

Chapter One

Patterns of Diversity and Evolution in Ray-finned Fishes

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Introduction

The ray-finned fishes (Actinopterygii) display the most spectacular pattern of evolutionary diversification among the vertebrates. More than half of the 40,000 or so species of vertebrates are actinopterygians, and the teleost fishes alone number approximately 23,000 species. In recent years systematists have made tremendous progress in unraveling the relationships of the ray-finned fishes, and in this chapter we review and summarize current views on the phylogeny of actinopterygian fishes and present it in a form that will be of use to comparative neurobiologists.

Many of the recent advances in our understanding of fish evolution and relationships have come through the application of the principles of phylogeny construction outlined by Hennig (1966). Eldredge and Cracraft (1980) have given an excellent recent summary of the theory and methodology of historical analysis. The goal of phylogenetic analysis is to identify monophyletic assemblages of organisms. A monophyletic taxon is a group stemming from a single common ancestor and containing all the descendants of that ancestor. A monophyletic group is to be distinguished from a polyphyletic group (a taxon containing members derived from more than one ancestor) and a paraphyletic group (a taxon not containing all descendants of the ancestral population). Systematic ichthyologists have regarded monophyletic lineages as representing natural entities, which are defined on the basis of shared derived characters common to all (or at least all primitive) members of a given monophyletic taxon. A phylogeny is a hypothesis of a relationship between taxa, and this hypothesis may be either corroborated or refuted by attributes of the component taxa (characters). A highly corroborated phylogeny results from the analysis of many characters which are used to define monophyletic groups at various levels in the phylogeny (see fig. 1, for example). The analysis of evolutionary grades tends to obscure relationships between groups and masks the evolutionary sequence of structural change as inferred from nested sets of shared derived features.

Historical hypotheses provide the basis for the interpretation of convergent and divergent evolutionary pathways, and it is our hope that comparative neurobiologists will both use the hypotheses of relationship summarized here as a framework for their investigations, and contribute to phylogenetic reconstruction using neuroanatomical characters.

Relationships of the Actinopterygii

The ray-finned fishes share a common ancestor with a monophyletic lineage composed of the coelacanth (Actinistia), lungfishes (Dipnoi), and choanates (the rhipidistian fishes and tetrapods). The Elasmobranchiomorpha (sharks, rays, and holocephalans) share a common ancestor with the teleostome fishes (= Actinopterygii + Actinistia + Dipnoi + Choanata). The bulk of the vertebrate radiation is thus composed of two coordinate clades, each with about 25,000 species: the actinopterygians on one hand, and the rest of the Teleostomi on the other.

A number of characters corroborate the hypothesis that the Actinopterygii are monophyletic. Primitive actinopterygians have a single dorsal fin, a unique pattern of ossification in the endocranium, and ganoid scales; these characters are not found in other primitive gnathostome groups.

Primitive Actinopterygian Fishes

Figure 1 summarizes the relationships of the Actinopterygii. Each character is represented by a black bar to indicate that this feature is shared by taxa above the bar and is thus indicative of relationship at that level. Many primitive actinopterygians have traditionally been grouped into the Chondrostei. It is now clear that this is not a natural group, although the relationships of many of the included fossil and Recent taxa are still a matter of dispute.

The living survivors of the early ray-finned fishes include the bichir and reedfish, *Polypterus* and *Calamoichthys*, and the sturgeons and paddlefishes. The Polypteriformes appear to be the most primitive living actinopterygians (fig. 1) based on their cranial anatomy, but the relationships of this group have been the subject of considerable controversy (see Lauder and Liem, 1982). The sturgeons (Acipenseridae) and paddlefishes (Polyodontidae) are believed to form a monophyletic group (fig. 1; character 8) but the evidence is slim and additional corroboration is needed.

The Neopterygii (fig. 1) includes as its two most primitive living members the gars (Division Ginglymodi) and *Amia*, the bowfin (Division Halecostomi). Both of these groups, together with a number of fossil forms, were formerly included in the Holostei, now known to be polyphyletic. The Ginglymodi have been recently reviewed by Wiley (1976), who recognizes

two genera, *Lepisosteus* and *Atractosteus*. *Amia calva* is the only extant member of the Halecomorphi (fig. 1) which also includes the probably paraphyletic Parasemionotidae and Caturidae (Patterson, 1973).

The Teleost Fishes

The Teleostei (fig. 2), with about 23,000 species (Cohen, 1970), are by far the most diverse lineage of ray-finned fishes. Patterson (1968a) first unequivocally established teleostean monophyly based on characters in the caudal skeleton (fig. 2: character 1). Teleost fishes are now known to share a large number of features (see Patterson, 1977, and Patterson and Rosen, 1977, for a summary). Major advances occur in both the mechanics of feeding and locomotion at the teleost level. Teleost fishes share a suction-feeding mechanism of prey capture mediated by two separate biomechanical mechanisms (Lauder, 1980). In the caudal fin, the elongate ural neural arches (uroneurals) function to stiffen the upper tail lobe and support a dorsal series of caudal fin rays. These modifications may have had the effect of providing anterior thrust directed through the center of body mass, rather than ventral to it as in primitive actinopterygians.

The study of teleostean phylogeny has undergone a renaissance since the classic paper by Greenwood et al. (1966). Recent discussions of teleostean phylogeny may be found in Greenwood et al. (1973), Patterson (1977), and Patterson and Rosen (1977). There are four major lineages of teleost fishes (fig. 2): the Osteoglossomorpha, Elopomorpha, Clupeomorpha, and Euteleostei (considered in detail below). The Euteleostei is composed of a number of additional monophyletic lineages, all of which are united by the presence of an adipose fin anterior to the caudal fin, the presence of nuptial tubercles, and modifications of the caudal skeleton (fig. 2: characters 7-9).

The Euteleostei is a speciose lineage with 25 orders, 375 families, and over 17,000 species; recent evidence corroborates the branching pattern depicted in figure 2, although the relationships of the Protacanthopterygii are still unclear. The major division within the Euteleostei, the Neoteleostei, is characterized by an extremely important specialization, the presence of a retractor dorsalis muscle. This muscle, which extends from the vertebral column to insert on the upper pharyngeal jaws (see below), is related to a structural and functional reorganization in the masticatory and swal-

lowing apparatus of euteleosteans, which has had significant consequences for trophic specialization and diversification.

We now consider in turn the major teleostean lineages.

The Osteoglossomorpha

The cohort Osteoglossomorpha (fig. 4) first appears in the Lower and Upper Cretaceous of Africa, Europe, North and South America, Australia, New Zealand, and Southeast Asia. Recent osteoglossomorphs are without exception freshwater fishes, mostly confined to the tropical regions of South America, Africa, Southeast Asia, New Guinea, and Australia. One notable exception is the genus *Hiodon*, which inhabits North American fresh waters.

The Osteoglossomorpha is a monophyletic lineage characterized by the typical "tongue-parasphenoid bite." The tongue (basihyal and glossohyal bones) is covered with a massive toothplate that "bites" against the roof of the mouth. The latter is formed by the parasphenoid and palatal bones, which are armed with a battery of teeth. The toothed tongue moves against the tooth-bearing palate in a fore-and-aft fashion.

Within the osteoglossomorph body plan a great variety of insectivorous and piscivorous forms has evolved, including rapacious predators, filter-feeders, and benthic feeders.

The gross morphology of the osteoglossomorph brain (fig. 3) can be characterized by a trend toward an enlarged cerebellum, culminating in the huge cerebellum of the electric forms. In general, the forebrain is primitive, although *Arapaima* is a notable exception.

The cohort Osteoglossomorpha contains only one order, the Osteoglossiformes, within which are three suborders (Greenwood, 1973).

Osteoglossoidei

Members of this suborder possess one muscle between the hyoid bar and the lower jaw, the protractor hyoideus. *Arapaima* is an air breather and uses a modified swim bladder as a lung. It has been suggested that as a response to the environmental exigencies in O₂-deficient waters, many fishes have evolved specialized mechanisms of parental care. This is certainly the case with the osteoglossids, which mouth brood the young. The family Pantodontidae is regarded as an early and highly specialized offshoot

ACTINOPTERYGII

'CHONDROSTEANS'

