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Design of Feeding Systems in Aquatic Vertebrates: Major Patterns and Their Evolutionary Interpretations

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INTRODUCTION

A MAJOR GOAL OF RESEARCH in functional morphology should be to produce general concepts and define patterns of structural and functional evolution. However, few general concepts have been identified from the study of structure and function of the vertebrate skull. The lack of concepts has not been due to any deficiency in the empirical data base. On the contrary, functional morphologists have been extremely successful in their descriptions of skull structure and function in vertebrates. As evidenced by these volumes on the vertebrate skull (Hanken and Hall 1993), many investigators have documented the diversity of skull morphology. In general, the major patterns of skull morphology are understood, although controversies exist on some aspects of skull structure (such as the extent of segmental organization of the skull).

To a lesser extent, functional patterns of vertebrate skull diversity have also been documented. While growth in our comparative knowledge of skull function has been relatively slow (perhaps in part owing to the complex nature of functional analyses and the relatively recent application of quantitative experimental techniques), a great deal is now known about skull function in individual vertebrate clades (Chondrichthyes: Frazzetta and Prange 1987; Moss 1972, 1977; Actinopterygii: Alexander 1967; Lauder 1980a, 1982; Liem 1970; Actinistia: Lauder 1980b; Dipnoi: Bemis 1987; Bemis and Lauder 1986; Amphibia: Bemis et al. 1983; Cundall et al. 1987; Druner 1904; Erdman and Cundall 1984; Findeis and Bemis 1990; Gans and Gorniak 1982; Lauder and Shaffer 1985, 1986; Lombard and Wake 1977; Ozeti and Wake 1969; Shaffer and Lauder 1985a, b; Reilly and Lauder 1989, 1990c; and Amniota: Bock 1964; Crompton et al. 1977; Gans et al. 1978; Smith and Hylander 1985; Weijs and Dantuma 1981).

Despite this growth in our basic knowledge of skull structure and function, there have been few attempts to summarize the key ideas that

have emerged from all this research. In consequence, virtually none of the generalities derived from research on vertebrate skull structure and function are available to workers in fields such as systematics, neurophysiology, evolutionary biology, population biology, and ecology.

Our goal in this paper is to provide a summary and analysis of the key conclusions derived from studies of form and function in the skull of aquatic vertebrates. We will make no attempt to review the many specific studies, as several volumes have provided substantial overviews of skull structure and function (Hildebrand et al. 1985; Kluge 1977). Also, we will limit ourselves to considering the head and feeding system in lower vertebrates (fishes and amphibians), and will not address aquatic feeding in amniotes (see Jenkin 1957; Lambertsen 1983; Pivorunas 1979; Zweers 1974). Filter feeding and feeding methods in other clades are covered elsewhere in this volume.

This chapter is divided into three parts. First, we consider major results of general interest that have been derived from research on the skull of aquatic vertebrates over the past twenty years: we have identified four dominant concepts that have emerged from the current data available on feeding systems. Second, we discuss the importance and evolutionary significance of each of the four major concepts. Finally, we address future directions of research on skull structure and function in aquatic vertebrates.

KEY CONCEPTS

Concept 1
Biomechanical patterns of aquatic prey capture are evolutionarily conservative.

A key conclusion of comparative studies on feeding mechanics in lower vertebrates is that many of the biomechanical mechanisms used in prey capture are highly conserved evolutionarily. That is, many biomechanical patterns in the skull are found throughout lower vertebrates, and have been retained across the aquatic-terrestrial transition in vertebrate evolution (Reilly and Lauder 1990a). This conservatism in functional systems across a broad range of vertebrate clades occurs despite the remarkable diversity in skull shape and gross morphology, as well as in habitats occupied by lower vertebrates. For example, taxa as diverse in morphology, life history, and ecology as axolotls, trout, lungfish, and nurse sharks all share common biomechanical mechanisms for opening the mouth.

The conservation of biomechanical systems applies primarily to the musculoskeletal mechanisms used to control the initial capture of prey by suction feeding (Alexander 1967; Lauder 1980a, 1985b; Liem 1970). Suction feeding is the process of aquatic prey capture whereby the mouth
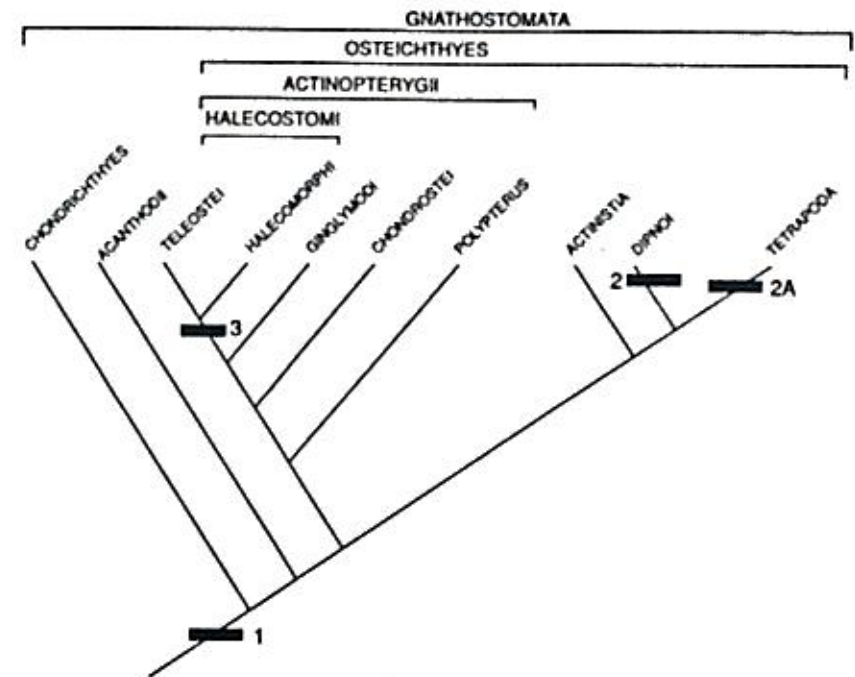
Fig. 3.1. A cladogram of lower vertebrate lineages with key functional and morphological characters relating to the skull and feeding mechanism mapped onto it. Functional aspects of skull design associated with characters denoted by the black bars (and representing specializations of the clades above the bars) are listed in table 3.1. As discussed in the text, lungfishes (Dipnoi) and tetrapods have independently acquired a depressor mandibulae muscle that functions as a second mandibular depression mechanism during feeding (characters 2 and 2A).

cavity is rapidly expanded, resulting in a negative (suction) pressure inside the oral cavity relative to the surrounding water (Lauder 1985a). This intraoral negative pressure creates a flow of water into the mouth that carries the prey within reach of the jaws. Suction feeding is a process proposed to have originated with the jawed vertebrates, and represents the dominant feeding mode in virtually all modern aquatic vertebrates.

Figure 3.1 and table 3.1 outline the major biomechanical pathways in osteichthyan fishes, and several of the major innovations in skull biomechanics in selected lineages are noted. There is still a paucity of experimental data on chondrichthyans, and thus the biomechanical basis of the feeding system in this clade has not been well worked out. The key biomechanical system that is retained throughout anamniotic vertebrates is the musculoskeletal apparatus controlling mouth opening. In lower vertebrate clades, the primary mechanism mediating mandibular depression in-

TABLE 3.1 Morphological and functional novelties in the feeding mechanism of vertebrates

Phylogenetic level for biomechanical novelties	Character in fig. 3.1*	Description of characters
Gnathostomata	1	i. Mandibular depression mechanism involving the hypaxialis and sternohyoideus muscles, the mandibulohyoid ligament, and posterodorsal rotation of the proximal end of the hyoid around the articulation with the interhyal bone or cartilage
		ii. Antero-posterior sequence of skull bone movement during suction feeding
		iii. Unidirectional flow of water through the buccal cavity during suction feeding
		iv. Elevation of the skull by the epaxial muscles
		v. Suction feeding as a prey-capture system
Dipnoi + Tetrapoda	2 and 2A	i. Mandibular depression mechanism involving a depressor mandibulae muscle (arising from the visceral musculature of the hyoid arch) that originates on the skull and inserts posterior to the jaw joint on the mandible
Halecostomi	3	i. Mandibular depression mechanism involving the levator operculi and opercular series (fig. 3.2), and a novel ligament, the interoperculomandibular ligament*

*Characters listed are keyed to the black bars on the cladogram in figure 3.1.

volves the ventral body and hyoid musculature and the hyoid apparatus. In salamanders and fishes (Lauder 1980a; Liem 1970; Lauder and Shaffer 1985), contraction of the hypaxial and sternohyoideus (= rectus cervicis) muscles causes a posteroventral translation of the hyoid arch. This movement causes the posterodorsal aspect of the hyoid to apply tension to the mandibulohyoid ligament. Because the mandibulohyoid ligament attaches to the mandible ventral to the axis of rotation of the quadratomandibular joint, the lower jaw is depressed. The major structural units involved in this system are diagramed in figure 3.2. This biomechanical pathway is present in all lower vertebrate clades, including taxa as diverse as coelacanths, salamanders, trout, sharks, and lungfishes. It thus forms the fundamental component of skull design in vertebrates.

