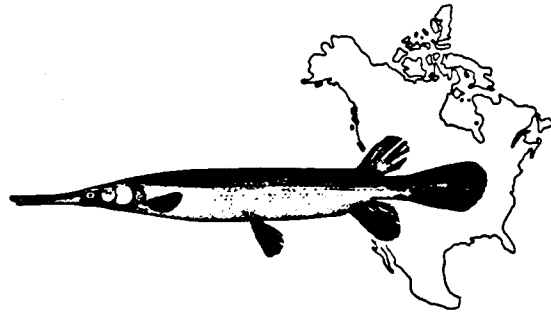# 15

Function and History:
The Pharyngeal Jaw Apparatus in Primitive
Ray-finned Fishes

George V. Lauder and Peter C. Wainwright

During the renaissance of systematic and comparative biology over the last twenty years the study of organismal structure has provided an extensive data base for constructing phylogenetic hypotheses. Morphometric, histological, amino acid and DNA base sequences, and gross anatomical methods have all been used to generate data for phylogenetic reconstructions, and the resulting phylogenies have been used extensively to study ecological and biogeographic patterns. As with most clades, morphological studies of ray-finned fishes have provided most of the characters used in phylogenetic analysis, and the structure of many features (e.g., jaw muscles, caudal osteology, the axial skeleton) have provided considerable phylogenetic information.

In contrast to the number of comparative papers published on biogeography, behavior, morphology, and phylogenetics, relatively few contributions have been aimed at understanding organismal *function* (Lauder, 1990). For the most part the study of function (i.e., the uses of structures) has either been physiological in focus, or "function" has been inferred from structure (often with little success). Moreover, research programs involving the actual measurement of function typically have not evaluated functional differences among species in terms of phylogenetic histories. Functional attributes of organisms represent another class of traits useful both in estimating phylogenetic branching patterns, and for providing insights into the evolution of biomechanics and the *uses* of structural characters. Exploration of how structural features are actually used by organisms is important if we wish to understand the mechanistic basis of behavioral evolution, and the extent to which structure and function may be dissociated during cladogenesis.

One morphological system in ray-finned fishes (Actinopterygii) that has received considerable attention since Nelson's classic paper in 1969 is the pharyngeal jaw apparatus (PJA). The pharyngeal jaw apparatus has been the focus of several functional analyses and a number of investigators have used the PJA as the basis for

phylogenetic or comparative analyses of form and function (Vanden Berghe, 1928; Nelson, 1967, 1969; Liem, 1973, 1986; Wiley, 1979; Liem and Greenwood, 1981; Sibbing, 1982; Lauder, 1983a, b, c; Liem and Sanderson, 1986; Gobalet, 1989; Wainwright, 1989a, b). The PJA consists of a set of toothed bony elements in the pharynx that act to hold, manipulate, and macerate prey after they have been captured. All functional and most morphological analyses of pharyngeal jaw function in ray-finned fishes have been conducted on euteleostean fishes. There is virtually no understanding of the primitive condition of the PJA in ray-finned fishes or of the historical patterns involved in the transformation of function in this complex system. The overall goal of this chapter is to provide a case study in the evolution of function using the PJA of some North American ray-finned fishes as an example. The North American fish fauna contains two clades critical to our understanding of the historical biology of ray-finned fishes (bowfins and gars). These two clades contain relic members of ancient speciation events in ray-finned fishes that provide a window into primitive functional characteristics and allow the functional attributes of recently derived taxa to be placed into an historical perspective.

This chapter has three specific aims. First, we consider phylogenetic patterns to pharyngeal jaw structure in order to define the primitive condition of PJA morphology in ray-finned fishes. Using a phylogeny as a basis for subsequent functional analysis allows us to determine (using the principle of parsimony) which morphological characteristics of the PJA are homologous and which are convergent. Second, we present new data on the function of the PJA in three "primitive" and relic clades of actinopterygians (bichirs, *Polypterus*; gars, *Lepisosteus*; and the bowfin, *Amia*) so that basic functional aspects of the PJA in early ray-finned fishes may be compared to more derived clades. Third, we assess the function of the PJA during airbreathing, and suggest a new hypothesis for the role of the PJA in allowing air to enter the respiratory gas bladder.

PHYLOGENETIC AND MORPHOLOGICAL BACKGROUND

While much recent research on the functional morphology and biomechanics of vertebrates has been conducted successfully from a non-historical perspective, the addition of a comparative phylogenetic framework allows analyses of vertebrate design to address new sets of questions (Lauder, 1990). Specifically, use of a corroborated phylogenetic hypothesis in conjunction with parsimony and optimization algorithms permits independent evolutionary origins of characters (whether morphological or functional) to be recognized. Similarly, the recognition that any given character is shared among several species due solely to the possession of that character in the common ancestor of those species is only possible given knowledge of genealogical relationships. Our efforts to understand the evolution of biomechanics and animal design are enhanced if we use phylogenetic data on morphology as a basis for both formulating and testing functional hypotheses. In this case study of the PJA in ray-finned fishes, the pattern of genealogical relationships among taxa is critical for recognizing, *prior* to the functional analysis, that a key morphological feature (the dorsal retractor muscle of the PJA) has evolved independently in (at least) two clades of ray-finned fishes.

The phylogenetic relationships of the major extant ray-finned fish clades (Actinopterygii) are depicted in Figure 1. The major living outgroup clades to the ray-
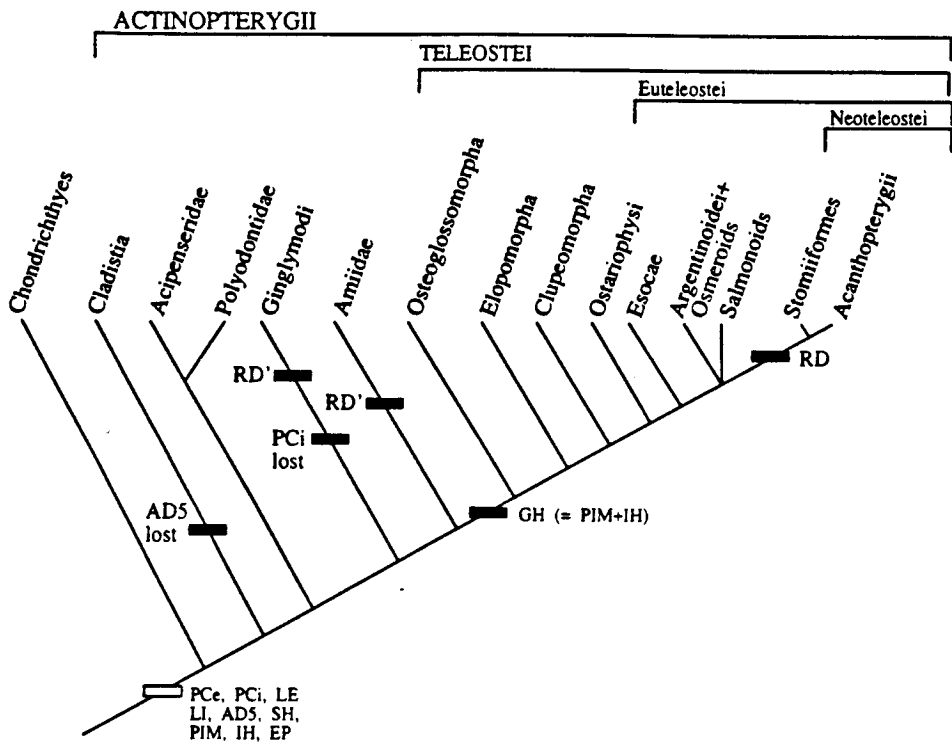
Figure 1.