NEOPTERYGII

HALECOSTOMI

HALECOMORPHI

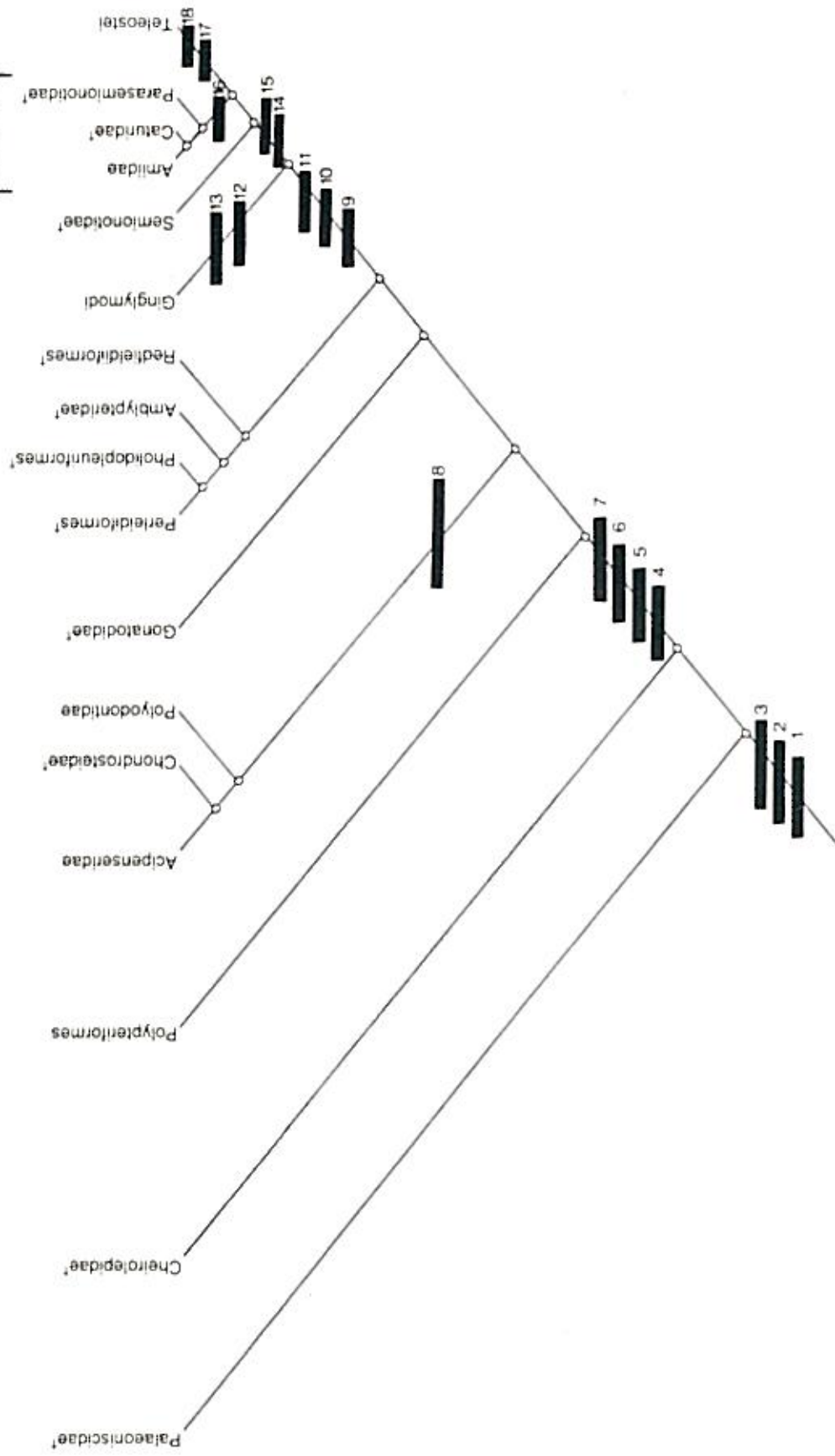


Fig. 1. A branching diagram (cladogram) showing the relationships between the main actinopterygian subgroups. Taxa having no living representatives are indicated with a dagger. Various characters are indicated by a black bar at the appropriate level. The characters are: 1, presence of a single dorsal fin; 2, unique endocranial ossification pattern, especially in the otic region; 3, unique scale histology; 4, absence of all superficial constrictors on the gill arches (Wiley, 1979); 5, obliqui ventrali gill arch muscles present (Wiley, 1979); 6, presence of a coracomandibularis muscle originating on the third gill arch (Wiley, 1979); 7, lateral cranial canal and other characters of Gardner (1973); 8, characters of Schaeffer (1973), including absence of myxodomes, fusion of premaxilla, maxilla, and dermo-

palatines; 9, fin rays equal in number to their supports in the dorsal and anal fins (Patterson and Rosen, 1977); 10, presence of a symplectic bone (Patterson and Rosen, 1977); 11, upper pharyngeal dentition is consolidated; 12, epistibioocular centra; 13, series of toothed infraorbital bones (Patterson and Rosen, 1977; see Wiley (1976) for many other characters); 14, mobile maxillary bone in the cheek; 15, presence of an interopercular bone; 16, both the symplectic bone and the quadrate contribute to the jaw articulation; 17, presence of uroneurals (elongated ural neural arches) in the caudal skeleton; 18, unpaired basibranchial toothplates (Patterson and Rosen, 1977).

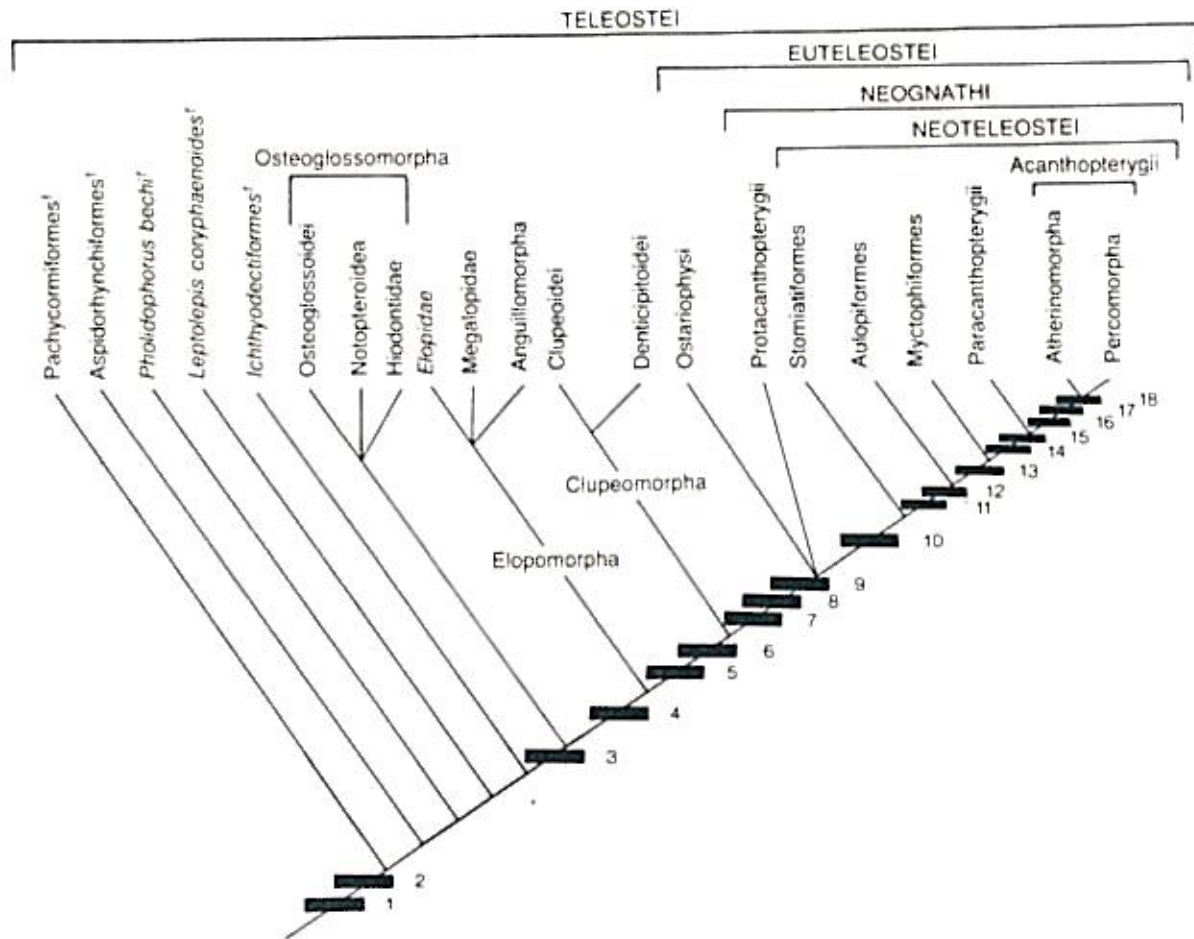


Fig. 2. Phylogeny of the Teleostei. Taxa known only from fossils are indicated with a dagger. The characters that define the levels of relationship are: 1, presence of uroneurals in the caudal skeleton (see fig. 1; character 17); 2, presence of unpaired basibranchial toothplates (see fig. 1; character 18). These two characters corroborate the hypothesis of teleostean monophyly; 3, shared features of caudal anatomy including only seven (occasionally eight) hypural bones as opposed to nine. For more characters, see Patterson and Rosen (1977); 4, only two uroneurals present as opposed to three or four; 5, articular bone co-ossified with the angular; 6, toothplates fused with first three pharyngobranchials and the fifth ceratobranchial. For further characters, see Patterson and Rosen (1977); 7, the presence of an adipose fin; 8, presence of nuptial tubercles (Wiley and Collette, 1970); 9,

presence of an anterior membranous outgrowth of the first uroneural that does not meet its antimeric in the midline (Patterson and Rosen, 1977); 10, presence of a retractor dorsalis muscle; 11, loss of the mandibulohyoid ligament and presence of an interperculohyoid ligament; 12, retractor dorsalis has a tendinous insertion on pharyngobranchial three; 13, reduction (or loss) of pharyngobranchial four and the main insertion of the retractor dorsalis on the third pharyngobranchial (Rosen, 1973); 14, presence of well-developed ctenoid scales; 15, expansion of ascending and articular premaxillary processes; 16, insertion of the retractor dorsalis on the third pharyngobranchial only; 17, ability to protrude upper jaw and the presence of an enlarged ascending process on the premaxilla; 18, spine on the second preural centrum is reduced to a low crest.

of the Osteoglossidae. Its only member, *Pantodon*, is a small surface-dwelling fish with an upturned mouth well suited to feed on insects caught in the surface film and to breathe well-oxygenated water from just below the surface.

Notopteroidei

In this suborder, the inner ear has the utriculus with its semicircular canals completely separated from the sacculus and lagena and the highly specialized cephalic lateral line system is without pores. The family Notopteridae has an enlarged cerebellum. Notopterids are elongate and laterally flattened nocturnal fishes that propel themselves by undulations of the long anal fin and are capable of breathing air. Unlike the other osteoglossiform families, the Mormyridae has undergone an evolutionary radiation differentiating into over 300 species. The most outstanding features characterizing this family are the electrogenic organs derived from caudal muscles and the greatly enlarged cerebellum. Mormyrids feed by electrolocation at night and exploit the rich bottom fauna of small worms and wormlike insects. The use of electric faculties may be correlated with feeding niches in the rivers of Africa.

Hiodontoidei

This small suborder is a phylogenetic relic in the sense that its living members (*Hiodon tergisus*, *H. alosoides*) form a lineage that has retained a large number of primitive features. The forebrain is very primitive and

the swim bladder has a diverticulum on each side extending anteriorly into the ear. In the ear region the diverticulum of the swim bladder is separated by a thin membrane from a vesicle that is filled with perilymph and connected with the utriculus of the inner ear via a foramen in the prootic bone.

The interrelationships of the major groups of the Osteoglossomorpha are summarized in figure 4.

The Elopomorpha

There are about 650 species of elopomorph fishes, which may be divided into seven major groups: the Elopidae, tenpounders; Megalopidae, tarpons; Albulidae, bonefishes; anguilloids, eels; saccopharyngoids, bathypelagic eels; halosaurids, deep-sea halosaurs; and notacanthids, the deep-sea spring eels. The anguilloids alone are subdivided into 19 families containing 600 species.

Although it has become increasingly clear that the Elopomorpha is a natural, monophyletic group, the relationships of fishes within the Elopomorpha are not well known. Forey (1973a,b), Greenwood (1977), and Patterson and Rosen (1977) have all examined elopomorph interrelationships to some degree. All elopomorph fishes share a peculiar elongate larval form called the leptocephalus, which has a small head and a greatly extended translucent body (other uniquely derived features for the Elopomorpha are discussed in Patterson and Rosen, 1977).

