Functional design and evolution of the pharyngeal jaw apparatus in euteleostean fishes

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Functional and structural patterns in the pharyngeal jaw apparatus of euteleostean fishes are described and analysed as a case study of the transformation of a complex biological design. The sequential acquisition of structural novelties in the pharyngeal apparatus is considered in relation to both current hypotheses of euteleostean phylogeny and patterns of pharyngeal jaw function. Several euteleostean clades are corroborated as being monophyletic, and morphologically conservative features of the pharyngeal jaw apparatus are recognized.

Functional analysis, using cinematography and electromyography, reveals four distinct patterns of muscle activity during feeding in primitive euteleosts (*Esox*) and in derived euteleostean fishes (*Perca, Micropterus, Ambloplites, Pomoxis*). The initial strike, buccal manipulation, pharyngeal manipulation, and the pharyngeal transport of prey into the oesophagus all involve unique muscle activity patterns that must be distinguished in analyses of pharyngeal jaw function. During pharyngeal transport, the upper and lower pharyngeal jaws are simultaneously protracted and retracted by the action of dorsal and ventral musculoskeletal gill arch couplings. The levator externus four and retractor dorsalis muscles, anatomical antagonists, overlap for 70–90% of their activity period. Levatores externi one and two are the main protractors of the upper pharyngeal jaws in the acanthopterygian fishes studied. The major features of pharyngeal jaw movement in primitive euteleosts are retained in many derived clades in spite of a dramatic structural reorganization of the pharyngeal region. Homologous muscles have radically changed their relative activity periods while pharyngeal jaw kinematics have been modified relatively little.

Patterns of transformation of activity may thus bear little direct relationship to the sequence of structural modification in the evolution of complex designs. Overall function of a structural system may be maintained, however, through co-ordinated modifications of the timing of muscle activity and anatomical reorientation of the musculoskeletal system. Deeper understanding of the principles underlying the origin and transformation of functional design in vertebrates awaits further information on the acquisition of both structural and functional novelties at successive hierarchical levels within monophyletic clades. This is suggested as a key goal of future research in functional and evolutionary morphology.

KEY WORDS:—Functional morphology – Euteleostei – pharyngeal jaws – evolutionary novelty – feeding mechanics – electromyography.

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INTRODUCTION

Of the two major themes in the history of morphology, functional design and diversity of form, functional morphologists have focused most intensively on organismal design. The diversity of morphology and its underlying theme of unity of type has, since the late nineteenth century, been the province mostly of phylogenetic research (Russell, 1916) which has run the gamut from reconstruction of ancestral morphotypes to modern cladistic analysis.

Functional design in organisms has been investigated primarily in relation to two goals. First, how do organisms work? For example, what are the mechanisms by which movement occurs during locomotion, feeding, or breathing in vertebrates? Biomechanical research of this type has benefited enormously from the infusion of new experimental techniques such as electromyography, cinematography, and pressure and strain recording devices. Experimental analyses are no longer limited by inferring muscle activity patterns or fluid pressures from bone kinematic patterns.

A second goal of research in functional morphology has been to clarify the relationship between organisms and the environment (Gans, 1974). How do different patterns of activity exhibited by organisms relate to the environments they inhabit and fluctuations of those environments? A frequently claimed aim of functional analyses of organism–environment interactions is the inference of selective pressures that have governed the origin of morphological novelties.

One approach to the analysis of biological design that has yet to be adequately explored concerns the historical origin and transformation of structure and function. The methodology of structural analysis in historical biology has been investigated in detail over the last 10 years (Eldredge & Cracraft, 1980; Nelson & Platnick, 1981; Wiley, 1981; Lauder, 1982) and has emphasized the reconstruction of historical changes in morphology and geographic distribution. But the historical relationship between the sequential acquisition of structural *and* functional novelties remains to be examined. Few investigations have analysed patterns of structural and functional novelties at successive hierarchical levels within a monophyletic clade.

In this paper I present a case study in the transformation of functional design that involves both structural analysis within an explicitly phylogenetic context and the experimental determination of functional patterns at several hierarchical levels. The pharyngeal jaw apparatus, a complex set of modified gill arches and associated muscles and ligaments in the pharynx of ray-finned fishes, is the structural system chosen for study. A general goal is to provide a foundation for evaluating the historical relationship between structural and functional novelties, especially in regard to the origin of complexity of design.

The phylogenetic hypothesis that serves as the basis for this paper is the cladogram of euteleostean fish relationships first proposed by Rosen (1973) and

subsequently modified by Fink & Weitzman (1982). A summary cladogram is presented in Lauder & Liem (in press). According to this hypothesis, the euteleostean fishes form a monophyletic lineage of about 17 000 species united by the possession of three derived characters: an adipose fin, breeding tubercles, and the structure of caudal uroneurals (Patterson & Rosen, 1977). The most primitive euteleostean clade is the Esocae (Fink & Weitzman, 1982) containing the pikes and pickerels. The interrelationships of other primitive euteleosteans are still poorly known and the Ostariophysi, Argentinoidei, Osmeroidei, Salmonidae and the neoteleostean fishes are grouped in an unresolved polychotomy near the base of the Euteleostei. The clade Neoteleostei is well-defined and includes the deep-sea stomiatoids (viperfishes), aulopiforms, myctophids (hatchetfishes), paracanthopterygians (cods and batrachoid fishes, among others), atherinomorphs, and percomorph fishes (a summary cladogram is presented in Fig. 28). It is important to note that the cladistic branching pattern within the Euteleostei is corroborated by the distribution of morphological features other than those found in the pharyngeal region. A non-circular approach to the historical analysis of design requires a cladogram to be corroborated by structural features other than those investigated experimentally.

Given an initial corroborated phylogenetic hypothesis, two further steps are involved in this analysis of pharyngeal design in fishes. First, a comparative morphological investigation of the pharyngeal jaw apparatus (especially branchial myology) in each of the major euteleostean clades is conducted to establish the sequence and nature of structural change during euteleostean evolution. Mapping the structural specializations in each terminal taxon onto the initial phylogenetic hypothesis reveals both features primitive for the Euteleostei and specializations of the pharyngeal jaw apparatus, if any, at each hierarchial level (Lauder, 1981). Second, the experimental study of pharyngeal jaw function in terminal taxa within the Euteleostei allows functional specializations (such as a unique muscle activity pattern) to be identified for each clade. Muscle activity patterns are treated in the same way as structural specializations and mapped, using parsimony, onto the initial phylogenetic hypothesis. This procedure reveals the distribution of functional novelties within the Euteleostei. Correlations or general relationships between structural and functional novelties at each hierarchical level can then be examined and used to test general explanations for the origin and transformation of 'character complexes', or the modification of central neural 'programmes' in relation to peripheral structural systems. Higher level historical hypotheses about the design of organisms can best be tested by comparing the predictions of such hypotheses against inferred sequences of structural and functional modification.

The analysis of evolutionary patterns in the pharyngeal jaw apparatus of fishes has been hindered both by the lack of a rigorous descriptive framework and by the scarcity of experimental data on generalized taxa. Cichlid pharyngeal jaw mechanisms have been studied in detail (Liem, 1973, 1978) but comparative data are lacking on generalized non-pharyngognath teleosts. Without such data, it is impossible to know which muscle activity patterns, for example, are derived for pharyngognath fishes and which are general acanthopterygian or teleost features.

The problem of defining a relevant descriptive classification of functional activity is analogous to the difficulties faced by mammalian functional morphologists in dividing the masticatory cycle into biologically relevant segments (Hiiemae, 1978). The aim of any functional classification is to reflect accurately biological

events and to order these events into natural clusters that facilitate interspecific comparisons. Unless distinct movements are recognized and divided into phases based on consistent kinematic patterns and muscle activities, biologically meaningful events will be hidden in a single highly variable descriptive class. The evaluation of chewing mechanics and the transformation of functional design is crucially dependent on an accurate division of organismal activity into natural units.

In this paper, I will use the classification presented in Lauder (in press), and describe electromyographic patterns that uniquely characterize each movement pattern. Four separate aspects of fish feeding behaviour have been identified: the initial strike, buccal manipulation, pharyngeal manipulation, and pharyngeal transport of prey into the oesophagus. Each of these four movements is distinct and recognizable by either the pattern of jaw bone movement or muscle activity, and the presence of three activity patterns following the initial capture of prey appears to be a primitive feature of euteleostean fishes.

MATERIALS AND METHODS

Preserved specimens of each of the major euteleost lineages were examined for morphological data on the pharyngeal jaw apparatus. The clades examined include the Esocae, Ostariophysi, Salmonae, Argentinoidei, Osmeroidei, Stomiiformes, Aulopiformes, Myctophiformes, Paracanthopterygii, Atherinomorpha and Percomorpha. In some lineages such as the Ostariophysi and Stomiiformes, species currently hypothesized to be primitive (e.g. *Chanos* and *Diplophos*) were selected for detailed analysis, and only certain characters were examined in more derived species. In lineages such as the Myctophiformes a broad range of comparative material was examined. Only the acanthopterygian species studied experimentally were dissected in detail. The genera, species, and museum numbers for specimens examined are available from the author.

Experimental analysis of feeding behaviour was conducted using high-speed cinematography and electromyography. A Photosonics 16-1PL high-speed camera was used in conjunction with Kodak 4X Reversal film to study jaw bone movement. Electromyographic signals were recorded through fine wire (0.051 mm) steel alloy bipolar electrodes as described previously (Lauder, 1980a), and recorded on a six-channel Bell and Howell 4020A FM tape recorder. Grass P511J preamplifers were used with the low pass filter set at either 30 Hz or 100 Hz and the high pass filter at 3000 Hz. The 60 Hz notch filter was used at all times. Electromyograms were recorded at 37.5 cm s^{-1} and played back at 4.7 cm s^{-1} through a Gould 260 chart recorder.

X-ray cinematographic data were available for the genus *Lepomis* (discussed in a forthcoming paper) and the results of that analysis in addition to high-speed films were used to establish the kinematic patterns associated with muscle activity.

A wave generator was used to test the frequency response of the entire electromyographic apparatus. Frequencies varying from 100 to 1000 Hz were accurately reproduced on the chart recorder after being amplified, recorded on FM tape and played back. Thus little loss in muscle signal amplitude should occur since the peak power of striated muscle electromyograms lies between 100 and 300 Hz.

Muscle electrical activity was analysed by the following procedure. A reference

muscle was chosen for each of the four categories of feeding behaviour outlined in the Introduction: initial strike and buccal manipulation—sternohyoideus; pharyngeal manipulation—obliquus inferioris; pharyngeal transport—retractor dorsalis. These reference muscles were selected on the basis of preliminary experiments and previous research which showed that they had a clearly definable action, consistent activity pattern, and lacked significant asymmetry in activity between the right and left sides. The onset of activity in the reference muscle was taken as the 'zero point' from which the onset and offset of activity in all muscles was determined (see Figs 13, 14 & 16 for examples). Mean times of onset and offset relative to reference muscle onset were calculated as was the standard error for each mean. This procedure is similar to that of Jenkins & Weijs (1979). Each bar diagram of muscle activity represents a summary of at least 15 recordings for each muscle, and often considerably more. For the analysis of pharyngeal transport, a repetitive cyclical process, two sequential bursts of activity in the reference muscle were chosen as the standard for comparison (e.g. Fig. 16).

Because choosing the onset of activity in one muscle limits the contribution that variability in the onset time of this muscle makes to the total electromyographic pattern, histograms of burst duration were constructed (e.g. Fig. 19) to illustrate the variability in total activity period of the reference muscles. In the case of the retractor dorsalis, burst duration was very similar in distribution to that of other muscles, while the sternohyoideus and obliquus inferioris showed considerably less variation in activity duration. The summary diagrams presented in this paper include variability between individuals, different prey types, and activity from different times in the chewing cycle.

Electrodes were implanted in the pharyngeal muscles while the experimental subject was anaesthetized as described in Lauder (1980a). Each of the pharyngeal muscles with the exception of the retractor dorsalis could be identified visually and the electrode placed through the thin mucous membrane over the gill arch muscles directly into the muscle belly. At least one of the reference muscles (sternohyoideus, obliquus inferioris, or retractor dorsalis) was always implanted. At the end of a series of experiments on a particular fish, the location of the electrode tips was confirmed by dissection.

Six species were studied experimentally: *Micropterus salmoides* (Lacepède) (3), *Ambloplites rupestris* (Rafinesque) (6), *Pomoxis nigromaculatus* (Lesueur) and *P. annularis* (Rafinesque) (2 each) (all in the perciform family Centrarchidae), *Perca flavescens* (Mitchill) (2), and *Esox niger* (Lesueur) (4). (The number in parentheses represents the number of individuals examined.) A wide variety of prey was used to assess the dependence of muscle activity pattern on prey type and size: earthworms (*Lumbricus*), crayfish (*Orconectes*), golden shiner (*Notemigonus crysoleucas* (Mitchill), fathead minnows (*Pimephales promelas* Rafinesque), goldfish (*Carassius auratus* (L.)), and emerald shiners (*Notropis atherinoides* Rafinesque).

This paper will focus on the pattern of functional activity in the most primitive euteleostean clade, the Esocae (as represented by *Esox niger*) in comparison to the pattern exhibited by acanthopterygian teleosts (*Micropterus, Ambloplites, Pomoxis* and *Perca*). Several euteleostean clades are not easily analysed experimentally because most species live in relatively inaccessible open ocean or deep sea habitats (e.g. Stomiiformes, Aulopiformes, Myctophiformes). Experimental data on the Salmonidae, Paracanthopterygii and Atherinomorpha will not be reported here. Monophyly of the Paracanthopterygii is not well established (Lauder & Liem, in

press) and the precise phylogenetic relationships of the Salmonidae and Atherinomorpha have yet to be ascertained.

RESULTS

Structural patterns

The pharyngeal jaw apparatus consists of gill arches, branchial muscles, and ligaments and articular capsules which interconnect gill arch elements. The musculoskeletal couplings involved in mediating gill arch movement extend beyond the branchial apparatus proper to connect to the mandible, hyoid, neurocranium and pectoral girdle. A diagrammatic guide to the pharyngeal jaw mechanisms of euteleostean fishes is presented in Fig. 1 as an aid to understanding the evolutionary modifications of this system, and as a general plan of the line of action of the numerous pharyngeal muscles. The following descriptions emphasize, but are not limited, to the species studied experimentally, and do not recapitulate anatomical information on euteleostean fishes available in the literature (e.g. Allis, 1903; Tchernavin, 1953; Gunther & Deckert, 1960; Kampf, 1961; Nelson, 1969; Joppien, 1970; Rosen, 1973; Winterbottom, 1974; Johnson, 1980; Parenti, 1981; Stiassny, 1981; Travers, 1981; Fink & Weitzman, 1982). Further comparisons are considered in the Discussion.

