

Functional Morphology of the Pharyngeal Jaw Apparatus in Perciform Fishes: An Experimental Analysis of the Haemulidae

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ABSTRACT A new mechanical model for function of the pharyngeal jaw apparatus in generalized perciform fishes is developed from work with the family Haemulidae. The model is based on anatomical observations, patterns of muscle activity during feeding (electromyography), and the actions of directly stimulated muscles. The primary working stroke of the pharyngeal apparatus involves simultaneous upper jaw depression and retraction against a stabilized and elevating lower jaw. The working stroke is characterized by overlapping activity in most branchial muscles and is resolved into three phases. Four muscles (obliquus dorsalis 3, levator posterior, levator externus 3/4, and obliquus posterior) that act to depress the upper jaws become active in the first phase. Next, the retractor dorsalis, the only upper jaw retracting muscle, becomes active. Finally, there is activity in several muscles (transversus ventrales, pharyngocleithralis externus, pharyngohyoideus, and protractor pectoralis) that attach to the lower jaws. The combined effect of these muscles is to elevate and stabilize the lower jaws against the depressing and retracting upper jaws.

The model identifies a novel mechanism of upper jaw depression, here proposed to be the primary component of the perciform pharyngeal jaw bite. The key to this mechanism is the joint between the epibranchial and toothed pharyngobranchial of arches 3 and 4. Dorsal rotation of epibranchials 3 and 4 about the insertion of the obliquus posterior depresses the lateral border of pharyngobranchials 3 and 4 (upper jaw). The obliquus dorsalis 3 muscle crosses the epibranchial-pharyngobranchial joint in arches 3 and 4, and several additional muscles effect epibranchial rotation. Five upper jaw muscles cause upper jaw depression upon electrical stimulation: the obliquus dorsalis 3, levator posterior, levator externus 3/4, obliquus posterior, and transversus dorsalis. This result directly contradicts previous interpretations of function for the first three muscles. The presence of strong depression of the upper pharyngeal jaws explains the ability of many generalized perciform fishes to crush hard prey in their pharyngeal apparatus.

The pharyngeal jaw apparatus of teleost fishes is a complex system of modified gill arch elements involving about 20 intrinsic bones and 24 muscles. Within the Perciformes this apparatus has undergone numerous anatomical and functional transformations and recently has drawn considerable attention as a case study in the evolution of a complex musculoskeletal system (Liem, '70, '74; Liem and Greenwood, '81; Kaufman and Liem, '82; Lauder, '83a,b; Stiassny and Jensen, '87). Much of this work has focused on a derived lineage, the Labroidei, a monophyletic group defined by specializations of the pharyngeal jaws (Kaufman and Liem, '82;

Stiassny and Jensen, '87). The functional anatomy of pharyngeal jaw mechanisms in this group is well known (Liem, '74, '86; Liem and Sanderson, '86), and much discussion has centered around its apparently profound ecological and evolutionary consequences (Liem and Greenwood, '81; Kaufman and Liem, '82; Stiassny and Jensen, '87; Wainwright, '88). Unfortunately, functional mechanisms are poorly understood in the many perciform taxa that exhibit the more generalized pharyngeal anatomy from which the labroid condition probably evolved.

An understanding of pharyngeal jaw mechanisms in primitive perciform fishes is nec-

essary for interpreting changes in derived lineages. Without this knowledge it is impossible to know which functional features exhibited by derived groups represent novel acquisitions and which are primitive for perciforms.

A few studies have examined pharyngeal jaw function in generalized perciform taxa and proposed models for the mechanisms of jaw movement. Liem ('70) inferred muscle actions in nandid fishes from manipulations of fresh specimens and from patterns of jaw movements resulting from tooth impressions left on swallowed prey. Lauder ('83a,b) presented electromyographic and cineradiographic data for some centrarchids but concluded that the patterns of muscle activity did not permit a complete explanation of the observed jaw movements. These studies illustrate the difficulties inherent in attempting to elucidate kinematic patterns of structures that cannot be directly observed because of their anatomical position deep in the pharynx. No study to date has tested hypotheses of pharyngeal muscle function in perciform fishes with electrical stimulation of anesthetized animals.

In this article I present a new model of pharyngeal jaw mechanics in generalized perciforms based on muscle stimulation data and electromyography from fishes in the family Haemulidae. The Haemulidae were selected for this study because they exhibit the primitive perciform branchial skeleton (as described by Nelson, '67; Johnson, '80) and thus should provide a good comparative foundation. The model departs from existing hypotheses in proposing drastically different functions for two key muscles of the upper pharyngeal jaws, the levator posterior and fourth levator externus. Further, it identifies previously unrecognized force couplings that account for the ability of generalized perciforms to crush prey in their pharyngeal apparatus.

MATERIALS AND METHODS

The anatomy of fresh and formalin-preserved specimens of nine Western Atlantic species of the marine family Haemulidae was studied. Between two and five preserved individuals were examined from each of the following species: *Anisotremus virginicus* (54–163 mm standard length [SL]), *Haemulon aurolineatum* (76–145 mm SL), *H. flavolineatum* (35–174 mm SL), *H. sciurus* (56–158 mm SL), *H. plumieri* (51–166 mm SL), *H. chrysargyreum* (71–111 mm SL), *H. bonair-*

iense (54–88 mm SL), *H. carbonarium* (46–167 mm SL), and *H. macrostomum* (123–387 mm SL). Specimens above 80 mm were usually sexually mature. Male and female specimens of most species were studied, although none of the species was found to exhibit sexual dimorphism in cranial morphology. Osteological observations were made on cleared and double-stained specimens (Dingerkus and Uhler, '77) of all but the last species listed above (no small specimens were available). Drawings were made with a camera lucida attachment mounted on a Zeiss SV-8 dissecting microscope. Skeletal terminology follows that of Nelson ('69), and muscle terminology follows that of Winterbottom ('74) and Lauder ('83b).

To test the functions of 12 branchial muscles a series of electrical stimulation experiments were performed on five living fishes: two *A. virginicus*, two *H. aurolineatum*, and one *H. plumieri*. These individuals ranged between 142 and 153 mm standard length. Living fishes were purchased from commercial suppliers in Florida and Belize (formerly British Honduras, Central America), housed in 100 liter aquaria (19–23°C), and fed a mixed diet of frozen shrimp (*Penaeus*) and living earthworms (*Lumbricus*). Each fish was first anesthetized (tricaine methane sulfonate), and then the opercle bone and the mucous epithelium separating the gills from the pharyngeal muscles were removed from one or both sides. This insured a clear lateral view of the muscles being stimulated and their actions. Monopolar stainless steel electrodes (0.051 mm diameter) were implanted directly into the belly of each muscle. All muscles were visible during implantation, but electrode placements were always verified by dissection following the experiments. Two electrodes were implanted into each muscle, one at each end of the muscle. Insulation was scraped away to expose 1 mm long electrode tips. The electrodes were attached to muscle stimulators (Grass S44 and S48) so that equal electrical stimulation could be delivered to a single muscle, a bilateral pair, or simultaneously to several muscles. Muscles were given both twitch (2–8 msec duration) and presumably tetanic stimuli (30–50 Hz, 2–8 msec pulse duration, 2–15 V). While muscles were being stimulated, their actions on the elements of the pharyngeal apparatus were observed and noted in writing. Each muscle was stimulated several times with varying electrical intensity, while observations were made from lateral and anterior aspects.

