Patterns of Evolution in the Feeding Mechanism of Actinopterygian Fishes¹

George V. Lauder

Department of Anatomy, University of Chicago, Chicago, Illinois 60637

SYNOPSIS. Structural and functional patterns in the evolution of the actinopterygian feeding mechanism are discussed in the context of the major monophyletic lineages of ray-finned fishes. A tripartite adductor mandibulae contained in a maxillary-palatoquadrate chamber and a single mechanism of mandibular depression mediated by the obliquus inferioris, sternohyoideus, and hyoid apparatus are primitive features of the Actinopterygii. Halecostome fishes are characterized by having an additional mechanism of mandibular depression, the levator operculi-opercular series coupling, and a maxilla which swings anteriorly during prey capture. These innovations provide the basis for feeding by inertial suction which is the dominant mode of prey capture throughout the haleco stome radiation. A remarkably consistent kinematic profile occurs in all suction-feeding halecostomes. Teleost fishes possess a number of specializations in the front jaws including a geniohyoideus muscle, loss of the primitive suborbital adductor component, and a mobile premaxilla. Structural innovations in teleost pharyngeal jaws include fusion of the dermal tooth plates with endoskeletal gill arch elements, the occurrence of a pharyngeal retractor muscle, and a shift in the origin of the pharyngohyoideus. These specializations relate to increased functional versatility of the pharyngeal jaw apparatus as demonstrated by an electromyographic study of pharyngeal muscle activity in Esox and Ambloplites. The major feature of the evolution of the actinopterygian feeding mechanism is the increase in structural complexity in both the pharyngeal and front jaws. Structural diversification is a function of the number of independent biomechanical pathways governing movement.

INTRODUCTION

The evolution of the feeding mechanism in ray-finned fishes (Actinopterygii) provides perhaps the best documented example in the Vertebrata of change in a structurally and functionally complex system. In the twenty years since the last review of the evolution of the feeding mechanism in ray-finned fishes (Schaeffer and Rosen, 1961), knowledge of both the historical pattern of diversification and the relation between structure and function has increased tremendously. Phylogenetic analyses of actinopterygian evolutionary patterns have provided an excellent baseline of information on the historical sequence of structural change (Greenwood et al., 1966, 1973; Patterson, 1977, 1982; Patterson and Rosen, 1977; Rosen, 1982), and as the discipline of experimental functional morphology has developed, a corresponding increase has occurred in the analysis of the relationship between form

and function in fishes and in the proposal and testing of functional explanations for structure (Alexander, 1966, 1967, 1970; Anker, 1974; Lauder, 1979; Liem, 1970; Osse, 1969). Functional analysis has become increasingly sophisticated and techniques such as high-speed cinematography (Elshoud-Oldenhave and Osse, 1976; Grobecker and Pietsch, 1979; Nyberg, 1971), electromyography (Ballintijn et al., 1972; Lauder, 1980a; Liem, 1973; Liem and Osse, 1975; Vandewalle, 1979), strain gauges (Lauder and Lanyon, 1980), and pressure transducers (Alexander, 1970; Lauder, 1980b, c; Osse and Muller, 1981) have largely obviated the need to base functional considerations on manipulations of preserved or freshly dead specimens. As a result, many hypotheses about the functional significance of morphological features in the actinopterygian skull have been tested, and many previously unsuspected relationships have emerged.

In this paper, I will focus on structural and functional specializations in the evolution of the actinopterygian feeding mechanism as they are reflected in nested sets of monophyletic lineages. I will em-

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FIG. 1. Structural network in the head of a primitive actinopterygian (A), a primitive halecostome (B), and a percomorph (C) to show the biomechanical pathways governing mouth opening, suction feeding, and jaw protrusion functions. Homologous biomechanical pathways are similarly numbered. Note the increase in complexity of the structural network in actinopterygian evolution. Only the function of jaw protrusion is shown in (C); the primitive functions of mouth opening and suction feeding are omitted for clarity. Solid rectangles = bony elements; dashed rectangles = ligaments; parallelograms = muscles. Arrows run from the muscle to the bone of insertion; doubleheaded arrows indicate ligamentous connections between bony elements. Three dimensional rectangles indicate major functions which are realized (r, arrows) by the biomechanical couplings indicated. This figure is not the same as the diagrams depicting the pattern of interrelationships and functional influences (see Dullemeijer, 1974, Fig. 62). Abbreviations: AM1, division A1 of the adductor mandibulae: AOP,



