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Functional morphology of the pharyngeal jaw apparatus

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Abstract

The pharyngeal jaw apparatus (PJA) of perciform fishes is a well-developed system of muscles and bones that functions in sophisticated prey processing behaviors. In being specialized for prey processing the PJA complements the prey capture functions of the oral jaw apparatus and thus greatly increases the overall diversity of feeding behavior seen in fishes. Formed from modified branchial arch elements the PJA is used to crack hard-shelled prey items, to separate edible from inedible material, to chew, and to transport prey into the esophagus. Central to PJA function is the jaw adduction mechanism that involves depression of the upper jaw as a consequence of being pressed from above by rotation of the epibranchial bone. The epibranchial is rotated by contraction of the external levator muscles that connect the underside of the neurocranium to the lateral margin of the epibranchials and by the obliquus dorsalis that crosses the epibranchial-pharyngobranchial joint dorsally. The central region of the epibranchial is stabilized by muscles that connect its ventral surface to the lower jaw and hence dorsal movement of the lateral region of the epibranchial causes ventral movement of the medial end of the epibranchial, pressing against the dorsal surface of the upper jaw. In spite of the challenge of viewing movements of the pharyngeal jaw cineradiography and sonomicrometry reveal that in generalized perciforms the pharyngeal jaws are capable of a variety of movements. This includes sheering actions between the upper and lower jaws, adduction with simultaneous retraction, and lateral motion of the lower jaws that is used to grip large prey. The major movements in the PJA of generalized perciforms are accomplished by the upper jaw, which can move extensively in three dimensions. The lower jaw has a more restricted orbit in lateral view but also moves in

three dimensions. Labroid fishes show a major morphological modification of the generalized condition in which the lower jaw bones are fused into a single element and external levator muscles connect the neurocranium directly to the lower jaw, providing a mechanically direct biting motion. Surprisingly, research has not revealed major changes in the functioning of the labroid PJA. The muscular sling effects jaw adduction, as these same muscles do in generalized perciforms, and the PJA muscle activity pattern of labroids is very similar to that seen in generalized taxa.

I. Introduction

No living group of vertebrates rivals teleost fishes in diversity. They make up about half of all living vertebrate species and they show stunning morphological, functional and ecological variety. Fishes live in nearly every aquatic habitat that has been invaded by metazoans, from the deep sea to high altitude torrential streams. As with any diverse group, it is useful to ask which functional systems underlie such staggering evolutionary success. One such axis of diversity in fishes is their feeding biology. There are fishes that feed on virtually every available food and this is associated with an equal range of functional specializations for capturing and processing these foods. Much of the functional diversity seen in fish feeding systems lies in the mechanics of prey capture that involves the oral jaws and buccal cavity (Wainwright & Bellwood, 2002; Wainwright & Richard, 1995). But an often overlooked element of fish trophic diversity lies in the functioning of a second set of jaws, the pharyngeal jaw apparatus (heretofore the PJA), that is used primarily in separating food from unwanted material and a variety of forms of prey manipulation and processing behaviors.

Fish trophic diversity is impacted by the PJA at two distinct levels. First, the presence of a second set of jaws in the feeding system promotes overall trophic diversity by increasing the range of musculo-skeletal specializations for feeding. The PJA can be thought of as an additional independent axis of morphological diversity that fish lineages have explored during evolution (Yamaoka, 1978). The structural independence of the oral and pharyngeal jaws permits potential autonomy in their evolution, and because the roles of prey capture and processing are potentially decoupled, the degree of specialization of each system is less constrained by the need to maintain secondary functions (Liem, 1973). As a result of this separation of functional role, the oral jaws of some fishes are mechanically specialized for the generation of suction or of gripping benthic prey to remove them from their holdfast, while some of the more extreme modifications to the PJA involve its use in crushing shells, grinding food, and winnowing edible material from unwanted debris, functions not often seen in the oral jaws of these fishes. Independent evolution of the oral and PJA has increased the range of fish feeding abilities and hence their feeding ecology.

The second way in which the PJA influences overall fish trophic diversity comes about because this system is itself structurally complex. The system involves a core group of 12 prominent skeletal element and is influenced by at least another 15. A similarly large number of muscles cross each joint in the system and provide the potential for intricate movements and in some cases awesome biting forces. The shape and organization of the bones is diverse and the attachment sites and sizes of muscles is highly variable, making for functional diversity that is only partly documented at present (Grubich, 2000; Lauder, 1983b; Sibbing, 1982; Wainwright, 1988; Winterbottom, 1974). Indeed, the functional diversity of the PJA may be far greater than seen in the oral jaw system. In a recent survey of 130 species of labrid fishes it was discovered that the mass of the levator posterior muscle, a prominent muscle of the PJA, ranged 500-fold across species as compared to a ten-fold range in the adductor mandibulae and sternohyoideus muscles, two prominent oral jaws muscles (Wainwright, Bellwood, Westneat, Grubich & Hoey, 2004). This result was found *after* accounting for body size!

In this chapter I review our understanding of the functional morphology of the PJA in perciform fishes. My aim is to emphasize what is known about the mechanisms of PJA action and to describe some examples of particularly notable functional innovations. Although much of what is covered applies very widely across teleosts, I focus on perciform fishes because this is where the majority of research has been concentrated. By focusing on this group of fishes I will omit a discussion of an excellent series of studies on the cyprinid, *Carpio carpio* by Sibbing and his colleagues (Sanderson, Cech & Cheer, 1994; Sibbing, 1982; Sibbing, 1988; Sibbing, Osse & Terlow, 1986) and recent, highly innovative work on mechanisms of suspension feeding (Cheer, Ogami & Sanderson, 2001; Sanderson et al., 1994; Sanderson, Cheer, Goodrich, Graziano & Callan, 2001).

II. The Pharyngeal Jaw Apparatus of Perciform Fishes

A. Overview and Anatomy

The PJA is located immediately rostral of the esophagus, suspended from the neurocranium dorsally and bounded posteriorly and ventrally by the pectoral girdle (Fig. 1A). The muscles and skeletal elements are modified components of the branchial arches (Fig. 1B). Except where indicated in the descriptions that follow, the bones and muscles of the PJA are bilaterally paired. The lower jaw is formed by tooth plates that are often fused to the fifth ceratobranchial (Nelson, 1967). These bones are oriented antero-posteriorly and converge medially at their anterior end to attach by ligaments to the basibranchials and by muscles to the fourth ceratobranchials and the pectoral girdle. The upper jaw is formed by tooth plates that are variably fused to one or more pharyngobranchial bones. In most perciform taxa the third pharyngobranchial is the largest and most dominant of these, with contributions from a reduced fourth pharyngobranchial (Nelson, 1967; Wainwright, 1989a). A functionally important second element of the upper jaw is the fourth, and often the third, epibranchial (Fig. 1 & 2). These bones form an arch dorsal and lateral to the pharyngobranchial and articulate with the latter through a rounded cartilaginous end (Galis & Drucker, 1996; Grubich, 2000; Wainwright, 1989a).

These jaw elements are stabilized by muscular connections among them and to the larger skeletal elements that surround them (Figs. 1A & 2). The fifth ceratobranchials are connected ventrally and posteriorly to the pectoral girdle by the pharyngocleithralis internus and externus muscles, and anteriorly to the hyoid bar by the protractor hyoideus muscle. The transversus ventralis muscle connects the left and right fifth and fourth ceratobranchials ventrally, helping to stabilize the lower jaw elements into a single functional structure. A small adductor branchialis muscle connects the posterior tip of the ceratobranchials to the epibranchial of the same arch. An obliquus posterior muscle also connects the fifth ceratobranchial dorsally to the fourth epibranchial. This muscle plays an important role in the PJA by providing a ventrally directed force on the epibranchial. The pharyngobranchials are connected dorsally to the neurocranium by levator interni muscles and posteriorly to several anterior vertebrae by the retractor dorsalis muscle. There is also an obliquus dorsalis muscle that connects the pharyngobranchial and epibranchial dorsally. Levator externi muscles connect each epibranchial to the neurocranium dorsally. The levator posterior muscle also connects the fourth epibranchial to the neurocranium.

B. Function in the PJA

Motion of the elements of the oral jaws can be directly observed in most taxa, but the location of the PJA in the pharynx makes observing movement more challenging. However, two approaches, cine-radiography and sonomicrometry, have permitted visualization of pharyngeal jaw movement. These approaches have yielded important insights into how the pharyngeal jaws move in several perciform taxa (Aerts, Devree &

Vandewalle, 1986; Liem & Sanderson, 1986; Vandewalle, Havard, Claes & Devree, 1992; Vandewalle, Saintin & Chardon, 1995). In conjunction with interpretations of the mechanisms of action in the PJA from anatomy and electromyography, these methods have made it possible to develop a picture of the basic patterns of movement in the PJA and the musculo-skeletal basis of those movements.

A mechanism of action of the PJA was initially identified in the perciform group Haemulidae (Wainwright, 1989a) and subsequently extended to the Centrarchidae and Sciaenidae (Galis and Drucker, 1996; Grubich, 2000). I have observed the anatomical elements of this mechanism in most perciform taxa that I have examined and numerous other teleosts (e.g. Carangidae, Girrelidae, Hexagrammidae, Lethrinidae, Lutjanidae, Percidae, Pomacanthidae, Serranidae, Scorpaenidae, Tatraponidae). Although the mechanism has never been formally mapped onto a phylogeny of actinopterygian fishes, its apparent presence in Osteoglossomorphs and *Amia* suggest that it may be at least as old as the teleosts.

The mechanism implicates the epibranchial bone as a key element in the mechanism for depression of the upper jaw bones (Fig. 2). Several muscles are oriented such that they can flex the joint between the pharyngobranchial (the upper jaw bone) and the epibranchial. If this joint is flexed while the midpoint of the shaft of the epibranchial is constrained or even pulled ventrally by the fifth adductor branchialis and the obliquus posterior muscles, then the subsequent rotation of the epibranchial bone presses ventrally on the dorsal surface of the upper jaw bone, depressing it (Fig. 2). The medial margin of the pharyngobranchial is typically connected loosely to the neurocranium by connective tissues, so that this mechanism actually causes a biting action in the PJA in which the lateral margins of the upper jaw are pressed ventrally toward the lower jaw (Fig. 2A). The joint between the epibranchial and pharyngobranchial can be flexed directly by the obliquus dorsalis muscle, and if the midpoint of the epibranchial shaft is constrained, the epibranchial can be rotated about this point by action of the levator posterior and fourth levator externus muscles that connect the lateral margin of the epibranchial to the neurocranium.