The suborder Anguilloidei is divided into two

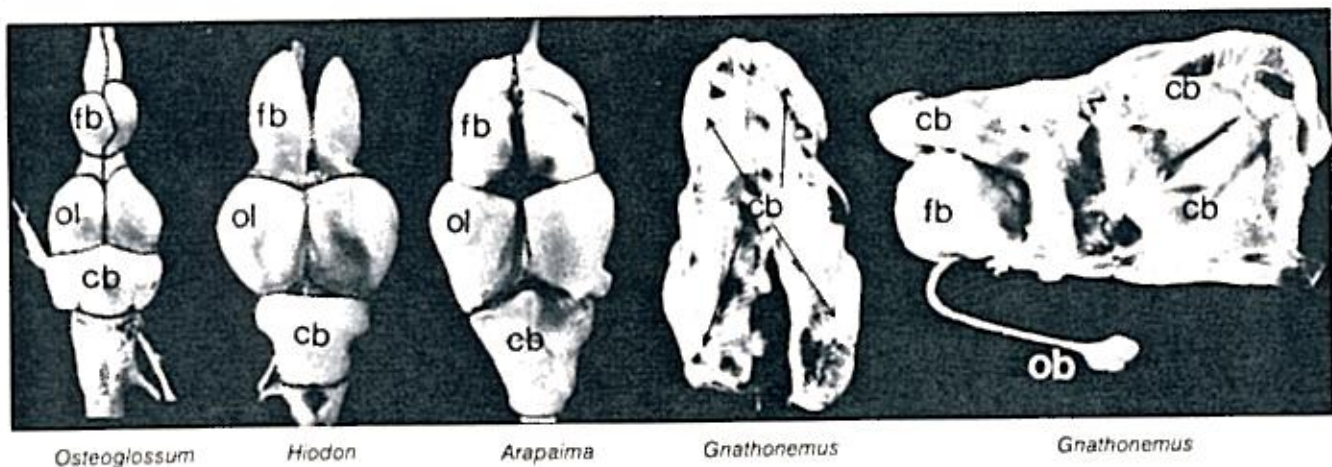


Fig. 3. Dorsal views of the brains of some representative osteoglossomorphs. The cerebellum (cb) in *Osteoglossum* and *Hiodon* exhibits only a moderate increase in size. In *Arapaima* the cerebellum is enlarged as in most osteoglosso-

morphs. In *Gnathonemus* the cerebellum is greatly enlarged enveloping the rest of the brain. cb, cerebellum; fb, forebrain; ob, olfactory bulb; ol, optic lobe.

groups—the Saccopharyngoidea and Anguilloidea. The saccopharyngoids are highly modified deep-sea predators which lack a swim bladder, ribs, scales, and pelvic and caudal fins. The Anguilloidea includes a diversity of eel-like fishes such as the well-known American eel (*Anguilla rostrata*), as well as the bonefish, *Albula*, and the halosaurs and notacanth. Halosaurs and notacanth both are deep-sea groups with a worldwide distribution and are primarily benthic in habit.

The two remaining groups of elopomorphs are the Elopidae, tenpounders, with a single genus (*Elops*) containing about five species, and the Megalopidae. *Elops* has a worldwide tropical distribution and is usually found in near-shore habitats and estuaries, while *Megalops* occurs in tropical and subtropical waters of the Pacific and Atlantic. *Megalops* is apparently unique among elopomorphs in possessing an otophysic (ear-swim bladder) connection.

The Clupeomorpha

The cohort Clupeomorpha (herringlike fishes) first appears in the Lower and Upper Cretaceous of West Africa, Europe, North and South America, and Southwest Asia. Most of the Recent members (four families and over 290 species) are primarily marine, although many move easily into brackish and fresh water. They inhabit oceans and seas all the way from

the warmest water in the tropics to very cold water in the far north and south. Most are plankton feeders with numerous long gill rakers.

Two specialized character complexes, shared by all members of the clupeomorphs, offer convincing evidence that the group is a monophyletic assemblage. The first feature is the specialized connection between the ear and swim bladder. The swim bladder's forward extension divides on each side of the skull to form two large vesicles which are lodged within the ossified bulbar or expansions of the prootic and pterotic bones. This type of ear-swim bladder connection is unlike that occurring in any other group of fishes. The second specialization affects the architecture of the neurocranium. Two prominent foramina are found in the temporal (bordered by the frontals and parietals) and the auditory region (surrounded by the prootic, exoccipital, and basioccipital).

The interrelationships between the various clupeomorphs are still a matter of speculation. Provisionally, one may recognize six recent families belonging to two suborders (Nelson, 1970).

The *Denticipitoidei* is monotypic, containing *Denticeps clupeoides* from the fresh waters of southwest Nigeria. This primitive living "herring" can be immediately distinguished from the second suborder, the Clupeoidei, by the presence of denticles on all the roofing bones of the skull and even on some trunk scales.

The *Clupeoidei* is the suborder to which all other clupeomorphs belong. It contains five families of uncertain interrelationships: Chirocentridae (the wolfherrings, one of the most voracious carnivores in the

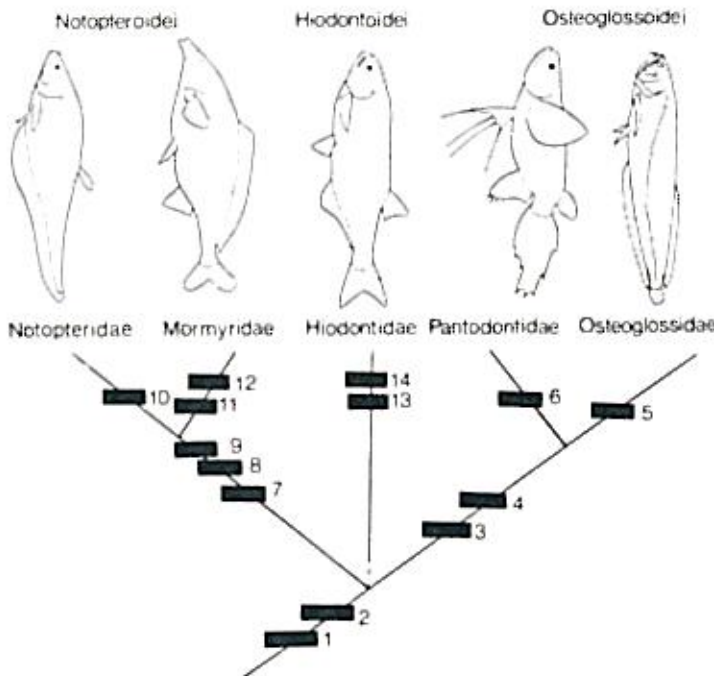


Fig. 4. Interrelationships of the major groups of the Osteoglossomorpha. Major specializations characterizing the various lineages are: 1, primary bite between tongue (basihyal armed with teeth) and toothed parasphenoid; 2, paired bony rods or bony processes at base of second gill arch, sometimes reduced to tendons; 3, upper hypural bones of caudal skeleton become fully fused; 4, muscle between hyoid and mandible is the protractor hyoideus; 5, scales are reticulate with elaborate surface ridges; 6, reduced number of vertebrae and dorsal and anal fin rays; 7, utriculus completely separated from sacculus and lagena; 8, lateral line without pores; 9, brain with greatly enlarged cerebellum; 10, toothplate on the tongue greatly enlarged; 11, cerebellum encloses the rest of the brain; 12, highly developed electrogenic and electroreceptive organs; 13, specialized infraorbital bones; 14, swim bladder connected with the utriculus via a foramen in the prootic bone.

sea), Clupeidae (herrings and menhadens), Dussumieriidae (round herrings), Engraulidae (anchovies), and the Pristigasteridae. Because the phylogenetic relationships are so poorly known, the five families are expressed as an unresolved polychotomy in figure 5. The brain of clupeoids is known for its lack of variation and the large subdivided optic lobes (Svetovidov, 1952).

The Protacanthopterygii

The Protacanthopterygii (fig. 2) include only one order, the Salmoniformes, which is composed of a number of monophyletic groups. Rosen (1974) has examined the evidence for protacanthopterygian monophyly and has shown that all protacanthopterygians possess upper pharyngeal jaws which are primitively formed by the fusion of two toothplates on the second and third pharyngobranchial elements of the gill arches. Extensive modifications of the pharyngeal teeth and toothplates have taken place during salmoniform evolution.

There are four major lineages of protacanthopterygians. The Esocoidei (pikes, pickerels, mudminnows) appears to be the most primitive lineage. Pike is voracious predators with posteriorly placed dorsal and anal fins for rapid acceleration. The Argentinoidei are large-eyed deep-sea fishes, some of which have bioluminescent organs. The Salmonoidei is characterized by large marginal fanglike teeth on the basihyal bone, and includes the family Salmonidae [trout, salmon

(*Salmo*, *Oncorhynchus*), charr (*Salvelinus*), whitefish (*Coregonus*), and grayling. The second salmonoid family, the Galaxiidae, is composed of small fishes which have an exclusively southern hemisphere distribution. Finally, the Osmeroidei contains the smelts (*Osmerus*), which live in marine, brackish, or coastal freshwater areas.

The Ostariophysii

Fishes of the division Ostariophysii (Rosen, 1973) (fig. 2) comprise about one fourth of all living actinopterygian fishes (with 5,000 to 6,000 species) and are by far the dominant group in the freshwater fish fauna. All ostariophysian fishes share a number of uniquely derived characters which support a hypothesis of monophyly [see Fink and Fink (1981) for a summary of ostariophysian relationships]. A particularly interesting feature is the presence of the epidermal "alarm substance cells," which exude an alarm substance when damaged (Pfeiffer, 1977). A wounded fish "leaks" alarm substance into the surrounding water and adjacent fish sense the substance and immediately alter their behavioral pattern. Behavioral changes such as scattering and diving for the bottom presumably reduce the chance of succumbing to a predator. Ostariophysian fishes also share a specialization of the anterior cervical vertebrae and ribs. The gonorynchiform fishes are the most primitive ostariophysians and have expanded cephalic ribs which lie posterior to the otic region of the cranium. The expanded first pleural rib

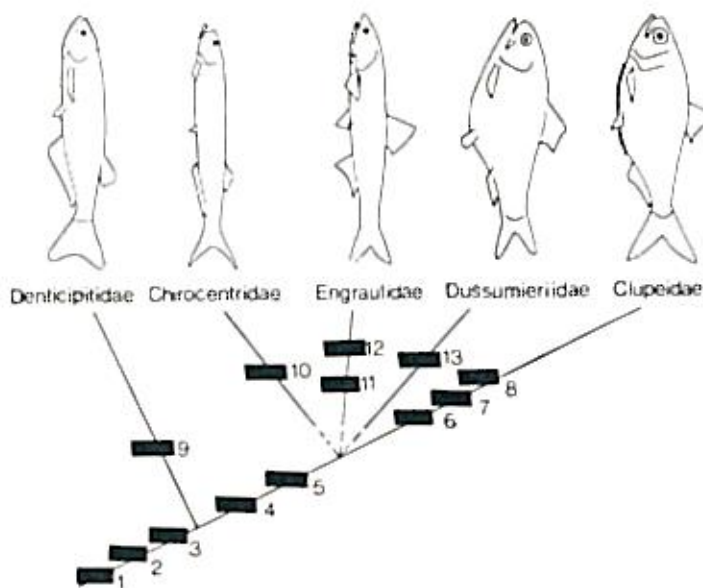


Fig. 5. Interrelationships of the major groups of the Clupeomorpha. Major specializations characterizing the various lineages are: 1, swim bladder extensions connect with prootic and pterotic; 2, presence of temporal and auditory foramina in the syncranium; 3, first hypural is free, being separate from the "urostyle"; 4, third pharyngobranchial bones with long medial processes; 5, fusion of toothplates with second basibranchial; 6, tendency to loose teeth; 7, proliferation of gill rakers; 8, elaboration of specialized epibranchial organs; 9, denticles on skull bones and some trunk scales; 10, dorsal gill arch elements of either side separated from each other across the midline; 11, reduction of the basihyal and loss or reduction of its toothplate; 12, fusion of the toothplate with first and third basibranchials; 13, rounded abdomen and loss of center row of sharp scales. In this unresolved polychotomy, the Pristigasteridae is not depicted. The Pristigasteridae can be recognized as yet another monophyletic lineage by the fusion of the toothplate with the second hypobranchial and sometimes also with the first and third hypobranchials.

supports a thickened peritoneum that partially invests the anterior chamber of the swim bladder. This appears to be the primitive condition from which the Weberian apparatus, characteristic of the remaining ostariophysan fishes, has evolved. The Weberian apparatus consists of five paired bony elements that form a link between the anterior chamber of the swim bladder and the ear. Differential movement of two membranes surrounding the anterior chamber of the swim bladder causes oscillations in the chain of Weberian ossicles which are transmitted to the ear (Alexander, 1966). Ostariophysan fishes appear to have improved hearing and an increased range over which sounds can be detected as a result of the Weberian apparatus (Popper and Fay, 1973; Tavolga, 1976).

