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The Evolution and Interrelationships  
of the Actinopterygian Fishes

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# THE EVOLUTION AND INTERRELATIONSHIPS OF THE ACTINOPTERYGIAN FISHES

GEORGE V. LAUDER<sup>1</sup> and KAREL F. LIEM<sup>2</sup>

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**ABSTRACT.** The phylogenetic relationships of ray-finned fishes are critically reviewed, and major features in the evolution of actinopterygian fishes are discussed and summarized. Significant progress has been made over the last fifteen years in defining the interrelationships of ray-finned fishes, but much of this progress has not been widely noted, especially by experimental biologists. Several currently accepted higher taxa are only poorly defined (e.g., the Acanthopterygii) while others are not corroborated by any uniquely derived features (the Protacanthopterygii and Paracanthopterygii). These taxa

exemplify areas in need of reexamination by systematic ichthyologists.

## INTRODUCTION

The ray-finned fishes comprising the subclass Actinopterygii form by far the most diverse group of vertebrates. With almost 23,000 species of actinopterygian fishes known, they total more than half of all extant vertebrate species and have diversified to an extent unparalleled within the chordates. This tremendous radiation has resulted in extensive variation not only in morphology but also in behavior and ecology, and members of the most advanced group of actinopterygians, the Teleostei, have penetrated virtually every conceivable habitat and range from the ocean depths (-11,000 m) to high mountain streams (+4,500 m) and from hot springs (43° C) to subfreezing water (-1.8° C) (Lagler *et al.*, 1977; J. Nelson, 1976; Somero and De Vries, 1967). Teleosts also contain the smallest adult vertebrates, with one species becoming adult at 7.5 mm or less (Miller, 1979). While this diversity has provided fertile ground for comparative studies on actinopterygian anatomy, behavior, and ecology, it has also compounded the problems faced by systematic ichthyologists in unravelling the interrelationships and evolutionary history of the actinopterygian fishes. In the last fifteen years, and especially since the monograph by Greenwood *et al.* (1966), considerable progress has been made in determining the relationships between the various major groups of ray-finned

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fishes. The primary goals of this review will be to summarize the recent advances in phylogenetic reconstruction, present these data in a form that will be of use to ichthyologists, vertebrate paleontologists, and comparative and experimental biologists in general, and to integrate major recent discoveries in functional morphology into a phylogenetic context. The lack of a current critical review of progress and problems in the analysis of actinopterygian evolution has stimulated this paper. We have not attempted an exhaustive survey of the literature on actinopterygian fishes, nor have we solved many of the current problems in fish phylogenetics. Rather, we highlight those areas most in need of further work, and rely heavily, but not exclusively, on the literature for characters supporting monophyly of the major actinopterygian subgroups. In providing a general critical review, we hope to clearly define the areas in which current data are inadequate to support both hypotheses of relationship and functional evolutionary scenarios, as well as to contribute new ideas and suggestions for resolving problems of pattern and process in actinopterygian evolution.

Recent advances in deciphering actinopterygian phylogenetic patterns have been primarily achieved by applying the principles of phylogeny construction formulated by Hennig (1966). (More recent summaries of genealogical methodology may be found in Eldredge and Cracraft, 1980; Gaffney, 1979; Wiley, 1975, 1976.) In presenting a review of actinopterygian relationships and biology, then, we will emphasize monophyletic assemblages of taxa (*sensu* Hennig) defined as follows: a monophyletic taxon is a group stemming from a single common ancestor and containing all known descendants of that ancestor. In recent years, systematic ichthyologists have increasingly regarded monophyletic lineages as representing natural evolutionary units, and have attempted to identify monophyletic taxa by

uniquely derived structural attributes. The large degree of recent success achieved in this endeavor is manifested by the number of corroborated nested sets of structural features (see, for example, Figures 1, 14, and 19) which can serve as a basis for interpretations of evolutionary trends and processes.

An alternative approach, the analysis of the pattern of diversification in terms of general grades of evolutionary "advancement," tends to obscure phylogenetic (genealogical) patterns and conceals evolutionary sequences of structural change. We will precisely define the various actinopterygian groups, where possible, in terms of monophyletic lineages; in several cases insufficient information is available to define certain currently accepted major taxa as natural groups.

The relationships of the actinopterygian fishes to the other major groups of lower vertebrates will be examined briefly before we turn to a consideration of the relationships and general biology of the actinopterygian subgroups. An understanding of structural patterns and trends in the diversification of the ray-finned fishes is of critical importance for a meaningful analysis of actinopterygian functional morphology and evolution.

## RELATIONSHIPS OF THE ACTINOPTERYGII

In recent years the interrelationships of the major groups of lower vertebrates have been considered in detail by various investigators, but a consensus has not emerged. Romer (1966), G. Nelson (1969a), Gardiner (1973), and Miles (1977) have all proposed differing hypotheses of how the Actinopterygii (ray-finned fishes), Actinistia (coelacanth), Dipnoi (lungfishes), and "rhipidistian" fishes and tetrapods are related (also see Forey, 1980; Jarvik, 1980; Lovtrup, 1977; Rosen *et al.*, 1981; Wiley, 1979a).

In Figure 1 we present one hypothesis of the interrelationships of these groups

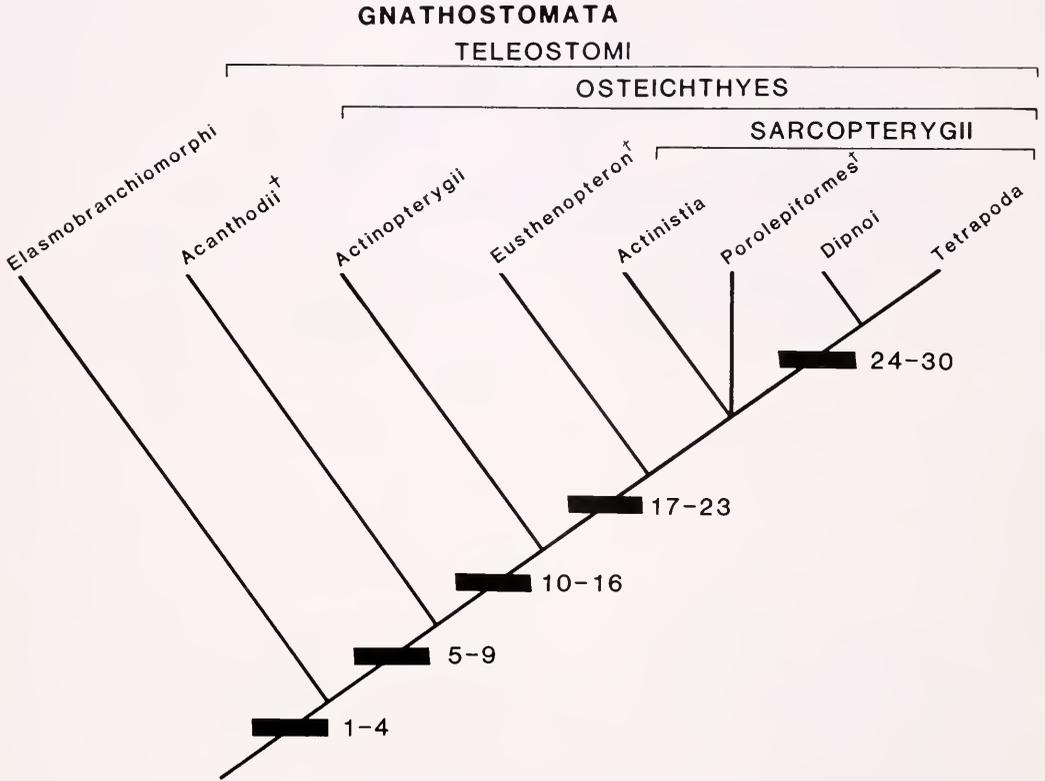


Figure 1. Branching diagram (cladogram) representing the phylogeny of the major groups of lower vertebrates. This and subsequent cladograms show the historical sequence of character acquisition in the lineage and reflects the genealogical relationships of the terminal taxa. The characters that indicate relationship between the various lineages are represented by a black bar at the appropriate level. Note that several of the characters listed on the cladograms apply only to living forms and thus do not corroborate the location of fossil taxa. The discovery of new fossil material or new anatomical features in extant taxa may change the level at which any given character indicates shared ancestry. The characters are: **1**, the presence of three semicircular canals (placoderms also share this feature); **2**, the presence of a ventral otic fissure between the embryonic trabecular and parachordal segments of the chondrocranium; **3**, the presence of a lateral occipital braincase fissure; **4**, five other characters listed by Rosen *et al.* (1981) including branchial arches consisting of basibranchial, hypobranchial, ceratobranchial, epibranchial and pharyngobranchial elements, and internal supporting girdles for the pectoral and pelvic appendages; for further discussion of elasmobranchiomorphs and other characters at this level see Maisey, 1980, 1982; Schaeffer, 1981; Schultze and Truab, 1981; **5**, ossified dermal opercular plate(s) covering the gills laterally; **6**, presence of an interhyal bone in the hyoid arch (Gardiner, 1973: 129); **7**, branchiostegal rays present (Miles, 1973); **8**, mandibular depression primarily mediated by posteroventral rotation of the hyoid apparatus (inferred from the similarity of the hyoid—palatoquadrate relationships to that in osteichthyans (see Lauder, 1980c; Miles, 1973), and a mandibulohyoid ligament is inferred to have been present); **9**, sclerotic ring present (see Miles, 1973; Moy-Thomas and Miles, 1971); **10**, transversi ventrales gill arch muscles present (Wiley, 1979); **11**, interarcuales ventrales muscles present (Wiley, 1979); **12**, hypohyal bones present in the hyoid arch (Gardiner, 1973; Miles, 1973); **13**, medial insertion of the adductor mandibulae complex in the mandibular fossa (Lauder, 1980b); **14**, pleural ribs present (Schaeffer, 1968); **15**, lepidotrichia present (see text); **16**, unique ossification pattern in the dermal shoulder girdle (suprascapular, supracleithrum, cleithrum, and clavicle; Schaeffer, 1968)—many other characters corroborating a monophyletic osteichthyans are listed in Rosen *et al.* (1981); **17**, true enamel present on the tooth surface (Smith, 1978); **18**, double articulation of the hyomandibula with the neurocranium (Gardiner, 1973); **19**, unique supporting skeleton in paired fins; **20**, presence of an endoskeletal urohyal (Patterson, 1977); **21**, last gill arch articulates with base of preceding arch (Rosen *et al.*, 1981: 257); **22**, muscular lobes form the base of pelvic and pectoral appendages (Rosen *et al.*, 1981); **23**, anocleithrum subdermal (Rosen *et al.*, 1981; additional characters are also given in this paper); **24**, presence of a choana (see Rosen *et al.* [1981] for a detailed discussion of this controversial character); **25**, structure of the pelvic girdle (Rosen *et al.*, 1981); **26**, the presence of multiple pharyngoclaviculari muscles (Wiley, 1979a); **27**, numerous other features of soft anatomy such as partially divided conus arteriosus, an atrial septum, and ciliation of larval forms (see Gardiner, 1973; Rosen *et al.*, 1981; Whiting and Bone, 1980); **28**, dermal bone pattern covering the braincase; **29**, loss of interhyal; **30**, structure of the pelvic and pectoral appendage (see Rosen *et al.* [1981] for an extended discussion).

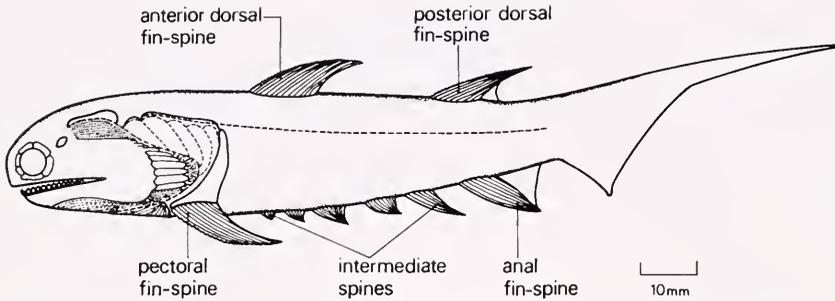


Figure 2. *Climatius reticulatus*, a Lower Devonian acanthodian fish. (From Moy-Thomas and Miles [1971], courtesy of W. B. Saunders Publishing Co.)

based on an analysis of the distribution of various characters (listed in the caption). This figure indicates that the actinopterygians share a common ancestor with a group consisting of the coelacanth (Actinistia), lungfishes, and tetrapods, and that these two groups together share a common ancestor with the acanthodian fishes.

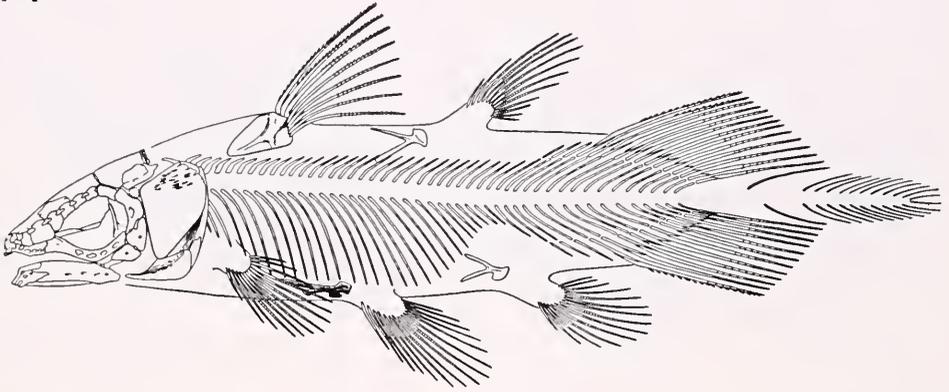
The Acanthodii, often very inappropriately called "spiny sharks," first appear in the fossil record in the Lower Silurian. They are the most primitive members of the teleostome fishes (Fig. 1) and are characterized by pectoral fin spines, strong spines anterior to the dorsal and anal fins, and the presence of numerous small bony plates which form a protective cover over the branchial chamber (Fig. 2). Primitively the acanthodian fishes possess two dorsal fins which have internal unsegmented stiffening rays (Moy-Thomas and Miles, 1971). These fishes have rather large eyes relative to their head size and are generally assumed to have fed in the midwater or on the surface.

The Actinistia or coelacanth (Fig. 3) are first known from the Middle Devonian and are represented today by the single genus, *Latimeria*, discovered in 1938 off East London, South Africa. The coelacanth has two dorsal fins, two external nostrils, and an intracranial joint—a division between the anterior and posterior portions of the cranium allowing the

anterior (ethmosphenoid) portion to be elevated during feeding (see Lauder, 1980a; Thomson, 1966, 1967). The caudal fin of coelacanth has a characteristic diphyccercal or "tassel shape" (Fig. 3) with a central caudal lobe flanked dorsally and ventrally by two additional lobes. In Devonian coelacanth the brain appears to have nearly filled the cranial cavity (Stensio, 1963) while in the recent *Latimeria* the brain in the adult is significantly smaller than the cranial cavity, occupying only the otico-occipital division of the braincase and less than 1 percent of the total endocranial volume (Nieuwenhuys *et al.*, 1977). Throughout the long evolutionary history of the actinists their morphology has remained remarkably constant although there has been a general trend towards a reduction in neurocranial ossification (see Forey [1981] for a consideration of coelacanth phylogeny).

The Dipnoi or lungfishes (Fig. 4) originated in the Lower Devonian and have a long history culminating in three extant genera (Thomson, 1969). The earliest lungfishes differ greatly from the living forms. Primitively lungfishes possess two dorsal fins, a mosaic pattern of dermal skull elements which are difficult to homologize with skull bones in other osteichthyan groups, and thick cosmoid scales. The modern genera of lungfishes, *Neoceratodus* (Australian; one species), *Protopterus* (African; four species), and *Lepidosiren* (South American, one

A



B

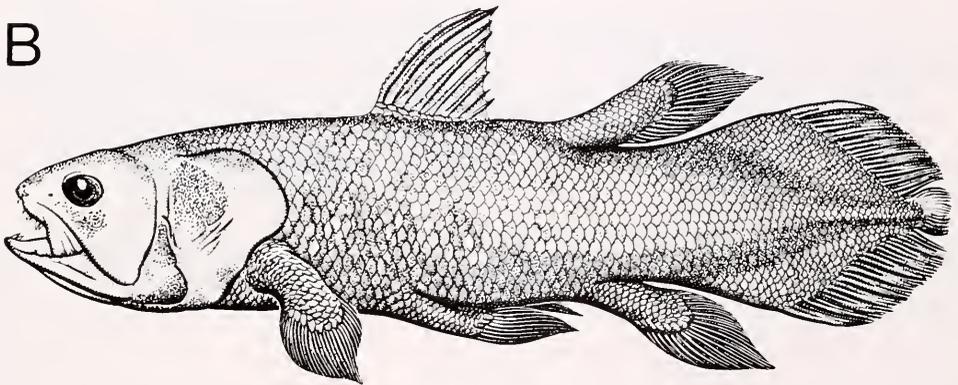
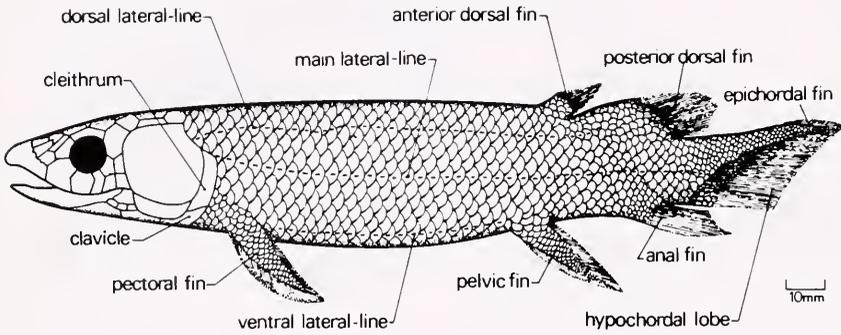


Figure 3. A. An early fossil coelacanth, *Diplurus newarki*. (From Schaeffer, 1952.) B. The living coelacanth, *Latimeria*. (From "The Vertebrate Body," 5th Ed. by A. S. Romer and T. S. Parsons. Copyright 1977 by W. B. Saunders Co. Reprinted by permission of Holt, Rinehart, and Winston Co.)

species) have scales embedded in the skin and have continuous dorsal, caudal, and anal fins (Fig. 4). Despite these specializations and reduced ossification in living forms, four primitive features have been retained in living lungfishes: three pairs of peculiar ridged tooth plates, the lack of marginal toothbearing jaw bones, an autostylic palatoquadrate fused to the neurocranium, and a greatly reduced hyomandibula. The Dipnoi share several important features of the circulatory system, as well as other characters (Fig. 1) with the Tetrapoda (Rosen *et al.*, 1981).

Rosen *et al.* (1981), in the course of examining the relationships of lungfishes, have also considered the phylogenetic position of the so-called rhipidistian fishes (Fig. 5). Although the rhipidistians have traditionally been considered as ancestral to tetrapods (Andrews and Westoll, 1970a, b; Romer, 1966; Thomson, 1964), Rosen *et al.* (1981) show that one group of "rhipidistians," the Porolepiformes, is related to coelacanth and choanates (Fig. 1), while *Eusthenopteron* is considerably more primitive than had previously been supposed (Fig. 1). The

A



B

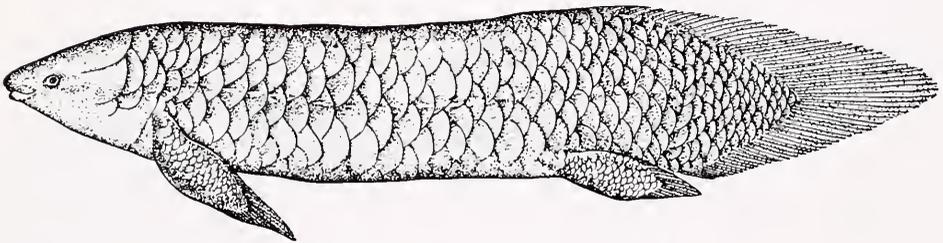


Figure 4. A. A Middle Devonian lungfish, *Dipterus valenciennesi*. (From Moy-Thomas and Miles [1971], courtesy of W. B. Saunders Publishing Co.) B. The living Australian lungfish, *Neoceratodus forsteri*. (From Romer and Parsons [1977], courtesy of C.B.S. College Publishing.)

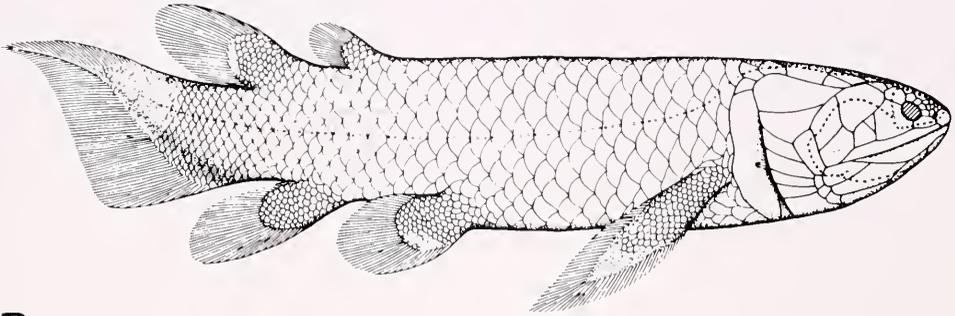
Rhipidistia are thus a paraphyletic group and are not characterized by uniquely derived features. Porolepiformes possess two dorsal fins, and many "rhipidistians" also have an intracranial kinetic joint. The ventral part of this joint appears to be a primitive teleostome feature (Fig. 1) while the dorsal portion of the joint appears to be nonhomologous in coelacanth and "rhipidistians" (Rosen *et al.*, 1981; Wiley, 1979b, 1980). The functional anatomy of the kinetic mechanism is also very different in these two groups (Thomson, 1967).

Turning now to the Actinopterygii or ray-finned fishes, named for the dermal, segmented, ray-like supports within the fins, it is clear that despite considerable research on other osteichthyan groups,

few if any investigators have explicitly tested the hypothesis of actinopterygian monophyly. The Actinopterygii have undergone an extensive radiation since their first well-established appearance in the Lower Devonian, and this tremendous diversity of morphology and habit as well as the historical interplay between neontology and paleontology (Patterson, 1982) has hindered the development of a comprehensive definition of the Actinopterygii. Actinopterygian monophyly is usually assumed.

Patterson (1982) has recently investigated the question of actinopterygian monophyly in detail and has concluded that the principal difficulty in characterizing the Actinopterygii has been the confusing pattern of character distribu-

A



B

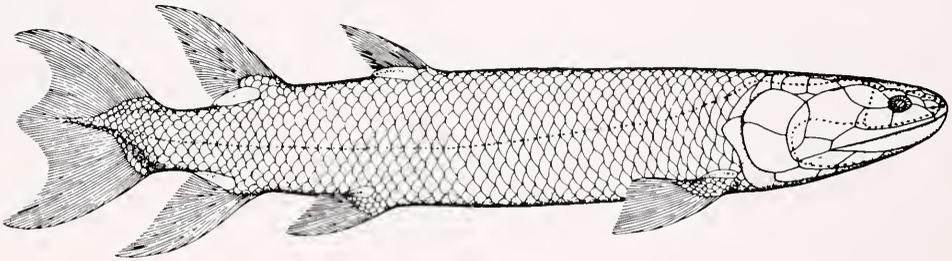


Figure 5. A. *Holoptychus*, a Late Paleozoic porolepiform. Rosen *et al.* (1981) place the porolepiforms at the node joining the actinists and the Choanata (Fig. 1) thus forming an unresolved trichotomy. Porolepiform anatomy is poorly known. B. *Eusthenopteron foordi*, an Upper Devonian sarcopterygian placed by Rosen *et al.* (1981) as the sister group to the sarcopterygians. Many of the characters shared by *Eusthenopteron* and early tetrapods and commonly believed to be indicative of relationship now appear also to be shared with coelacanth, porolepiforms, and lungfishes. These features thus corroborate a monophyletic assemblage composed of *Eusthenopteron* and the Sarcopterygii (Fig. 1). (From Andrews [1973], reprinted by permission of the Council of the Linnean Society of London.)

tion when living relic forms such as *Polypterus* and *Lepisosteus* are considered. Patterson (1982: Fig. 3B) lists seven characters of the Actinopterygii which unite the primitive fossil form *Cheirolepis*, *Polypterus*, and all higher ray-finned fishes into a monophyletic group (Fig. 6). Two of these are discussed here.

Actinopterygian fishes share a unique scale histology, the ganoid scale, with an outer lamellar layer (ganoine), a central dentinous layer with vascular canals, and a deep layer of spongy bone (Goodrich, 1908; Gross, 1966; Moy-Thomas and Miles, 1971; Patterson, 1982; Pearson, 1982; also Schultz, 1977). These scales are rhomboid in shape, have a dorsally

directed peg that fits into a socket on the adjacent dorsal scale (Fig. 7D), and are arranged in sloping diagonal rows along the body (Fig. 7). A unique pectoral fin structure is shared by all actinopterygians which have an expanded propterygial element of the pectoral fin base and an extensive articular surface with the endoskeletal shoulder girdle (Jessen, 1972; Rosen *et al.*, 1981).

Rosen *et al.* (1981) mention two additional characters relevant to actinopterygian monophyly. 1) Acrodin, a dentinous tissue (Orvig, 1978), forms a cap on the teeth of many ray-finned fishes (Patterson, 1982), including many primitive fossil taxa and *Polypterus*. 2) The pelvic gir-

dle of actinopterygians has a greatly expanded metapterygium which supports the fin radials. The metapterygium may be composed of smaller separate cartilages in juveniles, but in adults the cartilages are generally fused together. The ontogenetic fusion of internal pelvic cartilages into a larger adult structure is unique to ray-finned fishes. Early ray-finned fishes also possess a single dorsal fin (Figs. 6, 7). Acanthodians, actinistians, and lungfishes all primitively possess two dorsal fins while primitive actinopterygians, the paleoniscoid fishes, have only a single dorsal fin. This feature is remarkably constant throughout the entire actinopterygian radiation although the dorsal fin has been lost or highly modified in several groups, and in the more advanced teleostean fishes the fin is subdivided into an anterior spiny portion and a posterior soft-rayed section.

One last noteworthy feature of actinopterygians is the nature of the fin articulation: median fins are supported internally by paired segmented dermal rays (lepidotrichia), and these are attached to an internal skeleton which does not extend into the fin at the fin base. Between the distal ends of each pair of lepidotrichia lies an unsegmented actinotrich made of elastoidin, a fibrous collagenous protein (Arita, 1971; Geraudie and Meunier, 1980; Videler, 1975). This morphology may be correlated with an increase in fin mobility and greater maneuverability during locomotion. Actinotrichia are also found in coelacanth (Geraudie and Meunier, 1980) and bear a close similarity both in chemical composition and fine structure to selachian ceratotrichia. This raises the possibility that actinopterygian actinotrichia are homologous to selachian ceratotrichia (suggested by Goodrich, 1904), as both are composed of elastoidin, are not mineralized, and both consist of "giant collagenous fibers constructed of closely packed or fused fibrils aligned so that the banding (60–65 nm) of the collagen fibrils is in register throughout the fiber"

(Geraudie and Meunier, 1980: 637; also see Patterson, 1977a: 113). Based on these data and the work of Goodrich (1904), Geraudie (1980), Kemp (1977), and Patterson (1977a), the following phylogenetic hypothesis of intrinsic fin supports may be proposed for future detailed examination. Collagenous fin rays composed of elastoiden are primitive for gnathostomes, with a derived state consisting of a terminal "actinotrich" located at the distal end of the fin rays, and lepidotrichia which are both segmented and ossified, corroborating a monophyletic Osteichthyes (Fig. 1). An ontogenetic study of dipnoan fin rays is needed to flesh out this hypothesis, as Patterson (1977a) suggests that the dipnoan "camptotrichia" are really ceratotrichia/actinotrichia with an outer ossified face, a view not considered by Geraudie and Meunier (1982) in their analysis of camptotrich structure.

#### PRIMITIVE ACTINOPTERYGIAN FISHES

The early actinopterygian fishes are usually included in the Infraclass Chondrostei (Alexander, 1967; Bailey and Cavender, 1971; Gosline, 1971; Lagler *et al.*, 1977; J. Nelson, 1976; Romer, 1966). This grouping results more from a lack of information on the relationships of the early ray-finned fishes than from the expectation that "chondrosteans" actually form a natural group. The "Chondrostei" usually includes a diverse assemblage of fossil and living taxa and is demonstrably paraphyletic (Schaeffer, 1973). Since this grouping tends to obscure the phyletic relationships of primitive actinopterygians, we will follow Patterson (1982) in restricting use of Chondrostei to refer to a monophyletic clade composed of sturgeons, paddlefishes, and closely related fossil groups (Fig. 6; see below for further discussion).

The interrelationships of the primitive living actinopterygians have been relatively well established (Fig. 6) largely as

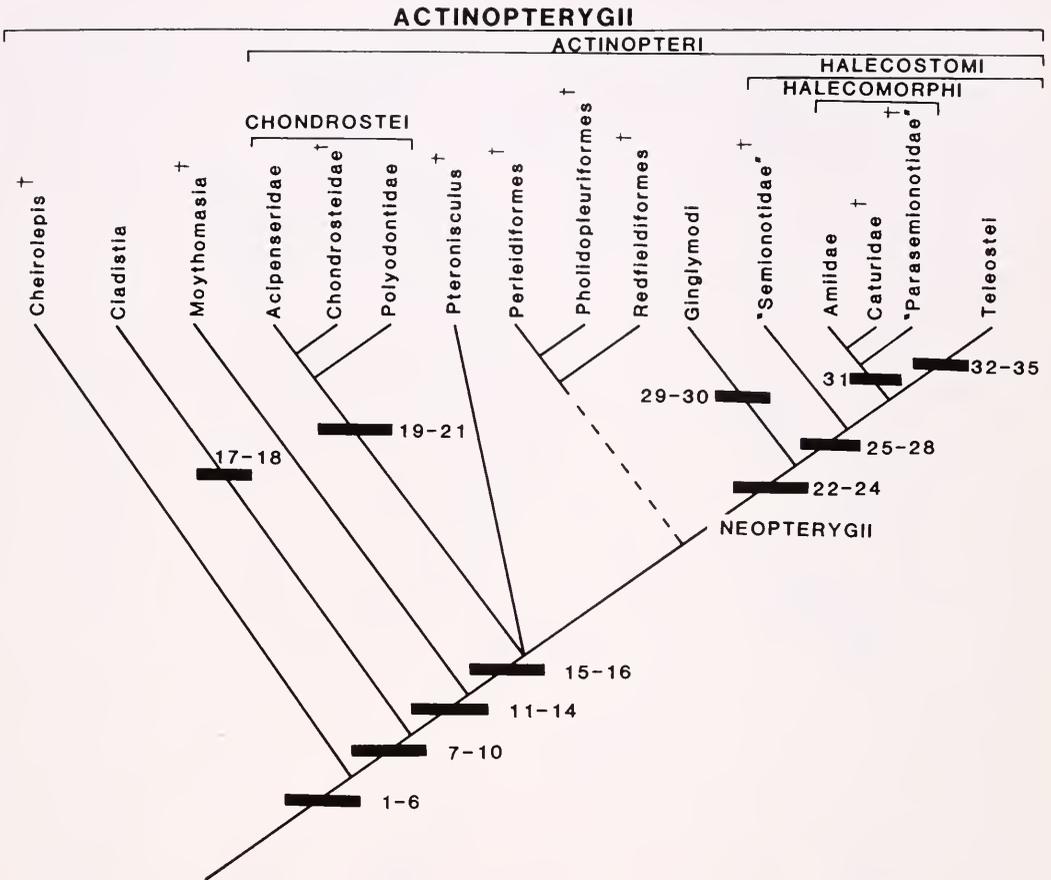


Figure 6. Branching diagram (cladogram) showing one hypothesis of the relationships between the main actinopterygian subgroups. Taxa with no living representatives are indicated with a dagger. Patterson (1982) provides an extensive discussion of the relationships of primitive actinopterygians and many of the characters listed here are abstracted from his paper. The characters are: 1, presence of a single dorsal fin; 2, a pectoral propterygium (see Rosen *et al.*, 1981); 3, ganoin; 4, anterodorsal peglike process on the scales; 5, jugal pitlines; 6, mandibular sensory canal enclosed in the dentary bone; 7, autosphenotic and large opisthotic bone in the braincase; 8, acrodin caps on teeth; 9, pelvic plate present (see Rosen *et al.*, 1981); 10, numerous features of soft anatomy including brain development, jaw muscles, and gill arch muscles (Wiley, 1979; Nieuwenhuys, 1982; Patterson, 1982; Lauder, 1980b); 11, a perforated propterygium; 12, basal fulcra on dorsal caudal margin; 13, supra-angular bone present in lower jaw; 14, hemopoietic organ above the medulla oblongata; 15, fringing fulcra on fins; 16, spiracular canal; 17, dorsal fin spines; 18, ontogenetic fusion of infraorbitals with the maxilla (see Patterson [1982] and Daget [1950] for additional characters); 19, absence of myodomes (Schaeffer, 1973); 20, fusion of premaxillae, maxillae, and dermopalatines (Schaeffer, 1973); 21, anterior palatoquadrate symphysis (Jollie, 1980); 22, fin rays equal in number to their supports in the dorsal and anal fins (Patterson and Rosen, 1977); 23, upper pharyngeal dentition consolidated (Patterson and Rosen, 1977); 24, clavicle lost or reduced to small plate lateral to cleithrum (see Patterson and Rosen [1977] who also provide several other characters); 25, mobile maxillary bone in the cheek; 26, interopercular bone present; 27, median neural spines; 28, quadratojugal lost or fused with quadrate (Patterson and Rosen, 1977); 29, opisthocoelous centra; 30, a series of toothed infraorbital bones (see Wiley [1976] for many other characters); 31, both the symplectic bone and the quadrate contribute to the jaw articulation (see Patterson [1973] for further discussion of this clade); 32, the presence of oroneurals (elongated ural neural arches); 33, unpaired basibranchial toothplates; 34, a mobile premaxilla; 35, internal carotid foramen enclosed in the parasphenoid (Patterson, 1977a). Patterson (1977) also mentions two other features as tentative teleostean features: seven epurals, and a pectoral propterygium fused with the first pectoral fin ray. Living teleosts share many features in the jaw musculature (see text; Lauder 1980c), including loss of the anterior (suborbital) jaw adductor component.

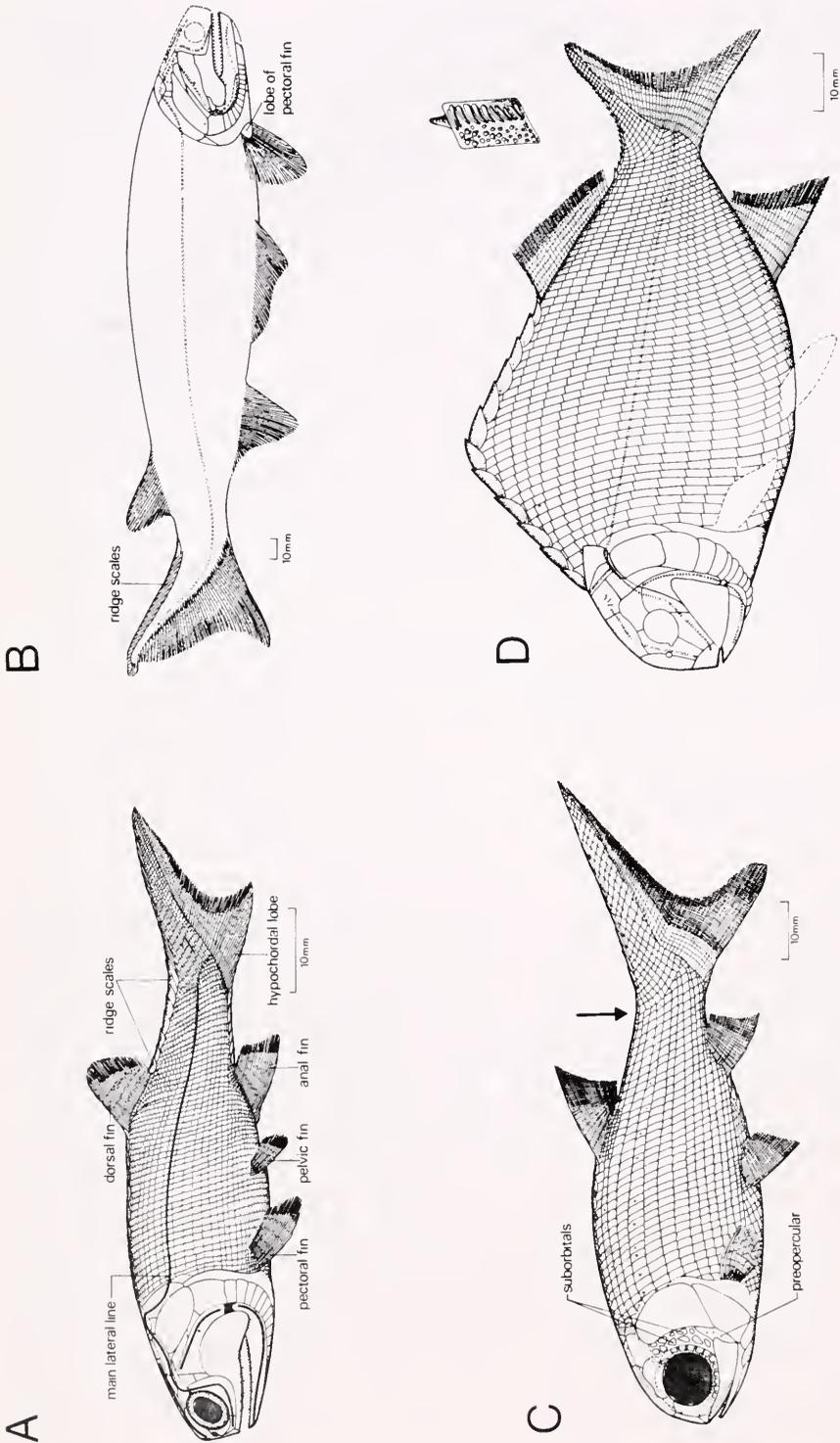


Figure 7. Gross morphology of some representatives of early actinopterygian fishes. A. *Moythomasia nitida* (Upper Devonian) (Fig. 6). B. *Cheirolepis canadensis* (Middle-Upper Devonian) (Fig. 6). C. *Adrella blairvillei* (Lower Permian), arrow points to the "chondrostean hinge." D. *Androichthys tuberculatus* (Lower Carboniferous), a member of the deep-bodied family Chirodontidae. Note the long closely fitting scale rows and the enlarged scale (D, upper right) showing the dorsal peg which inserts into a ventral socket on the scale above. (From Moy-Thomas and Miles [1971], courtesy of C.B.S. College Publishing.)

the result of the recent work of Jollie (1980), Patterson (1973, 1975, 1982), Rosen *et al.* (1981), and Wiley (1976). The interrelationships of the primitive fossil taxa remain problematical. Only three fossil genera have been assigned a position in actinopterygian phylogeny that is corroborated by uniquely derived characters: *Cheirolepis* (Fig. 7B), *Moythomasia* (Fig. 7A) and *Pteronisculus* (see Fig. 6; Patterson, 1982). Schaeffer (1973) has also identified several possible monophyletic assemblages among lower actinopterygians. The Devonian *Cheirolepis* (Pearson and Westoll, 1979) is the most primitive known ray-finned fish (Fig. 6).

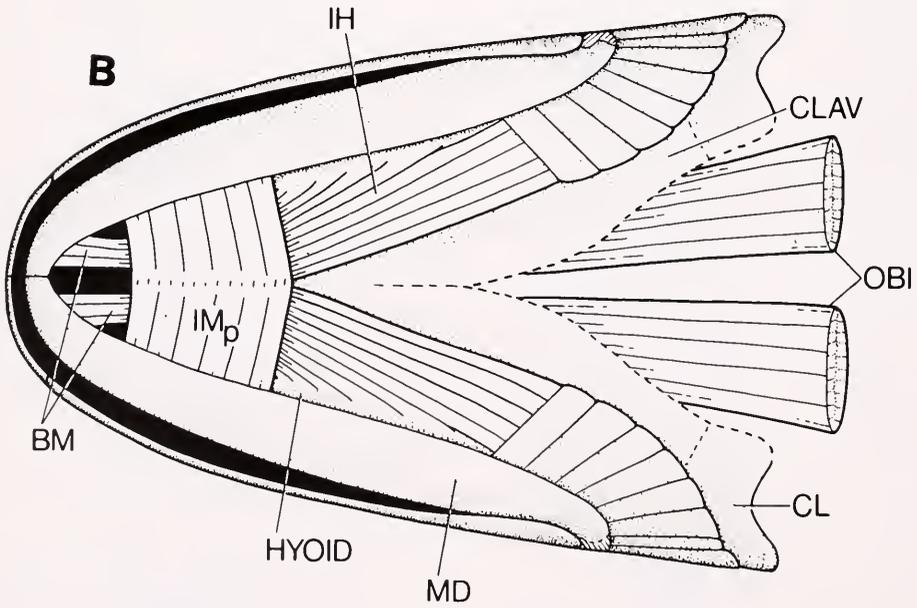
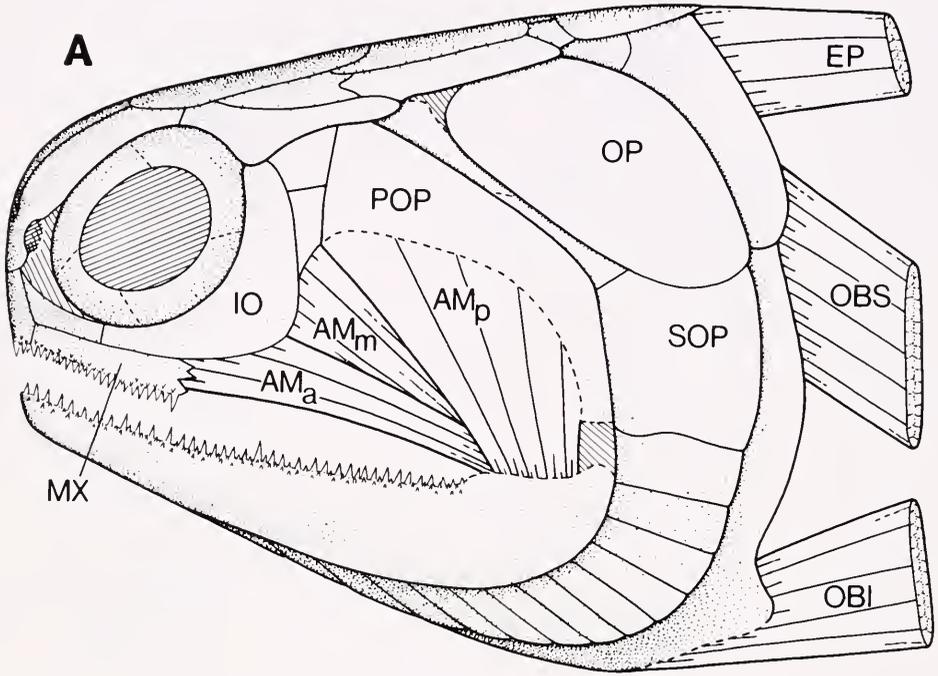
The structure of the skull in these early actinopterygians (Fig. 8) reflects their generally predaceous habit (Pearson and Westoll, 1979). Simple conical teeth are present along the marginal jaw bones and on many of the dermal bones lining the buccal cavity. The dermal cheek bones form a relatively solid plate with the large maxilla occupying much of the cheek and attaching posteriorly to the preoperculum. Lateral movements of the cheek and palatoquadrate were relatively limited (Lauder, 1982a). An operculum and suboperculum covered the gills laterally and a series of smaller bony plates, the branchiostegal rays, extended posterolaterally from the hyoid apparatus (Fig. 8). The eye and nasal openings were located far anteriorly. Paleonisciform fishes possessed a tripartite adductor mandibulae (Fig. 8: AMa,m,p) with a posteroventral fiber orientation. The primitive gnathostome condition is retained in the ventral head musculature (Fig. 8; Lauder, 1980b) with an intermandibularis posterior extending between the mandibular rami and an interhyoideus connecting the branchiostegal rays and hyoid to the fascia dorsal to the intermandibularis posterior. Incidentally, this general arrangement of the buccal floor musculature appears to have been a very conservative feature in lower vertebrate evolution, as a very similar

condition is found in coelacanths, lungfishes, and salamanders.

The braincase of these early ray-finned fishes exhibits several remarkable features (Fig. 9). A ventral otic fissure (Fig. 9: vof), cartilage filled in life, represents a persistent division between the embryonic parachordal and trabecular elements of the chondrocranium and lies just posterior to the hypophysis. An additional fissure, the lateral occipital fissure of the braincase (Fig. 9: lof) provides an exit for the vagus nerve, represents a persisting embryonic metotic fissure, and may not have been filled with cartilage in adult paleoniscoids (Gardiner and Bartram, 1977; Patterson, 1975; Schaeffer and Dalquest, 1978). It is important to note that the adult braincase of many primitive actinopterygians was fully ossified and completely sutureless, a condition that prohibited further growth (Patterson, 1975).

In contrast to the teleost and halecomorph actinopterygians (see below) in which a suction feeding mechanism is developed (a negative pressure is created in the buccal cavity and used to draw in prey with the inflow of water as the mouth is opened), most paleoniscoid fishes had only a limited ability to expand the buccal cavity (Schaeffer and Rosen, 1961; Lauder, 1982a) and thus must have primarily used their body velocity to overtake and capture prey rather than the "ambush predator" strategy used so successfully by many teleosts. Mouth opening in all non-halecostome actinopterygians is accomplished by contraction of the hypaxial and sternohyoideus muscles (Lauder, 1980c; 1982a). These muscles mediate posteroventral hyoid movement which causes mandibular depression. Elevation of the neurocranium during prey capture also contributes significantly to the increase in gape.