Observations on each muscle were replicated on at least two fish. To ensure that cross stimulations to other muscles were not confusing interpretations of function, each muscle was tested at least once with all other muscle insertions to the bone of attachment severed. Severing muscle attachments can alter the passive forces experienced by individual elements of the apparatus. With this in mind interpretations of these experiments were made only with reference to the possibility of the effects of cross stimulation.

To examine the functional role of the pharyngeal muscles during feeding behaviors, electromyographic recordings of muscle activity were made from five *A. virginicus*, three *H. aurolineatum*, three *H. plumieri*, three *H. sciurus*, and two *H. flavolineatum*. These specimens ranged between 146 and 169 mm standard length. Stainless steel bipolar electrodes (0.051 mm diameter) were constructed and implanted directly into the branchial muscles of anesthetized fishes as described earlier (Wainwright, '89). Briefly, the first 15 cm of paired electrode wires were glued together with a cyanoacrylate adhesive to reduce movements of electrode tips relative to each other during the experiment. The 0.5 mm bared electrode tips were threaded into a hypodermic needle (26 gauge) and bent back against the barrel. The needle was inserted into the muscle belly where the hooked tips anchored the electrodes in place as the needle was backed out carefully. Paired electrodes from up to 10 muscles were color coded, sutured to the fishes' back just anterior to the dorsal fin, and glued into a common cable. Each of the pharyngeal muscles with the exception of the retractor dorsalis, the levator interni, the third obliquus dorsalis, and the transversus ventrales could be identified visually through the mucous membrane over the branchial muscles. Electrode placements were confirmed by dissection following 9 of the 16 experiments.

During experiments fishes were fed 2–3 cm long pieces of fresh earthworm, 1 cm cubed pieces of shrimp flesh, and 1–2 cm long live mole crabs (*Emerita*). Electromyographic signals were recorded from up to six muscles simultaneously and stored on a Bell and Howell 4020A FM tape recorder. Grass P511J preamplifiers were used, with the low pass filter set at 100 Hz and the high pass filter at 3,000 Hz. The 60 Hz notch filter was always used. Electromyograms were recorded at a tape speed of 19 cm/sec and were later digitized with a Keithley 12-bit analogue-to-

digital converter at a sample rate of 2,050 Hz. This sample rate was used because 1) a Fast Fourier Transform of representative signals showed that these electromyograms contained insignificant energy (less than 5%) in the range above 1,000 Hz so that the Nyquist sample criterion was met and aliasing could be rejected, and 2) the variables that were measured from these digitized records were only onsets and cut-offs of activity (see below) rather than signal magnitude. The former two variables would not be affected by aliasing. A hard copy, for visual inspection, was made from the computer file of each feeding on a Gould 260 chart recorder.

The digital file of each feeding was played into a Tektronix 4107 color graphics terminal and a computer program assisted in measuring durations of activity in each muscle during the cyclical bursts characteristic of pharyngeal transport (Lauder, '83b; Wainwright, '89). Also, the temporal sequence of muscle activity was quantified by choosing the onset of activity of the retractor dorsalis muscle as a reference time, from which the onset of activity in each of the other muscles was measured. The retractor dorsalis was chosen as the reference muscle for this study, because it exhibited a conservative pattern of activity (was active in all cycles of muscle activity) and has been used in previous work on perciforms (Lauder, '83a,b), thus facilitating comparisons.

RESULTS

Morphology

The pharyngeal jaw apparatus is made up of gill arch bones, ligaments, branchial muscles, and articulating joints. Important mechanical couplings include linkages to the neurocranium, vertebral column, pectoral girdle, and the hyoid bar. The descriptions of haemulid pharyngeal anatomy that follow focus on areas of particular functional interest. All haemulids examined possessed the bone and muscle configuration described below. Additional anatomical descriptions of haemulids (Johnson, '80) and other teleostean fishes are available in the literature (e.g., Allis, '03; Tchernavin, '53; Nelson, '67, '69; Liem, '70; Rosen, '73; Winterbottom, '74; Travers, '81; Lauder, '83a,b).

Osteology of the pharyngeal jaws

The upper pharyngeal jaw is made up of dermal tooth plates fused to the ventral surfaces of pharyngobranchials 2, 3, and 4 (Fig. 1). Each of these broad elements articulates

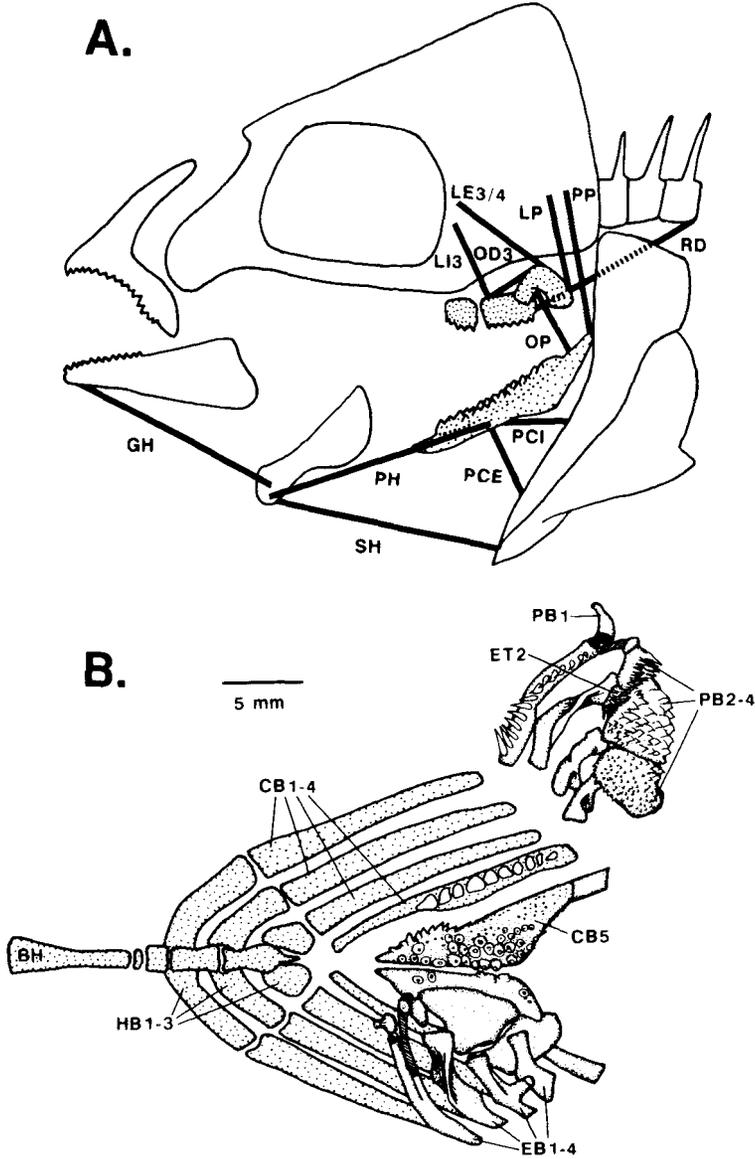


Fig. 1. A: Schematic lateral view diagram of the haemulid pharyngeal jaw apparatus. The opercular series, suspensorium, and most of the gill arches have been removed. Thick black bars represent lines of action of pharyngeal jaw muscles. B: Dorsal view of gill arch elements in *H. sciurus*. Right side dorsal elements are shown in ventral aspect. The hyoid bar is not shown. BH, basihyal; CB1-5, ceratobranchials 1 to 5; EB1-4, epibranchials 1 to 4; ET2, epibranchial 2 tooth plate; GH, geno-