The recent hypothesis of ostariophysan relationships proposed by Fink and Fink (1981) has a number of important implications for neurobiologists studying ostariophysan fishes, as it differs significantly from previous schemes. The superorder Ostariophysi is divided into two lineages: the Anotoptysi containing only the gonorynchiforms, and the Otophysi. The Otophysi include two monophyletic lineages, the Cypriniphysi, containing the cypriniform fishes (minnows, suckers, hill-stream fishes, carps, loaches), and the Characiphysi containing the order Characiformes (tetras, piranhas, pacus), and the order Siluriformes. The Siluriformes includes both the catfishes (Suborder Siluroidei) and the gymnotoids (Suborder Gymnotoidei). Thus, the catfishes and the gymnotoids are each others closest relatives, both groups together forming a monophyletic lineage.

The Gonorynchiformes is a monophyletic lineage with four families, three of which contain only one species. *Chanos*, the milkfish, is widespread in the Western Pacific and is important as a food fish in Southeast Asia. Other gonorynchiform fishes are placed in the Kneriidae, Phractolaemidae, and Gonorynchidae. The biology of these groups is poorly known.

The cypriniform fishes are usually divided into six families. One family, the Cyprinidae, contains about 1,600 of the 2,000 cypriniform species. Cypriniform fishes lack jaw teeth and have independently evolved the protrusible upper jaw which is characteristic of acanthopterygian fishes. Many cypriniforms are herbivores and the families Cyprinidae and Catostomidae possess especially strong pharyngeal jaws for grinding and crushing thick-walled algal cells.

Cyprinid fishes are widely distributed in the fresh waters of North America, Africa, Europe, and Asia, although they are absent from South America. The greatest diversity of cyprinids occurs in Africa and Eurasia, and European cyprinids include the carp (*Cyprinus*) and the goldfish (*Carassius*).

The other families of cypriniforms, the Gyriinocheilidae, Psilorhynchidae, and Homalopteridae, all inhabit fresh waters of Asia. Many species live in rapidly flowing streams and use suctorial mouths or modified pelvic fins to cling to the bottom. The Cobitidae, loaches, are elongate bottom-dwelling fishes which appear to be related to the Psilorhynchidae and Homalopteridae.

The characiform fishes include over 1,000 species which have diversified extensively in South America and to a lesser extent in Africa. In the Amazon River Basin, over 43 percent of the fishes are characoids (Roberts, 1972). Characiforms have been divided into about 16 families (Greenwood et al., 1966), of which five have African representatives. Trophic diversity is an important aspect of characiform evolution, and dental specialization and modifications of the jaw structure have occurred repeatedly. The Characiformes includes predaceous groups (Hepsetidae, some Characidae (which includes the piranhas), Erythrinidae, and Cynodontidae), as well as mud and detritus-eating fishes (Prochilodontidae, Curimatidae, and Anostomidae). Trophic interactions between ostariophysan fishes have been reviewed by Lowe-McConnell (1975) and Fink and Fink (1979).

The Siluriformes include the catfishes and gymnotoids. Catfishes (about 2,000 species in 31 families) are highly modified fishes with a distinctive morphology. Catfishes have large spiny first rays of the pectoral and dorsal fins which may be locked in the erect position. Thick bony plates may be present, and from one to four pairs of barbels presumably serve a tactile and gustatory function. Catfishes have a characteristic Weberian apparatus and a distinctive pectoral girdle.

The most primitive family is the relic South American Diplomystidae. The interrelationships of the other catfish families are presently unknown. Thirteen of the 31 catfish families are endemic to South America (Roberts, 1972), and the largest families are the Pimelodidae, Callichthyidae, and Loricariidae. In Europe, the Siluridae is the dominant group [some of which may attain a length of over 3 m (Nelson, 1976)], while in North America the Ictaluridae are the only native catfishes.

The gymnotoid fishes, which have in the past been considered to share a common ancestor with the characiforms, are of special interest to neurobiologists because of their electrogenic capabilities. The four families of gymnotoids, Apterontidae, Electrophoridae, Gymnotidae, and Rhamphichthyidae, are mostly nocturnal and insectivorous. The family Apterontidae is the most diverse family, with about 10 genera, although gymnotoid systematics at the genus and species level is in need of much further study. Apterontids presently appear to be unique among gymnotoids in having neurally derived electric organs which fire at much higher frequencies (1,000 to 1,800 Hz) than the myogenic organs of other families. *Electrophorus electricus*, the electric eel, is piscivorous and can produce a powerful electrical discharge. The gymnotoid fishes are restricted to South and Central America.

The Emergence of a New Pharyngeal Retractor Muscle

One of the most striking innovations during the evolution of the Euteleostei is the appearance and differentiation of a unique muscle associated with the upper pharyngeal jaws. This paired muscle is known as the retractor arcus branchialium (RAB; Rosen, 1973) or retractor dorsalis (RD; Winterbottom, 1974a). The anterior end of each retractor dorsalis inserts on the dorsal gill-arch elements (pharyngobranchials), and the posterior end originates from the first to sixteenth vertebrae (fig. 6). Fishes with an RD are grouped together in the subdivision Neoteleostei (fig. 2). Experimental studies (Liem, 1970, 1978) have shown that the retractors play a key role in manipulating, triturating, and swallowing of prey. This new functional design of the pharyngeal jaw apparatus is reflected in the spectacular adaptive radiation of the neoteleosteans. In the course of neoteleostean evolution the retractor dorsalis (RD) develops in numerous specialized ways that have proved to be helpful in phylogenetic analysis and very illuminating in studies of functional morphology.

The Stomiatiformes

It is often held (Weitzman, 1967) that the stomiatiforms are very closely related to the Protacanthopterygii (Salmoniformes). The stomiatiforms are considered to be the most primitive neoteleosteans. Stomiatiforms have the distinctly neoteleostean retractor dorsalis

muscle (RD). The stomiatiform RD insertion on the upper pharyngeal jaw is much more restricted and concentrated on the posterior element.

Stomiatiforms are composed of over eight families [e.g., Gonostomatidae (light fishes), Sternoptychidae (marine hatchet fishes), Chauliodontidae (viper fishes), Stomiatidae (dragonfishes)] and some 300 species that inhabit the middle depths of the Atlantic, Indian, and Pacific oceans. They are small, equipped with photophores, and have a mouth that extends posteroventrally past the eye.

The Aulopiformes

This small order of marine fishes contains among others the thread-sail fishes (Aulopidae) and greeneyes (Chlorophthalmidae). They form a primitive group of the neoteleosts (fig. 2). Thread-sail fishes live at moderate depths in the tropical and subtropical waters of the Indo-Pacific region and Atlantic; greeneyes have the same distribution but live at greater depths.

The most generalized condition of the RD is found in the aulopiforms. The RDs are still surrounded by the outer circular musculature of the esophagus. Anteriorly, the RDs fan out to form a flat sheet of muscle that inserts on the fourth epibranchial, and the ventromedial edge of the third pharyngobranchial (fig. 7).

The Myctophiformes

The lantern fishes (Myctophidae) with their photophores arranged along the side of the body like portholes, and pearleyes (Scopelarchidae) comprise a monophyletic assemblage of mostly deep-sea fishes possessing a suite of specialized characters which seem to indicate an intermediate level in neoteleostean evolution. This large and varied order is an ancient one, for myctophiforms were already abundant and diverse in the Upper Cretaceous. In the myctophiforms we can see the beginning of the evolutionary trend toward a shift of the insertion of the RD from the fourth, or third and fourth, entirely to the third pharyngobranchial. This change in insertion of the RD is related to the progressive reduction or loss of the fourth pharyngobranchial and its toothplate. As one ascends the neoteleostean evolutionary ladder, there is an increasing emphasis on the third pharyngobranchial as the dominant tooth-bearing element in the upper pharyngeal jaw.

Based on the structural and functional design of the upper pharyngeal jaws, the myctophiforms appear to be more closely related to the more advanced superorders Paracanthopterygii and Acanthopterygii (figs. 2, 8).

With the increased emphasis on the third pharyngobranchial and reduction of the fourth pharyngobranchial, the myctophiform RD is divided into a distinct medial component inserting on the third pharyngobranchial, whereas the lateral component retains the primitive insertion on the fourth pharyngobranchial (fig. 8). The dual insertions of the RD on the third and fourth pharyngobranchials in myctophiforms furnish the basic elements from which the more specialized upper pharyngeal jaws of the paracanthopterygians and acanthopterygians can be derived.

The lantern fishes (Myctophidae) occur in all oceans from the Arctic to the Antarctic and are known for their daily vertical migration. At night they migrate to the surface to feed; with the approach of day they start their return trip into the depths as far as 500 m down.

The Paracanthopterygii

No single character or combination of characters occurs in all paracanthopterygians (Rosen and Patterson, 1969). The taxa grouped under the Paracanthopterygii may in fact have evolved as discrete groups in parallel fashion from submyctophiform ancestors. Thus there are still doubts as to whether the Paracanthopterygii represent a monophyletic assemblage. Most paracanthopterygian orders date back to the Eocene and only the Percopsiformes is known from the Cretaceous. Other paracanthopterygians are not known from the Cretaceous, possibly because of the boreal Atlantic origin of the group. Explorations of the almost unknown marine vertebrate fauna of the Cretaceous of Greenland and Arctic Canada may provide fossils that can shed light on the origins and early evolution of the paracanthopterygians. Despite the lack of a uniquely distinguishing character for the paracanthopterygians, we are offering a provisional scheme of a monophyletic nature.