Three other aspects of skull function appear to be conserved across lower vertebrate clades (table 3.1; fig. 3.1). First, in all groups studied experimentally, there is a specific timing of skull bone movement during prey capture (Lauder 1979, 1980a; Lauder and Shaffer 1985). As the mouth opens and reaches peak gape, the hyoid is moving posteroventrally and is the major contributor to the increase in buccal cavity volume. Peak hyoid depression occurs after maximum gape is reached, and this is in turn followed by expansion of the posterior (opercular) region of the skull.
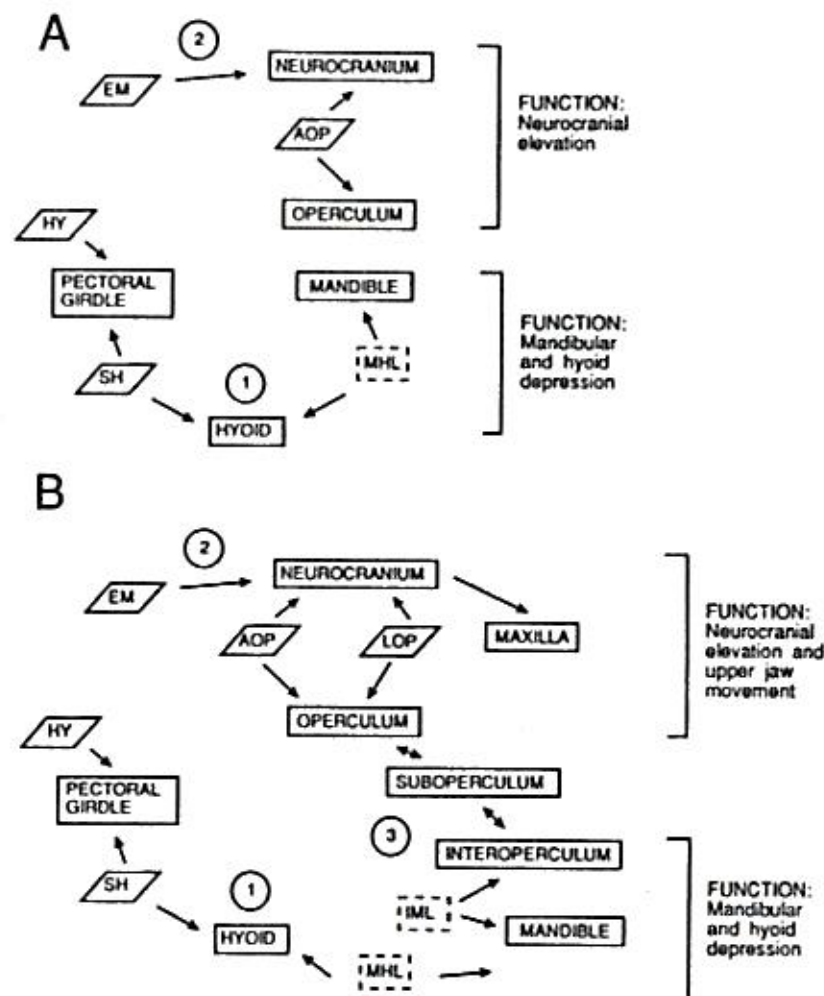

Fig. 3.2. Schematic diagram of the major structural components in the skull of ray-finned fishes at two phylogenetic levels. A. The primitive condition for ray-finned fishes (Actinopterygii, fig. 3.1). B. The primitive condition for the Halecostomi (fig. 3.1). This figure illustrates the addition of a novel biomechanical pathway (no. 3) to the two primitive systems (nos. 1 and 2). The new biomechanical pathway is added to the structural configuration of the head without modifying the primitive pattern, and the function of mandibular and hyoid depression in halecostome fishes is achieved via two biomechanical pathways. Solid rectangles represent bony elements; dashed rectangles, ligaments; parallelograms, muscles. Solid arrows extend from the muscle to the bone of insertion, and double-headed arrows indicate ligamentous connections between bones. Abbreviations: AOP, adductor operculi muscle; EM, epaxial muscles; HY, hypaxial muscles; IML, interoperculomandibular ligament; LOP, levator operculi muscle; MHL, mandibulohyoid ligament; SH, sternohyoideus muscle.

There is thus a consistent anterior-to-posterior sequence in timing of head movements during feeding.

Second, the flow of water into the mouth during suction is predominantly unidirectional, owing to the resistance of the gill bars to water flow at the back of the head. In both fishes and salamanders (Lauder 1985b; Lauder and Shaffer 1985), the branchial apparatus forms a dynamic resistance to water flow during feeding. As the mouth opens and water enters the buccal cavity, the gill arches at the back of the mouth cavity are adducted, preventing water influx from the back of the head. As peak gape is reached, the gill bars begin to abduct, allowing water drawn into the mouth to exit posteriorly. This dynamic resistance of the gill apparatus is fundamental to the suction-feeding mechanism, and is postulated to have been present in early osteichthyan fishes. No data are available on the nature of the gill resistance during feeding by sharks, and it is thus not yet possible to say whether a dynamic gill resistance is primitive for gnathostomes.

Third, in all clades studied experimentally, a key aspect of feeding biomechanics is elevation of the cranium by the epaxial muscles. Cranial elevation contributes to the increase in gape and to the increase in buccal volume.

There are two important corollaries to concept 1.

Corollary 1: *Major innovations in skull design related to initial prey capture typically occur by adding on functional/design features to those primitively present, not by changing existing biomechanical mechanisms.* Two examples of this phenomenon are shown in figure 3.1. Early ray-finned fishes possess only one mechanism of mandibular depression, the hypaxialis–sternohyoideus–hyoid apparatus–mandible coupling (fig. 3.1, character 1). However, halecostome fishes (the Halecostomi contain the family Amiidae and the teleost fishes, as well as several fossil taxa; fig. 3.1) possess a second biomechanical system for depressing the mandible, the levator operculi–opercular apparatus–mandible system (fig. 3.1, character 3; Lauder 1979, 1980a). Figure 3.2 diagrammatically illustrates the transformation in the structural network of the head from the primitive actinopterygian condition to the halecostome configuration. Note that the addition of a novel biomechanical system, the levator operculi coupling (fig. 3.2B: pathway 3), occurs while retaining all of the elements in the original system (fig. 3.2A: pathways 1 and 2). The new mechanism for lower-jaw depression utilizes several bony components of the head that are primitive for ray-finned fishes, such as the operculum (fig. 3.2A). The levator operculi and the ligamentous connection of the interoperculum to the mandible are novelties at the halecostome level (fig. 3.1, character 3; fig. 3.2B; table 3.1) that are *added on* to the primitive structural configu-

ration of the feeding mechanism (with minimal modification to the primitive system).

A second example is provided by lungfishes and salamanders, which also possess a novel mandibular depression mechanism: a biomechanically independent system that does not disrupt function of the hyoid-based depression mechanism. Lungfishes and salamanders have independently acquired a depressor mandibulae muscle (Bemis 1987; Bemis and Lauder 1986) that inserts directly on the lower jaw (fig. 3.1, characters 2 and 2A). In both lungfishes and salamanders this muscle has been demonstrated to function in concert with the primitive mandibulohyoid system (Bemis and Lauder 1986; Lauder and Shaffer 1985) to mediate mouth opening. Thus, in these clades a second novel muscular biomechanical mechanism has been added onto the primitive mouth opening system without modification of the original system.

Corollary 2: *Jaw muscle activity patterns (motor patterns) among closely related taxa may be phylogenetically conserved, and phylogenetic changes in feeding behavior within these clades is then a consequence primarily of changes in the design of peripheral morphology.*

Recent quantitative analyses of the jaw muscle activity patterns used during initial prey capture and in prey processing by lower vertebrates have shown that there tend to be relatively few interspecific differences in motor patterns, despite significant differences in feeding behavior and performance among these species (Lauder 1991; Sanderson 1988; Shaffer and Lauder 1985a; Wainwright and Lauder 1986; Wainwright 1989).

For example, Wainwright and Lauder (1986) studied the motor pattern of the jaw muscles in four genera in the family Centrarchidae (a clade of endemic North American fishes that includes the bass, *Micropterus*, and sunfishes, *Lepomis*). The four genera differ considerably in head shape and mouth size and have different natural feeding habits and abilities. Only one of the eleven electromyographic variables measured showed any significant difference among genera, indicating that the pattern of muscle activity used during feeding is very similar among the genera. Similar conservatism among closely related species has been found in the feeding motor pattern in ambystomatid salamanders (Shaffer and Lauder 1985a), and haemulid and labrid fishes (Sanderson, 1988).

Concept 2
Functional characters differ in their levels of intraspecific and interspecific variation.

Functional characters differ in their levels of variation, with those most important to suction-feeding performance exhibiting the greatest interspecific variation and the least intraspecific variation.

While the previous section suggests that certain general movement and muscle activity patterns are conserved across most suction-feeding vertebrates, recent detailed studies of variation within and among closely related species emphasize that interesting patterns of variability occur in some functional characters. In particular, certain movement and muscle activity patterns appear to be relatively stereotyped within species, and yet differ among related taxa. Others show the exact opposite pattern, with virtually all variation occurring within species, and species means exhibiting little or no differentiation. A key point in these population level analyses of suction feeding is the role of individual variation within species, and how it shapes the opportunity for selection to act on functional characters and their morphological constituents.