The significance of this mechanism is that it provides forceful adduction of the PJA. The importance of forceful adduction is clear in the case of behaviors such as mollusc crushing (Lauder, 1983a; Wainwright, 1987), but adduction also can be employed in concert with other actions, most notably sheering of the upper and lower jaws (Vandewalle et al., 1992; Vandewalle et al., 1995). Posterior and anterior translation of the upper jaws can be facilitated by the retractor dorsalis and levator interni muscles respectively. As we shall see below, studies have revealed that a major feature of pharyngeal jaw function in generalized perciform taxa is the combined motion of the upper jaw in both the anterior-posterior axis and the dorsal ventral axis.

C. Movement patterns of the PJA

Among generalized perciform fishes, previous studies have documented aspects of pharyngeal jaw movement patterns only in the Serranidae (Vandewalle et al. 1992) and the Sparidae (Vandewalle et al., 1995) while movements have been inferred from muscle activity patterns and anatomy in the Nandidae (Liem, 1970), Haemulidae (Wainwright 1989), Centrarchidae (Galis & Drucker, 1996; Lauder, 1983b) and the Sciaenidae (Grubich 2000). In the serranid, *Serranus scriba*, during routine pharyngeal transport behavior the upper jaw moves in a cyclic pattern that includes anterior-posterior and dorsal-ventral excursions of similar magnitude (Fig. 3; (Vandewalle et al., 1992). At the start of each cycle the upper jaw (the pharyngobranchial) moves posteriorly and ventrally until it meets the lower jaw. During the recovery stroke the upper jaw moves dorsally before also recovering anteriorly, so that the overall cycle does not involve the jaw exactly retracing its path (Fig. 3). Lower jaw motion is more restricted than upper jaw movement and occurs mostly in the anterior-posterior axis. The lower jaw cycle involves posterior retraction that peaks shortly before the upper jaw reaches its most posterior and ventral position.

I present unpublished data in figures 4, 5, 7 and 8 on pharyngeal jaw motion from three other perciform taxa, the cabezon *Scorpaenichthys marmoratus* (Cottidae), largemouth bass *Micropterus salmoides* (Centrarchidae), and the lingcod *Ophiodon elongates*, a member of the Hexagrammidae. From these data, two major points can be emphasized in relation to the observations made previously. First, all taxa were capable of a variety of pharyngeal jaw kinematic patterns, including sheering between upper and lower jaw and adduction with retraction as described for *Serranus*. Second, previously unrecognized movement in the medial-lateral axis was sometimes substantial (Fig. 7).

As with *Serranus*, the upper jaw of *Scorpaenichthys marmoratus* begins the cycle with posterior and ventral movement that culminates in a period when the upper and lower jaws adduct against the prey item (Fig. 4). There is considerable variation in the pattern from cycle to cycle with one of the primary differences being whether the upper and lower jaws are moving in the same direction together, or are moving against each other in a sheering action (compare Fig. 4A & B). A second point of variation is that the upper jaw often depresses rapidly before moving posteriorly (Fig. 4B). In these cycles the lower jaw reaches its most posterior position earlier than the upper jaw and the upper jaw moves ventrally and then posteriorly, raking the prey against the less mobile lower jaw. In the recovery stroke, both the upper and lower jaw move away from their point of adduction before being protracted into anterior positions that form the widest gape between the jaws during the cycle. During cycles when the jaws move in a sheering motion the movement orbit of the lower jaw is smaller than during cycles of simultaneous retraction. The capacity to show sheering motions and simultaneous retraction was also found in *Micropterus* and *Ophiodon*.

A slightly different picture is seen in the largemouth bass, *Micropterus salmoides* (Fig. 5). During rhythmic pharyngeal transport behavior in this species, the upper jaw undergoes relatively minor ventral excursion but travels about three times further in the posterior direction. As with *Serranus* and *Scorpaenichthys*, *Micropterus* shows both sheering and simultaneous depression and retraction of the jaws. Published data on the sparid, *Diplodus sargus*, illustrate sheering in this species (Fig. 6) as well as simultaneous retraction (Vandewalle et al., 1995).

In my recordings from *Scorpaenichthys*, I tracked motion of the medial margin of the pharyngobranchial and found that it showed very little ventral or medial movement during the adduction phase of the cycle, in marked contrast to the lateral margin of the pharyngobranchial (Fig. 7). This may be interpreted in the light of the working model of pharyngeal jaw function (Fig. 2). The epibranchial depresses the lateral margin of the upper jaw elements, but the medial section of the phayrngobranchial is expected to be relatively stationary during this motion. The medial movement of the lateral margin of the upper jaw appears to reflect the rotation of the pharyngobranchial about its medial region so that the lateral margin swings in an arc.

In generalized perciform fishes the left and right pharyngeal jaws are not constrained to move only in the dorsal-ventral and anterior-posterior axes. Data from *Serranus* (Vandewalle et al., 1995) and *Scorpaenichthys* show that the ventral movement of the upper pharyngeal jaw is associated with movement toward the midline of the pharynx (Fig. 7). It is important to recognize that this pattern is based on tracking movements of the lateral margin of the pharyngobranchial bone and thus much of this motion is probably due to the way in which the pharyngobranchial rotates when it is depressed. However, there may also be additional lateral motion in the entire pharyngobranchial bone involved. In *Ophiodon elongates*, a highly piscivorous species of hexagrammid common on temperate rocky reefs along the coast of Western North America, the medial-lateral motion of the lower pharyngeal jaw can be extensive (Fig. 8). Lateral motion occurs while the PJA is being protracted, such that the jaws are protracted while being strongly abducted in both the dorsal-ventral axis and laterally. This behavior was most apparent in this species when the fish was fed very large prey items. It appears that strong abduction during jaw protraction may aid in moving the jaws to a more anterior position on the prey before beginning the next cycle of retraction and adduction.

Finally, the left and right sides of the PJA may move in phase, as is most common, or they may move out of phase (Lauder, 1983b; Liem, 1970; Vandewalle et al., 1992). The structurally decoupled status of the right and left sides of the system in generalized perciform fishes permits some independent movements in the system and may allow greater dexterity and fine control of prey.

In summary, pharyngeal jaws movements are diverse and take place in three dimensions. It appears that in generalized perciform fishes the orbit of motion of the upper jaw is normally greater than that of the lower jaw. During the rhythmic pharyngeal transport behavior that dominates pharyngeal sequences, the upper jaw sweeps from an anterior-dorsal position to a posterior-ventral position. The upper jaw meets the lower jaw in this posterior-ventral region of its orbit and the relative motion of the lower jaw at this time indicates that either the jaws are being adducted or that the upper jaw is moving posteriorly as the lower jaw is moving anteriorly, creating a sheering action. As the jaws are protracted during the recovery stroke they are abducted. This action may involve considerable lateral spreading of the lower jaw bones in preparation for the subsequent cycle.

D. Motor Control of PJA Action

A considerable literature exists on the muscle activity patterns of the PJA in generalized perciform fishes (Grubich, 2000; Lauder, 1983a; Wainwright, 1989a; Wainwright, 1989b). My aim in this section is to describe the major patterns of muscle activity that have been described by various workers. This review will be slanted to accomplish two primary goals: (a) to interpret available motor pattern data in the light of the data on movement patterns, and (b) emphasize the extent to which motor patterns appear to be similar across diverse taxa. Among generalized perciform taxa, electromyographic data from the PJA muscles have been reported for members of the Centrarchidae (Lauder 1983a), the Haemulidae (Wainwright, 1989a, b), and the Sciaenidae (Grubich, 2000). Although we presently lack data from synchronized EMG and kinematics in the PJA, it is possible to identify the probable basis of actions such as sheering and retraction with adduction.

A similar pattern of motor activity is seen during pharyngeal transport behavior in several generalized perciform taxa (Fig. 9). The activity pattern is characterized by initial onset of the fourth levator externus, almost simultaneously with the onset of activity in the levator posterior. The retractor dorsalis muscle is activated during the middle 50% of the LE4 burst. The relative onset of the RD with respect to the LE4 and LP is quite variable among cycles of activity. The levator interni muscles and the second levator externus, both protractors of the upper jaw, are out of phase with the retractor dorsalis (Wainwright, 1989a). The fifth branchial adductor and obliquus posterior are active together, at the time of the retractor dorsalis. The obliquus dorsalis muscle that flexes the joint between the epibranchial and the pharyngobranchial is active simultaneously with the levator posterior. Given the anatomical interpretations of the functions of these muscles, these motor activity patterns are consistent with the expected motor basis of the kinematic patterns described above. Upper jaw depression is caused by the combined activity of the fifth adductor branchialis/obliquus posterior, the obliquus dorsalis, the fourth levator externus, and the levator posterior. Upper jaw retraction is caused uniquely by contraction of the retractor dorsalis. Protraction of the upper jaw is caused by the levator interni and possibly by the second levator externus.

Interestingly, lower pharyngeal jaw motor patterns are more variable than the upper jaw muscles and can be more difficult to summarize simply. Activity of the pharyngocleithralis externus and internus muscles are usually out of phase with each other (Fig. 9). When active, the PCi is activated simultaneously with the fourth levator externus and therefore functions during the posterior-ventral power stroke of the upper jaw. In contrast the PCe muscle is typically active out of phase with these muscles and appears to function during abduction and recovery of the lower pharyngeal jaws. However, the PCe often shows a second burst of activity that is in phase with all of the PJA adductors (Grubich, 2000; Lauder 1983a, b; Wainwright, 1989a, b). This activity burst may function to stabilize the lower jaw against the pectoral girdle during more forceful cycles of activity. Overall, the PCe functions to strongly abduct the lower jaw during the recovery stroke of the jaws, analogous to the inferred function of the levator interni muscles of the upper jaw. The lower jaws are protracted by the pharyngohyoideus muscle and also by the geniohyoideus muscle. The latter functions in this context to protract the hyoid apparatus toward the mandibular symphysis, which pulls the entire group of lower branchial structures anteriorly. These muscles can be active singly or together and may or may not be active while the upper jaw depressors are active (Fig. 9).