The Paracanthopterygii may be defined on the basis of an elongate neural spine on the second preural vertebra (fig. 9A). Furthermore, only two epural bones are present and the hypurals fuse into plates (fig. 9A). The functional significance, if any, of these specializations

in the caudal skeleton characterizing the Paracanthopterygii as a monophyletic lineage, remains unknown.

The paracanthopterygian radiation comprises five orders: Percopsiformes, Gadiformes, Batrachoidiformes, Lophiiformes, and Gobiesociformes, and contains between 200 and 250 genera. Only five genera of the percopsiforms, the gadiform *Lota*, a few brotulids, some batrachoidiforms, and the fluviatile gobiesocids are freshwater fishes. All other paracanthopterygians are primarily marine, many occupying dysphotic environments.

The Paracanthopterygii have diverged from ancestors of the basal acanthopterygian type along evolutionary pathways opposite to those of acanthopterygian fishes. The paracanthopterygian evolutionary trends that are the reverse of those characteristic of generalized acanthopterygians are: (1) a decrease in the depth of the head and trunk, (2) a reduction and eventual loss of median fin spines, (3) an increase in the number of abdominal vertebrae relative to the caudals, and (4) a reduction in spiny "ornaments" on the bones of the cheek and operculum.

Order Percopsiformes

The Percopsiformes [trout perches (*Percopsis*), pirate perches (*Aphredoderus*) and cave fishes (*Amblyopsis*, *Chologaster*)] is the only paracanthopterygian group confined to fresh water. It is restricted to North America. All percopsiforms have a reduced gape of the mouth and oral dentition. Although median fin spines are either reduced or lost, most percopsiforms have retained the spine ornamentation of the head.

The amblyopsids have sensory papillae or tactile organs in very prominent rows on the head, body, and tail. These sensory organs compensate for the lack of vision in the blind species or the rudimentary vision in the eyed forms.

Order Gadiformes

This order includes cods (Gadidae), hakes (Merluccidae), cusk eels (Ophidiidae), pearlfishes (Carapidae), eel pouts (Zoarcidae), grenadiers, and rattails (Macrouridae). Except for a few species, the Gadiformes are marine. The earliest gadiforms from the Eocene were similar in structure to early percopsiforms, but almost all remained marine and subsequently specialized to exploit a wide variety of environments.

Gadiforms (fig. 10) are elongate fishes, often of the deeper and colder dysphotic marine habitats, with the

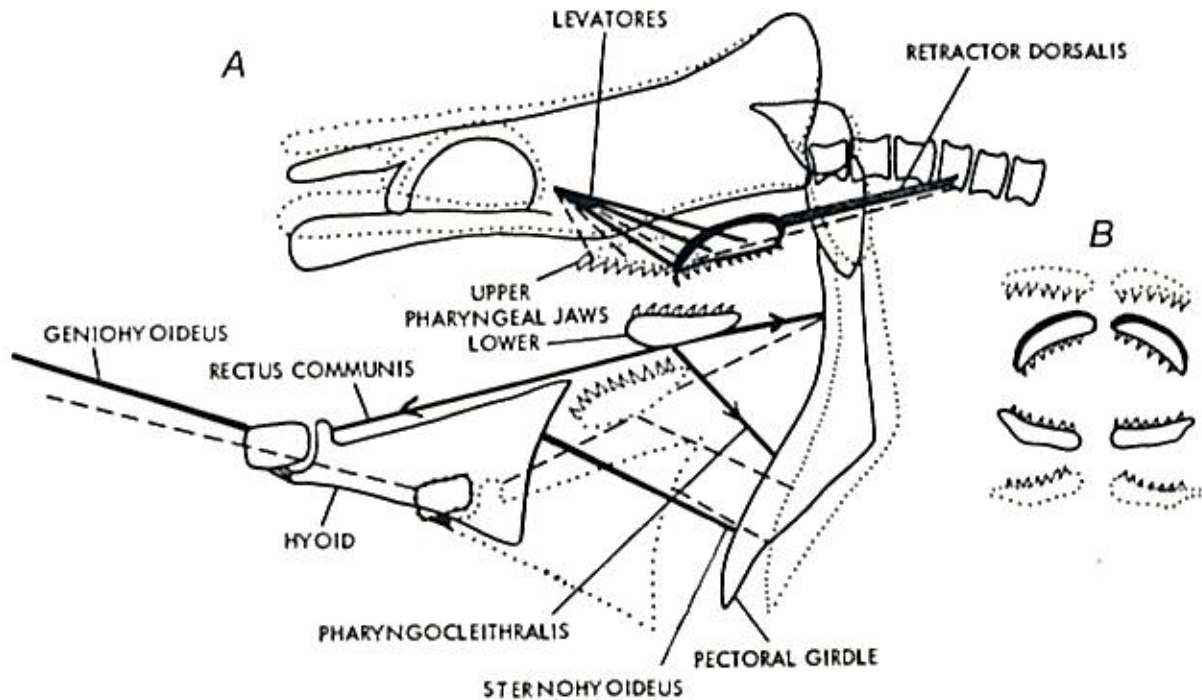


Fig. 6. (A) Simplified diagram depicting the retractor dorsalis (or retractor arcuum branchialium, RAB) muscle in euteleosts. Solid lines show position and condition of muscles during retraction of the pharyngeal jaws. Bony elements in

solid lines represent position during full retraction, while dotted outlines indicate positions during protraction. (B) Front view of upper and lower pharyngeal jaws during retraction (solid lines) and protraction (dotted lines).

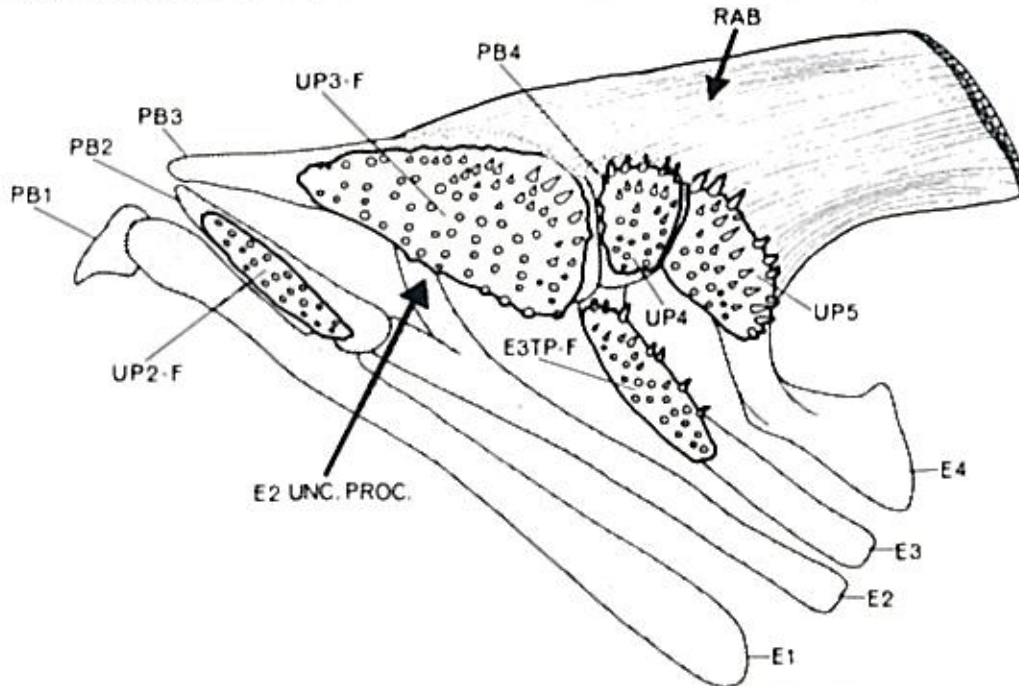


Fig. 7. Dorsal gill arch elements and the retractor dorsalis (RAB) muscle in the autopiform *Aulopus* (ventral view). The muscle fans out to insert on the third and fourth pharyngobranchials and fourth epibranchial. The second epibranchial (E2) has a prominent uncinat process (E2 UNC. PROC.).

E1-E4, epibranchials; PB1-PB4, pharyngobranchials; RAB, retractor arcuum branchialium or retractor dorsalis muscle; TP, toothplate; TP-F, toothplate fused with endoskeleton; UP, upper pharyngeal toothplates.

tail reduced or confluent with the dorsal and anal fins (which are long, many-rayed, and in many cases secondarily subdivided), with very reduced fin spines, and with a tendency to develop pelvic fins anterior to (jugular position) the pectoral fins and mental or circummental barbels. In the upper jaw the postmaxillary process on the premaxilla is distinctly notched. More advanced gadiforms have the olfactory bulbs at the olfactory organs and at a distance from the rest of the brain (Svetovidov, 1948).

It is postulated that the gadiforms are more closely related to the percopsiforms (fig. 10) than to any other paracanthopterygian, because the two orders share many specializations, which are thought to reflect common ancestry (e.g., the position of the olfactory bulb at the olfactory organ).

The Gadidae containing the cods, haddocks, pollocks, and whittings are predominantly a cold- and temperate-water group occurring mostly in the northern hemisphere. They represent the world's most valuable food fishes. Many species live near the bottom and exploit the benthic invertebrate fauna as food. Gadids also hold the record for being the most prolific egg producers, a single large female laying around 9,000,000 eggs in one spawning season.

The remaining lineage has radiated into three directions, the Batrachoidiformes, Lophiiformes, and

Gobiesociformes. Many specializations link these three groups together. The skull roof is greatly flattened and the parasphenoid either approaches (Gobiesociformes) or is sutured (Lophiiformes, Batrachoidiformes) to the frontals. With the flattening of the skull the sphenotics have become very large, flaring forward and laterally, while the infraorbital bones are represented only by a lacrimal.

Key features that relate the batrachoidiform lineages with the gadiforms are found in the gill cover, the median fins, and skin. In both the gadiforms and batrachoidiform lineages the operculum is reduced, while the suboperculum has become greatly enlarged, forming most of the distinctly angular gill cover and extending upward and backward to the posterodorsal tip of the operculum. Both lineages have usually reduced scales or lost them altogether.

The three orders within the batrachoidiform lineage differ in a number of structural specializations concerned with feeding and locomotion.