FIG. 2. Reconstruction of the superficial lateral (A) and ventral (B) cranial musculature in the paleonisciform fish Moythomasia nitida Gross. Osteological elements modified after Jessen (1968). The anterior branchiostegal rays have been removed in the ventral view to show the reconstructed throat musculature, and the maxilla in the lateral view has been partially removed to reveal the adductor musculature. The paired sternohyoideus muscles lie deep to the intermandibularis posterior and interhyoideus and are not visible in this view. This reconstruction results from deducing the most parsimonious primitive arrangement of adductor muscle character states in living actinopterygians. Abbreviations: AMa, anterior (suborbital) division of the adductor mandibulae; AMm, medial adductor division; AMp, posterolateral adductor division; BM, branchiomandibularis muscle; CL, cleithrum; CLAV, clavicle; EP, epaxialis; IH, interhyoideus; IMp, intermandibularis posterior muscle; IO, infraorbital bone; MD, mandible; MX, maxilla; OBI, obliquus inferioris; OBS, obliquus superioris; OP, operculum; POP, preoperculum.

adductor operculi muscle; EM, epaxial muscles; HY, hypaxial (obliquus inferioris) musculature; IHL, interoperculohyoid ligament; IML, interoperculomandibular ligament; LAP, levator arcus palatini muscle; LOP, levator operculi muscle; MHL, mandibulohyoid ligament; SH, sternohyoideus muscle.

phasize characteristic features of the Actinopterygii, Halecostomi, Teleostei, Neoteleostei, and Percomorpha with the goal of suggesting certain general propositions about the nature of change in structural and functional networks within lineages (also see Lauder, 1981).

PRIMITIVE FEATURES OF THE Actinopterygian Feeding Mechanism

Mouth opening in primitive actinopterygians is mediated by two musculoskeletal couplings (Figs. 1A, 2): the epaxial muscles-neurocranium coupling which elevates the head (Fig. 1A: coupling 2), and a ventral coupling involving the hypaxial musculature, cleithrum, sternohyoideus, and hyoid apparatus (Fig. 1A: coupling 1) which causes mandibular depression. Depression of the lower jaw is effected by retraction of the hyoid apparatus (by the sternohyoideus and obliquus inferioris muscles) which exerts a posterodorsal force on the mandible via the mandibulohyoid ligament (Fig. 1A: MHL). This posterodorsal force is applied at the insertion of the mandibulohyoid ligament ventral to the quadratomandibular articulation and thus causes mandibular depression (also see Lauder, 1980a, Fig. 18; 1980d). This mechanism of mandibular depression is also found in lungfishes, coelacanths, and sharks and is thus primitive for the Teleostomi.

A reconstruction of the jaw musculature in a palaeoniscoid is illustrated in Figure 2. Laterally, the adductor mandibulae is divided into three divisions: an anterior (suborbital) division, a medial division, and a posterolateral division (Fig. 2A). These three adductor components are hypothesized to be homologous with similarly located muscle divisions in Polypterus, Lepisosteus, and Amia (see Lauder [1980a, e] for a more extensive discussion of muscle homologies). An intramandibular adductor (Aw) occupies the mandibular adductor fossa. Ventrally, the paired sternohyoideus muscles extend anteriorly to insert on the urohyal. A flat, wide intermandibularis posterior spans the mandibular rami (Fig. 2B: IMp) and the interhyoideus extends anteriorly from the ceratohyal and dorsal surface of the branchiostegal rays to insert in the fascia dorsal to the intermandibularis posterior. The hyohyoideus musculature of halecostomes appears to be derived from the interhyoideus muscle fibers of primitive actinopterygians (Fig. 2B: IH).

