

Functional morphology of the feeding mechanism in lower vertebrates

G. V. LAUDER

Department of Anatomy; University of Chicago; 1025 E. 57th St.; Chicago, IL 60637; USA

Summary

Suction feeding is the basic method of aquatic prey capture in teleostomes. The functional morphology of aquatic feeding was studied experimentally in several lower vertebrate clades (ambystomatid salamanders, lungfishes, and ray-finned fishes) to determine general characteristics of the feeding mechanism in lower vertebrates. Four basic features of the vertebrate feeding mechanism have been found in each of these clades and are hypothesized to be primitive for teleostomes: 1) elevation of the head by the epaxial muscles during the strike at the prey; 2) excursion of the hyoid occurring at or after maximum gape has been reached; 3) mediation of mandibular depression and mouth cavity volume change by the hyoid; and 4) resistance of the branchial apparatus (gill bars, rakers, filaments, and associated soft tissues) within the mouth cavity. The gill bars function to restrict posterior flow of water into the mouth.

Introduction

The origin of tetrapods from aquatic vertebrates has long been a key topic of interest in vertebrate biology. One aspect of the transition to land that has received considerable attention is the change in skull structure and function associated with the acquisition of a terrestrial feeding mechanism (PANCHEN, 1980; WESTOLL, 1938, 1943). Paleontological investigations have been instrumental in documenting structural transformations of the head and in providing a framework for speculation on changes in function that occurred during the transition to terrestrial life (SZARSKI, 1976; THOMSON, 1967, 1969). Another avenue of research into early tetrapod skull structure and function addresses the functional morphology of living lower vertebrate clades. Function of the head during feeding and respiration can be studied experimentally, and the phylogenetic distribution of both structural and functional aspects of the head determined.

In this paper I will summarize the results of research on the functional morphology of aquatic prey capture in aquatic ambystomatid salamanders, lungfishes, and ray-finned fishes. Experimental analyses of feeding using high-speed cinematography, electromyography, and pressure transducers have provided several novel insights into the function of the skull in lower vertebrates. An especially important result of these experiments is the conservatism in kinematic pattern and in hyoid and branchial function throughout lower vertebrates. Many basic features of skull function in early tetrapods can thus be proposed on the basis of an analysis of living taxa.

Material and Methods

Four techniques have provided considerable insight into the functional morphology of the head in lower vertebrates, and most of these have been considered in detail elsewhere. Here I will only indicate the types of approaches that have proven essential in analyses of skull function. (1) High-speed cinematography has been instrumental in providing a data base of kinematic patterns on primitive lower vertebrates (e.g., LAUDER, 1980a; LIEM, 1970), and in demonstrating the phase relationship of different movements. (2) Electromyography has allowed the determination of muscle activity patterns during feeding and respiration, and the relation of muscle activity to bone movement (BEMIS et al., 1983; GORNIK et al., 1982). During high-speed prey capture events, considerable overlap in activity occurs between antagonistic muscles: for example, there may be little difference between the onset of electrical activity in the jaw adductors and the mouth opening muscles. Such results make predicting muscle activity from films and preserved specimens difficult. Recent work has emphasized that the amplitude of the electromyogram may be an important variable to consider in understanding the function of high-speed feeding mechanisms (GANS and GORNIK, 1982). (3) Pressure transducers have been used to measure pressure within the mouth cavity of fishes and salamanders, and these measurements play a key role in defining the branchial apparatus as a resistance within the mouth cavity. Polyethylene cannulae are implanted in the buccal and opercular cavities and these tubes are then filled with fluid. Earlier research used transducers with a relatively low frequency response (about 80 Hz), while recent results have been obtained with high-frequency catheter-tip transducers that are threaded down the implanted cannulae. All pressures reported in this paper (e.g. Fig. 2) were recorded with Millar PR-249 transducers with an outer catheter diameter of 0.7 mm. Relatively little difference has been found between the recordings obtained with the two types of transducers. (4) Impedance electrodes can be used to circumvent a significant difficulty in many analyses of aquatic prey capture by transducing distances between internal structures in the head. Light cinematography provides no information on the movement of gill arches, and even x-ray cinematography does not have the resolution to accurately measure small (1 to 2 mm) and rapidly changing distances between internal structures. Impedance is measured between two electrodes implanted on adjacent structures. If there is conducting medium between the electrodes, then the impedance between the tips will be a function of the distance between them. Changes in impedance are then amplified and displayed simultaneously with electromyograms and pressure recordings. The distances between the gill bars shown in figure 2 were recorded with a Biocom impedance converter.