While the motor pattern seen during pharyngeal transport behavior is similar in the generalized perciform taxa that have been studied all taxa show additional behaviors and motor patterns associated with prey capture, buccal manipulation of prey, swallowing behavior, and in some taxa, winnowing, and prey crushing. The overall picture that emerges is that the PJA is capable of a wide range of actions that are matched by diversity in motor control. Nevertheless, the general motor pattern during pharyngeal transport behavior tends to be largely conserved among groups of perciforms.

III. Innovation in the Pharyngeal Jaw Apparatus

Much as the oral jaw apparatus has undergone reorganization and functional specialization within various groups of perciform fishes, so too has the PJA. In this section I discuss two major modifications of the PJA that have received considerable attention. First, I review studies of the functional basis of pharyngeal jaw durophagy, or the modifications associated with feeding on very hard-shelled prey. This specialization is noteworthy because it has evolved many times within perciform fishes and the mechanical demands associated with the specialization are quite clear. Mollusc-crushing has provided an excellent system for studies of convergent evolution. Second, I review our understanding of the labroid pharyngeal jaw apparatus, the most famous of all teleost pharyngeal jaw innovations. This modification is particularly noteworthy because it was proposed to have a major effect on the trophic diversification of the fishes that posses the innovation, particularly cichlid fishes (Friel & Wainwright, 1999; Liem, 1973).

A. Durophagy

Specialized feeding on molluscs and other very hard-shelled prey types has evolved repeatedly within generalized perciform fishes. In some taxa the prey are crushed by oral jaw biting (Friel & Wainwright, 1999; Hernandez & Motta, 1997; Norton, 1988; Palmer, 1979) and in a few others holes are punched in the shell, allowing digestive juices access to soft-parts of the prey after they are swallowed (Norton, 1988). However, in the majority of instances of molluscivory the prey items are crushed in the PJA and the functional specialization involves being able to exert high forces during jaw adduction (Lauder, 1983a). Crushing strength constrains mollusc predation. This is indicated by ontogenetic studies that have shown in different groups that the youngest, and hence weakest, individuals in the species are not able to crush hard prey and do not eat them (Huckins, 1997; Osenberg & Mittelbach, 1989; Wainwright, 1988). Both within and between species, there is a strong correlation between the strength of the PJA and the percent of the diet made up by hard-shelled prey (Wainwright, 1987; Wainwright, 1988).

Durophagus taxa have larger pharyngeal jaw adductor muscles and enlarged jaw bones when compared to closely related taxa that do not crush hard prey (Lauder 1983a; Grubich, 2003). Enlarged muscles have higher cross-sectional area and can generate higher stresses, while the enlarged skeletal components are able to resist the higher loads. Within the centrarchid genus *Lepomis* two species are specialized mollusc predators, *Lepomis microlophus* and *L. gibbosus*. The PJA of these two species are greatly hypertrophied relative to their congeners, including muscular (Lauder, 1983a) and skeletal modifications (compare Fig. 2B with Fig. 10). All of the elements of the PJA that are expected to bear loads during jaw adduction are enlarged and the teeth have a wider, 'molariform' shape. There is also buttressing of the ventral side of the neurocranium, suggesting that increased loads are transmitted through the upper jaw bones to the neurocranium (Fig. 10). The muscles that show the greatest hypertrophication are the levator posterior, LE4 and the obliquus dorsalis (Lauder, 1983a; Wainwright, 1991), all major muscles involved in adduction.

Grubich (2003) has documented skeletal and muscular hypertrophication in molluscivorous sciaenids and carangids. In both groups muscles and bones are hypertrophied although there tend to be unique elements of the specialization in each group. For example, in the carangid *Trachinotus*, the protractor pectoralis is one of the most hypertrophied muscles. This muscle connects the neurocranium to the pectoral girdle and acts to protract the latter. Girdle protraction probably acts to stabilize and protract the lower jaw during prey crushing.

Because mollusc-shell crushing probably involves applying increasing forces against a stiff shell it can be expected that the muscular contractions during crushing are at times purely isometric. Movement patters of the PJA during mollusc crushing have not been directly observed, but it is well known that molluscivorous *Lepomis* use a derived pattern of muscle activity during crushing that is characterized by long simultaneous bursts of activity in all PJA muscles (Lauder, 1983c). Grubich (2000) found a similar pattern in the sciaenids, where the black drum exhibited crushing motor patterns very similar to those that have been reported in *Lepomis*. Interestingly, even the trophically generalized sciaenid, *Sciaenops ocellatus*, used this crushing motor pattern when feeding on relatively hard-shelled prey.

B. The Labroid PJA

Monophyly of the Labroidei (Cichlidae, Labridae, Pomacentridae and Embiotocidae) was proposed initially based on pharyngeal anatomy (Kaufman & Liem, 1982) and this hypothesis was further developed with additional characters (Stiassny & Jensen, 1987). Members of these four groups of perciform fishes share a derived condition of the PJA that has three major features: the lower jaw elements are fused into a single structure, the lower jaw is suspended in a muscular sling that runs from the neurocranium to the posterior muscular arms of the two fused fifth ceratobranchials, and the upper jaw elements have a diarthrotic articulation with the underside of the neurocranium (Fig. 11). The functional implications of this suite of modifications are primarily that the system appears to be better suited to strong adduction. This is facilitated by direct muscular connection between the neurocranium and the lower jaw, but also by the fused elements of the lower jaw (Galis & Drucker, 1996; Liem, 1973).

In a widely-cited series of papers the labroid PJA was proposed to be an important innovation that facilitated the radical evolutionary success and diversity found in the members of this group of perciform fishes (Liem, 1973; Liem, 1978; Liem, 1979). Liem's hypothesis was that this condition of the PJA, (1) allows labroids to process a wider range of prey types, (2) may permit a greater range of jaw behaviors, (3) and because the PJA and oral jaw systems are largely decoupled from each other the evolutionary potential of the labroid feeding system is particularly high. Unfortunately there are not enough comparative data on jaw function or trophic diversity to rigorously test each of these predictions, although there are some compelling circumstantial data. In the sections below I review what is known about the functioning of the labroid PJA and how this innovation distinguishes these fishes from generalized perciforms. The results are surprising. The labroid PJA appears to exhibit a range of behaviors very similar to that seen in generalized perciform fishes and because the lower jaw is fused there is less possibility of motion in the medial-lateral axis. While the labroid PJA appears to confer a more efficient and powerful bite, there is no evidence that it is behaviorally or functionally more versatile than found in generalized taxa that lack the specializations.

1. Morphology. Functional patterns have been inferred from morphology in several labroid taxa, primarily cichlids (Aerts, 1982; Galis, 1992; Galis, 1993; Galis & Drucker, 1996) but also the pomacentrids (Galis & Snelderwaard, 1997), embiotocids (Laur & Ebeling, 1983) (DeMartini, 1969) and labrids (Bullock & Monod, 1997; Claes & De Vree, 1989; Claes & De Vree, 1990; Clements & Bellwood, 1988; Gobalet, 1989; Liem & Greenwood, 1981; Monod, Hureau & Bullock, 1994). The chief functional distinctions between the labroid PJA and that of generalized perciforms are that (1) muscles that connect the neurocranium to the fused lower pharyngeal jaw are positioned to directly adduct the lower jaw, and (2) at least in most labrids (personal observations) and possibly in some cichlids (Galis and Drucker, 1996) the upper and lower pharyngeal jaws can move independently. The joint between the medial end of the fourth epibranchial and the dorsal surface of the pharyngobranchial in these taxa has been modified into a sliding joint that allows the pharyngobranchials to move anteriorly and posteriorly, supported dorsally by their articulation to the neurocranium, independent of motion of the lower jaw. The retractor dorsalis and the internal levators appear to effect these actions. Morphological positions indicate that the lower jaw can be strongly adducted by the muscular sling, can be protracted by actions of the pharyngohyoideus and geniohyoideus, and can be abducted and retracted by the pharyngocleithralis externus and internus. It is interesting to note that none of the primary PJA muscles appear to have altered their basic function in labroids, as compared to the generalized condition discussed above. Even the levator externus and levator posterior, that attach variably on the lower pharyngeal jaw instead of the epibranchial, act to adduct the jaws. The distinction appears to be that in labroids jaw adduction is accomplished mainly by actions of the lower jaw, whereas in generalized taxa adduction is accomplished mostly by depression of the upper jaw.

2. Kinematic patterns. Direct observations of pharyngeal jaw motion using cineradiography have confirmed most of the anatomically-based interpretations. Data from cichlids (Claes & De Vree, 1989; Claes & De Vree, 1990; Claes & De Vree, 1991), embiotocids (Liem, 1986) and labrids (Liem & Sanderson, 1986) reveal that the lower jaw undergoes the largest excursions during prey processing behaviors (Fig. 12). Sheering actions between the upper and lower jaws are frequent in these taxa, although all authors report that the upper and lower jaws can also move in concert as they swing in the anterior-posterior axis. Thus, observations confirm a large degree of independence in movement of the upper and lower pharyngeal jaws. However, it is unclear that these taxa show an advanced level of independence in jaw motion as compared to the generalized perciform condition where sheering actions and considerable independence of motion have also been found (Figs. 5-6).