The skull of primitive actinopterygians possesses only a few mobile elements (Blot, 1978; Saint-Seine, 1956). The maxilla and premaxilla are firmly attached to the other dermal skull bones and the opercle, subopercle, and branchiostegal rays have limited lateral mobility. The oblique angle of the suspensory apparatus (reflected by the position of the preoperculum, Fig. 2A: POP), results in a distinctly postorbital jaw articulation and limited lateral expansion. The three adductor mandibulae divisions are contained in a postorbital maxillarypalatoquadrate chamber.

The experimental study of prey capture in the primitive living actinopterygians Polypterus and Lepisosteus (Lauder, 1980a; Lauder and Norton, 1980) has revealed the importance of synchronous activity in the obliquus inferioris and sternohyoideus muscles for mouth opening. The ventral division of the hypaxialis (=obliquus inferioris) stabilizes the pectoral girdle so that the primary effect of the sternohyoideus is to cause posteroventral hyoid rotation, thus opening the mouth. Experimental analysis reveals no evidence for the posterior movement of the pectoral girdle which has been suggested to be involved in feeding (Hutchinson, 1973; Schaeffer and Rosen, 1961; Tchernavin, 1953). The ventral throat musculature plays little role in mediating mouth opening. The intermandibularis posterior, interhyoideus, and branchiomandibularis (Fig. 2B) are primarily active during chewing and intraoral manipulation of prey items, and may be used to control fluid flow through the oral cavity. These ventral muscles are not involved in opening the mouth.

Primitive actinopterygian fishes (e.g., *Cheirolepis, Moythomasia*) possessed a cephalic musculoskeletal system which is considerably less complex mechanically than that of the Halecostomi. There were relatively few mobile elements in the skull and expansion of mouth cavity volume during feeding was probably quite small due to the limited lateral mobility of the suspensorium, opercle, and branchiostegal elements. Water flow through the mouth cavity during feeding may thus have been primarily controlled by body velocity, and not by movement of skull elements.

The Halecostome Feeding Mechanism

The Halecostomi share two major structural innovations related to the feeding mechanism and possess a network of structural connections in the head which is considerably more complex than that of the paleoniscoid fishes (Fig. 1B). Halecostome fishes share two independent biomechanical pathways mediating lower jaw depression: the primitive coupling involving the hypaxial musculature, pectoral girdle, sternohyoideus, and hyoid apparatus (Fig. 1B: coupling 1), and a second, new coupling involving the opercular apparatus (Fig. 1B: coupling 2). This opercular series coupling is retained in nearly all of the 25,000 species of halecostomes and is a remarkably persistent component of the structural network of the head.

Mandibular depression by levation of the operculum is accomplished by contraction of the levator operculi muscle which is derived from the adductor operculi of primitive actinopterygians (Fig. 1A, B: AOP, LOP). The levator operculi causes a dorsal rotation of the opercular series (opercle, subopercle, and interopercle) which is applied as a posterodorsal force on the mandible via the interoperculomandibular ligament (Fig. 1B: IML). Both the levator operculi and interoperculum represent structural specializations at the halecostome level. The consequence of having two biomechanically independent pathways mediating mandibular depression is a dissociation of the primitive hyoid coupling (Fig. 1A, B: coupling 1) from obligatory mouth opening functions. This allows changes in the timing of hyoid depression in relation to mouth opening and increases the versatility of control of fluid movement through the oral cavity.