The primary use of body velocity in prey capture is reflected in the structure of the locomotory apparatus in the early ray-finned fishes and suggests several



functional correlates of body form. The early actinopterygians are unique among lower vertebrates in possessing a single dorsal fin, and generally lateral body and fin profiles are not concentrated far posterior to the center of gravity. Webb (1976, 1977, 1978) has examined fast-start performance in teleost fishes and has concluded that the ability to rapidly accelerate from a rest position (of great importance to ambush predators) is largely a function of lateral body and fin area and the mass of body musculature, higher values of both giving improved fast-start performance. The paleoniscoid fishes would have had a rather poor fast-start performance since fin area is relatively small, caudal fin shape is not designed to rapidly generate anteriorly directed forces (Thomson, 1976; Webb, 1982) and neural and haemal spines were not firmly attached to vertebral centra (Lauder, 1980d; Schaeffer, 1967).

The caudal fin in early actinopterygians is heterocercal in shape, the notochord and vertebral elements extending into the upper (epichordal) lobe while the hypochordal lobe (Fig. 7A) possesses little to stiffen it except the dermal fin rays. This external and internal morphological asymmetry in tail structure may have resulted in an "asymmetrical" thrust (Thomson, 1976) directed anteroventrally. One of the fundamental functional changes in actinopterygian evolution is often held to be the modification of tail structure to generate an anteriorly directed symmetrical thrust, the correlated reduction in scale weight (and thus specific

gravity), and evolution of a gas-filled swimbladder from the primitive lunglike pharyngeal diverticulum. The role of the swimbladder in allowing the achievement of neutral buoyancy was of potential importance both for a reduction in energy expenditure needed to maintain a constant level in the water column (Alexander, 1966a) and in the removal of functional constraints on caudal and pectoral fin structure. Many primitive actinopterygian fishes, however, possessed a very high aspect ratio tail with complete external symmetry (e.g., *Bobasatrania*, *Platysomus*, *Chirodus*, and *Dorypterus*; see Schaeffer, 1973: 217). These forms also had enlarged stiffening rays in the hypochordal fin lobe. In the absence of experimental data on the function of primitive actinopterygian caudal fins, it is perhaps unwise to speculate about the direction of thrust produced and to generalize too broadly about the "inefficiency" of asymmetrical caudal structure.

Two other groups of fossil ray-finned fishes deserve mention. A deep-bodied radiation of primitive forms is represented by the platysomoids, of which *Adroichthys* (Fig. 7D) is a member. A second lineage is composed of the redfieldiiform and perleid fishes (Fig. 6), although monophyly of this assemblage has not been conclusively established (see Schaeffer, 1973; Hutchinson, 1973; Brough, 1939). These fishes share several general features with the neopterygian fishes, including a nearly vertically oriented palatoquadrate allowing greater expansion of the orobranchial chamber, a

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Figure 8. General structure of the skull in a palaeoniscoid fish (*Moythomasia nitida*). The cheek is covered with a solid plate of dermal bone composed of infraorbital bones, a preoperculum, and a large expanded maxillary bone, partially removed to show the underlying adductor musculature. The oblique orientation of the preoperculum indicates the posterior inclination of the palatoquadrate. The dentary lacks a coronoid process. Mouth opening during feeding occurred by lifting of the upper jaw and by depression of the mandible via posterior movements of the hyoid apparatus. Primitive actinopterygians possessed three divisions of the adductor mandibulae, anterior (AMa), medial (AMm), and posterior (AMp). (From Lauder [1982a], courtesy of the American Society of Zoologists.)

*Other Abbreviations:* BM, branchiomandibularis; CL, cleithrum; CLAV, clavicle; EP, epaxial muscles; IH, interhyoideus muscle; IMP, intermandibularis posterior muscle; IO, infraorbital bones; MX, maxilla; OBS, obliquus superioris muscle; OBI, obliquus inferioris muscle; OP, operculum; POP, preoperculum; SOP, suboperculum.

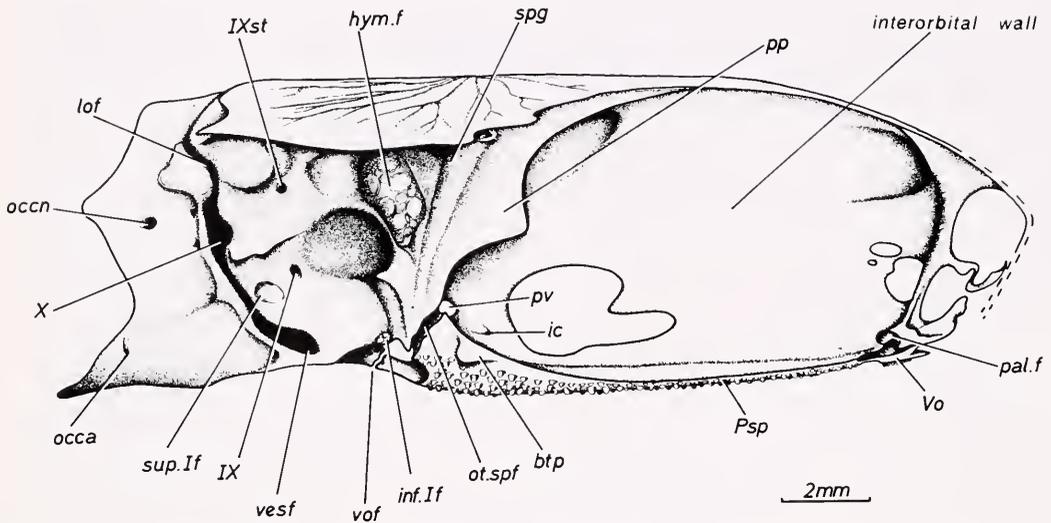


Figure 9. The braincase of a paleoniscoid fish (lateral view of the right side) showing the interorbital wall, the ventral otic fissure (vof), the lateral occipital fissure (lof) and exits for the vagus nerve (X), glossopharyngeal nerve (IX), supra-temporal branch of IX (IXst), the parasphenoid bone (Psp), vomer (Vo), foramen for the pituitary vein (pv) and for the internal carotid artery (ic). (After Gardiner [1973], reprinted by permission of the Council of the Linnean Society of London.)

*Other Abbreviations:* btp, basipterygoid process; hym.f, hyomandibular facet; inf.If, articular facet for infrapharyngobranchial I; occa, occn, foramina for the occipital artery and nerve; ot.spf, oticosphenoid fissure; pal.f, articular facet for palatine bone; pp, postorbital process; spg, spiracular groove; sup.If, articular facet for supraopharyngobranchial I; vesf, vestibular fontanelle.

coronoid process on the mandible, and the expansion of one of the upper branchiostegal rays.

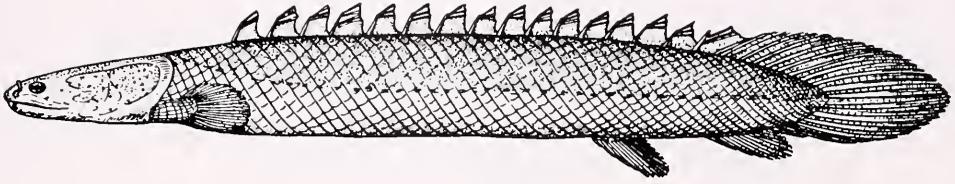
The early actinopterygian fishes represent a relatively limited radiation which remained morphologically rather uniform in basic plan. The first major changes in feeding and locomotory patterns occur in the neopterygian fishes, but first we must examine the living survivors of the early ray-finned fishes, the bichir and reedfish *Polypterus* and *Erpetoichthys* (Cladistia), and the sturgeons and paddlefishes (Chondrostei). Rosen *et al.* (1981) proposed using Cope's (1871) term Actinopteri to refer to all actinopterygians more derived than cladistians (see Fig. 6), and this usage is followed here (also see Patterson, 1982).

The Cladistia contains the single family Polypteridae with two genera, *Polypterus* and *Erpetoichthys* (= *Calauo-*

*ichthys*; see Swinney and Heppell, 1982), and has been the subject of extensive debate in the literature of the last hundred years. Probably no other group of living fishes has been placed, at one time or another, in so many widely differing major taxonomic groups. An early view (Huxley, 1861; Cope, 1871; see Patterson, 1982, for a historical review) was that the polypterids were members of the Sarcopterygii or "lobe-finned fishes" (Fig. 1), an hypothesis based primarily on the structure of the pectoral fin in *Polypterus* (Fig. 10), which consists of a proximal lobelike extension from the body and a fan-shaped distal array of fin rays (Fig. 10A). Jarvik (1980) still supports this view.

This suggestion has been largely supplanted in recent years by the hypothesis that polypterids are sufficiently distinct to warrant recognition as a separate subclass of the Osteichthyes, the Brachio-

A



B



C

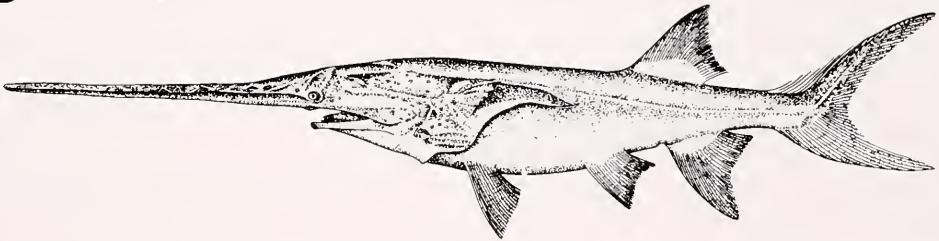


Figure 10. A. A representative of the genus *Polypterus*. B. *Scaphirhynchus*, a sturgeon from the Mississippi drainage. C. *Polyodon spathula*, also from the Mississippi. (From "The Vertebrate Body," 5th Ed. by A. S. Romer and T. S. Parsons. Copyright 1977 by W. B. Saunders Co. Reprinted by permission of Holt, Rinehart, and Winston.)

pterygii (e.g., McAllister, 1968; G. Nelson, 1969a). More recently, however, Gardiner (1973), Schaeffer (1973), Wiley (1979a), and especially Patterson (1982) have provided convincing evidence, summarized in Figure 6, that the polypterids represent highly specialized survivors of primitive actinopterygian fishes. Romer (1966), Gardiner (1967), and Andrews *et al.* (1967) have also held this view. Nieuwenhuys (1967, 1982) has al-

lied *Polypterus* with the Actinopterygii on neuroanatomical evidence, as has Lovtrup (1977) on otolith structure and lens proteins.

The Cladistia are hypothesized to be monophyletic based on the dorsal fin-spine pattern (Fig. 10A), the presence of a series of spiracular ossicles, and the structure of the urohyal and parasphenoid, among many other uniquely derived features (Daget, 1950; see Patter-

son, 1982). The genus *Polypterus* (bichirs) is composed of 10 species, all very similar in appearance. A row of dorsal finlets extends down the back (Fig. 10), each finlet having an anterior spine supporting a thin membranous web posteriorly. These finlets are elevated during active swimming but lie flat when the fish is inactive. A primitive actinopterygian feature retained by *Polypterus* is the thick covering of rhomboid scales arranged in oblique rows along the body (Pearson, 1981). The internal skeleton is well ossified, the tail is modified into a so-called diphyccercal or symmetrical shape, and a spiracle connects the buccal cavity with the surrounding water via a short spiracular canal opening onto the dorsal head surface. The cranial anatomy of *Polypterus bichir* has been described in detail by Allis (1922). Young *Polypterus* possess a pair of relatively large external gills which extend posteriorly from the hyoid arch. Adult *Polypterus* are able to breathe air and have a pair of highly vascularized lungs which arise ventrally from a diverticulum in the floor of the pharynx. The lungs are asymmetrical in size, the right extending much further posteriorly than the left. In view of the widespread occurrence of ventral lunglike diverticula in primitive osteichthyan groups, the presence of lungs and probably the occurrence of external gills in young may be a primitive feature of actinopterygian fishes that has been retained in *Polypterus*. Although most commonly seen at a size of about 15 to 20 cm, some species of *Polypterus* can grow to well over a meter in total length.

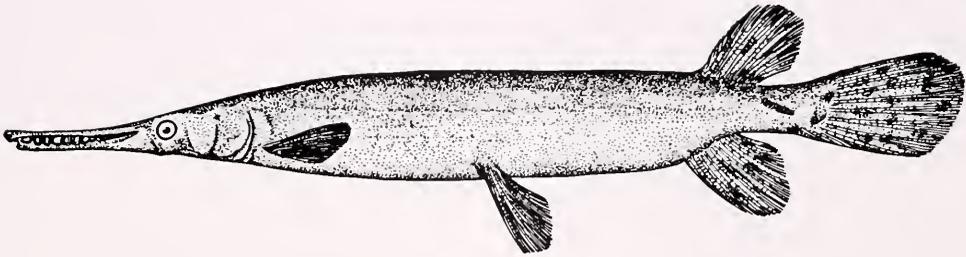
The other genus included in the Polypteriformes is *Erpetoichthys* with one species, *E. calabaricus* (the reedfish). This fish is elongate in form and considerably thinner than *Polypterus* with a round ropelike body. *Erpetoichthys* lacks pelvic fins but is similar to *Polypterus* in all major characters outlined above. The Polypteridae are only found in the fresh-

waters of tropical Africa and are generally distributed along lake shores.

The two remaining groups representing living survivors of early ray-finned fishes are the sturgeons, family Acipenseridae, and the paddlefishes, family Polyodontidae. These two families and the allied fossil forms such as *Chondrosteus* are united into the Chondrostei (Fig. 6). Schaeffer (1973), Jollie (1980), and Patterson (1982) have examined the evidence supporting the Chondrostei as a monophyletic lineage (see Fig. 6; characters 19–21). Several of the characters shared by the two living families are reductive ones (such as absence of myodomes) and may have evolved independently, but current evidence does seem to corroborate a monophyletic Chondrostei.

The family Acipenseridae, first known from Upper Cretaceous fossils, contains four genera arranged in two subfamilies. The subfamily Acipenserinae, containing *Acipenser* (about 20 species) and *Huso* (2 species), is found in Eurasia and North America; some species live only in freshwater (where all species spawn) while others have part of the lifecycle in the ocean. The subfamily Scaphirhynchinae includes the genus *Pseudoscaphirhynchus* (3 species), which is confined to Asia, and *Scaphirhynchus* (2 species) (See Fig. 10B). The different genera and species are distinguished on the basis of mouth shape and scalation, while the subfamilies differ in the occurrence of a spiracle: present in the Acipenserinae and absent in the Scaphirhynchinae. The body shape of sturgeons (Fig. 10B), the presence of a heterocercal tail, and a mainly cartilaginous skeleton suggested to several investigators early in this century that sturgeons should be included in the Selachii. These features are actually either reductions from a primitive actinopterygian condition (an ossified skeleton) or merely represent the retention of primitive characters (the heterocercal tail). Sturgeons

A



B

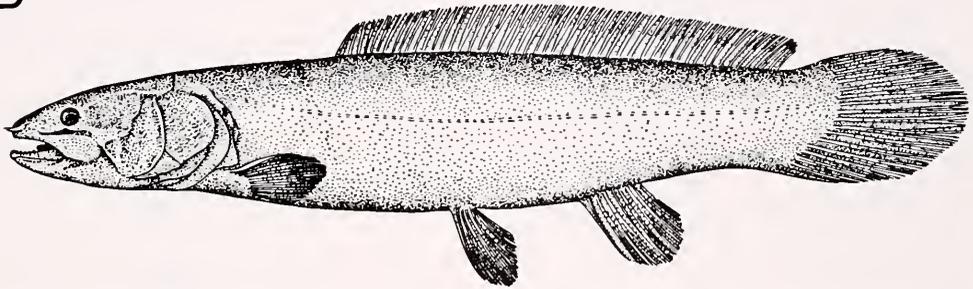


Figure 11. A. *Lepisosteus*, a living representative of the Ginglymodi. B. *Amia calva*, a living halecomorph fish. (From "The Vertebrate Body," 5th Ed. by A. S. Romer and T. S. Parsons. Copyright by W. B. Saunders Co. Reprinted by permission of Holt, Rinehart, and Winston.)

are peculiar in having scales modified into five rows of bony scutes which run the length of the body (Fig. 10B), greatly reduced teeth and jaws, and a large extended fleshy rostrum with barbels used in rooting for food on the bottom. Sturgeons, especially European species, may grow to an enormous size, record individuals weighing in at over 3,000 lbs.

The family Polyodontidae consists of two living genera, each with one species, with a disjunct distribution. *Polyodon spathula* (Fig. 10C) occurs in the Mississippi drainage of the United States. It has a very elongate snout with minute barbels, and long gill rakers for straining plankton from the water (Rosen and Hales, 1981). *Psephurus gladius* differs considerably in morphology from the American paddlefish and is found in the

Yangtze River basin of China. The mouth can be protruded to feed on small benthic organisms, and the snout is considerably shorter than in *Polyodon*. Both genera have greatly reduced scalation. Paddlefishes usually reach a maximum size of about 2 meters. The first fossil record of the Family Polyodontidae occurs in the Upper Cretaceous with the genus *Paleopsephurus wilsoni* from Montana.

#### THE GINGLYMODI AND HALECOMORPHI

The Neopterygii (Fig. 6) contains two major groups, the Ginglymodi containing only the family Lepisosteidae (gars), and the Halecostomi (Fig. 11). The Halecostomi also consists of two major groups one of which, the Halecomorphi, containing

several fossil taxa and the living genus *Amia*, will be considered here while the other, the Teleostei, will be examined extensively below. Patterson and Rosen (1977) have recently given both the Teleostei and Halecomorphi the rank of Subdivision in the Division Neopterygii.

Some of the characters which have been used to define the neopterygian fishes (Fig. 6: characters 22–24) are the presence of an equal number of fin rays and fin ray supports in the dorsal and anal fins (primitively the number of fin rays exceeds the number of supports) and the occurrence of a symplectic bone which develops as a separate ossification center in the hyomandibular cartilage. Patterson (1973), Patterson and Rosen (1977), Wiley (1976), and Bartram (1977) provide extensive evidence for monophyly of the Neopterygii.

The Ginglymodi have been recently reviewed by Wiley (1976), who has provided a long list of characters shared by members of this group, including very elongate jaws with toothed infraorbital bones on the upper jaw (Fig. 12A), opisthocoelous vertebral centra, and teeth containing plicidentine. Gars have elongate bodies with the dorsal fin located far posteriorly on the body (Fig. 11A) and oblique rows of ganoid scales. The posterior location of the dorsal and anal fins reflects the feeding strategy of gars as ambush predators. Wiley (1976) has divided recent and fossil gars (first known from the Cretaceous) into two genera: *Lepisosteus* (4 fossil species, 4 living) and *Atractosteus* (5 fossil species, 3 living). Although fossil gars are known from North America, Europe, Africa, and India, the living gar species are restricted in distribution to North America where they generally inhabit rivers, streams, and lakes, although some species also live in brackish or occasionally marine waters. Gars have a bilobed lung that arises from a dorsal pharyngeal diverticulum and frequently take air from the surface which is pumped into the lung. The lung is sim-

ilar to that in the living halecomorph *Amia* in having a highly subdivided interior to increase respiratory surface area (Rahn *et al.*, 1971). The largest living gar, *Atractosteus spatula*, the alligator gar, has been reported to reach a length of over 3 meters and occurs in brackish water along the Gulf of Mexico and in the Mississippi River.

The extinct family Semionotidae (Fig. 6) includes about 20 genera of fishes. Until recently the gars were grouped with the semionotid fishes in the order Semionotiformes, but as discussed above they now constitute a separate division, the remaining forms comprising the family Semionotidae within the division Halecostomi. While the semionotids may well represent an unnatural assemblage of fishes grouped together only because they share certain general similarities (many of the genera are known only from extremely poor fossils, Patterson, 1973) the majority share two characters of fundamental importance with the Halecomorphi and Teleostei: the presence of a mobile maxillary bone in the cheek and an interopercular bone (Fig. 6: characters 14 and 15), thus placing them in a more cladistically derived position than the gars.

Figure 13 depicts the major musculo-skeletal elements in the head of a primitive teleost and how they interact during prey capture. This same basic system is present in amiids and halecomorphs (with the exception of the *geniohyoideus* muscle, see below). The evolution of a separate interopercular bone (Fig. 13: iop) allowed a new system of muscles and bones to activate opening of the mouth. Contraction of the levator operculi muscle rotates the opercular bone dorsally (Fig. 13: lo, op) and this force is transmitted via the interopercular bone and ligament  $l_1$  to the lower jaw causing it to move ventrally and open the mouth. This mechanism for opening the mouth evolved at the halecostome level (Lauder, 1980c). The primitive actinopterygian mechanism for depressing the lower jaw in-

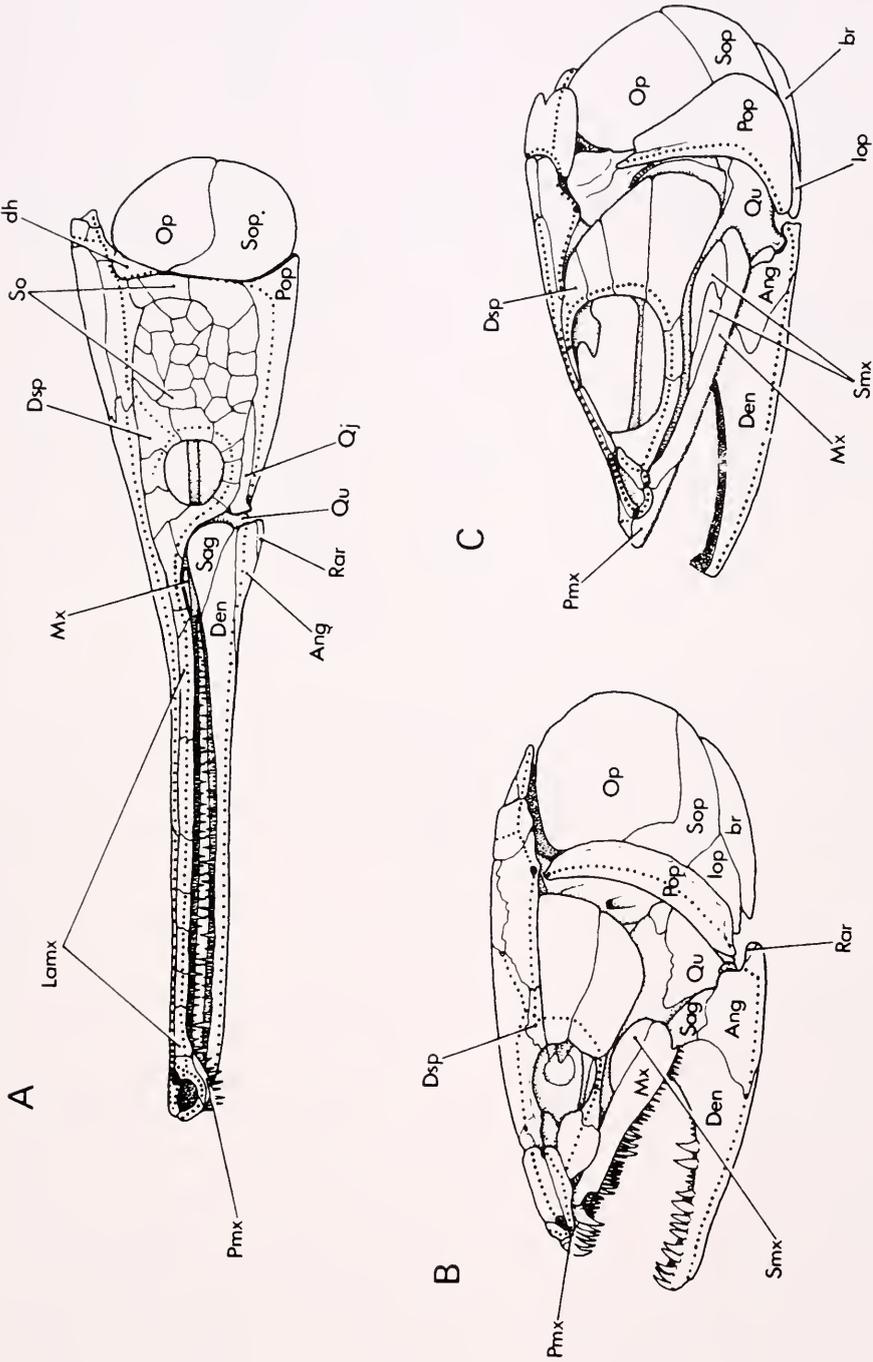


Figure 12. Lateral views of the skull of A, *Lepisosteus platostomus*, a ginglymod; B, *Amia calva*, a haliecomorph; C, *Elops saurus*, a primitive teleost (Elopomorpha). Dotted lines denote the course of the sensory canals. (From Patterson [1973]), reprinted by permission of the Council of the Linnean Society of London.)  
 Abbreviations: Ang, angular; br, branchiostegal rays; Den, dentary; Dsp, dermosphenotic; lop, interoperculum; Lamx, infraorbital bones; Mx, maxilla; Op, opercle; Pmx, premaxilla; Pop, preoperculum; Qj, quadrate; Rar, retroarticular; Qu, quadratojugal; Smx, surangular; Sog, retroarticular; So, suborbitals; Sop, suboperculum.

volves posterior movements of the hyoid arch caused by contraction of the sternohyoideus and hypaxial (obliquus inferioris) muscles and the transmission of this movement by ligament  $1_2$  (Fig. 13: hyoid, sh,  $1_2$ ) to the lower jaw. This last mechanism was present in paleoniscoids and is also found in *Polypterus*, *Lepisosteus*, halecomorphs, and many primitive teleosts. Use of the sternohyoideus, ventral body muscles, and the mandibulohyoid ligament as a system mediating mouth opening may in fact be primitive for gnathostomes, as the requisite anatomical features and mechanical relationships are found in elasmobranchs, coelacanth, and lungfishes, as well as in primitive ray-finned fishes. The salient specialization of the halecostome feeding mechanism is thus the occurrence of two biomechanical pathways controlling lower jaw depression. The presence of a maxillary bone that has been freed from the cheek (in contrast to the primitive actinopterygian condition; compare Figs. 12 and 13 to Fig. 8) contributes to the suction feeding mechanism since during mouth opening the maxilla swings towards the prey and creates a "tunnel" which directs water flow from the region immediately in front of the mouth into the buccal cavity (Lauder, 1979). The importance of the interopercular bone and the free maxilla is that they indicate the presence in the "semionotids," halecomorphs, and primitive teleost fishes of a suction feeding mechanism similar in all key features to that of higher teleosts. This mechanism has been slightly modified in advanced teleosts, but prey capture by inertial suction feeding was clearly present in the early halecostome fishes.

The halecomorph fishes (Fig. 6), all extinct except for the living *Amia calva* (Fig. 11B), are united by the possession of a unique jaw articulation: both the quadrate and the symplectic contribute to the jaw joint. The main fossil taxa included in the Halecomorphi are the Parasemionotidae and the Caturidae, almost cer-

tainly paraphyletic groups (Patterson, 1973). The main lineage of interest, however, to students of extant organisms is the Family Amiidae (Fig. 6) containing *Amia calva*, the bowfin. Although the Amiidae has an extensive fossil record beginning in the Jurassic and covering Europe, Asia, and North America (Borreske, 1974), the family today is confined to North America. *Amia* inhabits freshwaters of the south and midwest up through the Mississippi drainage, into the Great Lakes (except Lake Superior) and reaches down into Lake Champlain in the east. Its common name, bowfin, derives from the elongate dorsal fin (Fig. 11B) which is undulated in a bowlike fashion during slow locomotion. *Amia* is a voracious predator, often consuming large numbers of prey in a short time, and exhibits the main characteristics of the halecostome feeding mechanism outlined above. In *Amia* the maxilla may achieve a nearly vertical position during the strike at the prey and high-speed movies of feeding sequences show that this contributes significantly to suction efficiency by creating a tunnel-like mouth opening. The bowfin is also able to breathe air and possesses a lung that arises as a dorsal diverticulum of the pharynx in a similar fashion to the lung of the gar, *Lepisosteus*. *Amia* reaches a maximum length of about one meter.

## THE TELEOSTEI

### THE EARLY TELEOST FISHES

The Teleostei comprise by far the most diverse group of Actinopterygii and, with an estimated 20,000 species (Cohen, 1970), far exceed the diversity of any other vertebrate group. The various subgroups of the Teleostei will be treated in the remainder of this paper. Teleosts are first known from the Middle Triassic, and for most of this century it has been thought that the Teleostei form an unnatural assemblage derived polyphyletically by many independent lin-

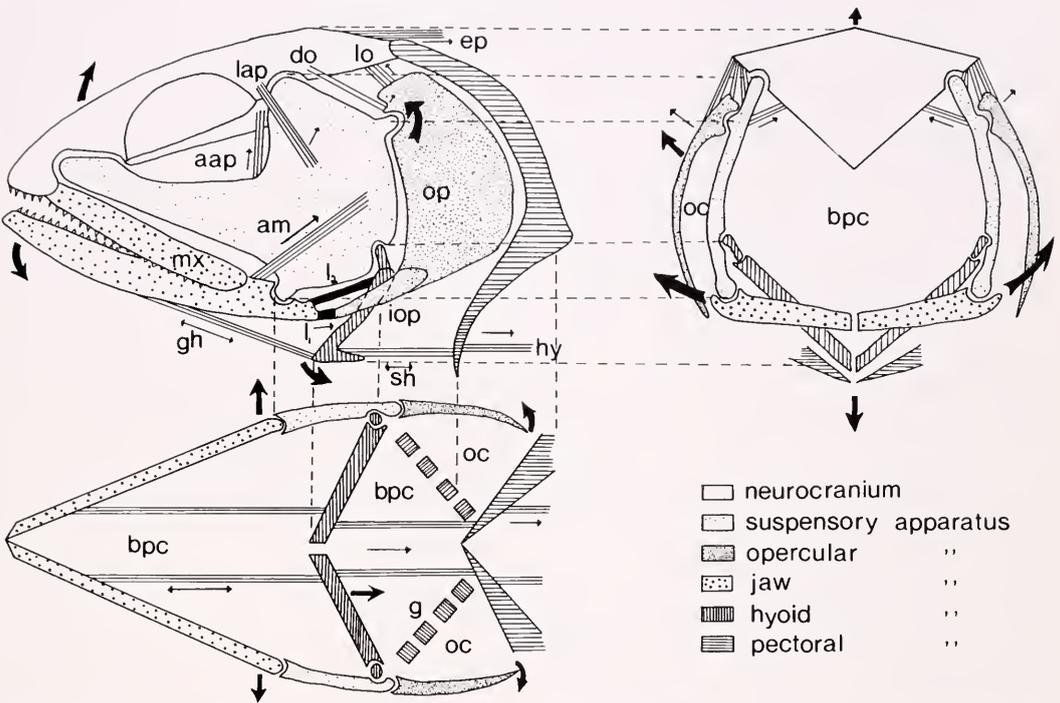


Figure 13. Diagrammatic model of the feeding apparatus in primitive teleost fishes. The major mechanical units of the jaw are shown in different patterns (see key). Heavy arrows indicate the major movements of the bony elements during mouth opening, light arrows indicate the major action of the muscles. (Modified from Lauder and Liem, 1980.)

Abbreviations: aap, adductor arcus palatini muscle; am, adductor mandibulae musculature; bpc, buccopharyngeal cavity; do, dilator operculi muscle; ep, epaxial muscles; g, gills; gh, geniohyoideus muscle; hy, hypaxial muscles; iop, interopercular bone;  $l_1$ , interoperculomandibular ligament;  $l_2$ , mandibulohyoid ligament; lap, levator arcus palatini muscle; lo, levator operculi muscle; mx, maxilla; oc, opercular chamber; op, operculum; sh, sternohyoideus muscle.

eages from the so-called pholidophorid fishes (Gosline, 1965; Patterson, 1967). Patterson (1968a) first proposed a precise definition of the Teleostei based on the anatomy of the caudal fin and showed that teleosts, as he defined them, do in fact constitute a natural, monophyletic assemblage of fishes which includes several groups previously thought not to be teleosts. The groups currently included in the Teleostei and their interrelationships are summarized in Fig. 14. Teleosts possess a caudal skeleton which differs from that of other neopterygian fishes (Rosen, 1982; Fig. 14: character 1) and is of key significance in the evolution of actinopterygian locomotor patterns. In haleco-

morph and ginglymod fishes (Fig. 15A, B) the caudal fin rays articulate with the posterior edge of the haemal spines and with flattened and expanded haemal arches and spines known as hypurals (Fig. 15: h1-h7). The caudal fin is heterocercal and is both internally asymmetrical (the vertebral column bends dorsally in the tail) and externally asymmetrical. A "chondrostean hinge" occurs at the base of the upper lobe of the primitive actinopterygian tail and represents a zone of weakness between the body scale rows (running in an obliquely posterior direction) and the scale rows in the epichordal tail lobe (with an anteroventral inclination) which serve to stiffen the tail (*Ad-*

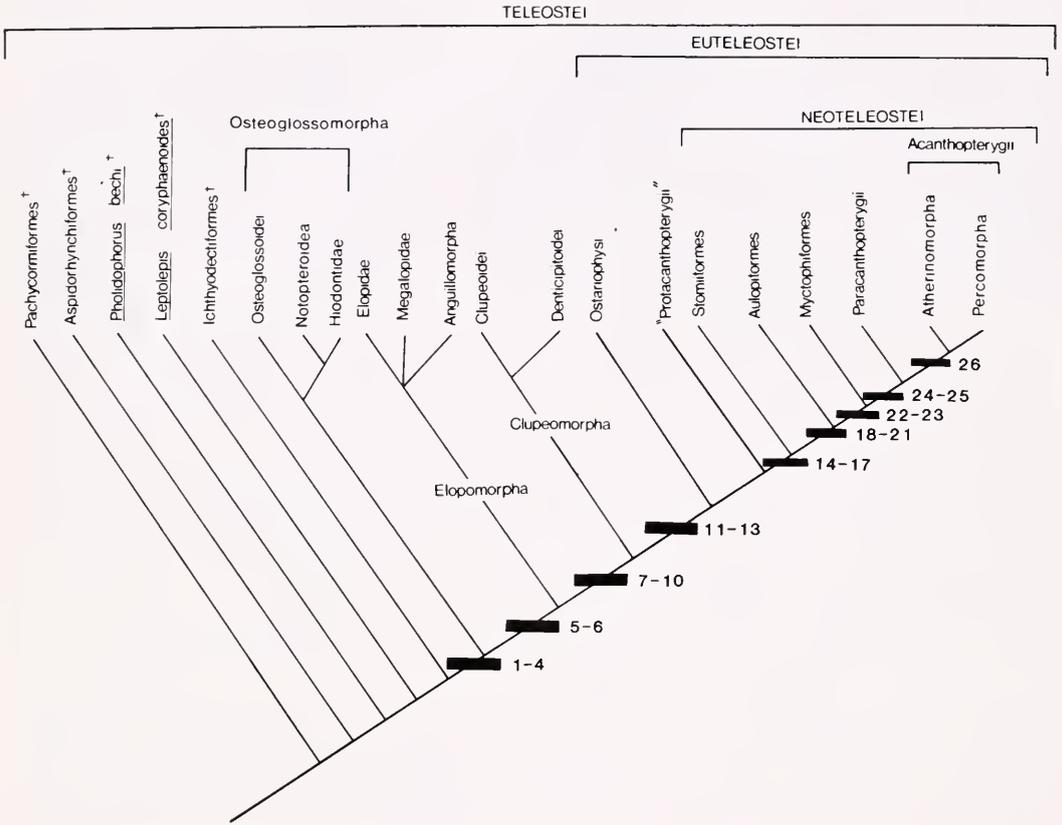


Figure 14. Phylogeny of the Teleostei. Taxa known only from fossils are indicated with a dagger. Monophyly of the Teleostei is established in Figure 6, and monophyly of the various subgroups is considered below. The "Protacanthopterygii" is discussed on p. 132, see Fig. 28. Characters corroborating the branching of the primitive teleostean fossil taxa are discussed and presented in Patterson (1977b). The characters are: **1**, presence of an endoskeletal basihyal (Nelson, 1969a; Patterson, 1977a); **2**, four pharyngobranchials; **3**, three hypobranchials present; **4**, basibranchial and basihyal cartilages overlain by median toothplates (Rosen, 1982); **5**, two uroneurals extend anteriorly over the second ural centrum (Patterson, 1977); **6**, "epipleural intermuscular bones developed throughout the abdominal and anterior caudal regions" (Patterson, 1977b: 630); **7**, retroarticular bone excluded from the quadratomandibular joint surface; **8**, toothplates fused with endoskeletal gill arch elements; **9**, neural arch on ural centrum one reduced or absent (Patterson, 1977b); **10**, articular bone co-ossified with the angular (Nelson, 1973); **11**, the presence of an adipose fin; **12**, presence of nuptial tubercles (Wiley and Collette, 1970); **13**, the presence of an anterior membraneous outgrowth of the first uroneural that does not meet its antimere in the midline (Patterson and Rosen, 1977); **14**, the presence of a retractor dorsalis muscle (see text; Rosen, 1973); **15**, a rostral cartilage (Fink and Weitzman, 1981); **16**, tooth attachment to bone is Type 4 (Fink, 1981); **17**, Aw division of adductor mandibulae has a posterior tendinous insertion on the quadrate, preoperculum, or operculum (Lauder, unpublished); **18**, reduction of second preural neural spine to a half-spine (Rosen, 1973); **19**, retractor dorsalis with a tendinous insertion on the third pharyngobranchial (Rosen, 1973); **20**, loss of the primitive mandibulohyoid ligament and the presence instead of an interoperculo-hyoid ligament (Lauder, 1982a); **21**, fusion of a toothplate to the third epibranchial. (Rosen (1973) lists several additional characters at this level, but these have been studied in more detail by Fink and Weitzman (1981) and are not found to be uniquely derived features); **22**, pharyngohyoideus (the primitive teleostean *rectus communis*) inserts on the urohyal, but see text for discussion (Lauder, 1982a); **23**, reduction or loss of pharyngobranchial four and the main insertion of the retractor dorsalis onto the third pharyngobranchial; **24**, the presence of well-developed ctenoid scales (Rosen, 1973; ctenoid scales, however, are also present in more primitive clades); **25**, expansion of ascending and articular premaxillary processes (Rosen, 1973; this level on the cladogram is not well defined); **26**, insertion of the retractor dorsalis onto the third pharyngobranchial only, and enlargement of epibranchials two and three. Various other features of the upper jaw mechanism are discussed by Rosen (1973, 1982) but none are unique to the Acanthopterygii and this group remains poorly defined. (But see character 1, Fig. 47, and Rosen and Parenti, 1981.)

*uella*, Fig. 7C, shows this well; an arrow points to the hinge). This asymmetrical shaped tail is presumed to generate an asymmetrical thrust with respect to the body axis.

In teleosts, however, the ural neural arches have become elongated into uroneurals (Fig. 15C: un 1-3) which function both to stiffen the upper tail lobe and to support a series of dorsal fin rays (Fig. 15C: epr). The hypurals have become expanded, and the net result is an internally asymmetrical but externally symmetrical caudal fin. In the earliest teleost fishes the uroneurals were rather small and dorsal fin rays were tightly bound to the dorsal hypurals to stiffen the upper lobe. In most teleosts, the uroneurals extend far anteriorly across the first and second preural centra (Fig. 15C: un 1-3) and completely eliminate the primitive line of flexion in the upper tail lobe. The functional significance of the anatomical changes in caudal structure for teleostean locomotion remains problematical. It is usually assumed that the externally symmetrical teleostean tail generates symmetrical thrust that passes through the center of mass of the fish, in contrast to the oblique (anteroventral) thrust generated by the asymmetrical chondrosteian tail (Patterson, 1968a). There is, however, very little experimental evidence to support such speculations, and all of the detailed experimental studies on caudal structure and function (e.g., Webb, 1975, 1982) have focused on euteleostean fishes. The first actual measurements of bone deformations in the symmetrical tail of teleost fishes (Lauder, 1982b; see Fig. 16) show that during continuous locomotion, the hypurals are probably being twisted about their long axis, and that the thrust may be anteroventrally inclined. During rapid fast-start accelerations, however, strain patterns are consistent with an anteriorly directed thrust (Fig. 16). These data underscore the need for caution in simple extrapolations ("symmetrical tail

equals symmetrical thrust") and the necessity for comparative functional data from living non-teleost actinopterygians such as *Amia*, *Lepisosteus*, and *Polypterus*. The oft-cited correlation between the reduction in weight of scalation, increased buoyancy control, and symmetry of caudal structure needs to be subjected to critical examination.

Teleost fishes may also be characterized by modifications in the jaw musculature. Non-teleost actinopterygians are all very similar in ventral throat musculature anatomy, closely resembling the primitive condition illustrated in Figure 8 with an intermandibularis posterior muscle spanning the mandibular rami, and an interhyoideus extending anteriorly from the ceratohyal and epihyal to insert on the branchiostegal rays and fascia dorsal to the gular plate(s) and intermandibularis posterior. In teleosts, the geniohyoideus muscle extends between the mandibular symphysis and the hyoid (Fig. 13: gh) and is composed of a fused intermandibularis posterior (trigeminal innervation) which forms the geniohyoideus anterior, and the interhyoideus (facial innervation) which comprises the geniohyoideus posterior (see Winterbottom, 1974a). The hyohyoideus musculature of teleosts, which regulates abduction and adduction of the branchiostegal rays and is instrumental in governing branchiostegal pump function during respiration (Gosline, 1971), appears to be derived from the interhyoideus of primitive actinopterygians. Finally, teleost fishes have lost the anterior component of the adductor mandibulae present in primitive actinopterygians (Fig. 8: AMa), and also in *Amia* as the "levator maxillae superioris" (Allis, 1897).

Teleostean phylogeny has been the subject of intensive investigation in the last decade, stimulated primarily by the publication in 1966 of the now classic paper by P. H. Greenwood *et al.* on teleostean phylogeny and classification. Prior

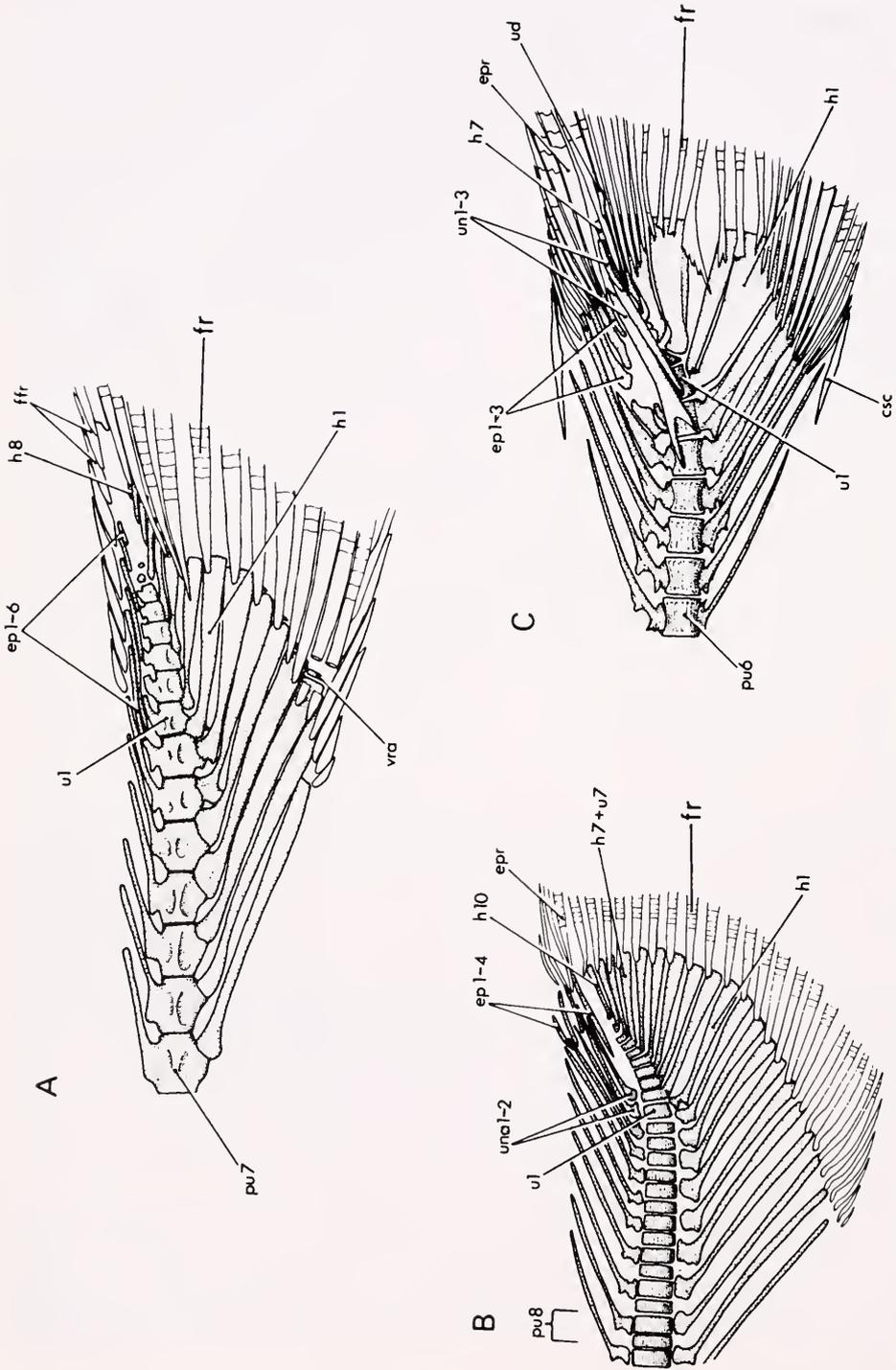


Figure 15. Caudal skeleton. A. A ginglymod (*Lepisosteus osseus*). B. A halecomorph (*Amia calva*). C. A teleost (*Elops saurus*). See text for discussion. (After Patterson [1973], reprinted by permission of the Council of the Linnean Society of London.)  
 Abbreviations: csc, caudal scute; ep, epurals; epr, lowermost epaxial fin ray; fr, fin ray; ffr, fringing fulcra; h, hypural; pu, pre-ural centrum; u, ural centrum; ud urodermal; un, uroneural; una, ural neural arch; vra, ventral caudal radial.