Detailed descriptions of populational variation in functional systems have been carried out in aquatic salamanders (Shaffer and Lauder 1985a, b; Lauder and Shaffer 1985, 1986) and fishes (Sanderson 1988; Wainwright 1986; Wainwright and Lauder 1986). While these studies cover only a small fraction of the morphological, taxonomic, and behavioral variation found in aquatic suction feeding, several patterns are emerging.

Perhaps most important is the lack of a one-to-one relationship between morphological divergence and functional output. In nontransforming ambystomatid salamanders (the axolotl, *Ambystoma mexicanum*, and its relatives), there is a great deal of variation in head size and shape (Shaffer 1984; Lauder and Shaffer 1985). However, when three morphologically divergent species were quantitatively tested for variation in kinematic variables (Shaffer and Lauder 1985b), similar functional divergence was not observed. Rather, functional variables display a range of variation, from maximum hyoid depression, where virtually all (90%) of the phenotypic variance is attributable to differentiation among species, to maximal cranial elevation, where an estimated 22% of the variance is attributable to among-species differences, and most (63%) is at the level of variation among trials of the same individual (table 3.2). These results emphasize the crucial importance of experimental verification of functional hypotheses based on morphology alone; they also stress the necessity of quantifying variation in *function* within species before general conclusions on divergence among species may be drawn (Lauder 1990).

A general trend that is emerging is that functional characters most important in generating suction during feeding show the least variation within species, and tend to differentiate closely related taxa. For virtually all suction-feeding vertebrates, the hyoid apparatus acts as the primary pump involved in generating negative pressures within the buccal cavity (Lauder 1985a). Thus, patterns of hyoid movement and electromyographic activity in its associated musculature (the rectus cervicus or sternohyoideus)

TABLE 3.2 Patterns of variation in the feeding mechanism of three species of ambystomatid salamanders (genus *Ambystoma*)

Kinematic variable in the feeding mechanism	Percentage of total variance			Mean value of the variable for each species		
	Among species	Among individuals within species	Among trials within individuals	A. dumerilii	A. mexicanum	A. ordinarium
Cranial elevation (in degrees)	22	15**	63	45.5	32.6	38.1
Maximum hyoid depression (in cm)	90**	6**	4	2.8	1.9	1.8
Maximum gape (in cm)	63**	16**	21	2.1	1.5	1.2
Time to maximum gape (in ms)	39*	19**	42	46.7	33.8	38.0
Time to maximum hyoid depression (in ms)	69**	15**	16	52.5	28.2	38.0
Total gape cycle time (in ms)	38*	18**	44	88.0	69.7	73.0

Source: Shaffer and Lauder (1985b).
Note: These three species are the most morphologically divergent in the family (Shaffer 1984). Six kinematic variables were digitized from high-speed films of feeding for several individuals in each species.
* Significant at the 0.05 level.
** Significant at the 0.01 level.

TABLE 3.3 Patterns of variation in the feeding mechanism of two species of ambystomatid salamanders (genus Ambystoma).

Electromyographic variable in the feeding mechanism	Percentage of total variance				Mean value of the variable for each species (in ms)	
	Among species	Among individuals within species	Among days within individuals	Among trials within days	A. dumerilii	A. mexicanum
Onset time difference between the depressor mandibulae and sternohyoideus muscles	51**	13	6**	30	2.80	-2.11
Onset time difference between the depressor mandibulae and adductor mandibulae internus muscles	7	4	2	87	0.45	-1.94
Duration of activity in the depressor mandibulae muscle	0	40*	15**	45	67.7	59.0
Duration of activity in the sternohyoideus muscle	25	33**	2	40	39.1	66.1
Duration of activity in the adductor mandibulae internus muscle	0	27	24**	49	116.5	98.1

Source: These data are abstracted from Shaffer and Lauder (1985a).

Note: Eleven electromyographic variables were digitized from recordings of cranial muscle activity during prey capture for several individuals in each species (five are shown here). Data are shown for three muscles: the depressor mandibulae (a muscle that contributes to mouth opening by depressing the mandible), the sternohyoideus (a muscle that causes both lower-jaw depression and buccal volume expansion), and the adductor mandibulae internus (one of the jaw-closing muscles).

* Significant at the 0.05 level.
** Significant at the 0.01 level.

consistently differentiate species of ambystomatid salamanders (table 3.3; Shaffer and Lauder 1985a, b; Lauder and Shaffer 1985) and centrarchid sunfishes (Wainwright and Lauder 1986). Interestingly, this is the only muscle showing significant electromyographic variation among species, and therefore a relatively stereotyped behavior within taxa, in these studies. All other muscles and kinematic variables demonstrate consistently high levels of variation among conspecific individuals and large amounts of within-individual variation. However, the mean values of congeneric species are often very similar to each other.

Unfortunately, we have virtually no information on how these levels of functional variation are related to morphological variation in the bones and muscles of the head. For head width, the only variable so far considered in salamanders, within-species correlations with mean values of kinematic variables range from 0.21 to 0.63, suggesting that morphometric and functional variation at the individual level may be related. Species means are even more highly correlated, with average head width and kinematic variable correlations ranging from 0.54 to 0.96 (Shaffer and Lauder 1985b).

Concept 3
Environmental transitions affect kinematic and EMG patterns, but these changes are not a direct consequence of the biophysics of the media.

Significant differences in feeding and breathing behavior are observed as vertebrates shift from water to air, but the patterns of cranial bone movement and muscle function used during the manipulation of prey in the two media are remarkably similar.

A central concern in functional analyses of morphology is the extent to which the physical environment sets limits to, or constrains, the functional performance attained with a given morphology. The transition from water to air has been emphasized as a particularly important one in vertebrates as so many species have shifted, both ontogenetically and phylogenetically, from aquatic to terrestrial lifestyles. In particular, amphibians, turtles, and a few fishes have both aquatic and terrestrial life history phases, and functional analyses of feeding by these organisms in water and on land have allowed a preliminary examination of the biophysical constraints imposed by these two very different media on the structure and function of the skull (Bramble and Wake 1985). Additionally, comparisons between aquatic and aerial respiration have illuminated the extent to which the same structures may serve dual functional roles in lower vertebrates (Liem 1985, 1987).

One conclusion to emerge from these studies has been the overall conservatism of movement and muscle activity patterns that may be used during respiration and prey manipulation in different environments. In
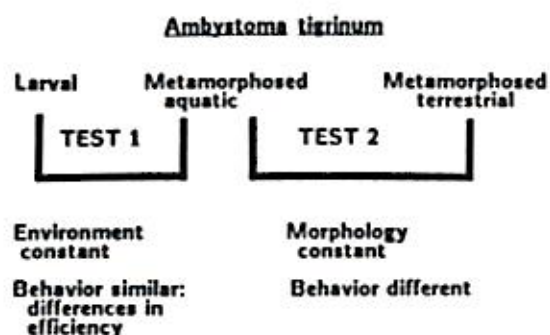
Fig. 3.3. Conceptual design of the experimental comparisons used in analyses of the effect of the environment on skull function by Lauder and Shaffer (1988) and Shaffer and Lauder (1988). The tiger salamander, *Ambystoma tigrinum*, was used as an experimental animal to investigate both the influence of the medium (water versus air) and the effect of morphological transformations at metamorphosis on skull function. Because metamorphosed animals will still feed in the water, we were able to conduct two sets of comparisons (tests). Test 1 involves comparing feeding behavior and muscle activity between larval and metamorphosed animals feeding in the water (termed the metamorphosed aquatic stage): the environment is constant, but the morphology is different. Test 2 involves comparing metamorphosed aquatic individuals with metamorphosed individuals feeding on land: morphology is constant but the feeding environment has changed. From Lauder and Shaffer (1986).

our work on the salamander *Ambystoma tigrinum*, we have used an experimental design that allows us to partition the variation in feeding kinematics and electromyographic muscle activity into distinct components reflecting the morphological changes at metamorphosis and the environmental transitions associated with feeding in the water and on land (fig. 3.3). This general design provides information on two aspects of the functional transition from aquatic suction to terrestrial lingual feeding. First, by comparing variation in function between larval and metamorphosed animals feeding in the water (fig. 3.3; test 1) we were able to assess the effect of morphological changes at metamorphosis alone on feeding function (the presence of the aquatic environment is a constant). Second, comparing metamorphosed animals feeding in the water and on land documents the magnitude of the functional shifts associated with the change in environment that occurs at metamorphosis (fig. 3.3: test 2). Partitioning the overall variation in feeding kinematics and muscle function into environmental and morphological components allows us to quantify the degree to which a given change in morphology of the skull and hyobranchial skeleton necessitates a change in function.