Primitive halecostomes possess two other structural innovations which relate to

control of fluid flow and suction feeding. The maxilla, primitively firmly attached to the neurocranium and forming the lateral wall of the adductor chamber (Fig. 2A; Gardiner, 1963; Schaeffer and Rosen, 1961) is free from the cheek and pivots on a medially directed process posterior to the vomer. High-speed cinematography of prey capture by Amia calva and several primitive teleosts (Lauder, 1979) has revealed that the maxilla swings anteriorly on its neurocranial pivot as the mouth opens, and by preventing fluid inflow through the corners of the mouth, results in anteroposteriorly oriented streamlines which increase the velocity of water movement from in front of the mouth into the oral cavity (see Fig. 3A: MX). Secondly, an increase in the volume change within the orobranchial cavity results both from the vertical orientation of the suspensorium and from increased ventral mouth cavity expansion as a result of a greater range of hyoid depression. A mobile maxilla, potentially large orobranchial volume changes, and increased kinematic versatility, are features which are maintained in suction feeding fishes throughout the halecostome radiation.

The kinematic pattern which is characteristic of primitive halecostome fishes is also maintained in all generalized predaceous fishes studied to date (Figs. 3, 4). As the mouth begins to open during feeding, the operculum and branchiostegal rays are adducted against the pectoral girdle (Fig. 3B: frames 1 and 2), preventing water inflow. Maxillary swing and opercular levation reach a peak nearly synchronously with peak mouth opening which is followed by hyoid depression and opercular dilation. The mouth then rapidly closes while hyoid depression, suspensorial abduction, and opercular dilation return to their initial positions (Figs. 3, 4). The process of buccal compression thus involves a sequence of movement different from mouth cavity expansion.

Patterson (1973) considers the extinct groups Parasemionotidae and Semionotidae to represent primitive grades of halecostome organization. Both groups include forms which show the structural



FIG. 3. Prey capture in *Amua calva* as seen in lateral (A) and ventral (B) views. This figure is traced from frames of high-speed films of two separate prey capture events. (Modified from figures 13 and 14 of Lauder [1980a].) Note the delay in opercular and branchiostegal expansion until the mouth is nearly completely open, and the anteroposterior sequence of peak excursion in mouth opening, hyoid depression, and opercular dilation. Abbreviations: GP, gular plate; MX, maxilla.

correlates of a suction feeding mechanism. For example, *Lepidotes* has a well-developed interopercle and a free maxilla bearing a prominent medial process (personal observation on MCZ 5304, *Lepidotes elvensis*). The hyoid apparatus of *Lepidotes* also appears to be very similar to that of other halecostomes.

THE TELEOST FEEDING MECHANISM

Major structural features

The teleost feeding mechanism is distinguished from that of more primitive halecostomes by the division of the premaxilla into a mobile lateral toothed portion and



FIG. 4. Pattern of jaw bone movement in *Salvelnus* fontinalis to illustrate the primitive halecostome kinematic profile. The relative sequence of bone movement at the strike is very similar in all predaceous halecostomes that have been studied experimentally (see text).

a medial portion which becomes associated with the ethmoid complex (Patterson, 1973). In a number of predaceous teleosts (e.g., Hoplias, Salmo) the premaxilla has become secondarily firmly attached to the neurocranium, but the primitive condition for teleosts as exemplified by *Pholidophorus, Leptolepis,* or ichthyodectiforms, is a small mobile premaxilla (Patterson, 1977; Patterson and Rosen, 1977).

Although there have been major modifications within the Teleostei in the overall shape of the jaw and its component elements, only three major types of change have occurred in the pattern of interconnections in the structural network of the head. The first specialization involves a shift in insertion of the mandibulohyoid ligament to the interoperculum (Fig. 1C: IHL). The interoperculohyoid ligament characterizes the feeding mechanism of eurypterygian fishes (=Aulopiformes + Myctophiformes + Paracanthopterygii + Acanthopterygii; Rosen, 1973) and effectively shifts the action of the hyoid and opercular coupling onto the interoperculum. Only the interoperculomandibular ligament transmits posterodorsal hyoid and opercular movement to the mandible in the Eurypterygii, while other teleosts retain the primitive two-coupling system of halecostomes (Fig. 1B).

The second major structural specialization within teleosts is the development of an elongate ascending process on the premaxilla and modification of maxillary and premaxillary articular surfaces and ligaments, all associated with protrusion of the upper jaw toward the prey during feeding (Fig. 1).