Order Batrachoidiformes (Toadfishes, e.g., *Opsanus*)

Batrachoidiforms are primarily coastal benthic fishes of the Atlantic, Indian, and Pacific Oceans. They made their first appearance during the Miocene. Batrachoidiforms are slow-moving bottom fishes with

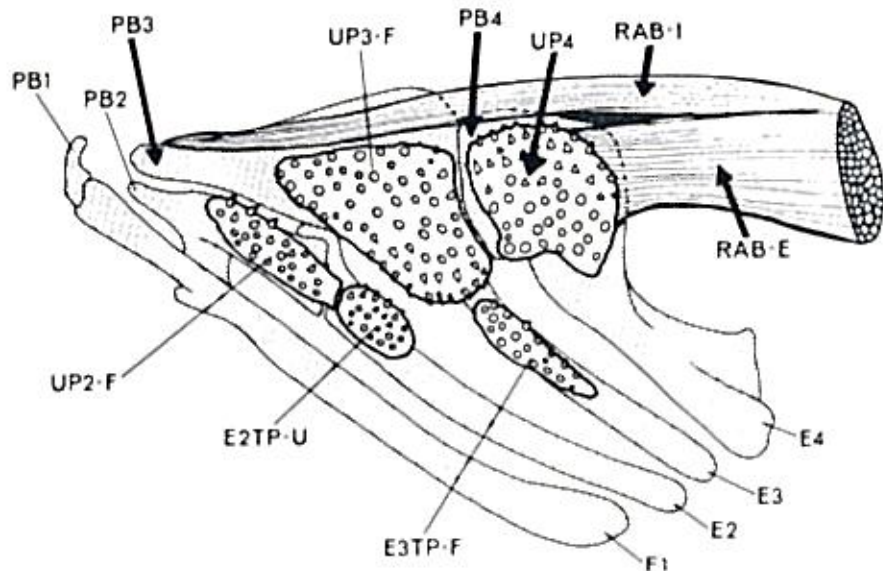


Fig. 8. Dorsal gill arch elements and the retractor dorsalis (RAB) muscle in the myctophiform *Neoscoptes* (ventral view). The muscle is subdivided into an internal (RAB-I) and external (RAB-E) division, inserting respectively on the third pharyngobranchial (PB3) and the fourth upper pharyngeal toothplate (UP4). E1-E4, epibranchials; PB1-PB4, pharyngobranchials; RAB-I, internal division of retractor dorsalis; RAB-E, external division of retractor dorsalis; TP-F, toothplate fused to endoskeleton; UP, upper pharyngeal toothplate.

(UP4). E1-E4, epibranchials; PB1-PB4, pharyngobranchials; RAB-I, internal division of retractor dorsalis; RAB-E, external division of retractor dorsalis; TP-F, toothplate fused to endoskeleton; UP, upper pharyngeal toothplate.

short spinous dorsal fins and long soft-rayed dorsal fins. The five radial bones supporting the pectoral fins are typically elongate. Toadfishes can live out of water, sometimes for hours, and make sounds, usually grunts, growls, or single boat-whistle blasts. The sound is produced by the swim bladder in association with specialized muscles.

Order Lophiiformes

The goosefishes (Lophiidae), anglerfishes (Ceratioidei), frogfishes (Antennariidae), and batfishes (Ogcocephalidae) date back to the Eocene. These often grotesque-looking marine fishes are widespread in shallow water as well as deep-sea habitats. Their best trademark is the modification of the spinous dorsal fin into a movable lure. However, most of the major specializations of lophiiforms concern the feeding mechanism, which in general is adapted to the taking of large prey at exceedingly high speeds. The pectoral girdle is greatly modified in accordance with the development of clasping, prehensile, and "walking" mechanisms in the wholly benthic forms. Many members have fewer than five elongate radials. The Lophiiformes has undergone a major radiation, comprising 15 families with about 215 species. During this radiation numerous highly specialized and bizarre forms emerged. In some families the males are parasitic on the females, attaching firmly with their jaws and becoming, in most cases, completely dependent on the female for their basic physiological functions.

Order Gobiesociformes

Gobiesociforms (clingfishes) are small, flattened, depressed fishes with a ventral sucker formed of the modified pelvic fin and surrounding tissue. They are marine and occasionally freshwater fishes in the tropics and along many temperate seacoasts. The extreme dorsoventral flattening of the head and body has much modified the orientation and shape of the bones in the jaw suspension and opercular apparatus. The jaws are adapted principally to the cutting and scraping of short adherent vegetation. Most of their specializations are closely related to their ecological preferences for regions characterized by rapid water exchange, such as the intertidal zone and steeply descending freshwater streams (fig. 10).

The Acanthopterygii

This vast group of advanced neoteleosts had its beginnings in the Cretaceous. The Acanthopterygii and Paracanthopterygii can be considered as members of a monophyletic lineage (fig. 2) because both groups show strong development of ctenoid scales (already present in the myctophiforms), armored opercular bones, and an elongation of the ascending and articular processes of the premaxilla. Furthermore, in both groups there are evolutionary trends toward an elevation of the pectoral fins on the flank and movement of the pelvic fins anteriorly. An obvious feature of generalized acanthopterygians, and one to which this term refers, is the differentiation of stiff spines in the

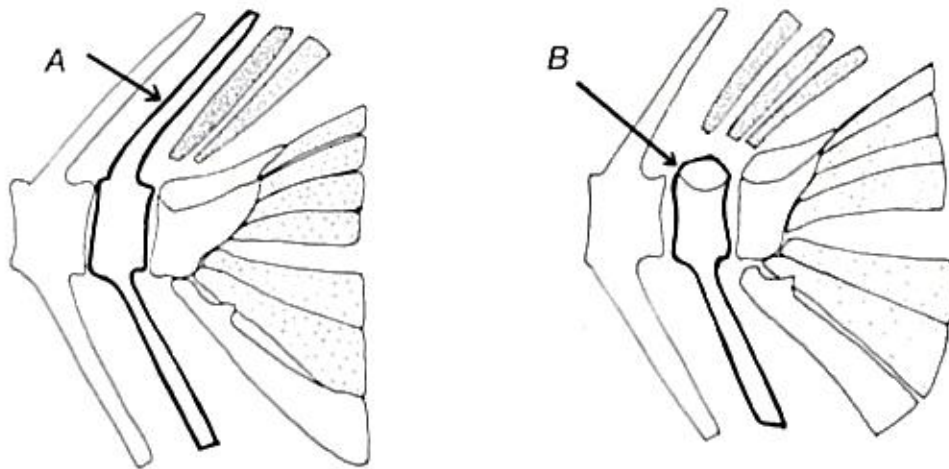


Fig. 9. (A) Caudal skeleton of a representative paracanthopterygian. (B) Caudal skeleton of a primitive acanthopterygian. Arrows indicate the second preural neural spine, which becomes reduced into a low crest in the acanthopterygians (B).

The second preural vertebra is emphasized by a heavier line. Epurals are densely stippled, and the hypurals are lightly stippled.

anal and dorsal fins. The lineage has undergone an immense radiation. It includes a great majority of modern marine fishes as well as a large number of freshwater forms. The acanthopterygians represent a monophyletic group because all members share several major structural and functional specializations. The upper pharyngeal jaw apparatus is characterized by a specialized retractor dorsalis muscle that inserts principally or entirely on the third pharyngobranchial. In the caudal skeleton the spine of the second preural vertebra is reduced to a low crest (fig. 9B).

Whereas in the myctophiform and paracanthopterygian feeding mechanism the upper jaw symphysis undergoes little or no forward movement, the acanthopterygian mechanism has developed a much more mobile upper jaw. With the emergence of a well-developed ascending process on the premaxilla, the symphyseal and alveolar parts of the bone are cap-

able of significant forward displacement or protrusibility. Upper jaw protrusion in acanthopterygians can be accomplished in at least four different ways (Liem, 1978) and can be modulated precisely by various patterns of muscle contractions. Thus, the acanthopterygian jaw apparatus is a truly prehensile device with a tremendous built-in versatility. As a result, the adaptive expressions seen in the acanthopterygian jaw apparatus are dramatically diverse.

Order Atheriniformes (Atherinomorpha)

This order originated in the Eocene and contains about 16 families, including the killifishes (Cyprinodontidae), live-bearing topminnows (Poeciliidae), silversides (Atherinidae), needlefishes (Belontiidae), and ocean flying fishes (Exocoetidae). Atheriniforms have a worldwide distribution inhabiting marine shores and fresh waters both in tropical and temperate climates.

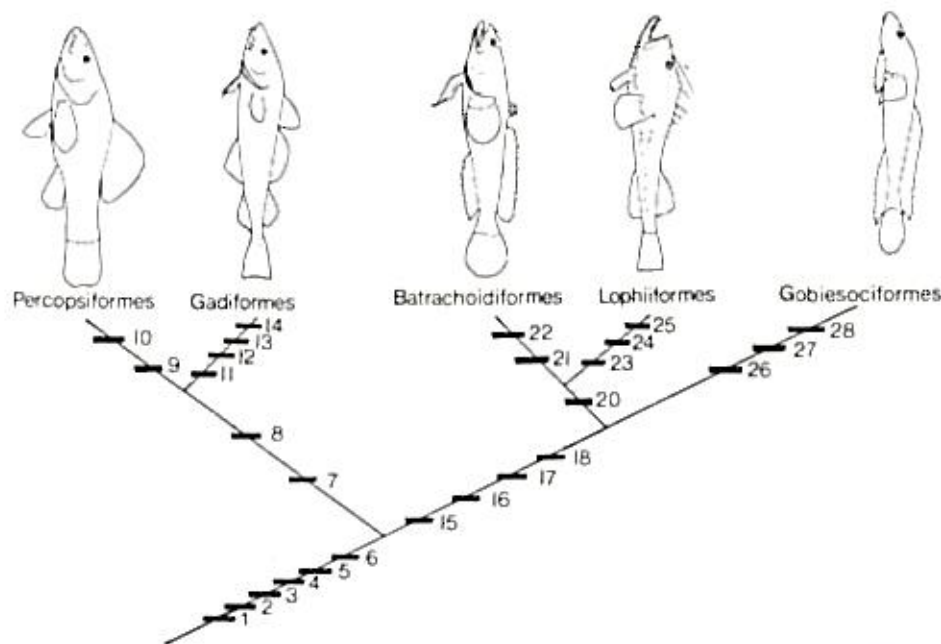


Fig. 10. Interrelationships of the major groups of the Paracanthopterygii. Major specializations characterizing the various lineages are: 1, increase in the number of abdominal vertebrae; 2, decrease in the depth of the head and trunk; 3, suboperculum becomes enlarged and the operculum is reduced; 4, anterior vertebrae crowded and linked; 5, trend toward various patterns of fusions of the hypurals; 6, in the caudal skeleton the second preural centrum possesses a complete spine; 7, pterosphenoïd and parasphenoïd are touching; 8, olfactory bulb at the olfactory organ and at a long distance from the rest of the forebrain; 9, in the caudal skeleton there are two large bony plates, representing fused hypurals borne on two separate centra; 10, reduced gape of the mouth and oral dentition; 11, postmaxillary process of

the premaxilla notched; 12, tail reduced or confluent with dorsal and anal fins; 13, pelvic fins in jugular positions; 14, presence of mental barbels; 15, skull of roof has become flattened; 16, parasphenoïd and frontal bones are either approaching each other or sutured to each other; 17, large sphenotics flaring forward and laterally; 18, progressive reduction in the ossification of the palatopterygoid; 20, radials have become very elongate; 21, entopterygoid is not ossified; 22, short spinous dorsal fin and long soft dorsal fin; 23, modified pectoral girdle correlated with "walking" mechanism; 24, spinous dorsal fin modified into a lure; 25, all palatopterygoid bones reduced; 26, extreme dorsoventral flattening; 27, all pterygoid bones lost; 28, pelvic fins modified into a sucker.