Figures 3.4 and 3.5 illustrate some of the morphological changes that occur during metamorphosis. Externally, the gills are lost, the gill slits close, the head narrows, and the eyes move to a more anterodorsal loca-
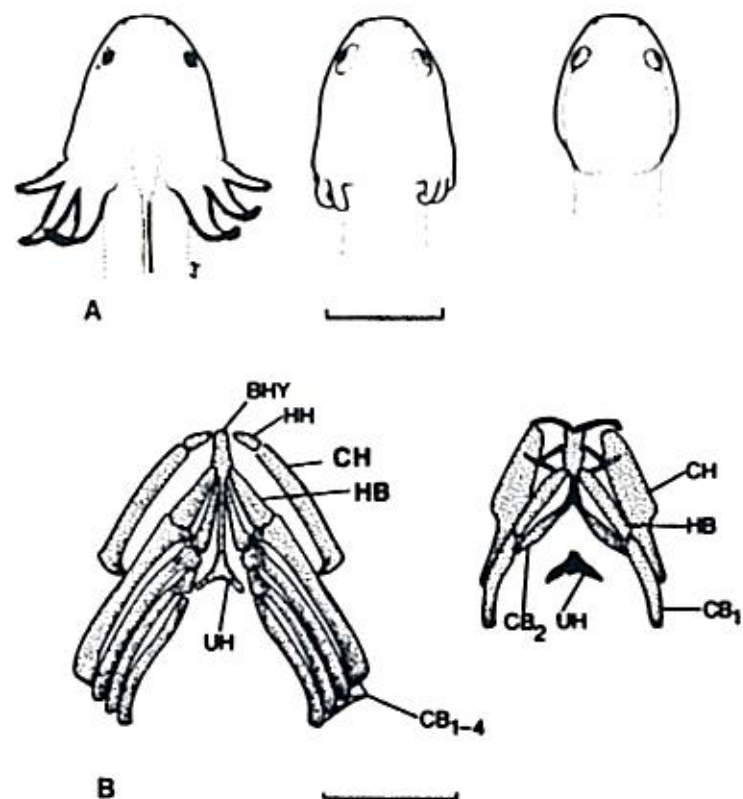
Fig. 3.4. A. Three dorsal views of the head of *Ambystoma tigrinum*. The left panel shows the head of a larva, the middle panel the head of an individual in the middle of metamorphosis, and the right panel the head of a metamorphosed individual. B. The hyobranchial apparatus of larva (on the left) and an adult (on the right) *Ambystoma tigrinum*. Note the major morphological changes that occur at metamorphosis: loss of ceratobranchials 2, 3, and 4, and extensive alterations in shape of the hyoid and branchial arches. Scale bars = 1.0 cm. Abbreviations: BHY, Basihyal cartilage; CB_{1-4}, Ceratobranchial bones 1 through 4; CH, Ceratohyal cartilage; BH, Hypobranchial cartilage; HH, Hypohyal cartilage; UH, Urohyal. Modified from Lauder and Shaffer (1988).

tion (fig. 3.4A). Changes in the skull at metamorphosis include the loss of the palatine and alterations in shape of the vomer, pterygoid, and prearticular bones. Many changes occur in the hyobranchial apparatus (fig. 3.4B). For example, the posterior ceratobranchials are lost, most hyobranchial skeletal elements change shape, the radials form, and a glandular tongue with lingual sinuses develops (see Duellman and Trueb 1986; Lauder and Reilly 1990; Reilly and Lauder 1989, 1990b; Yamasaki 1956). A great many changes also take place in the muscular system of the head (fig. 3.5):
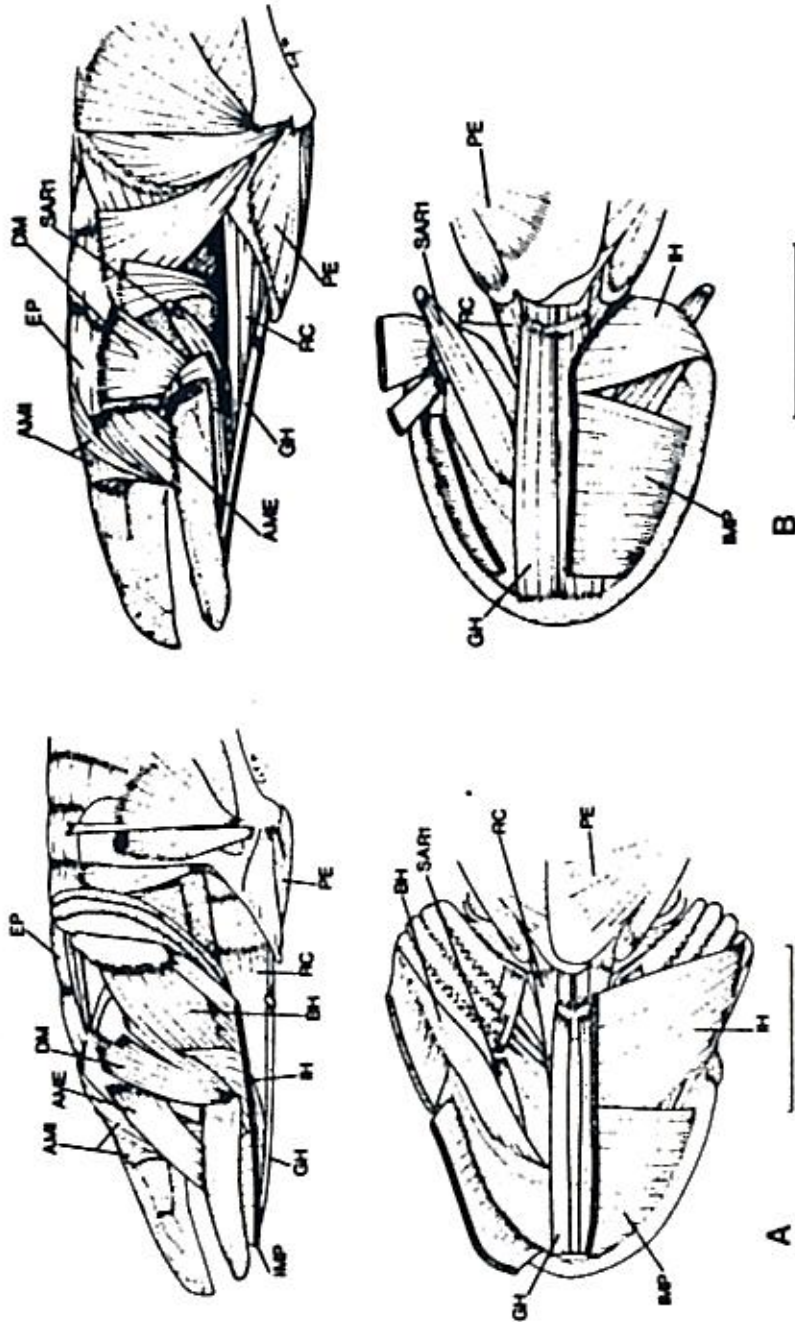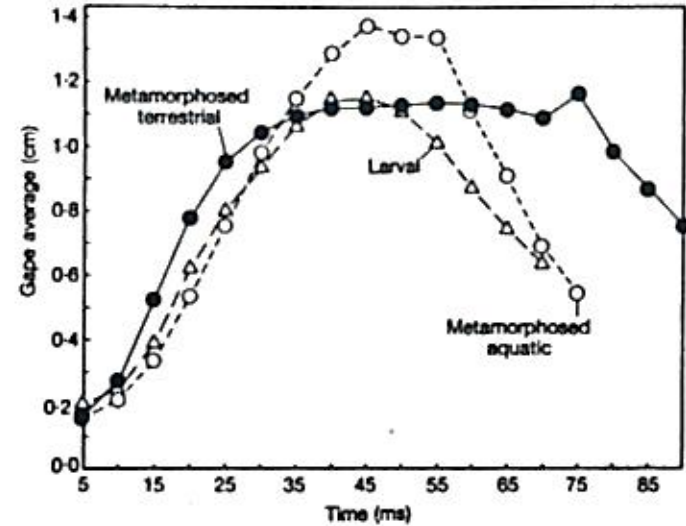
Fig. 3.6. Graph of the average pattern of mouth opening (gape) with respect to time for three individuals feeding as larvae, as metamorphosed animals in the water, and as metamorphosed individuals on land. Each point represents the mean gape distance for each time interval measured from high-speed films of feeding. There are no statistically significant differences among the three curves, although there is a tendency for terrestrial feedings to be longer in duration. Similar results were obtained for most other kinematic variables. Modified from Shaffer and Lauder (1988).

Fig. 3.5. A. Dorsal and ventral views of the muscles of the head of a larval *Ambystoma tigrinum*. Note the ventral branchial muscles and particularly the large branchiohyoideus muscle. B. Dorsal and ventral views of the muscles of the head of an adult *Ambystoma tigrinum*. Note the lack of gill bars and the branchiohyoideus muscle, and the subarcualis rectus 1 muscle that attaches to the distal end of ceratobranchial 1. Scale bars = 1.0 cm. Abbreviations: AME, Adductor mandibulae externus muscle; AMI, Adductor mandibulae internus muscle; BH, Branchiohyoideus muscle; DM, Depressor mandibulae muscle; EP, Epaxial muscles; GH, Geniohyoideus muscle; IH, Interhyoideus muscle; IMP, Intermandibularis posterior muscle; PE, Pectoralis muscle; RC, Rectus cervicis muscle; SAR1, Subarcualis rectus 1 muscle. Modified from Lauder and Shaffer (1988).

tongue muscles are formed, many gill arch muscles (such as the larval branchiohyoideus) are lost, and the subarcualis rectus 1 muscle elongates and moves its insertion to the distal end of ceratobranchial 1 (fig. 3.5). Given the extensive morphological changes at metamorphosis, one might predict that major functional transformations occur also.