hyoideus muscle; HB1-3, hypobranchials 1 to 3; LE3/4, levator externi 3 and 4 muscles; LI3, levator internus 3 muscle; LP, levator posterior muscle; OD3, obliquus dorsalis 3 muscle; OP, obliquus posterior muscle; PB1-4, pharyngobranchials 1 to 4; PCE, pharyngocleithralis externus muscle; PCI, pharyngocleithralis internus muscle; PH, pharyngohyoideus muscle; PP, protractor pectoralis muscle; RD, retractor dorsalis muscle; SH, sternohyoideus muscle.

dorsally with a cartilaginous knob on the proximal end of the epibranchial of the same arch. Epibranchials 2 and 3 also each make contact with the next most posterior pharyngobranchial (Fig. 1B). These articulations

(termed PB-EB joints) permit free movement of both bones in the dorsoventral plane. Epibranchials 2-4 are complexly shaped bones, each dorsoventrally flattened and bent into an arc that rises dorsally from its articu-

lation with the pharyngobranchial and curves ventrally to its distal attachment with the ceratobranchial. When the pharyngeal apparatus is viewed anteriorly, posteriorly, or laterally the pharyngobranchials can be seen suspended within the pharynx by their attachments to the epibranchials. Epibranchial 3 also possesses a well-developed uncinat process that projects posteriorly (Fig. 1B). This process overlaps epibranchial 4 and attaches to it by strong ligaments medial and distal to the process. Through these attachments epibranchials 3 and 4 form a single mechanical unit (Gans, '69), which permits very little independent movement of the two elements (during manipulations of fresh specimens).

The lower pharyngeal jaws (Fig. 1) are formed by broad tooth plates that are fused with the underlying fifth ceratobranchials. The paired lower pharyngeal jaw bones meet medially, and although they do not fuse they are attached by extensive ligaments and are capable of only limited independent movement. Anteriorly, these bones are connected by ligaments to the basibranchial and laterally via ligaments to ceratobranchial 4. Posteriorly and dorsally the tip of each ceratobranchial 5 attaches by muscles to the distal ends of ceratobranchial 4 and epibranchial 4. These attachments restrict movement of the fifth ceratobranchials relative to the rest of the branchial basket. All other connections of the lower pharyngeal jaw to peripheral structures are muscular.

Muscles of the pharyngeal jaws

The obliquus dorsalis 3 muscle (Figs. 1, 2) crosses the third PB-EB joint dorsally, running from a central ridge on pharyngobranchial 3 to insert broadly on the dorsal margin and uncinat process of epibranchial 3. Apparently, no anterior obliquus dorsalis is present; however, the transversus dorsalis anterior spans the PB-EB joint of arch 2, attaching medially to a thickened fibrous connective tissue pad that is connected on the midline to the anterior process of pharyngobranchial 3 and inserting broadly along the dorsal surface of epibranchial 2 (Fig. 2). In *Anisotremus* and *Haemulon* both the obliquus dorsalis and transversus dorsalis anterior are thick, robust muscles.

Levator externi 1-4 arise from the ventrolateral region of the neurocranium near the otic capsule and attach to the epibranchial of each arch (Figs. 1, 2). Levator externi 3 and 4 each insert on the tip of the uncinat process

of their epibranchial bone, but levator externus 4 is much more robust than the very slender levator externus 3. In the functional analyses these muscle could not be separated, so they were considered together. The levator interni arise medial to the external levators and insert on the pharyngobranchial of each arch. The levator posterior runs straight dorsoventrally from the skull to insert on the dorsal surface of the distal-most region of epibranchial 4 (Fig. 1). The retractor dorsalis arises from the second and third vertebrae and attaches to the posterodorsal surface of pharyngobranchials 3 and 4 (Figs. 1, 2).

In all haemulids examined the protractor pectoralis muscle runs from its origin on the skull immediately posterior to the levator posterior to insert primarily by a thick tendon on the distal tip of ceratobranchial 5 (Figs. 1, 2). This muscle also inserts into the connective tissue sheet that runs between the pectoral girdle and ceratobranchial 5. In other fishes the protractor pectoralis muscle, when present, inserts on the pectoral girdle or the connective tissue between the pectoral girdle and ceratobranchial 5 (Greenwood and Lauder, '81). Thus the attachment of this muscle by a thick tendon to ceratobranchial 5 is a phylogenetically derived and apparently unique condition in the Haemulidae. A complete discussion of the condition of the protractor pectoralis in haemulids will be presented elsewhere. Two muscles, the adductor 5 and the much larger obliquus posterior, attach the end of ceratobranchial 5 to the broad underside of epibranchial 4 (Fig. 1). Because of their close association, it was not possible to separate these two muscles during functional experiments; hence they are considered together in the discussions below. These muscles are surrounded laterally and anteriorly by a pronounced connective tissue sheet that connects the posterior margin of ceratobranchial 5 to the posteroventral margin of epibranchial 4. This connective tissue limits the extent to which these bones can separate.