All kinematic patterns described here were measured from films of unrestrained animals taken at 200 frames per second. All physiological measurements were recorded on a Bell and Howell 4020A FM tape recorder at 37.5 cm/sec and played back at a speed of 4.7 cm/sec on a Gould 260 chart recorder.

Results and Discussion

1. Ray-finned fishes

One of the most striking features of the feeding mechanism in ray-finned fishes is the large number of bones and muscles and the consequent complexity of motion that is displayed during feeding and respiration. As noted by Richard OWEN (1854), "It may well be conceived, then, that more bones enter into the formation of the skull in fishes than in any other animals; and the composition of this skull has been rightly deemed the most

difficult problem in Comparative Anatomy. «It is truly remarkable», writes the gifted Oken, to whom we owe the first clue to its solution, «what it costs to solve any one problem in Philosophical Anatomy. Without knowing the what, the how, and the why, one may stand, not for hours or days, but weeks, before a fish's skull, and our contemplation will be little more than a vacant stare at its complex stalactitic form».

The basic action of the muscles and bones in the head during feeding is to produce a change in volume within the mouth cavity. As the volume inside the mouth increases, water is drawn from in front of the head. Subsequently, as the mouth begins to close, this water passes over the gills and out the back of the head. The most fundamental aspect of the feeding mechanism is the segregation of the volume inside the head into two functionally and anatomically distinct areas: the buccal cavity anteriorly, and the paired opercular cavities posteriorly. The structures that separate the buccal and opercular cavities inside the head are the gill bars, gill rakers, and soft tissues on the bars. In many fishes the gill rakers interdigitate on adjacent arches so that as the gill bars are adducted, a rigid curtain is formed separating the opercular and buccal cavities (LAUDER, 1983). From an anatomical perspective, the branchial apparatus is capable of functioning as a dynamic resistance within the mouth cavity by changing the distance between the gill bars during prey capture. Experimental evidence for this will be presented below.

In addition to the anatomical segregation of the buccal and opercular cavities, these two areas of the head display different patterns of movement during feeding. Many studies over the past ten years have shown a definite phase relationship between the major bone movements of the head, and the overall pattern of movement is remarkably consistent even in taxa as phylogenetically diverse as the bowfin (*Amia*), gar (*Lepisosteus*), trout (*Salmo*) and sunfish (*Lepomis*). As discussed in more detail elsewhere (LAUDER, 1982), there is an anterior to posterior delay in peak excursion of major functional components in the head. Thus, mouth opening reaches its peak first, followed by hyoid depression, and finally by lateral movement of the operculum. Opercular abduction commonly may not begin until the mouth has begun to close.

Of all the functional components of the head, the hyoid apparatus plays the major role in changing the volume inside the mouth and thus creating suction. Two aspects of hyoid function are especially important for understanding the mechanism of aquatic prey capture in lower vertebrates. (1) The muscles controlling movement of the hyoid during mouth opening, the sternohyoideus and hypaxialis, have larger physiological cross-sections than other head muscles, and are coactivated as the mouth opens. These muscles also possess excellent mechanical advantage compared to other muscles (such as the levator arcus palatini) that function to expand the mouth cavity laterally. These attributes, combined with the fact that the hyoid apparatus produces a larger change in mouth cavity volume than other components of the head, mean that the hyoid can be regarded as the dominant effector of mouth cavity volume change. (2) In primitive members of all lower vertebrate lineages, a thick ligament extends from the ceratohyal anteroventrally to the mandible. This ligament transmits posterodorsal movement of the hyoid to the lower jaw and results in mandibular depression (LAUDER, 1980a, b). It is important to emphasize that this mechanism is found consistently in ray-finned fishes, coelacanth, lungfishes, and salamanders. In the primitive actinopterygian fishes *Polypterus* and *Lepisosteus* LAUDER (1980a) showed that the hyoid and the ligament from the hyoid to the mandible provide the only mechanism of mandibular depression. Thus the hyoid also plays a critical role in opening the mouth.

