1966). This remarkably prescient, precladistic study delineated for the first time the major groups of teleostean fishes and thereby laid an important foundation for the "modern era" of teleostean systematics that was to follow.

formes (mooneyes; two spp., one family) and mostly Old World Osteoglossiformes (bony tongues, knifefishes, and elephantfishes; 220+ spp., five families). Osteoglossomorpha are an ancient group with a long fossil history dating to the Jurassie (Patterson 1993, 1994, Li and Wilson 1996) and displaying a number of primitive characters as well as two evolutionary innovations; a complex tongue-bite mechanism and a gut that uniquely coils to the left of the stomach. The most speciose and perhaps the most interesting members of this group are the elephantfishes (Mormyridae), which ereate an eleetric field with muscles of the caudal region and use it to find prey and avoid obstacles in their turbid water habitats. Relationships among mormyrids and the evolution of their electric organs have reeently been elucidated with molecular data by Sullivan et al. (2000) and Lavoué et al. (2000). Other osteoglossiforms include the large (to 2.5 m) bonytongues of South America, Asia, and Africa. Li and Wilson (1996) analyzed phylogenetic relationships and discussed evolutionary innovations of osteoglossomorphs, and a reeent molecular analysis (Kumazawa and Nishida 2000) corroborates osteoglossomorph monophyly but differs in its assessment of osteoglossiform interrelationships.

Elopomorpha are a heterogeneous group united by the unique, leaflike, transparent leptocephalus larval stage, onee considered a distinct taxonomie group, and by the possession of derived sperm morphology (Mattei 1991, Jamieson 1991). All are marine, although some venture into brackish waters. Elopomorph intrarelationships are poorly understood; however, most studies agree in placing Elopiformes (tarpons and ladyfishes; eight spp., two families) as the basal order. Albuliformes (bonefishes, two spp., one family) are a small group highly prized by fishermen. Notacanthiformes (halosaurs and spiny eels, 25 spp., two families) are marine, deep-water fishes. The bulk of elopomorph diversity lies in the Anguilliformes (true eels, 750+ spp., 15 families), which includes morays (200 spp.), snake eels (250 spp.), conger eels (150 spp.), and the anadromous freshwater eels (15 spp.). Saccopharyngiformes (deep-water gulper eels, 25 spp., three families) contains among the most bizarre of living vertebrates, with luminescent organs and huge mouths capable of swallowing prey several times their body size. Forey et al. (1996) accepted elopomorph monophyly and presented a detailed study of their intrarelationships, using both morphological and molecular characters. However, two recent studies (Filleul and Lavoué 2001, Obermiller and Pfeiler 2003) have challenged elopomorph monophyly, and Filleul and Lavoué (2001) place the four orders as *incertae sedis* among basal teleosts.

Until 1996, the remaining teleost fishes were grouped into two putative lineages, Clupeomorpha (herrings and allies, 360+ spp., five families) and Euteleostei. Euteleostei have proven to be a problematic group, persistently defying unambiguous diagnosis (Fink 1984).

Following the molecular work of Lê et al. (1993), Lecointre (1995) and Lecointre and Nelson (1996) suggested, based on both morphological and molecular characters, that ostariophysans (minnows, catfishes, and allies) are not euteleosts but instead are the sister group of clupeomorphs. Further evidence is emerging, both molecular (Filleul and Lavoué 2001, G. Orti pers. comm.) and morphological (Arratia 1997, 1999, M. DePinna pers. comm.) to support this hypothesis, which removes one of the stumbling blocks to understanding the evolution of euteleosts, but its validity and implications are not yet fully understood. For example, Ishiguro et al. (2003) find mitogenomic support for an Ostariophysan-clupeomorph clade, but one that also includes the alepocephaloids (slickheads, see below) nested within it.

With the ostariophysans removed, Johnson and Patterson (1996) argued that four unique evolutionary innovations characterize the "new" Euteleostei and recognized two major lineages. The first, Protacanthopterygii, is a refinement of the group first proposed by Greenwood et al. (1966). The second (Neognathi) placed the small order Esociformes (the freshwater Holarctic pikes and mudminnows; about 10 spp., two families) as the sister group of the remaining teleosts (Neoteleostei). The relationships of the pikes and mudminnows remain problematic, but they share two unique evolutionary innovations with neoteleosts (Johnson and Patterson 1996).