The pharyngocleithralis internus and externus muscles exhibit the condition present in other percoids in connecting the pectoral girdle to the ventral surface of the lower pharyngeal jaw (Figs. 1, 2). Anterior coupling of the lower pharyngeal jaws to the hyoid bar is provided by the pharyngohyoideus muscle, which connects the urohyal to ceratobranchial 5. The transversus ventralis posterior is a large muscle that interconnects the fifth ceratobranchials ventrally (Fig. 2C). A trans-

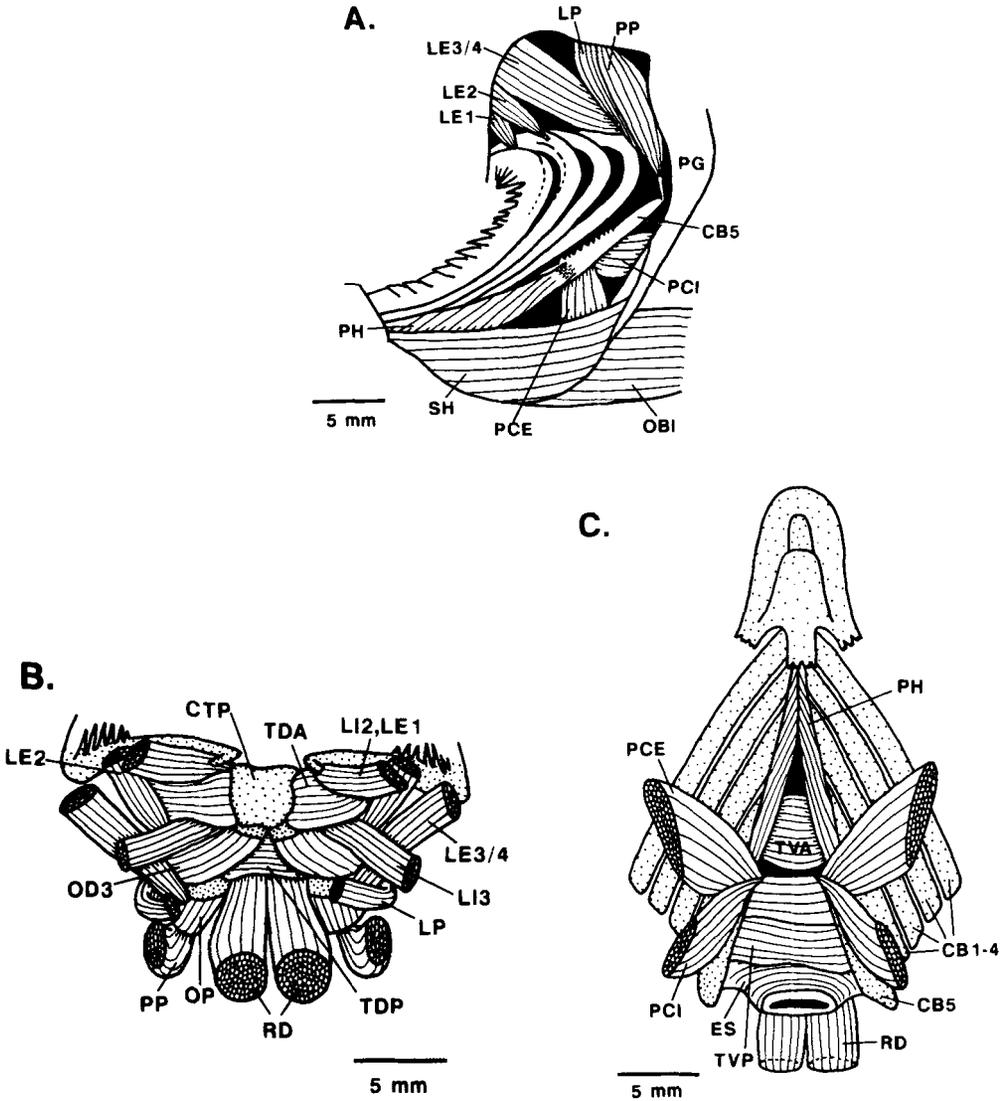


Fig. 2. **A:** Diagram of the lateral view of the branchial region of *H. flavolineatum*. The gills have been removed. **B:** Dorsal view of the branchial musculature in *H. flavolineatum*. **C:** Ventral view of the branchial musculature in *H. flavolineatum*. The urohyal and hyoid bar have been removed. CTP, central connective tissue pad; ES, esophagus;

LE1-3, levator externus 1 to 3; LI2, levator internus 2; OBI, obliquus inferioris portion of the hypaxialis muscle; PG, pectoral girdle; TDA, transversus dorsalis anterior; TDP, transversus dorsalis posterior; TVA, transversus ventralis anterior; TVP, transversus ventralis posterior. All other abbreviations as in Figure 1.

versus ventralis anterior is also present ventrally between the ceratobranchials of the fourth arch.

Muscle stimulation experiments

A summary of the movements caused by electrical stimulation of the 12 pharyngeal muscles is presented in Table 1. Although this type of information is valuable in this

kind of research, it is stressed that the results of electrical stimulation experiments should be interpreted with some caution. The effect of stimulated muscles can depend on the orientation of skeletal elements as well as on the activity of other muscles. In the descriptions that follow, *retraction* refers to posterior movement of the element (relative to the fish's body), *protraction* means movement in

TABLE 1. *Actions of pharyngeal muscles during direct electrical stimulation*

Muscle	Action
Retractor dorsalis	Retraction of upper jaws
Transversus dorsalis anterior	Depression of upper jaws, primarily tooth plates 2 and 3
Obliquus dorsalis 3	Depression of upper jaws, primarily tooth plates 3 and 4
Levator externus 3/4	Depression of upper jaws, dorsal rotation of lateral margin of epibranchials 3 and 4
Levator posterior	Depression of upper jaws, dorsal rotation of lateral margin of epibranchials 3 and 4
Obliquus posterior	Depression of upper jaws, elevation of posterior region of lower jaws
Levator internus 3	Protraction and elevation of upper jaws
Protractor pectoralis	Elevation of posterior region of lower jaws
Pharyngocleithralis externus	Depression of lower jaws
Pharyngocleithralis internus	Depression and retraction of lower jaws
Pharyngohyoideus	Protraction and elevation of anterior region of upper jaw
Transversus ventralis posterior	No movements, stabilization of articulation between left and right ceratobranchials

an anterior direction, *depression* refers to ventrally directed movement, and *elevation* to dorsal movements.

Upper pharyngeal jaw depression was caused separately by each of five muscles: the transversus dorsalis anterior, obliquus dorsalis 3, levator externus 3/4, levator posterior, and obliquus posterior. Of these muscles the obliquus dorsalis 3 and transversus dorsalis anterior caused the greatest depressive movements. The term *upper jaw depression* is heretofore used to indicate the ventral depression of the lateral aspect of the pharyngobranchials. The medial regions of the pharyngobranchials were never observed to move ventrally, as they are attached strongly to a medial cartilaginous pad that is firmly attached to the ventral surface of the neurocranium. During independent stimulations of the obliquus dorsalis 3, levator externus 3/4 and levator posterior epibranchials 3 and 4 rotated about the insertion of the obliquus posterior and its associated connective tissue. The lateral aspect of this mechanical unit rotated dorsally and the medial aspect rotated ventrally, depressing the lateral margins of pharyngeal tooth plates 3 and 4. When the posterior tip of ceratobranchial 5 was lifted dorsally to simulate the function of the protractor pectoralis, these three dorsal bran-

chial muscles were still able to cause depression of the pharyngeal tooth plates. However, when the insertion of the obliquus posterior and its associated connective tissue sheet onto epibranchial 4 was severed, the effect of these muscles was only to elevate the lateral aspect of the epibranchial; no pharyngobranchial depression was observed. The transversus dorsalis anterior caused dorsal rotation of the lateral margin of epibranchial 2, depressing pharyngobranchial 2.