A greatly simplified diagram of the phylogenetic relationships of the major living clades of ray-finned fishes (Actinopterygii; modified from Lauder and Liem, 1983) with pharyngeal jaw muscle characters discussed in this chapter indicated by black bars. All fossil clades and many living clades are omitted from this diagram for clarity. The Chondrichthyes are outgroups to ray-finned fishes. The muscle characters are not used to support this particular phylogeny; rather they indicate the distribution of the muscle characters on the phylogeny from Lauder and Liem (1983). Muscles labelled at the base of the cladogram next to the open bar are hypothesized to be primitive for the Actinopterygii (and thus may be present in outgroups too). A dorsal retractor muscle (the retractor dorsalis proper (RD) in neoteleost fishes) has evolved independently in *Lepisosteus* (Ginglymodi) and *Amia* (Amiidae) where it is labelled RD'. It is equally parsimonious to assume an independent origin of this muscle (twice) as to assume that it was gained once (below the Ginglymodi) and lost once (above the Amiidae). Current data do not allow a decision on this point. The Acipenseridae, Polyodontidae, Cladistia, and Chondrichthyes all lack an RD' muscle. One genus of osteoglossomorph (*Pantodon*) and one genus of osmeroid (*Lepidogalaxias*) also possess an RD' muscle. Ginglymodi are autapomorphic in lacking a PCi muscle and the Cladistia (*Polypterus*) lack an AD5. Outgroup taxa possess homologues of both these muscles (Allis, 1897, 1917, 1922; Edgeworth, 1935; Wiley, 1979). Teleost fishes are characterized by the possession of an antero-posteriorly oriented PIM muscle; in most teleosts the PIM is continuous anteroposteriorly with the interhyoideus (IH) to form the geniohyoideus (GH; Lauder, 1980). The pattern of branchiomandibularis muscle evolution is still unclear and is not treated on this figure. Abbreviations: AD5, fifth branchial adductor; EP, epaxialis; IH, interhyoideus; GH, geniohyoideus; LI, levatores interni; LE levatores externi; PCe, pharyngocleithralis externus; PCi, pharyngocleithralis internus; PIM, posterior intermandibularis; SH, sternohyoideus.

finned fishes are the Chondrichthyes (sharks, rays, and holocephalans) and the Sarcopterygii (*Latimeria*, lungfishes, "rhipidistians," and tetrapods). The two clades that will be the subject of most of the functional analyses reported in this chapter are the Ginglymodi (gars, including *Lepisosteus* and *Atractosteus*; Wiley, 1976; Wiley and Schultze, 1984), and the Amiidae (the bowfin, *Amia*; Boreske, 1974). Extant species in these clades are endemic to North and Central America (Patterson, 1981), although if fossil taxa are included the clades have a wider distribution. The Cladistia (which includes bichirs, *Polypterus*, and rope fishes, *Erpetoichthyes*) is the sister group to all other living ray-finned fishes (Fig. 1; Lauder and Liem, 1983; Patterson, 1982) and thus represents one of the most ancient speciation events for the Actinoptergyii. One species in the Cladistia will be used here as an outgroup for historical studies of function in the North American *Amia* and *Lepisosteus*. The Chondrostei includes the sturgeons and paddlefishes (Acipenseridae and Polyodontidae, both with North American representatives) and these two clades together with gars, *Amia*, and teleost fishes comprise a monophyletic Actinopteri (Patterson, 1982; Lauder and Liem, 1983). The Teleostei (Fig. 1) contains the vast majority of the approximately 23,000 living species of ray-finned fishes. Within the Teleostei, the neoteleost clade (Fig. 1) is an extremely diverse assemblage of fishes and contains many monophyletic groups including the Acanthopterygii (spiny-finned fishes).

The pharyngeal jaw apparatus (PJA) in "primitive" ray-finned fishes is diagrammed in Figure 2. This pharyngeal system is located ventral to the skull in the pharynx, and consists of gill arch elements and associated musculature (Allis, 1897, 1922; Tchernavin, 1953; Nelson, 1967, 1969; Liem, 1970; Wiley, 1979). The PJA is composed of paired upper pharyngeal jaws (Fig. 2; UPJ), consisting of one or more toothed bony plates, and paired lower pharyngeal jaws (e.g., Fig. 2b; LPJ) usually formed by ceratobranchial five. In *Polypterus* the lower pharyngeal jaw consists of paired fourth ceratobranchials (Fig. 2a; CB4). The PJA is used by fishes during the manipulation and swallowing of prey. During these movements the pharyngeal jaws are protracted, retracted, and adducted to crush, manipulate, and move prey items from the posterior portion of the buccal cavity into the esophagus (Vanden Berghe, 1928; Liem, 1970, 1973; Lauder, 1983a, b; Liem and Sanderson, 1986; Wainwright, 1989a, b).

The PJA is controlled by muscles that attach the upper and lower pharyngeal jaws to the skull, pectoral girdle, hyoid apparatus, lower jaw, and in some cases the vertebral column (Fig. 2; Nelson, 1969; Wiley, 1979; Lauder, 1983b). Primitively in ray-finned fishes the upper pharyngeal jaw is attached to the skull by levatores externi and interni muscles that act to protract and elevate the upper pharyngeal jaw (Figs. 2 and 3; LE and LI). The pharyngocleithralis externus and internus muscles (Fig. 2a; PCe and PCi) attach the lower pharyngeal jaw to the pectoral girdle and move the lower pharyngeal jaw ventrally and posteriorly. Primitively in ray-finned fishes the major muscle protracting the lower pharyngeal jaw is the branchiomandibularis (Fig. 2; BM), which originates near the mental symphysis on the lower jaw and inserts on the hyobranchial apparatus (Allis, 1922; Wiley, 1979; Lauder, 1980). Contraction of this muscle protracts the entire hyobranchial apparatus. Wiley (1979) hypothesized that the branchiomandibularis muscle is homologous to the coracomandibularis muscle of Chondrichthyes and sarcopterygians. Teleost fishes lack a branchiomandibularis.