The primary conclusion from both kinematic (Shaffer and Lauder 1988) and electromyographic (Lauder and Shaffer 1988; Reilly and Lauder 1990c) studies of feeding in salamanders is that while feeding *mode* changes across environments, many functional components of the feeding act are retained from the larval ontogenetic stage. For our kinematic data, there were no detectable differences between larval and metamophosed animals feeding in the water (figs. 3.6, 3.7), suggesting that the morphological changes at metamorphosis do not necessitate a shift in function. That is, both larval and metamorphosed animals can suction feed, and the metamorphosed animals retain the larval patterns of muscle activity and bone movement when they do feed by suction in the water. Feeding performance is reduced (with metamorphosed individuals capturing fewer prey; Lauder and Shaffer 1986), suggesting that the morphological
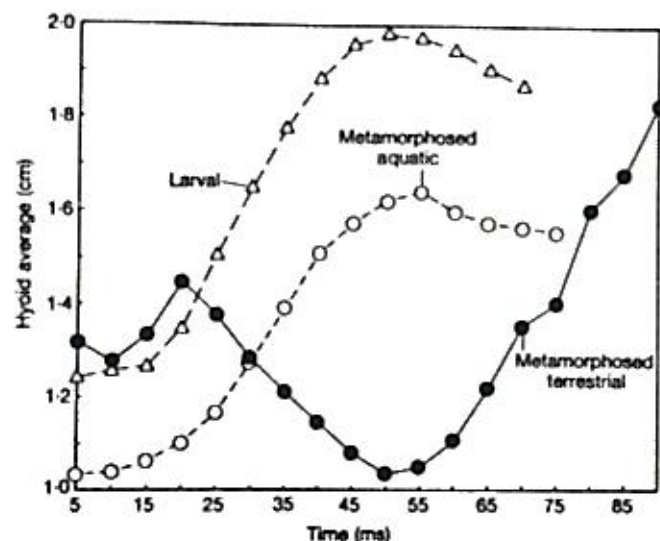
Fig. 3.7. Graph of the average pattern of hyoid depression with respect to time for three individuals feeding as larvae, as metamorphosed animals in the water, and as metamorphosed individuals on land. Each point represents the mean hyoid distance for each time interval measured from high-speed films of feeding (Shaffer and Lauder 1988). Note the close similarity of the larval and metamorphosed aquatic curves (offset vertically owing to morphological changes at metamorphosis) and the radical change in hyoid kinematics during terrestrial feedings: for this variable there is a major effect of the environment on feeding behavior. Modified from Shaffer and Lauder (1988).

changes (especially in the hyobranchial apparatus) have a profound influence on feeding ability. The muscle activity patterns used by larval and metamorphosed ambystomatid salamanders feeding in the water are not significantly different when motor pattern variables are compared using a MANOVA (Lauder and Shaffer 1988).

When metamorphosed animals feed on land, many kinematic and muscle activity patterns change as feeding mode shifts entirely from suction to lingual protrusion (Lauder and Shaffer 1988; Shaffer and Lauder 1988; Reilly and Lauder 1990c). For kinematic data, the variable showing the most pronounced shift is hyoid excursion (fig. 3.7), which changes from continuous abduction during the prey-capture phase of suction feeding in larvae, to protraction followed by retraction associated with tongue protrusion in adults (Shaffer and Lauder 1988). Muscle activity patterns exhibit a more complex pattern of change, with activity on land being longer in duration than in aquatic feedings (see Lauder and Shaffer 1988: epaxial muscles, rectus cervicis, and the adductor mandibulae externus).

The muscle activity patterns of metamorphosed animals feeding in the water and land (fig. 3.3: test 2) do show a significant overall effect of the environmental shift on motor pattern (Lauder and Shaffer 1988), with a significant MANOVA testing the global hypothesis of mean differences in muscle activity (P = 0.014) across environments.

These changes in electromyographic pattern are striking for two reasons. First, this pattern provides an example of a change in the motor pattern across environments. Second, the changes in the motor pattern represent a change in the *opposite* direction to that predicted on the basis of the biophysical properties of air and water alone, since muscles are active for a longer period in a less viscous medium (air). The longer durations of muscle activity on land compared to water may function to increase the duration of the gape cycle (allowing time for tongue extension and retraction), but the changes in motor pattern cannot be attributed to differences in resistance of the two media.

Following the initial capture of prey by ambystomatid salamanders, a series of discrete prey transport events occurs in which the prey is moved posteriorly in the mouth toward the esophagus for swallowing (Reilly and Lauder 1990a, 1991). Prey transport involves the use of a complex motor pattern in head muscles and a relatively stereotyped pattern of bone movement. Reilly and Lauder (1991) have hypothesized that the process of terrestrial prey transport in ambystomatid salamanders utilizes a kinematic and electromyographic pattern similar to the processes of aquatic prey capture and transport. In this view, the major behavioral novelty in salamander feeding is the process of terrestrial prey capture by tongue projection, with the other three behaviors (terrestrial prey transport, aquatic prey capture, aquatic prey transport) all being similar despite differences in environment between water and land.

Liem (1980, 1985, 1987), in his work on respiratory ventilation in air-breathing fishes, has conducted a set of interesting investigations on the effect of switching respiratory media on functional patterns in the head. His studies show many parallels with the results from ambystomatid salamanders discussed above. Liem identified triphasic and quadruphasic air ventilation as to the two basic patterns in advanced teleosts. Both patterns involve gulping a bubble of air at the surface and extracting oxygen by passing the air across a highly modified first epibranchial bone (Liem 1985). Using both pressure profiles and electromyographic data, Liem showed that the triphasic mode is very similar to prey capture during aquatic suction feeding; in this case, the "prey" is an air bubble. Similarly, in quadruphasic air ventilation, muscle activity and pressure profiles are identical to those used in coughing, a widespread response to novel aquatic environments in many teleosts. Thus, the "new" function of air ventilation

is achieved by using a conservative motor pattern for a new environment, while retaining the original function in the aquatic environment (Liem 1985; Gans 1970).

Concept 4
Unidirectional and bidirectional feeding systems are the two basic skull designs in aquatic vertebrates.

Feeding mechanisms in aquatic vertebrates can be divided into two fundamental hydrodynamic categories: unidirectional and bidirectional flow systems. Unidirectional flow systems are used during feeding by most fishes, larval salamanders, and some tadpoles (Ruibal and Thomas 1988; Wassersug and Hoff 1979). The feeding mechanism is said to be unidirectional because water drawn into the mouth during suction feeding passes through the buccal cavity to exit posteriorly between the gill bars and out the opercular opening. Flow is thus from anterior to posterior and travels in one direction.

In bidirectional flow systems, water drawn into the mouth anteriorly as the gape increases and buccal volume expands is expelled through the mouth as the jaws close. Thus, water both enters and leaves through the mouth, and flow during feeding is bidirectional. Aquatic vertebrates that feed with bidirectional flow systems include turtles, frogs, completely metamorphosed salamanders, and some mammals.

Relative to the considerable body of research on unidirectional flow systems (e.g., Alexander 1969, 1970; Lauder 1980c; Lauder and Clark 1984; Lauder and Shaffer 1985; Liem 1978), there are very few studies of feeding in vertebrates with bidirectional flow. Most of the research on prey capture and skull function in aquatic vertebrates has focused on fishes (e.g., Grobecker and Pietsch 1979; Lauder 1985b; Liem 1970; Osse 1969), and this has to some extent overshadowed the significant differences between these two fundamental suction-feeding systems. Indeed, it is remarkable that more attention has not been devoted to aquatic feeding in turtles and frogs, two groups that exemplify bidirectional feeding systems.

In an effort to investigate the functional significance of the difference between unidirectional and bidirectional feeding systems in vertebrates, Lauder and Shaffer (1986) and Lauder and Reilly (1988) studied the functional morphology of prey capture in salamanders. Salamanders, both by the ontogenetic changes that occur in the feeding mechanism and because of their amenability to experimental manipulation, make an excellent system in which to investigate the functional implications of different feeding designs.

Figure 3.8 illustrates the ontogenetic transformation between larval *Ambystoma tigrinum*, which possess a unidirectional feeding system, and
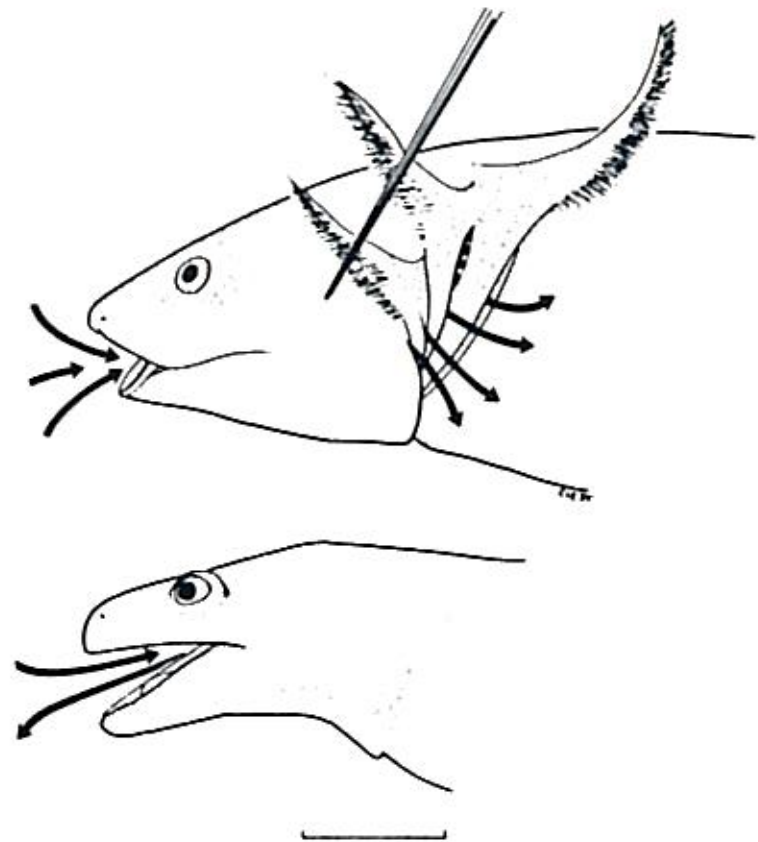
Fig. 3.8. Basic hydrodynamic design of the feeding mechanism in a larval tiger salamander, *Ambystoma tigrinum* (upper panel), and a metamorphosed individual (lower panel). Arrows indicate the direction of water flow in and out of the mouth during feeding. In larvae, gill slits are present and water that enters the mouth during suction feeding is expelled posteriorly out the gill slits. At metamorphosis the gill slits are lost, and adults feeding in the water must expel water anteriorly in a bidirectional flow regime. This transformation from a unidirectional to a bidirectional design of the feeding system during ontogeny has served as an experimental system for investigating the functional significance of the two designs in vertebrates. From Lauder and Shaffer (1986).