3. Motor patterns. Muscle activity patterns of the labroid PJA are surprisingly unmodified relative to those found in generalized perciforms (compare Figs. 9 and 13). This probably reflects the general conservation of overall muscle function noted above for the two groups rather than any constraint on the nervous system for generating variation in motor activity (Wainwright, 2002). One distinct modification that is seen in labroids is a very early onset of activity in the fourth levator externus (Fig. 13). This has been proposed to represent a recovery or preparatory period when this muscle protracts the jaws (Liem, 1986; Liem and Sanderson, 1986; Claes and De Vree, 1992). The interpretation of this pattern is made difficult because the LE4 muscle attaches both to the fourth epibranchial in most labroids, and also to the lower pharyngeal jaw in labrids, many cichlids and many embiotocids (Liem, 1986). As in generalized perciform taxa, muscles appear to be active during an adduction phase that includes retraction by the retractor dorsalis, or active during a recovery phase (e.g. the pharyngocleithralis externus). As is seen in other perciform groups, the activity patterns of muscles that control the lower jaws are especially variable and can show a pattern consistent with sheering actions of the upper and lower jaws or of synchronized retraction and adduction (Liem, 1986; Liem and Sanderson, 1986).

4. Labroid diversity. Comparative studies of morphological and functional diversity across groups of perciform have not been published, so it is not possible to rigorously assess the hypothesis that labroids exhibit greater functional diversity than other groups. As an initial exploration of this area figure 14 presents data on the diversity of the size of the levator posterior muscle in 154 labrid species and 20 centrarchid species. Variance is a useful measure of diversity as it describes the spread of a variable around its average value and because it does not scale with sample size (Foote, 1997). This comparison reveals that LP muscle diversity in centrarchids is about 60% of that seen in labrids, providing modest support for the expectation that labrids are more diverse than centrarchids.

IV. Summary

The pharyngeal jaws have been a more difficult nut to crack than the oral jaws, primarily because they are buried deep inside the head and cannot be observed directly. But anatomical observations, and data collected with cineradiography and sonomicrometry have helped in the development of functional models and documentation of how the jaws are used. One of the biggest surprises from this body of work is the lack of evidence to support the expectation that the labroid pharyngeal jaws show greater versatility and are used in a wider range of behaviors than the jaws of generalized perciform taxa. One remaining interpretation of the functional enhancement gained with the labroid condition is that proposed by Galis & Drucker (1996) who suggested that biting forces are more efficiently transferred to the prey in labroids than in generalized taxa. Thus, the advantage may be in the strength of the bite. This point raises the specter of a remaining serious challenge for students of the pharyngeal jaws, how to measure performance. The only PJA performance trait that has been both modeled (e.g. Galis, 1992) and measured, is biting strength (Wainwright, 1987; Osenberg, 1989). Without clear performance metrics upon which to compare taxa, it will not be possible to fully understand the implications of the diversity seen in teleost pharyngeal jaw systems.

Acknowledgements

I thank Justin Grubich, Darrin Hulsey and Lara Ferry-Graham for many conversations over the years on pharyngeal jaw function and diversity. Ian Hart prepared the anatomical diagrams shown in figures 2B, 10 and 11. Funding was provided by NSF grant IBN-0076436.

Literature Cited

Aerts, P. (1982). Development of the musculs levator externus IV and the musculus obliquus posterior in *Haplochromis elegans* Trewavas, 1933 (Telostei: Cichlidae): a discussion on the shift hypothesis. *J. Morphol.* **173,** 225-235.

Aerts, P., Devree, F., and Vandewalle, P. (1986). Pharyngeal jaw movements in Oreochromis niloticus (Teleostei, Cichlidae) - Preliminary results of a cineradiographic analysis. *Annales De La Societe Royale Zoologique De Belgique* **116,** 75-81.

Bullock, A. E., and Monod, T. (1997). Cephalic myology of two parrotfishes (Teleostei: Scaridae). *Cybium* **21,** 173-199.

Cheer, A. Y., Ogami, Y., and Sanderson, S. L. (2001). Computational fluid dynamics in the oral cavity of ram suspension-feeding fishes. *J. Theor. Biol.* **210,** 463-474.

Claes, G., and De Vree F. (1989). Effects of food characteristics on pharyngeal jaw movements in two cichlid species pisces perciformes. *Annales de la Societe Royale Zoologique de Belgique* **119,** 7.

Claes, G., and De Vree, F. (1990). Pharyngeal jaw movements during feeding in *Haplochromis burtoni* cichlidae. *Belgian Journal of Zoology* **120,** 15.

Claes, G., and De Vree, F. (1991). Cineradiographic analysis of the pharyngeal jaw movements during feeding in *Haplochromis burtoni* Gunther 1893 pisces cichlidae. *Belgian Journal of Zoology* **121,** 227-234.

Clements, K. D., and Bellwood, D. R. (1988). A comparison of the feeding mechanisms of two herbivorous labroid fishes, the temperate *Odax pullus* and the tropical *Scarus rubroviolaceus*. *Australian Journal of Marine and Freshwater Research* **39,** 87-107.

DeMartini, E. E. (1969)**.** A correlative study of the ecology and comparative feeding mechanism morphology of the Embiotocidae as evidence of the family's adaptive radiation. *Wasmann Journal of Biology* **27,** 117-247.

Foote, M. (1997). The evolution of morphological diversity. *Ann. Rev. Ecol System.* **28,** 129-152.

Friel, J. P., and Wainwright, P. C. (1999). Evolution of complexity in motor patterns and jaw musculature of tetraodontiform fishes. *J. Exp. Biol* **202,** 867-880.

Galis, F. (1992). A model for biting in the pharyngeal jaws of a cichlid fish: *Haplochromis piceatus*. *J. Theor. Biol.* **155,** 343-368.

Galis, F. (1993). Interactions between the phayrngeal jaw apparatus, feeding behavior, and ontogeny in the cichlid fish, *Haplochromis piceatus*: a study of morphological constrainst in evolutionary ecology. *J. Exper. Zool.* **267,** 137-154.

Galis, F., and Drucker, E. G. (1996). Pharyngeal biting mechanics in centrarchid and cichlid fishes: insights into a key evolutionary innovation. *J. Evol. Biol.* **9,** 641-670.

Galis, F., and Snelderwaard, P. (1997). A novel biting mechanism in damselfishes (Pomacentridae): The pushing oup of the lower pharyngeal jaw by the pectoral girdle. *Neth. J. Zool.* **47,** 405-410.

Gobalet, K. W. (1989). Morphology of the parrotfish pharyngeal jaw apparatus. *Amer. Zool.* **29,** 319-331.

Grubich, J. R. (2000). Crushing motor patterns in drum (Teleostei: Sciaenidae): functional novelties associated with molluscivory. *J. Exp. Biol.* **203,** 3161-76.

Grubich. J. R. (2003). Morphological convergence of pharyngeal jaw structure in durophagus perciform fish. *Biol. J. Linn Soc.* **80,** 147-165.

Hernandez, L. P., and Motta, P. J. (1997). Trophic consequences of differential performance: Ontogeny of oral jaw-crushing performance in the sheepshead, *Archosargus probatocephalus* (Teleostei, Sparidae). *J. Zool. (Lond.)* **243,** 737-756.

Huckins, C. J. F. (1997). Functional linkages among morphology, feeding performance, diet, and competitive ability in molluscivorous sunfish. *Ecology* **78,** 2401-2414.

Kaufman, L., and Liem, K. F. (1982). Fishes of the suborder Labroidei (Pisces: Perciformes): Phylogeny, ecology, and evolutionary significance. *Breviora (Museum of Comparative Zoology, Harvard University)* **472,** 1-19.

Lauder, G. V. (1983a). Functional and morphological bases of trophic specialization in sunfishes (Teleostei: Centrarchidae). *J. Morphol.* **178,** 1-21.

Lauder, G. V. (1983b). Functional design and evolution of the pharyngeal jaw apparatus in euteleostean fishes. *Zool. J. Linn. Soc.* **77,** 1-38.

Lauder, G. V. (1983c). Neuromuscular patterns and the origin of trophic specialization in fishes. *Science* **219,** 1235-1237.

Laur, D. R., and Ebeling, A. E. (1983). Predator-prey relationships in surfperches. *Environ. Biol. Fish.* **8,** 217-229.

Liem, K. F. (1970). Comparative functional anatomy of the Nandidae. *Fieldiana Zoology* **56,** 1-166.

Liem, K. F. (1973). Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Sys. Zool.* **22,** 425-441.

Liem, K. F. (1978). Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes. I. Piscivores. *J. Morphol.* **158,** 323-360.

Liem. K. F. (1979). Modulatory multiplicity in the feeding mechanism in cichlid fishes, as exemplified by the invertebrate pickers of Lake Tanganyika. *J. Zool.* **189,** 93-125.

Liem, K. F. (1986). The pharyngeal jaw apparatus of the Embiotocidae (Teleostei) - a functional and evolutionary perspective. *Copeia* 1986**,** 311-323.

Liem, K. F., and Greenwood, P. H. (1981). A functional approach to the phylogeny of the pharyngognath teleosts. *Amer. Zool.* **21,** 83-101.

Liem, K. F., and Sanderson, S. L. (1986). The pharyngeal jaw apparatus of labrid fishes - a functional morphological perspective. *J. Morphol.* **187,** 143-158.

Monod, T., Hureau, J. C., and Bullock, A. E. (1994). Cephalic osteology of two parrotfish (Scaridae: Teleostei). *Cybium* **18,** 135-168.

Nelson, G. J. (1967). Gill arches of some teleostean fishes of the families Girellidae, Pomacentridae, Embiotocidae, Labridae, and Scaridae. *J. Natur. Hist.* **1,** 289-293.

Norton, S. F. (1988). Role of the gastropod shell and operculum in inhibiting predation by fishes. *Science* **241,** 92-94.

Osenberg, C. W., and Mittelbach, G. G. (1989). Effects of body size on the predator-prey interaction between pumpkinseed sunfish and gastropods. *Ecol. Monogr.* **59,** 405-432.

Palmer, A. R. (1979). Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. *Evolution* **33,** 697-713.

Sanderson, S. L., Cech, J. J., and Cheer, A. Y. (1994). Paddlefish buccal flow velocity during ram suspension feeding and ram ventilation. *J. Exp. Biol.* **186,** 145-156.

Sanderson, S. L., Cheer, A. Y., Goodrich, J. S., Graziano, J. D., and Callan, W. T. (2001). Crossflow filtration in suspension-feeding fishes. *Nature (Lond.)* **412,** 439-441.