The atheriniforms represent a major radiation at the advanced neoteleostean level. The most distinctive specialization has evolved in the caudal skeleton, in which two large, triangular, hypural plates of opposite symmetry are borne on the terminal centrum. It is postulated (Rosen, 1964) that the left and right premaxillae are capable of and normally undergo independent movement during jaw protrusion. Typically, the upper jaw lacks crossed ligaments and rests on top of a disklike mesethmoid. Although the significance of the elongation and expansion of the alveolar (tooth-bearing) arm of the premaxilla is still unknown, the feature is pervasive within the atheriniforms. As a result of this elongation the alveolar arm of the premaxilla becomes interpolated between the maxilla and the mandible, and has gained a direct ligamentous connection with the mandible.

Included in this monophyletic assemblage is a large number (16 families, about 830 species) of small fishes of varied appearance and habits. Many are valued as aquarium fishes, and quite a few have served as exemplary experimental subjects: egg-laying topminnows (Cyprinodontidae) of which the brackish-water "chub" or common killifish, *Fundulus heteroclitus*, of the eastern United States is probably the best known to experimental biologists. Included here also are fishes whose eggs are impervious to desiccation and develop at varying rates to spread the risks in unpredictably varying harsh environments. Egg-laying cyprinodonts are often brightly colored and enter the aquarium fish trade as medakas, lyretails, and panchaxes. The viviparous topminnows (Poeciliidae), to which the guppy (*Poecilia reticulata*) and world-famous mosquitofish (*Gambusia affinis*) belong, practice internal fertilization during which one batch of sperm fertilizes several successive broods. Some molly species (*Mollienesia formosa*) are composed only of female populations and use a male of another species, which contributes nothing to the gene pool of his offspring. The famous four-eye fishes belong to the family Anablepidae. Each eye in *Anableps* is divided into an upper section for aerial vision and a lower for aquatic vision. Among types placed in the Atheriniformes are the "flying fishes" (Exocoetinae: e.g., *Exocoetus* and *Cypselurus*). Close relatives of the flying fishes are the half beaks (Hemiramphinae: e.g., *Hemiramphus*), in which the lower jaw protrudes forward, and the needlefishes (Belontiidae: e.g., *Belone*), in which both jaws are elongated. The silversides (Atherinidae) have lost

the lateral line. One of the best known silversides is the grunion *Leuresthes tenuis*, which spawns on the beach at night during the period of the highest tides in correlation with the phases of the moon.

Order Beryciformes

With the rise of the Beryciformes late in the Cretaceous, a major upward step in neoteleostean evolution was made. The rise must have been a rapid one since beryciforms became abundant and diverse before the end of the Cretaceous (Patterson, 1964). These relatively primitive acanthopterygians are still present in seas today: the squirrelfishes (Holocentridae), alfonsinos (Berycidae), lantern-eye fishes (Anomalopidae), and pinecone fishes (Monocentridae) are better known examples.

The Beryciformes occupy a central and basal evolutionary position among the Acanthopterygii (fig. 11). By virtue of their unique evolutionary position and current uncertainty over their interrelationships, the Beryciformes offer numerous challenging phylogenetic and evolutionary problems to neurobiologists.

Order Lampridiformes and Order Zeiformes

Although the main trends of acanthopterygian evolution occur in the Perciformes, there seem to have diverged, at an early beryciform stage, an assemblage of odd types of mainly deep-sea fishes, the very specialized Lampridiformes (opahs) and Zeiformes (the dories and boarfishes). The proposed relationships of the Lampridiformes and Zeiformes to other perciforms is depicted in figure 11.

At this point it seems appropriate to observe that important changes in methods of locomotion have taken place during the evolution of the acanthopterygian fishes. The trend in the Beryciformes, Lampridiformes, and Zeiformes (fig. 11) is toward a shortening and deepening of the body with a decrease in the number of vertebrae. The pectoral fins are almost always well developed and have moved, possibly for greater maneuverability, high up the side of the body. Concomitantly, the pelvic fins have moved forward to a position below the pectorals, with the pelvic girdle attached to the cleithrum. Such a forward shift may serve as an aid toward proper balance necessitated by the upward move of the pectorals. The end results of this evolutionary trend are especially discernible among the Perciformes (fig. 11).

Order Gasterosteiformes

In general, sticklebacks (*Gasterosteus*), pipefishes (e.g., *Syngnathus*), and sea horses (*Hippocampus*) are considered relatively more advanced acanthopterygians. The gasterosteiforms appear to be another early but highly specialized side branch of the early acanthopterygians, possibly sharing a distant common ancestor with the Berycoiformes (fig. 11). In this group there is a reversal in the evolutionary trend to the deepening of the body. Thus, the body has become typically elongate and slender, and encased in a bony armor; the small mouth is at the end of a tubular snout. The sticklebacks are famous for the numerous studies made on their behavior and physiology. All members are slow-moving fishes. Because the Gasterosteiformes are so specialized, they provide little evidence of their exact phyletic origin (Pietsch, 1978).

Order Dactylopteriformes

Dactylopteriformes (flying gurnards) is a small order of aberrant fishes (fig. 11) whose relationships are still unknown. The dactylopteriforms have large pectoral fins, giving them an ability to "fly" in a way paralleling the exocoetoids or true flying fishes (see the section on atheriniformes).

Order Perciformes

This possibly monophyletic group can best be described as extraordinarily vast, containing well over 140 families, divided among about 20 suborders involving at least 6,900 species. It is without doubt the most diversified and largest vertebrate order, an example of major adaptive radiation (fig. 11). Perciforms (perchlike fishes) dominate vertebrate ocean life and also form a major component of the fish fauna in many tropical and subtropical fresh waters. The Perciformes emerged during the Upper Cretaceous and must have undergone a truly explosive radiation, for we find at the dawn of the Tertiary not only more generalized types, but a host of very specialized suborders and families. By the end of the Eocene we encounter representatives of over 60 distinct families.

The basal perciform caudal skeleton has only five hypurals, no free second ural centrum, and only 17 principal rays. It is interesting to note that the typically perciform functional and structural design of the caudal skeleton occurs in a wide range of perciform groups, including forms with rounded, forked, emarginate, and lunate caudal fins living in habitats rang-

ing from pelagic, marine, benthic, and riverine to lacustrine. Thus, the basic plan of perciform caudal architecture is rigidly maintained during the greatest adaptive radiation known among vertebrates.

As mentioned before, it is in the Perciformes that the evolutionary trend toward a deeper body, an upward shift of the pectoral fins, and a forward shift of the pelvic fins comes to full fruition (fig. 11).

It is believed that the Perciformes is a specialized sister group of the lineage containing the Berycoidei and Zeiformes.

As depicted in figure 11 the perciforms share specializations of the caudal skeleton, caudal fin, and the pelvic fin with the Scorpaeniformes, Tetraodontiformes, Pleuronectiformes, Channiformes, and Synbranchiformes. Thus, the entire assemblage is probably monophyletic. However, monophyly of the Perciformes is still questionable, because neither a single specialized character nor a combination of specialized characters has been found for this vast assemblage of advanced fishes. Thus, the Perciformes remain without precise definition (fig. 11). As a consequence, the relationships between the Perciformes, Scorpaeniformes, Tetraodontiformes, Channiformes, and Synbranchiformes are depicted as an unresolved polychotomy (fig. 11). A more precise statement of phylogenetic relationships awaits future research. For a discussion and survey of the various suborders of the Perciformes, the reader is referred to Gosline (1966, 1968, 1971) and Freihofner (1963, 1978).

Order Channiformes (Ophicephaliformes) and Synbranchiformes

Channiforms (snakeheads) and synbranchiforms (swampeels) can be considered perciform derivatives that have penetrated O₂-poor tropical fresh waters. In both groups, the trend is toward elongation of the body (fig. 11). Although their phylogenetic relationships are still unknown, there is some evidence that these two orders and the Anabantoidei share a common ancestry. All members of both orders share a specialized forebrain (fig. 12) and a highly modified fourth branchial artery. The telencephalon in teleosts is usually divided into very distinct and clearly separated right and left hemispheres by the ventriculus medius telencephali. However, in the channiforms and synbranchiforms the two hemispheres are not separated but clearly united posteriorly (fig. 12). The hypothesis advanced here is that the two orders share

a common ancestry and that the channiforms represent the more primitive lineage, while the synbranchiformes have become very specialized by losing pectoral, pelvic, median, and caudal fins (fig. 11), and developed an eel-like body and a highly vascularized buccopharyngeal mucous membrane as their principal respiratory organ. The channiforms also have elongate bodies, but their fins are very well developed. They possess an accessory air breathing organ which involves not only the vascularized buccopharyngeal mucous membrane, but also elaborate treelike structures attached to the first epibranchial, parasphenoid, and hyomandibula. The gills of channiforms remain well developed and functional.

Order Scorpaeniformes

The scorpionfishes (Scorpaenidae), sculpins (Cottidae), flatheads (Platycephalidae), and sea robins (Triglidae) form a complex group of widely divergent marine fishes that may be polyphyletic. Scorpaeniforms share a peculiar architectural specialization in their skulls: a bony posterior extension of the third suborbital bone (one of the ossicles surrounding the eye) extends across the cheek to the preoperculum. Twenty-one families and about 1,000 species are grouped in the Scorpaeniformes, which contain the world's most venomous fishes (stonefishes have venom glands near the base of hypodermiclike dorsal fin spines containing neurotoxins fatal to humans). It has been suggested that scorpaeniforms are derived from percoids that have become semisedentary bottom forms.

Order Tetraodontiformes

The triggerfishes and filefishes (Balistidae), boxfishes (Ostracioidae), puffers (Tetraodontidae), and porcupine fishes (Diodontidae) are among the most advanced of all fishes (Winterbottom, 1974b). Numerous structural and functional specializations can be seen in the various evolutionary lineages. Among the more pervasive and important ones is the development of small, but mechanically very efficient and powerful shearing jaws. All tetraodontiforms demonstrate remarkable structural specializations that increase the maneuverability of the fish by appropriate movements of the fins. With this new functional design, precisely controlled movements can be made by passing undulations back and forth along the dorsal and anal fins. As

is often the case with slow-moving fishes, the tetraodontiforms have developed an impressive array of protective devices [i.e., spines (porcupine fishes), bony armor (boxfishes), poisonous flesh (puffers), or poisons that exude into the water (boxfishes, Ostracioidae)]. Tetraodontiforms have a restricted gill opening that never extends far below the base of the pectoral fin, no lateral line, and have maxillae with the premaxillae connected or fused. It is interesting that highly specialized tetraodontiforms differentiated as early as the Eocene.