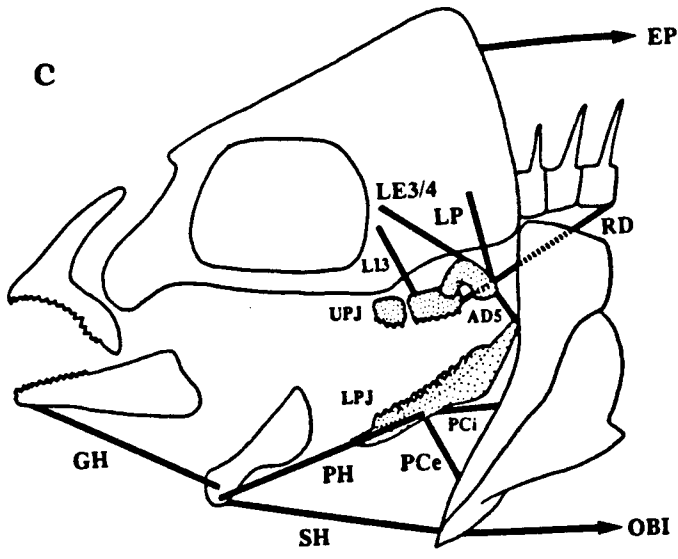Movements of the hyoid apparatus as a result of activity of the sternohyoideus
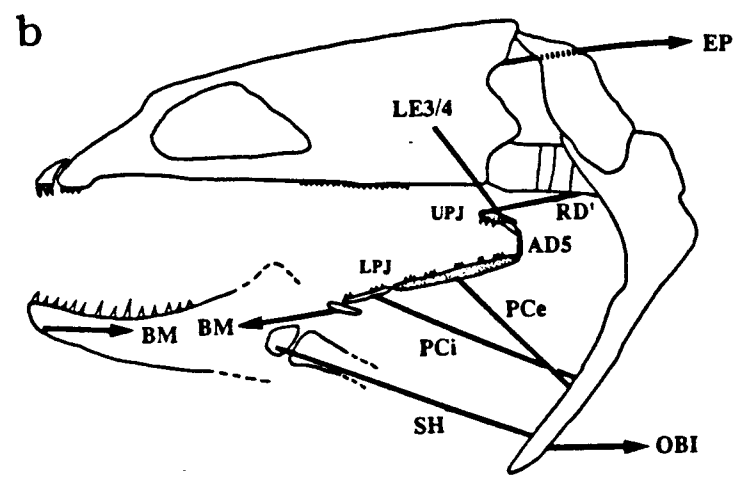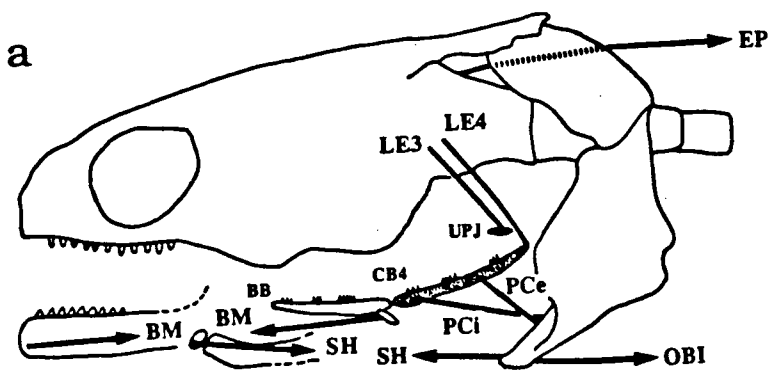
Figure 2.
Diagrammatic view of the pharyngeal jaw apparatus in three actinopterygian fishes: a, *Polypterus*; b, *Amia*; c, a percomorph such as *Haemulon*. Bones of the pharyngeal jaw apparatus (PJA) are stippled; note the upper and lower pharyngeal jaws (UPJ and LPJ). Black lines represent muscles with the line extending from the origin to the insertion. In these schematic diagrams the levatores interni (LI) muscles are not shown attaching the UPJ to the skull. Note that both neoteleost fishes and *Amia* possess a dorsal retractor muscle capable of pulling the upper pharyngeal jaw posteriorly. Abbreviations: AD5, fifth branchial adductor; BB, basibranchial; BM, branchiomandibularis; CB4, ceratobranchial 4; EP, epaxial muscles; GH, geniohyoideus; LE 3, 4, levatores externi three and four muscles; LI, levatores interni; LPJ, lower pharyngeal jaw; OBI, obliquus inferioris muscle; PCe, pharyngocleithralis externus; PCi, pharyngocleithralis internus; PH, pharyngohyoideus; RD, retractor dorsalis muscle; RD', dorsal retractor muscle in *Lepisosteus* and *Amia* (convergent with the RD in neoteleost fishes); SH, sternohyoideus; UPJ, upper pharyngeal jaw.

Figure 3.
Dorsal view of the branchial musculature in *Lepisosteus oculatus*. Note that the large dorsal retractor muscle passes anteroventrally beneath the transversus dorsalis (TD) to insert on the upper pharyngeal jaw. Abbreviations: ES, esophagus; LI, levatores interni; LE, levatores externi; OD,. obliquus dorsalis; RD', dorsal retractor muscle; TD, transversus dorsalis. Scale bar equals 0.5 cm.
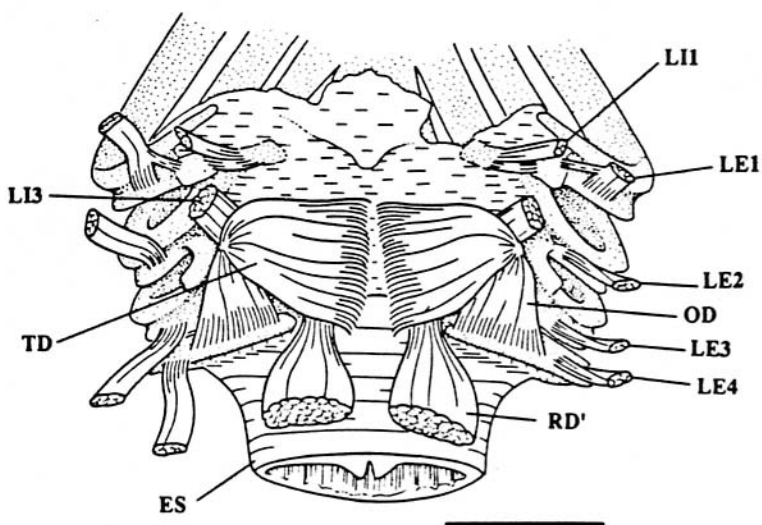
and intermandibular muscles may also influence the position of the pharyngeal jaw apparatus. In most ray-finned fishes (except *Polypterus*) there is a muscle that attaches the distal tip of the lower pharyngeal jaw to the upper pharyngeal jaw, the fifth branchial adductor (Fig. 2; AD5). This muscle adducts the distal ends of the lower and upper pharyngeal jaws.