Research on primitive ray-finned fishes has shown that several aspects of the feeding mechanism are probably primitive for this clade, and has demonstrated that even in fishes as highly specialized as *Lepisosteus*, the general components of the lower vertebrate feeding

pattern may be discerned. The general pattern may be summarized as follows: (1) Dorsal and ventral body musculature is important in the process of prey capture. Both hyoid depression and lifting of the head at the strike are largely the consequence of contraction of the large body muscles. (2) The hyoid apparatus is the dominant mediator of both mandibular depression and mouth cavity volume change. (3) There is an anterior to posterior sequence of peak excursion of the mouth, hyoid, and operculum.

Important insights into the mechanism of prey capture in fishes have been obtained by direct measurement of the pressures within the mouth cavity. As the mouth opens, the pressure in both the buccal and opercular cavities drops below ambient. While the first pressure measurements made by ALEXANDER (1969, 1970) confirmed that large negative pressures do in fact occur, several surprising results have since been obtained from simultaneous measurement of buccal and opercular cavity pressures during prey capture. Chief among these is the large pressure differential across the branchial apparatus. Work on *Lepomis* shows that buccal cavity pressure may reach negative values of $-650 \text{ cm H}_2\text{O}$ below ambient, while opercular pressure peaks at $-150 \text{ cm H}_2\text{O}$. There is a consistent ratio of 3–5:1 for buccal to opercular cavity pressures. In addition, the negative phase of the

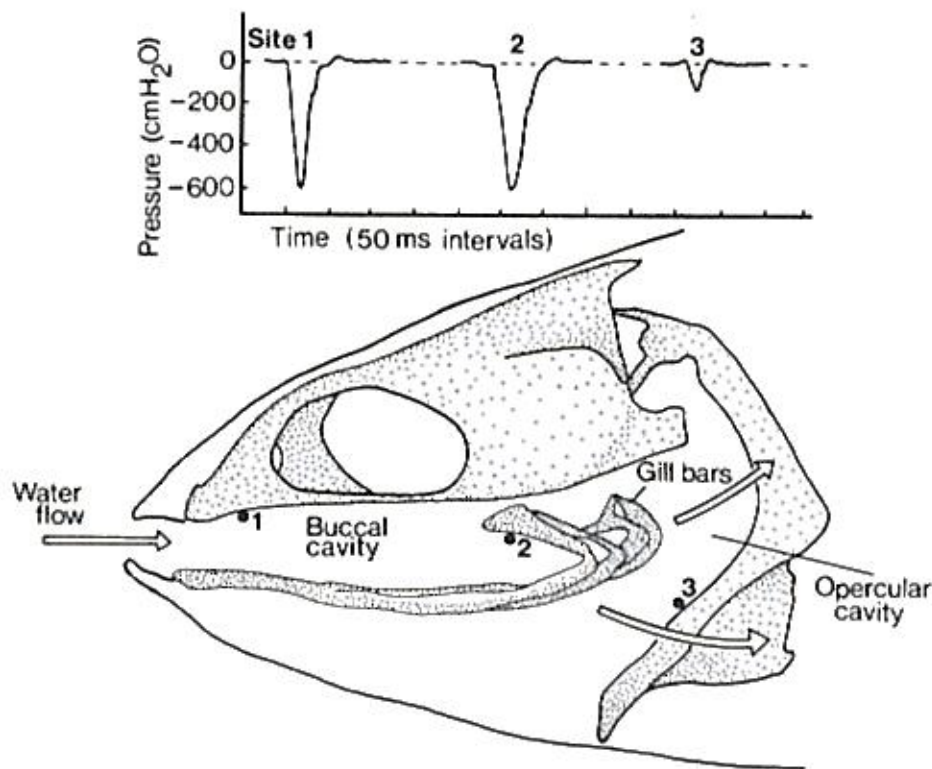


Fig. 1. Schematic diagram indicating the pattern of pressure change at three sites within the mouth cavity of a percomorph fish during prey capture. Pressure traces and morphology are based on centrarchid sunfishes. Note that the pressures within the buccal cavity (at both sites) are nearly five times more negative than the pressure in the opercular cavity. The large pressure differential across the gill apparatus is one indication that the gill bars and supports function as a resistance within the mouth cavity during feeding.

opercular pressure waveform is delayed relative to the buccal so that in the first 5–50 ms of prey capture, a pressure differential of up to 200 cm H₂O occurs across the gill bars. Representative pressure traces from the buccal and opercular cavities are shown in relation to basic anatomical features of the head in a percomorph fish in Fig. 1, and simultaneous pressure and electromyographic traces from *Lepomis* are shown in Fig. 2A. Pressures recorded immediately anterior to the gill bars are very similar to those in the front of the buccal cavity and do not differ significantly in magnitude (LAUDER, 1980c; Fig. 1).