Dorsal rotation of the lateral aspects of epibranchials 3 and 4 by levator externus 3/4 and the levator posterior caused some elevation of the posterior limb of ceratobranchial 5. Stimulation of either the obliquus posterior or the protractor pectoralis produced distinct elevation of the posterior region of the lower pharyngeal jaw. The protractor pectoralis also caused a protractive rotation of the pectoral girdle.

The upper pharyngeal jaws were retracted strongly and elevated by stimulation of the retractor dorsalis. The action of the levator internus 3 depended on the position of the pharyngobranchials. With the jaws in a relaxed state this muscle caused the third pharyngobranchial to be elevated and slightly protracted, but when the upper pharyngeals were first retracted, as if by retractor dorsalis action, its effect was strong upper jaw protraction.

The pharyngocleithralis muscles caused short depressive movements of the lower pharyngeals, with an additional retractive motion occurring when the pharyngocleithralis internus was activated. Stimulation of the pharyngohyoideus brought about a slight rocking of the lower pharyngeal jaws, as their anterior aspect was elevated in a short protractive excursion. No movements were caused by the transversus ventralis posterior, but contraction of this large muscle firmly stabilized the connection between left and right fifth ceratobranchials. In general, the movements of the lower pharyngeals were not as extensive as those of the upper jaws.

Patterns of muscle activity

Four distinct phases of pharyngeal jaw muscle activity have been identified by Lauder ('83b,c) during prey capture and processing by teleost fishes: the initial strike, buccal manipulations, pharyngeal manipulation, and pharyngeal transport. All haemulid species studied exhibited three of these phases: the initial strike, buccal manipulation, and pharyngeal transport.

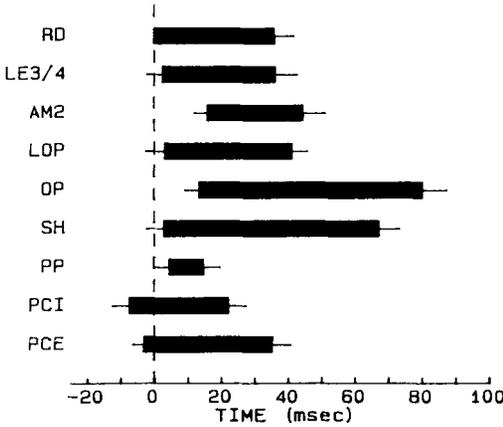


Fig. 3. Electromyographic bar diagram showing summary of muscle activity from the strike in *A. virginicus*. Bars represent mean durations of activity in each muscle (S.E. shown at right end of bar) and mean onset times relative to the retractor dorsalis onset (S.E. shown at the left end of the bar). Data shown are averages from three fish; sample sizes for each muscle vary from 11 to 36. AM2, division 2 of adductor mandibulae; LOP, levator operculi. All other abbreviations as in Figure 1.

During the initial strike all muscles simultaneously exhibited a single short burst of activity (Fig. 3). This was usually followed immediately by the pharyngeal transport phase, but in about 10% of feedings buccal manipulation occurred. During this phase a

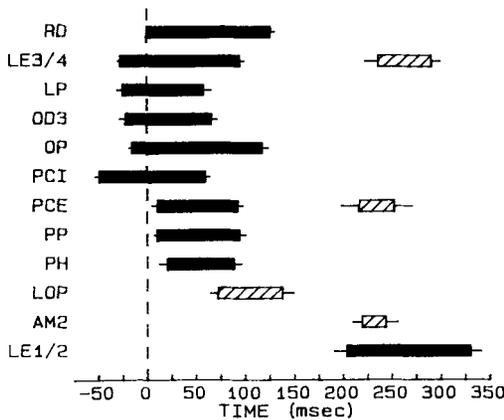


Fig. 4. Electromyographic bar diagram of muscle activity during pharyngeal transport in *A. virginicus*. The burst pattern for a single cycle of activity is shown. Conventions and abbreviations as in Figure 3. Data shown are from six different fish feeding on pieces of earthworm. Sample sizes for each muscle vary from 37 to 217 cycles of activity. Solid bars represent activity bursts that occur in 100% of activity cycles; hatched bars indicate activity bursts that occur in less than 50% of pharyngeal transport cycles.

motor pattern similar to the initial strike was repeated cyclically up to 12 times while the fish moved the prey back and forth between the anterior margin of the oral jaws and the buccal cavity. Pharyngeal transport involved activity in all muscles examined for much longer durations than either the initial strike or buccal manipulation (Figs. 4–8). Depending on factors such as prey hardness, pharyngeal transport continued for more than 60 cycles of muscle activity. Although this phase matches Lauder's definition of pharyngeal transport ('83b,c), much trituration of prey occurred during this behavior, indicating that the name for the behavior may not be entirely appropriate.

During pharyngeal transport most muscles overlapped activity with the retractor dorsalis (Figs. 4, 5). Of the muscles examined, only the adductor mandibulae, levator operculi, levator externus 1/2, and levator internus 3 did not overlap with retractor dorsalis activity. Before the onset of activity of the retractor dorsalis four upper pharyngeal jaw muscles begin activity almost simultaneously and stay active for about 100 msec: the obliquus dorsalis 3, the levator posterior, the levator externus 3/4, and the obliquus poste-

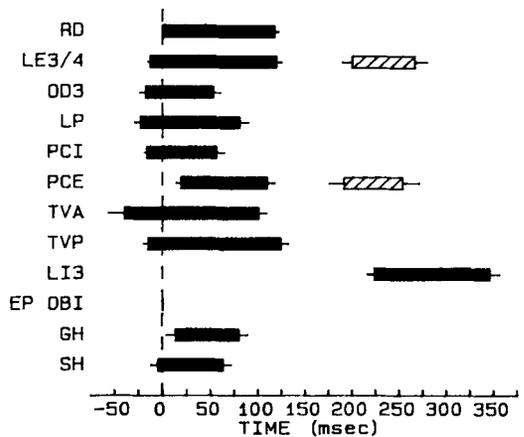


Fig. 5. Electromyographic bar diagram showing muscle activity during pharyngeal transport in *Haemulon*. This diagram is a composite from four species of *Haemulon* feeding on earthworm pieces. The first three muscles and the pharyngocleithralis muscles represent data pooled from feedings by three individuals each of *H. aurolineatum*, *H. sciurus* and *H. plumieri* (activity patterns in these muscles have been shown not to vary among these three species [see Wainwright, 1989]). Data for the levator posterior are from *H. sciurus*. All remaining data are from *H. aurolineatum*. Sample sizes vary from 23 to 389 cycles of activity. Conventions and abbreviations as in Figures 1 and 3.