Sibbing, F. A. (1982). Pharyngeal mastication and food transport in the carp (*Cyprinus carpio*): a cineradiographic and electromyographic study. *J. Morphol.* **172,** 223-258.

Sibbing, F. A. (1988). Specializations and limitations in the utilization of food resources by the carp, *Cyprinus carpio*: a study of oral food processing. *Envir. Biol. Fish.* **22,** 161-178.

Sibbing, F. A., Osse, J. W. M., and Terlow, A. (1986). Food handling in the carp (*Cyprinus carpio*): its movement patterns, mechanisms and limitations. *J. Zool., Lond* **210,** 161-203.

Stiassny, M. L. J., and Jensen, J. (1987). Labroid interrelationships revisited: morphological complexity, key innovations, and the study of comparative diversity. *Bulletin of the Museum of Comparative Zoology* **151,** 269-319.

Vandewalle, P., Havard, M., Claes, G., and De Vree, F. (1992). Movements of the pharyngeal jaw during feeding in *Serranus scriba* (Linneus, 1758) (Pisces, Serranidae). *Can. J. Zool.* **70,** 145-160.

Vandewalle, P., Saintin, P., and Chardon, M. (1995). Structures and movements of the buccal and pharyngeal jaws in relation to feeding in *Diplodus sargus*. *J. Fish Biol.* **46,** 623-656.

Wainwright, P. C. (1987). Biomechanical limits to ecological performance: Mollusc-crushing by the Caribbean hogfish, *Lachnolaimus maximus* (Labridae). *J. Zool., Lond* **213,** 283-297.

Wainwright, P. C. (1988). Morphology and ecology: the functional basis of feeding constraints in Caribbean labrid fishes. *Ecology* **69,** 635-645.

Wainwright, P. C. (1989a). Functional morphology of the pharyngeal jaws in perciform fishes: an experimental analysis of the Haemulidae. *J. Morphol.* **200,** 231-245.

Wainwright, P. C. (1989b). Prey processing in haemulid fishes: patterns of variation in pharyngeal jaw muscle activity. *J. Exp. Biol.* **141,** 359-376.

Wainwright, P. C. (2002). The evolution of feeding motor patterns in vertebrates. *Cur. Opin. Neurob.* **12,** 691-695.

Wainwright, P. C., and Bellwood, D. R. (2002). Ecomorphology of feeding in coral reef fishes. "Coral Reef Fishes. Dynamics and diversity in a complex ecosystem" (P. F. Sale, Ed.) pp. 33-55. Academic Press, Orlando.

Wainwright, P. C., Bellwood, D. R., Westneat, M. W., Grubich, J. R., and Hoey, A. S. (2004). A functional morphospace for the skull of labrid fishes: patterns of diversity in a complex biomechanical system. *Biol. J. Linn. Soc.* **82,** 1-25.

Wainwright, P. C., Osenberg, C. W., and Mittelbach, G. G. (1991). Trophic polymorphism in the pumpkinseed sunfish (*Lepomis gibbosus* Linnaeus): effects of environment on ontogeny. *Func. Ecol.* **4,** 40-55.

Wainwright, P. C., and Richard, B. A. (1995). Predicting patterns of prey use from morphology with fishes. *Envir. Biol. Fish.* **44,** 97-113.

Winterbottom, R. (1974). A descriptive synonymy of the striated muscles of the Teleostei. *Proc. Acad. Natur. Sci. Philad.* **125,** 225-317.

Yamaoka, K. (1978). Pharyngeal jaw structure in labrid fishes. *Publ. Seto Marine Biol. Lab.* **24,** 409-426.

Figure Legends

Figure 1. A) Schematic diagram of the pharyngeal jaw apparatus in teleost fishes with the connections of major muscles indicated by thick black lines. The PJA is positioned at the posterior end of the pharynx immediately anterior to the esophagus and is connected by muscles to structures in this region. B) Dorsal view of the skeletal elements of the branchial arches in *Haemulon sciurus*. The lower pharyngeal jaw is formed by the paired fifth ceratobranchial and the upper jaw by pharyngobranchials 3 and 4. Abbreviations: AD5, m. fifth adductor branchialis; BH, branchiohyoideus; CB, ceratobranchial; EB, epibranchial; ET2, epibranchial tooth plate; GH, m. geniohyoideus; HB, hyobranchial; HY, hyoid bar; LE4, m. fourth levator exernus; LI, m. levator internus; LP, M. levator posterior; PB, pharyngobranchial; PCe, m. pharyngocleithralis externus; PCi, m. pharyngocleithralis internus; PG, pectoral girdle; PH, m. protractor hyoideus; RD, m. retractor dorsalis; SH, m. sternohyoideus. Reproduced with permission from Wainwright (1989a).

Figure 2. A) Schematic representation of the mechanism of upper pharyngeal jaw depression in posterior view (modified after Wainwright, 1989a). Skeletal elements of the jaws are represented by shading and muscles indicated by thick black lines. Joints and rotation points indicated with small circles. Contraction of the LE, LP and OD muscles, in concert with stabilization from the AD5 and OP muscles, results in flexion of the joint between the pharyngobranchial and the epibranchial, resulting in depression of the lateral margin of the pharyngobranchial. B) Diagram of the pharyngeal jaw bones of *Lepomis punctatus* in posterior view for comparison with the schematic model in figure A. Abbreviations as in figure 1 and OD, m. obliquus dorsalis; OP, m. obliquus posterior.

Figure 3. Two-dimensional movement, in lateral view, of the upper and lower jaws of *Serranus scriba* (data redrawn from Vandewalle et al., 1992) illustrating a typical pattern of jaw movement during pharyngeal transport in generalized perciform fishes. Upper jaw motion involves simultaneous depression and retraction. Note that the upper jaw has greater motion in the dorsal ventral axis than the lower jaw. Data were collected from radio-opaque markers implanted in pharyngeal jaw bones, the relative positions of the upper and lower symbols in this graph do not reflect their positions with respect to each other. Numbers adjacent to points indicate homologous points in time. Points are separated by 40 ms

Figure 4. Two-dimensional later view kinematics of the upper and lower pharyngeal jaws in the cabezon, *Scorpaenichthys marmoratus*. Data were generated using sonomicrometry with crystals placed on the jaws and to fixed structures surrounding the jaws that allowed the reconstruction of three-dimensional movement. Here the data are reconfigured to show the motion in two dimensions. A) Single sequence that shows simultaneous adduction and retraction of both the upper jaw and lower jaw. B) Sequence from the same feeding bout that shows sheering action of the upper and lower jaws. Note that the positions of the upper and lower jaws in this graph are not meant to represent their position relative to one another. Numbers adjacent to points indicate homologous points in time. Points are separated by 10 ms.

Figure 5. Two-dimensional movement in lateral view of the upper pharyngeal jaw in a 207 mm *Micropterus salmoides*. Data were generated with sonomicrometry. Crystals were sutured to the jaw bones of the fish and to several non-moving structures in the pharynx and buccal cavity to determine movements in two dimensions. Note that in this

species, there is considerable anterior posterior motion of the upper jaw, in addition to movement in the dorsal-ventral axis.

Figure 6. Two-dimensional movement in lateral view of the upper and lower jaws in a 110 mm *Diplodus sargus* (Sparidae). Data are redrawn from cineradiographic observations presented in Vandewalle et al. (1995). This sequence illustrates sheering between the jaws during the depression and retraction of the upper jaw.

Figure 7. Two-dimensional kinematics in posterior view of two points on the upper pharyngeal jaw (the pharyngobranchial) in a 450 mm *Scorpaenichthys marmoratus*. Data were generated with sonomicrometry by attaching crystals to the lateral (blue) and medial (red) edge of the pharyngobranchial and to fixed structures in the pharynx that allowed resolution of motion in two –dimensions. Note that the pharyngobranchial appears to rotate about its medial edge while the lateral margin undergoes considerable excursions, ventrally and medially. Compare this pattern to the model shown in figure 2. Points are separated by 20 ms.

Figure 8. Simultaneous lateral spreading of the posterior ends of the fifth ceratobranchials during protraction of the lower jaw in a 580 mm lingcod, *Ophiodon elongates*. Data were generated with sonomicrometry by attaching crystals to the posterior tips of the fifth ceratobranchials and to fixed structures in the pharynx that allowed resolution of motion in the anterior posterior axis. Points are separated by 20 ms.

Figure 9. Average activity patterns of pharyngeal jaw muscles during pharyngeal transport behavior in representatives of three generalized perciform groups. Activity is expressed as a proportion of the duration of a single cycle of pharyngeal activity, measured as onset of the RD until onset of the subsequent burst. Data from *Micropterus* are previously unpublished personal observations. Data from *Anisotremus* are redrawn from Wainwright (1989a) and the data from *Scaienops* are redrawn from Grubich (2000). Muscle abbreviations are as in figure 1. Note that activity patterns in the three taxa are broadly similar.

Figure 10. Posterior view of the pharyngeal jaw apparatus in a 210 mm redear sunfish , *Lepomis microlophus*, a mollusc-crushing predator. Note that the skeletal elements of the PJA are greatly hypertrophied relative to that seen in trophically generalized taxa such as *Lepomis punctatus*, shown in figure 1B. Abbreviations as in figure 1, NC, neurocranium.

Figure 11. Diagrams of the pharyngeal jaw apparatus in three labrid species to illustrate the labroid condition. A) Lateral view of the neurocranium and branchial structures in *Bodianus axillaris* to show the position of the PJA at the posterior end of the pharynx. B) Posterior view of the PJA in *Halichoeres garnoti*. Note the lower jaw bones are fused into a single robust element. C) Dorsal view of *Cheilinus chlorourus* showing the development of the joint where the upper jaw contacts the underside of the neurocranium. Abbreviations as in figure 1, UH, urohyal.

Figure 12. Two-dimensional kinematic pattern of the upper (blue dots) and lower (red dots) pharyngeal jaws in a 200 mm *Oreochromis niloticus*. Note that the movement of

the lower jaw is considerably more extensive in the dorsal-ventral axis than is the upper jaw. However the upper jaw matches the lower jaw in the anterior-posterior excursions. Data are redrawn from Claes and DeVree (1991) and are based on cineradiographic observations. Note sheering action of lower and upper jaw. Units are arbitrary, following Claes and DeVree (1991).