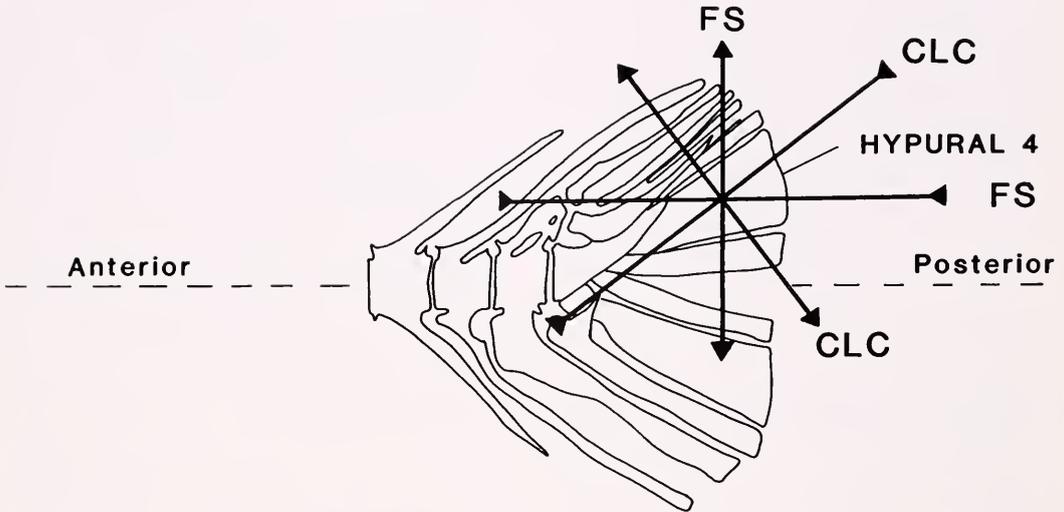


Figure 16. Caudal skeleton of a pumpkinseed sunfish (*Lepomis gibbosus*) showing the patterns of hypural compression and tension resulting from both continuous locomotion (CLC) and fast-start accelerations (FS). Hypural deformation was recorded with a strain gauge (see Lauder, 1982b). Note that during continuous locomotion the angle of the principal strain axes is tilted anteroventrally indicating that the hypurals are being twisted. There is no necessary correlation between the presence of an externally symmetrical tail and symmetrical patterns of thrust or deformation.

to 1966, views on the interrelationships of the major groups of living fishes had changed little since the work of C. T. Regan in the 1920's and teleostean phylogeny was poorly understood. Patterson (1977b: 634) has noted that "the mammalian analogy would be if the distinction between monotremes, marsupials, and placentals was not recognized until ten years ago." Greenwood *et al.* (1966) dismantled many of the clearly unnatural groups of teleost fishes, and the subsequent impact of the methodology of Hennig (1966) has resulted in a tremendous increase in our understanding of teleostean phylogeny (see Greenwood *et al.*, 1973; Patterson and Rosen, 1977). Patterson and Rosen (1977) have recently reexamined several of the early fossil teleostean groups, in particular the pholidophorids, leptolepids, and ichthyodectids, and have concluded that only the ichthyodectiforms constitute a natural group (Fig. 14). Many of the fishes assigned to the "Pholidophoridae" and "Leptolepidae" are so poorly known that

only a few forms can be placed with confidence (Fig. 14).

There are four major groups of living teleosteans, the Osteoglossomorpha, the Elopomorpha, the Clupeomorpha, and the Euteleostei; and while hypotheses of the interrelationships of these groups have changed considerably within the last decade, each appears to be a well corroborated monophyletic group. Each of these groups will be considered in detail below. The interrelationships of the four major living groups of teleosts have been most recently examined by Patterson and Rosen (1977) and their account is summarized in Fig. 14. The osteoglossomorph ("bony-tongued") fishes comprise the most primitive group of living teleosts (also see Gosline, 1980). The other three groups (elopocephalans) are united by the presence of only two unoneurals (Fig. 14: character 5). Gosline (1965; 1980: 21) has suggested that this group shares a nasal pumping system effected by movements of the antorbital bone, but this character has yet to be examined in de-

tail. Within the elopocephalan assemblage, the Elopomorpha (tarpons and eels) are the most primitive group. The more derived Clupeomorpha (herrings) and Euteleostei share several features of cranial and caudal anatomy (Fig. 14).

While the Euteleostei form the bulk of teleost fishes, this group has also been one of the most difficult to characterize with derived characters. Although three characters in particular are commonly used (Fig. 14: 11–13), these features are widely distributed only in primitive euteleostean fishes (many of which lack the characters) and do not form an entirely satisfactory definition of the group. A comprehensive defining set of characters for the Euteleostei remains a key goal of systematic ichthyology.

The feeding mechanism in the early teleost fishes, depicted diagrammatically in Figure 13, differs from both that of the early actinopterygian fishes and that of advanced teleosts with a protrusible upper jaw. The premaxilla is usually small and slightly mobile on the neurocranium although in some groups (e.g., the Osteoglossomorpha) it becomes immovably attached to it. The maxillary bone (Figs. 12 and 13: mx) forms the main tooth-bearing element of the upper jaw and swings anteriorly during prey capture to occlude the corners of the mouth. This system differs very little from the feeding mechanism of *Amia*. In general, the inertial suction feeding mechanism of teleost fishes involves expansion of the orobranchial chamber (Fig. 13: bpc) by elevation of the head, depression of the jaw, depression of the hyoid apparatus and lateral movements of the suspensory apparatus. These expansive movements create a low pressure center in the buccal cavity which creates a flow of water into the mouth. The inertial suction feeding mechanism is a feature of major significance to the evolution of teleostean fishes.

#### THE OSTEOGLOSSOMORPHA

The osteoglossomorph fishes have been subjected to close scrutiny by systematic

ichthyologists in recent years. Greenwood (1967, 1970, 1971, 1973), Nelson (1968, 1969b, 1972), and Taverne (1977, 1978, 1979) have conducted the most comprehensive analyses. Despite this literature, it is still not possible to show convincingly that osteoglossomorph fishes are strictly monophyletic. Although no recent author appears to have doubted this, other groups such as the ichthyodectiforms (Fig. 14) are often included in the Osteoglossomorpha (e.g., Taverne, 1979), and few of the characters proposed as corroborating monophyly stand up to close examination.

Osteoglossomorphs are first known from the Upper Jurassic, but the branching from the elopocephalan lineage (Fig. 14) may be considerably older than this. Of special interest to biogeographers is the fact that living or fossil osteoglossomorphs are known from every continent except Europe (Patterson, 1981a) and a new set of lycoperids, relatives of the living *Hiodon* (North American), have recently been reported from China.

Two characters are often mentioned as characteristic of osteoglossomorph fishes: the presence of a "tongue—parasphenoid bite," and paired bony rods or processes at the base of the second gill arch (see Lauder and Liem, in press; Greenwood, 1973; Nelson, 1968). The osteoglossomorph fishes take their name from the tongue bite in which the basihyal, covered by a massive toothplate, "bites" against the roof of the mouth which bears large teeth (Fig. 17). Nelson (1968: 271) has suggested that in mormyrids, the first basibranchial supports most of the tongue toothplate.) The biting action occurs following initial prey capture by inertial suction, and results in the shredding and decapitation of prey items. The utility of this chewing complex for characterizing the Osteoglossomorpha is called into question by the observation that *Heterotis* and *Gymnarchus* lack parasphenoid teeth, and that parasphenoid teeth are present in more primitive fossil teleostean clades (Patterson and Rosen, 1977;

Fig. 14). This chewing apparatus may thus be shared by more primitive teleost fishes and not be indicative of osteoglossomorph monophyly. All osteoglossomorphs do, however, appear to share an additional feature of the chewing complex. The palatal bones (mesopterygoid and ectopterygoid) are toothed (in *Heterotis* only the mesopterygoid is toothed), and as the basihyal teeth move dorsally to "bite" against the parasphenoid as a result of hyoid protraction, shearing of the prey occurs between the basihyal teeth and the lateral mesopterygoid and/or ectopterygoid teeth. This shearing action is thus in addition to the puncturing and crushing provided by the basihyal—parasphenoid bite, and the entire tongue-bite complex functions as a highly effective mechanism for immobilizing and preparing prey for digestion.

The second character often used to distinguish osteoglossomorph fishes is "the evolution of a discrete connection between the sternohyoid and the second gill arch near the midline" (Fig. 18; Greenwood, 1973: 309). An examination of sternohyoid—gill arch relationships in teleosts reveals that a widespread feature in elopomorphs, clupeomorphs, ostariophysans, paracanthopterygians, and many acanthopterygians is a tendinous connection between the sternohyoideus and a ventrally directed process on hypobranchial three (Lauder, 1983). This feature appears to be primitive at least for elopcephalans, although the possibility that ichthyodectids, *Pholidophorus*, or aspidorhynchiforms also possessed a sternohyoideus connection to the gill arches cannot be ruled out. However, the attachment of the sternohyoideus to hypobranchial two does appear to be confined to osteoglossomorphs. Most osteoglossomorphs have ventrally directed processes on both hypobranchials two and three, and unless this feature is found in more primitive fossil teleosteans it would seem to be unique to osteoglossomorph fishes.

One convincing character uniting all living osteoglossomorphs into a mono-

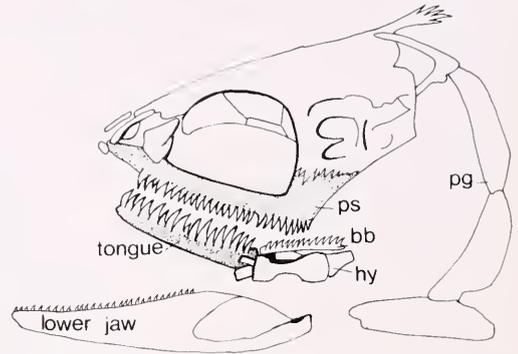


Figure 17. Lateral view of the synchranium, tongue, hyoid (hy), basibranchial (bb), lower jaw, and pectoral girdle (pg) of *Hiodon*, to show the major bony components of the "tongue-parasphenoid bite" which is common to many osteoglossomorph fishes. Note the massive dentition on the tongue and the parasphenoid (ps) of the roof of the mouth. Not shown are the toothed bones of the palatoquadrate located lateral to the tongue on each side. The shearing mechanism resulting from dorsoventral movements of the tongue with adducted palatoquadrates appears to be a shared feature of all osteoglossomorphs. More primitive teleosts have parasphenoid (and perhaps also basihyal) teeth and not all osteoglossomorphs possess a dentigerous parasphenoid.

phyletic group is the pattern of coiling in the gut (Nelson, 1972). In all primitive actinopterygians, "the anterior part of the intestine passes posteriorly to the right of the esophagus and stomach" (Nelson, 1972: 326), and this is true for higher teleosts as well. In osteoglossomorphs, the gut passes to the left of the esophagus and stomach, and one or two pyloric caeca are consistently present. A summary of the other characters that corroborate osteoglossomorph monophyly is presented in Figure 19.

Within the osteoglossomorpha, there is a great diversity in trophic biology. Insectivorous and piscivorous predators as well as filter feeders and benthic feeding fishes occur. *Heterotis*, a filter feeder, has a specialized epibranchial organ (Taverne, 1977; Nelson, 1967a) which apparently functions in the maceration of filtered material prior to swallowing. The gross morphology of the osteoglossomorph brain (Fig. 20) appears to be relatively primitive, although the forebrain of *Arapaima* and the enormously en-

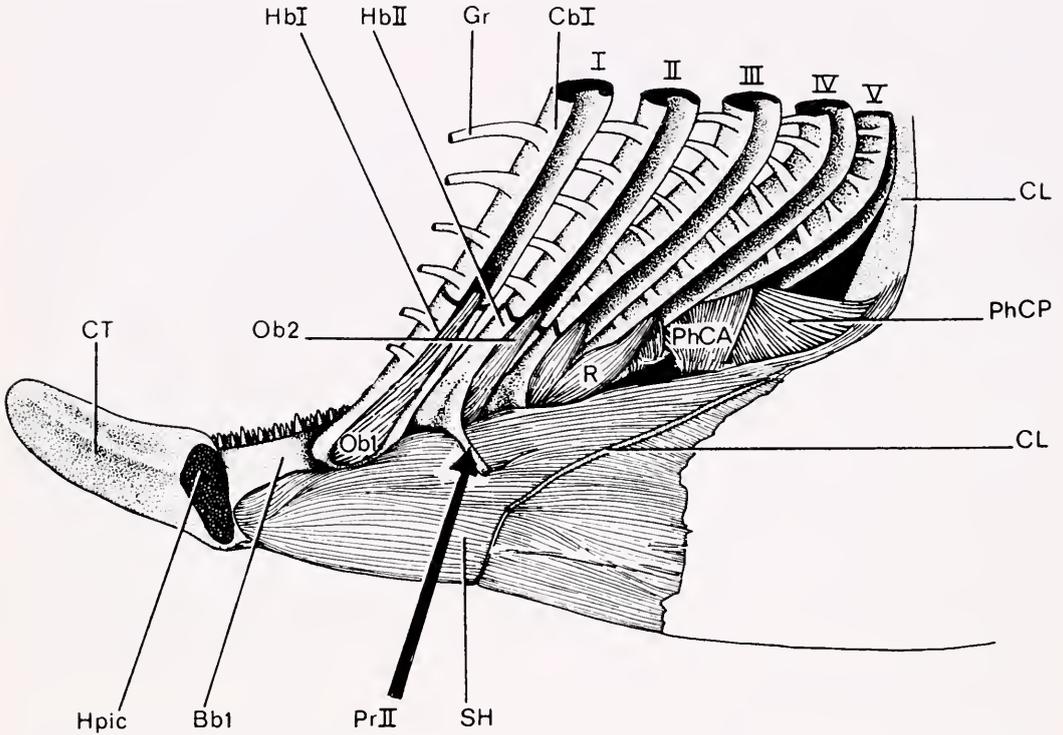


Figure 18. Ventral gill arch muscles and sternohyoideus (SH) of *Scleropages* in left lateral view (from Greenwood [1971], courtesy of the Trustees of the British Museum [Nat. Hist.]). The hypohyal has been partly cut away. Note the prominent bony process on the second gill arch indicated by the arrow.

**Abbreviations:** Bbl, basibranchial one; Cb I-V, ceratobranchials (arches I-V); CL, cleithrum; CT, connective tissue surrounding lateral and ventral edges of basihyal and its anterior tooth plate; Gr, gill rakers; Hb I and II, hypobranchial of first and second arch; Hpic, hypohyal (cut through); Ob 1-3, obliquus muscle (1st-3rd gill arches), PhC A and P, external and internal pharyngocleithralis muscles; PrII, bony process from second hypobranchial; R, rectus muscle; SH, sternohyoideus muscle.

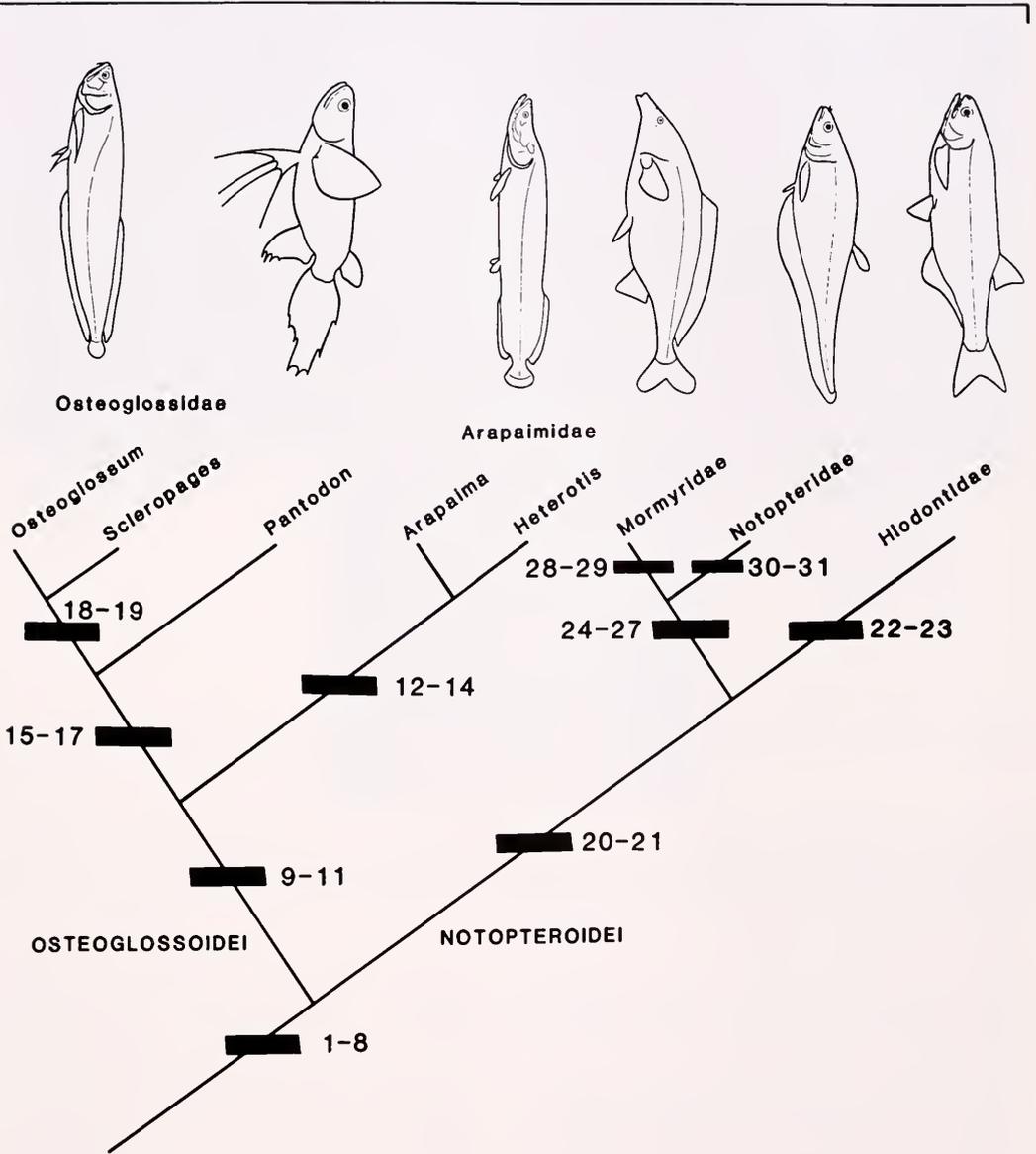
larged cerebellum of the electrogenic mormyrids clearly represent specialized conditions.

The Osteoglossomorpha may be divid-

ed into two major clades, the Notopteroidei, containing the families Notopteriidae, Mormyridae, and Hiodontidae, and the Osteoglossoidei containing the Os-

Figure 19. Phylogenetic relationships of the Osteoglossomorpha. Characters are: **1**, "shearing bite" between the basihyal teeth and lateral pterygoquadrate teeth; **2**, small premaxilla firmly fixed to the skull; **3**, intestine coils to left of esophagus and stomach (Nelson, 1972); **4**, Taverne (1979) has recently proposed (but also see Gosline, 1960; Greenwood *et al.*, 1966) that osteoglossomorphs share a distinctive caudal skeleton in which one or more epurals are fused with neural arches of the caudal to form "neurepurals"; **6**, parapophyses fused with vertebral centra; **7**, loss of supramaxillae; **8**, other, more questionable characters proposed for the Osteoglossomorpha include reticulate scales, 16 or fewer branched caudal rays, and a ventral process at the base of the second gill arch (see text); **9**, fusion of hypurals (usually 3, 4, and 5 at least); **10**, septum bisecting the eye, extending between the retina and lens (Haedrich *et al.*, 1973); **11**, articulation between ventrolateral peg of the parasphenoid and the entopterygoid (Greenwood *et al.*, 1966: 363); **12**, fusion of antorbital and lacrimal (Nelson, 1969b); **13**, uroneurals fused with the dorsalmost hypural; **14**, third infrapharyngobranchial "with medial portion segmented off as a distinct cartilage" (Nelson, 1968: 268); **15**, maxilla fixed to cheek and does not swing anteriorly on its dorsal palatal articulation during feeding; **16**, small "A1" division of the adductor mandibulae inserts on the maxilla (personal observation; Kershaw, 1976); **17**, single basibranchial toothplate "extending

OSTEOGLOSSOMORPHA



to the anterior end of a cartilagenous basihyal" (Nelson, 1968: 269) (see Taverne [1979] for numerous other characters); **18**, numerous unique features of the gill arches (Nelson, 1968) including the structure of the basibranchials and infra-pharyngobranchials; **19**, loss of the orbitosphenoid (Greenwood *et al.*, 1966: 362) (see Taverne [1979] for numerous other characters); **20**, "osteoglossomorph type" of otophysic connection (see Greenwood, 1973); **21**, ventral throat musculature containing an anteroposteriorly oriented intermandibularis posterior muscle that is not fused with the interhyoideus; **22**, medial process of the second and third infra-pharyngobranchials of each side overlapping in the midline (Nelson, 1968); **23**, uniquely specialized infraorbital bones (Nelson, 1969b); **24**, utricle completely separated from the sacculus and lagena; **25**, lateral line without pores; **26**, brain with greatly enlarged cerebellum; **27**, dentary sensory canal is an open groove rather than enclosed (Nelson, 1973); **28**, cerebellum encloses most of the rest of the brain; **29**, well-developed electrogenic and electroreceptive capability (amongst many other unique features of this family); **30**, ventral hypohyal lacking; **31**, ventral bony scutes present. (Drawings of fishes from J. S. Nelson [1976], courtesy of John Wiley Publishing Co.)

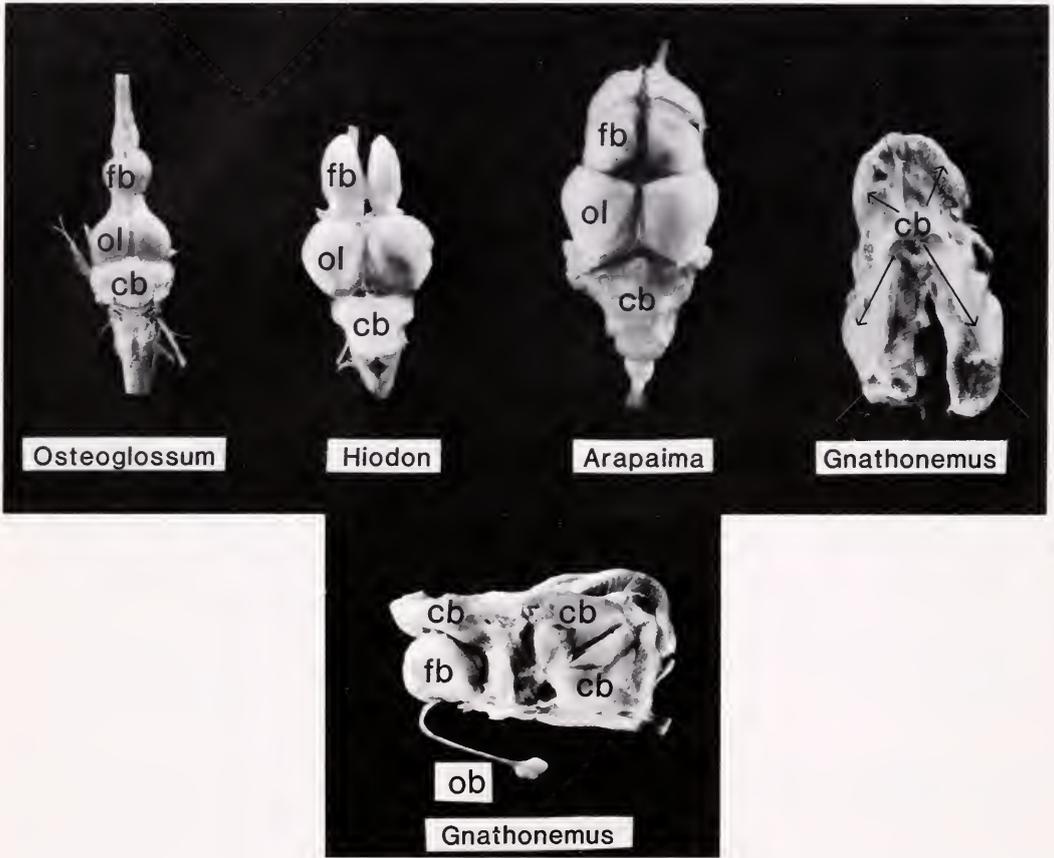


Figure 20. Dorsal views of the brains of some representative osteoglossomorphs. The cerebellum (cb) in *Osteoglossum* and *Hiodon* exhibits only a moderate increase in size. In *Arapaima* the cerebellum is enlarged as in most osteoglossomorphs. In *Gnathonemus* the cerebellum is greatly enlarged enveloping the rest of the brain.

Abbreviations: cb, cerebellum; fb, forebrain; ob, olfactory bulb; ol, optic lobe.

teoglossidae and *Arapaima* and *Heterotis*, here united into the Arapaimidae (Fig. 19).

*Osteoglossoidei*. Members of this clade possess one muscle, the geniohyoideus, extending between the mandible and the hyoid (Fig. 21A) (Greenwood, 1973; Kershaw, 1976). Although this character has been used as a shared derived feature for this group, the presence of a single geniohyoideus muscle is primitive for teleosts (Lauder, 1982a; see p. 117) and is not indicative of shared common ancestry. Most members of this group possess so-called reticulate scales (Fig. 22) with small sur-

face ridges ("circulae") aligned concentrically in a semicircle on the distal exposed aspect of the scale (see Nelson, 1969b: 24, 25; Taverne, 1979: 70). Reticulate scales are also found in the mormyrids as well as in several other teleosts.

*Osteoglossum*, *Arapaima*, *Scleropages*, and *Heterotis* have evolved a mouthbrooding behavior for caring for the young, and this pattern of parental care appears to be primitive for the Osteoglossoidei. *Pantodon*, a highly specialized member of this group, is a small surface-dwelling fish with an upturned

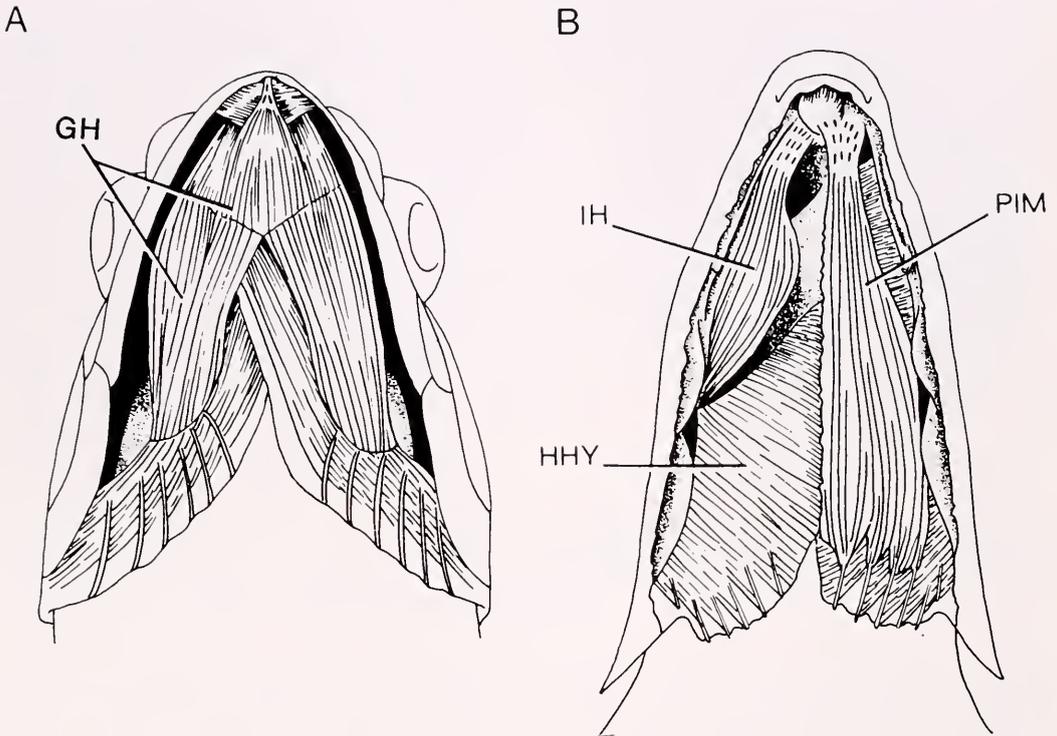


Figure 21. A. Ventral hyoid musculature of an osteoglossoid (*Pantodon*) showing the single muscle, the geniohyoideus (GH) between the mandible and the hyoid. B. Ventral hyoid musculature of a mormyrid (*Mormyrus*), showing the two muscles, the interhyoideus (IH) and posterior intermandibularis (PIM), between the mandible and the hyoid (From Greenwood [1971], courtesy of the Trustees of the British Museum [Nat. Hist.] )

mouth. Prey are small insects caught in the surface film, and *Pantodon* also breathes highly oxygenated water from just below the surface. It has been suggested that *Pantodon* is capable of air-breathing, a behavior well documented in *Arapaima* which uses a modified swimbladder as a lung.

*Notopteroidei*. The ventral throat musculature in the three clades comprising this suborder is distinctly modified (Fig. 21B). *Hiodon* shows the most generalized condition while mormyrids and notopterids show a specialized interhyoideus and posterior intermandibularis that is clearly a derived condition. The inner ear of mormyrids and the notopterid knife fishes shares a condition in which the utriculus and its semicircular canals are completely separated from the sacculus

and lagena (Fig. 23), and the highly specialized cephalic lateral line system is without pores. The family Notopteridae possesses an enlarged toothplate covering the tongue and 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 which have very few species, 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 (Fig. 20). Mormyrids feed at least in part by electrolocation (Hopkins, 1981) and exploit the rich bottom fauna of small

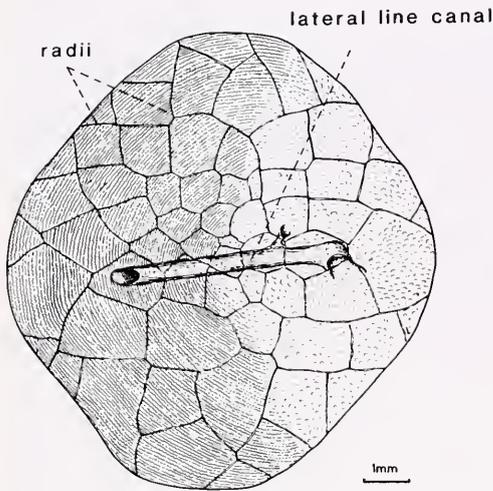


Figure 22. Lateral line scale of *Osteoglossum bicirrhosum*. The scale is typically ornamented. The radii form a coarse and irregularly reticulated pattern, both apically and basally. (After Taverne, 1977.)

worms and wormlike insects. The mormyrids largely occupy nocturnal bottom feeding niches in the rivers of Africa. *Gymnarchus niloticus*, often placed in a separate family Gymnarchidae, is a close relative of the mormyrid fishes.

The last clade in the Notopteroidei is the genus *Hiodon*, with two extant species, *Hiodon tergisus* and *H. alosoides*. These are the only osteoglossomorphs found in North American waters. Although *Hiodon* is often cited as being a very primitive teleost, it shows many specializations, especially in the braincase and swimbladder (Greenwood, 1973). The swimbladder has a diverticulum on each side extending anteriorly into the ear. Within the ear, this diverticulum is separated by a thin membrane from a vesicle which is filled with perilymph and connected with the utriculus of the inner ear via a foramen in the prootic bone.

#### THE ELOPOMORPHA

The Elopomorpha contains about 650 species (J. Nelson, 1976) which vary tremendously in body form and habit from the more conventionally shaped mega-

lopids (tarpons) to the highly aberrant saccopharyngoid deepsea eels. Elopomorph fishes may be divided into seven major groups: the Elopidae, tenpounders; the Megalopidae, tarpons; the Albulidae, bonefishes; the anguilloids, eels, containing about 600 of the 650 elopomorph species and about 19 families; the saccopharyngoids, bathypelagic eels; the Halosauridae, deep-sea halosaurs; and the Notacanthidae, deep-sea spring eels.

The interrelationships of these groups has been a matter of considerable debate in recent years, and elopomorph phylogeny has been most recently considered by Greenwood (1977) and Patterson and Rosen (1977). It has become increasingly clear, however, that the elopomorph fishes form a natural, monophyletic group which may be defined on the basis of several specializations (Forey, 1973a, b; Greenwood, 1977; Patterson and Rosen, 1977). The most remarkable feature shared by elopomorph fishes is the occurrence of a leptocephalus larva, an elongate ribbonlike larva with a small head and greatly extended body. See Hulet (1978) and Leiby (1981) for descriptions of eel leptocephali. The leptocephalus may be larger than the adult and is generally translucent with clearly visible segmented myotomes along the body. While the larval forms of all elopomorphs are not known, leptocephalus larvae do occur in all of the major elopomorph groups. A number of osteological features also may be used to define the Elopomorpha (Fig. 24): fusion of the angular and retroarticular bones of the lower jaw and the occurrence of rostral and prenasal ossicles in the snout.

The Suborder Anguilloidei contains the vast majority of the elopomorph fishes and is divided into two superfamilies, the Anguilloidea and Saccopharyngoidea (Fig. 24). The saccopharyngoids, with eight nominal species in three families, are highly specialized deep-sea fishes with elongate bodies and large mouths capable of engulfing extremely large prey rel-

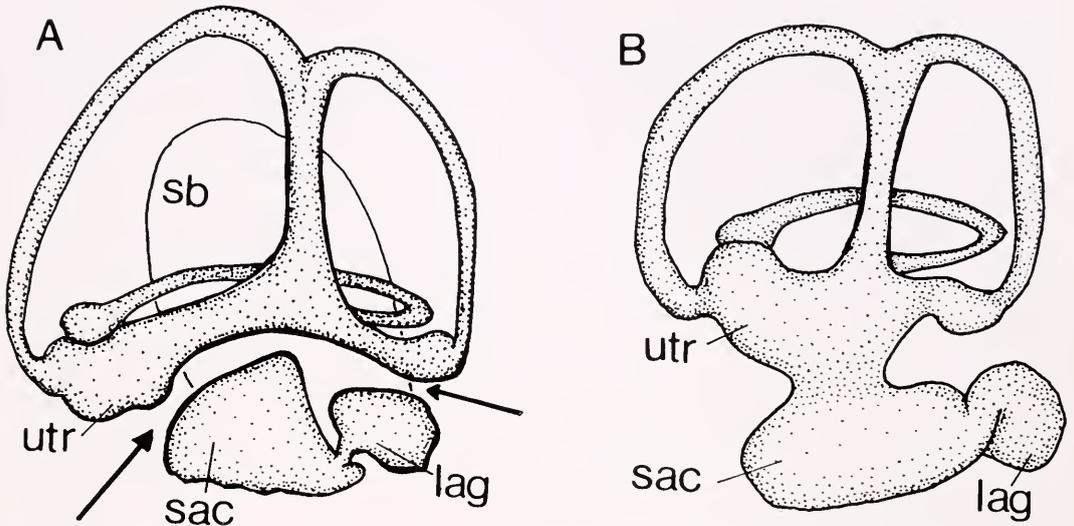


Figure 23. A. Medial view of the inner ear of a notoapteroid, showing the complete separation of the utricle (utr) with its semicircular canals from the sacculus (sac) and lagena (lag). The intraotic extension of the swimbladder (sb) is outlined. B. Medial view of the inner ear of an osteoglossoid exhibiting the primitive condition.

ative to their own body size. The skull is highly modified, and many bones are lacking as are scales, pelvic fins, the caudal fin, ribs, and swimbladder. These fishes are so bizarre that their relationships have been a matter of controversy in the past, although now it is generally recognized that the anguilloid eels are their closest relatives (Fig. 24). The Anguilloidea includes a wide diversity of eel-like fishes ranging from the well-known *Anguilla rostrata*, the American eel (Family Anguillidae), to the deep-sea snipe eels (family Nemichthyidae) and snake eels (Ophichthidae). All forms are highly elongate, and pelvic fins are absent in all Recent eels. The Anguillidae is the only family of eels containing members that spend part of their life in freshwater. All other eel families are exclusively marine. Spawning of the North American eel and the European eel (*A. anguilla*) takes place in the Sargasso Sea, and the leptocephalus larvae then drift either to North America or Europe where they metamorphose into elvers which often enter freshwater to mature into

adults. The lifecycle is completed when the adults migrate back into the sea and travel to the Sargasso where reproduction occurs and the adults die. The American eel differs from the European species in spawning site as well as in the length of larval life. Both have the same pattern of life history.

The sister group of the Anguilloidei is a group, the Albuloidei, composed of the Albuloidea (bonefishes) and Halosauroida (halosaurs and notacanth) (Fig. 24). The bonefishes, of which *Albula vulpes* is the best known, occur worldwide in tropical seas. They have a small mouth, and generally feed in schools on bottom living invertebrates. The halosauroids are divided into two groups, both found in the deep-sea with a worldwide distribution. The Halosauridae (3 genera) are elongate with a prominent lateral line and have a sensitive snout that is apparently used for food detection. Halosaurs are bathypelagic and retain a swimbladder (lost in many benthic fishes). The Notacanthidae, or spiny eels (Fig. 24), are similar in habit to the halosaurs although their

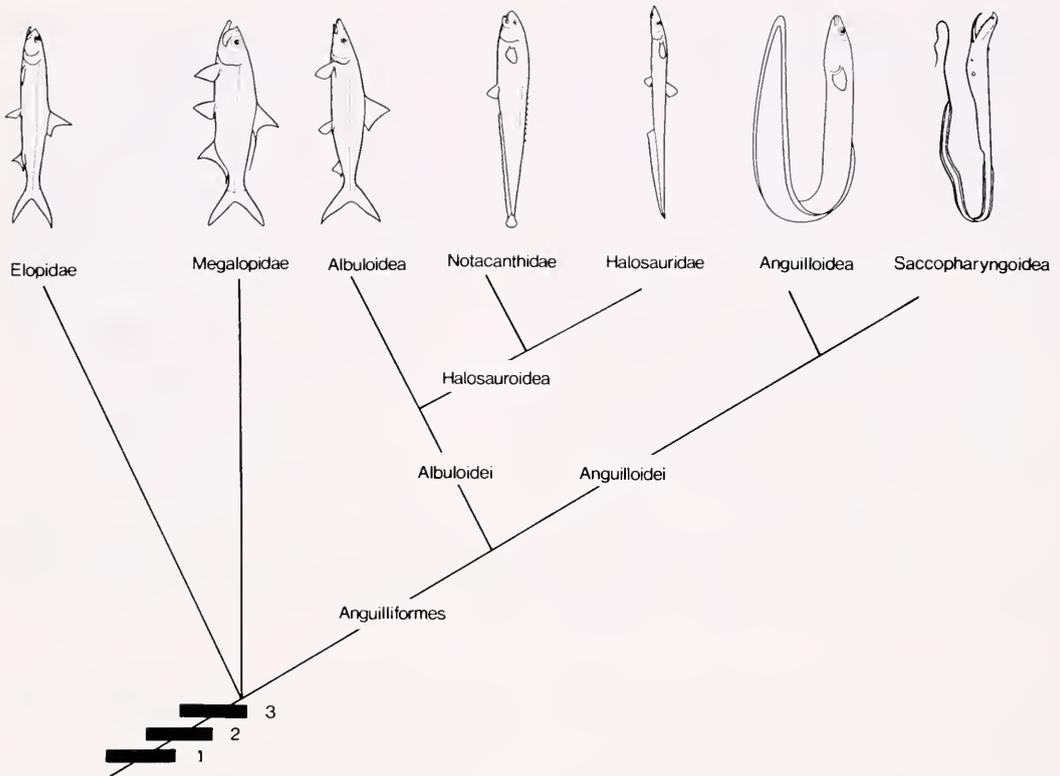


Figure 24. Phylogeny of the Elopomorpha. The Elopidae, Megalopidae, and Anguilliformes form an unresolved trichotomy based on present data. Shared derived characters of the Elopomorpha include 1, the presence of a leptocephalus larva; 2, fusion of the angular and retroarticular bones of the lower jaw; and 3, the presence of rostral and prenasal ossicles. See Patterson and Rosen (1977) for further characters. Justification of the branching pattern in the Anguilliformes may be found in Greenwood (1977) and Forey (1973). (Drawings of fishes from J. S. Nelson [1976], courtesy of John Wiley Publishing Co.)

food seems to consist more of soft-bodied deep-sea invertebrates. One rather modified notacanth, *Lipogenys*, often placed in a separate family, is poorly known but lacks teeth and possesses a small subterminal suctorial mouth (Greenwood, 1977).

The two remaining groups of elopomorphs, the Megalopidae and Elopidae, are often considered to be closely related to each other, together forming the sister group to the Anguilliformes. Patterson and Rosen (1977) have recently reviewed the evidence for this dichotomy and have concluded that little justification exists, and, on present evidence, the interrelationships of the Elopidae, Megalopidae,

and Anguilliformes are best represented as an unresolved trichotomy (Fig. 24). The family Elopidae, tenpounders, contains a single genus *Elops* with about five species which are distributed worldwide in tropical seas. Most commonly found in estuaries and near shore as adults, tenpounders may invade brackish waters. The Megalopidae, tarpons, with two species in tropical and subtropical waters of the Pacific and Atlantic, grow to a large size (maximum length about 2 m) and are unique among elopomorphs in possessing a connection between the ear and the swimbladder (Greenwood, 1970). This otophysic connection consists of paired

cranial swimbladder diverticula which extend anteriorly to form small air-filled bullae near the ear. The significance of this arrangement for sound reception in tarpons is as yet unclear.

### THE CLUPEOMORPHA

The Clupeomorpha (herringlike fishes) first appear in the Lower Cretaceous. Most of the Recent members (4 families and over 290 species) are primarily marine, although many move easily into brackish and freshwater. 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.

Four specialized character complexes, shared by the Recent Clupeomorpha offer convincing evidence that the group is a genuinely monophyletic assemblage (Grande, 1982a, b has recently provided new information on fossil clupeomorph fishes). The first feature is a specialized connection between the ear and swimbladder. The swimbladder's forward extension divides on each side of the skull to form two large vesicles which are lodged within ossified bullae or expansions of the prootic and pterotic bones (Greenwood *et al.*, 1966; Greenwood, 1973). This type of ear-swimbladder 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 basiooccipital) (Fig. 25A). The third characteristic feature is the recessus lateralis, a chamber in the pterotic bone into which several of the cranial lateral line canals empty (Greenwood *et al.*, 1966). Finally, extant clupeomorphs have a unique caudal skeleton (Forey, 1975; Gosline, 1960; Greenwood *et al.*, 1966). The urostyle (Fig. 25B) is composed of uroneural one and the terminal vertebral

centrum, and hypural one is autogenous—separated by a gap from the urostyle (Fig. 25B: arrow).

The Clupeomorpha and the next major clade to be discussed, the Euteleostei (Fig. 14), appear to be more closely related to each other than either is to any other group of teleosts (Patterson, 1977b; Patterson and Rosen, 1977). In both groups an important innovation is present, increasing the versatility of the feeding apparatus. The upper pharyngeal jaws, which are supported by the first three pharyngobranchials, have a well-anchored armor of teeth formed by the complete fusion of the toothplates to the endochondral pharyngobranchial elements (Nelson, 1969a). Similarly, in the lower pharyngeal jaw the tooth plates fuse to ceratobranchial five. One other significant character uniting the Clupeomorpha and Euteleostei is the co-ossification of the angular and articular bones of the lower jaw (Nelson, 1973). In more primitive groups, the dermal toothplates are only loosely attached to the gill arch elements, and other patterns of lower jaw bone fusion occur. Other features corroborating Clupeocephalan monophyly are summarized in Figure 14.

Clupeomorph relationships have yet to be precisely defined. We provisionally follow Nelson (1970) for most groups, and represent the interrelationships of the clupeoid lineages as an unresolved polychotomy (Fig. 26). The Denticipitoidei contains only the primitive *Denticiceps clupeoides* (Clausen, 1959; Greenwood, 1968) from the freshwaters of Nigeria. *Denticiceps* bears numerous small denticles on the skull and parts of the body. The Clupeoidei contains the remaining extant clupeomorphs: the Chirocentridae (Wolfherrings; the only predaceous clupeomorphs), Clupeidae (herrings and menhaden), Dussumieriidae (round herrings), Engraulidae (anchovies), and the Pristigasteridae (sometime ranked as a subfamily of the Clupeidae).