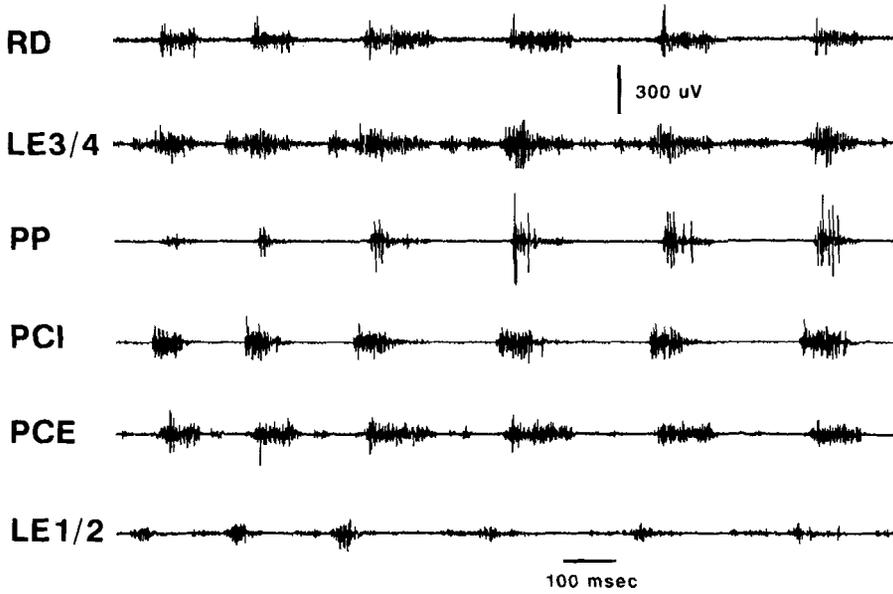


Fig. 6. Simultaneous recordings from six muscles during the pharyngeal transport phase in *A. virginicus*. Data shown are a printing of the digital file of this feeding as viewed on the Tektronix graphics terminal. Abbreviations as in Figures 1 and 2.

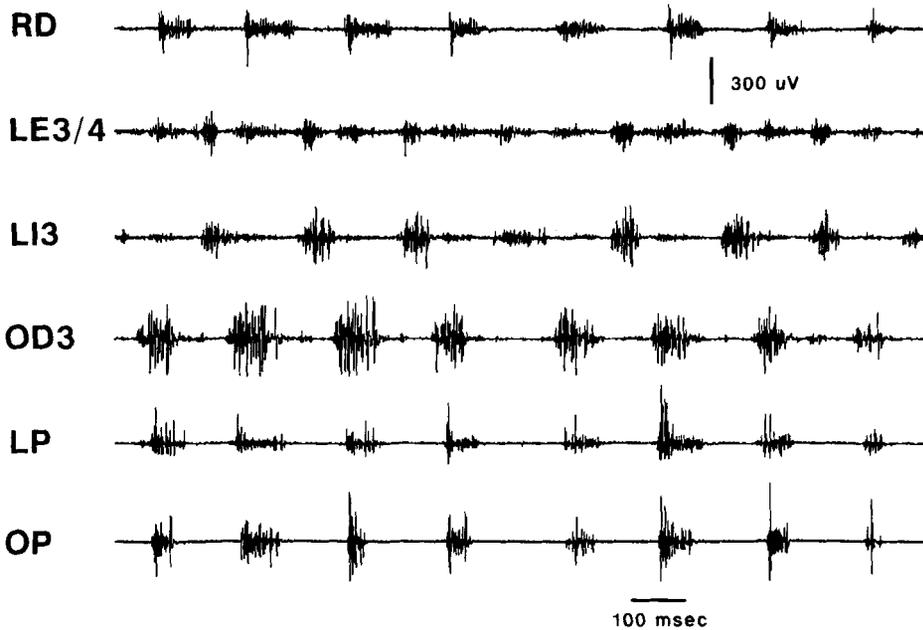


Fig. 7. Simultaneous recordings of six muscles during pharyngeal transport in *H. aurolineatum*. Note the broad overlap of activity in most muscles with the retractor dorsalis. Abbreviations as in Figure 1.

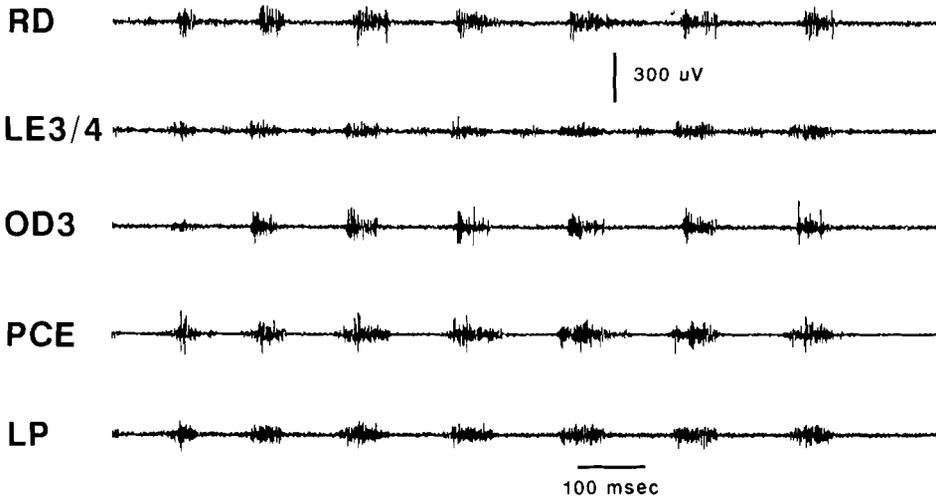


Fig. 8. Simultaneous recordings of five branchial muscles during pharyngeal transport in *H. sciurus*. Abbreviations as in Figure 1.

rior. There is also a group of muscles that insert on the lower jaws and, after the onset of the retractor dorsalis, begin activity together: the pharyngocleithralis externus, pharyngohyoideus, and protractor pectoralis. The transversus ventralis anterior and posterior were broadly active across these time periods (Fig. 5). The sternohyoideus and geniohyoideus muscles were mostly active within the duration of the retractor dorsalis burst. Two muscles also frequently showed a second period of activity per cycle; the levator externus 3/4 and pharyngocleithralis externus (Figs. 4, 5).

DISCUSSION

Pharyngeal jaw mechanisms

Based on the anatomical arrangement of branchial structures, the sequence of muscle activity during pharyngeal transport, and observations on the actions of directly stimulated muscles, the following mechanical model is proposed for function in the pharyngeal jaw apparatus of haemulid fishes. Because haemulids possess generalized perciform pharyngeal anatomy (Johnson, '80), this model is expected to apply broadly to other "basal" perciform fishes.

Function of the pharyngeal jaw apparatus during pharyngeal transport is dominated by the working stroke of the upper jaws, which can be defined by the activity pattern of several muscles that contribute to depression

of the upper tooth plates and the retractor dorsalis that retracts these elements (see Fig. 9). This simultaneous depression and retraction of the upper tooth plates is met by an elevation and stiffening of the lower jaws, resulting in a biting action as the jaws move against each other and the upper jaws rake across the lower tooth plates. The joint between the epibranchial and the pharyngobranchial of each branchial arch forms a previously unrecognized force coupling that is proposed to be the key to upper pharyngeal jaw function in haemulids (Fig. 9). Movement at this joint causes the epibranchial to push ventrally on the lateral margin of the pharyngobranchial, effecting an occlusal action of the upper jaws against the lowers. All four muscles that insert directly onto the epibranchial 3 and 4 complex cause this action when they are directly stimulated (Table 1; obliquus dorsalis 3, levator externus 3/4, levator posterior, and obliquus posterior).