Figure 13. Average pharyngeal muscle activity patterns in a representative embiotocid and a labrid. Data redrawn from Liem (1986) and Liem and Sanderson (1986). Note similarity in the activity pattern of the two species.

Figure 14. Histogram illustrating the diversity of mass of the levator posterior muscle in 154 labrid species and 20 centrarchid species. Data from all 174 species was fit to a Log-Log regression on body mass and residuals were calculated to remove body size effects. The histograms are of the residuals from that regression and show that variance of LP mass in centrarchids, a group of generalized perciforms, is about 60% of that in labrids. Since variance is expected to be independent of sample size this observation suggest that labrids have greater diversity in the size of the levator posterior muscle than do the centrarchids.

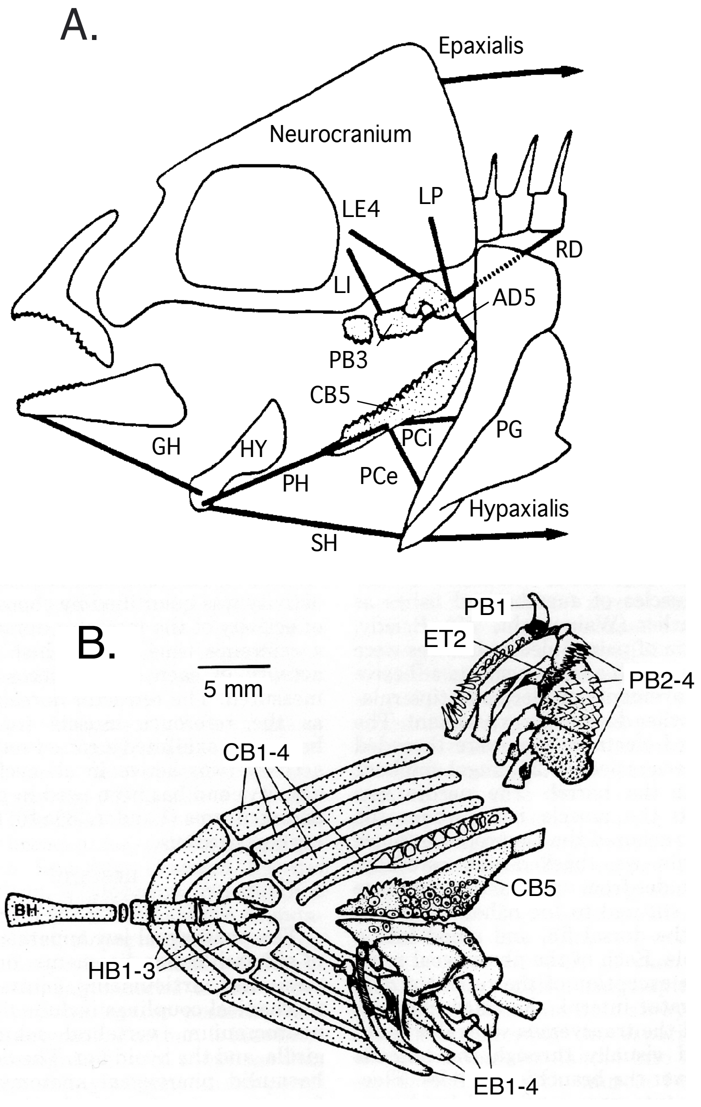

A.
Epaxialis
Neurocranium
LE4
LP
RD
LI
AD5
PB3
CB5
PCi
PG
GH
HY
PH
PCe
Hypaxialis
SH
B.
5 mm
PB1
ET2
PB2-4
CB1-4
CB5
BH
HB1-3
EB1-4

Figure 1

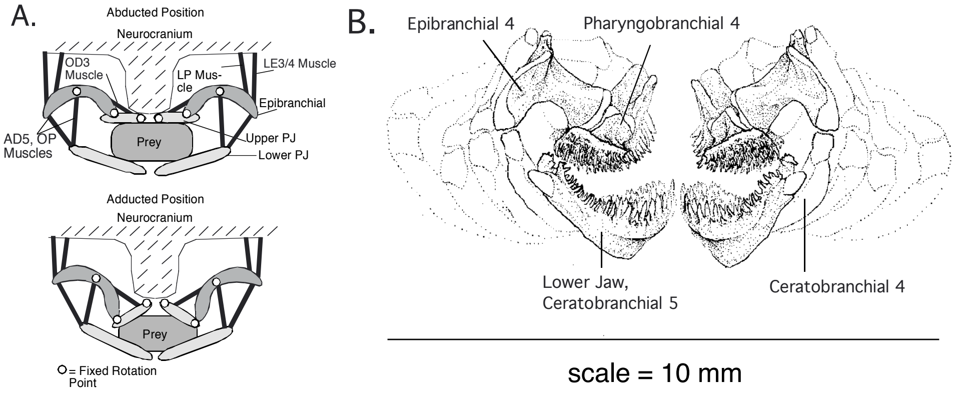
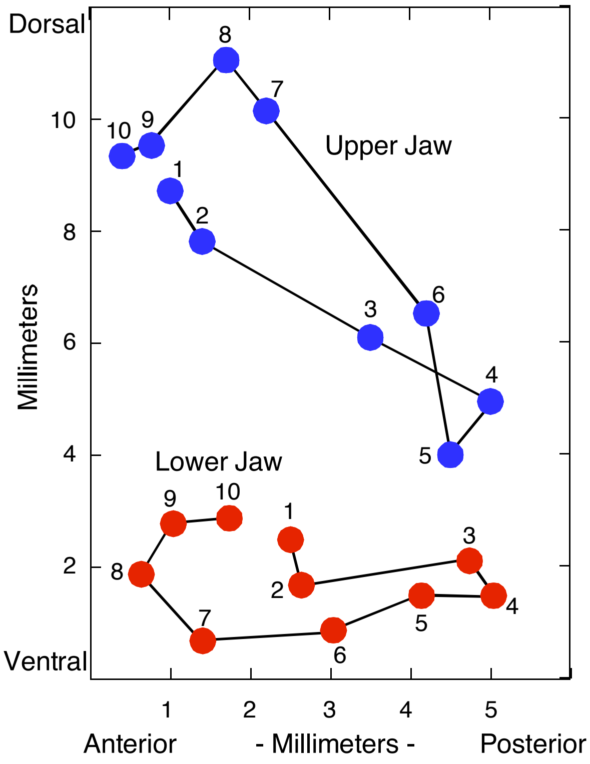

A.
Abducted Position
Neurocranium
OD3 Muscle
LP Muscle
LE3/4 Muscle
Epibranchial
AD5, OP Muscles
Prey
Upper PJ
Lower PJ
Adducted Position
Neurocranium
Prey
= Fixed Rotation Point
B.
Epibranchial 4
Pharyngobranchial 4
Lower Jaw, Ceratobranchial 5
Ceratobranchial 4
scale = 10 mm

Figure 2


Dorsal
10
8
6
4
2
Ventral
Millimeters
Upper Jaw
Lower Jaw
1
2
3
4
5
6
7
8
9
10
1
2
3
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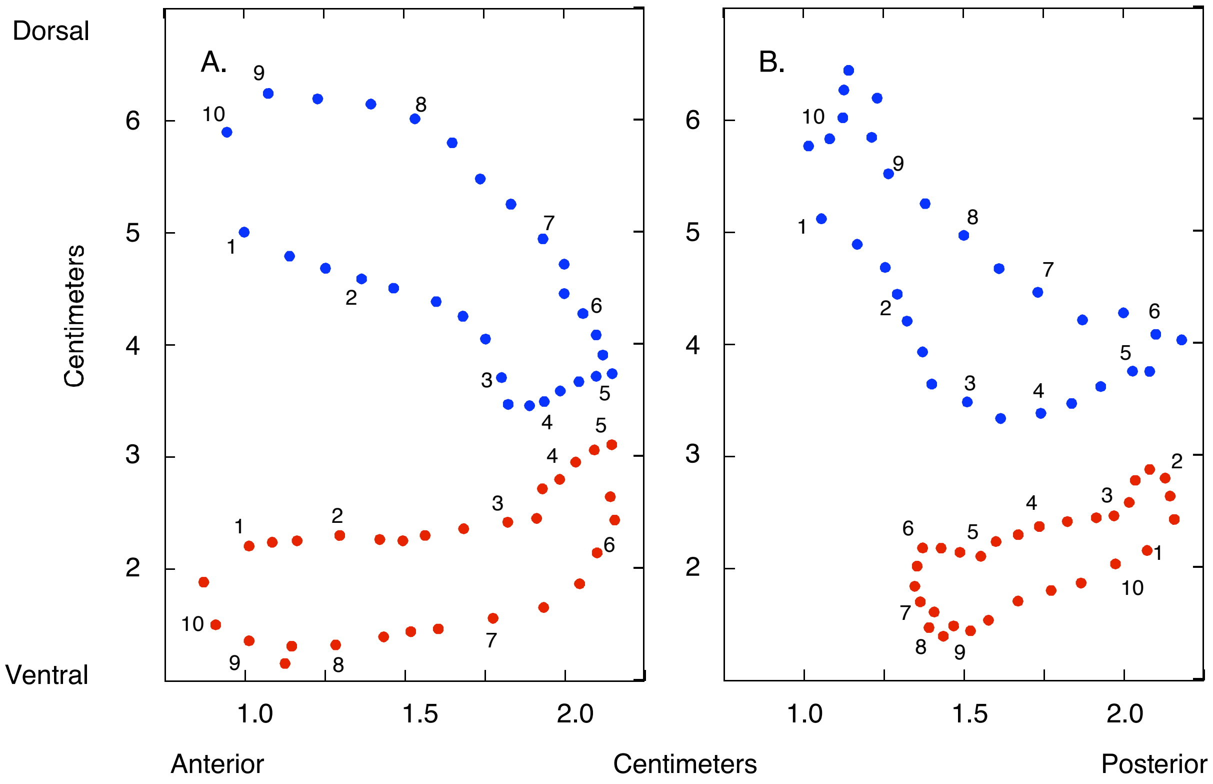
7
8
9
10
1
2
3
4
5
Anterior
- Millimeters -
Posterior