The reconstituted Protacanthopterygii consists of two orders, Salmoniformes and Argentiniformes, each with two suborders. Salmoniformes includes the whitefishes, Holarctic salmons and trouts, Salmonoidei (65+ spp., one family) and the northern smelts, noodlefishes, southern smelts and allies, and Osmeroidei (75+ spp., three families). The Argentiniformes include the marine herring smelts and allies (Argentinoidei; 60+ spp., four families), most of which occur in deep water, and the deep-sea slickheads and allies (Alepocephaloidea; 100+ spp., three families).

Morphological character support for a monophyletic Neoteleostei and the monophyly and sequential relationships of the three major neoteleost groups leading to Acanthomorpha, depicted in figure 24.1, appears strong (Johnson 1992, Johnson and Patterson 1993, Stiassny 1986, 1996), and it is perhaps at this level on the teleostean tree that most confidence can currently be placed. Stomiiformes (320+ spp., four families) are a group of luminescent, deep-sea fishes with exotic names such as bristlemouths and dragonfishes that complement their morphological diversity (fig. 24.4). Two genera of midwater bristlemouths (*Cyclothone* and *Gonostoma*) have the greatest abundance of individuals of any vertebrate genus on Earth (Marshall 1979). Harold and Weitzman (1996) provide the most recent analysis of stomiiform intrarelationships. Aulopiformes (220+ spp., 15 families) are a diverse group of nearshore and mostly deep-sea species, including the abyssal plain tripod fishes, the familiar tropical and temperate lizardfishes, and midwater predators such as the sabertooths and lancetfishes (for the most recent analyses of their intrarelationships, see Johnson et al. 1996, Baldwin and Johnson 1996, Sato and Nakabo 2002). Members of Myctophiformes—lanternfishes and allies (240+ spp., two families)—are also ubiquitous midwater fishes, most with luminescent organs. They are a major food source for economically important midwater feeders, from tunas to whales, and many undertake vertical migrations into surface waters at night to feed, returning to depths during the day, thereby contributing significantly to biological nutrient cycling in the deep ocean. Stiassny (1996) and Yamaguchi (2000) provide recent analyses of their intrarelationships.

Acanthomorpha and the "Bush at the Top"

The spiny-rayed fishes, Acanthomorpha, are the crown group of Teleostei. With more than 300 families and approximately 16,000 species, they comprise more than 60% of extant teleosts and about one-third of all living vertebrates. This immense group of fishes exhibits staggering diversity in adult and larval body form, skeletal and soft anatomy, size (8 mm to 15 m), habitat, physiology, and behavior. Acanthomorphs first appear in the fossil record at the base of the Late Cretaceous (Cenomanian) represented by more than 20 genera assignable to four or five extant taxa (fig. 24.1). By the late Paleocene the fauna is somewhat more diverse, but at the Middle Eocene, as seen in the Monte Bolca Fauna, an explosive radiation seems to have occurred, wherein the majority of higher acanthomorph diversity is laid out (Patterson 1994, Bellwood 1996). To date, because of the uncertainty of structure and relationships of many of the earlier fossils and the rapid appearance of most extant families, fossils have offered little to our understanding of acanthomorph relationships.

Acanthomorpha originated with Rosen's (1973) seminal paper on interrelationships of higher euteleosts and was based on five ambiguously distributed characters. In an attempt to define the largest and most diverse acanthomorph assemblage, Percomorpha, Johnson and Patterson (1993) proposed a morphology-based hypothesis of acanthomorph relationships. In so doing, they reviewed and evaluated support for previous hypotheses, including acanthomorph monophyly, for which they identified eight evolutionary innovations. Perhaps the most convincing of these are the presence in the dorsal and anal fins of true fin spines, as well as a single median chondrified rostral cartilage associated with specific rostral ligaments (Hartel and Stiassny 1986, Stiassny 1986) that permit the jaws to be greatly protruded while feeding. Johnson and Patterson (1993) proposed a phylogeny for six basal acanthomorph groups leading sequentially to a newly defined Percomorpha. Below, we briefly discuss acanthomorph diversity in this proposed phylogenetic order (fig. 24.5).