Fossil clupeomorphs have been de-

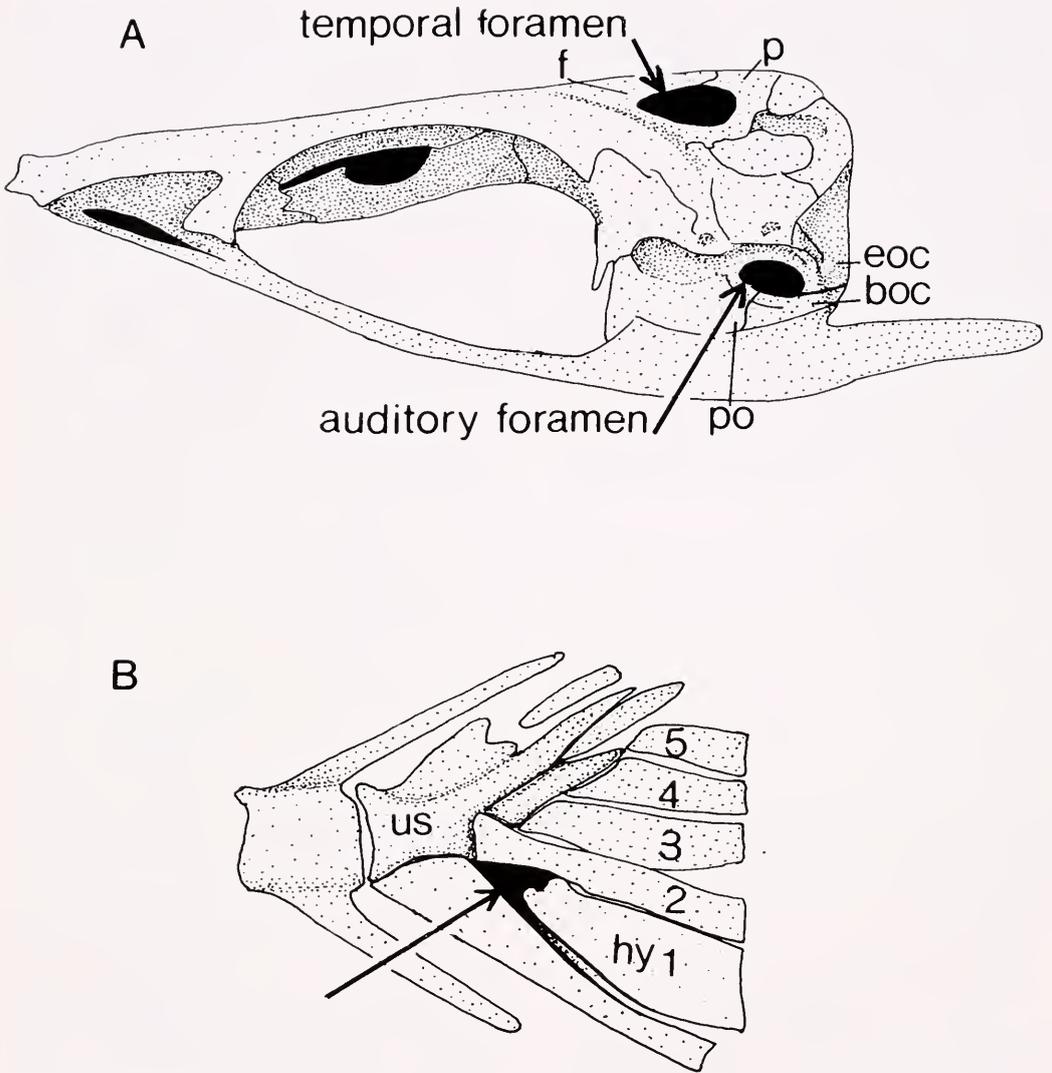


Figure 25. A. Lateral view of a clupeomorph neurocranium, showing the temporal and auditory foramina, surrounded respectively by the frontal (f) and parietal (p) bones, and by the prootic (po), basioccipital (boc) and exoccipital (eoc). B. Lateral view of a clupeomorph caudal skeleton showing the gap between the "urostyle" (us) and the first hypural (hy 1).

scribed by Forey (1973c; 1975), Greenwood (1960), and Patterson (1970), and the relationships of these forms to the Recent Clupeomorpha are summarized in Figure 26.

The major evolutionary trends within the Clupeomorpha are not yet clear due to the lack of a corroborated phylogenetic

hypothesis. However, it is evident that there has been a repeated and independent loss of teeth on the jaws and gill arches (Forey, 1975), a reduction and loss of branchiostegal rays, and the development of a long and very complex digestive tract with a "gizzard-like" structure (Nelson and Rothman, 1973). In addition,

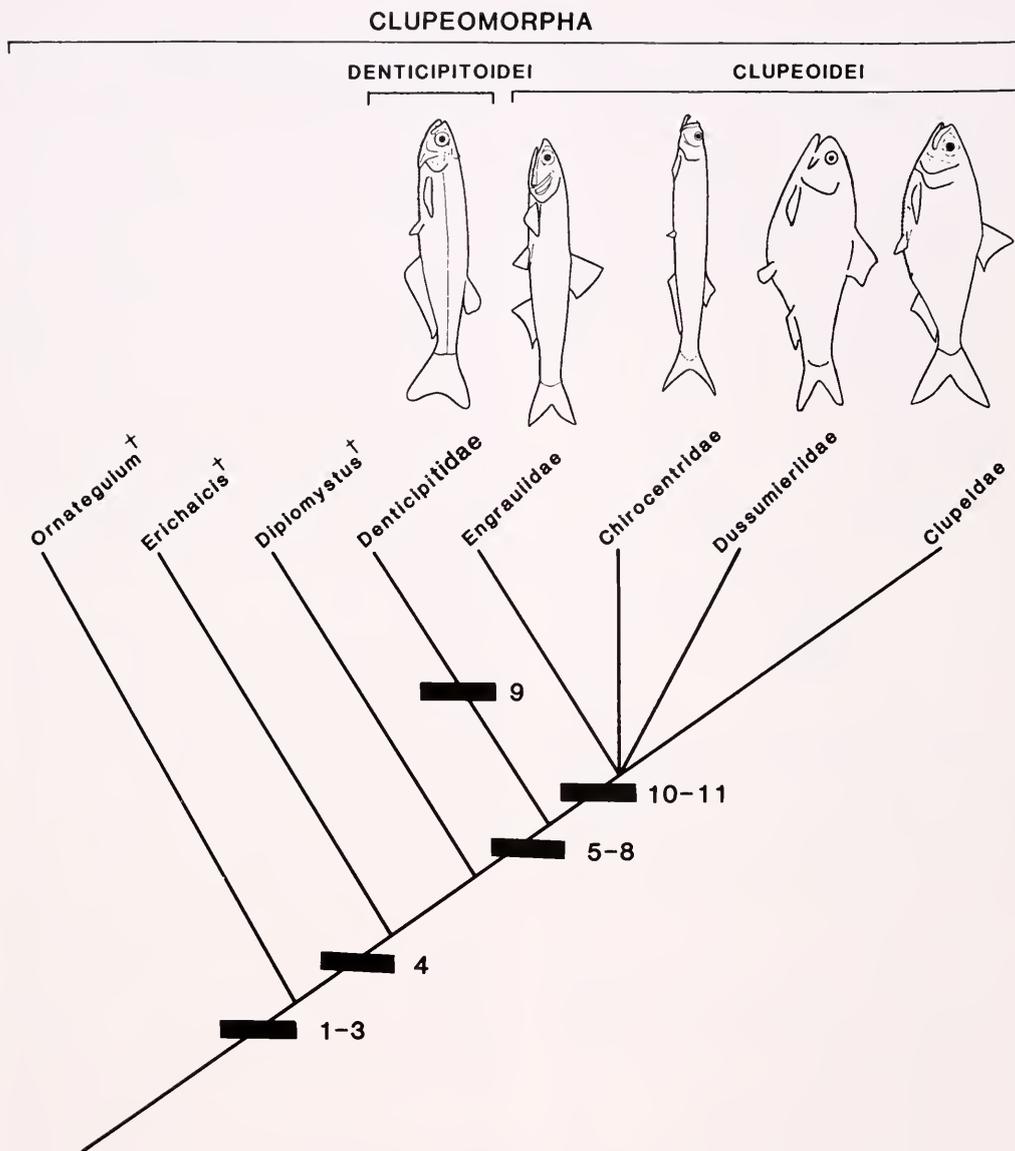


Figure 26. Interrelationships of the major groups of the Clupeomorpha. Three fossil taxa are included. Major specializations characterizing the various lineages are: 1, autogenous hypural number one; 2, hypural two fused with ural centrum one (these two characters are also found in several primitive euteleosteans and not in *Erichalcis* (Forey, 1975); 3, fusion of the median and lateral extrascapulars with the supraoccipital and parietal bones (indicated in part by the presence of a sensory canal in the supraoccipital, Patterson, 1970); 4, abdominal scutes present; 5, presence of a recessus lateralis; 6, temporal foramen present; 7, post-temporal groove present; 8, prootic and pterotic bullae present and enclosing an intracranial swimbladder diverticulum (this character is not known in fossil forms although Forey (1975) has suggested that the prootic bulla evolved before the pterotic bulla and may be a unique feature of all clupeomorphs); 9, denticles on skull bones and some trunk scales (see Greenwood (1968) for additional characters); 10, third pharyngobranchial bones with long medial processes; 11, two divisions of the levator arcus palatini muscle (Forey, 1975). The interrelationships of the clupeoids are a matter of dispute and additional families such as the *Pristigasteridae* and *Congothrissidae* may be recognized. (Drawings of the fishes adapted from J. S. Nelson [1976], courtesy of John Wiley Publishing Co.)

the clupeoids have evolved an upward extension of the space behind the fourth gill arch bordered anteriorly and posteriorly by the interdigitating edges of specialized gill rakers. The entire organ is called an epibranchial organ (Nelson, 1967a). As the gill arch elements bearing these rakers move toward one another, any small food in the epibranchial organs will be compacted into manageable masses or ground up. These morphological specializations are correlated with the development of mechanisms for the microphagous habits so characteristic of the vast majority of clupeoids.

### THE EUTELEOSTEI

The Euteleostei is an extremely large clade containing a greatly varying array of over 25 orders, 375 families, and 17,000 species. The current definition of the Euteleostei, although it has not been seriously challenged, is "far from satisfactory" (Patterson and Rosen, 1977). Three main characters corroborate euteleostean monophyly, although these are generally shared by primitive euteleosteans and have been lost in the more derived forms (Patterson and Rosen, 1977: 130): 1) the presence of an adipose fin posterior to the dorsal fin, 2) nuptial breeding tubercles on the head and body (Collette, 1977; Wiley and Collette, 1970), and 3) an anterior membranous component to the first uro-neural (Figs. 14, 28). Further evidence corroborating monophyly of this group is highly desirable.

### Primitive Euteleostean Fishes

In 1966, Greenwood *et al.* combined into a group, the superorder Protacanthopterygii, a wide variety of fishes which they considered to be basal "Division III" forms (Greenwood *et al.*, 1966: Fig. 1, p. 366). The Protacanthopterygii included the salmoniform, stomiatiform, alepocephaloid, myctophid, neoscopelid, and, questionably, the ostariophysan fishes. Rosen (1973) conducted a critical analy-

sis of the relationships of this assemblage and removed the stomiatiform, neoscopelid, myctophid, ostariophysan and alepocephalid fishes to their current location on the euteleostean cladogram (Fig. 14). These groups will be discussed below. Rosen (1974) then considered the only remaining subgroup, the Salmoniformes, to be monophyletic and coextensive with the Protacanthopterygii. The evidence for monophyly included 1) enlarged toothplates associated with but not fused to the fourth pharyngobranchial and 2) fusion of the third gill arch toothplate to the third pharyngobranchial (Fig. 27). As we have noted above, however (Fig. 14: sp. 129), fusion of toothplates to the endochondral gill arch elements is a clupeocephalan feature, and does not support monophyly of clades within the Euteleostei.

Fink and Weitzman (1982) have dealt the final blow to the concept of a natural Protacanthopterygii, and have shown that the esocoids do not belong in this assemblage, that present data are not sufficient to resolve a dichotomy between the Ostariophysi, Euteleostei, and argentinoids plus osmeroids. The Salmonidae is provisionally considered to be the sister group of the Neoteleostei. Their hypothesis of the relationship of these groups is depicted in Figure 28. Because of the well-corroborated monophyletic nature of the Ostariophysi, we will discuss this group in detail below. Here, under the admittedly inadequate heading "primitive euteleostean fishes," we consider the esocoids, salmonids, osmeroids (*sensu* Fink and Weitzman, 1982), and argentinoids. The phylogenetic relationships of these groups as depicted in Figure 28 should be regarded as highly tentative. Due to the importance of the taxa discussed here both for evolutionary research and for fisheries management and biology, the systematic relationships of these fishes deserve considerable attention. Because of the virtual obliteration of the original Protacanthopterygii, we do

not advocate use of this term, at least until lower euteleostean systematic research provides a well-documented monophyletic group to which the term can be applied.

*Esocae*. This clade, containing the pikes and pickerels (Esocidae) as well as the mudminnows (Umbridae), may be the most primitive euteleostean clade. Esocids retain the primitive dentigerous toothplates on the fourth basibranchial, lacking in more derived euteleosteans, and this may be evidence of their primitive position relative to other euteleosteans (Fink and Weitzman, 1982). The teeth on the tongue of esocids are small and uniform (Fig. 29), as are the teeth on the basibranchial elements behind the tongue. The adipose fin is absent, but this may be related to the posterior position of the dorsal fin. The maxillae of esocids are toothless, although they do form part of the gape, swinging anteriorly during prey capture as in *Amia* and *Salmo* (Lauder, 1979; Rand and Lauder, 1981). The body form of esocids, with most of the lateral fin area located far posterior to the center of mass, reflects the rapid accelerations used during prey capture and the generally poor cruising performance of these fishes (Webb and Skadsen, 1980). The pikes, pickerels, and mudminnows are restricted to the freshwaters of the northern hemisphere, although *Lepidogalaxias*, considered by Rosen (1974) to be an esocid, (Fink and Weitzman [1982] have questioned this) is a small fish from Western Australia.

*Salmonidae*. This group includes the trout, salmon (*Salmo* and *Oncorhynchus*), charr (*Salvelinus*), whitefish (*Coregonus*), and the grayling (*Thymallus*). These forms were originally confined to the northern hemisphere before shipment of salmonids to stock southern streams occurred. The small family Galaxiidae is often included with the Salmonidae in the order Salmonoidei, but we follow Fink and Weitzman (1982) in grouping galaxiids with Osmeroidei.

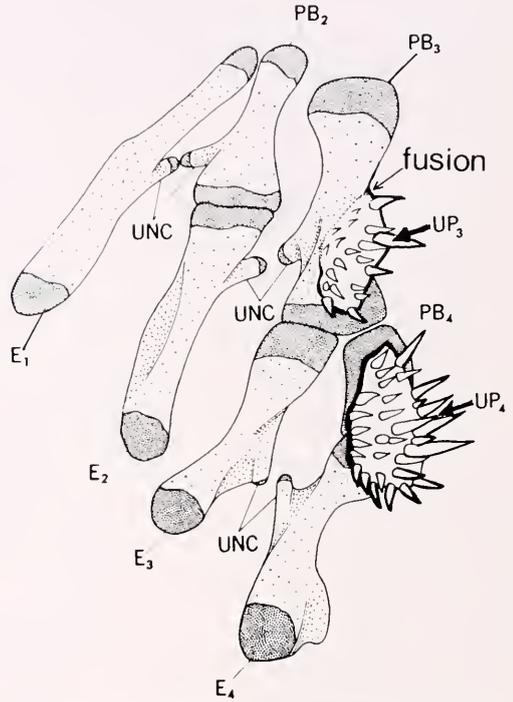


Figure 27. Dorsal gill arch skeleton, right side ventral view, of the "protacanthopterygian" *Novumbra*. Fusion of the toothplate ( $UP_3$ ) to the third pharyngobranchial ( $PB_3$ ) is indicated. Other tooth plates ( $UP_4$ ) are not fused to the gill arch elements. The fourth upper toothplate ( $UP_4$ ) is the dominant element. (Modified from Rosen, 1974.)

Other abbreviations:  $E_{1-4}$ , epibranchials; UNC, uncinat process.

There is relatively little evidence corroborating the monophyly of this group, although Rosen (1974) suggests that the tip of the posterior neural arch of the last caudal vertebra is joined to the first uroneural, and can be used to define osmeroids. Fink and Weitzman discuss two characters which link the salmonids to the Neoteleostei and are suggestive of a sister group relationship (Fig. 28). 1) In salmonids and neoteleosts, both the exoccipital and basioccipital articulate with the anterior vertebrae. In more primitive groups, only the basioccipital is involved in the articulation. 2) Paired cartilage nodules lying anterior to the ethmoid and attached to the premaxillae are suggested

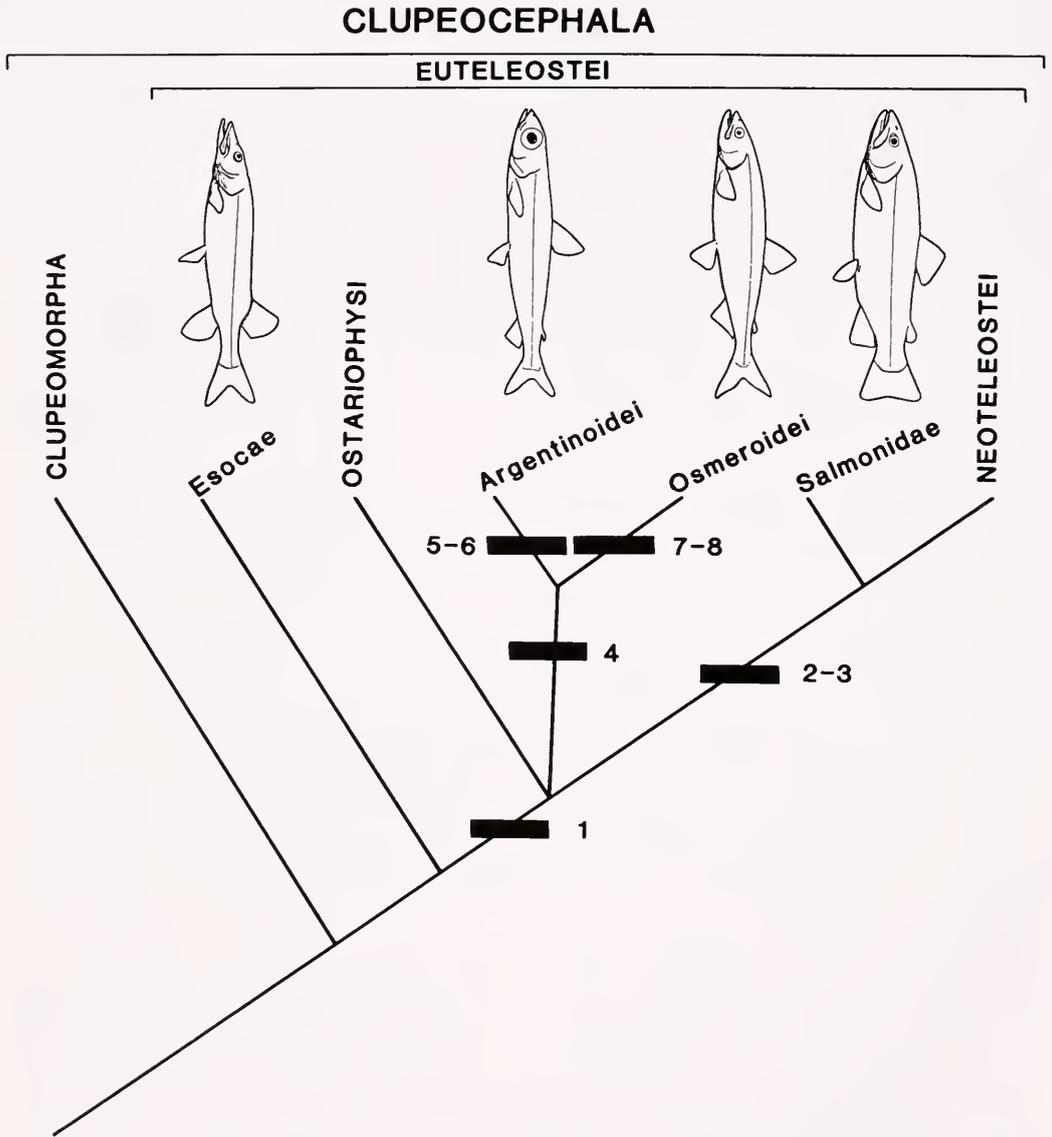


Figure 28. Interrelationships of primitive euteleosteans following the tentative hypothesis suggested by Fink and Weitzman (1982). Specializations characterizing the Clupeocephala, Euteleostei, and Neoteleostei are summarized in Figure 14. The characters are: 1, loss of the dentigerous toothplate on basibranchial four; 2, cartilage nodules (homologous to the rostral cartilage of euteleosts) between the ethmoid and premaxillae; 3, both the basioccipital and exoccipital articulate with the first vertebra; 4, fusion of the posterior neural arches in the caudal fin with either the uroneural or ural vertebra one; 5, specialized "tongue-bite" mechanism between basihyal and mesopterygoid teeth (Fink and Weitzman, 1982); 6, loss of basisphenoid (this bone is also absent in ostariophysans; Fink and Weitzman, 1982); 7, basibranchials toothless; 8, "crurenal organ" present and the posterior aspect of the fifth ceratobranchial associated with a complex accessory cartilage (see Greenwood and Rosen, 1971). (Drawings of fishes from J. S. Nelson [1976], courtesy of John Wiley Publishing Co.)

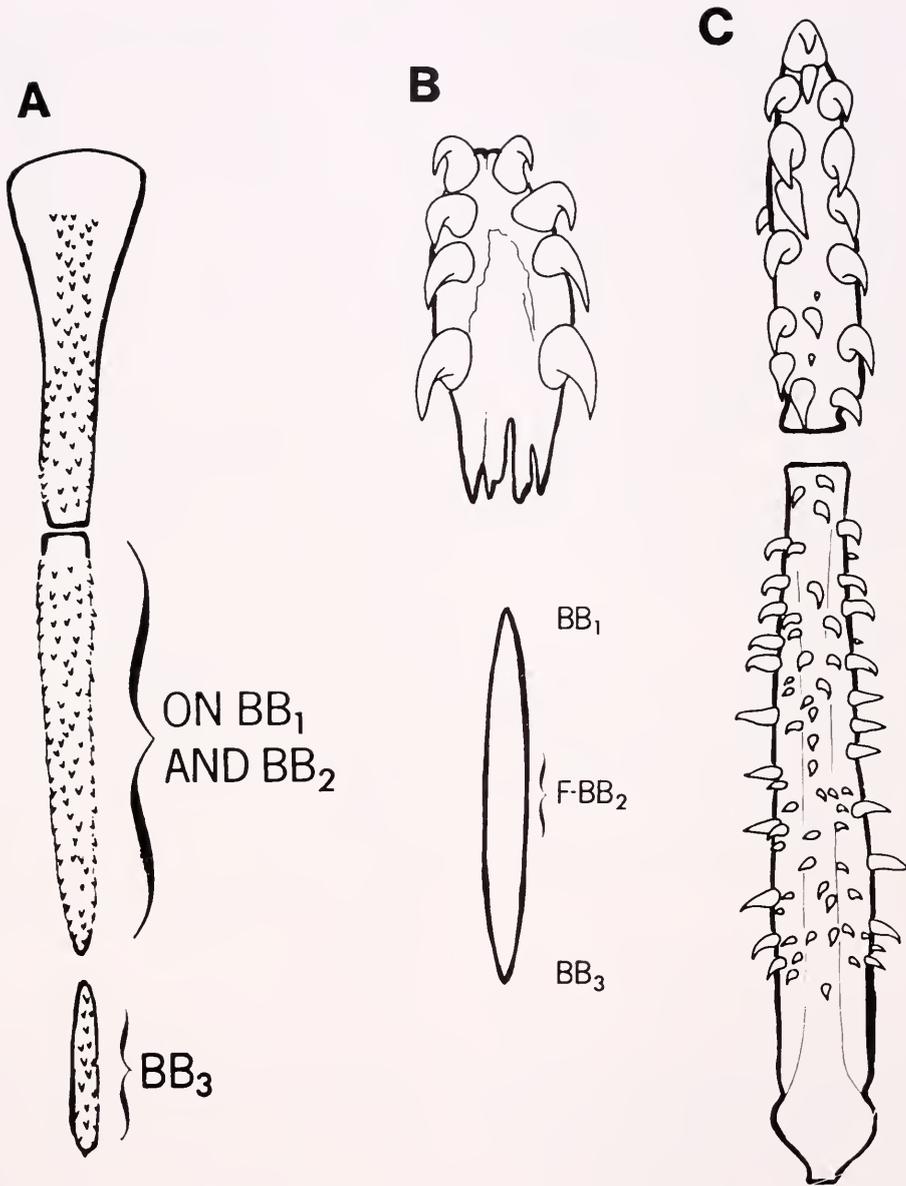


Figure 29. Dorsal view of dermal basihyal and basibranchial elements. A. Esocoids (*Esox*) with uniform and small teeth. B. Salmonoids (*Salvelinus*) showing the terminal pair and pattern of fangs. C. Osmeroids (*Retropinna*) with the alternating pattern and terminal fang. (Slightly modified from Rosen, 1974.)

to be homologous with the ethmoid cartilage of the Neoteleostei.

*Argentinoids and Osmeroids.* The evidence for including the galaxiids within

the Osmeroidei is threefold (Fink and Weitzman, 1982). First, both galaxiids and osmeroids lack an orbitosphenoid bone, although the lack of this bone in many

other primitive euteleosteans severely limits the utility of this character. Secondly, both taxa lack a basisphenoid bone. Finally, osmeroids and galaxiids have large fanglike teeth on the basihyal and basibranchial bones (Fig. 29C) which bite (shear) against palatal arch teeth in a similar manner to that described above for osteoglossomorph fishes. Most other primitive euteleosteans lack teeth on the palatoquadrate. Fink and Weitzman (1982) propose a sister group relationship between argentinoids and osmeroids (Fig. 28) on the basis of enlarged marginal basihyal teeth (Fig. 29C), and the occurrence of "platelike" bone on some neural and haemal spines. It should be clear from this discussion that the relationships of these "lower" euteleostean fishes are in need of a comprehensive analysis.

### The Ostariophysii

The ostariophysan clade comprises nearly three-quarters of the freshwater fishes of the world and is thus by far the dominant component of this fauna. The 6,000 species included in the Ostariophysii run the gamut from the small South American tetras to the poisonous marine catfishes and the weakly electric gymnotid "eels."

The four major monophyletic groups within the Ostariophysii, the Gonorynchiformes (milkfishes), Characiformes, Cypriniformes (carps and minnows), and Siluriformes (catfishes and gymnotids) are united by many shared characters (Fig. 30). A particularly interesting one is the presence of epidermal "alarm substance cells," a type of club cell (Fig. 30: character 3) which exudes an alarm substance (Pfeiffer, 1974, 1977; first discovered by Karl von Frisch, in 1938) when the cells are damaged. A wounded fish releases alarm substance into the surrounding water, and adjacent fish sense the substance and radically alter their behavior pattern, often scattering immediately in all directions and diving for the bottom—

presumably an anti-predation behavior. The fright reaction does not appear to be specific to taxa within the Ostariophysii, and alarm substance extracted from the skin of one group will cause a fright reaction in members of other taxa. The occurrence of fright cells and fright reaction is a shared feature of all ostariophysan fishes and has not yet been confirmed in any other actinopterygian. Another key character (in addition to the occurrence of histologically distinctive breeding tubercles on the body and shared features of caudal anatomy, Fig. 30) is a specialization of the anterior cervical vertebrae and ribs. In the gonorynchiform fishes, the first pleural rib, which articulates with the third vertebra, is expanded and supports a thickened peritoneum that partially invests the anterior chamber of the swimbladder. This condition represents a similar configuration of the swimbladder and pleural ribs to that which is proposed to have occurred in the evolution of the Weberian apparatus characteristic of the remaining ostariophysan fishes (Fig. 30: character 5; Rosen and Greenwood, 1970). Other characters in the anterior vertebrae which characterize all ostariophysans are 1) expanded anterior neural arches which form a roof over the neural canal posterior to the foramen magnum, and 2) loss of the free anterior neural arch (Fink and Fink, 1981).

The Weberian apparatus, named after its discoverer, characterizes the non-gonorynchiform ostariophysans, the Otophysii (Figs. 30, 31). This complex structure consists of five paired bony elements (homologous to neural arches, pleural ribs, and their parapophyses; Rosen and Greenwood, 1970) that form a link between the anterior chamber of the swimbladder and the ear. The five bony elements, the os suspensorium, the tripus, the intercalarium, the scaphium, and the claustrum (Fig. 31), are linked to each other by strong ligaments; the wall of the swimbladder, divided into two separate membranes, the tunica interna and the

## OSTARIOPHYSI

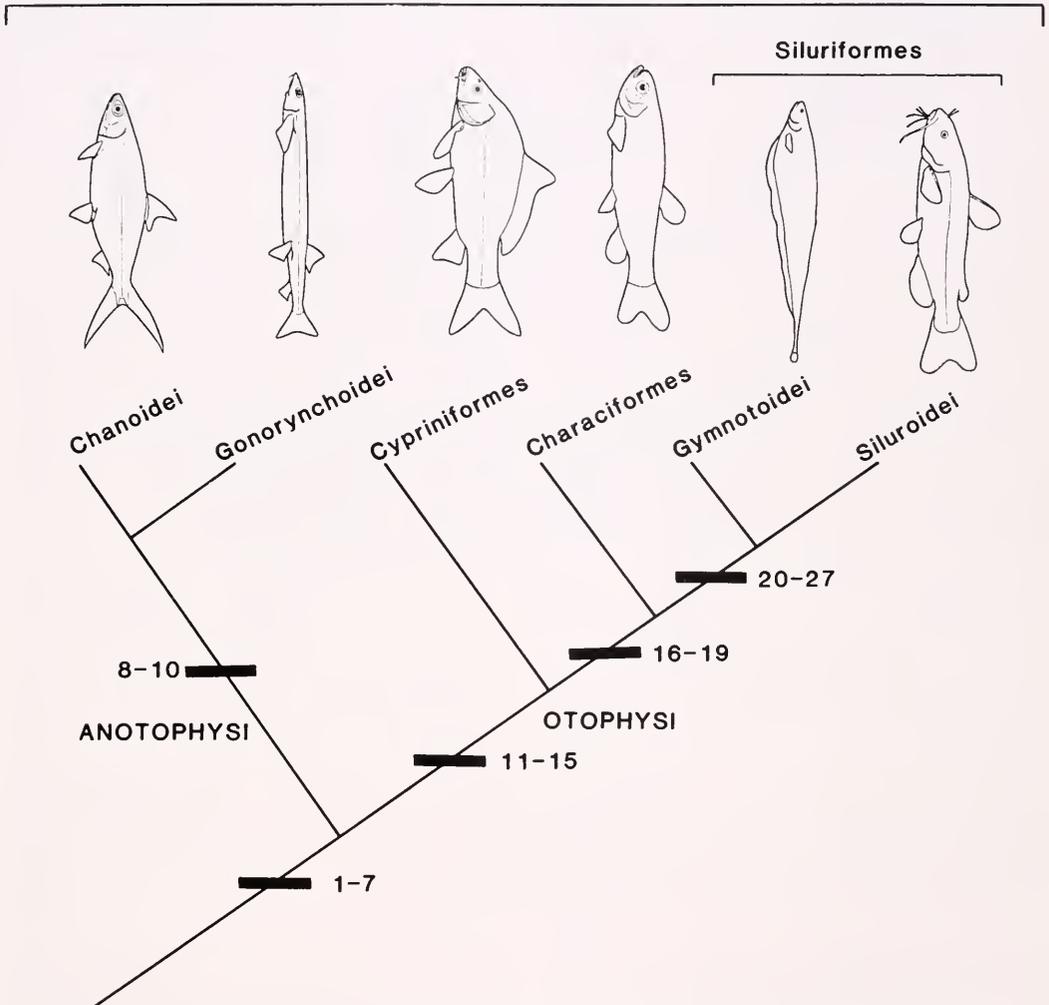


Figure 30. Phylogeny of the ostariophysan fishes (after Fink and Fink, 1981). Only a few of the many characters used by Fink and Fink (1981) to support this cladogram are presented here. The characters are: **1**, loss of dermopalatine; **2**, the swimbladder is divided into a smaller anterior and a larger posterior chamber and the pneumatic duct enters the bladder near the apposition of the two swimbladder chambers; **3**, the presence of fright cells and a fright substance (see text); **4**, swimbladder (anterior chamber) attached to the two anterior pleural ribs; **5**, modification of the anterior cervical vertebrae including loss of the anteriormost supraneural and an enlarged and mobile first pleural rib (see Fink and Fink, 1981); **6**, all anterior haemal spines are fused to the centra; **7**, great reduction in size of the parietal and interorbital septum; **8**, the presence of an epibranchial organ; **9**, absence of teeth on ceratobranchial five; **10**, extensive joint between the exoccipital and neural arch one; **11**, second supraneural is absent; **12**, distinctive specialization of several anterior supraneurals which form a joint with the third and fourth vertebrae; **13**, presence of a Weberian apparatus; **14**, caudal skeleton with a uniquely compound terminal centrum consisting of the last two ural centra, the first preural centrum, and the two anterior uroneurals; **15**, hypural two fused to the compound centrum; **16**, vomer articulates with the mesethmoid anterodorsally; **17**, maxilla positioned posterolateral to the mesethmoid and not articulating with it; **18**, the scaphium extends far anterior to the first vertebral centrum; **19**, Baudelot's ligament attaching to the posterior part of the skull; **20**, intercalar lacking; **21**, scleral bones absent; **22**, supraorbital bone absent; **23**, only one pharyngo-branchial toothplate present; **24**, absence of articular process of the intercalarium; **25**, distally bifurcate Baudelot's ligament; **26**, posterior pectoral fin rays offset from the anteriormost ray; **27**, medial ossification of the dorsal and anal fin radials is absent. (Drawings of fishes from J. S. Nelson [1976], courtesy of John Wiley Publishing Co.)

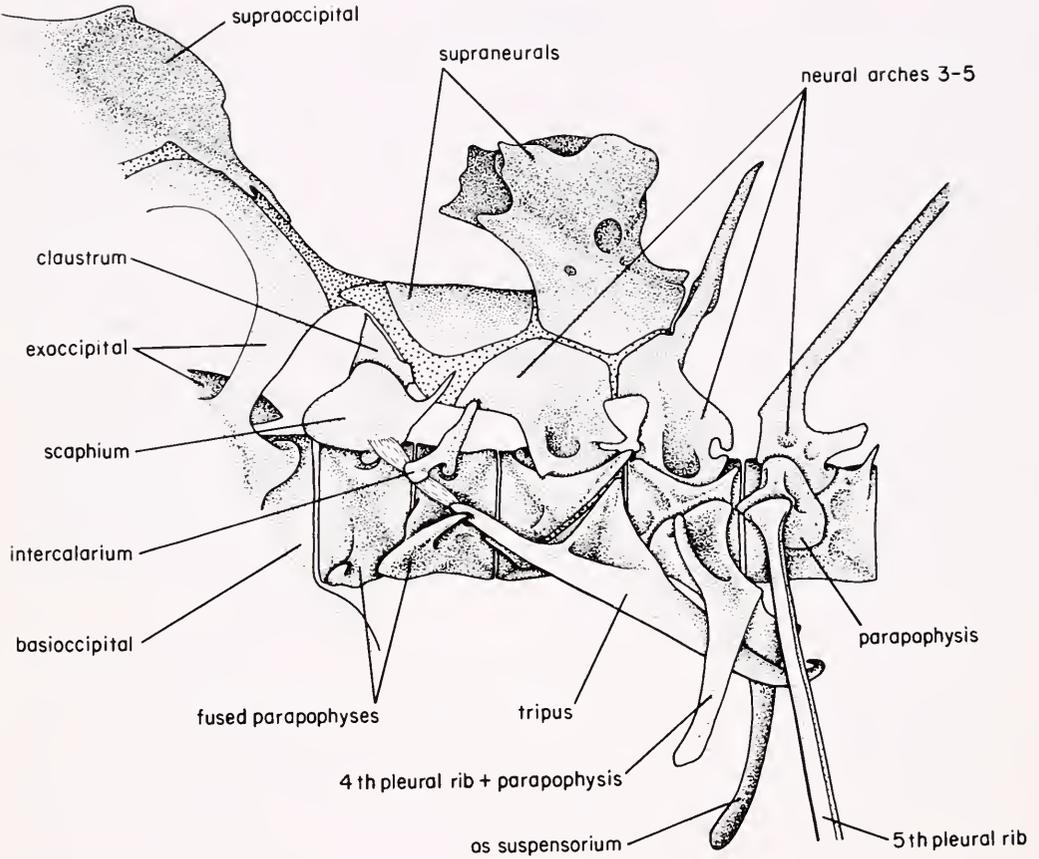


Figure 31. Lateral view of the Weberian apparatus in characiphysans. Anterior is to the left. (From Fink and Fink [1981], reprinted by permission of the Council of the Linnean Society of London.)

tunica externa, attaches to the os suspensorium and the tripus. Differential movement of these two membranes when sound waves impinge on the swimbladder causes oscillations in the chain of Weberian ossicles that are transmitted to the ear (Alexander, 1966a, 1975).

The ear and otic region of the skull are also highly modified in ostariophysan fishes in connection with the Weberian apparatus. The saccular and lagenar otoliths are located far posteriorly in the cranium, and a connection has developed between the two paired sacculi with a median posterior extension, the sinus impar. It is onto the wall of the endolymph-filled sinus impar that ligaments from the

scaphium attach, and this connection allows the transmission of sound into the inner ear. There is increasing evidence that this complex otophysic connection actually does result in a substantially improved hearing ability, especially at the higher frequencies (Popper and Coombs, 1982; Popper and Fay, 1973; Tavolga, 1976).

Until very recently, most hypotheses of the relationship of the major ostariophysan subgroups were based on concepts of ancestry and descent: many groups had specializations that prohibited them from being ancestral to other taxa. The publication of a major new synthetic analysis of ostariophysan relationships (Fink and

Fink, 1981) has focused on character distributions and has resulted in a detailed and highly corroborated hypothesis of relationship. This hypothesis is presented in Figure 30 with a portion of the extensive evidence supporting it. The Ostar-iophysyi is separated into two lineages, the Anotophysyi containing the order Gonorynchiformes and the Otophysi. The Otophysi in turn is divided into two monophyletic taxa, the Characiphysi with the orders Siluriformes and Characiformes (tetras, pacus, piranhas), and the Cypriniphysi (minnows, suckers, hill-stream fishes, carps, and loaches). The Siluriformes are in turn divided into two suborders, the Siluroidei (catfishes) and the Gymnotoidei (electric gymnotid fishes). This scheme of relationships differs significantly from past attempts to decipher ostar-iophysan phylogeny, especially in placing catfishes and gymnotids as sister groups (Fig. 30).

*Gonorynchiform Fishes.* The Order Gonorynchiformes contains four families, three with only one species and one with about twelve. Milkfish (Chanidae) are mostly marine and brackish water fishes found in southeast Asia where they are extremely important as a food fish, often reaching well over a meter in length. Two other families of gonorynchiforms, the Kneriidae and Phractolaemidae, have protrusible upper jaws and are found in the freshwaters of tropical Africa. The Family Gonorynchidae contains only one species and together with the Kneriidae and Phractolaemidae forms the Suborder Gonorynchoidei. *Gonorynchus* is found in Indo-Pacific marine habitats and has a very elongate body shape, and a protrusible jaw. It apparently feeds on small bottom-dwelling invertebrates, and its biology is poorly known. The gonorynchiforms are a well-corroborated monophyletic group (Fig. 30), and Fink and Fink (1981) have suggested that *Chanos* is the primitive sister group of all other gonorynchiforms.

*Characiformes.* The characiforms, together with the cypriniforms (minnows)

and siluroids (catfishes), comprise the bulk of the world's freshwater fauna. It is somewhat surprising given the importance of these groups and over a century of research that their interrelationships are not better known. One reason for the past difficulty in deciphering the interrelations of many ostar-iophysan fishes is the tremendous morphological and ecological diversity of each subgroup. The characiforms, for example, with over 1,000 living species (and maybe a quarter that number still undiscovered) have radiated extensively in South America and to a lesser extent in Africa and Central America. In the Amazon River basin, one of the most ichthyologically diverse areas in the world, over 43 percent of the fishes are characiforms (Roberts, 1972). The Ostar-iophysyi as a whole compose 85 percent of the Amazon fish fauna and 54 percent of the Congo fishes (Roberts, 1972). Reductive evolution and neoteny have also been common in characiform fishes (Weitzman, 1962) and have compounded the difficulties of working with such a vast species assemblage. Characiforms have been divided (somewhat arbitrarily) into sixteen families (Greenwood *et al.*, 1966) of which four are African. The family Hepsetidae contains only *Hepsetus odoe*, an elongate piscivorous and insectivorous pikelike fish, which is widely distributed in Africa and represents a relatively generalized morphology. The families Citharinidae and Distichodontidae (Vari, 1979) contain deep-bodied African fishes while the Ichthyboridae, also African in distribution, contains about nine genera of elongate fishes, many of which are reported to eat the fins and scales of other fishes. The remaining African taxa are usually grouped in the family Characidae, the best known African forms being *Alestes*, an omnivorous widely distributed genus, and *Hydrocynus*, a predator reaching over a meter in length. The remaining members of the Characidae are found in Central and South America and are enormously diverse, the family being divided into a

number of subfamilies. The American Characidae includes the piranhas (*Serrasalmus*), the glandulocaudine fishes which have specialized "caudal glands" on the caudal fin, the tetragonopterine characids, best known for the small colorful tetras but also including the generalized *Astyanax*, and the bryconine fishes (*Brycon*) and *Chalceus*. Other South American characiform families range from the family Erythrinidae (Roberts, 1969), with three genera of predaceous fishes, to the specialized Cynodontidae (Howes, 1976) and Gasteropelecidae—the freshwater hatchetfishes which are capable of making short (10 m) flights just above the surface of the water with their greatly enlarged pectoral fins. The family Ctenopomidae, the pike-characins, are elongate piscivorous fishes, while the Prochilodontidae, Curimatidae, and anostomidae are deeper bodied and eat mud, detritus, and insects.

Many characiforms show complex patterns of tooth morphology and replacement (Roberts, 1967), and their extensive radiation has resulted in a wide range of trophic specializations ranging from mud and detritus feeders to the specialized scale eating forms (Roberts, 1970). The trophic interactions between fishes in the world's tropical freshwaters have been recently reviewed in Lowe-McConnell (1975); also see Fink and Fink, (1979). Evidence for characiform monophyly is summarized in Figure 30.

*Cypriniform Fishes.* The primitive sister group of the characiphysi is the Cypriniformes (Fig. 30) which is a clearly monophyletic group based on characters such as the kinethmoid bone and the unique upper jaw mechanism (Alexander, 1966b), the dorsomedial palatal process, and the structure of the premaxilla and pharyngeal jaw complex (see Fink and Fink, 1981). Cypriniforms are usually divided into six families, one of which, the Cyprinidae, contains the vast majority (80%) of all cypriniform fishes.

Cypriniforms lack (except in a few species) the primitive euteleostean adipose fin (Fig. 14: character 11; see Fig. 30 for the presence of the small adipose fin, located posterior to the dorsal fin, in most characiform groups) and lack teeth on their oral jaws which are protrusible. The protrusible cypriniform jaw evolved independently from the acanthopterygian protrusible jaw discussed below. The cypriniform radiation is one of the few among the actinopterygian fishes that contains a large proportion of herbivores and very few piscivorous taxa are known (Howes, 1978). Correlated with extraction of nutrients from thick-walled algal cells, the two families containing the largest proportion of herbivores, the Cyprinidae and Catostomidae, possess strong grinding and crushing pharyngeal jaws. Primitively, teleostean pharyngeal jaws are of relatively limited mobility, being used primarily to aid the manipulation of prey in the buccopharyngeal cavity prior to deglutition. In cyprinids and catostomids, however, the lower pharyngeal jaws are hypertrophied and form massive bony elements which can be apposed to a horny pad located on the basioccipital bone (Eastman, 1971, 1977). Thus, the pharyngeal jaws in these cypriniforms "chew" against the base of the skull and are capable of strong grinding motions (Sibbing, 1982). The diversity in tooth structure on the lower pharyngeal jaws correlates with the diversity in feeding habits.

The speciose family Cyprinidae is widely distributed in the freshwaters of North America, Africa, Europe, and Asia; it is completely absent from South America. All Cyprinidae lack a true stomach and have an elongate intestine, a condition that would seem to correlate with a diet containing a high proportion of indigestible material (Kapoor *et al.*, 1975). The North American cyprinid fauna contains only about 200 species, much greater cyprinid diversity occurring in Africa and Eurasia and including the well-

known carp (*Cyprinus*) and goldfish (*Carassius auratus*). The family Catostomidae, suckers, has a highly disjunct distribution and occurs in North America and China. Suckers have large fleshy lips and are remarkable for the large number of hybrid populations which occur between species of the family. The remaining families of cypriniforms are small elongate forms with a subterminal mouth and inhabit the freshwaters of Eurasia and Africa. The Gyrimochelidae (suckerbelly loaches), Psilorhynchidae, and Homalopteridae (hillstream loaches) all inhabit freshwater streams and use suction mouths or modified pelvic fins as an aid in adhering to the substrate in fast-moving waters. The family Cobitidae (loaches) are elongate bottom dwellers occurring with greatest diversity in Southeast Asia but also with a very restricted African distribution.

*Siluroid Fishes.* The catfishes form a diverse group (about 2,000 species in 31 families) of highly modified fishes which have a distinctive morphology (Fig. 30). Characteristics of this group include large spiny first rays of the pectoral and dorsal fins which may be locked in the erect position, the absence of true scales—the body is naked or has thick bony plates, and from one to four pairs of barbels which presumably serve tactile and gustatory functions. Other specializations are the loss of a number of skull bones, characteristic modifications of the Weberian apparatus (Alexander, 1964), and a distinctive pectoral girdle modified to support and form the locking mechanism for the pectoral fin spines (Fig. 30; Fink and Fink, 1981). In many groups, a unique mechanism for moving the maxillary barbels occurs. This involves modifications of the palatoquadrate and jaw adductor musculature (Gosline, 1976) as well as the reduction of the maxillary bone to a toothless nubbin supporting the barbel.

The most primitive family of catfishes, the relic Diplomystidae of South Ameri-

ca, are the only catfish family to retain a toothed maxillary bone. With the exception of this one family, however, the phylogenetic position of the other catfish families is uncertain and further work is badly needed on the interrelationships of the catfishes. Three families are partially or completely marine in habit: the Aridae and Plotosidae are mainly salt water groups with the latter capable of inflicting painful wounds with their venomous dorsal spine, while the Aspredinidae occupy mostly freshwaters in tropical South America, but some species are brackish or marine in occurrence.