Figure 3


Dorsal
Ventral
Centimeters
A.
B.
6
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2
1.0
1.5
2.0
Anterior
Centimeters
Posterior
1
2
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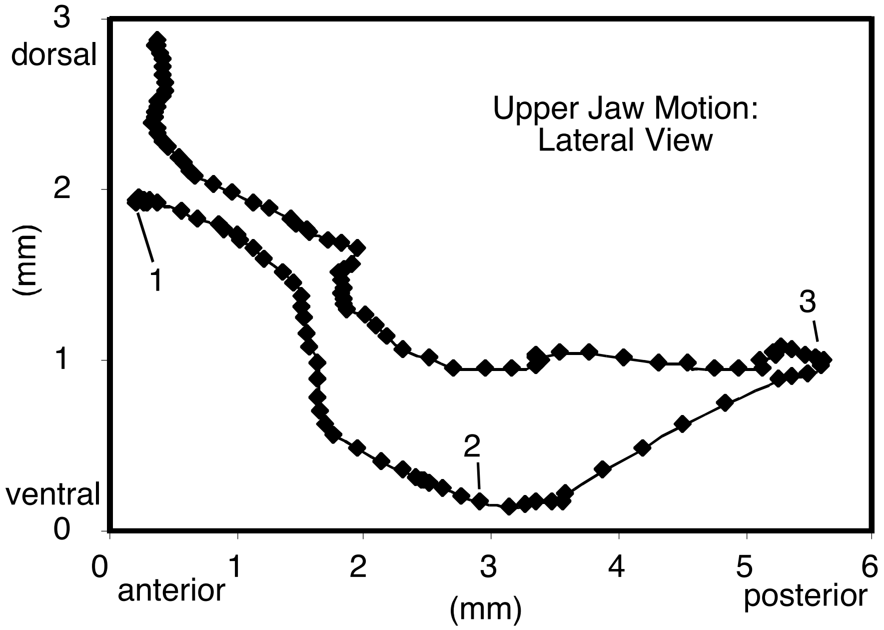
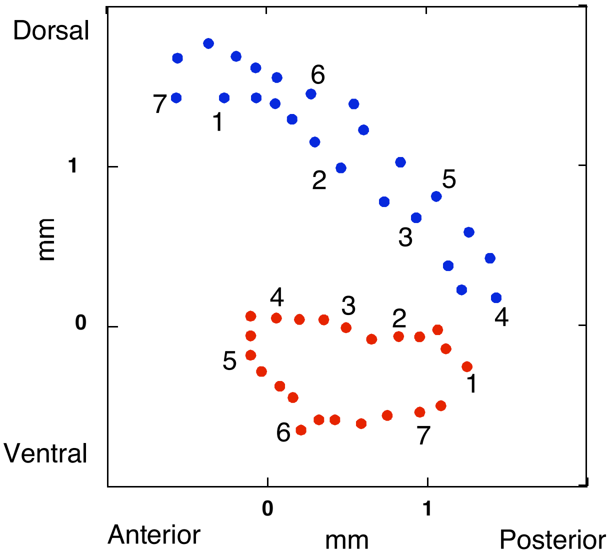
6
7
8
9
10

Figure 4



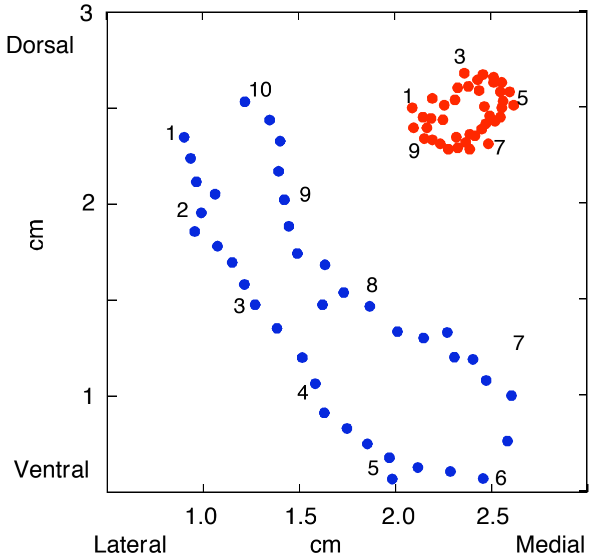
Upper Jaw Motion:
Lateral View
3
dorsal
2
(mm)
1
ventral
0
0
1
2
3
4
5
6
anterior
(mm)
posterior
1
2
3

Figure 5



Dorsal
Ventral
mm
1
0
0
1
Anterior
mm
Posterior
7
1
6
2
5
3
4
4
3
2
5
1
6
7

Figure 6


3
Dorsal
2
cm
1
Ventral
1.0
1.5
2.0
2.5
Lateral
cm
Medial
1
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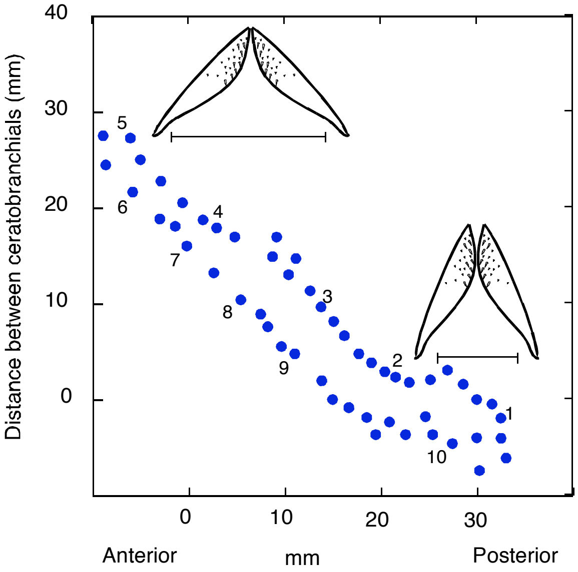
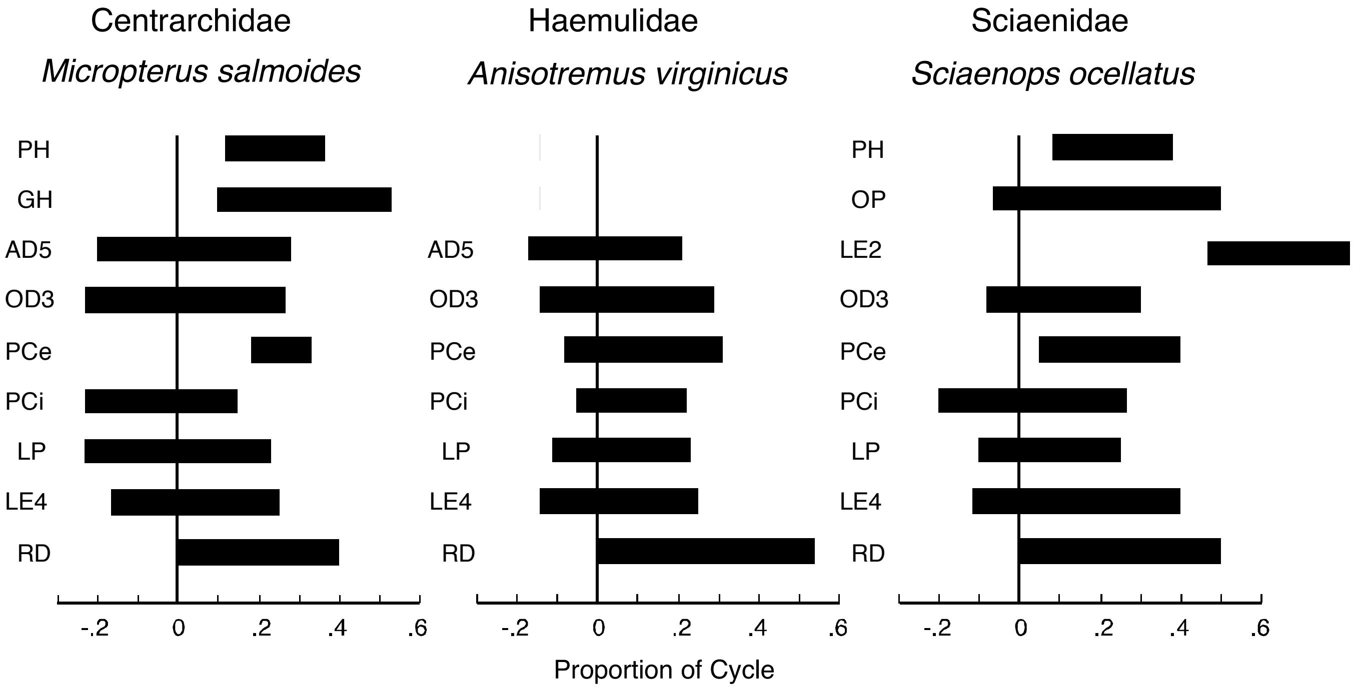
3
5
7
9

Figure 7



Distance between ceratobranchials (mm)
40
30
20
10
0
0
10
20
30
Anterior
mm
Posterior
5
6
4
7
8
3
9
2
1
10

Figure 8



Centrarchidae
Micropterus salmoides
Haemulidae
Anisotremus virginicus
Sciaenidae
Sciaenops ocellatus
PH
GH
AD5
OD3
PCe
PCi
LP
LE4
RD
AD5
OD3
PCe
PCi
LP
LE4
RD
PH
OP
LE2
OD3
PCe
PCi
LP
LE4
RD
-.2
0
.2
.4
.6
-.2
0
.2
.4
.6
-.2
0
.2
.4
.6
Proportion of Cycle