Fishes of the neoteleostean clade (Fig. 1) are characterized by (among other traits) the possession of a large muscle that extends posterodorsally from the upper pharyngeal jaw to the vertebral column, the retractor dorsalis (Fig. 2c; RD; Nelson, 1967; Rosen, 1973; Winterbottom, 1974; Lauder and Liem, 1983). This muscle is the dominant retractor of the upper pharyngeal jaw in neoteleostean fishes and is lacking in most primitive teleosts (although there are a few teleost species that appear to have a muscle similar in morphology to the neoteleostean retractor dorsalis). Both *Amia* and *Lepisosteus* (but not *Polypterus*, *Acipenser*, and *Polyodon*) possess a muscle that is morphologically similar to the neoteleostean RD, and is labelled here the RD' (Fig. 2b; Nelson, 1967, 1969). The RD' label in no way implies a homology of the dorsal retractor muscle between *Amia* and *Lepisosteus*. Rather, this label reflects current uncertainty in the homology of the retractor muscle in non-teleost clades. A schematic view of the RD' in *Amia* is shown in Figure 2b and a dorsal view of the pharyngeal jaw musculature in *Lepisosteus* is illustrated in Figure 3. In order to minimize confusion when discussing these muscles, we will refer to the RD' in *Lepisosteus* and *Amia* by the generic name "dorsal retractor muscle" and reserve the proper name "retractor dorsalis" (or RD) for fishes in the neoteleostean clade.

Given the limited distribution of a dorsal retractor muscle outside of neoteleost fishes, it is most parsimonious to conclude that the presence of a retractor muscle in *Amia* and *Lepisosteus* is convergent with that of neoteleost fishes (Fig. 1; Nelson, 1967:280, 1969:493). This conclusion is based on a parsimony analysis of the distribution of the dorsal retractor muscle character on the cladogram of Figure 1. For example, interpreting the evolution of the retractor muscle as involving one origin following the speciation of chondrosteans (Acipenseridae and Polyodontidae; Fig. 1), the subsequent loss of the muscle in the Teleostei (Fig. 1), and a second origin of a

retractor dorsalis muscle in the Neoteleostei involves three evolutionary steps. Interpreting the retractor muscle of *Amia*, *Lepisosteus*, and neoteleosts as homologous requires one origin and from four to ten independent losses (a total of five to eleven steps). These conclusions are not altered either by the presence within a few teleost lineages of a retractor muscle of some kind, or by the undoubted extinction of many clades of primitive teleost fishes with an undetermined condition for the retractor muscle. For example, Begle (1991) has commented on the presence of an RD' muscle in *Lepidogalaxias* (osmeroid, Fig. 1), and an RD' muscle appears to also be present in Pantodon (Osteoglossomorpha, Fig. 1). But as these are the only genera in those clades to possess an RD' muscle, it is most parsimonious to hypothesize that this muscle in *Pantodon* and *Lepidogalaxias* represents a novelty for those genera, and not a primitive teleost character.

The distribution of these myological features on the phylogeny of actinopterygian fishes is shown in Figure 1. Based on the distribution of muscle characters within ray-finned fishes and outgroup taxa (Chondrichthyes and Sarcopterygii; Fig. 1), the following anatomical features of the PJA are hypothesized to be primitive for the Actinopterygii. Primitive ray-finned fishes possess the following muscles: pharyngocleithralis internus and externus, levatores interni and externi, fifth branchial adductors, sternohyoideus, interhyoideus, posterior intermandibularis, and epaxial muscles. A dorsal retractor muscle is lacking, as is any mechanism for retracting the upper pharyngeal jaw. Swallowing of prey thus could only occur via retraction of the whole pharyngeal jaw apparatus by the pharyngocleithralis internus and externus muscles.

Muscular novelties that characterize the Teleostei include reorientation of the muscles of the buccal floor (posterior intermandibularis and interhyoideus) to form a geniohyoideus muscle (Fig. 1; Winterbottom, 1974; Lauder, 1980). *Polypterus* has lost the fifth branchial adductor and *Lepisosteus* has lost the pharyngocleithralis internus muscle.

FUNCTIONAL MORPHOLOGY OF THE PHARYNGEAL JAWS

Functional patterns in the pharyngeal jaw apparatus of *Polypterus ornatipinnis*, *P. senegalus*, *Lepisosteus oculatus*, and *Amia calva* were studied by measuring the sequence and timing of muscle activity with electromyography. As in previous research, we implanted fine-wire steel alloy bipolar electrodes into pharyngeal jaw muscles percutaneously while the animal was anesthetized with tricaine methanesulphonate (Lauder, 1983a, b; Wainwright, 1989a). Up·to six muscles were implanted simultaneously and the electrode pairs were glued together, color coded, and attached to the back of the fish with a loop of suture. Signals from the electrodes were amplified 10,000 times using Grass P511J preamplifiers and the data recorded on a Bell and Howell multitrack FM tape recorder. Animals were allowed to recover from the anaesthesia and were fed either later the same day or on subsequent days. Prey items were live goldfish (*Carassius auratus*) or earthworms (*Lumbricus*).