The existence of a large differential pressure across the gill bars suggests that they may function as a dynamic resistance within the mouth cavity during feeding. As the mouth opens initially, the sides of the head are adducted and oppose the gill bars. Resistance is high at this time. As peak gape is reached, the gill bars begin to abduct, opening a connection between the buccal and opercular cavities and allowing water to flow posteriorly and out of the gill cavity. The hypothesized presence of a gill resistance was tested in two ways, and in both cases it was corroborated. First, LAUDER (1983) implanted small plastic spacing elements separating the gill bars and preventing their adduction (and formation of a gill resistance) early in the strike. This resulted in a marked decrease in the differential pressure across the gills, and in several experiments abolished it completely. Secondly, the distance between the gill bars was transduced directly by small impedance electrodes implanted in adjacent gill bars. The results of one such experiment are shown in Fig. 2A. Note that as the buccal and opercular cavity pressures drop, the gill bars are adducted and that only when buccal pressure begins to return to ambient do the gill bars begin to abduct. The abducted condition is then maintained well after the mouth has closed on the prey. These results conform well to studies of head kinematics, and establish unequivocally the role of the branchial apparatus as a resistance within the mouth cavity of fishes feeding by high-speed suction.

2. Lungfishes

Although lungfishes are an important clade for discussions of the origin of tetrapod feeding mechanisms and analyses of patterns of lower vertebrate evolution, it is remarkable that this clade has not been the subject of an experimental analysis of feeding mechanics. It is of considerable interest to discover if lungfishes display the same general pattern of head kinematics as other lower vertebrates and to analyse the effect of the salient specializations in the lungfish skull, such as the unique jaw suspension and the presence of tooth plates, on the feeding mechanism.

Research currently in progress (BEMIS and LAUDER, 1983; in preparation) on the feeding mechanism of *Lepidosiren* has demonstrated that suction feeding is used to capture prey, and that considerable variability exists in the speed of the strike within individuals and between feeding events. The time from the start of mouth opening to mouth closing may vary from 20 ms to nearly a second. Kinematic analyses of suction feeding show a similar pattern of head movement to that of ray-finned fishes. As in actinopterygians, both cranial elevation and mandibular depression contribute to the gape, and hyoid depression reaches its peak value after peak gape. The mean values for relatively slow feedings by small *Lepidosiren* are: 0.30 sec average strike duration, 0.16 sec average time to peak cranial elevation, 0.19 sec average time to peak gape, and 0.27 sec average time to peak hyoid depression (BEMIS and LAUDER, 1983). The phase relationships of head movements thus are comparable to those of ray-finned fishes.

Electromyographic analysis also reveals a considerable range of variation in muscle activity patterns depending on the speed of the strike. During very rapid feedings, both the

sternohyoideus and depressor mandibulae depress the mandible, and the adductor mandibulae become active within 30 ms of the mouth opening muscles. In slow feedings, however, the depressor mandibulae may be the only muscle active, although commonly the adductor mandibulae does close the jaws on a prey item. Other muscles such as the sternohyoideus, interhyoideus, and epaxialis are not active in all strikes.