Figure 9

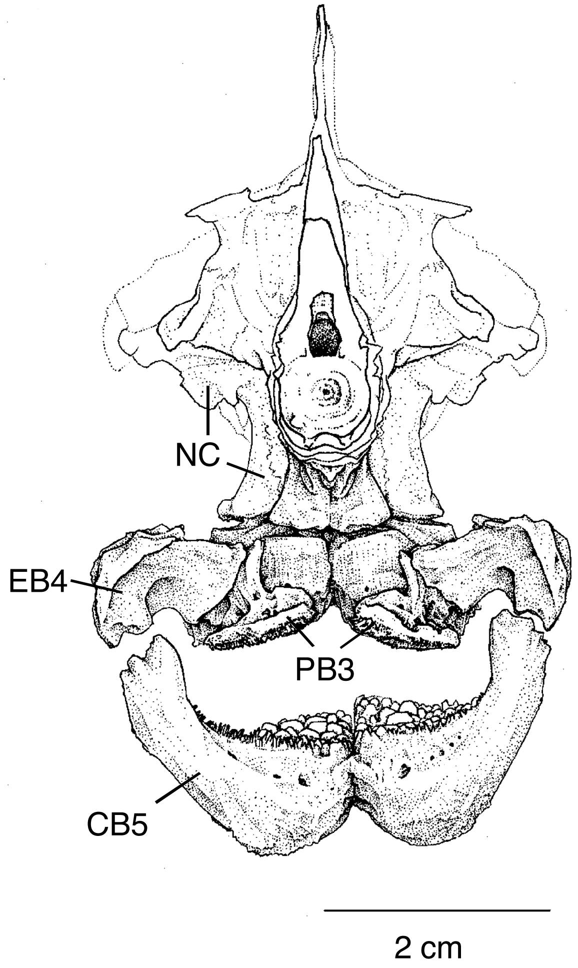


Figure 10

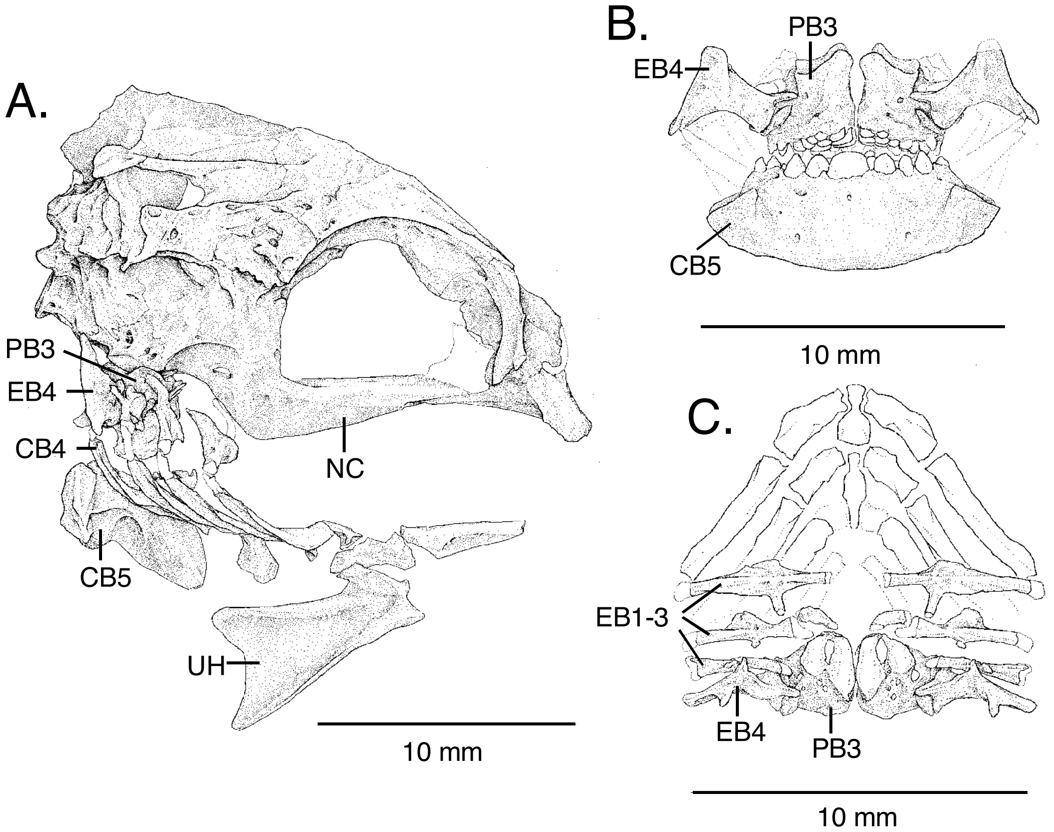
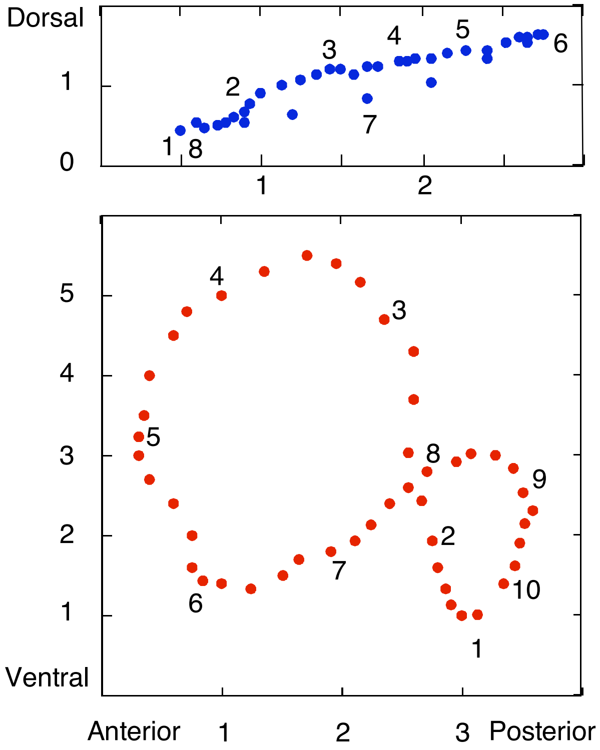

A.
PB3
EB4
CB4
CB5
NC
UH
10 mm
B.
PB3
EB4
CB5
10 mm
C.
EB1-3
EB4
PB3
10 mm

Figure 11



Dorsal
1
0
1
2
1
8
2
3
7
4
5
6
5
4
3
2
1
Ventral
Anterior
1
2
3
Posterior
4
3
5
8
9
2
7
6
10
1

Figure 12

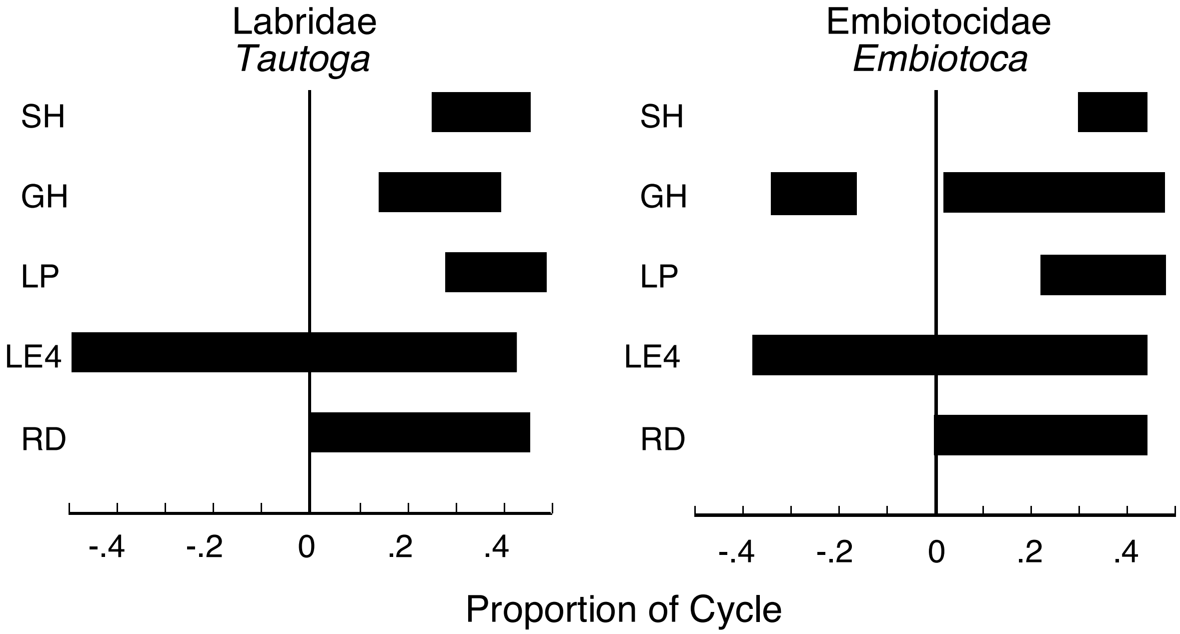

Labridae
Tautoga
Embiotocidae
Embiotoca
SH
GH
LP
LE4
RD
SH
GH
LP
LE4
RD
-.4
-.2
0
.2
.4
-.4
-.2
0
.2
.4
Proportion of Cycle

Figure 13

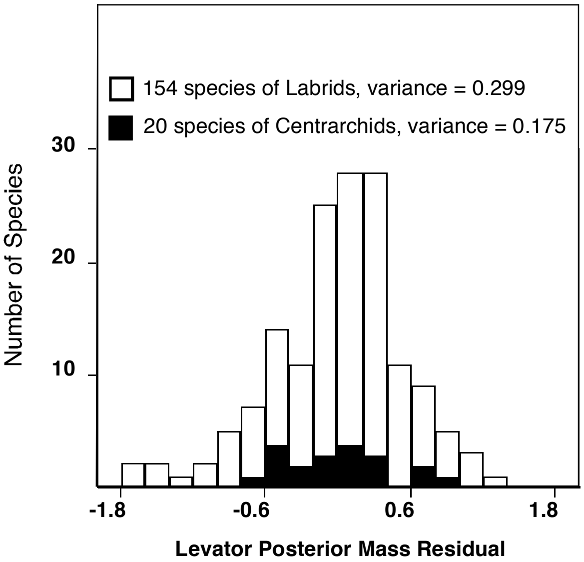

☐ 154 species of Labrids, variance = 0.299
■ 20 species of Centrarchids, variance = 0.175
Number of Species
30
20
10
-1.8
-0.6
0.6
1.8
Levator Posterior Mass Residual

Figure 14