In *Esox*, as in most other primitive euteleosteans, the endoskeletal components of the upper and lower pharyngeal jaws are well developed. The toothplate of ceratobranchial five is fused to, but does not completely cover, the endoskeletal
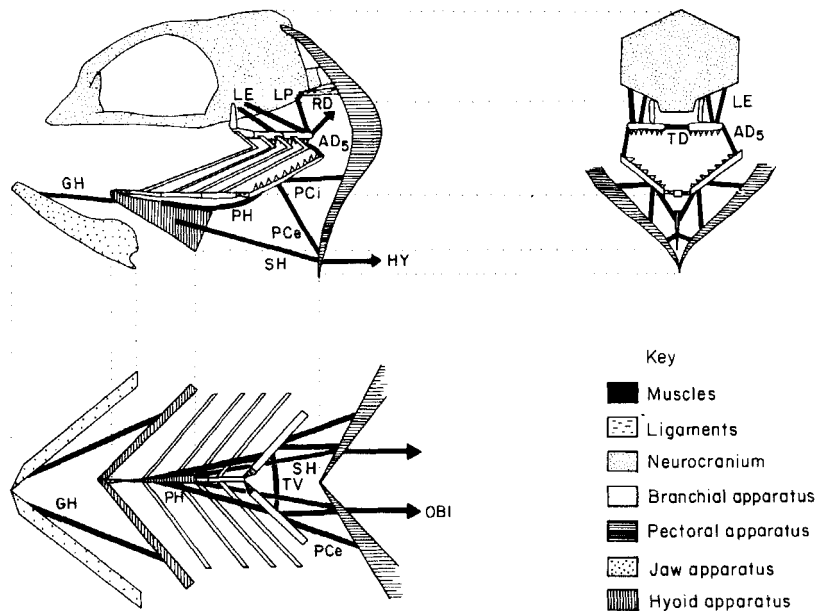

Figure 1. Schematic diagram of the musculoskeletal couplings in the pharyngeal jaw apparatus of euteleostean fishes. The pharyngeal jaws are tooth-bearing, modified components of the gill arch skeleton located postorbitally in the pharynx. This diagram may be used as a general guide to understanding the mechanical effects of the muscle activity patterns illustrated in Figs 10–18.
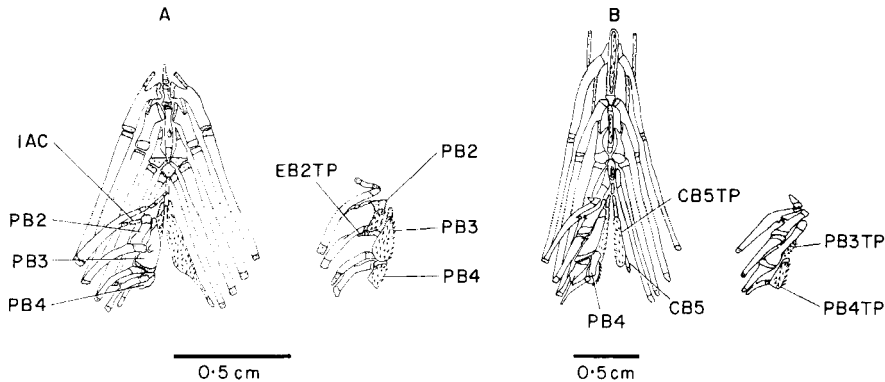
Figure 2. Gill arch skeleton of (A) *Micropterus salmoides* and (B) *Esox niger*. The dorsal gill arches on the right side have been displaced and are displayed in ventral view. Toothplates are only distinguished by labels from endoskeletal gill arch elements where both are clearly recognizable. The epibranchial two toothplate in *Micropterus* is not fused to the arch. Note the relative sizes of the toothed elements and the relationships of the upper to lower toothplates in the two species.

ceratobranchial (Fig. 2B) in contrast to *Micropterus*, for example, which possesses an extensive lower pharyngeal toothplate (Fig. 2A). The third and fourth epibranchials in both *Esox* and *Micropterus* articulate via uncinate processes, while the first two epibranchials are connected indirectly by pharyngobranchial two. The first two hypobranchials possess strong ligaments which extend anteriorly to attach to the hyoid and next anterior hypobranchial (Fig. 2A). In *Esox* the ventrally directed third hypobranchials also have thick ligamentous connections to the hypobranchials of arch two (Fig. 2B). In all myctophiform genera examined for this character (*Myctophum, Electrona, Notoscopelus, Lampanyctus, Ceratoscopelus, Gymnoscopelus*) the third hypobranchials extend ventrally to attach ligamentously to the urohyal (e.g. *Myctophum*, Fig. 5). The urohyal is in effect sandwiched between the third hypobranchials on each side. The close association between gill arches three and four indicated by the epibranchial articulations in *Esox* and *Micropterus* also occurs between the fourth and fifth ceratobranchials which are commonly attached by a broad band of dense connective tissue.

In non-neoteleostean euteleosts as well as in aulopiforms, the rectus communis (also called the pharyngohyoideus) originates from the third hypobranchial and inserts posteriorly on ceratobranchial five (Figs 3A, 6A). The Myctophiformes, Paracanthopterygii and Acanthopterygii all possess a pharyngohyoideus muscle originating from the lateral surface of the urohyal (Figs, 3B, 6B, 7A, 8B) or from both the urohyal and hypobranchial three (Fig. 5A). This change in origin represents an important structural specialization with significant consequences for pharyngeal jaw function. The origin of the pharyngohyoideus on the urohyal increases the range of anteroposterior excursion of the muscle origin due to increased mobility of the urohyal relative to the gill arches and the longer muscle fibres. This compares with an essentially immobile origin on hypobranchial three in primitive euteleosteans. In addition to greater potential anteroposterior excursions of the lower pharyngeal jaw, the pharyngohyoideus muscle is able to rotate the distal tip of ceratobranchial five anteriorly, around its ligamentous attachment to the posterior basibranchial (Fig. 1). Because the line of action of the pharyngohyoideus muscle is lateral to the vertical axis of rotation of the lower

pharyngeal jaw at its attachment to the basibranchials, anterior rotation of ceratobranchial five will occur.

The stomiiform rectus communis (homologous to the pharyngohyoideus muscle, see Discussion, p. 25 & 26), when present, is specialized with respect to the condition in other primitive euteleosts. This muscle is apparently absent in *Diplophos* and *Gonostoma* but is present in all other stomiiforms examined (*Yarella, Chauliodus, Malacosteus, Ichthyococcus, Stomias, Astronestes, Sternoptyx*). In these genera the rectus communis invariably inserts on ceratobranchial five and its origin is usually from
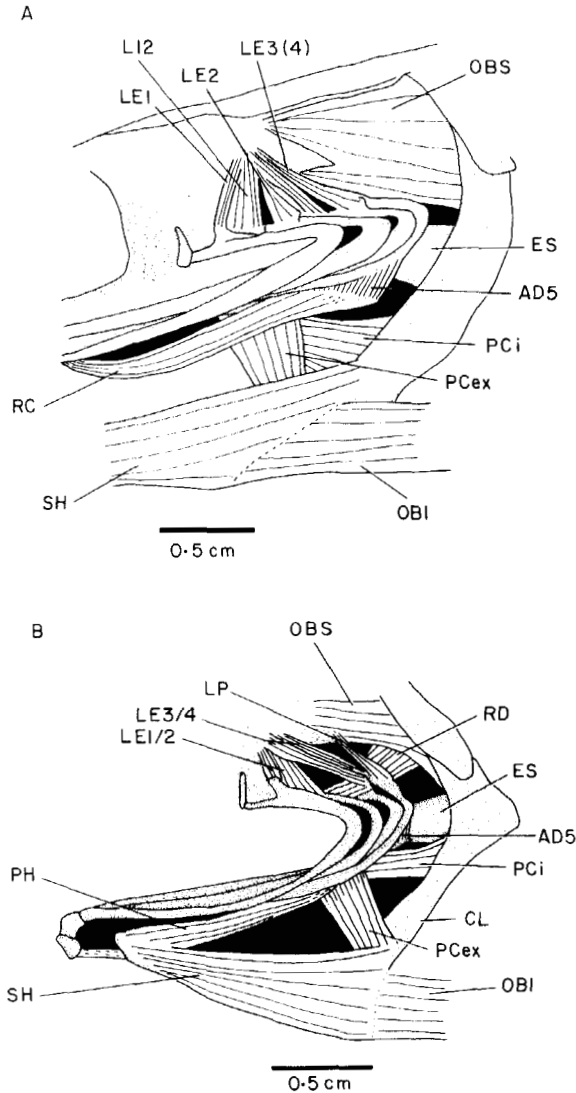
Figure 3. Lateral view of the gill arch musculature in (A) *Esox niger* and (B) *Micropterus salmoides*. The gills and mucous membrane covering the medial wall of the branchial chamber have been removed in this and all subsequent lateral views. The protractor pectoralis muscle has also been removed in *Micropterus*. Note the differing lines of action of the anterior and posterior branchial levator muscles and that in *Esox* many of the fibres from the fifth branchial adductor insert on ceratobranchial four.
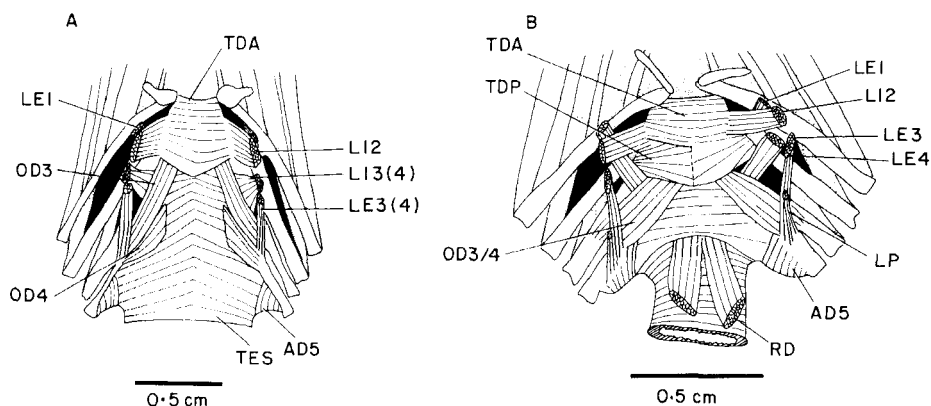
Figure 4. Dorsal view of the gill arch musculature in (A) *Esox niger* and (B) *Micropterus salmoides*. In (B), the left side of the transversus dorsalis epibranchialis two (TDP) has been removed to show the underlying fibre arrangement, and levator externus one on the left side has also been removed.

the ventral surface of the basihyal or anterior basibranchials. In *Astronestes* and *Yarella*, the rectus originates from hypobranchial three.

The anatomical antagonists of the pharyngohyoideus are the transversus ventralis posterior, pharyngocleithralis internus, and pharyngocleithralis externus (Fig. 1). These muscles exhibit little variation in line of action throughout the Euteleostei. The pharyngocleithralis internus, originating on the cleithrum and inserting anteriorly on ceratobranchial five, is oriented anteroposteriorly and is the dominant retractor of the lower pharyngeal jaw (Figs 3, 5–8). The pharyngocleithralis externus is usually nearly vertical in orientation and originates from the anteroventral limb of the cleithrum, often medial to the sternohyoideus. The pharyngocleithralis externus invariably inserts on the fifth ceratobranchial, and has a lateral component to its line of action in addition to the dominant posteroventral orientation. Both the pharyngocleithralis internus and externus may insert near the anterior tip of the lower pharyngeal jaws as in *Myctophum*, or onto cartilaginous basibranchial four (*Esox*), and in this case will have little effect on ceratobranchial five independently of the entire branchial basket.

The transversus ventralis posterior is present in all euteleosteans examined. This muscle extends between the two fifth ceratobranchials on each side and draws them toward the midline (Figs 1, 9A). In some species (e.g. *Perca*) the posterior fibres of the transversus ventralis posterior merge into the outer transverse muscle layer surrounding the oesophagus (Fig. 9A) which also attaches to the fifth ceratobranchials. Most euteleosts also possess a transversus ventralis anterior interconnecting the fourth ceratobranchials (Figs 6, 9A) on each side. At least some atherinomorphs are specialized in possessing transversus muscles between four gill arches. In *Fundulus majalis* (Walbaum), transversus ventralis one connects the first hypobranchials, and fibres from this muscle merge anteriorly with fibres of obliquus ventralis one from which the transversus appears to be derived. Transversus two interconnects the second hypobranchials of each arch; arch three has no transversus, and arches four and five have well developed transversus muscles.

Obliqui ventrales muscles are usually present between the hypobranchial and ceratobranchial components of the first three arches and often the fourth obliquus
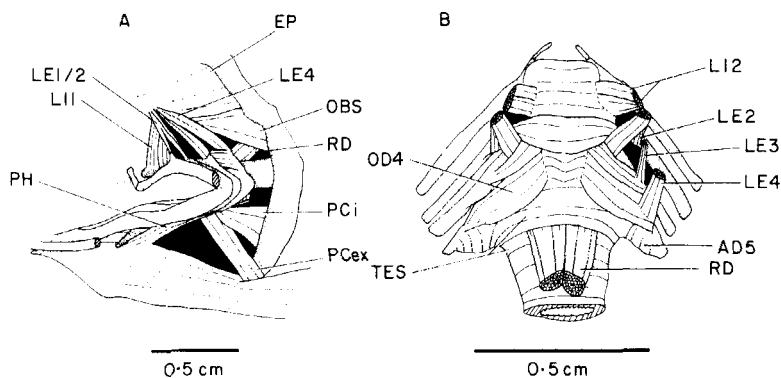
Figure 5. Lateral (A) and dorsal (B) views of the branchial musculature in *Myctophum nitidulum* Garman. The protractor pectoralis has been removed in (A) and levator externus one and the left levatores externi three and four in (B).

is present also (Fig. 9A). *Esox niger* lacks obliquus four as does *Micropterus salmoides* which possesses a rectus ventralis muscle originating from hypobranchial three and inserting on ceratobranchial four.

A fifth branchial adductor muscle is present in all species examined and connects the posterodorsal tip of ceratobranchial five with epibranchial four (Figs 3–9). The fibres of this muscle generally extend dorsoventrally but may, as in *Esox*, be inclined posterodorsally and partially insert on ceratobranchial four.