the bidirectional system of completely metamorphosed individuals. Larvae possess an extensive branchial apparatus with posterior gill openings (Lauder and Shaffer 1985, 1986) that allow water to exit posteriorly from the buccal cavity. At metamorphosis, the branchial apparatus is greatly reduced (Reilly 1986, 1987), the external gills are lost, and the gill slits close, converting the feeding system to a bidirectional flow regime (Reilly and Lauder 1988b).
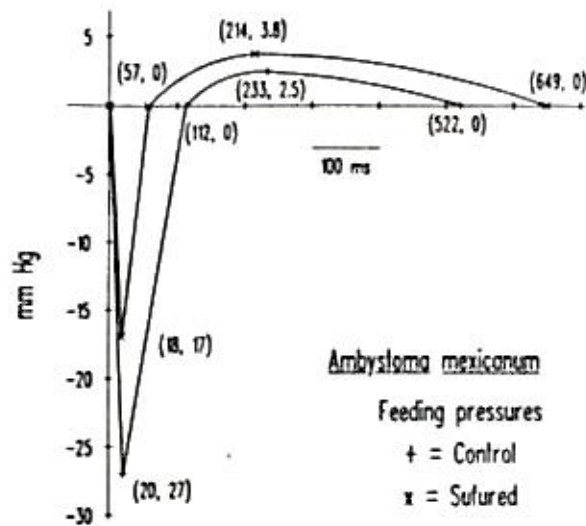
Fig. 3.9. Average pattern of buccal pressure change during feeding in normal axolotls (*Ambystoma mexicanum*) and in individuals which have had the gill slits sutured closed. Buccal pressure (in mm Hg) is given on the y-axis and time on the x-axis; coordinates indicate the time and pressure for various points on the curve. Note that suturing the gill slits reduces the negative buccal pressure and increases the positive portion of the pressure waveform. From Lauder and Reilly (1988).

Lauder and Shafer (1986) measured buccal cavity pressures in larval and metamorphosed *Ambystoma tigrinum* feeding in the water to determine the functional consequences of the ontogenetic shift from unidirectional to bidirectional feeding. They found that metamorphosed individuals generated significantly different buccal pressure curves, and specifically, that the amount of negative pressure produced declined after metamorphosis. This was correlated with a decrease in feeding performance by metamorphosed individuals: larval *Ambystoma tigrinum* were more effective at capturing freely swimming prey than were adults.

Lauder and Reilly (1988) specifically investigated changes in buccal pressure profiles that accompany the experimental transformation from a unidirectional to a bidirectional feeding system in *Ambystoma mexicanum* (with no change in morphology). By suturing the posterior gill openings, they experimentally converted individuals with a unidirectional feeding system into bidirectional feeding systems and compared buccal pressures and feeding performance in control and experimentally sutured individuals. The results of these experiments are summarized in figure 3.9, which shows that suturing the gill slits causes a decrease in negative pressure, and an increase in the positive portion of the pressure waveform. Because water

cannot flow posteriorly out of the mouth and is entering at a high velocity due to hyoid expansion, a larger positive pressure is created in bidirectional feeding systems. The reduction in negative pressure magnitude and duration (fig. 3.9) correlates with a dramatic reduction in feeding performance: sutured (bidirectional) individuals captured freely moving prey 5% of the time, while control (unidirectional) individuals captured prey 56% of the time.

The conclusion from these studies is that, all other things being equal, unidirectional feeding systems are more efficient than bidirectional systems, primarily because of the reduction in buccal pressure generated during feeding and the correlated increase in positive (backflow) pressure in bidirectional feeding systems.

Although these results on feeding systems in salamanders provide a basis for an understanding of the functional significance of unidirectional and bidirectional feeding systems, our knowledge of the diversity of such feeding systems among vertebrates is still woefully inadequate. With the exception of the preliminary reports by Bramble (1973), Shafland (1968), and Weisgram (1982), there are no studies of bidirectional aquatic feeding systems in frogs and turtles. Many lineages of fishes and salamanders possess reduced opercular openings that may have the effect of converting a primitively unidirectional feeding system into a bidirectional feeding system. Also, many of the specializations that occur in the feeding systems of turtles, such as the highly distensible esophagus, may function to circumvent the constraints of bidirectional feeding systems. The esophagus could function to store water drawn into the mouth and greatly delay the reversal of flow, thus effectively converting the feeding system into a unidirectional design. The functional consequences of these morphological transformations have yet to be investigated.

EVOLUTIONARY IMPLICATIONS AND PREDICTIONS: A DISCUSSION OF THE FOUR CONCEPTS

The four major concepts that emerge from research on aquatic vertebrate feeding systems invite explanation and analysis in the context of comparative and historical biology. What are the implications, predictions, and avenues for future research that emerge from these concepts?

Discussion of Concept 1
Evolutionary conservation of biomechanical patterns

The demonstration that certain critical biomechanical features of the feeding system in lower vertebrates are highly conserved may not appear especially noteworthy at first. After all, in phylogenetic terms this conclusion

amounts merely to documenting gnathostome or osteichthyan characters with little homoplasy. However, we emphasize several important features of concept 1 that point to its wider significance in comparative biology.

First, the number of synapomorphies for the Osteichthyes is not large (Lauder and Liem 1983), and complex morphological features that define major clades are rare and of critical importance in testing hypotheses of monophyly. Second, there are comparatively few biomechanical synapomorphies available for any vertebrate clade, and those provided by the feeding mechanism of lower vertebrates provide some of the best-documented examples to date of the use of biomechanical characters in phylogenetic analysis (also see Emerson 1982; Lauder 1983b; and Liem 1974, 1979 for other examples). Third, while morphological systems are widely used in phylogenetic analysis, only recently have historical patterns of functional transformation been studied in a rigorous manner (see Lauder 1990 for a review). If we are to understand the evolution of form *and* function, then we must attempt to identify functional characters and use them in a phylogenetic context. The research that underlies concept 1 attempts to do just this. Finally, the mere demonstration that certain complex biomechanical features of the vertebrate skull have been retained throughout hundreds of millions of years of divergent evolution in gross morphology is noteworthy. Very few other complex features of skull design have proven to be so invariant, and such highly conservative features point to interesting biological problems of functional constraint and versatility in relation to the evolution of morphological designs.

Why have biomechanical patterns in the skull, such as the relative timing of head movements or muscle activity patterns (table 3.1; fig. 3.1), been retained throughout lower vertebrate evolution? Two possible hypotheses (not necessarily mutually exclusive) might explain this result. First, the constraints of feeding in an aquatic medium that is 900 times as dense and 80 times as viscous as air may severely limit the range of functional solutions to the problem of obtaining prey from the water. If there is only one sequence of movements that will effectively work to extract quickly moving prey from water, then after the origin of such a system, perhaps at the base of the Gnathostomata, it may have been retained throughout all subsequent cladogenetic events. In this view, extrinsic (environmental) constraints on the design of the skull have limited the expression of functional diversity.

The second hypothesis states that conservative morphological substrates constrain function so that head kinematics and muscle activity patterns are preserved. In this view, conservative functional patterns are retained because of their close link to morphological features. These morphological features may themselves be retained as a result of developmental links with other skull features, and not because of any a priori

functional requirements. For example, the muscle activity pattern used during feeding might be conserved because of the difficulty of changing the morphological substrate for these functional characters: the complex neural circuitry that drives the jaw muscles. Thus, intrinsic (structural) constraints on the design of the skull may have limited the expression of functional diversity. It is also possible that changes in the central nervous system may occur that are masked by changes in peripheral morphology so that the final behavior stays the same even though changes have occurred at several levels.

It is our view that both hypotheses are needed to fully explain the historical pattern of conservative biomechanical features in the lower vertebrate skull. The results of experiments on unidirectional and bidirectional feeding systems in salamanders (Lauder and Shaffer 1986; Lauder and Reilly 1988) have shown unequivocally that unidirectional feeding systems outperform bidirectional systems (all other things being equal), when both feeding modes exist in closely related taxa sharing the same basic anatomical design. Our interpretation of these results is that certain extrinsic (hydrodynamic) constraints exist on skull design.