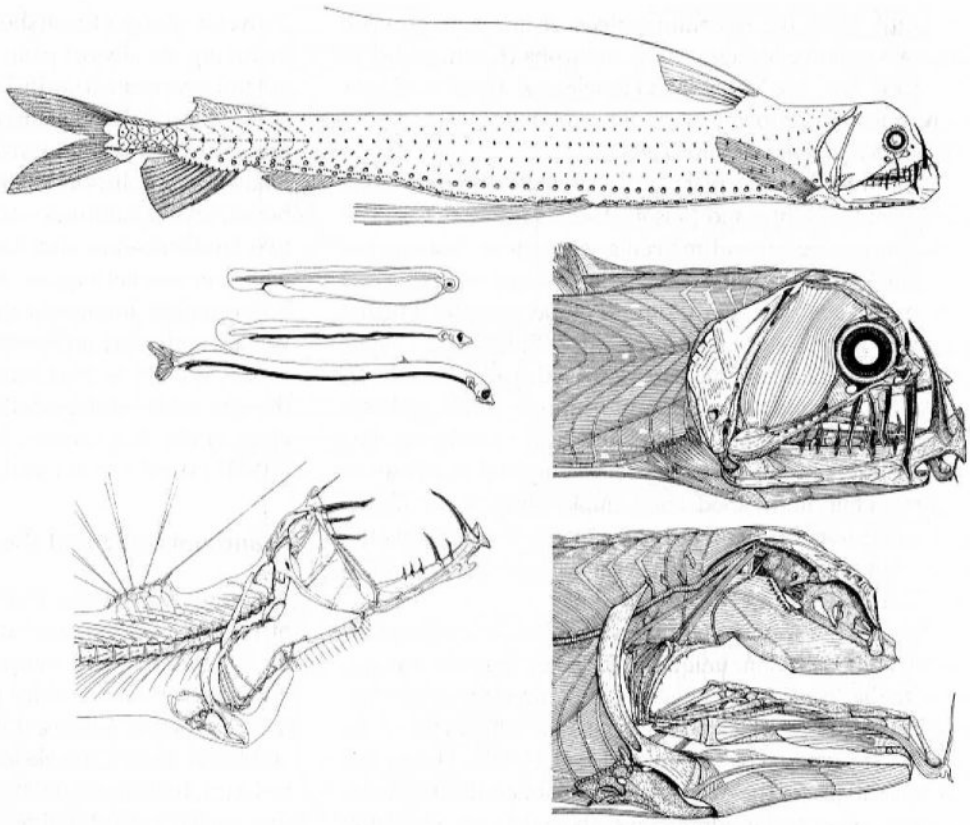

Figure 24.4. The viperfish, *Chauliodus sloani*; anatomical detail from Tchernavin (1953). Larvae redrawn after Kawaguchi and Moser (1984). Teleostean fishes are biomechanically complex; the head alone is controlled by some 50 muscles operating more than 30 movable skeletal parts. Such anatomical complexity, plus a wide range of ontogenetic variation, ensures a continued pivotal role for anatomical input into systematic study.

Interestingly, Lampridiformes (opahs and allies) were once placed among the perciform fishes at the top of the tree. They are a small (20 spp., seven families) but diverse group, characterized by a uniquely configured, highly protrusible upper jaw mechanism. Except for the most primitive family, the velifers, which occur in near shore-waters, the remaining families are meso- and epipelagic. In body shape they range from the deep-bodied opahs to extremely elongate forms such as the oarfish (*Regalecus glesne*), which is the longest known bony fish, reported to reach 15 m. The position of lampridiforms as a basal acanthomorph group has been supported by both morphological (Olney et al. 1993) and molecular data sets (Wiley et al. 2000, Miya et al. 2001, 2003, Chen et al. 2003).

Polymixiiformes (beard fishes; 10 spp., one family) are characterized by two chin barbels supported by the first branchiostegals and occur on the continental shelf and upper slope. The fossil record for this group is considerably more diverse than its living representation. Recent molecular studies have confirmed a basal position for these fishes, but some suggest a placement within a large clade consisting otherwise of paracanthopterygian and zeoid lineages (e.g., Miya et al. 2001, 2003, Chen et al. 2003).