The dorsal branchial muscles in euteleosteans have undergone considerably greater modification in line of action, number, and origin and insertion than the ventral gill arch muscles. In *Esox* the anterior branchial levators, levator externus one and levator internus one, are inclined posterodorsally from their origin on epibranchial one and pharyngobranchial two (Figs 3A, 4A). These levators have a line of action that is directed posterodorsally and laterally. They are thus capable of mediating posterior movements of the upper pharyngeal jaws, as well as serving as antagonists to the transversus dorsalis anterior which spans the second pharyngobranchials (Fig. 4A).
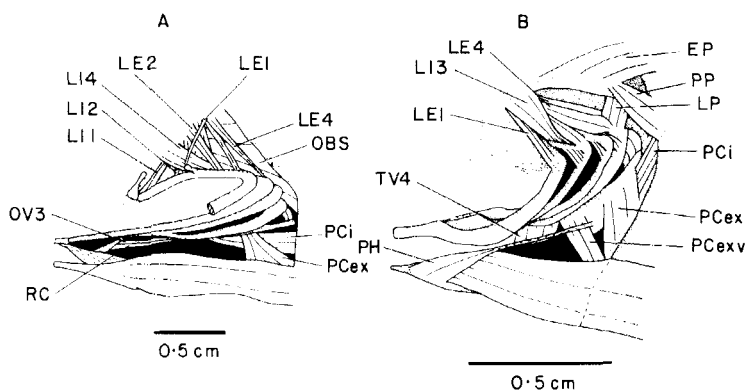
Figure 6. Lateral views of the branchial musculature in (A) *Bathypterois quadrifilis* Günther and (B) *Fundulus majalis*. The protractor pectoralis has been removed in (A) and the retractor dorsalis is not visible in this view. In (B), neither the retractor dorsalis nor adductor arcus branchialium one are visible.

Many non-acanthomorph fishes (Acanthomorpha = Paracanthopterygii + Acanthopterygii, Rosen, 1973) have either the anterior levatores interni or externi inclined posterodorsally. In myctophiforms all the levatores externi have a posteroventral line of action (Fig. 6A), a derived condition for ctenosquamate fishes as this orientation is also found in *Micropterus* (Fig. 3B), *Fundulus* (Fig. 6B), *Pollachius* (Fig. 7A) and *Perca* (Fig. 8B). The anterior internal levators in myctophiforms are vertically oriented and have only a slight posterior inclination in their line of action, a condition also present in *Diplophos* and *Salvelinus*. Aulopiform fishes display considerable variability in dorsal gill arch musculature. *Alepisaurus* has no internal levators, while levatores externi three and four are posteroventrally inclined, the primitive euteleostean condition. *Bathypterois*, on the other hand, possesses all four levatores externi and interni which are arranged in a complex crossed pattern (Fig. 6A). Levatores interni one and two and levator externus one are posterodorsally inclined while all other levators are oriented posteroventrally. The orientation of branchial levators is important in considering the possible functions of these muscles, and in relation to the evolution of the dominant pharyngeal retractor in neoteleostean fishes, the retractor dorsalis.

The retractor dorsalis originates from one or more of the first 10 vertebrae and extends anteroventrally to insert on the pharyngobranchials (Figs 3B, 4, 5A). The retractor dorsalis may pass between the transversus dorsalis posterior and the circular layer of oesophageal muscle (e.g. Fig. 4B), or it may pierce through the oesophageal muscles and extend anteriorly to insert on the pharyngobranchials (Figs 5B, 7B, 9B). Rosen (1973) described a separation of the retractor dorsalis into internal and external divisions in ctenosquamate fishes, and this division has been confirmed here for some species. In *Perca*, there is a prominent, well-developed, parallel-fibred band of muscle that merges posteriorly with the longitudinal oesophageal muscle layer. This band extends anteriorly to insert along the medial margin of pharyngobranchial three. The retractor dorsalis in *Perca* inserts on pharyngobranchials three and four.

Although the separate band of fibres inserting on pharyngobranchial three in *Perca* arises from the oesophageal muscles, it appears to be homologous with a thin strap-like internal division of the retractor dorsalis in *Myctophum* that inserts on pharyngobranchial three. The main external retractor division inserts only on
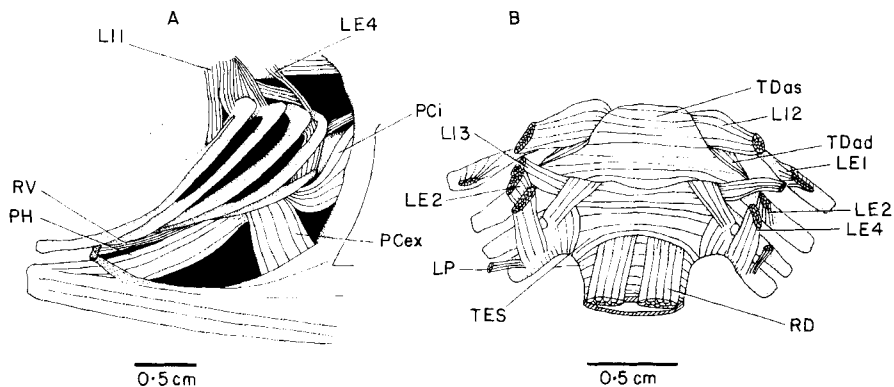

Figure 7. Lateral (A) and dorsal (B) views of the branchial musculature in *Pollachius virens* (L.). The protractor pectoralis has been removed in (A).

A

HB3

PBI

IAC

PB3

EB2

CB5

PB4

0·5 cm
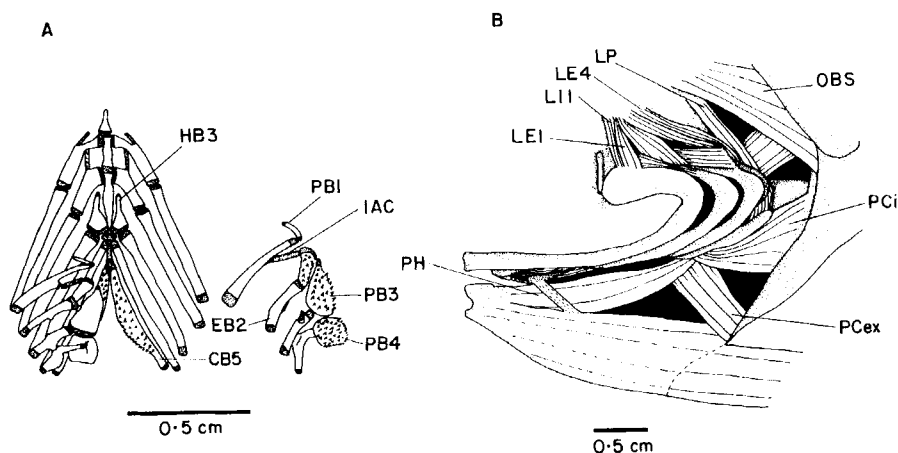
B

LP
LE4
LI1
LEI

OBS

PCi

PH

PCex

0·5 cm

Figure 8. The branchial skeleton (A) and lateral gill arch muscles (B) of *Perca flavescens*. The toothplate on epibranchial three is fused to the underlying bone, and the protractor pectoralis in (B) has been removed.

pharyngobranchial four. In *Pollachius*, the retractor dorsalis also inserts on pharyngobranchial four, and a thin internal strap of longitudinal oesophageal muscle extends anteriorly to attach to pharyngobranchial three. *Fundulus* lacks an internal section of the retractor dorsalis and this muscle inserts exclusively on pharyngobranchial four.

The retractor dorsalis functions both to move the upper pharyngeal jaws posteriorly and to elevate the pharynx (Fig. 1). The anatomical antagonists of this muscle are the anteriorly inclined levatores interni and externi. These muscles elevate, protract, and also have a lateral component to their line of action (Fig. 1). Levatores externi three and four in centrarchids and *Perca* are closely apposed to each other throughout their length and are oriented predominantly in an anteroposterior direction. The third external levator inserts on the uncinate process of epibranchial three, while the fourth attaches to the base of the fourth epibranchial uncinate process, near the insertion of the levator posterior; there is relatively little dorsal component to their line of action. The muscle with the largest mechanical advantage for elevating the upper pharyngeal jaws is the levator posterior. This muscle is often absent in euteleosteans, and like the protractor pectoralis, has a sporadic phylogenetic distribution (Greenwood & Lauder, 1981). A levator posterior is present in centrarchids, *Perca* and *Fundulus* in which a posteriorly shifted origin gives the levator posterior a slight retractive line of action (Fig. 6B). No levator posterior was found in *Esox*, myctophiforms, or aulopiforms. A levator posterior does occur in some ostariophysans.

There is no distinct negative correlation in euteleosteans between the presence of a retractor dorsalis and posterodorsally inclined anterior levator muscles. Aulopiforms possess a retractor dorsalis as well as branchial levators with a 90° difference in line of action between the anterior and posterior levator muscles (Fig. 6A). Euteleosteans that lack the retractor dorsalis tend to have posterodorsally oriented anterior levators which have the capability of producing upper pharyngeal jaw retraction (see Fig. 3A).

Both transversus dorsalis anterior and posterior muscles are present primitively in all major euteleostean clades (Figs 4, 5, 7, 9B). In *Perca* and *Pollachius*, the caudal
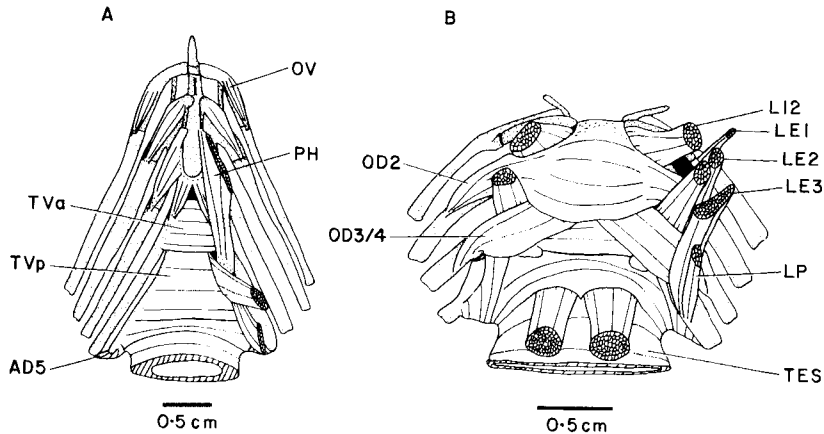
Figure 9. Ventral (A) and dorsal (B) gill arch musculature in *Perca flavescens*. The pharyngohyoideus and pharyngocleithralis internus and externus have been removed on the right side in (A). In (B), all levatores externi have been removed on the left side.

limit of the transversus dorsalis posterior is difficult to distinguish from the anterior transverse oesophageal muscle fibres. The transversus dorsalis anterior may originate from epibranchials one and two (as in *Myctophum*, Fig. 5B) or mostly from pharyngobranchial two (*Fundulus*).

Transversus dorsalis muscle fibres are often difficult to distinguish from anterior fibres of the obliqui dorsales muscles and some intermixing of fibres can occur. In *Perca*, for example, obliquus dorsalis two, which originates from epibranchial two on each side, merges medially with the transversus dorsalis anterior (Fig. 9B). Obliqui dorsales three and four are inseparable except at their origin from the two posterior epibranchials. In most euteleosts, the obliqui dorsales extend anteriorly to insert on the pharyngobranchials. The transversus dorsalis anterior in *Pollachius* has both a superficial and a deep component (Fig. 7B) which may represent a modified obliquus dorsalis two. Obliqui dorsales three and four are only rarely missing in euteleosts and are present primitively in all major euteleostean clades.

Overall, the pharyngeal jaw apparatus of generalized euteleostean fishes is a complex system of bones and muscles coupled to the skull, hyoid, mandible and pectoral girdle. Anteroposterior excursions of the gill basket are limited by the attachment of pharyngobranchial one to the skull (Fig. 1) and by movements of the hyoid and pectoral girdle. The upper pharyngeal jaws are constrained in their movement by extensive articulations with lateral epibranchials and by interconnections between the epibranchials themselves (Figs 2, 8A). Anteroposterior movement is only possible with concomitant motion at epibranchial·pharyngobranchial articulations, at ceratobranchial–epibranchial joints, and at the ventral joints between the ceratobranchials and hypobranchials.

Although the multiple muscular attachments to the lower pharyngeal jaw give the impression, especially in posterior view (Fig. 1), that the fifth ceratobranchials are suspended in a 'muscular sling' (Liem, 1978), movement of these bones is severely restricted in many generalized euteleosteans by two attachments. Anteriorly, the lower pharyngeal jaws attach via strong ligaments to the basibranchials, severely limiting anteroposterior movement of the ceratobranchials relative to the hyoid arch. Secondly, the fifth ceratobranchials are often

ligamentously attached to the fourth ceratobranchials. In centrarchids this connection may be very broad so that there is little independent movement between these two bones.

Finally, ceratobranchial five is attached to the upper pharyngeal jaws by the relatively short-fibred fifth branchial adductor. This muscle will limit the degree of independent motion between the upper and lower pharyngeal jaws, although some species (e.g., *Esox*) have a relatively long adductor muscle.

Functional patterns

Esocae

The process of prey capture and swallowing in *Esox* can be divided into four distinct phases, each with a unique electromyographic profile (Fig. 10): the initial strike, buccal manipulation, pharyngeal manipulation, and pharyngeal transport. Very little 'chewing' or maceration of the prey takes place other than that due to the upper jaw and mandibular teeth during positioning of the prey. Elongate prey items are often held crossways between the upper and lower jaws and then manipulated, turned, and swallowed headfirst using a similar set of motions to *Lepisosteus* (Lauder & Norton, 1980). No preparatory phase was observed in *Esox* (Fig. 10). All branchial muscles are active during the initial strike although considerable variability was found in the onset of activity in several of the muscles. The fifth branchial adductor and levator externus three and four, for example, become active from 120 to 10 ms prior to activity in the sternohyoideus.