Finally, a number of changes in the jaw adductor musculature have occurred. Primitive teleosts are characterized by the presence of a geniohyoideus muscle extending anteroposteriorly between the mandibular symphysis and the ceratohyal and epihyal. The geniohyoideus muscle of teleosts represents a fused intermandibularis posterior and interhyoideus (Fig. 2) of primitive actinopterygians (Winterbottom, 1974). Teleosts have lost the branchiomandibularis of primitive actinopterygians (Lauder, 1980a; Wiley, 1979), as well as the suborbital adductor component (Fig. 2A: AMa). Only a single unsubdivided lateral adductor muscle is present in primitive members of the Osteoglossomorpha, Elopomorpha, and Clupeomorpha, whereas in many euteleostean lineages both lateral and medial subdivisions of the main adductor mass (A2/3-Winterbottom, 1974) are present. Of particular importance for the evolution of protrusile mechanisms in teleosts is the independent evolution in many lineages of one or more adductor divisions with insertions on the maxilla. Stomiiforms, myctophiforms, some paracanthopterygians, and some primitive acanthopterygian fishes possess a medial subdivision of the main adductor mass, Alb, which inserts on the maxilla (Fink

and Weitzman, 1982; Rosen, 1973). In many other lineages, a lateral subdivision of A2/3, A1, inserts tendinously on the maxilla. Based on the diversity of lineages within the Acanthopterygii which possess a so-called A1 adductor division, it is unlikely that this division is homologous throughout advanced teleosts, and muscular attachments to the maxilla have certainly arisen independently in various more primitive teleostean lineages. A number of percomorph lineages have a subdivided main adductor mass with separate A2 and A3 components. The A3 usually inserts on the coronomeckelian bone in the Meckelian fossa, while A2 may insert along the coronoid process and medial face of the dentary and anguloarticular. A well-developed intramandibular adductor division (Aw) is present in most teleosts.

Models and mechanisms of upper jaw protrusion: The Acanthopterygii

The ability of many acanthopterygians to extend the premaxilla and maxilla toward the prey during feeding (protrusion) is one of the most widely discussed features of the teleost feeding mechanism (Alexander, 1967; Eaton, 1935; Gregory, 1933; Lauder and Liem, 1981; Liem, 1970, 1979, 1980; Nyberg, 1971; Pietsch, 1978; Schaeffer and Rosen, 1961; van Dobben, 1937). It is now clear that acanthopterygians possess a number of different mechanisms of protrusion involving non-homologous articular surfaces, ligaments, and possibly also muscular control mechanisms.

Alexander (1967) has provided a mechanical explanation for premaxillary protrusion which seems to apply to some primitive acanthopterygians. He suggested that rotation of the maxilla along its long axis is caused by depression of the lower jaw and contraction of the A1 division of the adductor mandibulae. Maxillary rotation causes the premaxillary process of the maxilla to press against the articular process of the premaxilla which forces the premaxilla to protrude anteriorly. The two prerequisites for this mechanism are (1) maxillary twisting and (2) apposition of the premaxillary articular surface with the

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premaxillary condyle of the maxilla. Alexander (1967) also noted that movements of the suspensory apparatus may limit retraction of the protruded premaxilla. Suspensory abduction causes the maxillary process of the palatine to move medially and block retraction which can only be accomplished with an adducted suspensorium. Thus suspensorial, maxillary, and premaxillary movements are all coupled with kinematic systems involved in mouth opening, and mandibular depression ultimately controls protrusion (Liem, 1970).

Liem (1979, 1980) has proposed a "decoupled model" for cichlid fishes which lack the requisite anatomical articulations for Alexander's (1967) model. This model involves contraction of the epaxial muscles and concomitant stabilization of the premaxilla, maxilla, and mandible by contraction of the adductor mandibulae (parts A1 and/or A2) and geniohyoideus. By lifting the neurocranium, jaw protrusion can be modulated and varied in relation to the degree of synchronous activity in the geniohyoideus and adductor mandibulae. Experimental analysis of prey manipulation in cichlids (Liem, 1979, 1980) shows that the epaxial musculature is involved in modulating upper jaw movement during manipulation of prey and that the decoupled protrusion system allows complex kinematic patterns of jaw movement not seen in fishes with coupled mechanisms.