Of the 31 currently recognized catfish families, 13 are endemic to South America (Roberts, 1972). The most speciose families are the Pimelodidae (with about 285 species), the armored Callichthyidae and Loricariidae, together with about 550 species, and the parasitic Trichomycteridae, some of which live on blood obtained through the gills and skin of other fishes. Some species of the genus *Vandellia* may enter the human urethra causing considerable pain. Among the African families, one of the more unusual is the family Malapteruridae, the electric catfishes. These thick-bodied fishes are capable of delivering a strong electric shock. Other families include the air breathing Clariidae, of which one Asian species, the "walking catfish," has been introduced to American waters; the Mochokidae, several species of which normally swim with the ventral side uppermost; and the Amblycipitidae and Amphiliidae that inhabit fast-moving streams. The native European catfish family is the Siluridae, although the introduced ictalurids are now more common; one silurid species reportedly can attain a length of over three meters (J. Nelson, 1976). In North America, the Ictaluridae (bullheads) are the only group of catfishes and are widely distributed throughout the continent.

The feeding habits of catfishes encompass the range from pure herbivory to car-

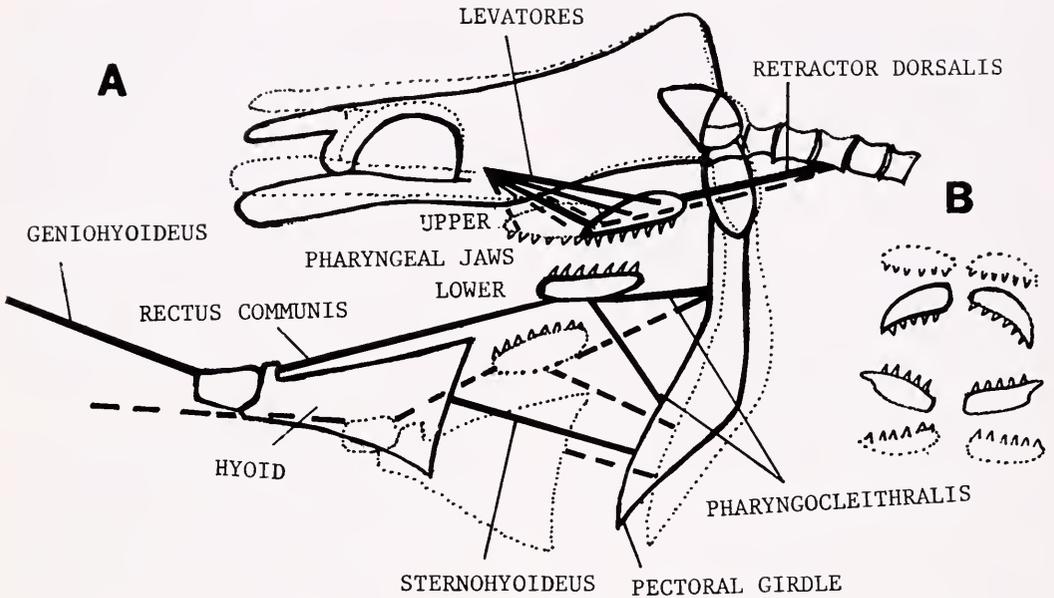


Figure 32. A. Simplified diagram depicting the retractor dorsalis (or retractor arcuum branchialium, RAB) muscle in euteleosts. Solid lines show position and condition of muscles during retraction of the pharyngeal jaws. Bony elements in dotted lines represent positions during protraction. B. Front view of upper and lower pharyngeal jaws during retraction (solid lines) and protraction (dotted line). (After Liem, 1977 in A. Kluge (ed.), "Chordate Structure and Function," courtesy of Macmillan Publishing Co.)

nivorous forms, and locomotor habit may vary from the bottom-dwelling loriciariids with suction mouths to the fast-moving streamlined cetopsid catfishes of South America.

*Gymnotoidei.* The gymnotoid fishes, a group of special interest to neurobiologists and students of animal behavior because of their electrogenic ability, share a common ancestor with the catfishes (Fig. 30). Characters shared by these two taxa include the structure of the mesethmoid, absence of scleral bones, a greatly reduced ectopterygoid, a single pharyngo-branchial toothplate, and electroreceptive capability (Fink and Fink, 1981). The gymnotoids, grouped into four families, are mostly nocturnal and insectivorous, and are remarkable for their ability to generate and detect weak electric signals which are used in navigation and for intraspecific communication. Recent articles on gymnotoid electroreception in-

clude Hopkins (1976), Hopkins and Heiligenberg (1978), and Heiligenberg (1977). The family Apterontidae is the most diverse family of gymnotoids with about ten genera, although gymnotoid systematics at the genus and species level is in need of much further study. Apterontids are unique among gymnotoids in having neurally derived electric organs which fire at higher frequencies (1000-1800 Hz) than the myogenic organs of the other wave-generating families. The Electrophoridae contains only one species, *Electrophorus electricus*, the electric eel, which can produce a powerful electric discharge and may reach 2.3 meters in length. *Electrophorus* is piscivorous. Gymnotids (Gymnotidae), with about three species, and the Rhamphichthyidae are more elongate than apterontids and lack a caudal fin. Wave-mode firing of electric organs appears to have evolved at least twice in the gymnotoid

fishes. The gymnotoid fishes are restricted to South and Central America.

### The Neoteleostei: The Emergence of a 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 bilaterally 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 may originate from any of the first to sixteenth vertebrae (Fig. 32). Fishes with an RD are grouped together in the Neoteleostei (Fig. 14). Experimental studies (Lauder, 1983; Liem, 1970, 1978) have shown that the retractor muscles play a key role in the manipulation, trituration, and swallowing of prey. In primitive euteleosteans such as *Esox* that lack the retractor dorsalis, protraction and retraction of the upper pharyngeal jaws occurs by alternate activity in the levatores externi one and two which produce posterior movement, and the levatores externi three and four causing protraction (Lauder, 1983). In neoteleosteans the retractor dorsalis forms the retractive component of the upper pharyngeal jaw complex.

Based on both phylogenetic and ontogenetic evidence (summarized in Rosen, 1973; also see Winterbottom, 1974a), the RD's originated from the dorsal, inner striated, longitudinal muscle fibers of the esophagus. Thus the evolution of RD control of the upper pharyngeal jaw had to be preceded by the development of a substantial longitudinal muscle layer at the beginning of the esophagus. The evolutionary history of the neoteleosteans is closely related to changes and specializations of the RD. In this summary, the ba-

sic premise is that the Neoteleostei represents a monophyletic assemblage characterized by the specialized upper pharyngeal jaw (among other features), which have a unique functional design with the appearance of an RD (Fig. 14). The following subchapters will trace the evolution of the major groups of the Neoteleostei, starting with the Stomiiformes and Aulopiformes and proceeding to the more advanced Myctophiformes, Paracanthopterygii, and Acanthopterygii.

Characters corroborating the hypothesis of neoteleostean relationships presented here (essentially that of Rosen, 1973) are summarized in Figure 14. Rosen's (1973) hypothesis has been examined and tested by Fink and Weitzman (1982) and Lauder (1983). Several conclusions have emerged from these recent analyses that have special importance for neoteleostean relationships and evolution. 1) The protractor pectoralis muscle, formerly believed to separate the Stomiiformes (which lack this muscle) from all other neoteleosteans (Rosen, 1973; Winterbottom, 1974a) appears to be a primitive gnathostome feature of very scattered distribution within teleosts (Greenwood and Lauder, 1981). It thus does not serve to define a monophyletic taxon within the Neoteleostei. 2) The "A1" division of the adductor mandibulae appears to have evolved independently in at least three lineages of neoteleosteans and is not indicative of neoteleostean monophyly (Fink and Weitzman, 1982). A muscle, termed the A1 $\beta$ , that arises medially on the palatoquadrate and inserts on the maxilla, occurs in stomiiforms, some acanthopterygians, some paracanthopterygians, and some aulopiforms, but not in atheriniforms or neoscoelids. 3) The presence of a median rostral cartilage between the premaxillae and the neurocranium characterizes the Neoteleostei (Fink and Weitzman, 1982). Finally 4), at a higher cladistic level, the occurrence of apharyngochoideus muscle, with an origin on

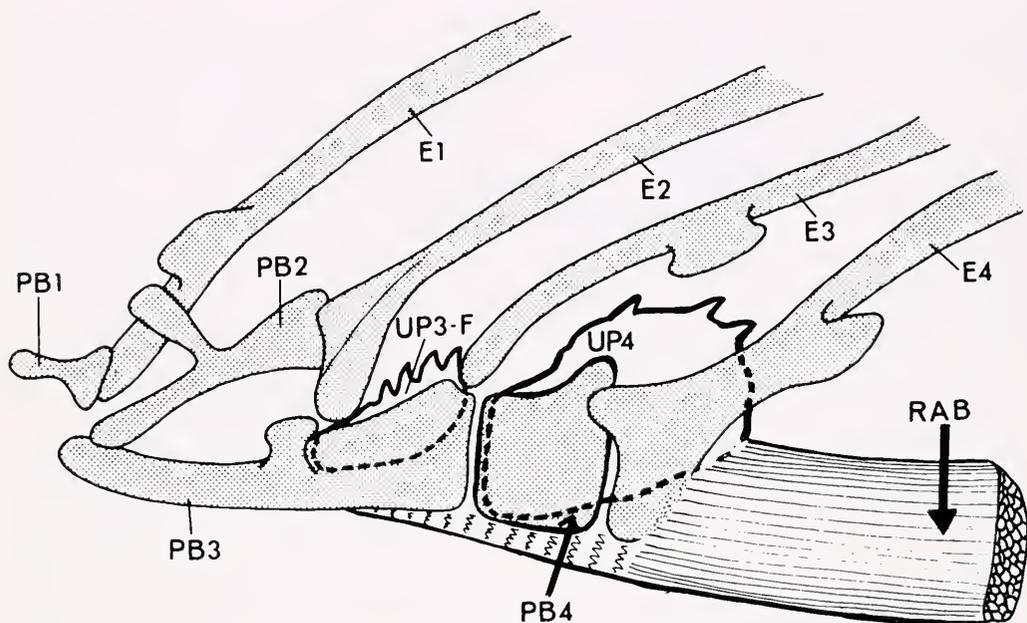


Figure 33. Dorsal gill arch elements and the retractor dorsalis (RAB) muscle in the stomiiform *Astronesthes* (dorsal view). The major muscle insertion is on the dominant fourth upper tooth plate (UP4) and fourth pharyngobranchial (PB4). (Modified from Rosen, 1973.)

Other Abbreviations: E 1-4, epibranchials; PB 1-4, pharyngobranchials; UP, upper pharyngeal tooth plate; UP3-F, upper pharyngeal tooth plate fused to endoskeleton.

ceratobranchial five and insertion on the urohyal, is a characteristic feature of the ctenosquamate fishes (= myctophiforms, paracanthopterygians, and acanthopterygians; Lauder 1982a). Stiassny (in preparation) has found a muscle apparently homologous to the ctenosquamate pharyngohyoideus in several aulopiforms. It is not yet clear if the aulopiforms are non-monophyletic or if this muscle has been independently acquired in a few aulopiform taxa. The pharyngohyoideus is homologous to the rectus communis muscle of lower teleosts which inserts on hypobranchial 3. The change in insertion to the urohyal marks an important functional shift, because the pharyngohyoideus is then no longer an intrinsic gill arch muscle, and forms the anterior element controlling anteroposterior and lateral movement of the lower pharyngeal jaw. Thus, the Ctenosquamata (Rosen, 1973) possess two functionally important pharyn-

geal jaw innovations allowing greatly increased control of prey transport and preparation in the pharynx (Lauder, 1983). Other characters relevant to neoteleostean relationships are summarized in Figure 14.

### The Stomiiformes

Although stomiiforms are considered to be the most primitive neoteleosteans, the condition of the retractor dorsalis muscle appears to be specialized from the probable primitive condition. The stomiiform upper pharyngeal jaw apparatus has the uncinat process of the second epibranchial obliterated by the development of a direct and broad articulation with the third pharyngobranchial, and the stomiiform RD insertion on the upper pharyngeal jaw is confined to the most posterior toothplate, which is associated with the 4th pharyngobranchial (Fig. 33).

As a result the alignment of the RD is longitudinal. It seems likely that the retractor dorsalis can produce greater excursions in a longitudinal direction than tilting or rocking (dorsoventral) movements of the upper pharyngeal jaws.

Stomiiforms are composed of over eight families, including Gonostomatidae (light fishes), Sternoptychidae (marine hatchet fishes; Weitzman, 1974), Chauliodontidae (viperfishes; Tchernavin, 1953), Stomiidae (dragonfishes), and some 300 species that inhabit the middle depths of the Atlantic, Indian, and Pacific oceans. They are small, possess photopores, and have a mouth that extends posteroventrally past the eye.

Fink and Weitzman (1982) have discussed characters that establish monophyly of the Stomiiformes. These include: 1) a unique photopore histology, 2) type 3 tooth attachment (Fink, 1981), 3) morphology of the adductor mandibulae muscle, and 4) some branchiostegal rays articulating with the ventral hypohyals.

### The Aulopiformes

This relatively small order of worldwide marine fishes embraces two distinct groups: 1) the Aulopoidei, which contains the thread-sail fishes (Aulopidae), greeneyes (Chlorophthalmidae), Bathysauridae, Scopelosauridae, Bathypteroidae and the large-eyed but lens-less Ipnopidae, and 2) the Alepisauroidei, which contains the Synodontidae (lizard fishes), Harpadontidae (Bombay ducks), Alepisauridae, Scopelarchidae, and Evermannellidae (Johnson, 1974).

All aulopiform fishes share a highly specialized feature in the dorsal elements of the second and third gill arches. The second pharyngobranchial is greatly elongated posterolaterally so that its long axis is directed away from the third pharyngobranchial. As a result a gap is present between the second epibranchial and the third pharyngobranchial. This gap is bridged by an uncinat process of the

second epibranchial (Rosen, 1973; Fig. 34). It is possible that this bridge offers additional structural strength to the upper pharyngeal jaw apparatus and that it has developed as a response to the new mechanical loading by the retractor dorsalis muscle.

The most generalized condition of the retractor dorsalis muscle (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. 34). Aulopiforms have a protractor pectoralis muscle which originates from the pterotic and inserts on the anterodorsal surface of the cleithrum.

Alepisauroids differ from aulopoids in having longer pharyngobranchials, the loss of the second and fifth upper pharyngeal toothplates, and the development of a very long jaw with an oblique suspension. There is myological evidence that the aulopoids represent the more primitive and generalized forms among the aulopiforms (Rosen, 1973).

### The Myctophiformes

This large group of pelagic marine fishes has been abundant and diverse since the Upper Cretaceous and contains the families the Myctophidae (the lanternfishes), with their photophores arranged along the side of the body like portholes, the Neoscopelidae, Evermannellidae (sabertooth fishes, Johnson, 1982) and the Scopelarchidae (the pearl fishes, Johnson, 1974).

The Myctophiformes are thought to be monophyletic since in all species the toothed third pharyngobranchial is the largest toothed element of the upper pharyngeal jaw. The fourth tooth-plate is only half the size of the third and is movably hinged to the third tooth plate. Consistent with these size relations of the toothplates in myctophiforms is the reduction in size of the fourth pharyngobranchial

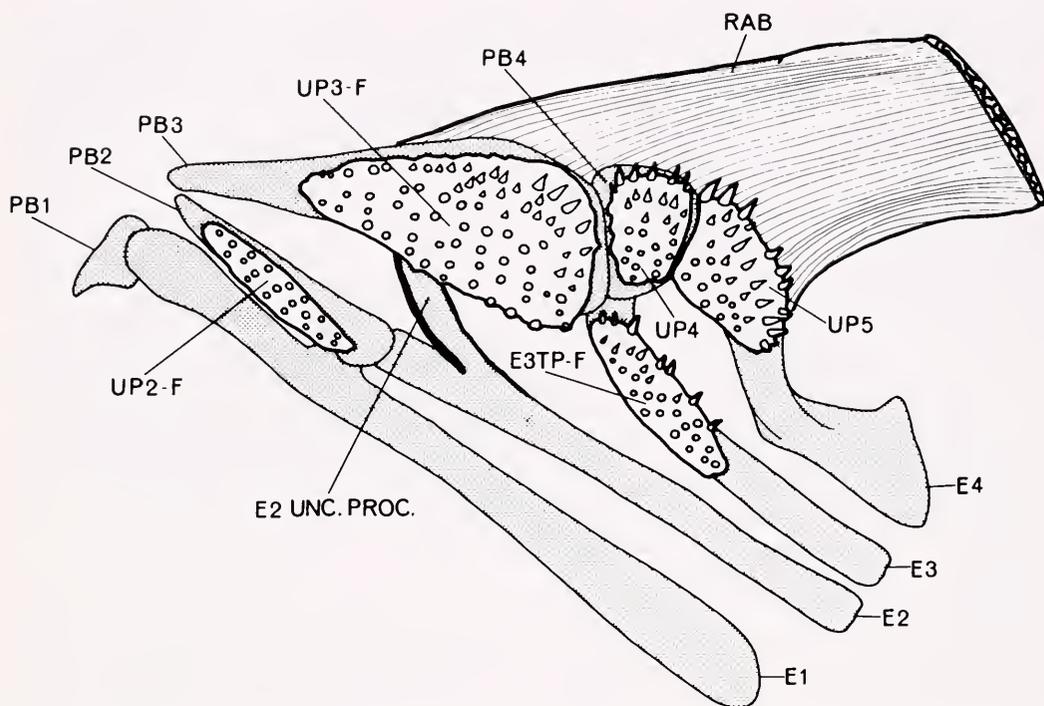


Figure 34. Dorsal gill arch elements and the retractor dorsalis (RAB) muscle in the aulopiform *Aulopus* (ventral view). The muscle fans out to insert on the third and fourth pharyngobranchials and fourth epibranchial. The second epibranchial ( $E_2$ ) has a prominent uncinete process ( $E_2$ UNC. PROC.). (Modified from Rosen, 1973.)

Other Abbreviations:  $E_{1-4}$ , epibranchials;  $PB_{1-4}$ , pharyngobranchials; RAB, retractor arcuum branchialium or retractor dorsalis muscle; TP, toothplate; TP-F, toothplate fused with endoskeleton; UP, upper pharyngeal element.

and the division of the retractor dorsalis muscle into distinct medial and lateral components or heads (Rosen, 1973). The smaller medial head inserts on the third pharyngobranchial, whereas the lateral component retains the original or primitive insertion on the fourth pharyngobranchial and its tooth-plate (Fig. 35). The appearance of the medial head of the retractor dorsalis inserting exclusively on the third pharyngobranchial indicates that the myctophiforms are aligned with the paracanthopterygians and acanthopterygians rather than with the Aulopiformes (Rosen, 1973). The dual insertions of the retractor dorsalis on the third and fourth pharyngobranchials in myctophiforms furnish the basic system from which the more specialized upper pharyngeal jaws

of the paracanthopterygians and acanthopterygians were derived. In myctophiforms we can see the beginning of the trend towards an increasing emphasis on the third pharyngobranchial as the dominant tooth-bearing element in the upper pharyngeal jaw in advanced euteleosteans. Concomitantly in some Acanthomorpha there is a shift of the insertion of the retractor dorsalis from the fourth, or third and fourth, to an exclusive insertion on the third pharyngobranchial.

The Myctophidae (lantern fishes) comprise about 32 genera and about 220 species (Paxton, 1972; Nafpaktitis, 1978; Nafpaktitis *et al.*, 1977). They occur in all oceans from the Arctic to the Antarctic and are known for their daily vertical migrations. At night they migrate to the sur-

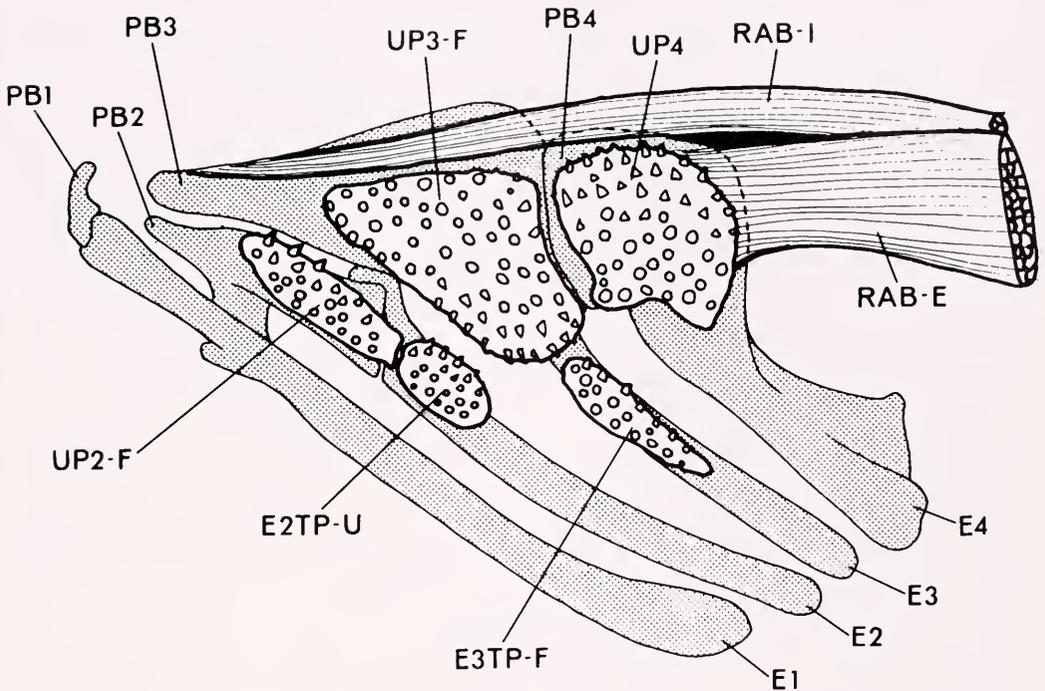


Figure 35. Dorsal gill arch elements and the retractor dorsalis (RAB) muscle in the myctophiform *Neoscopelus* (ventral view). The muscle is subdivided into an internal (RAB-I) and external (RAB-E) division, inserting respectively on the third pharyngobranchial (PB<sub>3</sub>) and the fourth upper toothplate (UP<sub>4</sub>). (Modified from Rosen, 1973.)

*Other Abbreviations:* E<sub>1-4</sub>, epibranchials; PB<sub>1-4</sub>, pharyngobranchials; RAB-E, external division of retractor dorsalis; RAB-I, internal division of retractor dorsalis; TP-F, toothplate fused to endoskeleton; UP, upper pharyngeal toothplate.

face to feed; with the approach of day they start their return trip into the depths as far as 500 meters. Of course, myctophids are well known for the possession of small photophores arranged in groups and rows on head and body. Because lanternfishes make up a considerable biomass and are able to convert plankton to food for organisms higher on the food chain, they occupy an important position in the trophic ecology of the ocean.

The Neoscopelidae is a small family containing five species (Nafpaktitis, 1977).

### The Paracanthopterygii

The concept of the Paracanthopterygii as a monophyletic assemblage has been plagued with problems, ambiguity, and confusion ever since its inception (Rosen

and Patterson, 1969). The major difficulty is the lack of a shared derived feature characterizing all paracanthopterygians (Rosen, 1973). Here we offer a provisional scheme of paracanthopterygian relationships, realizing that we may be including unrelated groups.

We include the Percopsiformes (troutperches), Gadiformes, Batrachoidiformes (toadfishes), Lophiiformes (anglerfishes), and Gobiesociformes (clingfishes), groups representing over 200 genera. The Percopsiformes is known from the Cretaceous, whereas the other four orders date from the Eocene. Paracanthopterygians are predominantly marine fishes. Only five genera of the percopsiforms, the gadiform *Lota*, a few brotulids, some batrachoidiforms and the fluviatile gobiesocids are freshwater fishes.

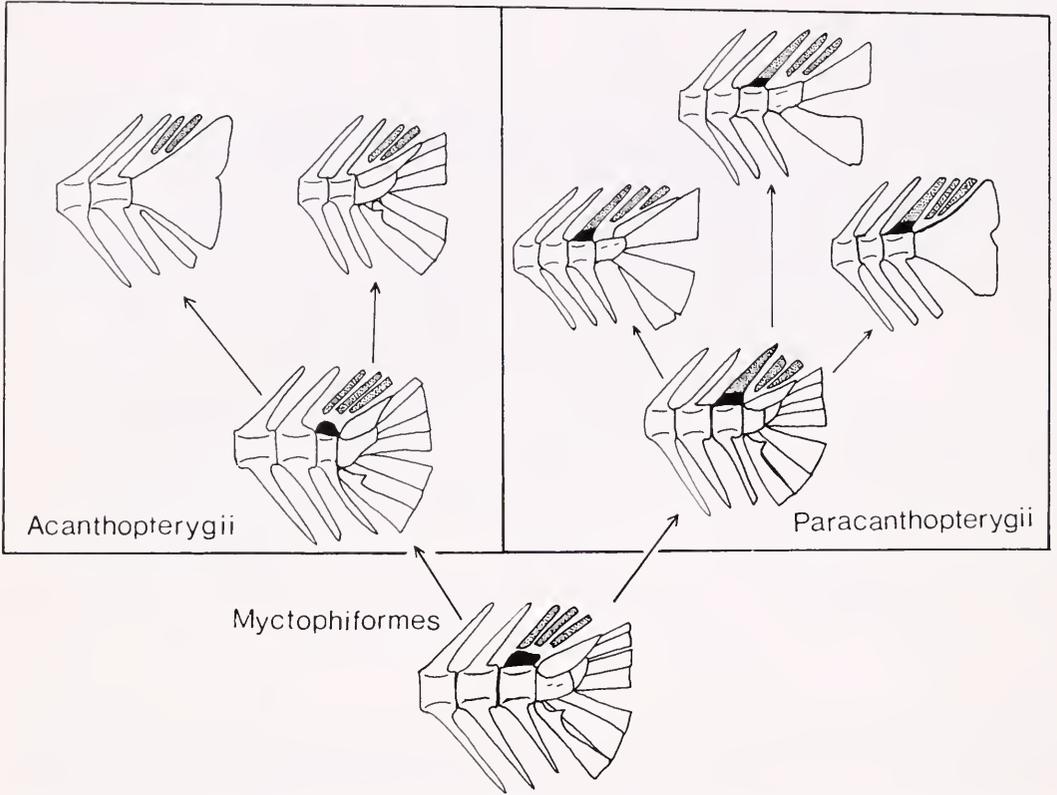


Figure 36. Evolution of the caudal skeleton in the advanced neoteleosts. The arrows connecting the different types indicate possible structural changes, not phyletic lineages. The epurals are stippled, the second preural neural spine crest is black. The primitive configuration of the caudal skeleton is exhibited in the Myctophiformes. In the Paracanthopterygii the most anterior epural fuses with the second preural neural spine crest. Further specializations involve the fusions of the hypurals into platelike elements. In the Acanthopterygii fusions occur of two preural vertebrae, of which one has a complete neural spine and the other a reduced or no neural spine crest. The result of this vertebral fusion is a caudal skeleton configuration which is convergent to that of the Paracanthopterygii. Among more specialized Acanthopterygii fusions occur of the hypurals to form hypural plates.

The Paracanthopterygii is at best an ill-defined group. The pharyngeal jaw apparatus does not furnish any phylogenetic information because in percopsiforms the retractor dorsalis muscle still has two heads, as in myctophiforms, in which the lateral head inserts on the fourth pharyngobranchial. The lateral jaw muscles of paracanthopterygians furnish conflicting evidence. In primitive paracanthopterygians (percopsids and gadids) the maxilla is associated with two muscles, the  $A_1$  and  $A_1\beta$ . More advanced paracanthopterygians resemble the Myctophidae in having only  $A_1\beta$  inserted on the maxilla. The

paracanthopterygians were first defined as a superorder (Rosen and Patterson, 1969) on the basis of the structural specialization in the caudal skeleton. In all adult paracanthopterygians the caudal skeleton is characterized by the presence of a full neural spine on the second preural centrum, and two epurals (Fig. 36). Such a structural configuration can be developed by three possible pathways: 1) elongation of a short spine on the second preural centrum, 2) a spineless second preural centrum may fuse with the normally spine-bearing third preural to form a compound centrum with one neural and

two hemal spines, 3) fusion of the first epural with the crest on the second preural centrum. It is hypothesized that in the Paracanthopterygii the third developmental mode has prevailed because the number of epurals is invariably reduced in the paracanthopterygian caudal skeleton. Paracanthopterygians are tentatively defined by the full neural spine on the second preural centrum thought to be the result of epural fusion, and the presence of not more than two epurals. Unfortunately the question of paracanthopterygian relationships cannot be resolved on caudal evidence. It has been suggested by Rosen (1973) that paracanthopterygians, polymixioids, trachichthyoids and stephanoberycoids are all part of a single monophyletic group in which there are "strong predispositions to develop common features of the head and tail." Polymixioids can also be considered as the primitive sister group of the trachichthyoids plus stephanoberycoids and the paracanthopterygians may be the primitive sister group of all three (Rosen, 1973).

Many paracanthopterygian evolutionary patterns are the reverse of those characteristic of generalized acanthopterygians: 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 caudal vertebrae, and 4) a reduction in spiny "ornaments" on the bones of the cheek and operculum.

The precise interrelationships of the paracanthopterygians are still unknown. Consequently we can offer only a tentative scheme of the paracanthopterygian interrelationships leaving many problems unresolved (Fig. 37).

*The Percopsiformes.* The Percopsiformes, trout perches (*Percopsis*), pirate perches (*Aphredoderus*), and cave fishes (*Amblyopsis*, *Chologaster*), is the only paracanthopterygian group confined to freshwater. It is restricted to North America.

All percopsiforms have a reduced gape

of the mouth and reduced oral dentition. In the caudal skeleton there is a sequence of fusions resulting in support of the caudal fin by two large bony plates (fused hypurals) borne on two separate centra. Although median fin spines are either reduced or lost, most percopsiforms have retained spine ornamentation on the head.

The amblyopsids have sensory papillae or tactile organs in very prominent rows on the head, body, and tail. These sensory organs correlate with the lack of vision in the blind species or rudimentary vision in the eyed forms. The distribution of the cave-dwelling amblyopsids is closely correlated with the limestone formations in the central United States (Woods and Inger, 1957).

*The Gadiformes.* This order includes cods (*Gadidae*), hakes (*Merlucciidae*; Marshall, 1966), cusk eels (*Ophidiidae*), pearlfishes (*Carapidae*), eel pouts (*Zoaridae*), grenadiers and rattails (*Macrouridae*). With only a few exceptions, members of the Gadiformes are marine. The earliest known gadiforms, from the Eocene, were similar in structure to early percopsiforms, but almost all remained marine and subsequently specialized to inhabit a wide variety of environments.

Gadiforms (Fig. 37) are elongate fishes, often of the deeper and colder dysphotoc marine habitats. The tail is reduced or confluent with the long dorsal and anal fins, which have very reduced fin spines. There is also 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 (Fig. 38). The brains of more advanced gadiforms have the olfactory lobes located at the olfactory bulb, at a distance from the forebrain (Svetovidov, 1948).

It is postulated that the gadiforms are more closely related to the percopsiforms (Fig. 37) than to any other paracanthopterygian (Rosen and Patterson, 1969), because the two orders share several spe-

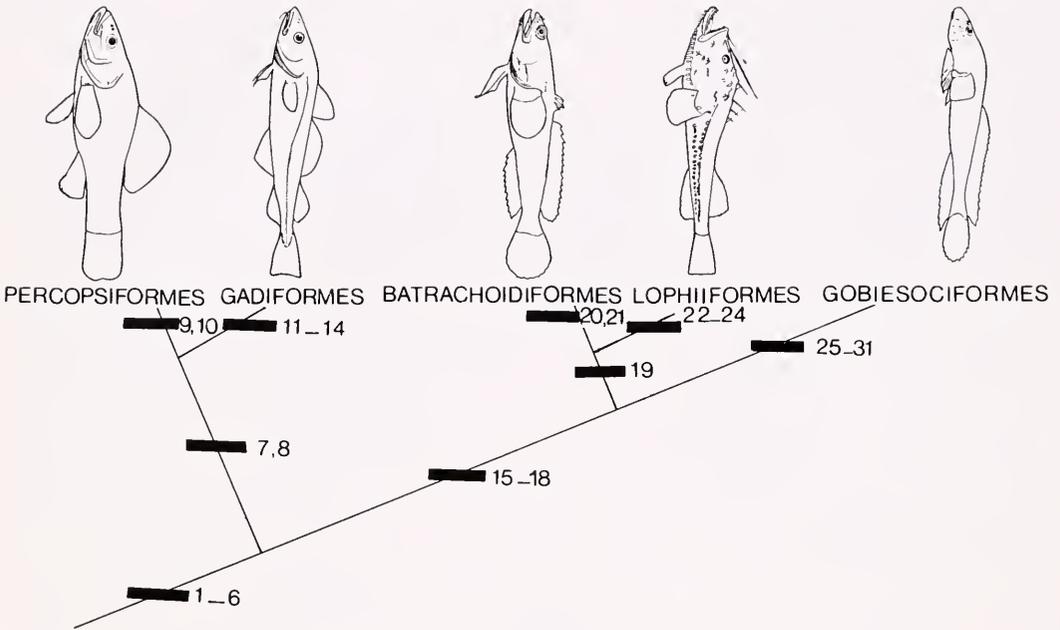


Figure 37. Interrelationships of the major groups of the Paracanthopterygii. Major specializations characterizing the various lineages are: 1, increase in the number of abdominal vertebrae; 2, decrease in the depth of the head and trunk; 3, suboperculum enlarged and operculum reduced; 4, anterior vertebrae 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 which is formed by fusion of the first epural with the crest on the 2nd preural centrum; 7, pterosphenoid and parasphenoid in contact; 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 reduced oral dentition; 11, postmaxillary process of the premaxilla notched; 12, tail reduced or confluent with dorsal and anal fins; 13, pelvic fins in jugular position; 14, presence of mental barbels; 15, skull roof flattened; 16, parasphenoid and frontal bones 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; 19, pectoral radials elongate; 20, the entopterygoid not ossified; 21, short spinous dorsal fin and long soft dorsal fin; 22, modified pectoral girdle correlated with "walking" mechanism; 23, spinous dorsal fin modified into a lure; 24, all palatopterygoid bones reduced; 25, extreme dorsoventral flattening; 26, joint between cleithrum and supracleithrum; 27, pelvic fins modified into a sucker; 28, joint between a convex condyle of interoperculum and concave fossa of epihyal; 29, hypertrophied sternohyoideus with a medial and lateral head; 30, asymmetrical heart with reduced sinus venosus and large accessory common cardinal chambers; 31, short ventral aorta with only three afferent branchial arteries.

cializations which are thought to reflect common ancestry: 1) position of the olfactory lobe at the olfactory organ, and 2) a tendency to establish contacts between parasphenoid and pterosphenoid bones in the skull (Fig. 37: characters 7, 8).

The Gadidae and Merlucciidae, containing the cod, haddock, pollock, ling, hake, and whiting, are predominantly cold- and temperate-water groups occurring mostly in the northern hemisphere. Gadids and merlucciids share an epihyal-

interopercular joint. A medially directed process arises from the medial surface of the interoperculum, and its concave articular surface meets the convex protuberance on the posteroventral corner of the epihyal. The general configuration of the joint shows some resemblance to the epihyal-interopercular joint of the gobiesociforms. However, the relative position and the shape of the articular surfaces of the gadid-merlucciid epihyal-interopercular joint differ from

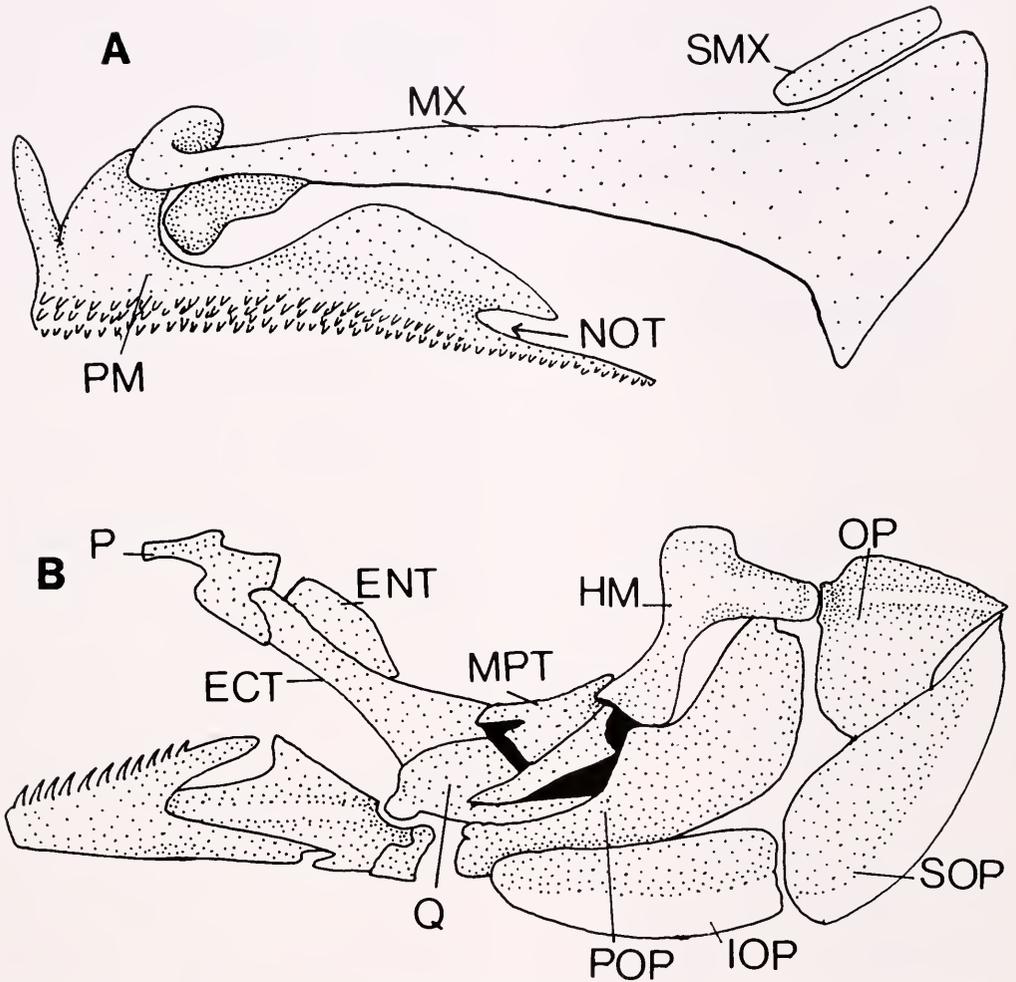


Figure 38. A. Bones of the upper jaw in the gadiform *Ogilbia*. Note the notched postmaxillary process (NOT) of the premaxilla (PM). B. Opercular apparatus and jaw suspension in the gadiform *Pollachius virens*.

*Other Abbreviations:* ECT, ectopterygoid; ENT, endopterygoid; HM, hyomandibula; IOP, interoperculum; MPT, meta-terygoid; MX, maxilla; OP, operculum; P, palatine; POP, preoperculum; Q, quadrate; SMX, supramaxilla; SOP, suboperculum.

those of the gobiociforms. The former represent the world's most valuable food fishes. Many species live near the bottom and utilize 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 Macrouridae (rattails; 15 genera and about 250 species) have large heads

and eyes, long tapering tails and live in the depths of all the oceans in tremendous abundance (Okamura, 1970). Some of the eelpouts (Zoarcidae) are viviparous, giving birth to as many as 40 young. Zoarcids are common fishes in the cold waters of both the Arctic and Antarctic. Twenty-eight zoarcid genera with 65 species have been described (Nielsen, 1968; McAllister and Rees, 1964). The

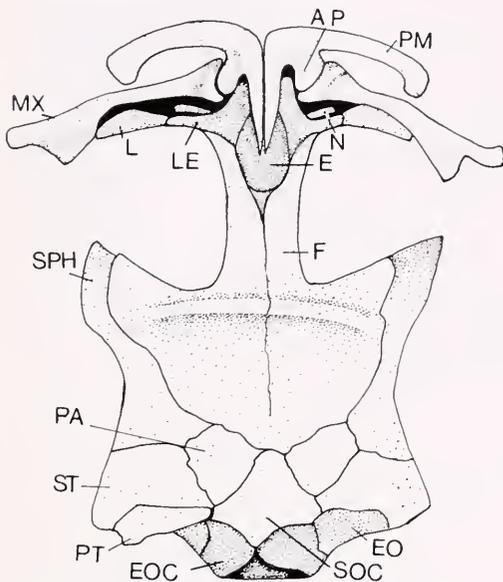


Figure 39. Dorsal view of the skull of *Thalassophryne* to show flattening of the skull and the large, laterally flaring sphenotics (SPH).

*Other Abbreviations:* AP, articular process of the premaxilla; E, ethmoid; EO, epiotic; EOC, exoccipital; F, frontal; L, lacrimal; LE, lateral ethmoid; MX, maxilla; N, nasal; PA, parietal; PT, posttemporal; SOC, supraoccipital; SPH, sphenotic; ST, pterotic.

Carapidae (pearlfishes) are small fishes that live commonly (some even parasitically) in mollusks and sea cucumbers both in tropical and temperate oceans (Arnold, 1956). The Ophidiidae (brotulas and cusk eels; Nielsen, 1969) contains about 16 genera with 190 species (Gosline, 1971). A specimen of the ophidiid *Abyssobrotula galatheae* has been dredged at a depth of about 8,000 meters which is the deepest record of a captured teleost fish (Nielsen, 1977).

*The Batrachoidiform Lineage.* This group has diversified into three orders, the Batrachoidiformes, Lophiiformes, and Gobiesociformes (Fig. 37). Four specializations link these three groups together (Fig. 37: characters 15–18). The skull roof is greatly flattened, and the parasphenoid either approaches (Gobiesociformes) or is sutured to (Lophiiformes, Batrachoid-

iformes) 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 (Fig. 39). All three groups have well-differentiated ascending processes of the premaxilla and show trends toward a strong connection of the hyomandibula with the preoperculum and reduction in ossification of the palatopterygoid arch.

Key features that relate the batrachoidiform lineages with the gadiforms are found in the gill cover, the anterior vertebral column, the median fins, and skin (Fig. 37; Rosen and Patterson, 1969). In both the gadiforms and batrachoidiform lineages the operculum is reduced, while the sub-operculum has become greatly enlarged, forming most of the distinctly angular gill cover and extending upward and backward to the posterodorsal tip of the operculum (Fig. 38). The anterior vertebrae are not only compressed but are joined via overlapping pre- and postzygapophyses, while the median fins are long and many-rayed, mostly confluent with the caudal except in specialized members. Finally, both lineages have reduced scales or have lost them altogether (Fig. 37).

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

Batrachoidiforms (toadfishes, e.g., *Opsanus*) are primarily coastal benthic fishes of the Atlantic, Indian, and Pacific Oceans. They are first known from the Miocene. Batrachoidiforms are slow-moving bottom fishes with a short spinous dorsal fin and long soft-rayed dorsal fin. In the palatopterygoid arch the entopterygoid is the only element that is not fully ossified. The radial bones (Fig. 40) supporting the pectoral fins are typically elongate. Toadfishes can live out of water, sometimes for hours, and can make sounds, usually grunts, growls, or a single boat-whistle blast. Sound is produced by

specialized “sonic muscles” in association with the swimbladder (Skoglund, 1961). The 55 species of batrachoidiforms are primarily marine benthic fishes, except for two species confined to fresh water.

Lophiiformes, comprising the goosefishes (Lophiidae), anglerfishes (Ceratoidae), frogfishes (Antennariidae), batfishes (Ogcocephalidae; Bradbury, 1980), Tetrabrachiidae, Lophichthyidae, Brachionichthyidae, and Chaunacidae, are widespread marine fishes in shallow water as well as deep-sea habitats (Bertelsen, 1951). In the lophiiforms all pterygoid bones in the palatopterygoid arch are reduced. However, most of the major specializations of lophiiforms concern the feeding mechanism, which in general is adapted to the taking of large prey at high speeds (Grobecker and Pietsch, 1979). Lophiiforms are thought to be monophyletic sharing the following synapomorphies (Pietsch, 1981): 1) Spinous dorsal fin primitively of six spines, the anterior-most three of which are cephalic in position and modified as a luring apparatus; 2) epiotics separated from parietals and meeting on the midline posterior to the supraoccipital; 3) gill opening restricted to a small, elongate, tubelike opening situated immediately dorsal to, posterior to, or ventral to the pectoral base; 4) eggs spawned in a double, scroll-shaped mucous sheath. In the wholly benthic forms, the pectoral girdle is greatly modified in accordance with the development of clasping, prehensile, and “walking” mechanisms. Many members have fewer than five narrow and elongate radials, of which the ventral most is considerably expanded distally. The Lophiiformes comprises 18 families with about 255 species, including numerous highly specialized and bizarre forms. In some families the males are parasitic on the females, attaching firmly with their jaws and becoming, in most cases, completely dependent upon the female for their basic physiological functions (Fig. 37).