Order Pleuronectiformes

This order dates back all the way to the Eocene, and contains the left-eye flounders (Bothidae), right-eye flounders (Pleuronectidae), soles (Soleidae), and tonguefishes (Cynoglossidae). Adults of all pleuronectiforms have both eyes on the same side, and the group is thus bilaterally asymmetrical. Pleuronectiforms have evolved very pronounced adaptations to a truly bottom life. They are best known for their ability to blend their body colors with the substrate and their asymmetrical body shape. It is postulated that flatfishes have been derived from compressed, deep-bodied percoid ancestors, which have settled to the bottom on one side, with subsequent asymmetrical developments of the new upper (eyed) and lower (blind) surfaces. In flounders the crossing of the optic nerves is so arranged that when the eye crosses over to the eyed side the chiasm untwists.

Summary

The interrelationships of the major lineages comprising the Actinopterygii or ray-finned fishes are reviewed with particular regard to currently unsolved taxonomic problems. We summarize recent research on the phylogeny of fishes to provide a basis for interpreting the evolution of the nervous system. Both the Actinopterygii and its major subgroup, the Teleostei, are monophyletic. Within the Teleostei there are a number of monophyletic lineages such as the Clupeomorpha (herrings), Osteoglossomorpha (bony-tongued fishes), and Ostariophysii (characins, catfishes, and minnows), but the relationships within the largest teleost subgroup, the Acanthopterygii, are only poorly known.

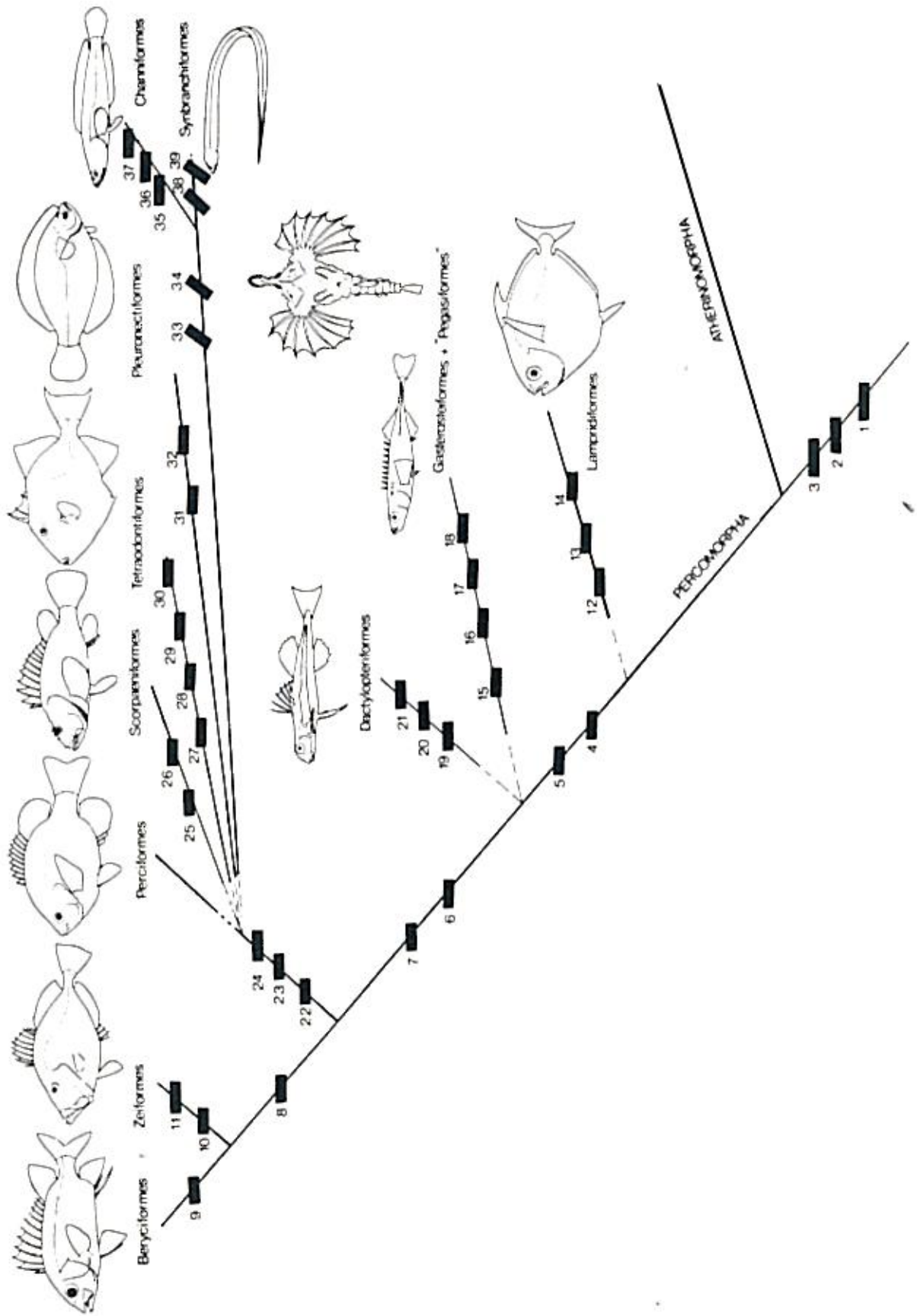


Fig. 11. Interrelationships of the major groups of the percomorph Acanthopterygii. Major specializations characterizing the various lineages are: 1, retractor dorsalis muscle inserts principally or entirely on the third pharyngobranchial; 2, symphyseal and alveolar parts of the premaxilla are capable of significant downward displacement; 3, spine of second preural vertebra is reduced to a low crest; 4, separate soft and spinous dorsal fins; 5, pelvic girdle attached to cleithrum; 6, second circumorbital bone with subocular shelf; 7, pelvic fin with spine and five rays; 8, saccule (otolith) morphology specialized; 9, presence of specialized procurrent caudal spines; 10, decrease in number of vertebrae; 11, deepening of the body; 12, maxilla slides out with premaxilla during jaw protrusion; 13, no true spines in fins; 14, pelvic girdle attached to a large specialized hypacoracoid; 15, body encased in bony armor; 16, small mouth at end of tubular snout; 17, number of branchiostegals reduced (1-5); 18, trend to either reduce or modify

gills; 19, no lateral line; 20, enlarged pectorals; 21, body covered with scutelike scales; 22, no free second urol centrum; 23, 17 principal caudal rays; 24, caudal skeleton with five hypurals; 25, hypurals fused into two distinct, large plates; 26, third circumorbital bone with an extension attached to the preoperculum; 27, maxilla and premaxilla fused; 28, no lateral line; 29, gill opening restricted to a very small slit; 30, specialized dermal protective devices; 31, median fins extend along much of body profile; 32, bilateral asymmetry affecting topography of the eyes and coloration; 33, fourth branchial arteries modified; 34, hemisphere of forebrain coalesced; 35, fins without spines; 36, specialized air-breathing organs derived from first and second epibranchial, hyomandibular, and parasphenoid bones; 37, attachment between pelvic girdle and cleithrum lost; 38, body elongate, pelvic and pectoral fins lost, and median fins reduced; 39, gill openings fused into a single, median, ventral slit.

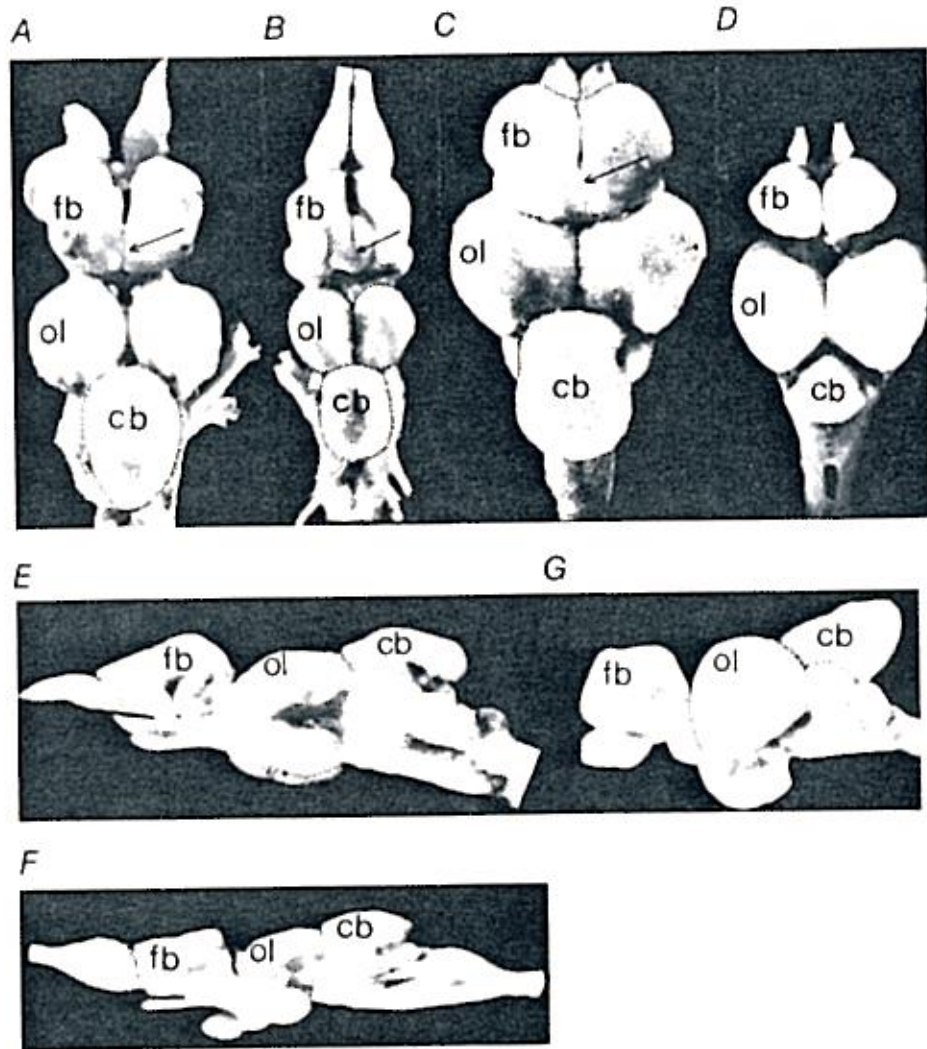


Fig. 12. Dorsal views of the brains of the channiform *Channa* (A), synbranchiform *Monopterus cuchia* (B), anabantoid *Helostoma* (C) and the luciocephaloid *Luciocephalus* (D). Note the interconnected forebrains in A–C. In *Luciocephalus* the two halves are separate. Lateral views of the

brains of *Channa* (E), *Monopterus* (F), and *Helostoma* (G). Note the striking similarities in specializations of the brains of *Channa* (A,E) and *Monopterus* (B,F). cb, cerebellum; fb, forebrain; ol, optic lobe (arrows indicate forebrain fusions).

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