Function of the PJA in *Polypterus*

The pattern of pharyngeal jaw muscle activity during swallowing in *Polypterus* is shown in Figure 4. During vigorous manipulation of prey within the oral cavity the
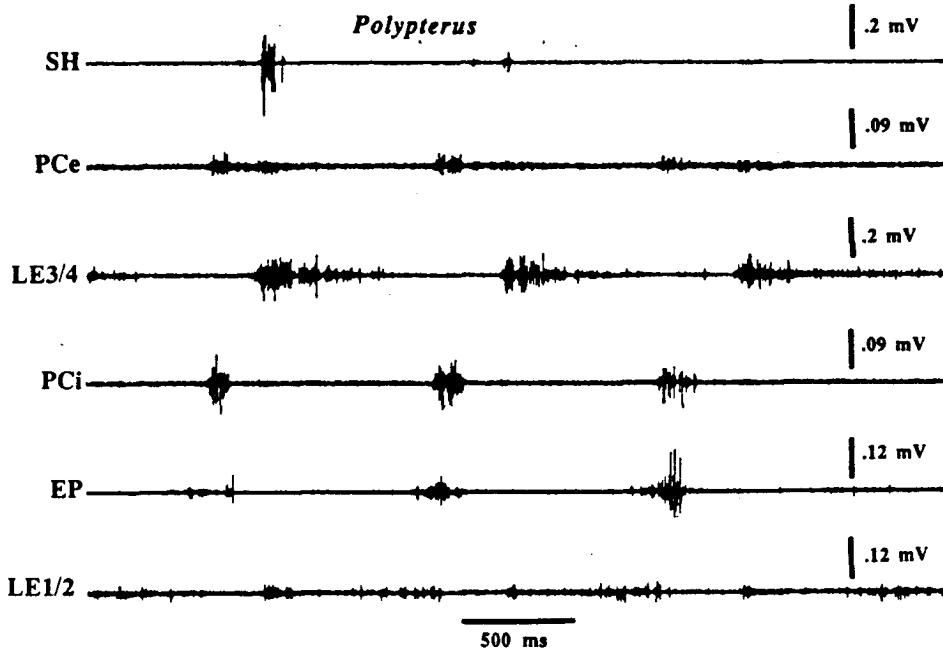
Figure 4.
Representative muscle activity pattern (all six muscles were recorded simultaneously) during pharyngeal prey transport in *Polypterus*. Muscle activity patterns are presented in the order in which they were recorded. The prey item (a goldfish) has been captured and is being swallowed. We were not able to distinguish electrode location within the levatores externi 3 and 4 and so recordings from this channel are labelled as LE3/4. Note the alternating pattern of activity in the PCi and the LE3/4. Abbreviations: EP, epaxial muscles; LE 1/2, levatores externi one and two; LE 3/4, levatores externi three and four; PCi, pharyngocleithralis internus; PCe, pharyngocleithralis externus; SH, sternohyoideus.

sternohyoideus muscle is active, but it is typically inactive during the actual swallowing of food by the pharyngeal jaws. All other muscles show a regular rhythmic bursting pattern as the prey is transported from the buccal cavity into the esophagus by the action of these pharyngeal jaw muscles. The pharyngocleithralis externus, pharyngocleithralis internus, and epaxial muscles all show strongly overlapping bursts of activity, and we interpret this activity to reflect retraction of the lower pharyngeal jaw. This activity alternates with activity of the levator externi three and four which effect anterodorsal movement of both the upper and lower pharyngeal jaws.

We interpret this motor pattern to indicate that swallowing in *Polypterus* is achieved via alternating protractive and retractive movements of the pharyngeal jaw apparatus, and that the lower and upper pharyngeal jaws probably are moving in an alternating pattern to transport the prey into the esophagus.

Function of the PJA in *Lepisosteus*

The pattern of pharyngeal jaw muscle activity during swallowing in *Lepisosteus* is illustrated in Figure 5a. While the levatores externi, pharyngocleithralis externus, and sternohyoideus are all active during the initial strike and during intraoral
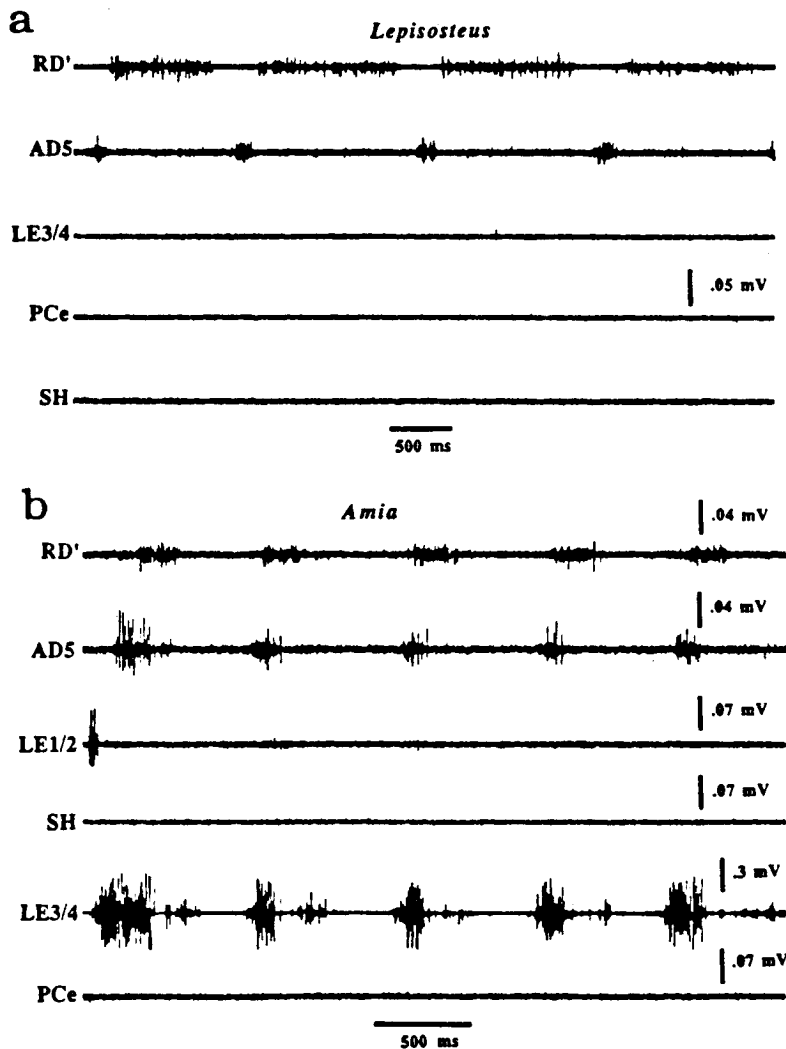
Figure 5.
a) Representative muscle activity pattern (all six muscles were recorded simultaneously) during pharyngeal prey transport in *Lepisosteus*. Note the low amplitude rhythmic activity in the RD' muscle and the lack of activity in the LE3/4, PCe, and SH muscles. Also note that *Lepisosteus* does not possess a PCi muscle (see Fig. 1). b) Pharyngeal muscle activity pattern in *Amia*. Note the extensive LE3/4 activity and the relative timing of activity in the RD' and AD5. Abbreviations: AD5, fifth branchial adductor; LE1/2, levatores externi one and two muscles; LE3/4, levatores externi three and four muscles; PCe, pharyngocleithralis externus; RD', dorsal retractor muscle; SH, sternohyoideus.

manipulation of prey items, only the dorsal retractor (RD') and fifth adductor (AD5) show consistent activity during swallowing. The RD' is active at a low amplitude in a regular bursting pattern that may continue for many seconds. Activity in the AD5 alternates with that in the RD, and the sternohyoideus is not active during swallowing (Fig. 5a). Swallowing of prey items is thus accomplished primarily by the dorsal retractor. The very low level of activity in the levatores externi suggests that recoil of the muscles and connective tissue surrounding the pharyngeal jaw apparatus might be responsible for protraction of the jaws during swallowing. There is little electromyographic evidence for active pharyngeal protraction during prey transport.