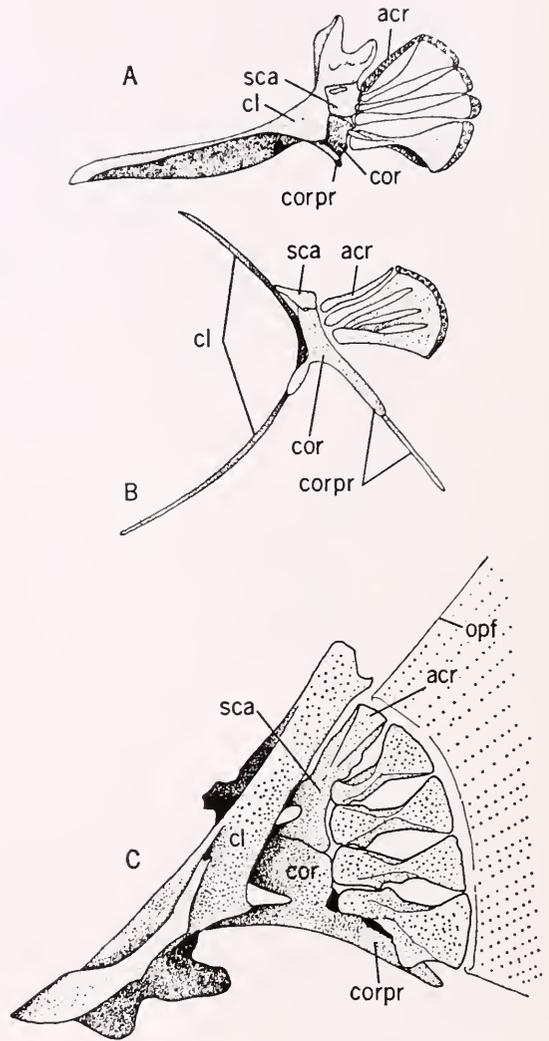


Figure 40. Shoulder girdle in members of the batrachoidiform lineage. A. *Batrachoides*, a batrachoidiform, after Monod (1960). B. *Gigantactis*, a lophiiform, after Waterman (1948). C. *Gobiesox*, a gobiesociform, after Rosen and Patterson (1969).

Abbreviations: acr, accessory upper pectoral radial; cl, cleithrum; cor, coracoid; corpr, posteroventral process of coracoid; opf, outline of pectoral fin; sca, scapula.

Gobiesociforms (clingfishes) are small, dorsoventrally flattened fishes with a ventral sucker formed of the modified pelvic fin and surrounding tissue (Briggs, 1955; Gosline, 1970). They inhabit ma-

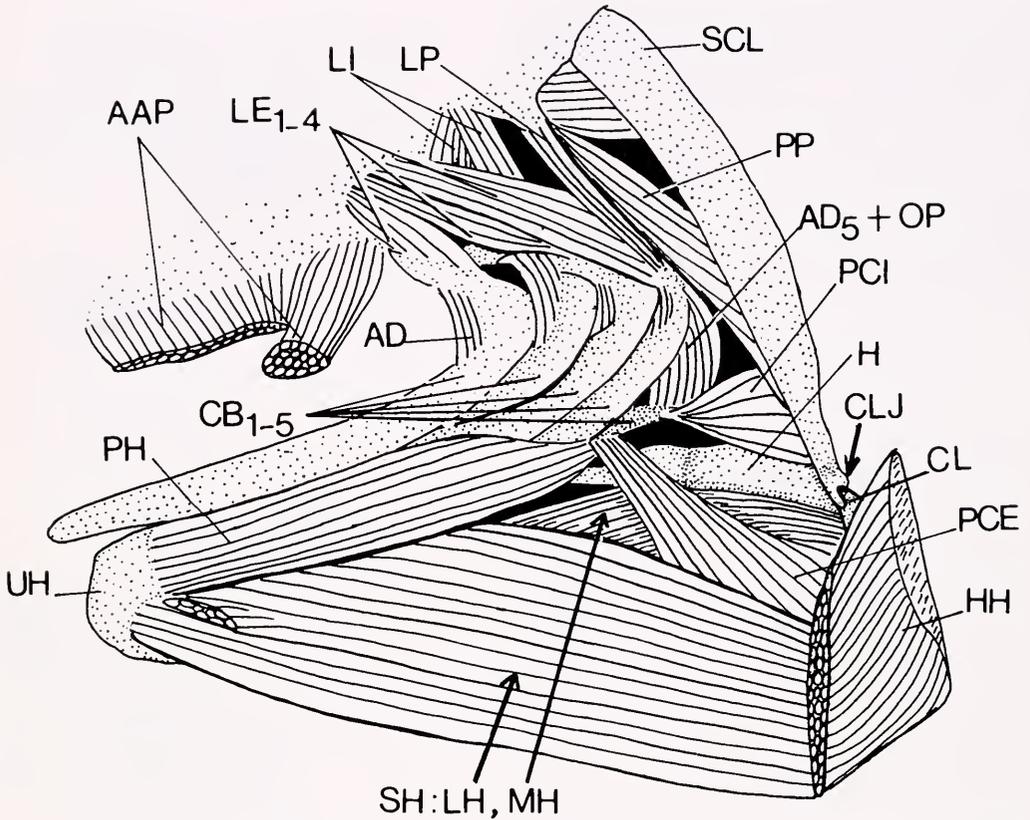


Figure 41. Lateral view of the branchial musculature after removal of the gills and mucous membranes in the gobi-sociform *Alabes rufus*. The sternohyoideus (SH) has well-differentiated lateral (LH) and medial heads (MH); the ventral end of the supraclithrum (SCL) forms a distinct joint (CLJ) with the cleithrum.

*Other Abbreviations:* AAP, adductor arcus palatini; AD, adductor branchialis; AD<sub>5</sub>+OP, fifth adductor and obliquus posterior muscles; CB<sub>1-5</sub>, ceratobranchials 1-5; CL, cleithrum; CLJ, supraclithrum-cleithral joint; H, heart; HH, hyohyoideus, cut and reflected to expose sternohyoideus; LE<sub>1-4</sub>, levatores externi 1-4; LI, levator internus; LP, levator posterior; OP, obliquus posterior; PCE, pharyngocleithralis externus; PCI, pharyngocleithralis internus; PH, pharyngohyoideus; PP, protractor pectoralis; SH, sternohyoideus with lateral head (LH) and medial head (MH); UH, urohyal.

rine and occasionally freshwaters in the tropics and along many temperate sea-coasts. The dorsoventral flattening of the head and body is correlated with the orientation and shape of the bones of the jaw suspension and opercular apparatus. The pterygoid bones in the palatopterygoid arch are lost (Rosen and Patterson, 1969). Most of the specializations of the gobi-sociforms correlate with ecological zones involving rapid water exchange, such as the intertidal zone and steeply descending freshwater streams (Fig. 37).

As observed by Springer and Fraser

(1976), most of the specialized osteological characters shared by the gobi-sociforms are reductional in nature: the loss of scales, basisphenoid, pterosphenoid, metapterygoid, mesopterygoid, suborbitals (except lacrymal), and first infrapharyngobranchial. According to Springer and Fraser (1976), the single most significant synapomorphy of the Gobi-sociformes is the presence of a joint between the supraclithrum and the cleithrum: the supraclithrum has a shallow, concave process on its distal end that articulates with a convex condyle on the anterior

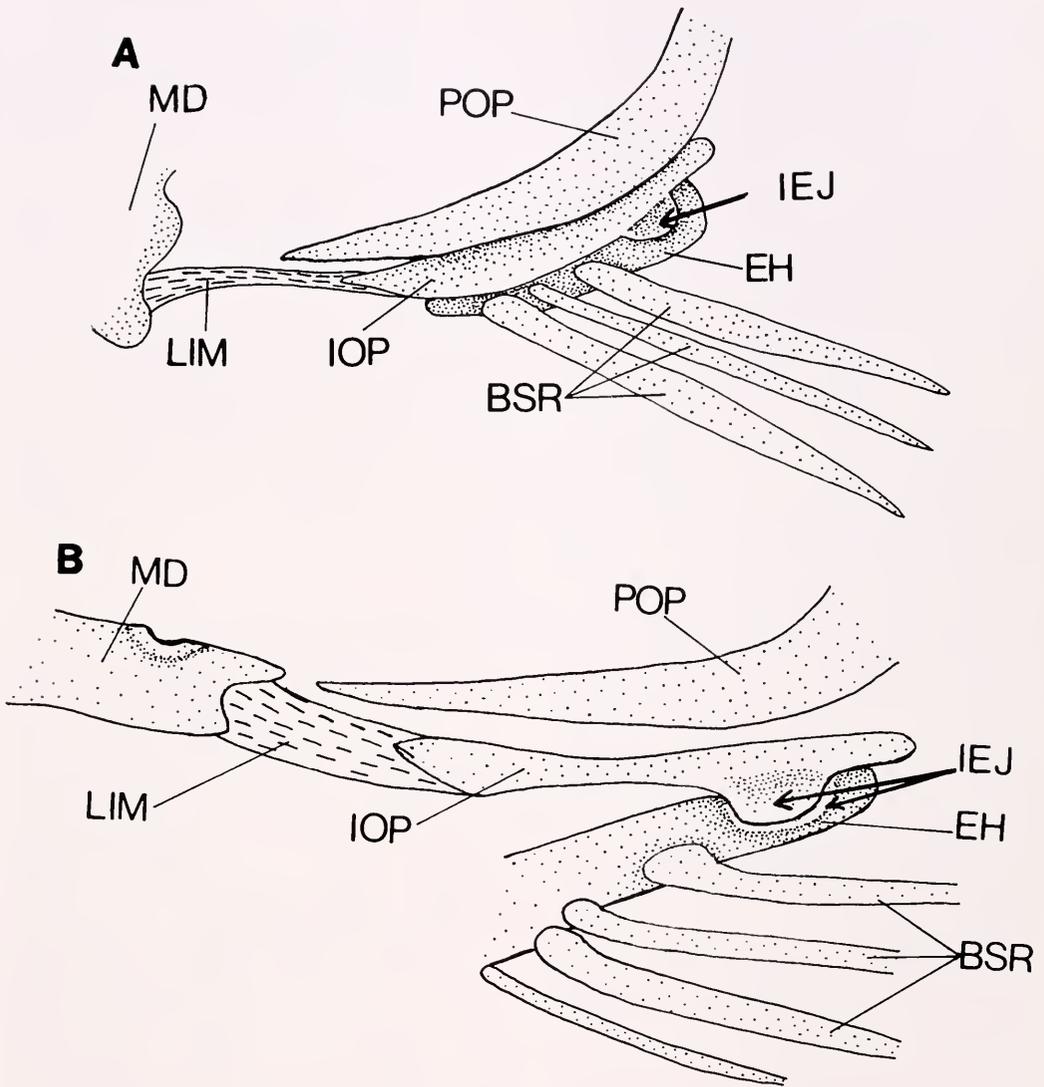


Figure 42. Ventrolateral view of the association of the epiphyal (EH) and interoperculum (IOP) of *Alabes dorsalis* (A) and *Gobiesox papillifer* (B) (MCZ 44836). The interoperculum has been dissected away from the preoperculum, and the hyoid ramus pulled down, to reveal the epiphyal-interoperculum joint (IEJ).

Other Abbreviations: BSR, branchiostegal rays; EH, epiphyal, with a condyle of the interoperculum and a fossa in the epiphyal; IOP, interoperculum; LIM, interoperculomandibular ligament; MD, mandible; POP, preoperculum.

surface of the proximal end of the cleithrum (Fig. 41). Such a joint is not duplicated in other fishes. Because *Alabes* (Alabetidae or Cheilobranchidae) possess a similarly specialized supracleithrum-cleithrum joint, it has been placed in the

Gobiesociformes (Springer and Fraser, 1976). Previously, the Alabetidae has been classified with the Synbranchiiformes (Regan, 1912) or the Blenniidae (Vaillant, 1905; Greenwood, 1975).

We present additional synapomorphies

characterizing the Gobiesociformes as a monophyletic assemblage and offer supporting evidence that *Alabes* is indeed a gobiesociform (Fig. 37: characters 28–31).

Gobiesociforms (including *Alabes*) have a joint between the interoperculum and epihyal bone superficially resembling the condition in gadids and merlucciids. From the medial surface of the interoperculum toward the rear third of the bone, a distinct process arises. The process is directed medially and has a cartilage lined convex condyle, which fits in a matching, shallow concavity on the lateral aspect of the epihyal (Fig. 42). This linkage establishes a firm connection between the epihyal and interoperculum. A second linkage between interoperculum and hyoid is present in the form of a very strong cordlike ligament. The functional significance of this linkage is still unknown, but it is possible that the sternohyoideus-hyoid-interoperculum coupling to open the mouth (Liem, 1970) is dominant in the gobiesociforms, because of the strong double linkages of the interoperculum and the hyoid, and the hypertrophied sternohyoideus muscle with two characteristic heads (Fig. 41): a medial and lateral head, separated by a hypertrophied pharyngocleithralis externus muscle.

Gobiesociforms (including *Alabes*) have a very specialized cardiac morphology not encountered in other teleosts. The heart is distinctly asymmetrical, with the ventricle on the right side and the atrium on the left (Fig. 43). The sinus venosus is greatly reduced, but two large chambers form at the point where the anterior and posterior cardinal veins enter the heart. These accessory common cardinal chambers are much larger than the sinus venosus and bulbus arteriosus. The presence of these accessory common cardinal chambers represents a synapomorphy of the gobiesociforms. Anteriorly the ventral aorta tends to be short and only three afferent and efferent branchial arteries are present. The fourth afferent and efferent

branchial arteries are lacking. The first afferent branchial arteries originate independently from the ventral aorta. The second and third afferent branchial arteries originate by a long common root from the ventral aorta (Fig. 43).

The additional synapomorphies given here seem to indicate that the gobiesociforms with the inclusion of the Cheilobranchidae (Alabetidae, with 1 genus *Alabes* and 4 species) is a monophyletic assemblage defined by the presence of a joint between the supracleithrum and cleithrum, a joint between the interoperculum and the epihyal, the accessory common cardinal chambers in the heart, asymmetry of the heart, and the characteristic configuration of the three afferent branchial arteries.

### The Acanthopterygii

This vast group of advanced neoteleosts is first known in the Cretaceous. The Acanthopterygii and Paracanthopterygii can be considered members of a monophyletic lineage (Fig. 14) 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. These characters, however, are less than satisfactory, and a convincing definition of this lineage is lacking. An obvious feature of generalized acanthopterygians, and the one to which this term refers, is the differentiation of stiff spines in the anal and dorsal fins. This radiation includes the great majority of modern marine fish species as well as a large number of freshwater forms. The acanthopterygians represent a monophyletic group characterized by several major structural and functional specializations. The specialized acanthopterygian char-

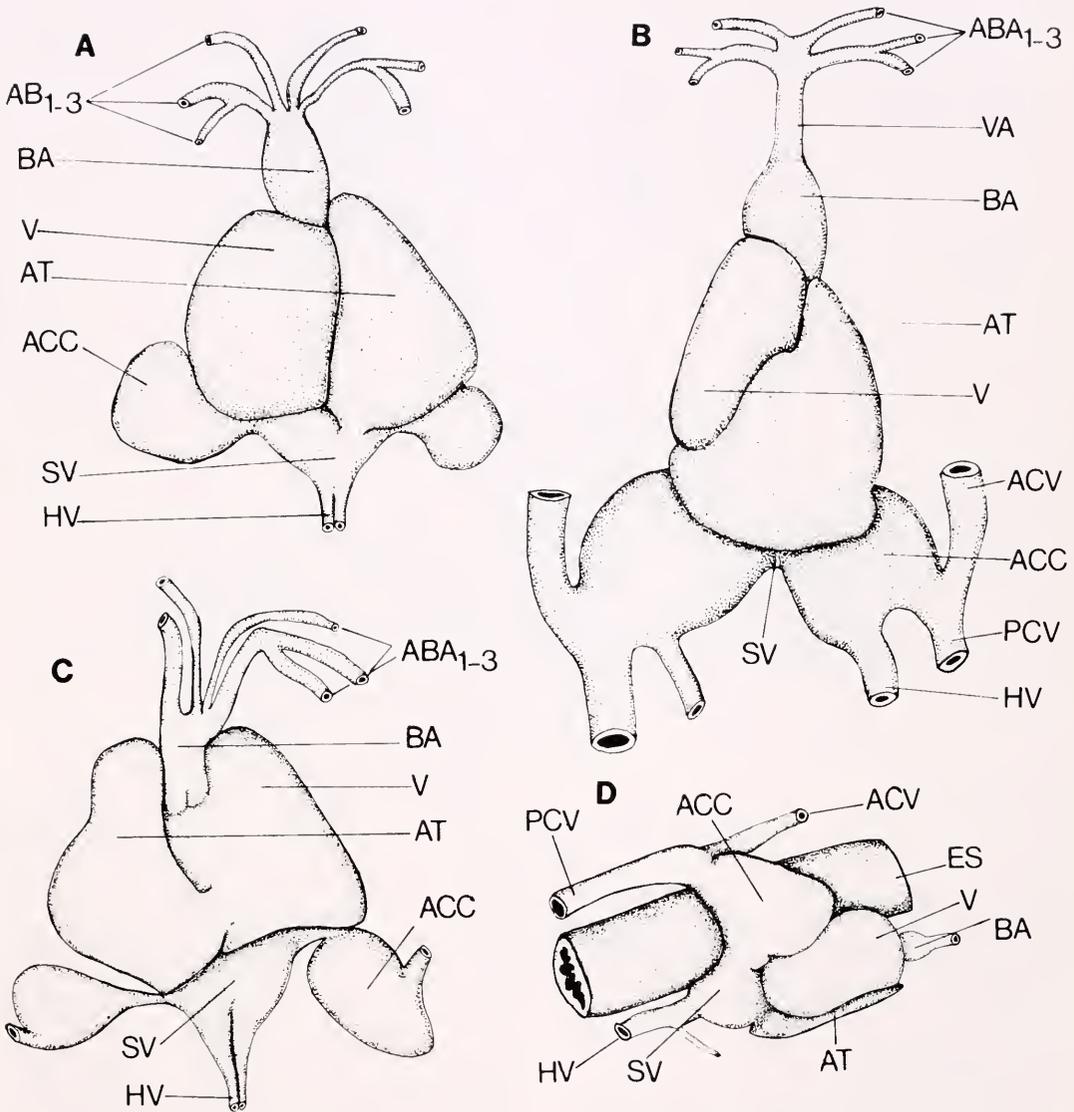


Figure 43. Cardiac morphology in the gobiesociforms *Alabes dorsalis* and *Gobiesox papillifer*. A. ventral view of the heart and great vessels in *Alabes*; B. ventral view of the heart and great vessels in *Gobiesox*. C. dorsal view of the heart and great vessels in *Alabes*. D. lateral view of the right side of the heart of *Alabes*.

Abbreviations: ABA<sub>1-3</sub>, afferent branchial arteries 1-3; ACC, accessory common cardinal chamber; ACV, anterior cardinal vein; AT, atrium; BA, bulbus arteriosus; ES, esophagus; HV, hepatic vein; PCV, posterior cardinal vein; SV sinus venosus; V, ventricle; VA, ventral aorta.

acter complexes occur in two functional units: the pharyngeal jaw apparatus and the oral jaw mechanism.

The upper pharyngeal jaw apparatus is characterized by a specialized retractor

dorsalis muscle (Fig. 44:RD) that inserts principally or entirely on the third pharyngobranchial. In addition, the second and third epibranchials are enlarged, forming the principal structural support

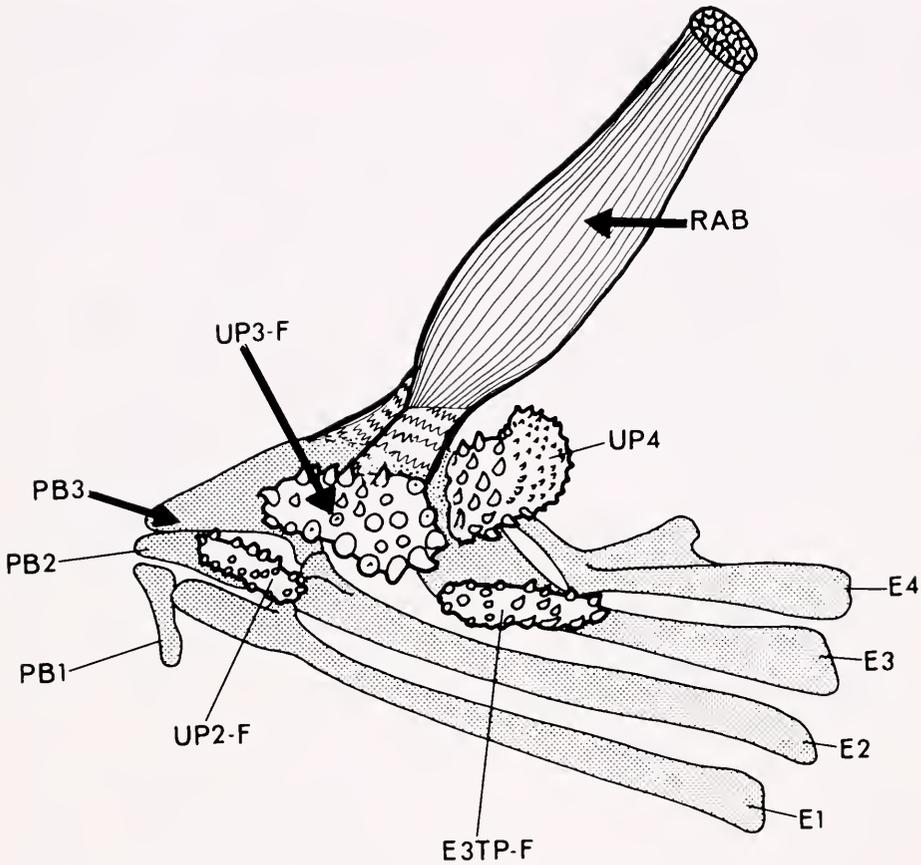


Figure 44. Dorsal gill arch elements and the retractor dorsalis (RAB) muscle in the acanthopterygian *Epinephelus* (ventral view). Muscle is inserted on the upper toothplate (UP3-F) fused to the third pharyngobranchial (PB3).

Other Abbreviations: E<sub>1-4</sub>, epibranchials; PB<sub>1-3</sub>, pharyngobranchials; TP-F, toothplate fused to endoskeleton; UP, upper toothplate; UP-F, upper toothplate fused to endoskeleton (Modified from Rosen, 1973).

for the upper pharyngeal jaws (Fig. 44; Rosen 1973).

In myctophiform and paracanthopterygian fishes the upper jaw symphysis is capable of little or no forward movement, while acanthopterygians have 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 capable of significant forward displacement or protrusibility (Fig. 45; Alexander, 1967). Upper jaw protrusion in acanthopterygians can be accomplished in at least

four different ways (Liem, 1979) and can be modulated precisely by various patterns of muscle contraction. Thus the acanthopterygian jaw apparatus is a prehensile device of great versatility. The structural diversification seen in the acanthopterygian jaw apparatus is great and may be correlated with the multiple kinematic pathways underlying upper jaw protrusion. The 13 orders within the Acanthopterygii may be divided into two groups (categories or series): the Atherinomorpha, and the poorly defined Percomorpha.

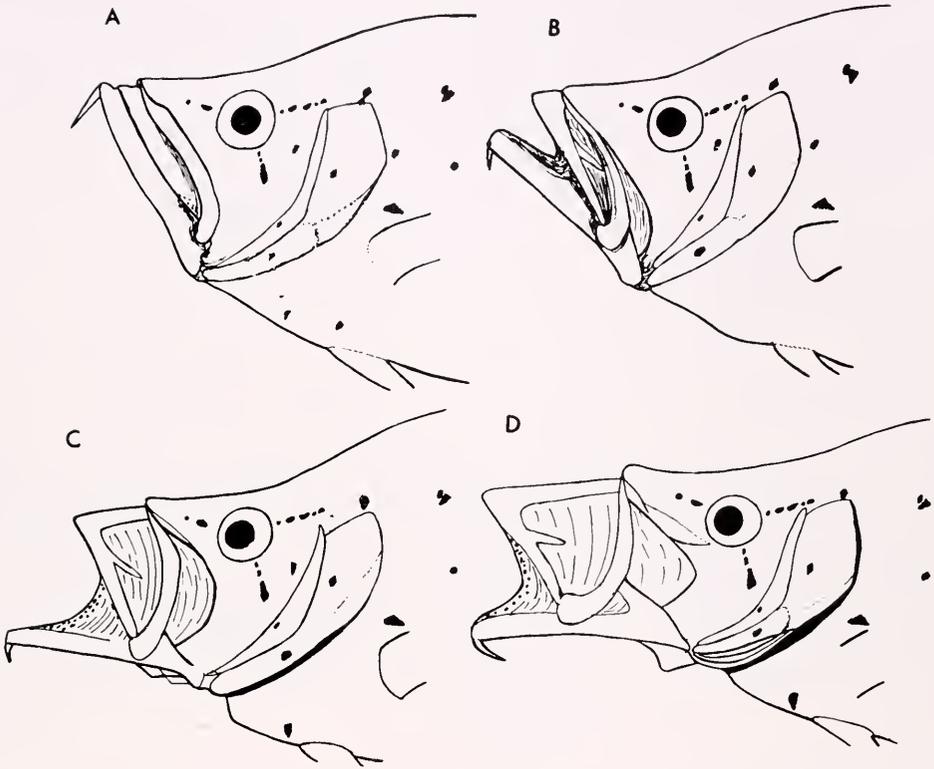


Figure 45. Jaw protrusion in the percoid fish *Monocirrhus* during the capture of prey. A–D. Four representative stages of mouth opening and jaw protrusion. D. fully protruded condition. (From Liem, 1970.)

### *Atherinomorpha*

This group is first known from the Eocene and according to the most recent classification (Parenti, 1981; Rosen and Parenti, 1981) contains 11 families and about 830 species, including the killifishes (cyprinodontids), live-bearing top minnows (Poeciliidae), silversides (Atherinidae), four-eyed fishes (Anablepidae), ricefishes (Adrianichthyidae), half-beaks (Hemiramphidae), needlefishes (Belonidae), and ocean flying fishes (Exocoetidae). Atherinomorphs have a nearly world-wide distribution and inhabit marine waters and freshwaters both in tropical and temperate climates.

There is considerable evidence that the atherinomorphs are members of a mono-

phyletic assemblage (Rosen and Parenti, 1981) representing a major radiation at the advanced neoteleostean level. Atherinomorphs share, among others, the following derived characters (Rosen and Parenti, 1981): 1) A specialized oral jaw mechanism in which the rostral cartilage is not attached to the premaxilla and the protrusible upper jaw has crossed palatomaxillary ligaments with a maxillary ligament to the cranium. It is postulated that the left and right premaxillae are capable of and normally undergo independent movement during upper jaw protrusion (Rosen, 1964; Karrer, 1967). 2) A large demersal egg with many oil droplets that coalesce at the vegetative pole and rather long adhesive filaments. 3) The absence

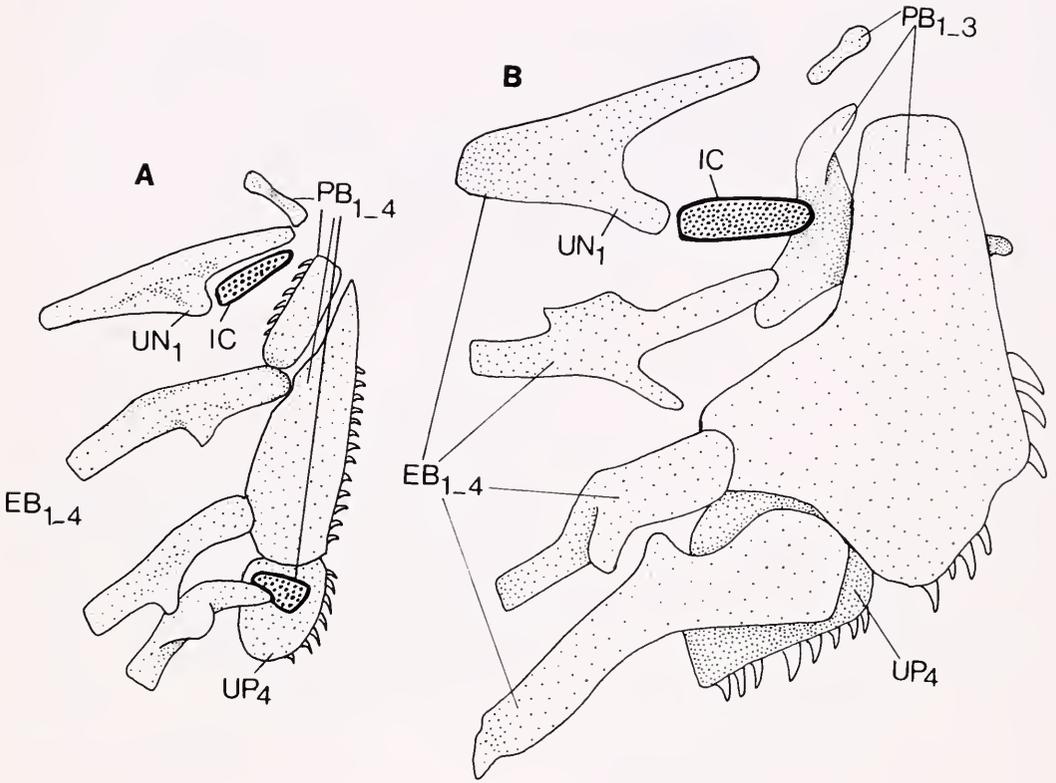


Figure 46. Dorsal gill elements seen from dorsal view. A. Generalized percoid (*Morone*). B. Atherinomorph (*Thelmatherrina*). In generalized percoids the fourth pharyngobranchial is present, while in atherinomorphs the element is lost. (Modified from Rosen and Parenti, 1981.)

Abbreviations: EB<sub>1-4</sub>, epibranchials 1-4; IC, interarcual cartilage; PB<sub>1-4</sub>, pharyngobranchials 1-4; UP<sub>4</sub>, upper toothplate of fourth branchial arch.

of the third, fourth, and fifth infraorbital bones and the fourth pharyngobranchial (Fig. 46; Rosen and Parenti, 1981).

The relationship between atherinomorphs and the Percomorpha is specified by the presence in the dorsal gill arch skeleton of an interarcual cartilage between the first epibranchial and second pharyngobranchial (Fig. 46; Rosen and Parenti, 1981); however, see Travers (1981) for the distribution of the interarcual cartilage. Atherinomorphs have four bladelike branchiostegals inserting laterally on the hyoid bar, the anteriormost located just posterior to a notch on the anterior ceratohyal.

Included in the Atherinomorpha are the

“atherinoids” (Atherinidae, Bedotiidae, Isonidae, Melanotaeniidae, Phallostethidae, and Telmatherinidae), the Cyprinodontiformes (Parenti, 1981), and the Beloniformes (Adrianichthyoidei and Exocoetoidei).

Within the atherinomorphs, the “atherinoids” are still problematic since they cannot be regarded as a monophyletic group, and at present the Atherinoidei cannot be characterized. Among the atherinoids are the Atherinidae (silversides) most of which are marine. However, many species live in freshwater (Barbour, 1973). The grunion, *Leuresthes tenuis*, is probably the best known atherinid because of its peculiar spawning behavior which is

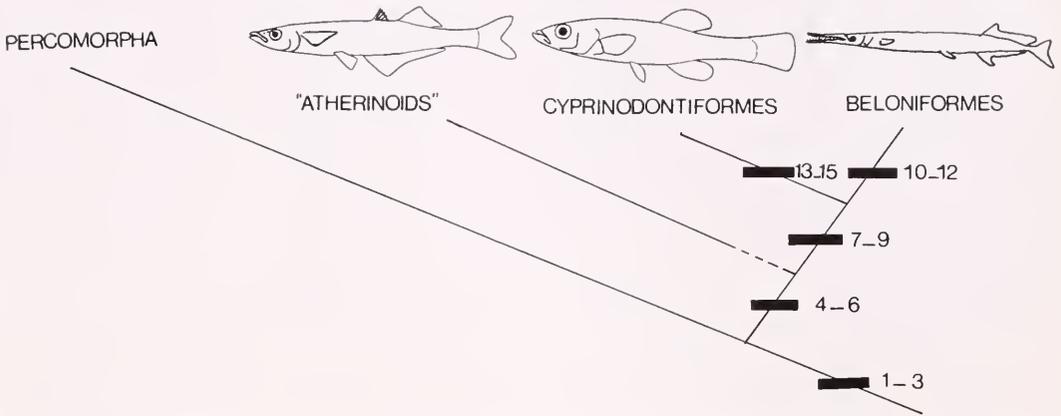


Figure 47. Phylogenetic relationships of the Atherinomorpha. Note that, at present, the Percomorpha are not characterized by any shared derived character(s). The "Atherinoids" are probably not monophyletic, since they lack unifying specialized characters. **1**, presence of an interarcual cartilage in the dorsal gill arch skeleton between the first and second pharyngobranchial; **2**, retractor dorsalis inserts principally or entirely on the third pharyngobranchial; **3**, symphyseal and alveolar parts of the premaxilla are capable of significant downward and forward displacement; **4**, a specialized oral jaw mechanism in which the rostral cartilage is not attached to the premaxilla and the protrusible upper jaw has crossed palatamaxillary ligaments with a maxillary ligament to the cranium; **5**, a large demersal egg with many oil droplets and adhesive filaments; **6**, the third, fourth, and fifth infraorbitals and the fourth pharyngobranchial are absent; **7**, the first epibranchial has an expanded base; **8**, second and third epibranchials reduced; **9**, 1st and 2nd infraorbital lacking; **10**, symmetrical internal skeleton of the caudal fin; **11**, caudal fin is not lobed; **12**, low-set pectoral fins associated with a large, scalelike postcleithrum; **13**, presence of a large ventral flange on the fifth ceratobranchials; **14**, second and third epibranchials distinctly smaller than other epibranchials; **15**, second pharyngobranchial vertically reoriented.

determined by the lunar cycle (Clark, 1925; Walker, 1952). More than 150 atherinid species belonging to 29 genera have been described. The rainbow fishes (*Melanotaeniidae*) inhabit freshwaters of Australia, Aru Island, and New Guinea. The *Phallostethidae* are peculiar atherinoids possessing highly specialized, muscular and bony copulatory organs under the throat of the male (Bailey, 1936; Roberts, 1971a, b).

The remaining two atherinomorph lineages are the Cyprinodontiformes and Beloniformes (Fig. 47) which share several specialized characters in the dorsal gill arches (Fig. 48): 1) the first epibranchial has an expanded base, 2) the second and third epibranchial are reduced, and 3) the first pharyngobranchial and the second infraorbital bone are lost.

Beloniformes are readily characterized by the presence of a large ventral flange on the fifth ceratobranchial, relatively

small second and third epibranchials, a vertical reorientation of the second pharyngobranchial and the loss of the interhyal.

The beloniforms are composed of the exocoetoids, characterized by a median lower pharyngeal toothplate (Rosen, 1964) and more than three anterior branchiostegal rays, and the *Adrianichthyoidei* with a greatly expanded articular surface of the fourth epibranchial and the loss of the metapterygoid or ectopterygoid. Among the exocoetoids (Karrer, 1967) are the marine flying fishes (*Exocoetidae*), the marine and freshwater halfbeaks (*Hemiramphidae*), the predominantly marine needlefishes (*Belonidae*), and the marine sauries (*Scomberesocidae*). The *adrianichthyoids* contain one family, the *Adrianichthyidae* (which includes the *Oryziidae* and *Horaichthyidae*). The medakas (*Oryzias*) from the fresh- and brackish waters of India and Japan to the Indo-

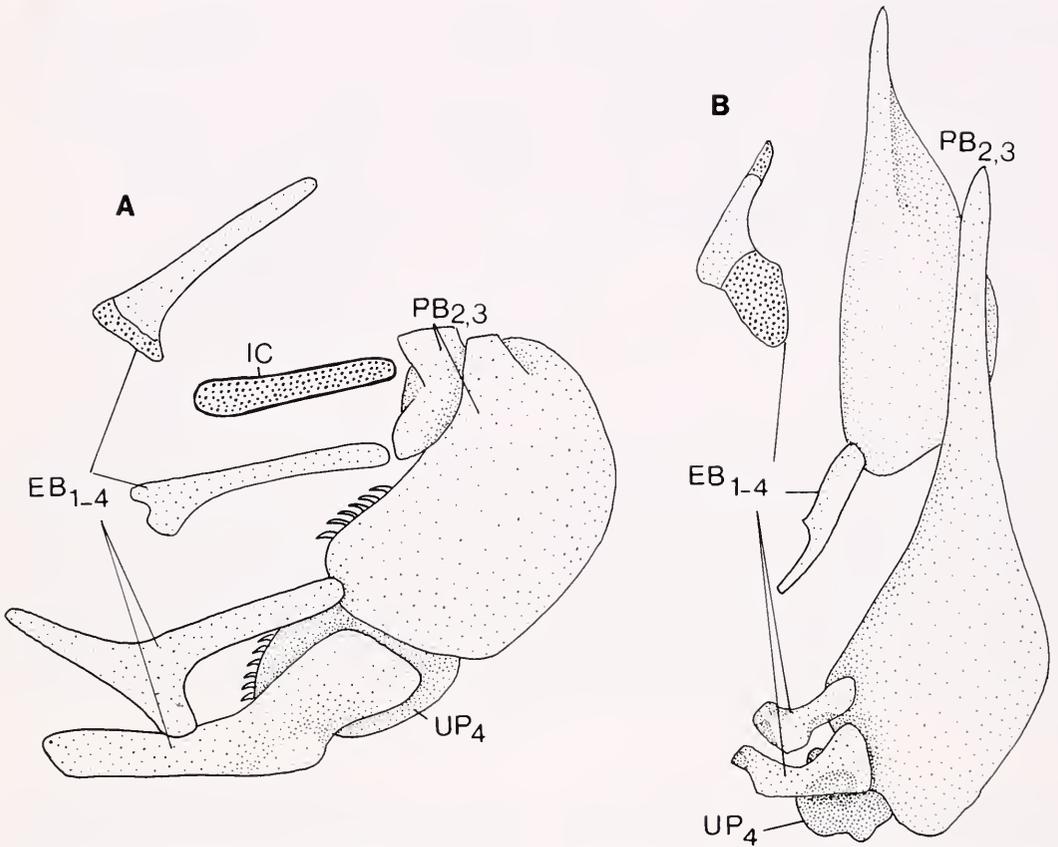


Figure 48. Dorsal gill arch elements seen from dorsal view. A. Representative cyprinodontiform (*Aplocheilus*). B. Representative beloniform (*Xenentodon*). (Modified from Rosen and Parenti, 1981.)

Abbreviations: EB<sub>1-4</sub>, epibranchials 1-4; IC, interarcual cartilage; PB<sub>2,3</sub>, pharyngobranchials 2, 3; UP<sub>4</sub>, upper toothplate of fourth branchial arch.

Australian Archipelago, are often used for developmental studies.

Cyprinodontiforms are characterized by several unique features (Parenti, 1981): 1) the internal skeleton of the caudal fin is symmetrical because the epural symmetrically opposes the parhypural, 2) the unlobed caudal fin, and 3) the low-set pectoral fins with a large, scalelike postcleithrum. In general, cyprinodontiforms have a pattern of early sexual maturation and prolonged embryonic development. In the most recent classification (Parenti, 1981), nine families are recognized within the cyprinodontiforms. Quite a few

have served as exemplary experimental subjects and many are very popular with aquarists. Among the killifishes are annual fishes with eggs that can withstand desiccation and possess different developmental rates so they can survive unpredictable fluctuations in the environment (Wourms, 1972). One of the best known members of the neotropical Rivulidae is *Rivulus marmoratus*, the self-fertilizing hermaphroditic species (Harrington, 1961). The four-eyed fishes (Anablepidae) of the freshwaters of southern Mexico to northern South America have their cornea and retina divided into up-

per and lower "eyes," the upper eye above the waterline serving for aerial vision. Among the Poeciliidae and lamp-eyes (*sensu* Parenti, 1981) are the famous guppy, *Poecilia reticulata*, and the mosquitofish (*Gambusia affinis*). The up-turned mouth opening serves to exploit the oxygen-rich surface layer for respiration. Contrary to common belief, guppies are not surface feeders, but feed on benthic detritus, invertebrates, and algae (Dussault and Kramer, 1981). *Poeciliopsis* is another cyprinodontoid genus which has an all-female species in northwestern Mexico (Schultz, 1973). *Poecilia formosa* consists almost exclusively of females using males of another species (which contribute nothing to the gene pool of the offspring) to stimulate development of the egg. Other cyprinodontiform families are the Old World Aplocheilidae (of which many members are often brightly colored and are popular in the aquarium trade), the viviparous Goodeidae from the freshwaters of west central Mexico (Miller and Fitzsimons, 1971), the Profundulidae, and the Fundulidae of which the brackish water species *Fundulus heteroclitus* is well known to experimental biologists. It is not only very common on the coast of the northeastern U.S. (Bigelow and Schroeder, 1953) but is a very hardy fish with interesting developmental and physiological features.

#### *Percomorpha*

The remaining groups in the Acanthopterygii belong to the Percomorpha. The percomorphs are ill-defined (Rosen, 1973) and their internal classification is very tentative, confusing, and problematic. Existing "phylogenetic" schemes are at best grade classifications adopted as temporary expedients. It is certain that many of the major taxa are polyphyletic groups that simply link most of the "primitive" members of a phyletic unit. Forthcoming investigations of phylogenetic relationships based on rigorous and objective approaches and principles will doubtless

generate new schemes that depart radically from existing ones. It is almost certain that the Beryciformes and Perciformes are polyphyletic assemblages. Since they occupy key positions in the present scheme, any change in their phylogenetic schemes will greatly affect the classification of the other percomorphs. The classification offered here will serve to identify the weaknesses in our current knowledge of the evolutionary relationships among the percomorphs.

#### The Beryciformes

Beryciforms are abundant and diverse in the fossil record of the Cretaceous (Patterson, 1964, 1967, 1968b). These primitive marine acanthopterygians include the squirrelfishes (Holocentridae), alfonsinos (Berycidae), lantern-eye fishes (Anomalopidae), and pinecone fishes (Monocentridae) (Zehren, 1979; Woods and Sonoda, 1973). Beryciforms exhibit all the major features that characterize the Acanthopterygii, but, as one might expect in a "basal" group, they differ from more advanced orders by the retention of such primitive features as an orbito-sphenoid bone in the neurocranium, the presence of 18 or 19 rays in the tail fin, the full complement of three epurals, and a low crest on the second preural vertebra in the caudal skeleton. All beryciforms share a peculiar specialization in the tail: the presence of true, unpaired procurrent caudal fin spines (Fig. 49), rather than unsegmented bilaterally paired rays as in other acanthopterygians (Patterson, 1968b); but see Rosen, 1973, page 452 for contradictory observations.

The beryciforms and perciforms appear to share a common ancestry, and the Beryciformes may represent the primitive sister group. Both taxa have the pelvic girdle firmly joined to the pectoral girdle, pelvic fins with a spine and five soft rays, and the second circumorbital bone with a suborbital shelf underlying the eye (Fig. 50). There is little doubt that

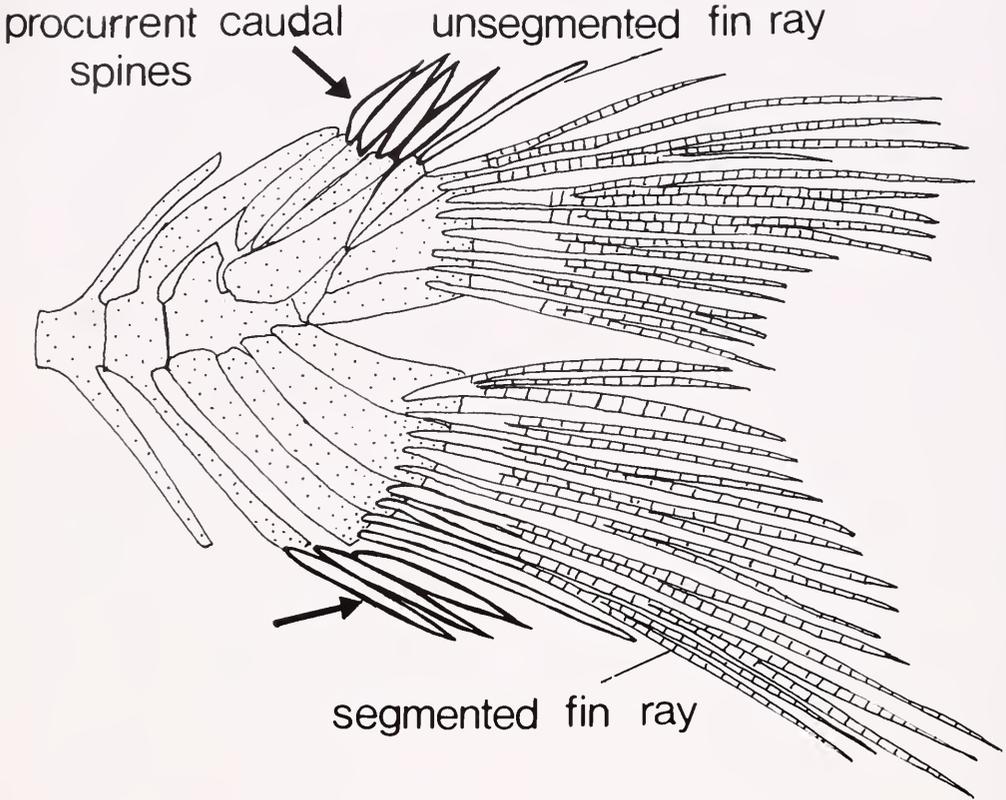


Figure 49. Lateral view of the caudal skeleton of a beryciform, showing the characteristic unpaired, truly spinous structures: the procurrent caudal spines.

these features reflect close phylogenetic relationships between the beryciforms and the largest known order, the Perciforms (perchlike fishes).

Based on the specialized morphology of the otoliths (Fig. 51), Patterson (1964) suggested that the order Zeiformes (dorries) is a sister group of the Beryciformes and that both groups are the sister group of the perciform assemblage.