A number of functions have been proposed for premaxillary protrusion, but few of these hypotheses have been tested experimentally. Protrusion may be related to bottom feeding by allowing the mouth opening to be pointed ventrally while the predator's body remains horizontal (Alexander, 1966, 1967). For midwater suction feeding, Nyberg (1971), Gosline (1971), and Alexander (1967) have hypothesized that protrusion provides an added velocity component to the predator's approach. Nyberg (1971) measured an "added velocity" of 89% of the average attack velocity in Micropterus, and Lauder and Liem (1981) measured an additional velocity of 39% of average attack velocity in Luciocephalus. It remains to be demonstrated whether the added velocity resulting from protrusion actually increases the success of prey capture, and how jaw protrusion effects the hydrodynamic properties of the feeding mechanism.

Pharyngeal jaw evolution

Upper pharyngeal jaw dentition in primitive actinopterygians consists of numerous dermal tooth plates aligned with (but not fused to) the pharyngobranchial and epibranchial gill arch elements. Amia and Lepisosteus are unique among non-teleost actinopterygians in having many small tooth plates grouped into a large posterior patch so that individual tooth plates are not referable to a particular arch (Nelson, 1969). Ventrally, small dermal tooth plates are aligned with a long and slender fifth ceratobranchial (Nelson, 1969; Nielsen, 1942). These plates become closely associated in Amia, Lepisosteus, Hiodon, and Elops but are not fused to the fifth ceratobranchial.

In the Teleostei, upper pharyngeal dentition is consolidated into one to five paired tooth plates (Nelson, 1969). Clupeomorphs and euteleostean fishes (the Clupeocephala, Patterson and Rosen, 1977) are derived in having the upper pharyngeal tooth plates fused to the bony endoskeletal gill arch elements, and a single large tooth plate fused to ceratobranchial five. In many euteleostean lineages, only one or two large toothplates are present in the upper pharyngeal dentition (Nelson, 1969, p. 492), and pharyngobranchial one commonly serves as the suspensory element of the gill basket (see Fig. 5).

A particularly important specialization during higher teleostean evolution, and one which characterizes the Neoteleostei (Rosen, 1973), is the occurrence of a retractor dorsalis muscle. The retractor dorsalis (=retractor arcus branchialium) is a paired muscle which originates on the vertebral column (anywhere from the first to the sixteenth vertebra) and extends anteroventrally to insert mainly on pharyngobranchials three and four (Rosen, 1973; Fig. 5B: RD). A second important innovation is the shift in origin of the pharyngohyoideus muscle (Fig. 5: PH), which primitively originates on ventral gill arch



F1G. 5. Diagrammatic view of the pharyngeal jaws and their relation to the skull in (A) Esox niger and (B) Ambloplites rupestris. Heavy lines indicate pharyngeal jaw muscles and their approximate line of action. Thin lines represent the branchial basket. Black bars represent electromyographic activity in selected branchial muscles during manipulation and deglutition; white bars indicate occasional activity. The short vertical line anterior to levator externus one connects the gill basket with the neurocranium and represents pharyngobranchial one. Note the two salient specializations which distinguish advanced euteleosteans such as Ambloplites from more primitive forms (Esox): (1) the shift in origin of the pharyngohyoideus muscle (PH) to the urohyal, and (2) the occurrence of a retractor dorsalis muscle (RD). Abbreviations: AD5, fifth branchial adductor; GH, geniohyoideus; LE1-4, levator externi muscles; PCi, e, pharyngocleithralis internus and externus muscles; PH, pharyngohyoideus; RD, retractor dorsalis; SH, sternohyoideus.

elements (usually hypobranchial three). In all myctophiform, paracanthopterygian, and acanthopterygian teleosts (Subsection Ctenosquamata, Rosen, 1973) the pharyngohyoideus originates from the urohval (Fig. 5: PH).