During buccal manipulation of prey located in the anterior region of the mouth cavity, both the sternohyoideus and obliquus inferioris are active simultaneously in a much shorter duration burst than at the strike (Fig. 10). Some branchial muscles show little (levator externus one) or no activity (adductor five). Manipulation of prey located in the pharynx is unequivocally distinguished by the absence of activity in the sternohyoideus and the consistent occurrence of obliquus inferioris activity (Fig. 10). Cinematography reveals that the pectoral girdle is being retracted by the obliquus inferioris, and activity in the pharyngocleithralis internus and externus indicates that the lower pharyngeal jaws are being pulled
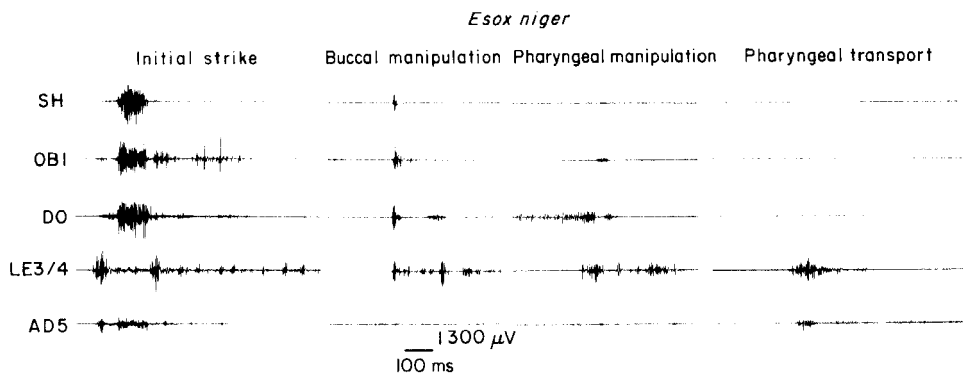

Figure 10. Simultaneous recordings of five jaw and branchial muscles during one feeding cycle in *Esox niger*. Different times during the feeding cycle have been selected to illustrate the four distinct electromyographic patterns associated with the initial strike, buccal manipulation, pharyngeal manipulation, and pharyngeal transport.

posteroventrally (confirmed by X-ray cinematography; Lauder, in prep.). The fifth adductor is inactive during pharyngeal manipulation and the upper pharyngeal jaw is elevated by activity in the levatores externi muscles. The overall effect of pharyngeal manipulation is to increase rapidly the distance between the upper and lower pharyngeal jaws allowing repositioning of the prey prior to transport.

In contrast to the three activity patterns just described which are not cyclical events and are of short duration, the process of pharyngeal transport involves repeated cycles of muscular activity (e.g. Figs 11, 15). Transport of prey items into the oesophagus may take up to several minutes if the prey is large.

Neither the sternohyoideus, obliquus inferioris, nor adductor mandibulae are active during pharyngeal transport (Fig. 11) and the pharyngocleithralis externus and the geniohyoideus are only active in less than half of the recorded swallowing sequences. A salient feature of the electromyographic profile during swallowing is the overlap in activity period between the two muscles capable of causing pharyngeal jaw retraction: the pharyngocleithralis internus and the anterior branchial levators (Fig. 11). Both the pharyngohyoideus and pharyngocleithralis internus are active for a significantly shorter period than the anterior branchial levators.

Protraction of the pharyngeal jaw apparatus occurs as a result of the posterior levators externi. These muscles are active just as the anterior levators stop and there is thus little overlap between the two sets of muscles.

Very little asymmetrical activity was observed in the pharyngeal muscles. Only levatores externi three and four exhibited significant asymmetry during
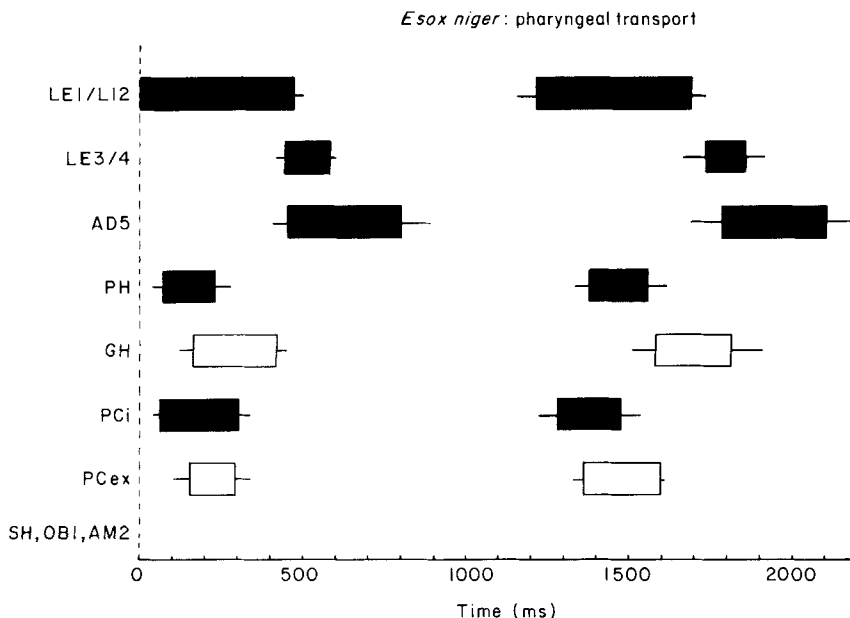

Figure 11. Bar diagram to illustrate the pattern of muscle activity during pharyngeal transport by *Esox niger*. Black bars indicate the duration of muscle activity. Thin lines indicate one standard error of the mean onset and offset times for each muscle. White bars indicate that activity was observed in less than 50% of the recordings. More information on the construction of this and subsequent bar diagram figures is given in Materials and Methods.

pharyngeal transport. The pattern of muscle activity during transport is relatively stereotyped as defined by the small standard error of mean (s.e.) onset and offset times for pharyngeal muscles (Fig. 11) relative to burst and interburst duration. The standard error is small even though muscle activities from different individuals, electrode placements, and prey are all averaged together to produce Fig. 11.

Acanthopterygii

All four of the distinct muscle activity patterns described for *Esox* were observed in the acanthopterygian fishes studied experimentally (see Materials and Methods); *Ambloplites* will be described in the most detail.

Figure 12 shows original recordings from one feeding sequence to illustrate the changing nature of muscle activity patterns. The initial strike possesses four discrete phases (Lauder, in press) including a preparatory phase. Several buccal manipulations may occur shortly after initial prey capture, and these show similar characteristics to buccal manipulations in *Esox*. Pharyngeal manipulation events then follow with rhythmic bursts of activity in the retractor dorsalis and other branchial muscles indicating the onset of pharyngeal transport.

All three muscle activity patterns prior to transport exhibit distinguishing features that uniquely define each pattern. 'Intermediate' patterns of muscle activity between these three categories do not occur. The initial strike (Fig. 13) contains a preparatory phase in which activity in the geniohyoideus, pharyngohyoideus and pharyngocleithralis externus is always present. The pharyngocleithralis internus is active in less than 50% of recorded feedings. All branchial, hyoid and mandibular muscles become active within a mean time of 25 ms from the onset of sternohyoideus activity. The variability in offset time is
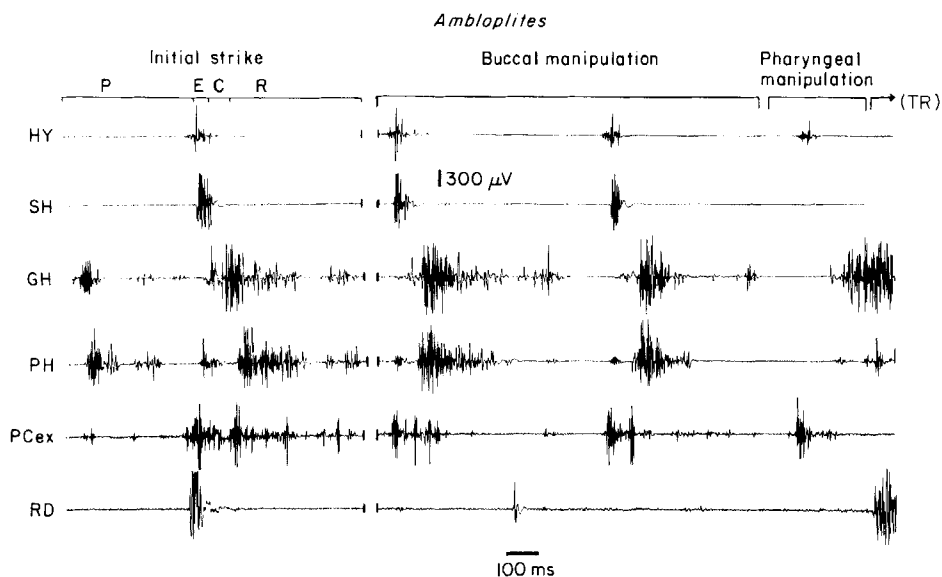

Figure 12. Simultaneous recordings of six jaw and branchial muscles during one feeding cycle in *Ambloplites rupestris*. Note the different patterns of muscle activity during the initial strike, buccal manipulation, pharyngeal manipulation, and pharyngeal transport (TR). See text for discussion.

slightly greater than onset time for several of the branchial muscles. The pharyngohyoideus exhibits a triphasic pattern during feeding (Fig. 13) with two significantly different bursts in the expansive and recovery phases. The adductor mandibulae becomes active with a mean of only 25 ms after the onset of activity in the sternohyoideus. The branchial muscle activity periods extend through the time of mouth opening and closing, into the recovery phase when the head bones are returning to their initial position (Lauder, in press).

Buccal manipulation and pharyngeal manipulation exhibit a significantly different pattern (Fig. 14). No preparatory phase is present and the duration and variability in offset time of several branchial muscles is considerably greater than during the initial strike. Buccal manipulation most closely resembles the initial strike (compare Figs 13 & 14). No activity in the sternohyoideus muscle is ever recorded during pharyngeal manipulation, and the retractor dorsalis and pharyngocleithralis internus are active less than half the time.

Neither the sternohyoideus nor the obliquus inferioris are active during pharyngeal transport (Figs 15, 16, 21). The pharyngocleithralis internus and the retractor dorsalis overlap for most of their activity periods, although the pharyngocleithralis does initiate and end activity significantly earlier than the retractor. There is also extensive overlap in activity period of levatores externi three and four, the levator posterior, and adductor five in all three centrarchids
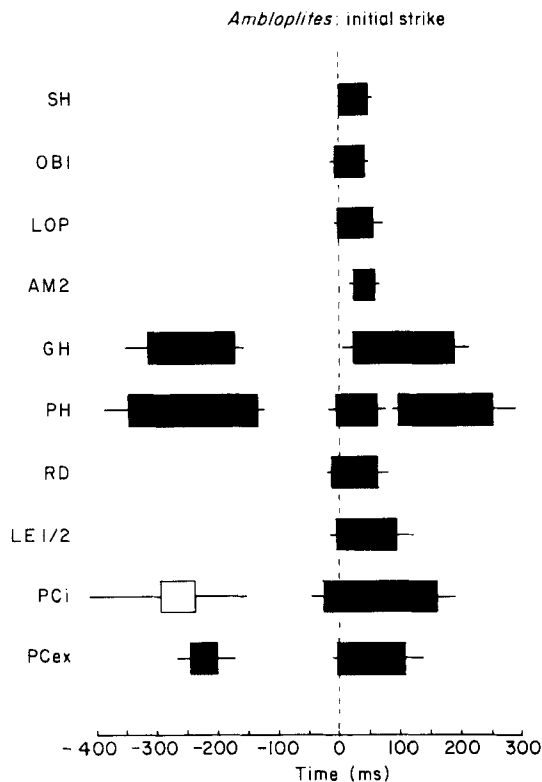

Figure 13. Summary pattern of muscle activity and variability during the initial strike by *Ambloplites rupestris*.
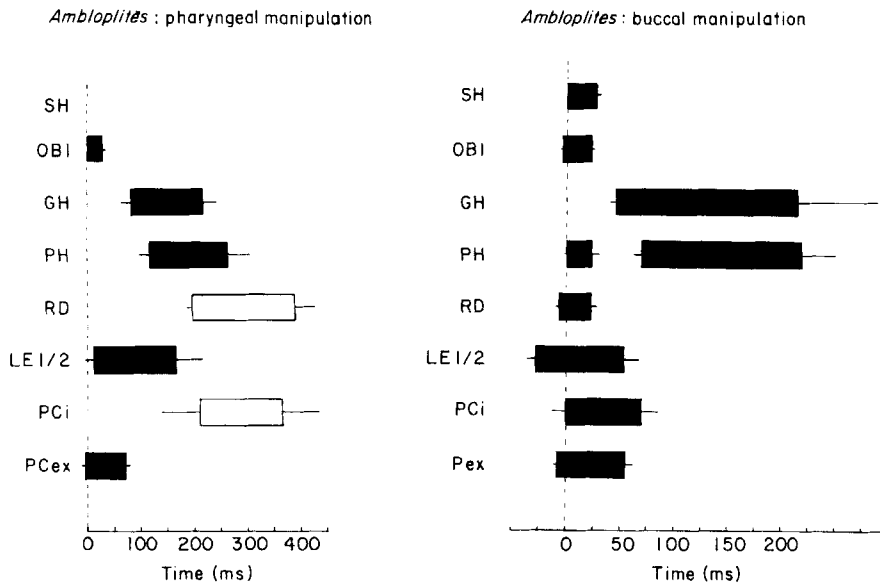
Figure 14. Summary pattern of muscle activity and variability during pharyngeal manipulation and buccal manipulation in *Ambloplites rupestris*.

examined (Figs 15–18). Levatores externi one and two consistently alternate in activity with levatores three and four, and in *Ambloplites* overlap extensively with activity in the pharyngohyoideus. This muscle shows very different activity patterns in the four acanthopterygians examined, and the differences correlate with patterns in the pharyngocleithralis externus muscle. In *Ambloplites*, both the pharyngohyoideus and pharyngocleithralis internus are active for a single burst which alternates with the retractor dorsalis (Fig. 16). Both muscles are active with the retractor dorsalis in *Micropterus*, *Pomoxis* and *Perca* although in these last two significant differences in timing do occur. But only in *Ambloplites* does pharyngohyoideus and pharyngocleithralis externus activity alternate with the retractor dorsalis.

The geniohyoideus muscle is also variably active during pharyngeal transport, the level of activity being mostly determined by the size of the prey. During swallowing of large prey, the geniohyoideus is active in concert with the pharyngohyoideus and adductor mandibulae (Fig. 17) to protract the branchial basket.

Retractor dorsalis burst duration was measured for the four species of centrarchids studied experimentally (Fig. 19). There was no significant difference between the two species of *Pomoxis*, but each of the three genera did have different mean burst durations. *Micropterus*, with the shortest mean of 298 ms, also displayed the least variance and thus the most stereotyped pattern. There was no difference in the range of food types or sizes fed to these species.