A critical functional component of this joint is the obliquus posterior muscle, which, together with its associated connective tissue sheet, forms a mechanical linkage that prevents purely dorsal movements of epibranchials 3 and 4 (Fig. 9). Indeed, when this muscle was severed during the stimulation experiments the other three posterior upper jaw depressors (obliquus dorsalis 3, levator posterior, and levator externus 3/4) move the epibranchials dorsally without causing de-

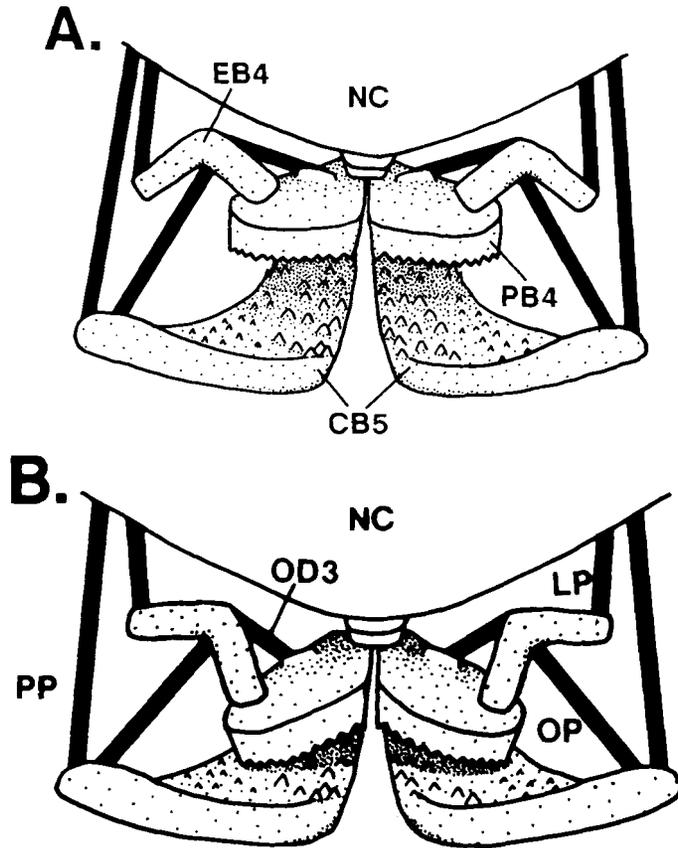


Fig. 9. Schematic diagram showing the pharyngeal jaw apparatus in its posterior aspect. This diagram illustrates the mechanism of upper jaw depression observed in haemulids. **A:** Apparatus in a relaxed state. **B:** Apparatus following contraction of all four paired muscles. Note the nature of the coupling between the epibranchial and pharyngobranchial. Rotation of the epibranchial about the insertion of the obliquus posterior is caused by the levator

posterior and the obliquus dorsalis 3. This causes the epibranchial to depress the lateral margin of the pharyngobranchial (the upper jaw). The obliquus posterior and associated connective tissue provide a mechanical linkage that resists dorsal movements of its attachment site on the epibranchial. NC, neurocranium. Abbreviations as in Figures 1 and 2.

pressive movements of the pharyngobranchial tooth plates. The intact obliquus posterior restricts dorsal movements of the central region of epibranchial 4 and causes it to pivot around the insertion of this muscle (Fig. 9).

The pattern of pharyngeal jaw movements proposed above is based largely on the sequence of muscle activity observed during pharyngeal transport. The working stroke of the upper jaw begins with nearly simultaneous activity in the four muscles that act primarily to depress the upper jaws: the obliquus dorsalis 3, the levator externus 3/4, the obliquus posterior, and the levator posterior. Immediately following the onset of this

action the retractor dorsalis muscle becomes active, retracting the upper tooth plates. During these events the transversus ventralis posterior muscle stabilizes the connection between the two fifth ceratobranchials, allowing these two bones to act as a single lower jaw element. About 25 msec after the onset of retractor dorsalis activity, three muscles that insert on the lower jaws begin to act: the pharyngocleithralis externus, protractor pectoralis, and pharyngohyoideus. Their net effect is to stabilize the lower jaws and elevate them toward the depressing upper jaws. Lower jaw elevation is accompanied by a protractive movement of the pectoral girdle

caused by the simultaneous activity of the geniohyoideus, sternohyoideus, and protractor pectoralis muscles, combined with inactivity in the obliquus inferioris. This contributes to overall constriction of the pharynx.

The presence of food items between the jaws may be expected to have one primary consequence for this model. The physical presence of food items will maintain a space between ceratobranchial 5 and pharyngobranchials 3 and 4; this will tend to maintain tension in the obliquus posterior. As long as the obliquus posterior resists (actively or passively) dorsal movements of the epibranchial, upper jaw depression can be accomplished by the upper jaw muscles. It is important to emphasize that even when the posterior tip of ceratobranchial 5 is elevated dorsally strongly the obliquus posterior resists dorsal movements of the epibranchial 3/4 complex, enabling the dorsal muscles to effect upper jaw depression.

Comparisons with other models

The pharyngeal jaw movement patterns proposed by this model draw broad support from the literature. The only published data on pharyngeal jaw kinematics in a perciform that does not exhibit specialized pharyngeal function were presented by Sponder and Lauder ('81), who used cineradiography to observe directly the pharyngeal jaw movements during feeding in *Periophthalmus*. These investigators observed that 1) the upper jaw underwent strong depression and retraction during its major working stroke and 2) the lower jaw had a much smaller orbit of movement than the upper jaw. Based on manipulations of fresh specimens and observations of the marks left on swallowed prey, Liem ('70) inferred that the working stroke of the upper jaws in nandid fishes involves simultaneous retraction and depression of the lateral border of the upper tooth plates. In an anatomical and electromyographic analysis of centrarchids and *Perca*, Lauder ('83a,b) emphasized upper jaw retraction as the primary pharyngeal jaw movement in these fishes. Lauder's electromyographic data ('83a,b) show strong congruence with the muscle activity patterns observed in haemulids. As in haemulids, there is broad overlap in activity of most pharyngeal muscles that can be divided into three phases: 1) an initial phase, when a group of upper jaw muscles begin activity before the retractor

dorsalis onset; 2) the onset of retractor dorsalis activity; and 3) a later phase that begins after retractor dorsalis onset, when a group of lower jaw muscles are active. The only muscle that exhibits a qualitatively different pattern of activity in centrarchids is the sternohyoideus, which is never active in centrarchid pharyngeal transport. Activity in this muscle was so consistently absent that it was used by Lauder ('83b,c) to define the pharyngeal transport phase in generalized perciforms, suggesting that the presence of activity seen in haemulids is a derived condition.