Function of the PJA in *Amia*

The pattern of pharyngeal jaw muscle activity during swallowing in *Amia* is summarized in Figure 5b. As in *Lepisosteus* the dorsal retractor muscle is active in a regular rhythmic pattern at a low level and the burst of activity in this muscle follows (with significant overlap) activity in the fifth adductor (AD5) and levatores externi

(LE 3/4). The sternohyoideus, levatores interni, and pharyngocleithralis externus are typically inactive during swallowing (Fig. 5b). This pattern of muscle activity suggests that swallowing is accomplished by alternating retraction of the upper pharyngeal jaw (caused by the RD') with protraction of the upper pharyngeal jaw (caused by the levatores externi). As in *Lepisosteus*, the lower pharyngeal jaw appears to play little role in swallowing.

Comparison to Other Actinopterygian Fishes

Muscle activity patterns in the PJA have been studied in several clades of teleost fishes (e.g., Centrarchidae: Lauder, 1983a, b, c; Cichlidae: Liem, 1973; Liem and Kaufman, 1984; Cyprinidae: Sibbing, 1982; Embiotocidae: Liem, 1986; Esocidae: Lauder, 1983b; Haemulidae: Wainwright, 1989a, b; Labridae: Liem and Sanderson, 1986; Percidae: Lauder, 1983b; several pharyngognath perciform lineages: Liem and Greenwood, 1981). It is thus possible to compare the function of muscles within teleostean fishes to those of non-teleosts such as *Polypterus*, *Lepisosteus*, and *Amia* in order to test for possible convergence in function. Labroid fishes possess structural specializations in the pharyngeal jaw apparatus (such as an upper pharyngeal jaw that articulates with the cranium) that make comparisons with outgroup clades difficult (Kaufman and Liem, 1982; Liem and Kaufman, 1984). This comparative analysis will thus be restricted to two relatively unspecialized perciform clades for which the most extensive data are available, the families Centrarchidae and Haemulidae.

In both centrarchids and haemulids the activity period of the retractor dorsalis muscle overlaps significantly with that of the levatores externi (Lauder, 1983a, b; Wainwright, 1989a, b; also see Wainwright and Lauder, Chapter 16). The levatores externi three and four invariably begin activity prior to the onset of activity in the retractor dorsalis. In addition, the fifth adductor (AD5) in centrarchids typically exhibits a characteristic pattern in which extensive overlap occurs with both the retractor dorsalis and levatores externi.

The similarities between the motor pattern in *Amia* and a centrarchid (*Ambloplites*) are illustrated in Figure 6. Despite the fact that the retractor muscle is not homologous in these two fishes, the overall pattern of activity is remarkably similar. Phylogenetically, the most parsimonious interpretation is that the motor pattern of the pharyngeal jaw muscles in *Amia* is convergent to that of the centrarchid and haemulid neoteleostean clades. Given the diversity of percomorph fishes, it is certainly not possible to assume that the pattern of muscle activity in the PJA described for centrarchids and haemulids is representative of all neoteleostean fishes. However, even if the motor pattern in *Amia* were discovered to be similar to that of many other Neoteleostei, the finding that the motor pattern is convergent would still stand. The determination of convergence in functional characters, like that of morphological features, ultimately rests on the pattern of character distribution on a phylogeny (Lauder, 1990).

While initially it might seem counter-intuitive that two muscles with such superficially dissimilar functions (levator externus three/four [a protractor of the upper pharyngeal jaw] and the retractor dorsalis [a retractor of the upper pharyngeal jaw]) should overlap so much in activity period, Wainwright (1989b) has shown that
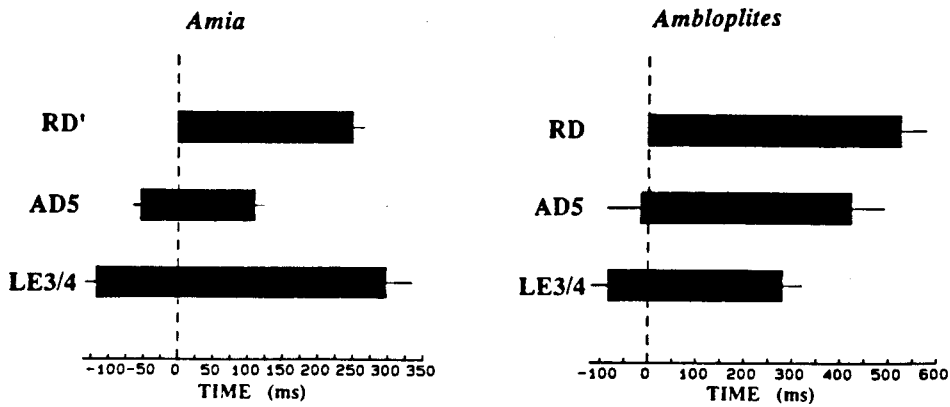
Figure 6.

Bar diagram depicting the average pattern of muscle activity in *Amia* (Amiidae) and *Ambloplites* (Centrarchidae) measured relative to the onset of activity in the dorsal retractor muscle (RD or RD'). The end of each black bar indicates the mean onset and offset of muscle activity while the thin line indicates one standard error of that mean. Note the similarity in relative activity periods for muscles in these two taxa. Abbreviations: AD5, fifth branchial adductor; LE3/4, levatores externi three and four muscles; RD, retractor dorsalis muscle; RD', dorsal retractor muscle (not homologous with the RD of *Ambloplites*).

in many perciform clades the LE3/4 muscle acts to depress the upper pharyngeal jaw by rocking epibranchial four medially and ventrally. In these clades the levatores externi are more than levators or protractors: they act to hold the prey between the pharyngeal jaws. Seen in this light, the pattern of muscle activity recorded from the pharyngeal jaw apparatus suggests that the LE3/4 muscle in centrarchids and haemulids is acting to clamp the upper pharyngeal jaw down onto the prey as the retractor dorsalis muscle pulls the entire upper pharyngeal jaw posteriorly (Fig. 6). This action pulls the prey into the esophagus. The mechanical actions of the LE3/4 muscle are unknown in *Amia*, but if the perciform mechanism is not found in bowfins, then this muscle will possess a convergent motor pattern with perciform fishes but a divergent function.