Within a particular swallowing sequence both the duration of retractor dorsalis activity and the length of time between bursts tends to increase (Fig. 20). This is more marked in some feedings than in others but the pattern is consistently present regardless of prey type. For small prey, the duration of pharyngeal
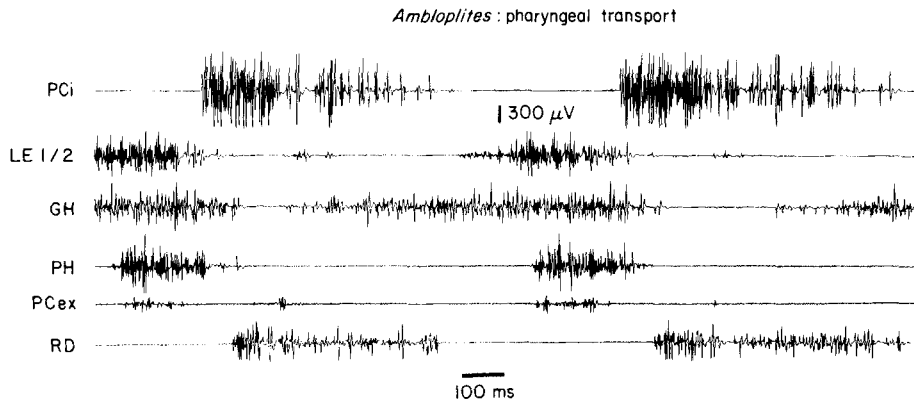
Ambloplites : pharyngeal transport

Figure 15. Simultaneous recordings from six branchial and hyoid muscles during the pharyngeal transport stage of feeding in *Ambloplites rupestris*. The rhythmic cyclical pattern of muscle activity used to transport prey into the oesophagus contrasts with the short duration non-repetitive activities recorded during buccal and pharyngeal manipulation.

transport may be so short that no increase in either interburst interval or retractor dorsalis activity duration is evident.

While most recordings of pharyngeal transport showed symmetrical activity between right and left muscles, two consistent patterns of asymmetry were found in all species. Figure 22 illustrates the maximum difference observed between activity

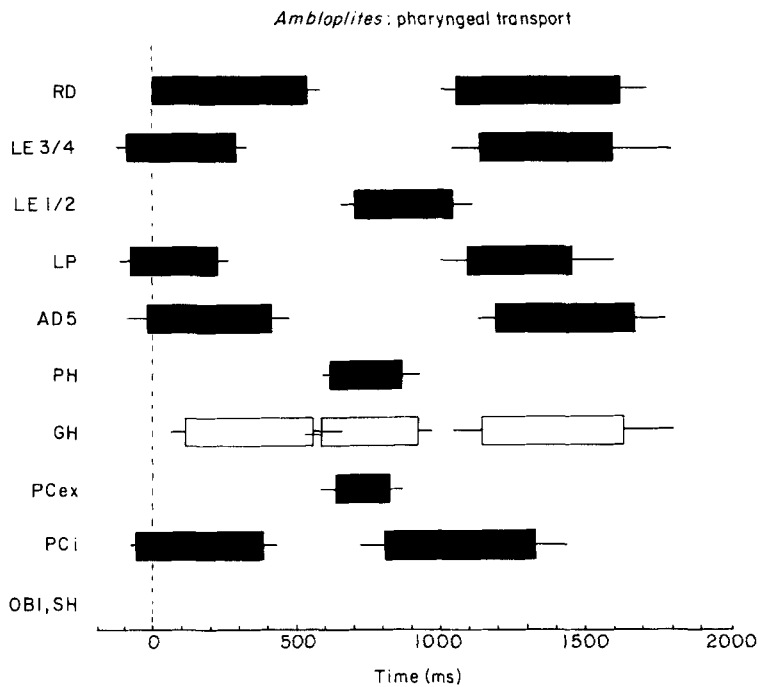*Ambloplites* : pharyngeal transport

Figure 16. Summary pattern of muscle activity during pharyngeal transport in *Ambloplites rupestris*. Note the extensive overlap in activity of the retractor dorsalis, levator posterior, levator externus three and four, and the fifth branchial adductor. Also note the lack of activity in the sternohyoideus and obliquus inferioris.
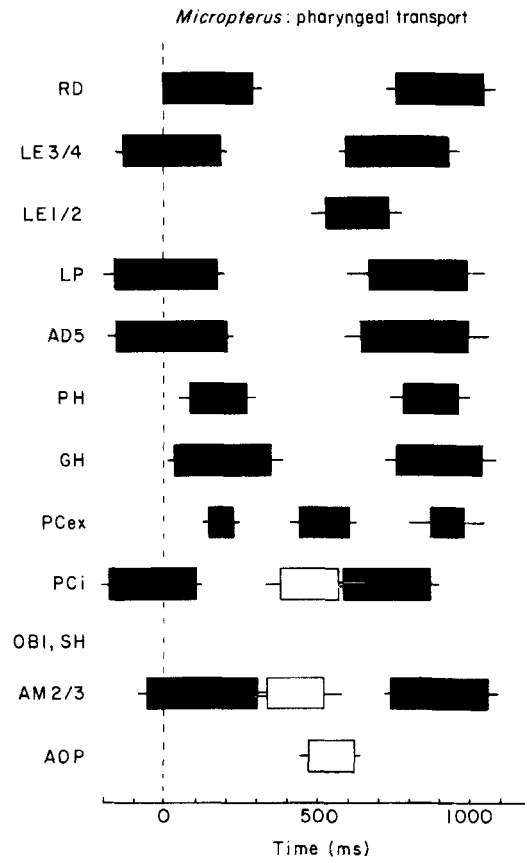
Micropterus : pharyngeal transport

Figure 17. Summary pattern of muscle activity during pharyngeal transport in *Micropterus salmoides*.

in the right and left retractor dorsalis and asymmetry of activity duration and relative timing in the anterior branchial levators. Minor (less than 100 ms) differences between right and left muscles were not considered as significant asymmetry because of (1) variation in electrode location between muscles of each side, (2) the lack of a consistent pattern to these small differences within a single swallowing cycle, and (3) these differences in timing are small relative to total burst duration.

The first asymmetrical pattern involves the timing of levator externus one and two activity relative to the retractor dorsalis. Two asymmetrical variations were found. (1) In contrast to the symmetrical activity illustrated in Fig. 16 in which anterior levators alternate with the retractor dorsalis, the anterior levatores interni occasionally showed extended bursts which overlap 50% of the retractor dorsalis activity (Fig. 22:RD(1), LE1/2(1)). Occasionally the anterior levators on both sides show this pattern, but usually one side retains the alternating pattern while the other levators show considerable overlap with the retractor dorsalis. During extended swallowing sequences, the side deviating from the symmetrical pattern may change several times and symmetrical activity usually occurs between a change of side. (2) The second pattern of asymmetry involving the anterior levators produces a complete overlap of levator activity with the retractor dorsalis
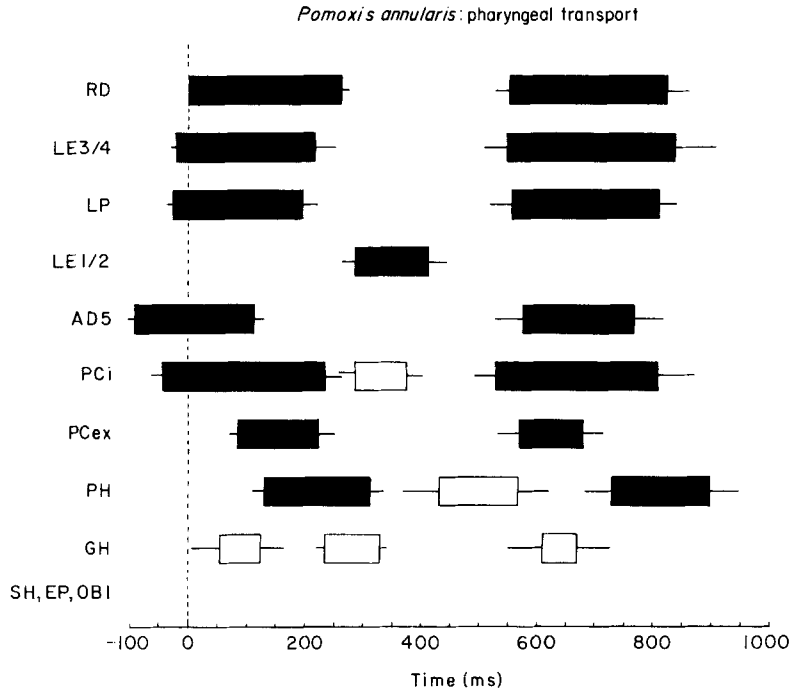
Figure 18. Summary pattern of muscle activity during pharyngeal transport in *Pomoxis annularis*.

(Fig. 23). The symmetrical pattern of activity in four muscles from one side is shown on the left of Fig. 23 and the asymmetrical pattern, 2 s later in the same swallowing sequence, on the right. When asymmetrical activity of this type was occurring, both sides (at different times) showed asymmetry.

The second major pattern of asymmetrical pharyngeal muscle activity is a co-ordinated change in the relative timing of muscles in both the upper and lower pharyngeal jaws. A small segment of a long swallowing sequence illustrating correlated asymmetry is shown in Fig. 24. The pharyngohyoideus muscle (PH) is the reference against which the activity patterns in the right and left posterior levators (LE 3/4) and the pharyngocleithralis internus (PCi) can be judged. In the first set of activity, the left side muscles display the normal symmetrical alternating pattern with the PH while the right side LE 3/4 and PCi begin activity 300 ms before the left side. In the very next sequence, on the right in Fig. 24, the relative timing of the two sides is reversed, and the left side muscles are now active throughout the last half of PH activity.

DISCUSSION

Phylogenetic patterns

The pharyngeal jaw apparatus of teleost fishes has been of particular importance as a source of information for phylogenetic analysis since Nelson focused attention on gill arch morphology with an extensive series of papers in the late 1960s and early 1970s (e.g. Nelson, 1967a, 1969). Most research on
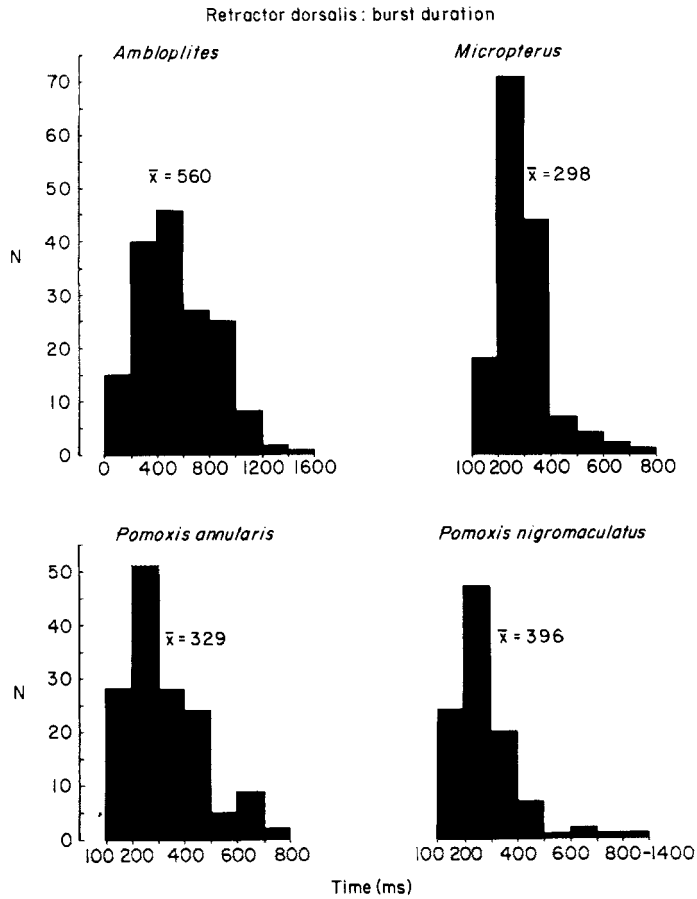
Retractor dorsalis : burst duration

Figure 19. Histograms to illustrate the variability in burst duration of the retractor dorsalis muscle in four of the species studied. This muscle was used as the reference muscle for summary diagrams of pharyngeal transport (see Materials and Methods).
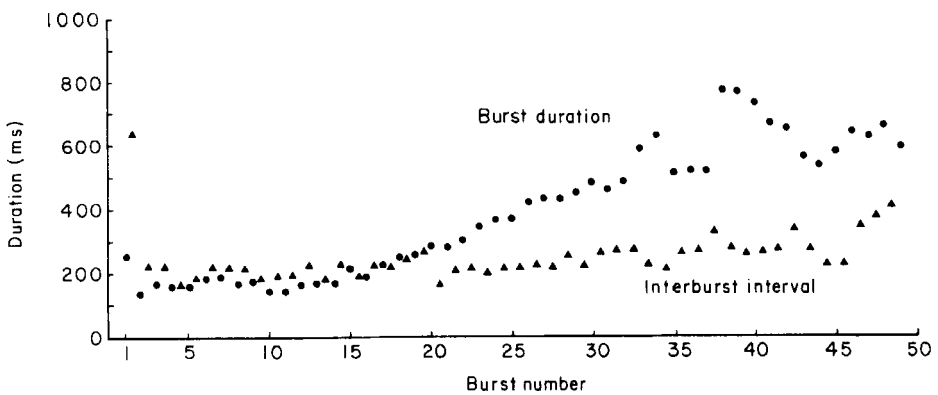
Figure 20. Scattergram of retractor dorsalis burst duration and the interburst interval versus time (Burst number) in one representative swallowing cycle in *Ambloplites rupestris*.
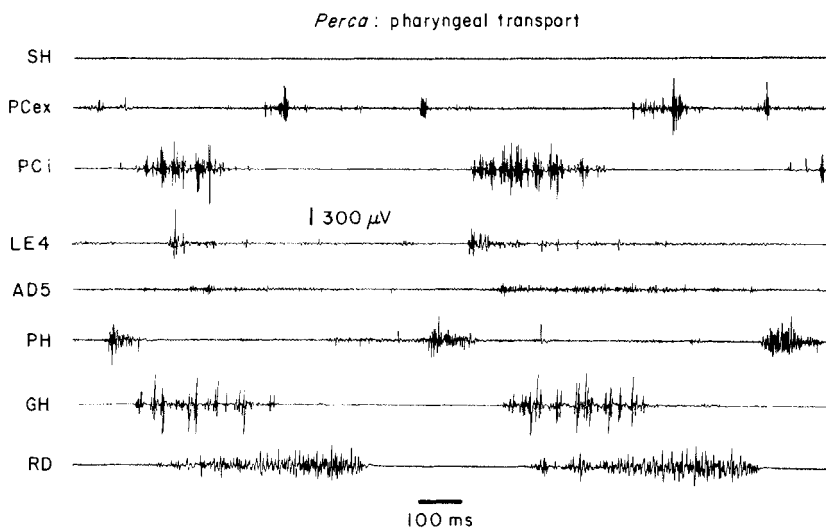
Perca : pharyngeal transport

SH

PCex

PCi

| 300 μV

LE4

AD5

PH

GH

RD

100 ms

Figure 21. Summary of muscle activity patterns during pharyngeal transport in *Perca flavescens*.