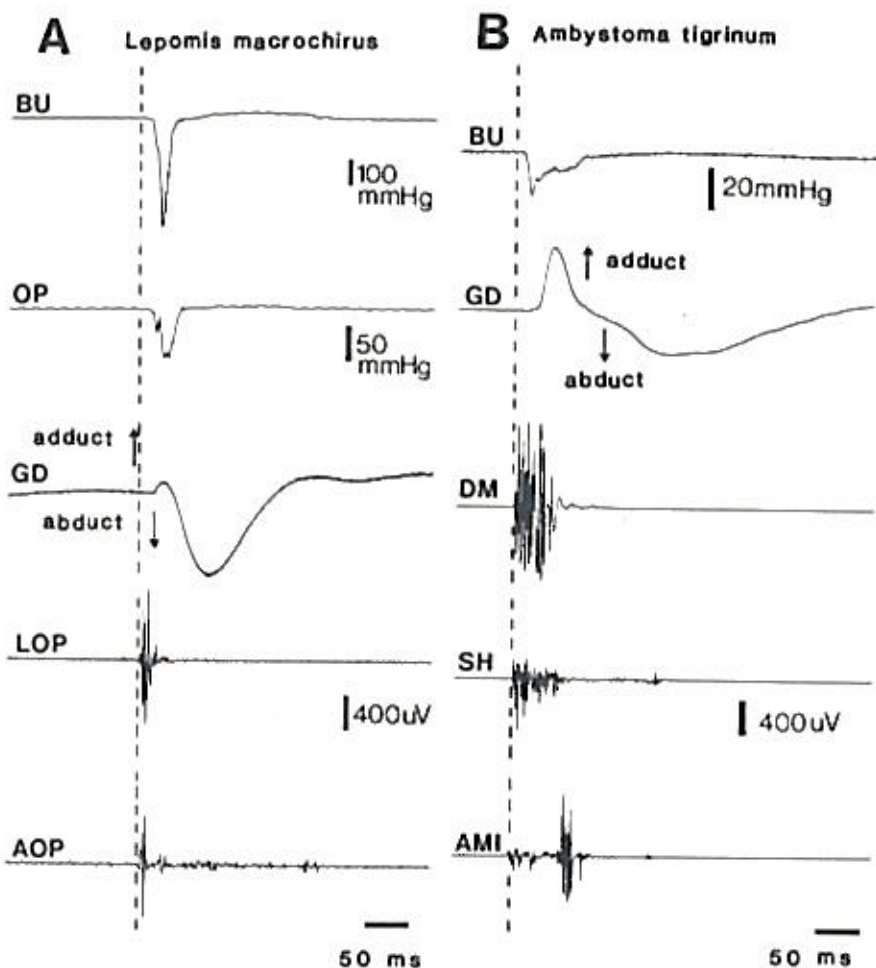


Fig. 2. Simultaneous recordings of cranial muscle activity, mouth cavity pressure and gill bar distance (see text for a discussion of experimental techniques) in (A) *Lepomis macrochirus*, and (B) *Ambystoma tigrinum*. Buccal pressure is much less negative in *Ambystoma*. Note the different pressure magnitudes in the buccal and opercular cavities in *Lepomis*. In both species, gill bar distance clearly reveals an initial adduction phase as the mouth opens, and subsequent abduction as the jaws close. The abducted condition is maintained for some time after the mouth has closed.

Abbreviations: AMI, adductor mandibulae internus muscle; AOP, adductor operculi muscle; BU, buccal cavity pressure; DM, depressor mandibulae muscle; GD, gill bar distance; LOP, levator operculi muscle; OP, opercular cavity pressure; SH, sternohyoideus muscle (= rectus cervicis).

Lungfishes possess two distinct mechanical systems that mediate mandibular depression. (1) The hyoid apparatus exerts a posterodorsal force on the mandibulohyoid ligament that causes the mandible to move ventrally. The muscular driving force for this mechanism is the sternohyoideus and hypaxial muscles. This is the homologous system to that of ray-finned fishes and coelacanth (LAUDER, 1980b). The morphological requisite for this mechanism, the mandibulohyoid ligament, is present in all lower vertebrate lineages. (2) A well-developed depressor mandibulae muscle is present that inserts on the lower jaw. Electromyographic analysis (BEMIS and LAUDER, in preparation) clearly shows that electrical activity in this muscle is correlated with mandibular depression. The depressor mandibulae of dipnoans is innervated by the facial nerve and is derived embryologically from the constrictor muscles of the hyoid arch. In these respects, it is similar to the depressor mandibulae of salamanders and would seem to be homologous.

3. Aquatic salamanders

Aquatic salamanders are of special interest for the analysis of lower vertebrate feeding mechanisms because (1) they retain many primitive features of the cranial musculature found in lungfishes, coelacanth, and ray-finned fishes, (2) their skull is of a sufficiently different design from that of fishes that salamanders are extremely useful experimental subjects on which to test hypotheses about the function of certain components of the head, and (3) as tetrapods, they provide important comparative data on the generality of patterns in the feeding mechanism elucidated for non-tetrapod gnathostomes. With virtually the sole exception of the early work of Matthes (1934) who investigated suction feeding in aquatic salamanders, little is known about the mechanics of the skull during suction feeding and the patterns of pressure change and muscle activity associated with aquatic prey capture.