In spite of the extensive and excellent osteological studies by Zehren (1979) and Patterson (1964) the monophyly of the Beryciformes has yet to be demonstrated. All recent beryciform families may represent monophyletic groups (Zehren, 1979). The Monocentridae (pinecone fishes) have a body armor of thick scales and the dentary has a distinct notch on

the ventral border. Lantern eye fishes (Anomalopidae) have the anterolateral portions of the nasal prolonged into a distinct process which articulates with the lateral ethmoid and a subocular light organ. In the Berycidae (alfonsinos) the lacrimal is extended posteriorly below infraorbital 1 to articulate with infraorbital 2. Squirrelfishes (Holocentridae) possess a transverse crest on the dorsal surface of the supraoccipital. Other beryciform families are the Trachichthyidae (slimeheads), Diretmidae, Polymixiidae, Gibberichthyidae, Stephanoberycidae (pricklefishes), and Anoplogasteridae (fangtooths). By virtue of their possible sister group relationship to the Perciformes, and uncertainty over their interrelationships, the Beryciformes offer nu-

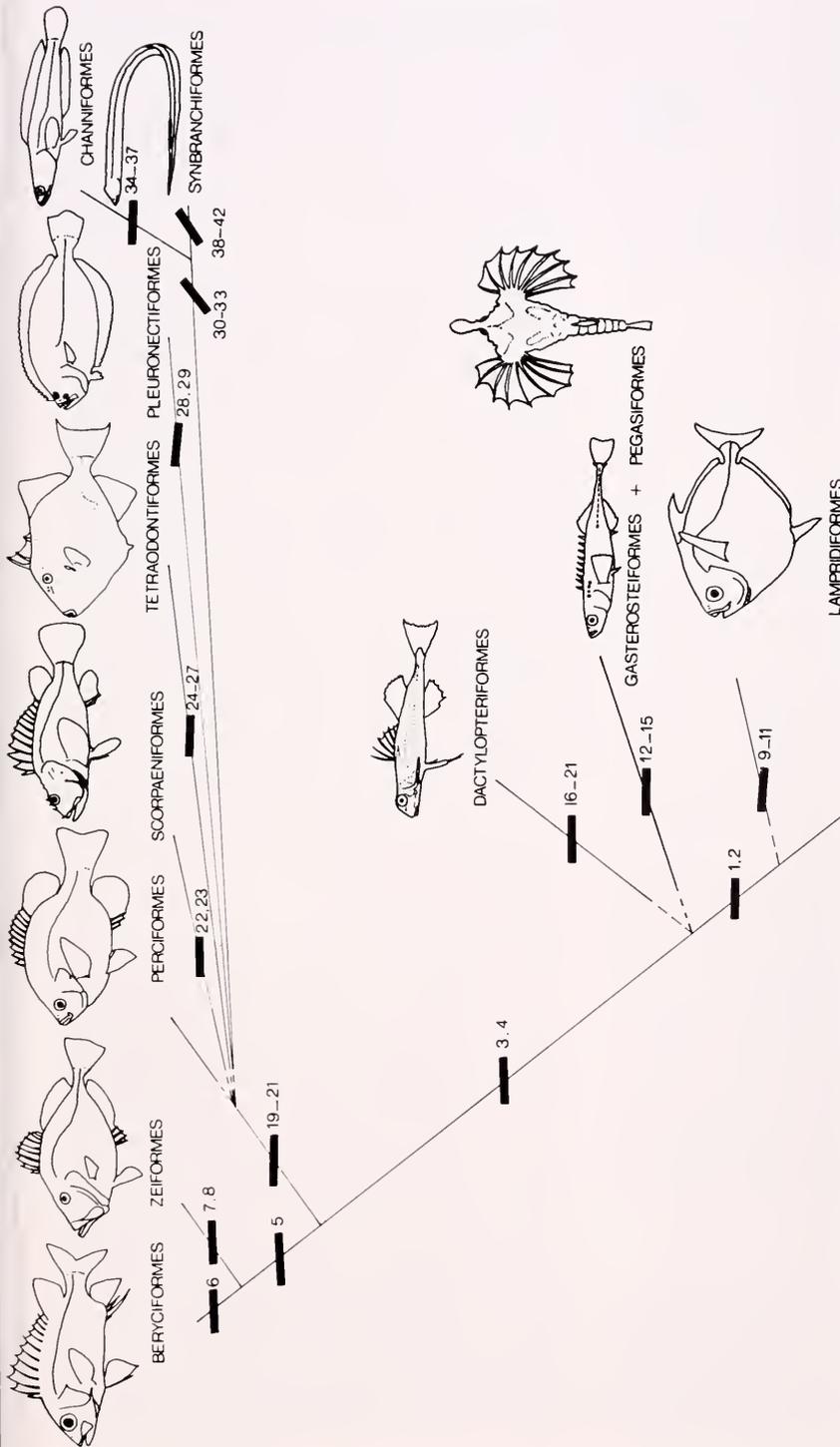


Figure 50. Interrelationships of the major groups of the percomorph Acanthopterygii. Major specializations characterizing the various lineages are: 1, separate soft and spinous dorsal fins; 2, pelvic girdle attached to cleithrum; 3, second circumorbital bone with subocular shelf; 4, pelvic fin with spine and five rays; 5, sacculith (otolith) morphology specialized (Fig. 51); 6, presence of specialized procurrent caudal spines; 7, decrease in number of vertebrae; 8, deepening of the body; 9, maxilla slides out with premaxilla during jaw protrusion; 10, no true spines in fins; 11, pelvic girdle attached to a large specialized hypocroracoid; 12, body encased in bony armor; 13, small mouth at end of tubular snout; 14, number of branchiostegals reduced (1-5); 15, trend to either reduce or modify gills; 16, no lateral line; 17, enlarged pectoral; 18, body covered with scutelike scales; 19, no free second urol centrum; 20, 17 principal caudal rays; 21, caudal skeleton with 5 hypurals; 22, hypurals fused into two distinct, large plates; 23, third circumorbital bone with an extension attached to the preoperculum; 24, entire branchiostegal region covered by a thick layer of scaleless or scaled skin; 25, no suborbitals, parietals, nasals, sensory canals in the skull, and anal spines; 26, gill opening restricted to a very small slit just below the base of the pectoral fin; 27, specialized dermal protective devices; 28, median fins extend along much of body profile; 29, bilateral asymmetry affecting topography of the eyes and coloration; 30, hemispheres of forebrain coalesced (Fig. 60); 31, adductor mandibulae complex with specialized  $A_1$  and  $A_2$  divisions (Fig. 61); 32, fourth branchial arteries modified; 33, fins without spines; 34, otic bullae for sacculith, utricle and lagenolith are contained in the prootic bone; 35, metapterygoid with prominent anterodorsally directed uncinata process; 36, two ventral aortae emerge separately from the bulbous arteriosus; 37, gas exchange with air in the suprabranchial and buccopharyngeal cavities, which remain in open communication throughout the breathing cycle; 38, frontals turned down and sutured to basisphenoid; 39, large parietals meet in midline; 40, suspensorium articulates with basisphenoid, frontal, vomer and lateral ethmoids; 41, interarcual cartilage ossified; 42, the elongate heart is located far posteriorly in the body cavity. (Many of these characters, e.g., 1-3, 10, and 17, are poor and considerable future work will be necessary to clarify the relationships of the Acanthopterygii.)

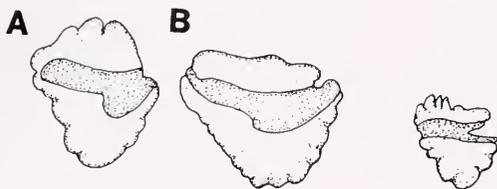


Figure 51. Inner face of the sacculith (otolith with the sacculus). A. The most primitive zeiform *Antigonina*. B. The berycoid *Beryx*. C. The zeiform *Capros*. (Modified from Stinton, 1967.)

merous challenging phylogenetic and evolutionary problems for future workers.

### The Lampridiformes

Although the main radiation of acanthopterygian fishes occurs in the Perciformes, there seem to have diverged, at an early stage, an assemblage of odd types of percomorphs. The highly specialized Lampridiformes (opahs) are an assemblage of mainly deep sea fishes (Walters, 1960; Walters and Fitch, 1960). The lampridiform caudal skeleton shows similarities to that of some beryciformes. The proposed relationships of the Lampridiformes to other percomorphs is depicted in Figure 50. Lampridiformes have no true spines in their fins and possess an unusual jaw mechanism in which the maxillae slide out with the premaxillae during protrusion (Oelschläger, 1978; Pietsch, 1978a). The pelvic girdle is not attached to the cleithrum, but instead it is connected to a greatly enlarged special bone of the pectoral girdle, the hypocoracoid (Oelschläger, 1978). *Lampris*, the opah or moonfish, is perhaps the best known for its odd appearance and size (about 1 m, and 300 kg).

### The Zeiformes

The dories (Zeidae) and boarfishes (Antigoniidae) together are considered the sister group of the beryciformes (Fig. 50) because of the shared specializations in the morphology of the otoliths (Patterson,

1964). In zeiforms, the caudal skeleton has specialized along the lines characteristic for the perciforms and the zeiform pelvic fin with one spine and five to nine branched rays also approaches the perciform condition. The dories (*Zeus*) are thin, deep-bodied fishes with enormously distensible jaws set at an oblique angle. They are marine and widespread (Myers, 1960).

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 pattern in the Beryciformes, Lampridiformes, and Zeiformes (Fig. 50) 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 are located, possibly for maneuverability, high up on the side of the body. 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 trend are especially discernable among the Perciformes (Fig. 50).

### The Gasterosteiformes

The Gasterosteiformes appear to be another highly specialized side branch of early acanthopterygians (Fig. 50). Pietsch (1978b) has included the former order Pegasiformes in the Gasterosteiformes on the basis of some shared specializations in the feeding apparatus. We follow the provisional phyletic scheme proposed by Pietsch and have put the sea moths (pegasoids), the sticklebacks (Gasterosteidae), sea horses (Syngnathoidei), and trumpet fishes (Aulostomidae, Fistulariidae) in a presumably monophyletic assemblage, the Gasterosteiformes.

The Gasterosteiformes are first known from the Lower Eocene and are widely distributed today in both marine and

freshwaters. In this group the body is typically elongate and slender and may be encased in bony plates; the small mouth is usually located at the end of a tubular snout. All members are slow-moving fishes. The sticklebacks (*Gasterosteidae*) are famous for the numerous studies made on their behavior and physiology (Wootton, 1976).

Because the *Gasterosteiformes* are so specialized they provide little evidence of their phylogenetic position. In all *gasterosteiformes* the spinous and soft parts of the dorsal fin are separated. In the *pegasoids* the pelvic girdle is attached to the cleithrum, and they possess a pterygiophore in the dorsal fin indicating that the spinous dorsal fin has been lost secondarily. It is postulated that in *gasterosteids* the pelvic girdle has lost its attachment with the cleithrum secondarily. Monophyly of the *Gasterosteiformes* has not been convincingly demonstrated (Gosline, 1971; Greenwood *et al.*, 1966). Some authors (e.g., McAllister, 1968; J. Nelson, 1976) prefer to recognize two groups at the ordinal level, i.e., *Syngnathiformes* and *Gasterosteiformes*. In the *Gasterosteidae* (sticklebacks) and the *Aulorhynchidae* (tubesnouts) the postcleithrum is lost. The loss of the postcleithrum is a derived character, suggesting a closer relationship between the *Gasterosteidae* and *Aulorhynchidae* than to any other *gasterosteiform*.

The remaining *gasterosteiformes* have lost all infraorbitals except for the lacrimal and possess very specialized tufted lobelike gills (Rauther, 1937). Included in this group are six families. The tropical marine trumpetfishes (*Aulostomidae*) which inhabit reefs and often rest with their bodies in a vertical position with the head downward. The *Fistularidae* (Cornetfishes) are also tropical marine fishes with exceptionally long tubular snouts (Jungersen, 1910) functioning as pipette-like suction devices. Snipefishes (*Macrorhamphosidae*) and ghost pipefishes (*Solenostomidae*) are both small families of

mainly tropical marine fishes. The shrimpfishes (*Centriscidae*) have a peculiar locomotor mode: they swim in a vertical position with the snout downwards. The *Syngnathidae* (pipefishes and seahorses) are mostly marine fishes inhabiting shallow waters. In *syngnathids* the males care for the brood the females attach to them in a pouchlike structure or on the ventral surface of the trunk or tail.

### The Dactylopteriformes

The *Dactylopteriformes* (flying gurnards) is a small order of specialized tropical marine fishes (Fig. 50) whose relationships are still unknown. The *dactylopteriforms* have large pectoral fins giving them an ability to "glide" in a way paralleling the *exocoetids* or true flying fishes. The *dactylopteriforms* have the pelvic girdle attached to the cleithrum, and have lost the lateral line. The spinous and soft dorsal fins are separated. *Dactylopterids* are benthic fishes that can "walk" on the sea floor by alternately moving the pelvic fins (J. Nelson, 1976).

### The Perciformes

The order *Perciformes* (perchlike fishes) cannot be defined cladistically and is almost certainly a gradal and unnatural assemblage. Even though the *Perciformes* is clearly polyphyletic, many attributes have been assigned to the group: 1) It is the most diversified of all fish orders, 2) It is the largest vertebrate order comprising about 20 suborders containing 150 families and at least 6,900 species, 3) *Perciforms* dominate vertebrate ocean life and also form a major component of the fish fauna in many tropical and subtropical freshwaters, and 4) It is the basal evolutionary group from which numerous other groups are believed to have been derived (Gosline, 1968). None of the above-mentioned attributes commonly ascribed to *perciforms* in evolutionary discussions is meaningful because mon-

ophyly of the group has not been established. If the Perciformes is polyphyletic, no statements can be made about their morphological, functional, and taxonomic diversity, evolutionary patterns, evolutionary rates, biogeography, and ecological dominance in the oceans and fresh-water. It is better to refrain from perpetuating such evolutionary scenarios so prevalent in the present ichthyological literature and to focus on the problems and inconsistencies of the internal classification of the Perciformes, and offer hypotheses of relationships of some of the major taxa. Because the Perciformes is presently ill defined and the internal classification so poorly known, this discussion will focus on some specific problems rather than offer a general classification of over 150 families.

To date the Perciformes cannot be defined by either a single specialized character or a combination of specialized characters. The perciform categories discussed below do not necessarily delimit monophyletic groups.

*Suborder Percoidei.* The most generalized and several specialized perciforms are included in this undefined assemblage. Included in the Percoidei are such important food fishes as the Serranidae (Smith, 1971; Gosline, 1966), the seabasses, with about 370 species of which many are protogynous hermaphrodites (Smith, 1965); the Carangidae, jacks and pompanos with their distinctly compressed bodies; the Mullidae, goatfishes, with their two long chin barbels used for detecting food; the Lutjanidae (Johnson, 1980), snappers, which are sometimes responsible for ciguatera or fish poisoning. Other percoids include the Pomadasyidae (grunts) and Sciaenidae (drums and croakers; Trewavas, 1977), which make sounds, using the swimbladder as a resonating chamber; the wide-spread remoras (Echeneidae; Gosline, 1971) in which the spinous dorsal fin is transformed into a sucking disc; and the Coryphaenidae (dolphins, mahi mahi; Gibbs

and Collette, 1959), which are composed of very fast swimming, streamlined oceanic fishes. More generalized percoids include the Centropomidae (Greenwood, 1976), the snooks; the Percidae (Collette, 1963) the perches and darters; and the Centrarchidae, the sunfishes. Many percoid families are strictly marine, e.g., the Grammistidae (soapfishes), Chaetodontidae (butterflyfishes); Kyphosidae (sea chubs), Ephippidae (bonnetmouths); Bramidae (Mead, 1972), pomfrets; Pomatomidae (bluefish); Branchiostegidae (tilefish); Apogonidae (cardinalfishes, Fraser, 1972); Priacanthidae (bigeyes); Teraponidae (tigerperches, Vari, 1978), Grammididae (basslets); Pleusiopidae (roundheads); and Leiognathidae (ponyfishes).

Some of the percoid families are thought "to have given rise" to the derived perciform suborders. For example, the Nandidae (leaf fishes) has been hypothesized to be related to the Anabantoidei (Nelson, 1969a; Gosline, 1971). Liem and Greenwood (1981), have argued that the evidence for such a close relationship is questionable. On the basis of functional morphological data it has been shown that the features associated with the tongue-parasphenoid bite in pristolepids are specialized and unique, making them autapomorphic for *Pristolepis*, an important taxon in efforts to relate Nandidae with the Anabantoidei. The dentition on the parasphenoid, basihyal, and third hypobranchial and all features associated with the swallowing apparatus in nandids and channiforms are primitive, and do not indicate relationships with either *Pristolepis* or the Anabantoidei. Thus, the efforts to demonstrate monophyly of the Nandidae, Anabantoidei and Channiformes have failed. However, Barlow *et al.* (1968) and Liem and Greenwood (1981), have discovered evidence that *Badis badis*, which is traditionally classified with or very near the Nandidae (Gosline, 1971) may share specializations with the Anabantoidei: a

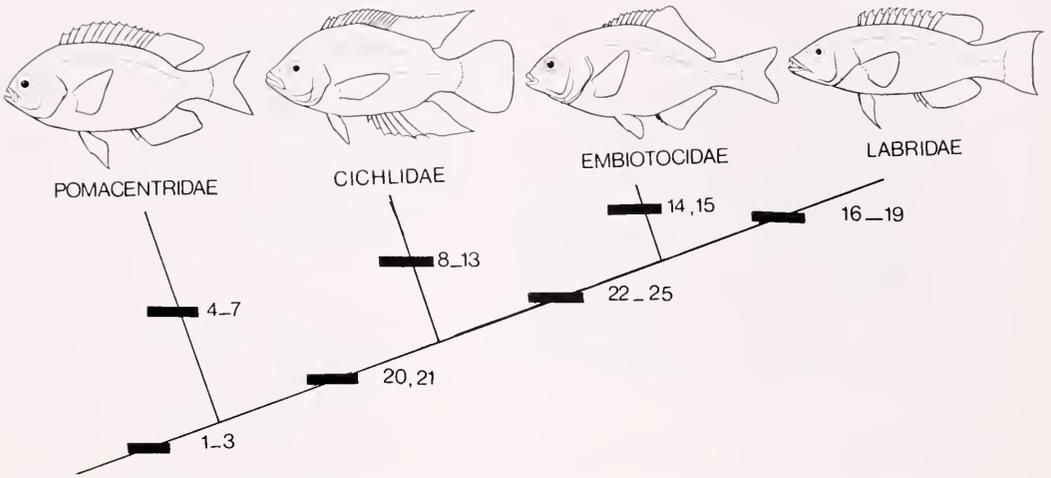


Figure 52. Interrelationships of the major labroid lineages based on the following specialized characters: 1, United or fused fifth ceratobranchials; 2, true diarthrosis between upper pharyngeal jaws and basicranium; 3, undivided sphincter oesophagi muscle; 4, strong sheet of connective tissue joining lower jaw with a ligament, which inserts on the ceratohyal bone; 5, nipple-like bony process on ventral surface of lower pharyngeal jaw; 6, pharyngo-cleithral articulation of characteristic form; 7, obliquus posterior dominant muscle to lower pharyngeal jaw; levator externus 4 and obliquus posterior vertically aligned on fourth epibranchial, separated by oblique aponeurosis or tendon; 8, transversus dorsalis muscle subdivided into four parts; 9, premaxillae and maxillae functionally decoupled; 10, cartilagenous cap on anterior border of epibranchial 2; 11, microbranchiospinae of characteristic form present on outer faces of second, third, and fourth gill arches; 12,  $A_2$  and  $A_w$  portions of adductor mandibulae complex separated completely; insertion of large ventral division of  $A_2$  onto angulo-articular; 13, head of epibranchial 4 distinctly expanded; 14, intra-uterine development of young with highly modified vascularized median fins; 15, muscular sheet joining  $A_1$  and  $A_{2,3}$  portions of adductor mandibulae; 16, levator posterior dominant muscle to the lower pharyngeal jaw, forming a force couple with the pharyngocleithralis muscle; 17, toothplates of fourth pharyngobranchials absent or reduced; 18, fourth epibranchials highly modified, articulating with upper pharyngeal jaws; 19, true pharyngo-cleithral articulation functioning as sliding and hinge joint; 20, levator externus 4 is a continuous muscle joining prootic region to muscular process on lower jaw; 21, predisposition for insertion of levator posterior muscle on lower pharyngeal jaw; 22, loss of second pharyngobranchial toothplates; 23, first three branchial adductor muscles cover anterodorsal faces of the epibranchials; 24, ligament connecting postmaxillary process of maxilla with anterior border of palatine and ectopterygoid; 25, tooth rows arranged radially across the lower pharyngeal jaw, teeth located directly over the symphysis between left and right fifth ceratobranchials, dominant mode of tooth replacement from posterior margin of toothplate. (From Kaufman and Liem, 1982.)

functional separation of the lower pharyngeal jaw-parasphenoid bite from the swallowing mechanism. It is therefore possible that *Badis* is the primitive sister group of the Anabantoidae.

The Pomacentridae (damselfishes), Embiotocidae, and the Cichlidae have been considered members of the percoids for many years (Regan, 1913). We deviate from this traditional scheme and link the three families together with the Labridae, Odacidae, and Scaridae into one monophyletic assemblage (Fig. 52) at the subordinal rank: The Labroidei (also see Stiassny, 1981; Kaufman and Liem, 1982).

*The Labroidei.* The Labroidei are composed of the Pomacentridae (damselfishes), Cichlidae, Embiotocidae (surfperches), Labridae (wrasses), Odacidae, and Scaridae (parrotfishes). The Labroidei are characterized by (Stiassny, 1980; Kaufman and Liem, 1982): 1) united or fused fifth ceratobranchials resulting in the formation of one lower pharyngeal jaw, 2) a true diarthrosis between the upper pharyngeal jaws and the skull base without an intervening muscular part of the transversus dorsalis anterior muscle (Fig. 53), and 3) the presence of an undivided sphincter oesophagi muscle forming a continuous sheet (Fig. 53).

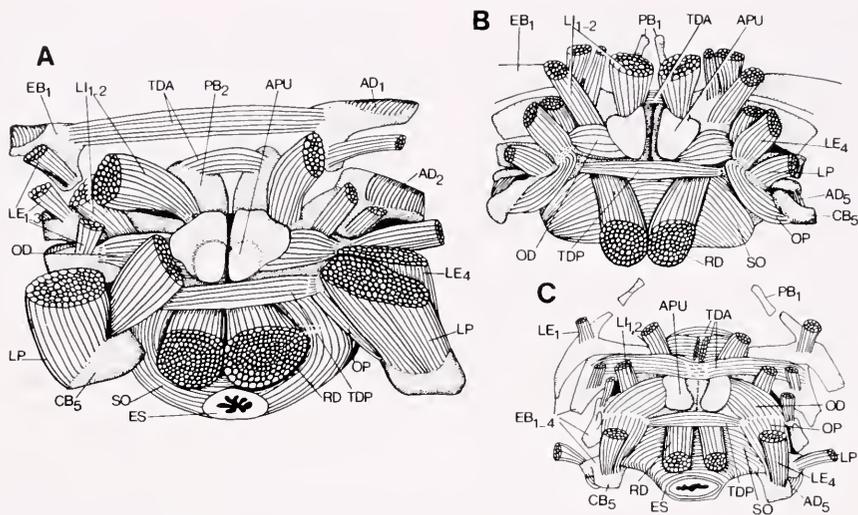


Figure 53. Dorsal aspect of the branchial musculature viewed from posterior to elucidate the muscles surrounding the esophagus and posterior branchial arches in representative Pomacentridae (A. *Tautoglabrus adspersus*. B. *Amphiprion xanthurus*); representative cichlid (C. "*Haplochromis*" *leuciscus*) (From Kaufman and Liem, 1982).

**Abbreviations:** AD, adductor branchialis; APU, apophysis of upper pharyngeal jaw (third pharyngobranchial); CB<sub>5</sub>, fifth ceratobranchial (lower pharyngeal jaw, LPJ); EB, epibranchial; ES, esophagus; LE, levator externus muscle; LI, levator internus muscle; LP, levator posterior muscle; OD, obliquus dorsalis; OP, obliquus posterior muscle; PB, pharyngobranchial; RD, retractor dorsalis muscle; SO, sphincter oesophagi muscle; TDS, transversus dorsalis anterior muscle; TDP, transversus dorsalis posterior muscle.

The Pomacentridae is considered the primitive sister group of all other labroids (Stiassny, 1980). In pomacentrids the fourth levator externus and levator posterior muscles insert on the fourth epibranchials, a plesiomorphous condition found also in all primitive perciforms. Pomacentrids can be defined by 1) the presence of a strong connective tissue sheet connecting the medial face of the lower jaw via a cylindrical ligament with the ceratohyal (Stiassny, 1981); 2) a pair of nipplelike processes are present on the ventral surface of the lower pharyngeal jaw serving as insertion sites for the pharyngohyoideus muscle; 3) the muscular processes of the lower pharyngeal jaw abut the cleithra; and 4) the obliquus posterior muscle is prominent and is separated from the fourth levator externus by a distinct aponeurosis (Fig. 53). The fibers of the fourth levator externus and obliquus posterior muscles are not continuous. Pomacentrids are represented by

about 23 genera with 230 species inhabiting all tropical seas, but primarily the Indo-Pacific.

The freshwater family Cichlidae has recently been defined (Liem and Greenwood, 1981; Stiassny, 1980, 1981; Kaufman and Liem 1982) by at least five shared derived characters: 1) the transversus dorsalis muscle is subdivided into four parts (Fig. 53); 2) microbranchiospinacae of characteristic form are present on the gill arches; 3) the presence of an extensive cartilaginous cap on the anterior border of the second epibranchial (Fig. 54); 4) the A<sub>2</sub> and A<sub>w</sub> portions of the adductor mandibulae complex are separate; and 5) the head of the fourth epibranchial is expanded. The Cichlidae comprise about 85 genera and well over 1,000 species. Cichlids are known for their complex territorial, agonistic and courtship behavior (Baerends and Baerends-van Roon, 1950; Wickler, 1962, 1963; Keenleyside, 1979), and the frequent occurrence of color and

trophic polymorphism (Fryer and Iles, 1972; Sage and Selander, 1975; Kornfield and Koehn, 1975). A spectacular evolutionary radiation occurs amongst the endemic cichlids inhabiting Lakes Victoria, Malawi and Tanganyika (Fryer and Iles, 1972; Greenwood, 1974). Speciation (Greenwood, 1974), morphological and functional diversification (Liem, 1978, 1979, 1980) and ecological dominance (Fryer and Iles, 1972; Liem, 1982) of the cichlids of Lakes Victoria, Malawi, and Tanganyika are considered accentuated if compared with similar phenomena in other vertebrates.

Phylogenetically, the Cichlidae represent the most primitive labroid in which the fourth levator externus becomes inserted on the lower pharyngeal jaw (Liem, 1974). Ontogenetically the fourth levator externus gains its attachment of the lower pharyngeal jaw by fusing with a large medial head of the obliquus posterior muscle (Aerts, 1982; Fig. 53). Thus the cichlid lower pharyngeal jaw is suspended in a muscular sling, part of which can be kept in continuous tension. Such a structural specialization facilitates the controlled protrusion, retrusion, and lateral translation, as well as rotation about three axes of the lower pharyngeal jaw (Liem, 1978). This specialized pharyngognathly of the cichlids is shared with the more derived Embiotocidae and Labridae (Fig. 52).

The Embiotocidae (surfperches) are coastal marine fishes (one species lives in freshwater), which are fully viviparous, delivering large well-developed young. The males have a small, intromittent organ, representing a modified forward end of the anal fin. Monophyly of the embiotocids can be established by the highly specialized viviparity and associated structural, physiological and behavioral features involving specialized and vascularized median fins (Webb and Brett, 1972). In respect to the jaw mechanisms, embiotocids share a specialized feature: a small slip of parallel muscle fibers aris-

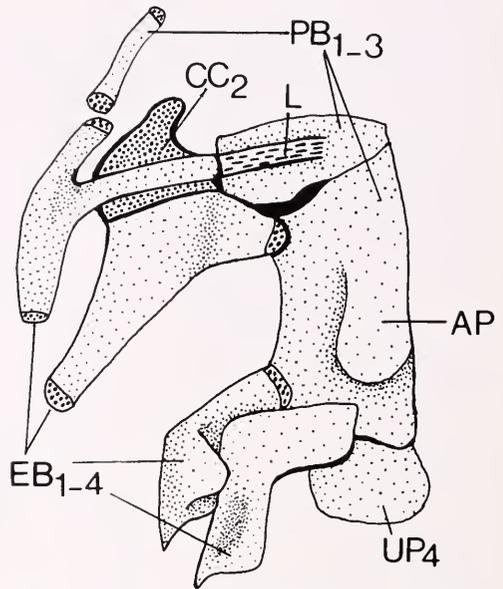


Figure 54. Dorsal view of dorsal gill arch elements of a representative member of the Cichlidae ("*Haplochromis leuciscus*").

*Abbreviations:* AP, articular process of the upper pharyngeal jaw on the third pharyngobranchial; CC<sub>2</sub>, cartilaginous cap on the 2nd epibranchial; EB<sub>1-4</sub>, epibranchials 1-4; L, ligament; PB<sub>1-3</sub>, pharyngobranchials 1-3; UP<sub>4</sub>, upper toothplate of the fourth branchial arch.

ing from the anteromedial region of the part A<sub>1</sub> of the adductor mandibulae muscle and inserting upon the dorsal aponeurosis of part A<sub>2,3</sub> of this muscle complex (Stiassny, 1981).

The Labridae as defined by Kaufman and Liem (1982) include the wrasses (formerly known as the Labridae), Odacidae, and the parrotfishes (Scaridae). The inclusion of the odacids and scarids in the Labridae reflects the monophyletic nature of the assemblage and the recency of their common descent. The Labridae (including "odacids" and "scarids") can be defined as follows: 1) The levator posterior muscle is the dominant muscle of the lower pharyngeal jaw forming a force couple with the pharyngocleithralis externus muscle (Liem and Greenwood, 1981); 2) The toothplates of the fourth pharyngobranchials are absent (Nelson,

1967b; Stiassny, 1981); 3) The fourth epibranchials are highly modified and of a characteristic form; 4) The adductor branchialis muscles of all arches are hypertrophied (Fig. 53); and 5) There is some form of physical contact between the lower pharyngeal jaw and the cleithrum (pharyngocleithral joint of Liem and Greenwood, 1981). The labrids comprise over 70 genera and about 470 species, and play a key role in modern tropical marine communities. Many labrids cause patchy disturbances to sessile invertebrates (Kaufman and Liem, 1982) and represent a principal factor regulating food abundance for other reef organisms. The disproportionate role of labrids in determining the distribution and abundance of benthic organisms in tropical marine hard-bottom communities may be correlated with the specialized lower pharyngeal jaw (LPJ) which is functionally versatile in processing a broad range of prey.

In the phylogenetic scheme of the Labroidei (Fig. 52), the Embiotocidae and Labridae are considered sister groups on the basis of four synapomorphies: 1) The second pharyngobranchial toothplates are absent (G. Nelson, 1967b; Stiassny, 1981); 2) The first three branchial adductor muscles cover the anterodorsal surfaces of the epibranchials (Stiassny, 1980); 3) a ligament connects the postmaxillary process of the maxilla with the anterior border of the palatine and ectopterygoid (Stiassny, 1980); and 4) tooth rows are arranged radially across the LPJ, with teeth located directly over the symphysis between left and right fifth ceratobranchials.

*Other Suborders.* The Acanthuroidei, the marine surgeonfishes (Acanthuridae) and rabbitfishes (Siganidae), is often thought to form the link between the more generalized perciforms and the Tetraodontiformes. Although the relationship between acanthuroids and tetraodontiforms is often implied (Winterbottom, 1974b, Tyler, 1980), no synapomorphies have so far been found. Acanthuroids all have deeply compressed bodies, large

swimbladders, and pass through a highly specialized planktonic acronurus larval stage. The mesethmoid bone is positioned well in front of the lateral ethmoids and is distinctly separated from the vomer by a forward extension of the parasphenoid (Starks, 1926). Many of the over 85 species of acanthuroids are herbivorous and feed on algae.

The Blennioidei, which includes 35 families, 245 genera, and over 900 species (Springer, 1968, 1972; Smith-Vaniz and Springer, 1971) is most likely a polyphyletic assemblage (Gosline, 1968). According to Bertin and Arambourg (1958) blennioids can be distinguished by the firm attachment of the fin rays of the pectoral fin to the hypertrophied pterygiophores. Blennioids have elongate bodies with long dorsal and anal fins, large pectoral fins and small pelvic fins placed far forward. Included among the blennioids are the sandfishes (Trichodontidae), jawfishes (Opisthognathidae), sandperches (Mugiloididae), sanddivers (Trichonotidae), venomous weeverfishes (Trachinidae), stargazers (Uranoscopidae) which have very venomous spines at the edge of the opercle and electric organs behind the eyes, sand stargazers (Dactyloscopidae), cod icefishes (Nototheniidae) from coastal antarctic waters living at an average temperature of  $-1.9^{\circ}\text{C}$  and using a glycoprotein in the blood as antifreeze (DeVries and Wohlschlag, 1969), crocodile icefishes (Chaenichthyidae) which lack hemoglobin in their blood, eelblennies (Congrogadidae), snake blennies (Ophichlinidae; Springer, 1970), threefin blennies (Tripterygiidae), clinids (Clinidae; Stephens, 1963; Springer, 1964), combtooth blennies (Blenniidae; Springer 1968, 1972; Springer and Smith-Vaniz 1972; Smith-Vaniz and Springer, 1971) comprising over 275 species, pricklebacks (Stichaeidae; Makushok, 1958), and wolf fishes (Anarhichadidae). Generally, blennioids are semisedentary bottom forms that live along rocky shores. But the sand-living species have special fea-

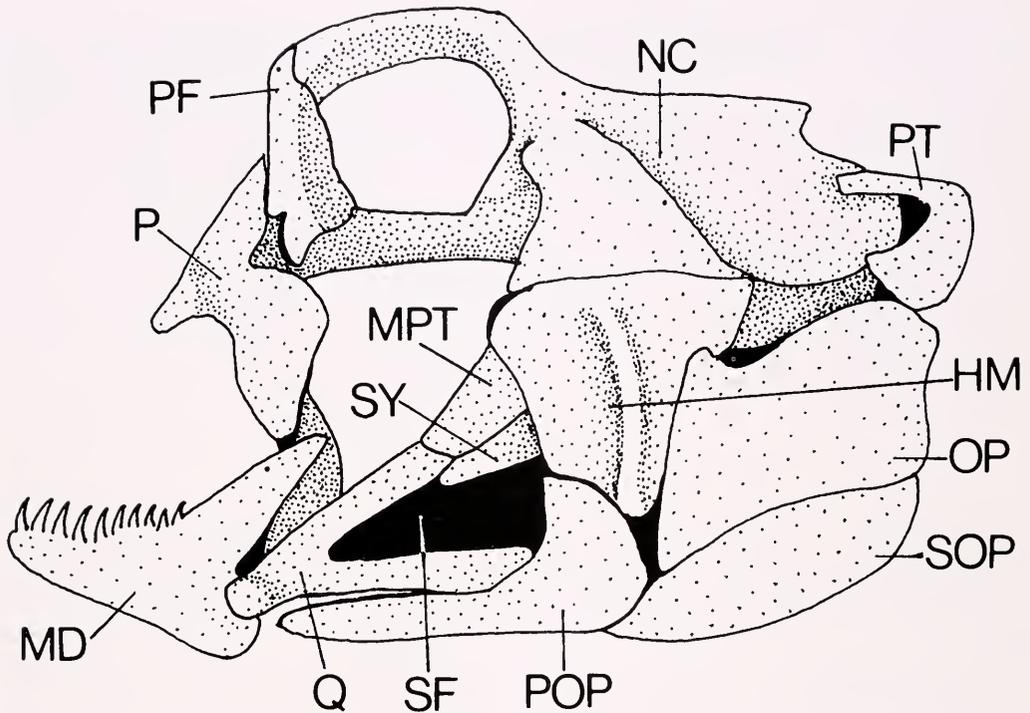


Figure 55. Lateral view of neurocranium, suspensorium, and opercular apparatus in a representative gobioid *Periophthalmus* (Modified from Gregory, 1933).

Abbreviations: SF, the large foramen in the suspensorium; HM, hyomandibula; MD, mandible; MPT, metapterygoid; NC, neurocranium; OP, operculum; P, palatine; PF, lateral ethmoid complex; POP, preoperculum; PT, posttemporal; Q, quadrate; SF, foramen in suspensorium; SOP, suboperculum; SY, symplectic.

tures such as eyes placed on the top of the head, and their upward-directed mouths have fringes, or flaplike structures thought to prevent the intake of sand with the respiratory current which is produced by a dominant opercular suction pump.

The Gobioidae is another extremely speciose suborder containing 7 families, 235 genera and over 1,000 species. Although monophyly is relatively well documented, internal classification is still chaotic (Gosline, 1968). Gobioids are characterized by the loss of the parietals, circumorbitals, the lateral line, and pyloric caeca. A very large space ("foramen") is located in the center of the suspensorium surrounded by the two arms of the quadrate bone, the symplectic and

preoperculum giving the gobioid suspensorium a very characteristic structural pattern (Fig. 55). Among the gobioids (Bohlke and Robbins, 1960, 1968; Koumans, 1953) are the sleepers (Eleotridae), gobies (Gobiidae), which is the largest family of marine fishes forming together with blenniids and clinids the dominant element in the benthic habitat of tropical reefs, sand gobies (Kraemeriidae), eellike gobies (Gobioididae), burrowing gobies (Trypauchenidae), and wormfishes (Microdesmidae).

The marine Stromateoidei is unquestionably monophyletic since all members have very specialized toothed saccular outgrowths of the esophagus (Haedrich, 1967). Stromateoids comprise 6 families, 15 genera and about 60 species and in-

clude the medusafishes (Centrolophidae), driftfishes (Nomeidae), squaretails (Tetragonuridae), and butterfishes (Stromateidae).

The marine Scombroidei includes the world's fastest swimming fishes. Scombroids are specialized in many ways for high speed swimming (Gibbs and Collette, 1966; Fierstine and Walters, 1968). The single synapomorphy is the highly modified upper jaw: the premaxillae are not only united with each other but also with the maxillae, forming a rigid non-protrusible upper jaw which can become elongate to form a rostrum. Scombroids comprise 6 families with 36 genera and over 90 species. Included are the snake mackerels (Gemphylidae), cutlassfishes (Trichiuridae), mackerels and tunas (Scombridae; Gibbs and Collette, 1966), swordfish (Xiphiidae), and billfishes (Istiophoridae) (Gregory and Conrad, 1937, 1943).

Smaller perciform suborders include the following: 1) The Kurtoidei, with a single genus. These forehead brooders possess hooks developed from the supra-occipital bone and have expanded ribs forming a bony tube enclosing the swimbladder; 2) The burrowing Ammodytoidei, the sand lances, with elongate bodies, protrusible premaxillae (Kayser, 1962), the lower jaw projecting forward beyond the upper jaw, and neither fin spines nor pelvic fins; 3) The Callionymoidei (Kayser, 1962), the dragonets, resemble the blennioid trichodontids in having a specialized pectoral fin skeleton in which the scapula is aligned together with the pterygiophores and functions as a direct articulation for the top three pectoral fin rays (Starks, 1923); 4) The elongate Mastacembeloidei, the spiny eels, with the dorsal fin preceded by a series of isolated spines and the supracleithrum attached to the second and third vertebra by a distinct ligament while the posttemporal is absent. The premaxillae are firmly united with the maxillae. Travers (personal communication) has proposed that

the mastacembelooids are more closely related to the synbranchiforms than to any other teleost; 5) The Sphyranoidei encompassing one family, the Sphyrnidae (barracudas; de Sylva, 1963), with elongate bodies and jutting jaws with strong fanglike teeth, and small gill rakers; 6) The Polynemoidei (threadfins) with a subterminal mouth; and 7) The Mugiloidei (mulletts), in which the oral dentition is often reduced and the pharyngeal jaw apparatus and gill rakers are modified to form a filtering device.

The Anabantoidei comprise five families, 16 genera and about 70 species. All anabantoids have accessory air breathing organs and possess a dual respiratory strategy: aquatic and aerial, the proportions of each depending on the oxygen and carbon dioxide content of the water, and the pH and temperature of the water. Anabantoids, as defined here, represent a monophyletic assemblage (Fig. 56) containing the Anabantidae (climbing gourmies), Belontiidae (gouramis, bettas and paradise fishes), Helostomatidae (kissing gouramis), Osphronemidae (giant gouramis), and the Luciocephalidae (pikehead). Monophyly is based on the following shared derived characters. 1) The suprabranchial air chamber is clearly separated from the buccopharyngeal cavity, and respiratory air is confined to the suprabranchial cavity (Fig. 57; Liem, 1981). Communication between the buccopharynx and suprabranchial cavity (Fig. 58) is by means of a) a pharyngeal opening protected by a valve which is derived from modified gill rakers and/or b) a branchial opening located between the first and second arches. (In the Luciocephalidae the pharyngeal opening is absent and communication between suprabranchial cavity and buccopharynx is restricted to the branchial opening.) 2) The principal organ for aerial respiration is supported by an enlarged and modified first epibranchial bone. 3) All members have the swimbladder extending posteriorly as far as the parhypural. 4) A distinct foramen

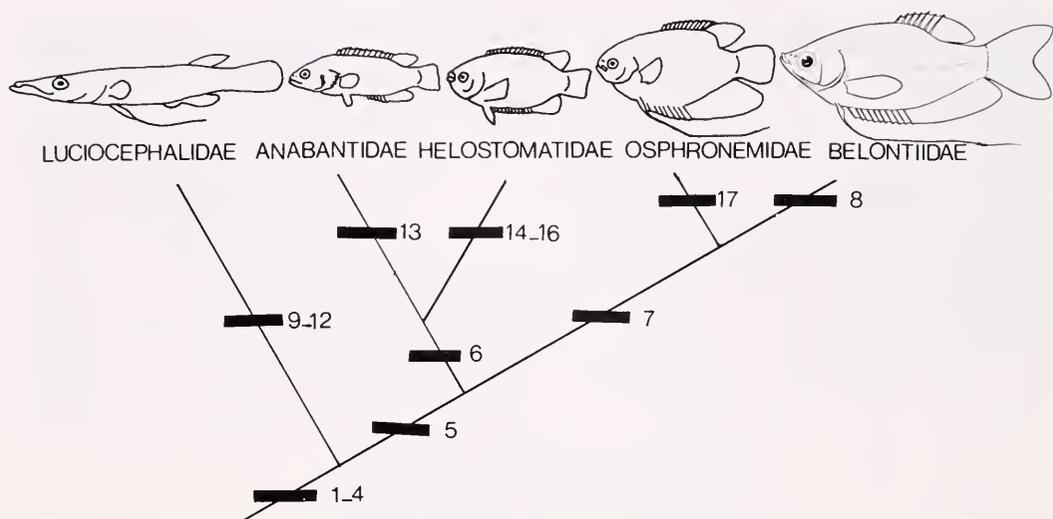


Figure 56. Interrelationships of the Anabantoidei based on the following specialized features: **1**, the suprabranchial air chamber is clearly separated from the buccopharyngeal cavity and respiratory air is confined to the suprabranchial cavity; **2**, principal organ for aerial respiration is supported by an enlarged and modified first epibranchial bone; **3**, swimbladder extends posteriorly into the tail as far as the parhypural (Liem, 1967a); **4**, a distinct foramen exoccipitale, covered by a tympanumlike membrane is present in the exoccipital bone; **5**, basioccipital with distinct pharyngeal processes (see Liem, 1963, Figs. 14–26, and 40–50); **6**, parasphenoid with very distinct transverse processes (Liem, 1963, Figs. 40–42, 44); **7**, parasphenoid with prominent, median ventrally directed pharyngeal process (Liem, 1963, Figs. 17, 19–93); **8**, loss of the ectopterygoid; **9**, median gular element present (Liem, 1967a); **10**, highly specialized premaxillae, lower jaw, and jaw protrusion mechanism (Lauder and Liem, 1981); **11**, dorsal and anal spines lost; **12**, no pharyngeal opening between the suprabranchial and buccopharyngeal cavities, and a specialized second adductor branchialis muscle running in the posterior margin of the floor of the suprabranchial cavity; **13**, fifth ceratobranchials are connected to each other to form a lower pharyngeal jaw, which bites against the toothed transverse process of the parasphenoid with the actions of the levatores posterior and externi muscles (Liem and Greenwood, 1981); **14**, the dentary rotates freely in the vertical plane around the articular; **15**, dentary and premaxillae are toothless; **16**, basibranchial with median, prominent, vertical, shelflike processes; **17**, a well-developed rostral fossa extending posteriorly nearly reaching the level of the posterior border of the orbit, formed by the ethmoid and frontals (Liem, 1963, Fig. 4).

exoccipitale, covered with a tympanumlike membrane overlying the sacculus, is present in the exoccipital bone (Liem, 1963, 1967), except in *Helostoma temminckii* and *Sandelia capensis*. Within the Anabantoidei we can recognize four major clades, each of which is defined by major specialized characters (Fig. 56). The Luciocephalidae (formerly classified as a separate order, e.g., Liem, 1963, or as a separate suborder, e.g., J. Nelson, 1976) represents a very specialized monotypic clade with numerous autapomorphic features (see Liem, 1967; Lauder and Liem, 1981; and Fig. 56). The Anabantidae, Helostomatidae, Osphronemidae, and Belontiidae possess distinct transverse processes of the basioccipital. The

Belontiidae have lost the ectopterygoid bone. On the basis of the characters summarized in Figure 56, the Anabantidae and Helostomatidae are considered sister groups, and so are the Osphronemidae and Belontiidae. This new hypothesis of the interrelationships of the Anabantoidei differs significantly from that proposed by Liem in 1963. The predominant mode of air ventilation in Anabantoidei is quadruphasic (Peters, 1978; Liem, 1980): First, the fish rises to the surface and exhales all the air by flushing out the entire air bubble from the suprabranchial cavity into the oropharynx and out of the mouth (Fig. 58). This is accomplished by a coughing-like mechanism, which produces a reversed water current entering

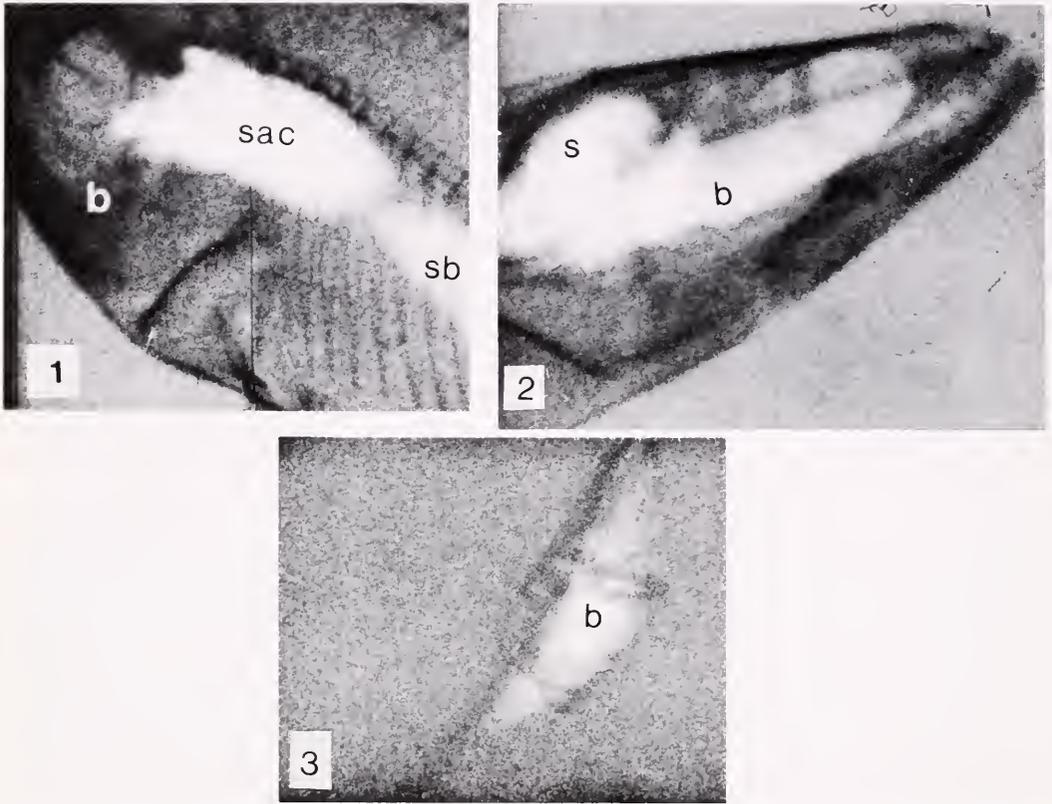


Figure 57. Prints of selected frames of x-ray film taken at 50 frames/sec. during the air breath in the anabantoid *Helostoma temminckii* (1), the channiform *Channa striatus* (2), and the synbranchiform *Monopterus albus* (3), to show where the respiratory air is stored in the live fish.