Lauder (1983a, b) has shown that activity in the pharyngocleithralis internus muscle, the major retractor of the lower pharyngeal jaw, overlaps significantly with activity in the retractor dorsalis in centrarchid fishes. This suggests that the upper and lower pharyngeal jaws are moving posteriorly and anteriorly synchronously in a rhythmic pattern to move the prey into the esophagus. Active retraction of the lower pharyngeal jaw plays an important role in swallowing in centrarchid and haemulid fishes.

The overall morphological pattern of the PJA in *Lepisosteus* and *Amia* is similar to that of derived teleost clades which means that the basic structure of the PJA has been conserved throughout most of ray-finned fish evolution. Specifically, nearly all ray-finned fishes share ventral pharyngocleithralis muscles, a branchial adductor 5, sternohyoideus, and levatores externi and interni muscles (Fig. 1). In addition, the evolution of a major morphological novelty in *Lepisosteus* and *Amia* (the RD' muscle) is convergent on the RD muscle of derived teleosts, and is associated with functional convergence in the motor pattern.

Major changes in pharyngeal jaw function have also occurred, and the pattern of pharyngeal jaw function differs considerably among the taxa for which we now have data. For example, swallowing in *Polypterus* is achieved primarily by activity in the ventral pharyngeal muscles because there is no dorsal retractor muscle. We hypothesize that this is the primitive condition for ray-finned fishes because outgroups (Chondrichthyes and Sarcopterygii; Fig. 1) also lack dorsal retractor muscles as do *Acipenser* and *Polyodon*. In *Lepisosteus* and *Amia* the upper pharyngeal jaw plays the major role in prey swallowing. In centrarchid and haemulid fishes, both the upper and lower pharyngeal jaws are important during swallowing. Thus, on the basis of the relatively limited functional data now available, it appears that similar, non-homologous, morphological conditions in the PJA are not obligatorily accompanied by similar functional patterns.

AIRBREATHING

Although the pharyngeal jaw apparatus has to date been analyzed only in terms of feeding function it is important to consider alternative functions for this system. Both *Amia* and *Lepisosteus* are air-breathing fishes and regularly surface to exchange deoxygenated air from the respiratory gasbladder (or lung) with fresh air. In both species the lung (which serves as a major component in gas exchange; Johansen et al., 1970; Johansen, 1972) possesses a pneumatic duct which opens dorsally into the esophagus at a glottis, located posterior to the upper pharyngeal jaw (pers. obs.). The pneumatic duct allows air to pass into and out of the lung during air ventilation (Deyst and Liem, 1985; Liem, 1989). In *Polypterus* the pneumatic duct opens ventrally into the esophagus posterior to the lower pharyngeal jaws (pers. obs.; Liem, 1988).

In *Lepisosteus* and *Amia* the dorsal retractor inserts on the upper pharyngeal jaws, and anatomical manipulation of the pharyngeal jaws and esophagus indicates that as the retractor muscle contracts the esophageal wall is deformed and opens the glottis. This observation suggests the following hypothesis: the dorsal retractor muscle functions during airbreathing to open the glottis as air passes into and out of the lung. Thus, this muscle is a critical and previously unrecognized component of air ventilation in bowfins and gars, and may possess other functions than those studied during prey swallowing. This hypothesis may be tested by recording muscle activity in the PJA during air ventilation.

Electromyographic recordings of the pharyngeal jaw musculature confirm that the dorsal retractor, fifth branchial adductor, and sternohyoideus are all active during air ventilation (Fig. 7a). Indeed the retractor muscle is active in a double burst pattern and the second burst is nearly twice the amplitude of the highest activity seen during swallowing of prey. We hypothesize that this double burst pattern of activity in the dorsal retractor facilitates air entry into and out of the pneumatic duct by opening the glottis. Activity of the sternohyoideus muscle in between the two RD' bursts may reflect depression of the hyoid apparatus (thus expanding buccal volume) and the drawing of air out of the lung as well as the subsequent inspiration of fresh air into the mouth. This interpretation is supported by the recordings of Liem (1989:337) who showed in *Amia calva* that air intake into the buccal cavity is occurring during the burst of activity in the sternohyoideus muscle. Our recordings of the double-burst pattern in the dorsal retractor muscle (Fig. 7a; RD') closely match the double burst found by Liem (1989) in the interhyoideus muscle. The two
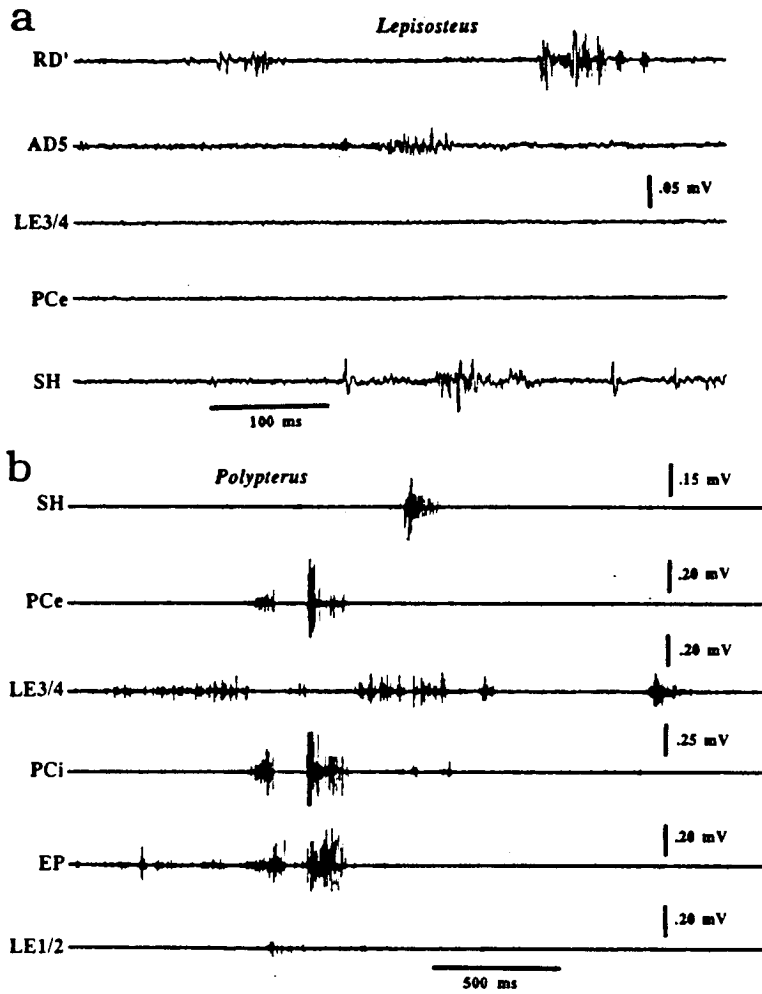
Figure 7.
a) Pattern of electromyographic activity in pharyngeal jaw muscles during air ventilation in *Lepisosteus*. Note the double burst pattern in the RD' and the presence of SH activity between the RD' bursts.
b) Pattern of electromyographic activity in pharyngeal jaw muscles during air ventilation in *Polypterus*. Note the high-amplitude activity in the ventral pharyngeal muscles (PCe and PCi) and the similar pattern of activity in the epaxial muscles (EP). Abbreviations: AD5, fifth branchial adductor; EP, epaxial muscles; LE3/4, levatores externi three and four muscles; LE1/2, levatores externi one and two muscles ; PCe, pharyngocleithralis externus; PCi, pharyngocleithralis internus; RD', dorsal retractor muscle; SH, sternohyoideus.