While the data presented here support previous interpretations of perciform pharyngeal jaw movements, they do not support some of the mechanisms that have been hypothesized to produce these actions. In particular, the levator posterior and levator externus 3/4 have previously been inferred to function in upper pharyngeal jaw elevation and protraction (Vanden Berghe, '28; Liem, '70; Lauder, '83a-c). Both hypotheses are directly refuted by the results of the stimulation experiments (Table 1), since each of these muscles produced upper jaw depression. The anatomical basis for this function becomes apparent only when the previously unrecognized interaction between the epibranchials and the pharyngobranchials is considered (Fig. 9).

The fourth levator externus does, however, appear to have a secondary role in upper jaw protraction. This is seen in less than 50% of chewing cycles when a second burst of activity occurs in the fourth levator externus (Figs. 4, 5, 7). This second burst occurs after the primary working stroke and coincides with activity in the third levator interni (Figs. 5, 7). The third levator internus effects strong protraction and elevation when the upper jaws are retracted (as will be the case following retractor dorsalis activity), and the fourth levator externus may contribute to this movement if no other depressors are active and the pharyngobranchial is being directly acted on by the levator internus.

In the only previous discussion of function of the obliquus dorsalis muscle, Liem ('70) hypothesized that this muscle acts to elevate the lateral border of the upper pharyngeal jaws. The opposite action was observed when this muscle was directly stimulated; the lateral margin of the upper jaw was depressed (Table 1; Fig. 9). For all other muscles tested the results of the stimulation experiments were congruent with previous hypotheses of function (Vanden Berghe, '28; Gunther and

Deckert, '55; Kayser, '62; Karrer, '67; Liem, '70; Lauder, '83a-c).

The primary significance of the model proposed here is that it identifies a mechanism for upper pharyngeal jaw depression and hence an effective pharyngeal jaw bite. Such a mechanism explains the ability of many generalized perciforms to crush prey in their pharyngeal apparatus. In work with mollusc crushing centrarchids, Lauder ('83a,d) found that this feeding behavior was associated with a derived pattern of intense, simultaneous activity in many pharyngeal muscles, including the levator posterior and levator externus 3/4. Lauder ('83a) concluded that crushing actions could not be inferred from this motor pattern under existing models of pharyngeal muscle function, and he proposed that the pharyngohyoideus muscle causes a shearing action of the lower jaws against the upper jaws to crack mollusc shells. While this function for the pharyngohyoideus muscle is consistent with data presented here, additional strong upper jaw depression is predicted to occur because of activity in the levator posterior and levator externus 3/4. Simultaneous activity in most branchial muscles would be expected to stabilize the pharyngeal apparatus while the primary crushing force is provided by upper jaw depression, through activity of the obliquus dorsalis 3, levator posterior, levator externus 3/4, and obliquus posterior muscles (Table 1; Fig 9).

Evolutionary patterns

The phylogenetically derived condition of the protractor pectoralis muscle in haemulids, connecting between the neurocranium and the lower pharyngeal jaw, is a novel functional innovation. This muscle elevates the lower pharyngeal jaws (Table 1), contributing to the overall occlusion that occurs during the working stroke of the apparatus. This functional innovation is analogous to the condition found in many labroids and exocoetid beloniforms in which either the levator posterior or the fourth levator externus inserts on the fifth ceratobranchial rather than on the fourth epibranchial (Stiassny and Jensen, '87). Here, too, a direct attachment between the neurocranium and the lower pharyngeal jaw provides these fishes with a mechanism for a strong lower pharyngeal jaw bite.

With the exception of the unique attachment and function of the protractor pecto-

ralis muscle the haemulid pharyngeal jaw apparatus represents the generalized perciform condition (as described by Liem, '70; Johnson, '80; Travers, '81; Lauder '83b). Functionally, this system is dominated by the working stroke of the upper jaws, during which the posterior pharyngobranchial tooth plates are depressed and retracted. The key functional attributes of the perciform pharyngeal apparatus, as adduced here, are the presence of 1) the retractor dorsalis muscle, which acts to retract the upper jaws; and 2) the epibranchial-pharyngobranchial joint, which permits upper jaw depression by dorsal branchial musculature. Rosen ('73) has identified the presence of a retractor dorsalis muscle as a shared derived character for the neoteleostei, indicating that this feature is not unique to perciform fishes. A key goal in future work will be to identify the phyletic distribution of the epibranchial-pharyngobranchial joint and its function in upper jaw movements. This is of interest because this feature is hypothesized here to represent the most primitive occurrence of the ability of teleostean fishes to depress the upper pharyngeal jaws forcefully.

In contrast to the primitive perciform condition, the labroid pharyngeal apparatus is dominated by movements of the lower jaw (Liem and Sanderson, '86; Wainwright, '87, '88). This functional transition has involved a suite of anatomical changes, including fusion of the fifth ceratobranchials and, usually, insertion of dorsal branchial muscles on the lower jaw (Kaufman and Liem, '82; Liem, '86). Function of the upper jaw has changed from being a dorsoventrally working element in generalized forms to moving almost entirely in the anteroposterior axis in labrids (Liem, '86; Liem and Sanderson, '86). In essence, the upper and lower jaws have reversed roles as the primary bite-force generator and a stabilized platform against which the other element works. It is interesting to note that, although the levator externus 4 and levator posterior muscles of labroids usually exhibit a derived insertion on the lower jaw (instead of on the fourth epibranchial), their role in prey processing does not change from the primitive perciform condition. These muscles are primary effectors of forceful occlusion of the pharyngeal jaws in both fish groups.

The labroid pharyngeal apparatus is capable of strong crushing actions (Brett, '79; Liem, '86; Wainwright, '87). Widespread

crushing of hard-shelled prey (e.g., molluscs, armored crustaceans, and coral rock) is a trophic innovation of the Labroidei (Freyer and Iles, '72; Yamaoka, '78; Kaufman and Liem, '82; Wainwright, '88) that permits these fishes to exploit food resources not available to functionally unspecialized perciforms. Nevertheless many generalized perciform taxa exhibit intermediate feeding habits and are capable of crushing some hard-shelled prey in their pharyngeal apparatus. For example, several haemulids, centrarchids, and members of numerous other generalized perciform lineages crush molluscs, echinoderms, and crustaceans (Randall, '67; Liem and Greenwood, '81; Savitz, '81). This is accomplished in the absence of labroid specializations (Liem and Greenwood, '81; Lauder, '83a) and indicates that the generalized perciform condition can be slightly modified (e.g., hypertrophied muscles and more robust jaws [Lauder, '83a,d]) and used to crush prey effectively. Based on the present model it is predicted that these taxa exhibit enlarged epibranchial-pharyngobranchial joints and hypertrophied upper jaw depressing muscles as part of the specialization for a strong pharyngeal bite. Support for this is provided by Lauder ('83a), who found that the levator posterior muscle exhibits about a 10-fold increase in physiological cross-sectional area in molluscivorous centrarchids compared with unspecialized species.

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