Ambloplites : pharyngeal transport

PH(r)

| 300 μV

LE I/2(r)

RD(r)

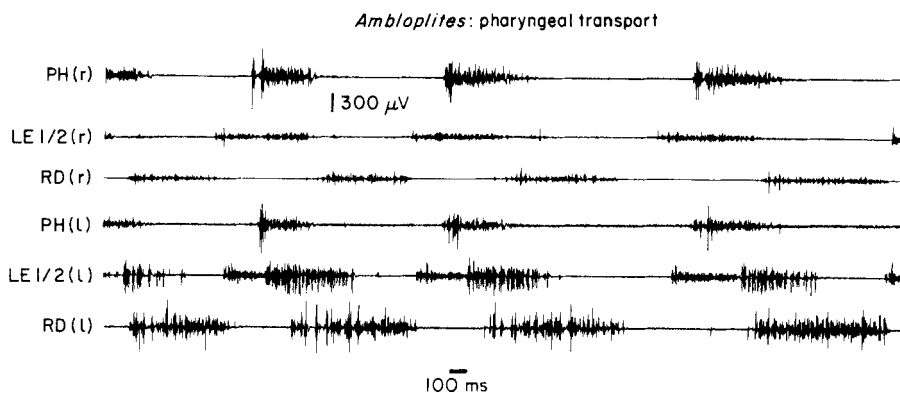PH(L)

LE I/2(L)

RD(L)

100 ms

Figure 22. Muscle activity pattern (simultaneously recorded) during a portion of a swallowing sequence in *Ambloplites rupestris* to illustrate one type of asymmetry between right (r) and left (l) muscles (see text for discussion).

Pomoxis annularis : asymmetrical transport
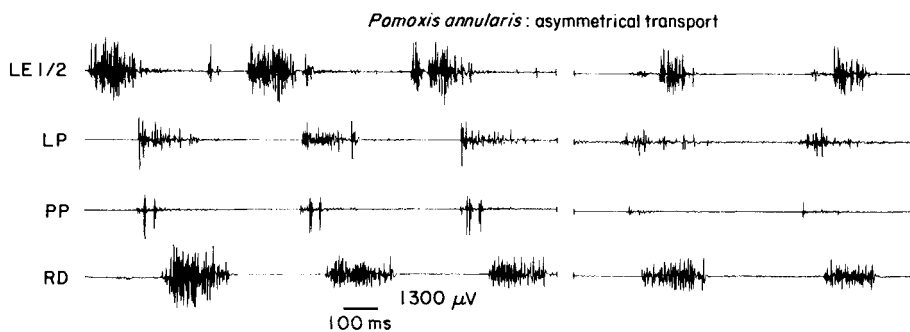
LE I/2

LP

PP

RD

| 300 μV

100 ms

Figure 23. *Pomoxis annularis*. Muscle activity pattern in four simultaneously recorded muscles during two separate times of a single swallowing sequence. These recordings illustrate the change in timing of anterior levator activity relative to the retractor dorsalis.
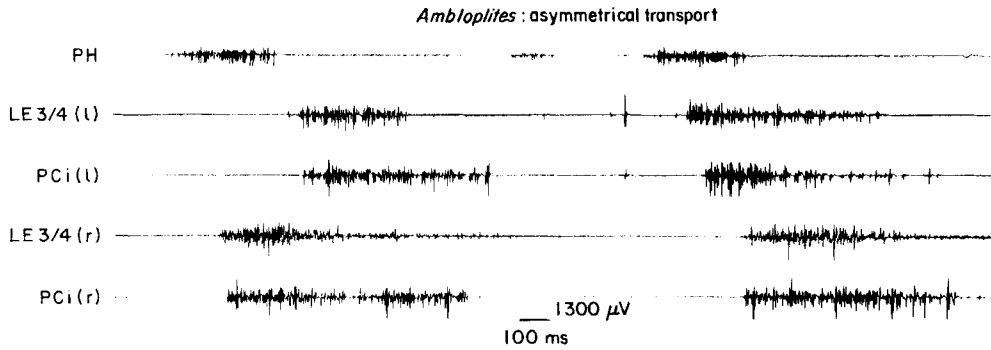
Figure 24. *Ambloplites rupestris*. Five simultaneous recordings from right (r) and left (l) branchial muscles demonstrating asymmetrical activity during pharyngeal transport.

branchial anatomy has emphasized osteology although Nelson (1967b, c) did discuss some general features of teleostean branchial musculature, and Holstvoogd (1965) considered the presence of the retractores arcuum branchialium (= retractor dorsales) to be a useful feature separating 'lower' from 'higher' teleosts.

Rosen (1973) utilized gill arch anatomy extensively in his proposed phylogeny of the euteleostean fishes and defined the major euteleostean clade, the Neoteleostei, by the presence of a retractor dorsalis muscle. Rosen (1974) subsequently examined the relationships of the Protacanthopterygii in detail, and this clade has recently been shown to be non-monophyletic by Fink & Weitzman (1982).

Although the interrelationships of primitive euteleosteans are still unsolved, this comparative anatomical analysis of representatives of each of the major euteleostean clades, with emphasis on the Neoteleostei, has revealed several new aspects of pharyngeal evolution in euteleosts and has served to define the primitive condition of the euteleostean branchial musculature. Although the features listed below do not uniquely define the Euteleostei, they do characterize the basic structural pattern from which morphological diversification within the Euteleostei has occurred. Primitively, the euteleostean pharyngeal apparatus lacks a retractor dorsalis, possesses a rectus communis originating from hypobranchial three and inserting on ceratobranchial five, possesses two dorsal and two ventral transversus muscles, a pharyngocleithralis internus and externus, obliqui dorsales three and four, dermal toothplates fused to the endoskeletal gill arch elements (Nelson, 1969; Patterson & Rosen, 1977) and dorsoventrally oriented anterior branchial levators. This pattern is retained in most generalized euteleosteans with two key additions.

Rosen (1973) demonstrated that the occurrence of a retractor dorsalis muscle defines the Neoteleostei and this result has been confirmed here. Within the Neoteleostei, however, the retractor dorsalis has undergone several specializations which do not conform to a clear trend toward posterior insertion of the retractor dorsalis. In *Perca*, for example, the retractor dorsalis inserts on both pharyngobranchials three and four, while in *Myctophum* the main external portion of the retractor inserts only on pharyngobranchial four. In myctophiforms, as described by Rosen (1973), the retractor dorsalis appears to be subdivided into an internal division inserting on the third pharyngobranchial, and an external division inserting on pharyngobranchial four. In *Perca*, *Myctophum* and *Pollachius*, however, the internal division actually is a direct continuation of the longitudinal

oesophageal muscle layer and does not arise from the retractor dorsalis externus. *Fundulus* and *Belonesox* (Karrer, 1967) lack this anterior extension of the longitudinal oesophageal muscles, but whether this loss is characteristic of all atherinomorphs or not remains to be established. Many acanthopterygians also lack the anterior band of oesophageal muscle (e.g. the Pharyngognathi, Liem & Greenwood, 1981; Stiassny, 1981). The occurrence of a thin band of oesophageal muscle parallel to the retractor dorsalis proper which inserts on the pharyngobranchials provides additional evidence, albeit indirect, for the derivation of the retractor dorsalis from the sphincter oesophagi (Winterbottom, 1974).

In addition to the retractor dorsalis, a second key specialization in the evolution of the euteleostean pharyngeal apparatus is the shift in origin of the rectus communis, which primitively originates from hypobranchial three, to the urohyal. This specialized origin is characteristic of the Ctenosquamata (Myctophiformes + Paracanthopterygii + Acanthopterygii), first defined by Rosen (1973) on the basis of other characters. In some ctenosquamates, the pharyngohyoideus may originate from both hypobranchial three and the urohyal. Stiassny (in prep.) has found a muscle similar to the pharyngohyoideus with an origin on the urohyal and insertion on ceratobranchial five in some aulopiform taxa. It is not yet established if the Aulopiformes are not monophyletic or if the 'pharyngohyoideus' has evolved independently in ctenosquamates and some aulopiforms.

In euteleosteans, the rectus communis primitively inserts on ceratobranchial five. Most ostariophysans examined lacked the rectus communis, and when it was present (e.g. *Hepsetus, Hoplias, Brycon, Arius, Apteronotus*) its origin was usually from one of the first three hypobranchials. In other primitive euteleosteans (*Alepocephalus, Galaxias, Aplochiton, Osmerus, Thymallus*) the rectus communis originates from hypobranchial three and inserts on ceratobranchial five. Occasionally, as in *Retropinna*, the origin of the rectus communis may be from the anterior hypobranchials.

The insertion of the rectus communis on ceratobranchial five appears to be a clupeocephalan character. In *Eutrumeus, Dussumieria* and *Opisthopterus* the rectus communis originates from hypobranchial three and inserts on ceratobranchial five. Kirchhoff (1958) illustrated the rectus of *Clupea* as inserting on ceratobranchial four with the pharyngocleithralis internus muscle and this appears to be a specialized condition within clupeomorphs. Elopomorphs either lack a rectus communis (*Elops, Megalops, Albula*), or its arises from hypobranchials two and three to insert on ceratobranchial four (pers. obs.; Nelson, 1967b). In osteoglossomorphs this muscle most commonly originates from hypobranchial two (although this is variable, and some genera lack a rectus communis; Greenwood, 1971), and inserts posteriorly on ceratobranchial four. Only *Amia* among non-clupeocephalans convergently possesses a rectus communis inserting on ceratobranchial five (Wiley, 1976, 1979).

This proposed pattern of rectus communis evolution emphasizes that there now exist two names which define different stages in the evolution of the acanthopterygian pharyngohyoideus muscle. Given the longstanding usage of these terms, it is probably best that they both be retained with the understanding that they refer to homologous muscles. Thus, the rectus communis would be used in non-ctenosquamate taxa for the muscle, derived from rectus ventralis four

(Nelson, 1967c; Winterbottom, 1974), that originates on one of the anterior hypobranchials (occasionally basibranchials) and inserts on ceratobranchial four or five. The term pharyngohyoideus would be retained for the rectus communis homologue in the Ctenosquamata which originates from the urohyal. In many cases, a rectus ventralis four occurs with the rectus communis or pharyngo-hyoideus, and the embryonic posterior rectus muscle anlage is generally considered to have separated into two divisions, one giving rise to the rectus of the fourth arch and the other to the rectus communis (Nelson, 1967c). Rectus ventralis four is sporadically distributed throughout euteleosts and has probably evolved independently in many lineages by (re-) splitting of the pharyngohyoideus or posterior obliqui muscle anlage.

Although, as noted above, the presence of two transversus muscles on both the dorsal and ventral gill arch elements is primitive for euteleosts, these muscles do not appear to have a uniform derivation. Winterbottom (1974:256) described the transversus dorsalis as originating "by subdivision of the sphincter oesophagi, which itself is derived from the upgrowth around the esophagus of the ventral ends of the muscle plates of the fifth branchial arches". The transversus ventralis posterior also seems to be derived from the outer transverse oesophageal muscle layer so the two muscles are often difficult to distinguish (Fig. 9A). But the transversus ventralis anterior, at least in some cases, appears to be derived from the obliqui ventrales. Nelson (1967c:281) noted that "there seems to be no known case among generalized teleosts in which a transversus and an obliquus occur on the same arch". In *Perca* (Fig. 9A) the fourth arch has both a transversus and an obliquus, suggesting that the transversus ventralis anterior is derived, in this species, from the oesophageal muscles. In *Fundulus* and *Belonesox* (Karrer, 1967), at least four transversi ventrales are present which exchange large numbers of fibres with the obliqui ventrales of the same arch. Several of the obliqui in *Fundulus* are nearly horizontal in orientation and meet at their origin in the midline. Distinguishing this condition from a transversus ventralis is difficult; it is still unclear how common the derivation of transversi ventrales muscles from obliqui is within teleosts.

Three other features of phylogenetic significance have been found in the euteleostean pharyngeal jaw apparatus. First, all myctophiforms (including neoscopelids; Rosen, 1973) possess a unique attachment of the branchial skeleton to the urohyal. Hypobranchial three, which in most teleosts is directed ventrally, contacts the urohyal (Fig. 5A) in a firm ligamentous attachment. The branchial apparatus is thus directly connected to hypobranchial and hypaxial musculoskeletal couplings, and posteroventral movement of the hyoid apparatus during mouth opening (a primitive feature of teleosts as well as gnathostomes; Lauder, 1980b) will cause the branchial apparatus to move posteroventrally also. In most teleosts, and in all immediate outgroups to the Myctophiformes, the hyoid has no ventral bony connection to the branchial apparatus but does have an anterior ligamentous connection to the urohyal. This attachment has a greater mechanical advantage for posteroventral hyoid movement than the direct bony link of myctophiforms (because of its greater distance from the articulation of pharyngobranchial one with the neurocranium; Fig. 1), but permits considerably greater independence of hyoid and branchial movement. Nearly all teleosts (with the notable exception of the Osteoglossomorpha where the tendon usually attaches to hypobranchial two) also possess a tendinous extension of the sternohyoideus

muscle to hypobranchial three. This tendon is illustrated in Figs 7A and 8B, but has been removed in the other lateral views of the pharyngeal region to show the ventral gill arch musculature. A tendinous connection between the sternohyoideus and hypobranchial three was present in most members of all the euteleostean clades examined as well as in clupeomorph and elopomorph fishes. It may thus represent an elopocephalan synapomorphy.

A second specialization of the pharyngeal region with phylogenetic implications is the division of the pharyngocleithralis externus into dorsal and ventral sections, both inserting on ceratobranchial five, in *Fundulus* (Fig. 6B). This condition was also observed in *Belonesox* by Karrer (1967) and is not present in any of the numerous outgroup taxa examined. The distribution of this feature within the Atherinomorpha remains to be determined. Sponder & Lauder (1981) described a similar separation of the pharyngocleithralis externus into two muscles in *Periophthalmus*, but in this species the ventral section inserts anteriorly on ceratobranchial three.

The third remaining feature of phylogenetic interest is the condition of the rectus communis in stomiiforms. In no other teleostean clade has the rectus communis been found to originate on the basihyal or basibranchials. Due to the origin of the rectus from hypobranchial three (the primitive condition) in some stomiiforms and its absence in two other genera examined, the significance of the anterior shift in rectus communis origin within stomiiforms cannot be assessed until more species are examined. The basihyal site of origin may characterize a monophyletic group within stomiiforms and the lack of the rectus communis in *Diplophos* and *Gonostoma* may be autapomorphic.