SHAFFER and LAUDER (1984) have studied the patterns of head movement in three species of *Ambystoma* during suction feeding. Their data show considerable similarity to the results described above for ray-finned fishes, although the timing of hyoid depression differs somewhat. Cranial elevation is an important event early in the strike and may reach a maximum angle of nearly 50°. Peak gape is reached in a mean time of from 34 to 47 ms in the three species, while the total time of the strike ranged from a mean of 70 ms for *Ambystoma mexicanum* to 88 ms for *A. dumerilii*. Maximum hyoid depression occurs earlier in *Ambystoma* than in any of the ray-finned fishes or lungfishes that have been investigated to date: the mean time to peak hyoid depression varied from 5 ms before peak gape to 6 ms after peak gape. From the limited data available, then, it appears that hyoid depression in ambystomatid salamanders is shifted earlier in the strike and occurs near peak gape, in contrast to the greater delay in ventral hyoid movement that has been recorded in other lower vertebrates. The earlier depression of the hyoid may be related to the lack of a mechanism for the lateral expansion of the buccal cavity and the absence of posterior bony elements in the head such as the opercular series and branchiostegal apparatus of fishes.

The two mechanisms of mandibular depression noted above for lungfishes, the hyoid and the depressor mandibulae, are both found in salamanders. A large mandibulohyoid ligament occurs in ambystomatid salamanders and serves the same function as in lungfishes, coelacanth, and ray-finned fishes. This ligament is also present in terrestrial plethodontid salamanders (LOMBARD and WAKE, 1977), and it appears to be a fundamental component of the feeding mechanism in all lower vertebrate clades.

Electromyographic analysis of muscle activity during prey capture in aquatic ambysto-

matid salamanders reveals extensive synchrony in the onset of the mouth opening muscles (depressor mandibulae and sternohyoideus) and the two mandibular adductors (Fig. 2B). Both the internal and external adductor mandibulae muscles become active within 4 ms of the depressor mandibulae. Usually, there is a brief (5–15 ms) silent period in the adductors after the initial activity which is then followed by a second larger amplitude burst to close the mouth.

Electromyography confirms that the epaxial muscles and sternohyoideus are active at the onset of mouth opening to elevate the cranium on the vertebral column and to move the hyoid apparatus posteriorly and ventrally.

The major difference in the basic design of the feeding mechanism in salamanders and ray-finned fishes is the lack of an opercular cavity in salamanders. In most aquatic salamanders, only fleshy posterior extensions of each gill arch occur and there are no bony elements in the posterior region of the head that can play a role analogous to the opercular series of fishes. While the operculum has been suggested to play a role in regulating the pattern of water flow through the mouth cavity of teleost fishes (MULLER et al., 1982; LIEM, 1978), such a function cannot be present in aquatic salamanders. On the other hand, if the gill bars, rakers, and soft tissues form a dynamic resistance to water flow within the mouth cavity as in fishes, then flow will be prevented from entering the buccal cavity posteriorly by the gill resistance. One would predict that if there were no «valve» at the back of the head, then during suction feeding water would be drawn into the mouth both anteriorly and posteriorly. This would cause a significant reduction in the effectiveness of prey capture, as both the volume and velocity of fluid in front of the mouth would be reduced.

The results from one experiment on *Ambystoma tigrinum* in which buccal pressure, cranial muscle activity, and gill bar distance were simultaneously measured is shown in Fig. 2B. Buccal pressure begins to drop below ambient 10 ms after activity in the mouth opening muscles, and reaches a peak value of -50 cm H₂O. In contrast to results from ray-finned fishes, buccal pressure then increases and plateaus at slightly less than ambient pressure before returning to its resting value (Fig. 2B). Gill bar distance during suction feeding (Fig. 2B) shows surprising similarity to ray-finned fishes. A clear initial adduction is present as the mouth opens and pressure drops inside the mouth. Then as buccal pressure increases, the gill bars begin to abduct and allow water to flow out posteriorly. Activity in the adductor mandibulae is high at this point and the jaws are closing.