interhyoideus bursts occurred as air was being expired from and inhaled into the lung (Liem, 1989).

In *Polypterus* the ventral pharyngeal jaw musculature is strongly active in a complex pattern during air ventilation (Fig. 7b). Especially noteworthy is the nearly synchronous double burst pattern of activity in the pharyngocleithralis externus and internus and the epaxial muscles. Head elevation and retraction of the lower pharyngeal jaw may facilitate air entry and exit from the ventrally opening pneumatic duct into the lung.

SUMMARY AND SYNTHESIS

When a muscle arises convergently in a clade does it also show convergence in function? The results presented in this case study indicate that at least for the retractor dorsalis muscle the answer is yes. The pharyngeal jaw apparatus in the "primitive" living ray-finned fishes *Polypterus*, *Lepisosteus*, and *Amia* has two impor-

tant biological roles: swallowing of prey and air ventilation. Electromyographic data confirm that the dorsal retractor muscle is critical to both functions in *Lepisosteus* and *Amia*.

During swallowing, the PJA functions primarily to macerate prey and to transport food from the buccal cavity into the esophagus. The morphology and function of the PJA in the ray-finned fishes *Polypterus*, *Lepisosteus*, and *Amia* provide a guide to primitive features of the PJA in actinopterygians and to the pattern of historical transformation in form and function. Primitively, the actinopterygian PJA possesses levatores interni and externi muscles dorsally, and pharyngocleithralis externus and internus muscles ventrally. *Lepisosteus* and *Amia* possess a dorsal retractor muscle convergent to that characterizing the Neoteleostei. Primitively in ray-finned fishes swallowing of prey is achieved using the lower pharyngeal jaw because a dorsal retractor muscle is lacking. Electromyographic analysis of the activity pattern (motor pattern) of pharyngeal jaw muscles shows that the dorsal retractor muscle (RD') of *Lepisosteus* and *Amia* is active at low amplitude during swallowing in a rhythmic bursting pattern. The RD' shows a muscle activity pattern that is convergent to that of the retractor dorsalis in neoteleost fishes. Inactivity of the sternohyoideus during swallowing is hypothesized to be a primitive functional feature of ray-finned fishes.

During airbreathing the ventral pharyngeal jaw muscles of *Polypterus* are strongly active while in *Amia* and *Lepisosteus* it is the RD' and other dorsal muscles that show strong activity. We hypothesize that the RD' (of *Amia* and *Lepisosteus*) functions to open the glottis (located ventrally in *Polypterus* and dorsally in *Amia* and *Lepisosteus*) allowing air to pass into and out of the lung during air ventilation.

The electromyographic patterns illustrated here show clearly that convergence in function of the dorsal retractor muscle between *Amia*, *Lepisosteus*, and neoteleost fishes has also been accompanied by apomorphic functional patterns associated with air breathing. Thus, convergence of function in one biological role is associated historically with specialization in another biological role. The origin of the RD' in *Lepisosteus* and *Amia* might be correlated historically with the origin of a lung containing a dorsal pneumatic duct with a glottis opening into the anterior part of the esophagus. The use of the RD' in swallowing may be historically incidental to the role of this muscle in air breathing.

In addition, the origin of a dorsal retractor muscle as a novelty in primitive actinopterygian fishes (Fig. 1) produced a major shift in function of the pharyngeal jaw apparatus as a whole. Primitively (as reflected in *Polypterus*), the upper pharyngeal jaw played only a limited role in the swallowing of prey: the lower pharyngeal jaw performed the major protraction and retraction movements that move prey items into the esophagus. With the origin of a dorsal retractor muscle in *Lepisosteus* and *Amia*, the major actions of swallowing shifted to the upper pharyngeal jaws; this shift is associated with a major change in the motor pattern to pharyngeal jaw muscles. Primitive teleosts lack an upper pharyngeal jaw retractor muscle, and the lower pharyngeal jaw plays the dominant role in swallowing (Lauder, 1983b).

These results suggest that in the pharyngeal jaw apparatus both congruent and incongruent changes have occurred between morphological and physiological characters. Congruent specialization in the PJA has occurred in the relative activity patterns of the retractor dorsalis, levatores externi, and fifth branchial adductor: convergence has taken place in both morphological and functional characters. In contrast, while both *Lepisosteus* and *Amia* possess a dorsal retractor muscle, the ac-

tivity patterns of the levatores externi muscles are distinct (Fig. 5), indicating that not all functional characteristics of the pharyngeal jaw apparatus are correlated with the presence of a dorsal retracting muscle. This case study emphasizes the necessity of experimentally determining the function of structural features and of empirically examining the pattern of historical congruence between structure and function.

Finally, it is apparent that function (or muscle activity pattern) is no guide to homology as earlier proposed by Baerends (1958:409). Convergence in morphology of the retractor muscle has been accompanied by convergent function (during swallowing) *and* by divergent function (during airbreathing). The tool most useful for examining the historical congruence of form and function is a corroborated phylogenetic hypothesis.

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