Paracanthopterygii (1,200+ spp., 37 families) are an odd and almost certainly unnatural assemblage of freshwater and marine fishes first proposed by Greenwood et al. (1966) and refined to its present form by Patterson and Rosen (1989). Most of the hypothesized evolutionary innovations proposed by these authors are suspect (Gill 1996), and molecular studies by Wiley et al. (2000) and Miya et al. (2001) suggest that although the freshwater Percopsiformes (trout perches; six spp., three families) and Gadiformes (cods; 500+ spp., nine families) are basal acanthomorphs, the other groups may be scattered through the higher acanthomorph lineages. These orders include Ophidiiformes (cusk eels; 380+ spp., 18 families), Batrachoidiformes (toadfishes; 70 spp., three families), and Lophiiformes (anglerfishes; 300+ spp., 18 families). Most species belonging to these orders are marine. The dismemberment of all or part of Paracanthopterygii will have significant implications for acanthomorph relationships, perhaps particularly those within the perciforms.

Between the paracanthopterygians and the immense diversity of Percomorpha are three small, but phylogenetically critical, marine lineages. Stephanoberyciformes (90 spp., nine families) is a monophyletic group of marine benthic and deep-water fishes commonly called pricklefishes and whalefishes. Johnson and Patterson (1996) separated this group from Beryciformes, but molecular data suggest that at least some members of the group might rejoin Beryciformes (Wiley et al. 2000, Colgan et al. 2000, Chen et al. 2003). Zeiformes (45 spp., five families) includes the dories, a marine group of deep-bodied fishes that includes the much-valued John