Functional morphology

A fundamental feature of the functional morphology of prey manipulation and swallowing in the euteleostean fishes examined here is the separation of three activities: buccal manipulation, pharyngeal manipulation and pharyngeal transport. The analysis of mean onset and offset times for jaw, hyoid and branchial muscles in *Ambloplites* (Figs 13, 14, 16) clearly shows that each represents a distinct pattern and that all muscle activity following the initial strike cannot be averaged into one meaningful summary bar diagram. This division of postcapture behaviour is proposed as the basis for comparing functional patterns within the Euteleostei (see below: Comparisons).

Within the context of current hypotheses of euteleostean phylogeny, as corroborated by the characters presented above, the functional analysis of branchial muscle activity in *Esox* and 'generalized' acanthopterygians has revealed several functional attributes of the primitive euteleostean pharyngeal apparatus. These conclusions are presented as tentative and subject to revision when experimental data on gill arch function become available for more euteleostean lineages. Because of the difficulties involved in obtaining and conducting experiments on stomiiform, aulopiform, and myctophiform fishes, future research on euteleostean pharyngeal jaw function will focus on salmoniforms, ostariophysans, paracanthopterygians, atherinomorphs and basal percomorphs.

Several muscle patterns were found in all species studied experimentally and are thus suggested to be primitive for the Euteleostei. (1) There is a sharp distinction between the pattern of activity in anterior and posterior branchial

levator muscles. The anterior levators in *Esox* begin and end activity significantly earlier in the chewing cycle than the posterior levators (Fig. 11) and there is little overlap in activity period. In *Ambloplites*, the same pattern is observed (Fig. 16) although the function of the anterior levators is reversed: the anterior levators protract the upper pharyngeal jaw, the opposite of their function in *Esox*. Even though the retractor dorsalis and levatores externi three and four are anatomical antagonists in *Ambloplites* these muscles overlap for 70% or more of their activity period. It is the anterior levators which are active inbetween bursts of the retractor dorsalis. The levator posterior also extensively overlaps retractor activity (Figs 16–18), and in *Pomoxis annularis*, there is no significant difference between relative activity periods of the retractor dorsalis, levatores externi three and four, and levator posterior. These data indicate that the posterior gill arch levators may function primarily to elevate the upper pharyngeal jaws during the retraction stroke (see below), as the combined action of these dorsal gill arch muscles will move the upper pharyngeal jaws toward the base of the skull. (2) The pharyngocleithralis internus is active with those dorsal gill arch muscles causing retraction (either the retractor dorsalis in acanthopterygians or the anterior levators in *Esox*). In *Perca* (Fig. 21), *Ambloplites* (Fig. 16) and *Pomoxis* (Fig. 18) the onset time of the pharyngocleithralis internus is significantly earlier in the swallowing cycle than the onset of the retractor dorsalis. In *Micropterus* (Fig. 17), at least half of the activity occurs prior to the onset of retractor dorsalis activity perhaps indicating considerable asynchrony in the protractive and retractive movements of the upper and lower pharyngeal jaws. (3) The sternohyoideus and obliquus inferioris muscles are not active during pharyngeal transport of prey into the oesophagus. (4) The obliquus inferioris is active during pharyngeal manipulation of prey. Pharyngeal manipulation involves pectoral girdle retraction and posteroventral branchial basket movement mediated by the pharyngocleithralis externus. (5) Both the sternohyoideus and obliquus inferioris are active during the initial strike and buccal manipulation, as are all branchial muscles. The timing of activity in the levatores, retractor dorsalis, and pharyngocleithrales muscles suggests that active expansion of the branchial basket is occurring, increasing the volume of the posterior portion of the buccal cavity and contributing to negative mouth cavity pressure. (6) Several branchial muscles are active during the preparatory phase of suction feeding. The pharyngohyoideus and geniohyoideus function together to protract the hyoid and reduce buccal volume. In *Ambloplites* (Fig. 13) the adductor mandibulae is only rarely active but the pharyngocleithrales muscles are active. It is unclear what role these muscles play during the preparatory phase as their major action is to move the lower pharyngeal jaws posteroventrally causing an increase in mouth cavity volume. The anterior levatores and fifth branchial adductor are also frequently active during the preparatory phase.

Although no direct observations of pharyngeal jaw movement were obtained in this study, an analysis of the mechanical relationships of the pharyngeal apparatus, the lines of muscle action, and relative muscle activity periods permit a well founded hypothesis of the pattern of upper and lower pharyngeal jaw movement. This analysis is facilitated by the relatively long durations of muscle activity (up to 1 s) relative to the rapid sequence of events occurring at the initial strike.

In primitive euteleosteans such as *Esox*, the upper pharyngeal jaw is able to move relatively little in an anteroposterior direction because the dorsal gill arch muscles have little mechanical advantage (Figs 3A, 25). Upper pharyngeal retraction is

especially limited and in fishes such as *Salmo*, in which the branchial levators are oriented dorsoventrally, may be accomplished only passively in conjunction with retraction of the entire branchial apparatus. The lower pharyngeal jaw is capable of undergoing greater anteroposterior excursions than the upper and appears to be the dominant element in the swallowing mechanism (Fig. 25). Both the upper and lower jaws move in a counterclockwise direction (in left lateral view) during the repetitive cyclical raking movements of pharyngeal transport. Both jaws move medially during the retraction phase and then dorsally and laterally during protraction. Protraction of both pharyngeal jaws is proposed to occur primarily as a result of levatores three and four and indeed activity in the adductor arcus branchialium does begin with that in the posterior levators. The rectus communis is also active during pharyngeal jaw retraction (Fig. 11) and may aid in keeping the pharyngeal teeth against the prey. This muscle is intrinsic to the branchial basket and thus does not play a significant role in protracting the lower pharyngeal jaw. At the end of the protraction phase of pharyngeal jaw movement there is a pause of about 200 ms during which no muscle activity is observed and this presumably reflects a temporary halt in movement of the prey into the oesophagus.

In generalized acanthopterygians, as exemplified by *Micropterus* (Fig. 26) the upper pharyngeal jaw undergoes greater anteroposterior excursion than the lower.
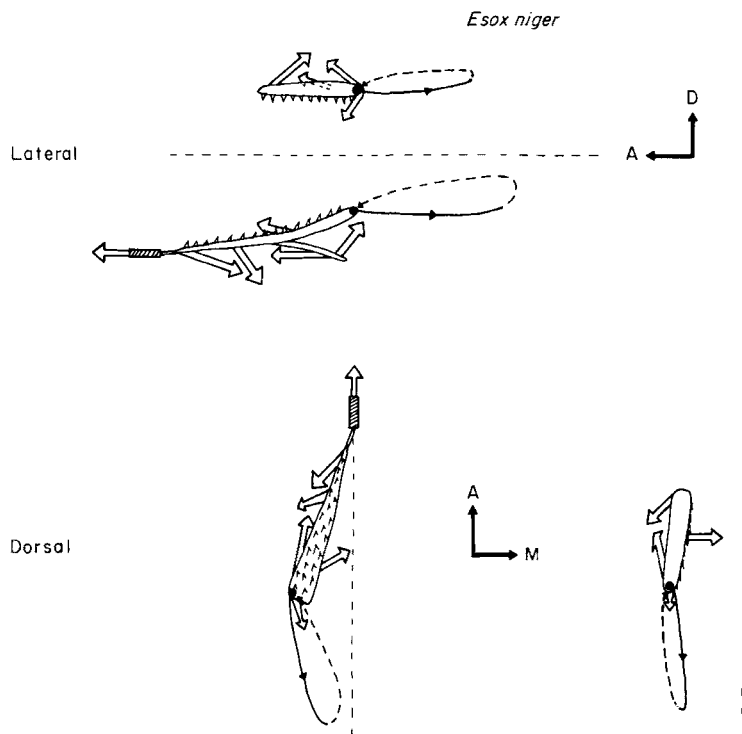
Figure 25. *Esox niger*. Diagrammatic lateral and dorsal views of pharyngeal jaw orbits reconstructed from the mechanical relationships and muscle activity patterns in the pharyngeal jaw apparatus. Some of the muscles acting on the upper and lower pharyngeal jaws are shown as arrows to indicate their major line of action. The direction of jaw movement during transport is indicated by the arrow. A, anterior; D, dorsal; M, medial.
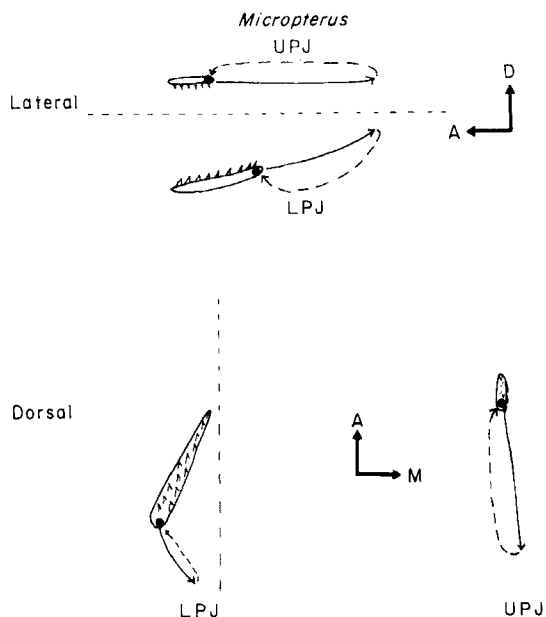
Figure 26. *Micropterus*. Diagrammatic lateral and dorsal views of pharyngeal jaw orbits reconstructed from the mechanical relationships and muscle activity patterns in the pharyngeal jaw apparatus. The orbits drawn indicate the motion of a point on the posterodorsal aspect of the upper (UPJ) and lower (LPJ) pharyngeal jaws. The dashed line indicates the midline in lateral and dorsal view. A, anterior; D, dorsal; M, medial.

Both the retractor dorsalis and posterior levators are long, mostly parallel-fibred muscles, and can produce large protractive and retractive movements. The lower pharyngeal jaw, while it can undergo greater relative excursion than in *Esox*, is hypothesized to be limited to about three-quarters of the range of upper jaw movement (Fig. 26). The upper and lower pharyngeal jaws are retracted together although because the pharyngocleithralis internus is usually active prior to the retractor dorsalis, retraction of the lower pharyngeal jaw will begin (and also end) before retraction of the upper. Both pharyngeal jaws move posteriorly and medially during retraction. Little movement is proposed to occur in the lower pharyngeal jaw during the final stages of upper jaw retraction (Fig. 26).

Protraction of the pharyngeal jaws, in contrast to *Esox*, causes the distance between the jaws to increase because of activity in the pharyngocleithralis externus (Figs 16, 17) and the dorsal component of the anterior levator line of action. The short-fibred adductor muscle connecting the upper and lower jaws is active throughout most of the retraction phase of jaw movement, beginning shortly after the onset of activity in the pharyngocleithralis internus. The adductor muscle effectively couples the upper and lower pharyngeal jaws and may result in passive protraction or retraction of either jaw when only upper or lower jaw musculoskeletal couplings are active.

Asymmetrical activity between right and left side pharyngeal muscles can change the synchronous pattern of jaw movement during transport into an alternating pattern in which the right upper and lower jaws are protracted while the left jaws are retracted. Yet another asymmetrical pattern occasionally seen at the start of pharyngeal transport is an alternating pattern in which the upper jaws

move anteriorly as the lower jaws retract. These movements are inferred from electromyograms which, instead of fitting the symmetrical pattern of transport (Fig. 16), display alternating activity between the retractor dorsalis and pharyngocleithralis internus for several cycles.

The general pattern of euteleostean pharyngeal jaw movement as inferred from muscle activity and pharyngeal mechanics is one of predominately symmetrical and synchronous protraction and retraction. In euteleosts that lack a retractor dorsalis muscle, the lower pharyngeal jaw plays the dominant role in transporting prey into the oesophagus, although the upper jaw is capable of active posterior movement in those taxa with posteriorly inclined levator muscles. The retractor dorsalis muscle mediates extensive posterior movement of the upper pharyngeal jaws, largely because of its length and mechanical advantage. In taxa possessing a retractor dorsalis muscle, the upper pharyngeal jaw contributes more to prey transport than the lower, undergoing greater excursions and continuing to move posteriorly when the lower pharyngeal jaw has stopped. The change from lower to upper pharyngeal jaws as the dominant element of the prey transport mechanism is postulated to have taken place with the origin of the Neoteleostei. The increased use of the upper pharyngeal jaw in prey transport may be related to changes in dentition, pharyngobranchial size, and supporting framework of epibranchials during euteleostean evolution, but the details of the form-function relationship remain to be investigated.

Comparisons

Although the conclusions regarding pharyngeal jaw movement in this paper are based on the mechanical arrangement of the branchial region and on patterns of muscle activity during swallowing, the hypothesized movements of the pharyngeal jaws accord extremely well with previous investigations. Liem (1970) investigated deglutition in nandid fishes by examining tooth marks left by pharyngeal teeth on albino, scaleless prey. Sponder & Lauder (1981) directly examined pharyngeal jaw movement in *Periophthalmus* using cineradiography of terrestrial swallowing so that the small pharyngeal bones could be visualized without X-ray scattering by water. Non-experimental studies of pharyngeal function in euteleosteans include the muscle stimulation research of Vanden Berghe (1928) on *Cottus* and *Blennius*, and the work of Tchernavin (1953), Günther & Deckert (1960), Kayser (1962) and Karrer (1967). Experimental research of pharyngeal function in cichlid fishes (Liem, 1973, 1978) has provided a source of comparative information from pharyngognath fishes.

The cycle of pharyngeal jaw movement described by Sponder & Lauder (1981: fig. 4) matches that proposed here for generalized acanthopterygians (Fig. 26) almost exactly. The upper pharyngeal jaw is the major element mediating prey transport and the lower pharyngeal jaw pauses at the posterior limit of its movement while the upper pharyngeal jaw completes its retraction stroke. Liem (1970:132–133) emphasized the morphological coupling between the upper and lower pharyngeal jaws and disagreed with the view of Karrer (1967) that protraction of the upper pharyngeal jaws occurs while the lower jaws are being retracted: "There is strong morphological evidence in favour of the simultaneous protraction and retraction of the upper and lower pharyngeals hypothesis over that of the alternating hypothesis proposed by Karrer (1967)". Liem also emphasized the mobility of the lower pharyngeal jaws.

The experimental data presented here, completely congruent with that of Sponder & Lauder (1981), indicate that when both pharyngeal jaws move posteriorly they do so together. But because the lower pharyngeal jaw in the acanthopterygian taxa studied undergoes a significantly smaller range of movement, it is not moving during much of pharyngeal retraction and lags behind at the start of the protractive phase. As in *Periophthalmus*, it is the lower pharyngeal jaw that first begins to move posteriorly. Thus, although most of lower jaw protraction and retraction occur together with the upper jaw, some asynchrony results from the different sizes of the movement orbits. No experimental evidence to date has demonstrated strict alternating movements of the jaws to be frequent during deglutition.