On the other hand, there is no a priori reason why the timing of muscle activity and kinematic patterns could not have been modified to a greater extent than has been observed. An example of a cranial muscle activity pattern that has been altered during cladogenesis is provided by Lauder (1983a, c). While this case study demonstrates that motor patterns can be modified, it focused on a chewing behavior that takes place over a relatively long period of time (on the order of seconds to minutes) and presumably involves considerable sensory feedback during execution of the behavior. Neuronal circuitry that drives behaviors of this type may be more malleable over evolutionary time than circuitry that drives initial prey capture (a behavior that occurs in 10 to 150 msec, is noncyclical, and does not involve sensory feedback during its execution). Thus, the hypothesis that functional features of the feeding mechanism have been retained because of intrinsic structural constraints holds that complex, preprogrammed behaviors (and their associated motor and kinematic patterns) are likely to be evolutionarily conservative owing to the difficulties of modifying complex circuitry. This hypothesis has yet to be tested, but is one possible explanation for the conservatism in functional features of the lower vertebrate skull.

The question of conservative motor patterns is important, for it directly addresses the issue of how one explains behavioral and functional transformations in animals. How does behavior evolve: by alterations in central nervous output to the musculature, or by reorganization of peripheral musculoskeletal design so that conservative motor patterns have a different effect (Lauder 1986)? The data obtained so far from quantitative
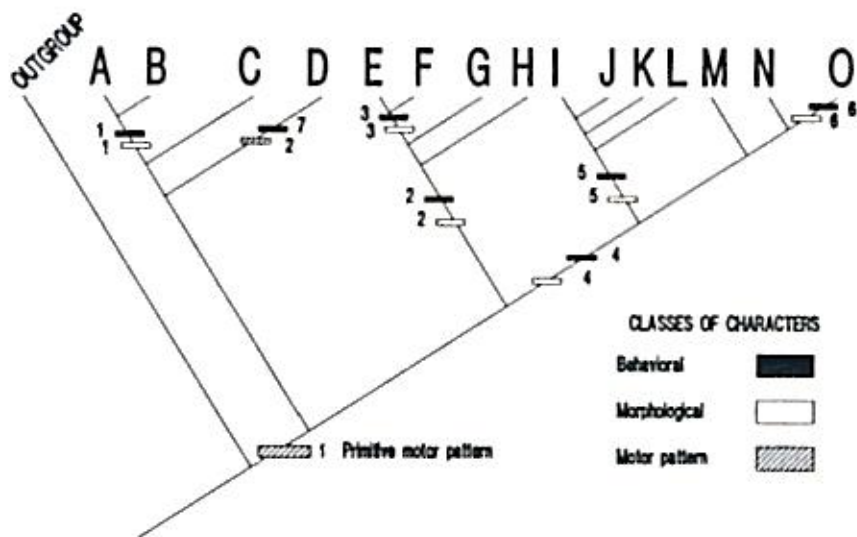
Fig. 3.10. Hypothetical cladogram of species A to O showing the phylogenetic pattern of morphological, motor pattern, and behavioral/performance characters if behavioral evolution is largely a consequence of changes in peripheral morphology and not of alterations in muscle activity patterns. Thus, all species in the clade retain the primitive pattern of muscle activity (hatched bar 1), while some species have acquired behavioral novelties (black bars 1 to 6). Alterations in the topology of the musculoskeletal system have occurred in those species that possess behavioral novelties (open bars 1 to 6). Note that a novel aspect of the motor pattern (hatched bar 2) is present in species D along with a behavioral novelty (black bar 7). It is important that the morphological characters analyzed be related (by a causal biomechanical model and experiments) to the behaviors being mapped onto the cladogram, so that a *causal* link is established between the morphological changes and the behavioral novelties (Lauder, 1991).

analyses of jaw muscle motor patterns indicate that motor patterns may be phylogenetically (historically) conservative and that peripheral musculoskeletal reorganization is often the basis for differences in feeding behavior.

There are a variety of ways in which one might attempt to explain changes in the behavior and behavioral performance of animals. For example, if two species differ in the pattern of jaw bone movement during feeding, these kinematic differences might be due to distinctions in the pattern of jaw muscle activity between the species. Alternatively, the topology of the musculoskeletal system could differ between the species so that a given muscle, activated by the central nervous system in exactly the same way in both species, has a different effect because of differences in the lever arms of the muscle (Lauder, 1991).

Figure 3.10 shows an example of an expected phylogenetic pattern to the transformation of peripheral morphology, motor patterns, and behav-

ior, if motor patterns are historically conserved during behavioral evolution. Under these conditions, congruence between morphological novelties and behavioral novelties will be high, while novelties in motor patterns should be rare and plesiomorphic to alterations in peripheral morphology and behavior.

The extent to which this view of motor patterns as conservative evolutionary units can be extended to other vertebrates (or to larger clades of more distantly related taxa) is as yet unknown because of the scarcity of quantitative analyses of muscle activity variation. Testing the generality of this hypothesis will be an important avenue for future research in functional and evolutionary morphology.

Discussion of Concept 2
Functional characters vary in their levels of intraspecific and interspecific variation

This result, stemming from population-level analyses of functional characters, is in our opinion one of the most important and potentially general results to emerge from recent functional studies on lower vertebrate feeding. Two findings in particular deserve further mention: the generally high levels of stereotyped behavior in hyoid movement patterns within species of suction-feeding vertebrates, and the high levels of among-individual variation in virtually all other functional characters examined to date.

That the hyoid has repeatedly been identified as the key functional unit in suction feeding (e.g., Lauder 1985c) suggests that this structure and its associated musculature may be under strong selection in nature. Current evidence indicates that movement of the hyoid apparatus determines the velocity of water entering the buccal cavity, and hyoid function is predicted to be related to the size and activity level of prey that may be captured. Unfortunately, there are no studies explicitly linking prey-capture performance to either intra- or interspecific variation in hyoid morphology, and such analyses are critical for future formulations of hypotheses on the reduced intraspecific variation in hyoid function (see Arnold [1983, 1986] for a general discussion of this research program). However, one reasonable interpretation of this pattern postulates strong stabilizing selection on hyoid function, and therefore feeding performance. Such stabilizing selection will tend to reduce both phenotypic and additive genetic variance in hyoid characters (Falconer 1981), leading to the observed pattern of stereotyped responses within species, and relatively great variation among taxa.

If this scenario is correct, then several predictions follow from population genetic and evolutionary theory. First, the heritability (defined as V_A/V_T where V_A is the additive genetic variance, and V_T is the total phenotypic variance; Falconer 1981) of functional characteristics of the hyoid

should be less than that of other, less strongly selected characters such as maximum gape, head lift, etc. The extent of this difference in heritabilities will depend on the intensity of selection on these characters and their polygenic mutation rates (Lande 1976; Turelli 1984). However, as long as mutation rates are roughly equivalent in both sets of characters, strong selection should reduce the additive genetic variance. In addition, if morphological variation in hyoid elements is responsible for variation in functional output, one should find reduced morphometric variation, and lower heritability estimates, in these characters as well. This prediction may prove especially useful since studies of morphometric variation are far easier to accomplish than corresponding functional analyses.

A final prediction involves measuring either functional or morphological variability in several characters early and late in ontogeny in a single cohort of animals. If strong stabilizing or directional selection is actively maintaining reduced variation in hyoid or other strongly selected characters, then one should find a reduction in phenotypic variance (and possibly a shift in population mean) as a cohort is exposed to these selection pressures over time (Arnold 1986). This research program is especially important since it involves actively measuring fitness effects on functional characters in a natural situation.

An additional and extremely important consideration is the functional and genetic correlations of different sets of characters. As Lande (1979) and many subsequent authors have emphasized, selection does not operate on single characters, and the correlated responses to selection on one character may effect the mean and variance of others. This may be especially true for functional "complexes" of characters, like those associated with different aspects of the feeding mechanism during underwater prey capture. Although no definitive work on the correlations (genetic or phenotypic) of characters important in underwater suction feeding has been carried out, such correlations have been shown to be important components of variance in other studies. Several studies have demonstrated large phenotypic and genetic correlations between morphological and functional components of locomotion (Garland 1988; Tsuji et al. 1989), although metamorphosis can apparently decouple such correlations, at least in the one amphibian studied so far (Shaffer et al. 1991). In the most complete analysis of a vertebrate known to us, Cheverud (1982) showed that phenotypic correlations among characters within the same "functional set" were large compared to such character correlations between functional sets. Interestingly, this difference in correlation structure was not found at the genetic level, suggesting that the patterns may reflect selection shaping the multivariate character distribution rather than underlying genetic covariances.

Whether or not considerations such as the genetic correlations of characters are important in understanding the patterns of variation and di-

vergence among aquatic vertebrates remains almost completely unknown, as does the fundamental relationship between morphological and functional variation. However, on the basis of a single study, it is known that genetic correlations of morphometric characters in the head can be extremely high in ambystomatid salamanders (Shaffer 1986). Obviously, the generality of this result requires further empirical testing, but it at least raises the possibility that selection on one part of a functional complex may have cascading effects on other aspects of skull morphology (e.g., Emerson 1988).