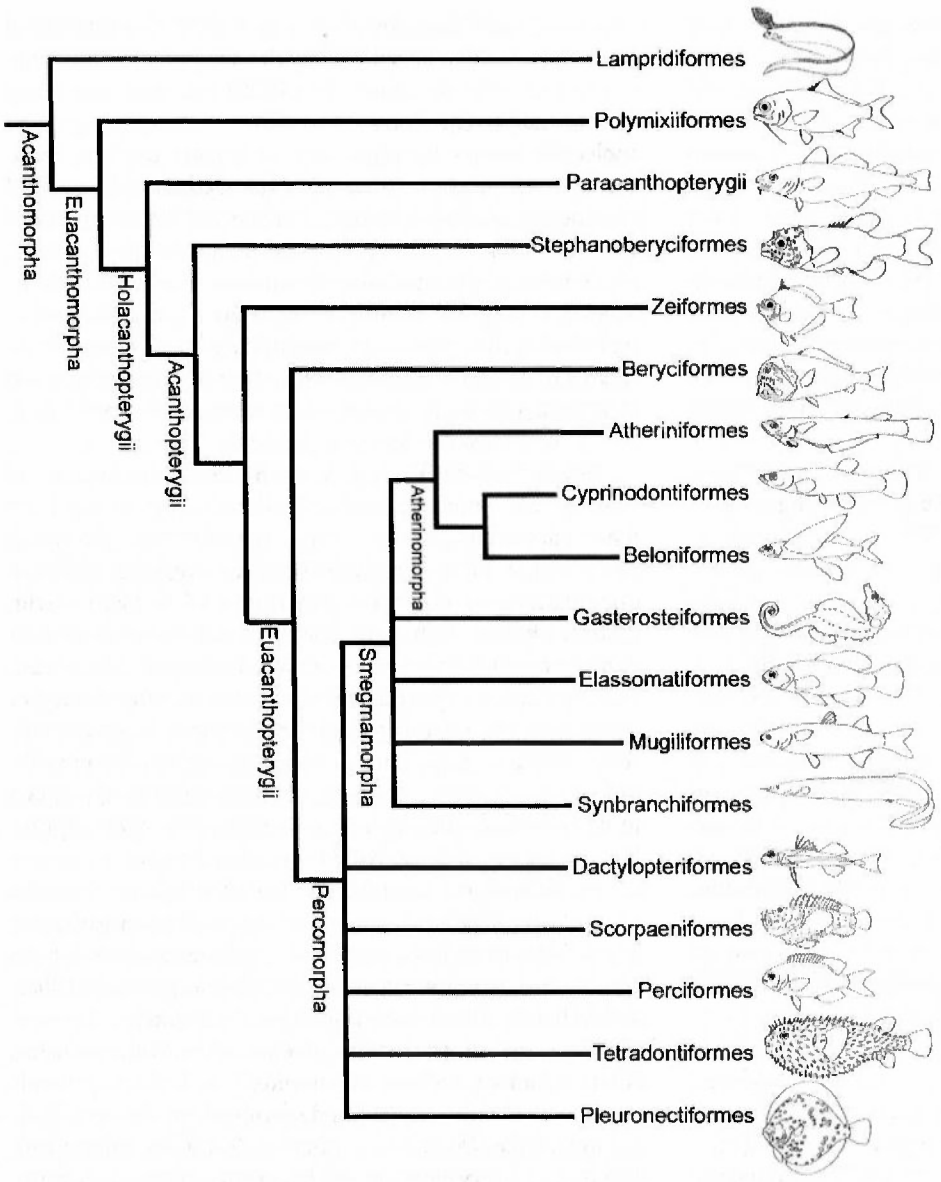

Figure 24.5. Intrarelationships among acanthomorph lineages after Johnson and Patterson (1993).

Dory of the Atlantic. Recent molecular studies suggest a relationship between the dories and the codfishes and/or beardfishes (Wiley et al. 2000, Miya et al. 2001, Chen et al. 2003), but this conclusion might be due to the relatively low numbers of species included in these studies. Beryciformes (140+ spp., seven families) includes some of the most familiar reef-dwelling fishes, the squirrelfishes. Beryciforms are entirely marine and occur worldwide from shallow depths, where they are nocturnal, to the deep sea. External bacterial luminescent organs characterize the pinecone fishes and flashlight fishes, the latter having a complex mechanism for rapidly occluding the large subocular light organ by rotating it downward or covering it with a lidlike shutter. Two genera of the closely related roughies (Trachichthyidae) have internal luminescent organs, and the orange roughy (*Hoplostethus atlanticus*) is an overexploited food fish.

Percomorpha, the Bush at the Top

Percomorph (14,000+ spp., 244 families) are the crown group of the spiny-rayed fishes and best represent what Nelson (1989) called the "bush at the top." The name Percomorpha originated with Rosen (1973) and was essentially the equivalent of Greenwood et al.'s (1966) Acanthopterygii, which consisted of beryciforms, perciforms, and groups placed between and beyond those two, such as lampridiforms, zeiforms, gasterosteiforms, scorpaeniforms, pleuronectiforms, and tetraodontiforms. Rosen presented no characters in support of his Percomorpha, nor have any been supported subsequently (but see Stiassny 1990, 1993, Stiassny and Moore 1992, Roberts 1993). The major goal of Johnson and Patterson's (1993) analysis was to sort out basal lineages of acanthomorphs and revise the composition of Percomorpha to represent a monophyl-

etic group diagnosed by derived characters. In the process, they erected a new, putatively monophyletic assemblage, Smegmamorpha, which, together with "the perciforms and their immediate relatives," constituted the newly defined Percomorpha. They identified eight evolutionary innovations of the Percomorpha, all of which are homoplasious. Although monophyly of Johnson and Patterson's Percomorpha has not been challenged subsequently with morphological analyses, it is considered tenuous, particularly in view of our ignorance of the composition and intrarelationships of Perciformes and allies (below) and strong doubts about paracanthopterygian monophyly. To date, no molecular analyses have captured a monophyletic Percomorpha without the inclusion of certain "paracanthopterygian" lineages.