The consequence of these two muscular

specializations is the presence in higher euteleosts of mechanical couplings which increase the versatility of the pharyngeal apparatus. In primitive teleosts (Fig. 5), protraction and retraction of the upper pharyngeal tooth plates must be accomplished by the levator externus muscles. Levator externus one (and the anterior levator interni) have a posteriorly inclined line of action which results in retraction of the upper pharyngeal jaw (Fig. 5A: LE1). Levator externi two and three mediate upper pharyngeal jaw protraction. In higher euteleosts (Fig. 5B), the retractor dorsalis and antagonistic levator externi three and four provide a coupling which allows extensive anteroposterior movement of the upper pharyngeal jaws. In addition, the levator posterior mediates dorsal movement of the upper jaws.

Ventrally, the change in origin of the pharyngohyoideus (Fig. 5B) to the urohyal increases the range of anterior movement of the lower pharyngeal jaw, and, in conjunction with the pharyngocleithralis internus, provides a coupling mediating anteroposterior excursions.

Experimental evidence from electromyographic analyses of pharyngeal musculature in euteleosteans (Fig. 5) reflects these constraints on lower pharyngeal jaw movement. In *Esox*, swallowing is accomplished by synchronous activity in levator externus one and the pharyngocleithralis internus (Fig. 5A: LE1, PCi) indicating that both the upper and lower pharyngeal jaws are retracted together. After retraction, levator externus three is active, elevating and protracting the upper pharyngeal jaw before the second retraction stroke of the lower jaw.

In Ambloplites (Fig. 5B), the pharyngohyoideus and geniohyoideus are active synchronously to protract the lower pharyngeal jaw, while the upper jaw is being protracted by the levator externi muscles (Fig. 5B: LE4). Retraction of the upper jaw occurs via the retractor dorsalis which is active with the pharyngocleithralis internus (Fig. 5B: RD, PCi). The upper and lower jaws thus are retracted together, although the excursion of the lower jaw is only one-half that of the upper jaw. In certain acanthopterygian lineages, the lower pharyngeal jaws are fused in the midline and osteological and myological specializations of the entire pharyngeal apparatus result in radically different kinematic and electromyographic patterns from generalized euteleosts (Liem, 1973, 1978; Liem and Greenwood, 1981).

CONCLUSIONS

Considerable progress has been made over the last twenty years in understanding patterns of structural and functional evolution in the feeding mechanism of fishes, and actinopterygians provide an excellent case study for analyzing the nature and pattern of structural changes in a complex system. In particular, an analysis of how the structural network in the front jaws has changed (Fig. 1) may be correlated with a similar analysis for pharyngeal jaw structural and functional systems (Fig. 5) to gain an understanding of evolutionary interactions between these two coupled structural features.

One of the major features of the evolution of the actinopterygian feeding mechanism is an increase in structural complexity. As more cladistically derived monophyletic lineages of actinopterygians are considered, structural complexity (defined as the number of connections in the structural network, Fig. 1) increases. Certain changes in the structural network are related to structural diversification. For example, the occurrence of two biomechanical pathways mediating jaw opening at the halecostome level permits structural and functional diversification by removing functional constraints on the primitive hyoid coupling. A similar relationship between structural diversity and number of biomechanical pathways holds for mechanisms of jaw protrusion and upper jaw morphology in acanthopterygians (Lauder, 1981).

In the pharyngeal jaws, three major structural and functional modifications have occurred in teleosts and the distribution of these modifications is congruent with currently accepted monophyletic lineages. Consolidation and fusion of pharyngeal tooth plates with underlying endochondral gill arch elements characterizes the Clupeocephala; the presence of a retractor dorsalis is shared by neoteleostean fishes; and the pharyngohyoideus muscle originates from the urohyal in the Ctenosquamata. These anatomical specializations result in increased control over prey manipulation and mastication in the pharynx and reflect the increasing functional versatility of pharyngeal jaw elements in actinopterygian evolution.

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