Discussion of Concept 3
Environmental transitions affect kinematic and EMG patterns, but these changes are not a direct consequence of the biophysics of the media

The limited data available on the biophysical constraints associated with aquatic versus terrestrial feeding provide two primary results. First, while many aspects of motor control (as summarized by electromyograms) and kinematic output are highly conservative, they are not totally fixed. Just as suction-feeding fishes modulate muscle activity patterns with different prey types (Wainwright and Lauder 1986), salamanders modulate certain aspects of the feeding act depending on the environment. Second, this modulation is not explainable simply in terms of the physical properties of water and air as fluids with different densities and viscosities. Given this result, we are then faced with explaining the functional differences across environments that we do find. In particular, why is the duration of feeding longer in air, where resistance to movement is less than in water? Since the opposite trend follows from purely biophysical considerations (and, in a sense, might be considered a null hypothesis), there does seem to be a phenomenon in need of explanation.

Before these trends can be investigated, we need a much larger series of studies describing feeding on land and in the water. Our work on one population of *Ambystoma tigrinum* is the only quantitative assessment of kinematic and electromyographic variation across environments to date; future studies on air-breathing fishes (e.g., Liem 1985, 1987) and turtles (e.g., Bramble and Wake 1985) may reflect similar patterns. The study of other salamander families would greatly add to our understanding of the generality of these patterns, especially in the newts (Salamandridae), where the life history of many species necessitates metamorphosed adults returning to the water for long periods of time (Duellman and Trueb 1986; Reilly 1986). Quantitative assessments of kinematic patterns in the primitive salamander family Hynobiidae would also be of interest in testing the generality of this result across the phylogenetic diversity of urodeles. Additional work on turtles and crocodilians is also crucial, since some species can feed on land and in water (Gans 1969; Bramble and Wake 1985).

These taxa should be particularly useful in testing the tenet of Bramble and Wake (1985, 232) that "the major functional and biomechanical distinctions between aquatic and terrestrial feeding stem mainly from morphological differences reflecting adaptation to the physical properties of the two fluids," since the same morphology is used in both media.

The currently available data suggest at least two hypotheses concerning the impact of different physical environments on feeding mechanics. First, some muscle activity patterns may change as a result of differential recruitment of muscles in water and on land. Most electromyographic analyses consider only relatively crude measures of muscle activity (such as onset, offset, amplitude, and integrated activity), and the quantitative assessment of recruitment or power output of muscles (or parts of muscles) has not been a primary focus of most studies. The results of Lauder and Shaffer (1988), while useful as an indicator of environmental effects on feeding function in one species (*Ambystoma tigrinum*), need to be compared to other quantitative studies of feeding function across environments in other taxa.

Second, primarily terrestrial metamorphosed individuals may simply not perform well in the water, and may in fact be overcompensating for physical differences in the two media by truncating the strike early in the more viscous aquatic environment. If the pattern seen in *A. tigrinum* reflects poorly coordinated feeding activity in the water, then it should not constitute a general trend in other urodele taxa; additional comparative data on species that routinely feed in the water after metamorphosis will help resolve this issue.

Discussion of Concept 4
Unidirectional and bidirectional feeding systems are the two basic skull designs in aquatic vertebrates

The results obtained on the relative efficiency of unidirectional and bidirectional feeding mechanisms in salamanders suggest several hypotheses regarding the evolution of suction feeding in aquatic vertebrates. However, discussion of historical patterns of the transformation of feeding designs must, at this point, be highly speculative, as not even the rudimentary bases for a historical analysis are currently available.

To our knowledge, all secondarily aquatic lower vertebrates possess a bidirectional feeding system. The transformation to terrestrial life involves the loss of branchial arches and associated posterior openings to the gill cavity, and these openings are never regained with the transition back to the aquatic environment. Thus, there has been no ontogenetic or phylogenetic morphological transformation from a bidirectional to a unidirectional feeding design. The sole exception to this pattern appears to be nontransforming salamanders, in which lineages with a derived unidirec-

tional adult form have evolved from bidirectional ancestors. However, the paedomorphic mechanism by which this transformation occurs involves the truncation of development in the normal bidirectional adult, not a transformation from a bidirectional to unidirectional system (Shaffer 1984). The scarcity of bidirectional-to-unidirectional transformations indicates that the loss or severe reduction of the branchial apparatus and the acquisition of a terrestrial respiratory system (Wake 1982) may constrain the nature and extent of morphological reorganization that can occur in the posterior region of the head.

If, as indicated by current data (e.g., Lauder and Reilly 1988; Lauder and Shaffer 1986; Reilly and Lauder 1988b), unidirectional designs are more efficient than bidirectional systems in capturing prey (when the morphology of other head features is held constant), lineages that have reinvaded the aquatic environment either have suffered a competitive disadvantage in feeding or have evolved morphological and functional systems to circumvent the hydrodynamic disadvantages of bidirectional systems. (However, in areas with little competition for food, as in fish-free ponds of the central and western United States where adult *Ambystoma tigrinum* feed routinely [Miller and Larsen 1986; Reese 1969], there may be little selection for an increase in aquatic feeding efficiency.)

The hypothesis that morphological specializations have accumulated in secondarily aquatic lineages to mitigate the deleterious effects of a bidirectional feeding system could be tested with a corroborated phylogenetic hypothesis of a secondarily aquatic lineage with a concomitant functional analysis of the living taxa in the clade. Basal taxa, which generally possess plesiomorphic character states for that clade, would be predicted to possess reduced feeding performance when compared to more derived taxa. These derived taxa would be predicted to have acquired morphological and functional novelties that aid in circumventing the hydrodynamic constraints of bidirectional feeding systems. Examples of such potential novelties include forming a distensible posterior region of the buccal cavity to mitigate the increase in positive pressure, increasing the lever arm of the hyoid apparatus and the cross-sectional area of muscles depressing the hyoid (such as the rectus cervicis), and lengthening the buccal cavity.

Confidence that such observed changes were causally related to changing function of the feeding mechanism would be increased by two observations. The first is the occurrence of multiple lineages, each of which has independently become secondarily aquatic. If each lineage exhibits similar morphological modifications, and those changes are specifically those predicted on the basis of functional analyses of uni- and bidirectional feeding systems (Lauder and Shaffer 1986; Lauder and Reilly 1988), then this convergence suggests a causal link between changes in the morphology and feeding function. The second observation is an experimental test of the

significance of the morphological modifications. To demonstrate the causal basis of the phylogenetic correlation between the changes in morphology and feeding system design, experimental modification of derived clades in a secondarily aquatic lineage is needed. Reduced feeding performance is expected when morphological changes that increase the effectiveness of bidirectional feeding systems are eliminated experimentally.

Taken together, these phylogenetic and experimental functional data would make a strong argument for the constraints of the aquatic medium on the design of the vertebrate skull. Turtles would appear to provide the best possibilities for testing this hypothesis, but as yet few data are available.

CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

Throughout this chapter, we have emphasized certain directions for future research on the functional design of the aquatic vertebrate skull. In this final section, we discuss two new avenues that we feel will be critical in further investigating the evolution of the skull, and in linking morphological and functional studies with current theoretical work in evolutionary biology.

First, what are the links, both phenotypically and genetically, between form and function? There are three prerequisites for evolution by natural selection: there must be phenotypic variation in natural populations, it must be heritable, and variants must confer differential fitness. We have stressed the individual variation component of much of our functional work; it appears to be generally true that there is considerable variation among individuals in functional attributes. However, the extent to which this variation is based on additive genetic variation that can respond to selection, as opposed to learning or other environmentally induced variation, is completely unknown. In addition, the relationship between fine-scale morphometric variation, which often has a heritable basis, and functional output remains unknown. This is true both at the phenotypic and genetic levels; yet, understanding these relationships is crucial for modeling the evolution of functional characters.

To forge the links between functional, morphological, and population genetic levels of analysis requires a research strategy that is different from those generally employed by morphologists. Within-population sample sizes must be large if correlations between morphometric variation and functional output at the individual level are to be determined (Jayne and Bennett 1990; Shaffer et al. 1991). Furthermore, for an understanding of the genetic basis of the relationship between morphological variation and functional response, animals from a known pedigree must be available. While these are large orders, they are feasible for a wide range of aquatic vertebrates. Fishes and aquatic salamanders in particular have had suffi-

cient descriptive work done to document the accessibility of phenotypic variation at the individual level; the next phase requires the integration of these results with phenotypic and genetic analyses of population variation in morphology.

Second, the concept of constraints has been much discussed in the recent literature in evolutionary biology (e.g., Raup and Jablonski 1986; Maynard Smith et al. 1985). However, there are very few examples of precisely identified constraints on any morphological feature for which it is possible to say unequivocally why (in the causal sense) the proposed constraint has limited pathways of historical differentiation. The aquatic vertebrate skull provides an ideal system to study such constraints, several of which have been proposed in this chapter. Some strengths of the lower vertebrate skull as a model system are that: (1) a solid phylogenetic foundation exists for formulating and testing historical arguments, (2) the biomechanics of skull function is now reasonably well established, and (3) the discipline of biomechanics provides (through its use of physical laws and mechanical models) a method of precisely quantifying and defining performance curves. The aquatic vertebrate skull may be the first system in which the concept of a functional and historical constraint can be quantified and its effect on performance clearly documented.

These two avenues are by no means an exhaustive survey of future directions in the study of functional design of aquatic vertebrate skulls. However, they represent new paths targeted at integrating functional and comparative morphology into the mainstream of evolutionary biology. We feel that this integration is one of the key directions for future research, and we emphasize the importance of moving functional studies toward their proper place as a central discipline in evolutionary biology.

ACKNOWLEDGMENTS

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