If the pattern described in this paper for *Perca* and certain centrarchids is a general one (as comparisons with nandids and *Periophthalmus* suggest it is) then the pharyngognath pattern of muscle activity and jaw movement is specialized. Pharyngognaths have added a further activity pattern, pharyngeal mastication, to the three intraoral activities defined here: buccal manipulation, pharyngeal manipulation and pharyngeal transport. Pharyngeal mastication in cichlid fishes involves all pharyngeal muscles as well as the sternohyoideus in a co-ordinated masticatory cycle lasting about 400 ms in piscivorous taxa (Liem, 1978). Prey are crushed and pierced by the pharyngeal teeth during two power strokes. Liem (1978) has presented some electromyographic data on swallowing that show considerable similarity to the proposed general acanthopterygian pattern. Swallowing is accomplished primarily by the upper pharyngeal jaw, and the levator posterior and retractor dorsalis overlap extensively in activity period. These muscles alternate with activity in the first levator internus (the only anterior levator recorded). This is exactly the pattern found in *Micropterus, Ambloplites, Pomoxis* and *Perca* and the cichlid upper pharyngeal jaws may have retained the primitive neuromuscular couplings involved in pharyngeal transport.

The lower pharyngeal jaw takes relatively little part in transport (Liem, 1978:354) and little activity was found in the ventral branchial musculoskeletal couplings. Liem reported activity in the geniohyoideus, sternohyoideus and pharyngocleithralis externus prior to swallowing and this may represent a pharyngeal manipulation stage in cichlids comparable to that of more generalized percomorphs.

Future studies of euteleostean pharyngeal jaw function will be most useful if attention is paid to the basic divisions of feeding behaviour and if muscle activity periods are summarized separately for each behaviour with statistically adequate sample sizes and an indication of the variability (standard error) in mean timing of each muscle. The structural specializations shared by many derived euteleostean clades are relatively well known compared to functional patterns and innovations. The lack of outgroup information on jaw function has seriously hindered our understanding of the origin of evolutionary and ecological trophic specialization in fishes. A general euteleostean pattern now seems to be emerging that can serve as a baseline for future analyses.

Functional design and evolutionary patterns

Within the last 10 years, research on cladistic methods has provided an extensive body of literature on patterns of structure in organisms and the ways in which

morphological and biochemical novelties can be grouped into hierarchies that may reflect genealogy or earth history (e.g. Rosen, 1978; Patterson, 1980). Relatively little attention has been paid to functional or behavioural novelties and the patterns exhibited by these features. Within a monophyletic clade, for example, what is the relationship between the sequential acquisition of structural and functional novelties at successive hierarchical levels? Are there any general patterns to structural and functional transformation that relate to intrinsic organizational properties of designs (Lauder, 1981)? In order to address these questions, a corroborated phylogenetic hypothesis is needed *a priori* to establish the basic hierarchical pattern, so that structural and functional novelties can be mapped onto that pattern.

In this paper the pharyngeal apparatus in euteleostean fishes has been used as an example of a complex structural system. In order to summarize the transformation of this system within a phylogenetic context, the branchial region may be abstracted into a structural network (Fig. 27). This network illustrates the pattern of connections between structural elements, not all of which were acquired at one time. In euteleostean evolution, connecting link number one (Fig. 27), the retractor dorsalis, was acquired before link number two, the interoperculohyoid ligament, which defines a larger clade than link number three, the pharyngohyoideus muscle (Fig. 27). These three features of the network define monophyletic clades within the Euteleostei (Lauder & Liem, in press) while the remainder of the structural pattern is primitive for euteleosts.

Functional specializations at several hierarchical levels are also shown in Fig. 28. Associated with structural change 2 in Fig. 27 is the dominant role of the upper pharyngeal jaw in the pharyngeal transport stage of feeding, and greater

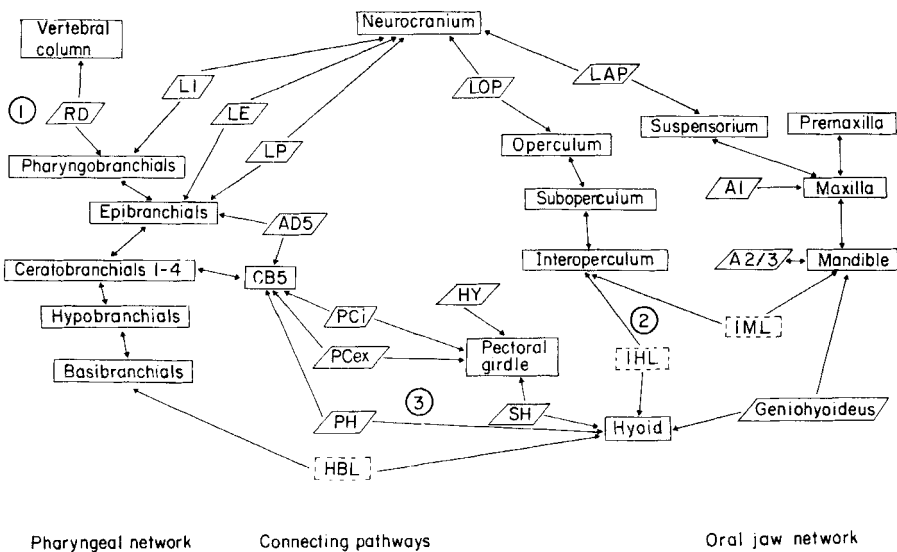Pharyngeal network   Connecting pathways   Oral jaw network

Figure 27. Structural network of the head in a generalized percomorph such as *Micropterus*. The oral jaw network, pharyngeal network, and connecting pathways between them are illustrated. Arrows run from the muscle to the bone of insertion or to the insertion site of ligaments. Solid rectangles—bones; dashed rectangles—ligaments; parallelograms—muscles. Three structural innovations in the network are numbered. These innovations occurred at different phylogenetic levels (Fig. 28). See text for discussion.
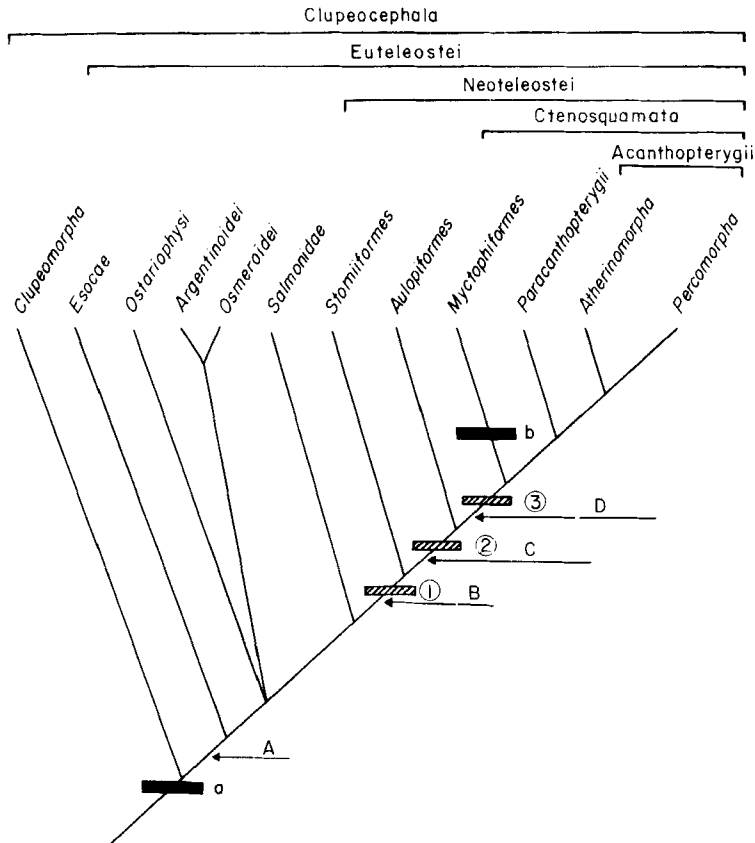
Figure 28. Phylogeny of the Euteleostei based on the work of Rosen (1973), Fink & Weitzman (1982), and characters presented in Lauder & Liem (in press). The three structural novelties (synapomorphies) from Fig. 27 are (hatched bars): (1) the presence of a retractor dorsalis muscle, (2) the presence of an interoperculohyoid ligament (homologous to the mandibulohyoid ligament), and (3) the change in origin of the rectus communis muscle to the urohyal (some aulopiforms may also possess a pharyngohyoideus—see text). Two other synapomorphies corroborating the initial phylogenetic hypothesis have been discovered (black bars): (a) the rectus communis muscle inserts posteriorly on ceratobranchial five (see text for discussion), and (b) the urohyal is attached firmly to hypobranchial three on each side. The cladogram shown is corroborated by many other characters (see Lauder & Liem, in press). Four levels (A–D) have been identified with specific functional innovations. A: anterior branchial levators elevate and/or retract the upper pharyngeal jaw; anterior branchial levators active with the pharyngocleithralis internus; the lower pharyngeal jaw plays the dominant role in prey transport. B: the upper pharyngeal jaw is the major effector of prey transport. C: hyoid retraction is transmitted directly to the interoperculum. D: the lower pharyngeal jaw is coupled to the hyoid apparatus and undergoes greater anteroposterior excursions as a result of the shift in pharyngohyoideus origin; the anterior levatores have a protractive function and alternate with activity in the pharyngocleithralis internus and retractor dorsalis; activity of the fifth branchial adductor and levatores externi three and four shifts into the retraction stroke of the upper pharyngeal jaw. Functional novelties are associated with structural innovations in a hierarchical pattern. The initial phylogenetic hypothesis of the Euteleostei can thus be used as a guide to examine patterns in the acquisition of both structural and functional novelties (see text for further discussion).

anteroposterior excursions of the upper pharyngeal jaw as compared with the lower. The anterior branchial levator muscles at this phylogenetic level are inferred not to overlap activity of the pharyngocleithralis internus, in contrast to the primitive condition at level A (Fig. 28) where these dorsal and ventral branchial muscles are active synchronously (as in Fig. 11). At level D, the shift in

origin of the rectus communis to the urohyal couples the lower pharyngeal jaw directly to hyoid movement and, via the geniohyoideus muscle, to the mandible (Fig. 1). This greatly increases the absolute anteroposterior mobility of the lower pharyngeal jaw, although because of its anterior attachment to the basibranchials it still undergoes less movement than the upper pharyngeal jaw.

This analysis reveals two key steps in the evolution of the acanthopterygian pharyngeal jaw apparatus. First, at the neoteleostean level, the upper pharyngeal jaw acquired the capability of significant prey transport functions and this event is inferred to have been accompanied by a shift in timing of contraction in a large number of gill arch muscles into the retraction stroke (Fig. 28: level B). Second, at the ctenosquamate level (Fig. 28:level D), the lower pharyngeal jaw beame coupled to the hyoid apparatus and is inferred to have been capable of a greater range of movement than in prectenosquamate taxa. Only with the origin of the Ctenosquamata, then, did the pharyngeal jaw apparatus acquire the general acanthopterygian configuration shown in Fig. 1. And it is important to emphasize that the mechanical linkages and activity patterns of muscles in Fig. 1 were acquired in a definite historical sequence only discernable by a phylogenetic analysis of structural and functional novelties (Fig. 28).

The pattern of structural and functional transformation discovered for the euteleostean pharyngeal jaw apparatus has several important implications for the evolution of functional design in vertebrates. Homologous muscles have been proposed to possess evolutionarily conservative action patterns which are maintained in the face of significant reorganizations of muscle line of action and function (Bramble, 1980). In euteleostean fishes this appears not to be the case as homologous muscles radically altered their activity patterns with the advent of the retractor dorsalis. However, the overall kinematic pattern of pharyngeal jaw movement was changed relatively little as in both primitive and derived euteleosts the retraction stroke of the upper and lower jaws largely coincides. It thus appears that as structural and functional novelties in the pharyngeal region were acquired, the overall pattern of jaw movement was maintained, although, to be sure, each novel feature modified the primitive kinematic pattern to some degree. Data are not yet available from other case studies in the historical analysis of form to show whether co-ordinated modification in structural and functional patterns and the consequent maintenance of the primitive movement sequence, are general features in the transformation of vertebrate design (Fig. 28).

A key aim of future research in the transformation of design is the relationship between the arrangement of connecting pathways in structural networks (Fig. 27) and patterns of morphological and functional diversity in monophyletic clades.

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ABBREVIATIONS USED IN FIGURES

A1, A2/3, AM2, AM2/3 divisions of the adductor mandibulae muscle
AD5 adductor arcus branchialium muscle
AOP adductor operculi muscle
C compressive phase of the initial strike
CB5 ceratobranchial five
CB5TP toothplate of ceratobranchial five
CL cleithrum
DO dilator operculi muscle
E expansive phase of the initial strike
EB2 epibranchial two
EB3TP tooth patch, unfused, on epibranchial three
EP epaxial muscles
ES oesophagus
GH geniohyoideus muscle
HB3 hypobranchial three
HBL ligament between urohyal and hypohyals

HY hypaxial musculature, synonymous as used here with the obliquus inferioris (OBI)
IAC interarcual cartilage
IHL ligament from the interoperculum to the hyoid
IML ligament from the mandible to the hyoid
LAP levator arcus palatini muscle
LE, LE1-4 levatores externi muscles
LI, LI1 4 levatores interni muscles
LOP levator operculi muscle
LP levator posterior
LPJ lower pharyngeal jaw
OBI obliquus inferioris muscle
OBS obliquus superioris muscle
OD, OD1-4 obliqui dorsales muscles
OV, OV1-4 obliqui ventrales muscles
P preparatory phase of the initial strike
PB1,2,3,4 pharyngobranchial bones

PB3TP toothplate (fused) to pharyngobranchial three

PB4TP toothplate (fused) to pharyngobranchial four

PCe, PCex pharyngocleithralis externus

PCexv pharyngocleithralis externus, ventral division

PH pharyngohyoideus muscle

PCi pharyngocleithralis internus muscle

PP protractor pectoralis muscle

R recovery phase of the initial strike

RC rectus communis muscle

RD retractor dorsalis muscle

RV rectus ventralis muscle

SH sternohyoideus muscle

TD transversus dorsalis muscle

TDad deep division of the transversus dorsalis anterior muscle

TDas superficial division of the transversus dorsalis anterior muscle

TDP transversus dorsalis epibranchialis two muscle

TES transverse muscle layer of the oesophagus

TR pharyngeal transport phase of feeding

TVa,p anterior and posterior transversi ventrales muscles

TV_{1-4} transversi ventrales of arches one to four

UPJ upper pharyngeal jaw