Smegmamorpha (1,700+ spp., 37 families) of Johnson and Patterson (1993) are a diverse group consisting of spiny and swamp eels (Synbranchiformes; 90 spp., three families), gray mullets (Mugiliformes; 80 spp., one family), pygmy sunfishes (Elassomatiformes; six spp., one family), sticklebacks, pipefishes and allies (Gasterosteiformes; 275 spp., 11 families), and the speciose silversides, flyingfishes, killifishes, and allies (Atherinomorpha; 1225+ spp., 21 families, four orders). The recognition of this group was greeted with some skepticism because swamp and spiny eels had traditionally been allied with the perciforms whereas pygmy sunfishes had been considered centrarchids (sunfish and basses), a family deeply embedded in one suborder of Perciformes. Smegmamorpha is united by a single evolutionary innovation, a specialized attachment of the first intermuscular bone (epineural) at the tip of a prominent transverse process on the first vertebra, but several additional specializations are shared by most smegmamorphs. There have been no comprehensive morphological analyses to challenge smegmamorph monophyly; however, Parenti (1993) suggested that atherinomorphs might be the sister group of paracanthopterygians, and Parenti and Song (1996) identified a pattern of innervation of the pelvic fin in mullets and pygmy sunfishes that is shared with more derived perciforms. Molecular analyses have failed to capture monophyly of smegmamorphs, although major components of the group are recognized (e.g., Wiley et al. 2000, Miya et al. 2003, Chen et al. 2003). Although relationships among smegmamorphs remain unknown, Stiassny (1993) suggested grey mullets (Mugilidae) may be most closely related to atherinomorphs, and Johnson and Springer (1997) presented evidence suggesting a possible relationship between pygmy sunfishes and sticklebacks.

The remaining groups comprise some 12,000+ species in more than 207 families. In their cladogram of percomorph relationships (fig. 24.4), Johnson and Patterson (1993) placed Perciformes (perches and allies) in an unresolved polytomy with Smegmamorpha and four remaining groups traditionally classified as orders: the scorpionfishes and allies (Scorpaeniformes), flying gurnards (Dactylopteriformes), flatfishes (Pleuronectiformes), and triggerfishes, pufferfishes, and allies (Tetraodontiformes). However, they saw no reason to exclude these last four orders from the traditional Perciformes and believed it likely that they are nested within it. Subsequently, Mooi and Gill (1995) classified Scorpaeniformes within Perciformes. To date, no morphological or molecular synapomorphies support a monophyletic Perciformes in either the restricted or expanded sense that would include any or all of the orders Johnson and Patterson (1993) placed in their terminal polytomy. Many questions remain about monophyly and interrelationships of a number of the approximately 25 suborders and more than 200 families included in that polytomy. Certainly the possibility that affinities of some members lie with other acanthomorphs, or vice versa, cannot be dismissed. With these observations in mind, we review the remaining orders.

Perciformes (9800+ spp., 163 families) are the largest and most diverse vertebrate order. Perciforms range in size from the smallest vertebrate, the 8 mm *Trimmatom nanus* (for which an estimated 3674 individuals would be needed to make up one quarter-pound gobyburger), to the 4.5 m black marlin (*Makaira indica*). Although there are a number of freshwater perciforms (mostly contained within the large cichlid clade), most species are marine, and they represent the dominant component of coral reef and inshore fish faunas. In a taxonomic sense, Perciformes is a catchall assemblage of families and suborders whose relationships have not been convincingly shown to lie elsewhere. Although there is reasonably good support for monophyly of about half of the suborders, others remain poorly defined, most notably the largest suborder, Percoidei (3,500+ spp., 70 families), another catch-all or "wastebasket group," for which not a single diagnostic character has been proposed. Percoids are usually referred to as perchlike fishes, and although this general physiognomy characterizes many families, such as freshwater perches (Percidae), sunfishes (Centrarchidae), sea basses (Serranidae), and others, percoids encompass a wide range of body forms, from the deep-bodied moonfishes (Menidae), butterflyfishes (Chaetodontidae), and more, to very elongate, eel-like forms such as bandfishes (Cepolidae) and bearded snakeblennies (Notograptidae). For lists and discussions of perciform suborders and percoid families, see Johnson (1993), Nelson (1994), and Johnson and Gill (1998), each of which, not surprisingly, differ somewhat in definition and composition of the two groups.

Scorpaeniformes (lionfishes and allies; 1,200+ spp., 26 families) were included within Perciformes by Mooi and Gill (1997) based on a specific pattern of epaxial musculature shared with some perciforms. It is a large, primarily marine group characterized by the presence of a bony stay of questionable homology that extends from the third infraorbital across the cheek to the preopercle. Monophyly, group composition, and relationships remain controversial, but most recent work supports two main lineages, scorpaenoids and cottoids (e.g., Imamura and Shinohara 1998), and preliminary molecular studies suggest a close relationship between zoarcoids and the cottoid lineage (Miya et al. 2003, Smith 2002, Chen et al. 2003). Whether the scorpaenoid and cot-

toid lineages are sister groups is open to question, and clarification of scorpaeniform relationships is an important component of the "percomorph problem."