Abbreviations: b, buccopharyngeal cavity; s and sac, suprabranchial chamber; sb, gas bladder (swimbladder).

from underneath the gill cover into the suprabranchial cavity and then into the buccopharynx and out of the mouth. Exhalation is followed by inhalation during which air is compressed from the buccopharynx into the suprabranchial cavity via the pharyngeal and branchial openings. This pattern is found in all adult anabantoids except *Anabas*, which ventilates air triphasically: The fish rises to the surface and inhales air into the buccopharynx and compresses the air into the suprabranchial cavity (Liem, 1980). In this way "deoxygenated" air in the suprabranchial cavity escapes from underneath the gill cover and is replaced by fresh air (Liem, 1980; Peters, 1978). Adult

*Helostoma* is capable of both quadruphasic and diphasic patterns of air ventilation. In most anabantoids the male builds foam nests and engages in parental care. According to our data and hypothesis, the Channiformes (Ophicephaliformes) is not closely related to the Anabantoidei (see p. 178).

### The Scorpaeniformes

The order Scorpaeniformes containing 21 families, over 250 genera and about 1,000 species can be defined readily by two specializations: 1) In the skull a peculiar bony posterior extension of the third circumorbital (suborbital, infraor-

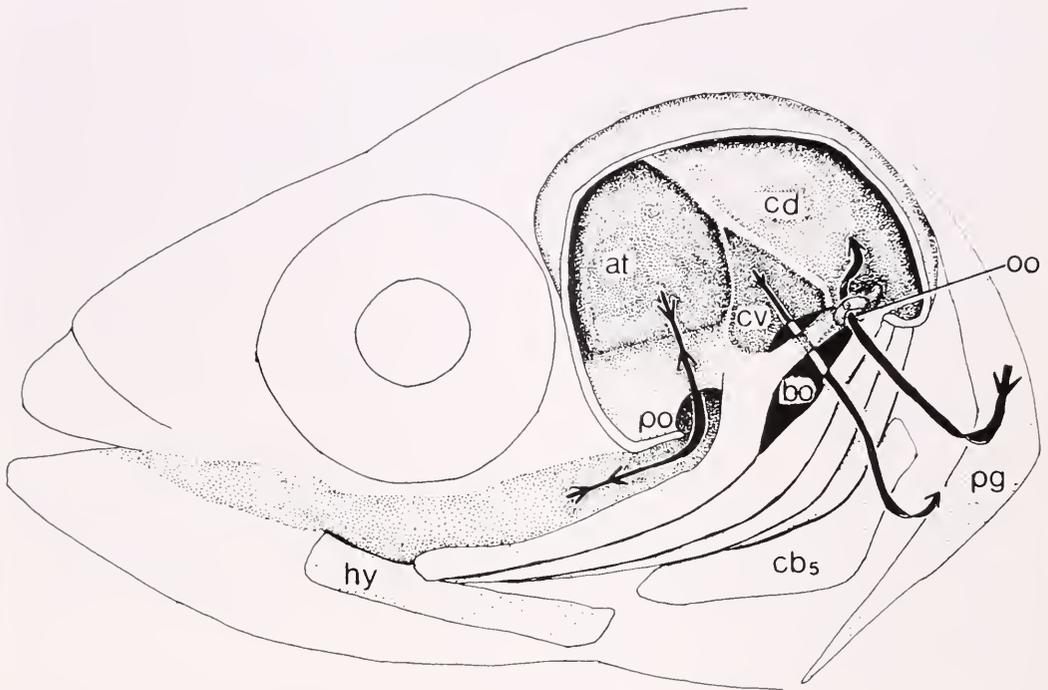


Figure 58. Lateral view of the suprabranchial cavity of a representative anabantoid fish after removal of the side of the head. Gills and "labyrinth organ" have been removed. Arrows indicate pathways for air and water. Structure over oo is a thickening of the operculum, shown here separately as a C-shaped sausagelike bulge. This bulge can be pressed tautly against the muscular process of the first epibranchial on which it lies, closing the opercular opening (oo). (From Liem [1980b], courtesy of Plenum Publishing Co.)

Abbreviations: at, atrium; bo, branchial opening;  $cb_5$ , fifth ceratobranchial; cd, caudodorsal compartment; cv, caudodorsal ventral compartment; hy, hyoid; oo, opercular opening; pg, pectoral girdle; po, pharyngeal opening in floor of the suprabranchial cavity.

bital) bone extends across the cheek to contact the outer surface of the preoperculum (Gutberlet, 1915; Rendahl, 1933); 2) In the caudal skeleton two platelike hypurals are sutured to the terminal half centrum. In general the scorpaeniform head and body tend to be spiny or bony-plated as a result of hypertrophied or otherwise specialized integumentary ossifications. The phylogenetic relationships of the scorpaeniforms are unknown (Fig. 50) and the internal classification is still chaotic (Quast, 1965). Provisionally, we subdivide the scorpaeniforms into four suborders. The Scorpaenoidei, which remains ill defined, containing among others, the Scorpaenidae (rockfishes; Eschmeyer, 1965, 1969; Eschmeyer and

Collette, 1966) with venom glands in the dorsal, anal, and pelvic spines and with internal fertilization as the dominant reproductive mode. The family contains about 60 genera with 330 species. The live-bearing genus *Sebastes* is the largest family with about 100 species. The Synanceiidae (stonefishes), has venom glands near the base of hypodermiclike dorsal fin spines and the neurotoxin of stonefishes is the most deadly of fish venoms (Halstead, 1970). The Triglidae (sea robins), have the lower two or three pectoral rays independent and greatly elongated. The Hexagrammoidei (greenlings and sablefishes), is a poorly defined taxon and greenlings constitute the richest family endemic to the North Pacific. The Platy-

cephaloidei (flatheads; Matsubara and Ochiai, 1955) have a very depressed head. The Hoplichthyidae (ghost flatheads) and Congiopodoidei (pigfishes) represent two small suborders of unknown phyletic status. The Cottoidei, which can be characterized by the loss of the basisphenoid bone, contain, among others, the Cottidae (sculpins, Bolin, 1947; Watanabe, 1960) with over 65 genera with about 300 species, Agonidae (poachers), and Cyclopteridae (lumpfishes and snailfishes).

### Channiformes (Ophiocephaliformes) and Synbranchiformes

We will discuss the Channiformes (snakeheads) in conjunction with the Synbranchiformes (swamp eels, rice eels), in order to emphasize our hypothesis that the two orders are closely related to each other. Travers (personal communication) has put forward a hypothesis in which the Mastacembeloidei are included in the Synbranchiformes. In most previous classifications the Channiformes is considered to be closely related to the Anabantoidei on the basis of the presence of a modified first epibranchial as a support for the accessory air breathing organ. Here we will present data refuting the hypothesis that the Channiformes is a sister group of the Anabantoidei and formulate a competing hypothesis that the Channiformes are closely related to the Synbranchiformes. First we will define the Channiformes and Synbranchiformes and then discuss the relationships of the two groups.

*The Channiformes.* This assemblage contains only one genus *Channa* (*Ophiocephalus*, *Ophiocephalus*; Myers and Shapovalov, 1931). All species are relatively large predaceous fishes (15 cm–1.2 m) with elongate bodies, long dorsal and anal fins and no fin spines. They are capable of breathing air. Because many inaccuracies concerning the cranial osteology continue to be repeated in recent literature, we present several illustra-

tions of the skull (Fig. 59) in order to define the Channiformes more accurately. Contrary to previous accounts (Day, 1914; Bhimachar, 1932; Gregory, 1933; Liem, 1963), the frontals of channiforms do not articulate with the parasphenoid (Fig. 59) and the metapterygoid (Fig. 59) does not articulate with the frontal and sphenotic. The channiforms can be defined by the following apomorphies: 1) The otic bulla for the sacculith is mostly contained in the prootic bone (Fig. 59). 2) The metapterygoid has an anterodorsally directed prominent uncinat process which approaches the neurocranium. It seems that the presence of this uncinat process of the metapterygoid has led to the misconception that an articulation between the palatoquadrate and neurocranium exists. Actually the process serves as an attachment of a strong, flat tendon of the massive levator arcus palatini muscle. The process is more prominent in larger specimens but does not achieve physical contact with the neurocranium. 3) Two ventral aortae emerge separately from the bulbus arteriosus (Ishimatsu *et al.*, 1979). The anterior ventral aorta supplies the first and second branchial arches, while the posterior ventral aorta gives rise to the third and fourth branchial arches, which are associated with the systemic circulation. 4) The accessory air breathing organs are the buccopharyngeal epithelium, the lining of the suprabranchial cavity, and the respiratory nodules on the first and second epibranchials, the hyomandibula and parasphenoid. The suprabranchial cavity is in open communication with the buccopharyngeal cavity (Liem, 1980b). Consequently air is present in both the buccopharyngeal and suprabranchial cavities (Fig. 57). 5) The first epibranchial is a greatly expanded plate, which is not folded, and is suspended by a very small first pharyngobranchial bone (Fig. 59).

*The Synbranchiformes.* The synbranchiformes (swampeels) comprise one family, the Synbranchidae, composed of

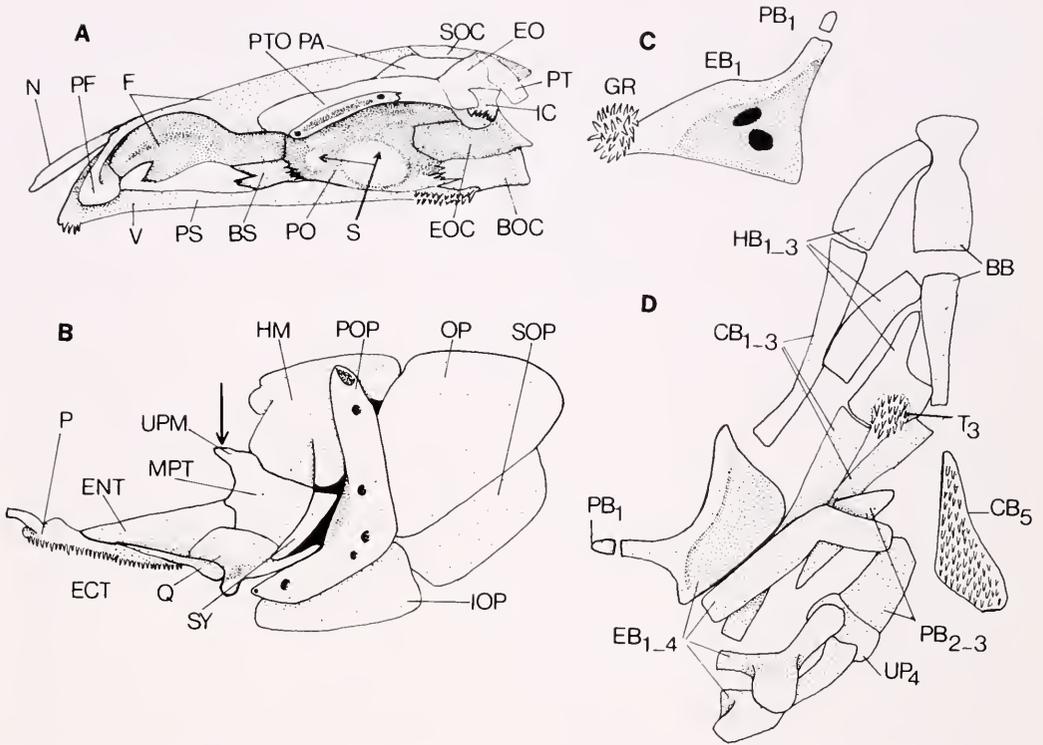


Figure 59. Osteology of the skull of a representative Channiform, *Channa striatus*. A. Lateral view of the neurocranium. B. Lateral view of suspensory and opercular apparatus. C. Ventrolateral view of first epibranchial bone. D. dorsal view of gill arches.

**Abbreviations:** BB, basibranchial; BOC, basioccipital; bs, basisphenoid; CB<sub>5</sub>, fifth ceratobranchial; EB<sub>1-4</sub>, epibranchials 1-4; ECT, ectopterygoid; ENT, entopterygoid; EO, epiotic; EOC, exoccipital; F, frontal; GR, gill raker on first epibranchial bone; HB<sub>1-3</sub>, hypobranchials 1-3; HM, hyomandibula; IC, intercalary; IOP, interoperculum; MPT, metapterygoid; N, nasal; OP, operculum; P, palatine; PA, parietal; PB<sub>1-3</sub>, pharyngobranchials 1-3; PF, lateral ethmoid complex; PO, prootic; POP, preoperculum; PS, parasphenoid; PT, posttemporal; PTO, pterotic; Q, quadrate; S, otic bullae; SOC, supraoccipital; SOP, suboperculum; SY, symplectic; T<sub>3</sub>, toothplate on third hypobranchial; UP<sub>4</sub>, upper toothplate of fourth branchial arch; UPM, uncinat process of metapterygoid; V, vomer.

4 genera (*Macrotrema*, *Ophisternon*, *Synbranchus* and *Monopterus*) with 15 species (Rosen and Greenwood, 1976). Travers (personal communication) includes the Mastacembeloidei within this order. This very specialized assemblage is unquestionably monophyletic and shares the following specializations: Eel-shaped fishes without pectoral fins in the adults, no pelvic fins or girdles and dorsal or anal fins. The gill membranes are united and continuous around the isthmus. In the uniquely specialized neurocranium the frontal bones are turned

down and sutured to the basisphenoid (Rosen and Greenwood, 1976) and the large parietals meet in the midline. Synbranchiforms are the only teleosts with the suspensorium (palatoquadrate) articulating with a prominence on the basisphenoid, frontal or both, and with the vomer and lateral ethmoids, making the jaw suspension "amphistylic." The anterior and posterior nares are separated by a long distance, and are associated with an elongate nasal sac containing a highly developed nasal rosette. The circulatory system is remarkably specialized (Liem,

1961; Rosen and Greenwood, 1976) with a complete fourth aortic arch, which has important functional implications. Most synbranchiforms are protogynous hermaphrodites (Liem, 1968), are amphibious (Liem, 1967; Johansen, 1966), and have uniquely modified urinary bladders, which may function in the reabsorption of water when the fish is on land (Liem, in preparation). The larvae of some synbranchiforms have a special vascular specialization and large pectoral fins to exploit the oxygen-rich surface layer by creating an effective counter current of the blood stream and the respiratory current to maximize gas exchange (Liem, 1981). Thus the synbranchiforms are among the most specialized teleosts known in terms of skull structure, respiratory and vascular design, reproduction, development, and ecology.

*Synbranchiform-Channiform Relationships.* We offer a hypothesis that the Synbranchiformes and Channiformes are closely related to each other. Sister group relationships of the channiforms and synbranchiforms (excluding the Alabetidae or Cheilobranchidae, which are Gobiociformes, p. 156) are based on the following synapomorphies. 1) The brain is elongate and the forebrain is characteristically modified by a fusion of the left and right hemispheres in the posterior half (van der Horst, 1918). The fusion occurs at the level where the sulcus ypsilanti stops. Anterior to this point a deep fissure between left and right hemispheres is present. The extensive cross-connection (commissure) of the posterior halves of the left and right hemispheres of the forebrain (Fig. 60) is a highly specialized feature occurring only in the channiforms and synbranchiforms among teleosts (van der Horst, 1918). In outgroups the left and right hemispheres of the forebrain are separated. In general, the brains of channiforms and synbranchiforms resemble each other very closely, except that the optic lobes of the channiforms are much larger than those

of the synbranchiforms (Fig. 60). Such a difference can be correlated with the fact that channiforms are large-eyed visual fishes, while synbranchiforms have drastically reduced vision. 2) The adductor mandibulae complex is specialized in several ways. The entire complex is hypertrophied (Fig. 61). In synbranchiforms the adductor mandibulae part  $A_1$  is no longer inserted on the maxilla and, instead, is attached to the mandible (Van Conner, 1966; Liem, 1980c). However, in the most primitive synbranchiform, *Macrotrema caligans*, the adductor mandibulae part  $A_1$  is still inserted on the maxilla by means of a tendon on the lateral surface of the maxilla, in the middle of the ramus, as is the case in all channiforms. Such an insertion of  $A_1$  on the ramus way below the maxillary head and halfway along the shaft of the bone is a specialization shared with all channiforms (Fig. 61). It is hypothesized that in advanced synbranchiforms the insertion of the maxilla is lost. In channiforms, the  $A_1$  is also associated with a muscle that inserts on the mandible (Fig. 61). The channiforms and synbranchiforms also share a specialization of the adductor mandibulae part  $A_2$ , which occupies the most anterior position just behind the orbit, and completely overlies other muscles (Fig. 61). In both groups, the fiber direction, topography, hypertrophy, and insertion of  $A_2$  on the ascending process of the dentary are identical. Further evidence that the synbranchiforms and channiforms are sister groups is the forward position of the orbits and the modified fourth aortic arch. In channiforms and the primitive *Macrotrema* the fourth aortic arch is composed of functionally almost continuous afferent and efferent branchial arteries which are connected by arterial loops (Ishimatsu *et al.*, 1979). In advanced synbranchiforms the fourth aortic arch is structurally and functionally one continuous vessel responsible for the systemic circulation. Both the Channiformes and Synbranchiformes (except for *Macrotrema*) use the bucco-

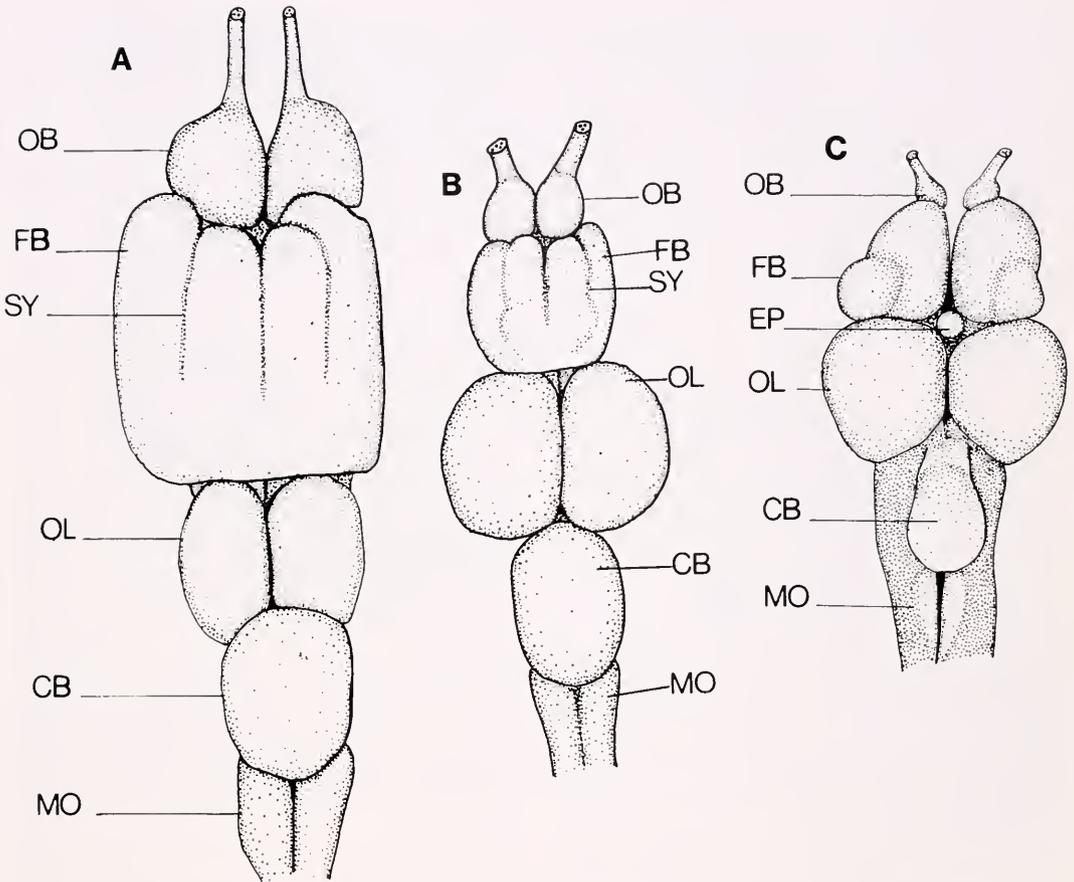


Figure 60. Dorsal views of the brains of: A. a primitive synbranchiform *Macrotrema caligans*. B. the channiform *Channa striatus*. C. the gobiesociform *Alabes dorsalis*. In A and B the forebrains are specialized in having the left and right halves coalesced posteriorly, while in C the primitive state of completely separated forebrain hemispheres is represented. Abbreviations: CB, cerebellum; EP, epiphysis; FB, forebrain; MO, medulla oblongata; OB, olfactory bulbs; OL, optic lobes; SY, sulcus ypsilanti.

pharyngeal epithelium and the linings of outpocketings of the buccopharynx (e.g., *Monopterusuchia*, all channiforms) for gas exchange with atmospheric air. These outpocketings maintain a continuously open communication with the buccopharynx.

Both groups have enlarged mesopterygoids (or entopterygoids). In channiforms (Fig. 59) the large mesopterygoid is very closely associated with the large toothed palatine and the small toothless ectopterygoid. Rosen and Greenwood

(1976: 45–48) imply that the mesopterygoid in synbranchiforms is missing and that the ectopterygoid is large and toothed. Such an interpretation seems unlikely, if synbranchiforms and channiforms are sister groups. The topographical features of the bone in the synbranchiforms and the condition of the element in the channiforms indicate that the bone in synbranchiforms is an enlarged mesopterygoid (as in channiforms). The ectopterygoid is present as a small toothless element (Fig. 59). The olfactory rosette

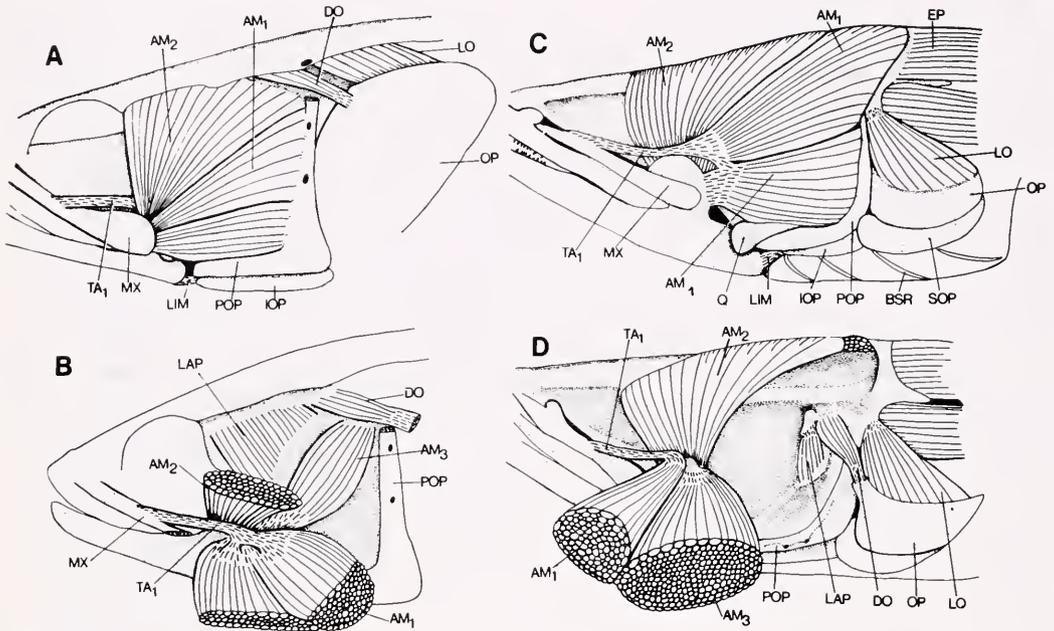


Figure 61. Lateral view of the main jaw musculature in: A and B, a representative channiform (*Channa striatus*); C and D, a primitive synbranchiform (*Macrotrema caligans*). A and C show the superficial musculature; B and D depict the deep jaw musculature.

**Abbreviations:** AM<sub>1</sub>, part A1 of the adductor mandibulae complex; AM<sub>2</sub>, part A2 of the adductor mandibulae complex; AM<sub>3</sub>, part A3 of the adductor mandibulae complex; BSR, branchiostegal ray; DO, dilator operculi; EP, epaxial muscle; IOP, interoperculum; LAP, levator arcus palatini; LIM, interoperculomandibular ligament; LO, levator operculi; MX, maxilla; OP, operculum; POP, preoperculum; Q, quadrate; SOP, suboperculum; TA, tendon of part A<sub>1</sub> of the adductor mandibulae complex.

in both groups is enlarged and has undergone complex elaborations.

The synbranchiforms differ from the channiforms in several important ways: Synbranchiforms have a greatly reduced levator arcus palatini muscle, which is hypertrophied in channiforms (Fig. 61). Synbranchiforms have an ossified interarcual cartilage while channiforms lack such an ossification, but have an expanded first epibranchial bone (Fig. 59). The heart of channiforms is located near the gill arches and shows a generalized structural configuration, while in synbranchiforms the heart is located far posteriorly (Liem, 1961), and its structural configuration deviates significantly from that of other teleosts. Finally, channiforms have a large swimbladder with a distinct cau-

dal extension, while a swimbladder is lacking in synbranchiforms.

The channiforms are traditionally aligned with the anabantoids rather than with the synbranchiforms. Based on the above-mentioned synapomorphies, we hypothesize that channiforms may represent the plesiomorphic sister group of the synbranchiforms. With the available evidence we have not been able to establish sister group relationships of the channiforms with the anabantoids. Recently, Travers (1981) has described the presence of an ossified interarcual cartilage in the Carapidae, raising the question of possible synbranchiform-carapid relationships. However, the forebrain, the heart and aortic arches, the adductor mandibulae complex, and the urogenital

anatomy of the Carapidae are all in their primitive state. Thus, carapid-synbranchid relationships have not been established.

### The Tetraodontiformes

This order dates back to the lower Eocene and is also known as the Plectognathi. It comprises about 320 species of mostly shallow water, circumtropical, and subtropical marine forms (Tyler, 1980). Tetraodontiforms are morphologically much more diversified than the great majority of fish groups of a comparable number of species. They range from 22 mm and 30 g to 2 m and 1,000 kg, from relatively normal shapes to strangely specialized forms with long tubular snouts and aborted caudal regions, from scaleless to heavily armored. Because tetraodontiforms show striking examples of extreme reductive evolution and represent one of the major end lines of the teleost radiation, the group is of considerable biological interest.

The tetraodontiforms are thought to represent a monophyletic assemblage based on the following characters (Tyler, 1980; Fig. 62). 1) The entire branchiostegal region is covered by a thick layer of scaleless or scaled skin, 2) The gill opening is greatly restricted and does not extend far below the base of the pectoral fin, 3) All members have lost the suborbital (circumorbital) bones, parietals, nasals, sensory canals in the skull bones, and anal fin spines.

Unfortunately the primitive sister group of the Tetraodontiformes remains unknown, although preliminary observations (Patterson, 1964; Tyler, 1968) indicate that it is the Acanthuroidei among the Perciformes. The Balistidae, Acanthuroidei and the berciform Pharmacichthyidae (Patterson, 1964) share a much elongate preorbital region of the neurocranium (as long as the lengths of the orbit and postorbital neurocranium combined), a ventrally bent parasphenoid in

front of the orbit, a very small mouth, a long, strongly inclined suspensorium, and a very long and slender pelvic girdle, which ends between the much expanded coracoids. Actually it has been suggested (Patterson, 1964) that because adult balistids resemble larval acanthuroids, they may have been derived from acanthuroids by pedomorphosis. The phylogenetic scheme of the Tetraodontiformes presented here (Fig. 62) is tentative (Winterbottom, 1974b; Tyler, 1980) and awaits corroboration by the combined studies of R. Winterbottom and J. C. Tyler now in progress.

The Triacanthodidae (spikefishes) and Triacanthidae (triplespines) are considered sister groups of the lineage called Sclerodermi. The pelvis has large pelvic spines which can be locked, and the following pelvic muscles are hypertrophied: arrector dorsalis pelvici, arrector ventralis pelvici, and adductor superficialis pelvici. The remaining six families share the single levator operculi and a distinct medial subdivision of the sternohyoideus muscle.

The Balistidae (triggerfishes and filefishes) and Ostraciidae (Ostraciotidae; boxfishes, trunkfishes and cowfishes) represent sister groups sharing the following specializations: The development of a deep A<sub>1</sub> subdivision of the adductor mandibulae complex, and the presence of a distinct retractor arcus palatini muscle (Winterbottom, 1974b). Some trunkfish produce ostracitoxin, which will kill other fishes in confined quarters.

The Triodontidae (three-toothed puffer), the lineage representing the Tetraodontidae (puffers) and Diodontidae (porcupine fishes), and the Molidae (molas) are tentatively represented by an unresolved trichotomy. All share the following specializations: 1) The loss of the intermandibularis and sternobranchialis muscles; 2) The A<sub>1</sub> part of the adductor mandibulae complex acquires an attachment to the prefrontal region of the skull; and 3) the A<sub>2</sub> part of the adductor man-

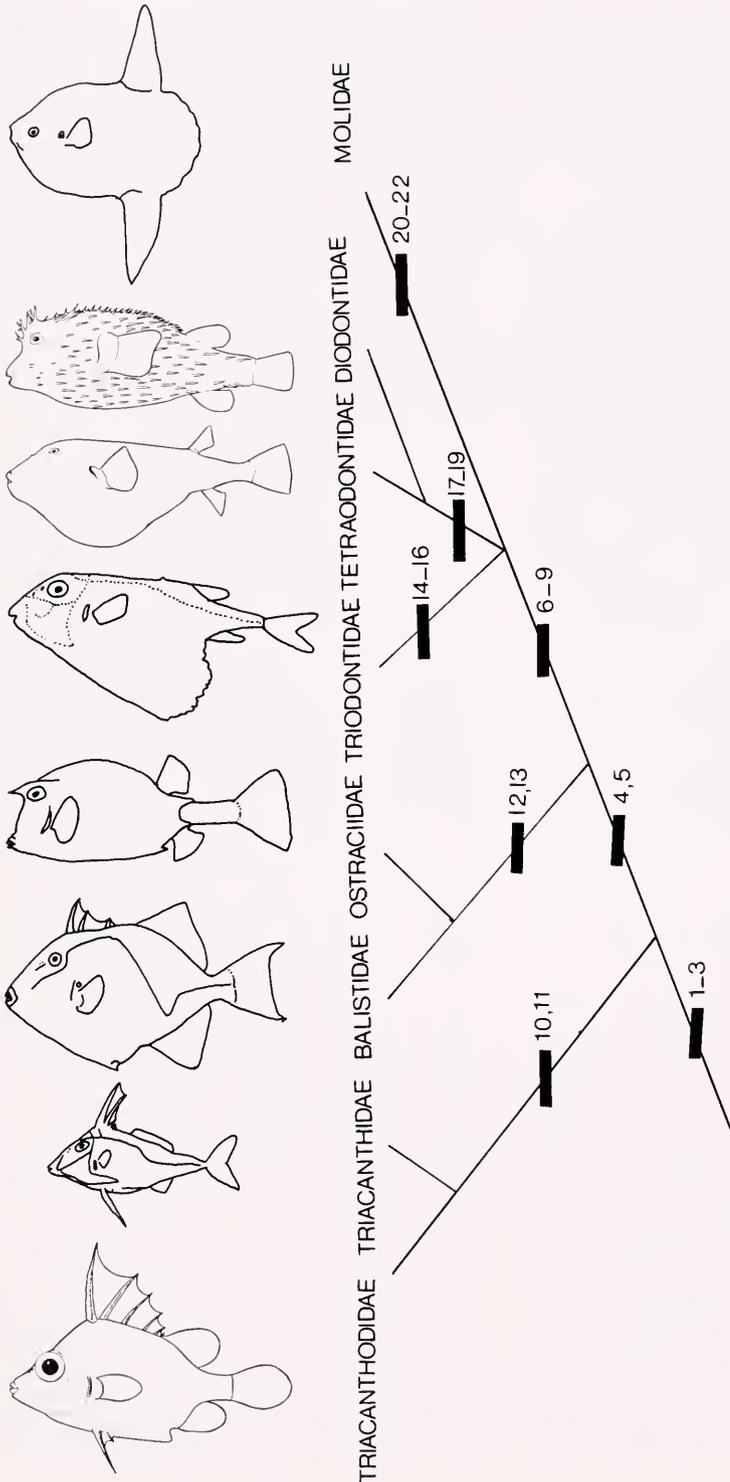


Figure 62. Interrelationships of the tetraodontiform fishes on the basis of the following specialized features: **1**, the entire branchiostegal region is covered by a thick layer of skin; **2**, the greatly restricted gill opening does not extend far below the base of the pectoral fin; **3**, suborbital bones, parietals, nasals, sensory canals in the skull bones and anal fin spines are absent; **4**, only a single levator operculi is present; **5**, a distinct medial subdivision of the sternohyoideus is present; **6**, the intermandibularis and sternobranchialis muscles are lost; **7**,  $A_1$  muscle acquires an attachment to the prefrontal region of the skull; **8**,  $A_1$  muscle is expanded dorsally and medially above  $A_3$  to include the parasphenoid and prootic as the sites of origin; **9**, teeth are either small rounded units or long rodlike structures; **10**, pelvis with large pelvic spines, which can be locked in position; **11**, hypertrophy of the arrector dorsalis pelvificus, arrector ventralis pelvificus, and adductor superficialis pelvificus muscles; **12**, a distinct retractor arcus palatini muscle is present; **13**, differentiation of a deep  $A_1$  muscle in the adductor mandibulae complex; **14**, cleithrum greatly elongate reaching forward underneath the lower jaw; **15**, a huge expansible dewlap of skin is present between the end of the pelvis and anus; **16**, presence in the spiny dorsal fin of one or two small spines borne on two basal pterygiophores; **17**, an inflatable diverticulum of the gut is present; **18**, fourth gill arch is lost and there is no gill slit between it and the fifth arch; **19**, muscle fibers from the dilator operculi insert on the interoperculum, preoperculum and suboperculum; **20**, only a single ovary is present; **21**, otoliths are presumably lost; **22**, caudal region with numerous structural and functional specializations creating a unique mode of locomotion.

dibulae complex is expanded dorsally and medially above  $A_3$  to include the parasphenoid and prootic as sites of origin. Each lineage of the unresolved trichotomy can be defined by synapomorphies (Fig. 62).

### The Pleuronectiformes

The flat fishes represent a very specialized assemblage dating back to the Eocene. Pleuronectiformes (Heterosomata) contain 6 families, over 500 species and approximately 115 genera (Norman, 1934; Hubbs, 1945; Amaoka, 1969). All flatfishes are benthic and carnivorous.

The coherence of the pleuronectiforms as a monophyletic entity is based on the asymmetrical position of the eye. The condition wherein both eyes are on the same side of the head is clearly a derived one relative to all other vertebrates (Chabanaud, 1936, 1938). However, the position of the pleuronectiforms in relation to other major fish groups and the phylogenetic relationships within the order are still problematic.

Here we offer a tentative phylogenetic hypothesis of the Pleuronectiformes (Fig. 63). We recognize eight families, even though their delineation is often unclear. The most primitive family is the Psettodidae, with one genus *Psettodus* and two species, which retain the primitive character of the dorsal fin not extending onto the head (Fig. 63). No specialized characters set this family aside from the other seven.

All other seven families share the specialization of the loss of the following structures: palatine teeth, basihyal teeth, dorsal fin spines, and anal fin spines; the dorsal fin extends onto the head (Fig. 63). Among this lineage, the Citharidae (citharids; Hubbs, 1945) is the most primitive member and can be distinguished by the fact that the anus is deflected onto the eyed side. In the remaining six families the pelvic spines are lost (Fig. 63). Of the pelvic spineless members the Scopthalmidae may be the plesiomorphous group

since the other five families are further specialized by the loss of vomerine teeth and having the branchiostegal membranes fused to one another rather than overlapping. The relationships between the Pleuronectidae (righteyed flounders; Norman, 1934) and the Bothidae (left-eyed flounders; Chabanaud, 1940) are still uncertain. The Rhombosoleidae shares the loss of a postcleithrum with the Soleidae and Cynoglossidae (Fig. 63), which are considered the most specialized members of the Pleuronectiformes. The Soleidae (soles) and Cynoglossidae (tonguefishes, tongue soles; Menon, 1977) are considered sister groups since both groups have lost their ribs and have the gill covers bound to one another across the throat by a thick layer of tough skin, which covers both the gill covers and the throat in between. Cynoglossids (Chabanaud, 1940) have pectoral fins without rays, becoming either unsupported membranous structures or lost altogether.

The phylogenetic interrelationships as hypothesized here are still problematic since they are based mostly on reductive characters. It is clear that further studies are needed to determine the phyletic relationships of the members of the Pleuronectiformes with greater confidence.

### CONCLUSIONS

In this paper we have attempted to summarize current knowledge of the interrelationships of the ray-finned fishes. After more than a century of intensive study many of the major actinopterygian taxa remain poorly delimited and several cannot be defined by any uniquely derived characters (e.g., the Percomorpha). In providing a critical review of certain key aspects of actinopterygian evolution we have sought also to point out those areas where future research is badly needed. Above all, we consider that characters and their distributions must be the focus of a research program in actinopterygian phylogeny if progress is to be made. Theories of ancestry and descent,

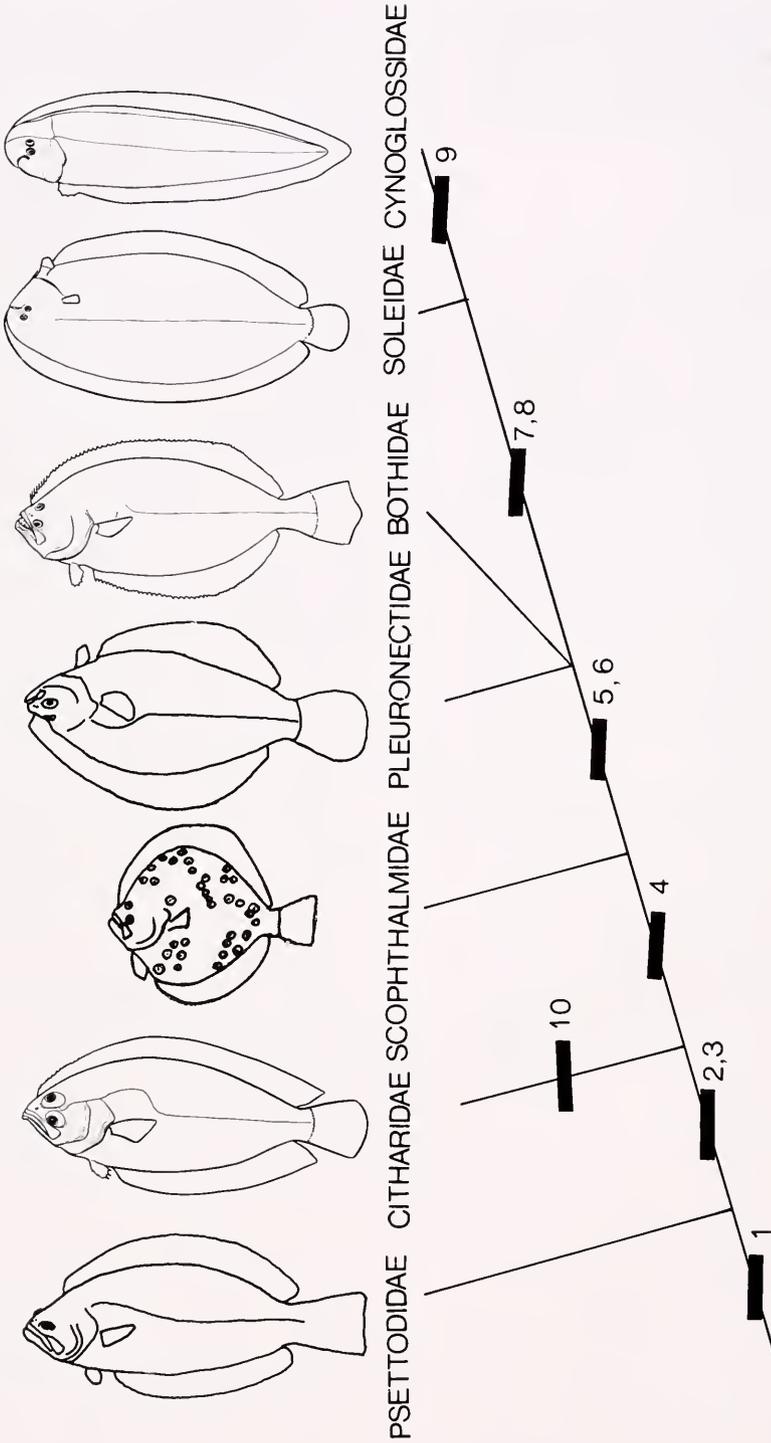


Figure 63. Interrelationships of the major lineages of the flatfishes (Pleuronectiformes) based on the following specialized characters: 1, both eyes on the same side of the head; 2 loss of palatine teeth, basihyal teeth, dorsal spines and anal fin; 3, dorsal fin extends onto the head; 4, the spines of the pelvic fin are lost; 5, vomerine teeth are lost; 6, branchiostegal membranes from the left and right sides are fused; 7, the postcleithrum is lost; 8, ribs are lost; 9, rayed pectoral fins absent; 10, deflection of the anus onto the eyed side.

specialization, trends, "adaptive" radiation, and patterns of functional evolution should be founded on a corroborated set of statements about phylogenetic patterns of structural features. The emphasis on theories of process and evolutionary transformation, for example, has obfuscated the analysis of tetrapod origins throughout this century (Patterson, 1980; Rosen *et al.*, 1981).

If progress in this decade continues at the rapid pace with which problems in ray-finned fish evolution have been solved in recent years, actinopterygians will soon be a model group for the analysis of evolutionary patterns and processes.

#### ACKNOWLEDGMENTS

We thank W. L. Fink, S. Fink, P. H. Greenwood, L. Parenti, and M. Stiassny for critically reading the manuscript and for their helpful comments. G. Howes and R. Travers discussed several parts of this paper with us, and we especially thank M. Stiassny for her cooperation, comments, and unpublished data. We are grateful to S. Fink, W. L. Fink, P. H. Greenwood, D. E. Rosen, C. Patterson, and especially J. S. Nelson for permission to reprint and/or modify illustrations from their papers. We are greatly indebted to: Christine Fox for her skills and patience in typing many versions of this manuscript and assistance in literature searches; Karsten Hartel has been instrumental in improving many key aspects of the manuscript; Karel Liem did the lettering of many of the figures; Elizabeth Campbell Elliott for her editorial efforts. The Milton Fund of Harvard University has provided support for reproducing the illustrations. George Lauder was supported by the Penrose Fund of the American Philosophical Society, a Louis Block Fund Award from the University of Chicago, the Andrew W. Mellon Foundation, The Whitehall foundation, and National Science Foundation DEB 81-15048. Karel Liem was supported in part by a fellowship from the John Guggenheim Me-

morial Foundation and Grants PCM 80-03874 and DEB 82-06888. An early and greatly condensed version of this paper appears in *Fish Neurobiology and Behavior* (Lauder and Liem, in press), courtesy of R. Davis and R. G. Northcutt. Publication costs of this study were covered in part by a grant from the Wetmore Colles Fund.

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