Dactyloptcriformes (flying gurnards; seven spp., one family) are a small, clearly monophyletic, group of inshore bottom-dwelling marine fishes characterized by a thick, bony, "armored" head with an elongate preopercular spine and colorful, greatly enlarged, fanlike pectoral fins. Their relationships are obscure (Imamura 2000), and they have been variously placed with, among other groups, the scorpaeniforms and gasterosteiforms. Molecular studies to date have shed little light on placement, with weak support for an alignment with flatfishes (Miya et al. 2001), gobioids (Miya et al. 2003), or syngnathoids (Chen et al. 2003).

Pleuronectiformes (flatfishes; 540+ spp., seven families) are widely distributed, bottom-dwelling fishes containing a number of commercially important species. These are characterized by a unique, complex evolutionary innovation in which one eye migrates ontogenetically to the opposite side of the head, so that the transformed juveniles and adults are asymmetrical and lie, eyeless side down, on the substrate. Their relationships as shown by morphological analysis have most recently been reviewed by Chapleau (1993) and Cooper and Chapleau (1998). A molecular analysis of mitochondrial ribosomal sequences by Berendzen and Dimmick (2002) suggests an alternative hypothesis of relationship. Interestingly, a recent mitogenomic study provides quite strong nodal support for a relationship with the jacks (Carangidae), but taxon sampling in this region of the tree is quite sparse (Miya et al. 2003).

Tetraodontiformes (triggerfishes, puffers, and allies; 350+ spp., 10 families) are a highly specialized and diverse order of primarily marine fishes, ranging in size from the 2 cm diamond leatherjacket (*Rudarius excelsus*) to the 3.3 m (>1000 kg) ocean sunfish (*Mola mola*). They are characterized by small mouths with few teeth or teeth incorporated into beaklike jaws, and scales that are either spine like or, more often, enlarged as plates or shields covering the body as in the boxfishes (Ostraciidae). Members of three families have modified stomachs that allow extreme inflation of the body with water as a defensive mechanism. Relationships of tetraodontiforms have been treated in large monographs dealing with comparative myology (Winterbottom 1974) and osteology (Tyler 1980). Although tetraodontiforms have been considered as highly derived percomorphs, Rosen (1984) proposed that they are more closely related to caproids and the apparently more basal zeiforms. Johnson and Patterson (1993) rejected that hypothesis, as do ongoing molecular studies (Holcroft 2002, N. I. Holcroft pers. comm.). However, it is defended in a recent morphological analysis (Tyler et al. 2003).

Concluding Remarks

Systematic ichthyologists were early to adopt Hennig's methods and have made great progress toward understanding the evolutionary diversification of fishes. Much of the new phylogenetic structure is underpinned by morphological character data, most of it from the skeleton and much of it gathered anew or reexamined and refined during the last 35 years. Another seminal innovation appeared fortuitously on the cusp of the cladistic revolution—the use of trypsin digestion in cleared and stained preparations, followed by the ability to stain cartilage as well as bone. These techniques revolutionized fish osteology and greatly facilitated detailed study of skeletal development adding significantly to our understanding of character transformation and homology. However, there is still much to do. Our understanding of the composition and relationships of Percomorpha, with more than half the diversity of all bonyfishes, remains chaotic—a state of affairs proportionally equivalent to not knowing the slightest thing about the relationships among amniote vertebrates.

Fishes are a tremendously diverse group of anatomically complex organisms (e.g., fig. 24.4) and undoubtedly morphology will continue to play a central role in systematic ichthyology. However, as in other groups of organisms, molecular analyses are increasingly beginning to make significant contributions, especially for fish groups with confusing patterns of convergent evolution. The combination of molecular and morphological data sets, and the reciprocal illumination they shed, augurs an exciting new phase in systematic ichthyology. We are, perhaps, at the halfway point of our journey.

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