These results clearly indicate the importance of the branchial apparatus as a resistance within the mouth during suction feeding. This resistance changes with time so that as the mouth opens and water begins to flow in, gill resistance is high. As the jaws close on the prey, gill resistance is low as the bars have abducted and slits several millimeters wide have opened between adjacent gill bars. Thus, in both salamanders and ray-finned fishes, unequivocal experimental data now exist to support the role of the branchial apparatus as a resistance.

Conclusions

In this overview of the feeding mechanism in lower vertebrates, several aspects of the process of prey capture stand out as common to the clades studied experimentally. First, suction feeding appears to be the basic teleostome feeding behavior. The capture of prey by filter feeding or by biting pieces off of larger prey are secondary specializations to phylogenetically primitive suction feeding. Secondly, the hyoid apparatus is a fundamental component of the feeding mechanism and mediates mandibular depression and volume

change within the mouth cavity. Thirdly, the body muscles, especially those inserting on the skull and pectoral girdle (epaxialis and hypaxialis) are important in producing of mouth opening and hyoid depression. Fourthly, the branchial apparatus plays an important role as a resistance within the mouth cavity, preventing water inflow posteriorly. Functionally, the buccal and opercular cavities play different roles in the suction feeding mechanism. Finally, there is a consistent phase relationship between movements of the anterior and posterior head elements such that posterior elements reach their peak excursion later than anterior ones.

It is important to emphasize that there is still an inadequate comparative basis for the general patterns of lower vertebrate feeding proposed in this paper. In particular, our understanding of the mechanism of aquatic prey capture in tetrapods is still sketchy, and considerably more work is needed on all groups of amphibians. Research on aquatic feeding in reptiles, especially turtles, will provide some important insights into the process of suction feeding because of the unidirectional flow system in which water drawn into the mouth during prey capture is expelled anteriorly after the mouth has closed (for preliminary reports on turtles see BRAMBLE, 1978; WEISGRAM, 1982). Within non-tetrapod teleostomes, elasmobranchiomorphs remain the last major clade for which we have almost no experimental data on prey capture. If current views of the phylogenetic patterns and generality of feeding mechanisms in lower vertebrates are to be tested and critically evaluated, then it is essential to broaden the comparative basis of investigation.

Acknowledgements

I am indebted to Dr. W. Bemis for comments on a draft of this manuscript, and to Drs. Bemis and H. B. Shaffer for their collaborative work on lungfishes and salamanders. Preparation of this manuscript and the new research reported herein was supported by NSF grants DEB 81-15048 and PCM 81-21649.

References

- Alexander, R. McN.: Mechanics of the feeding action of a cyprinid fish. - *J. Zool. Lond.* 159, 1-15 (1969).
- Alexander, R. McN.: Mechanics of the feeding action of various teleost fishes. - *J. Zool. Lond.* 162, 145-156 (1970).
- Bemis, W.E., Schwenk, K., Wake, M.: Morphology and function of the feeding apparatus in *Dermophis mexicanus* (Amphibia: Gymnophiona). - *Zool. J. Linn. Soc. Lond.* 77, 75-96 (1983).
- Bemis, W., Lauder, G.V.: Kinematics and electromyography of feeding in the lungfish *Lepidosiren paradoxa*. - *Amer. Zool.* (23, 1010).
- Bramble, D.W.: Functional analysis of underwater feeding in the snapping turtle. - *Amer. Zool.* 18, 623 (1978).
- Gans, C., Gorniak, G.: Functional morphology of lingual protrusion in marine toads (*Bufo marinus*). - *Amer. J. Anat.* 163, 195-222 (1982).
- Gorniak, G.C., Rosenberg, H.I., Gans, C.: Mastication in the tuatara, *Sphenodon punctatus* (Reptilia: Rhynchocephalia): structure and activity of the motor system. - *J. Morph.* 171, 321-353 (1982).
- Lauder, G.V.: Evolution of the feeding mechanism in primitive actinopterygian fishes: a functional anatomical analysis of *Polypterus*, *Lepisosteus*, and *Amia*. - *J. Morph.* 163, 283-317 (1980a).

- Lauder, G.V.: The role of the hyoid apparatus in the feeding mechanism of the coelacanth *Latimeria chalumnae*. – *Copeia* 1980, 1–9 (1980b).
- Lauder, G.V.: The suction feeding mechanism in sunfishes (*Lepomis*): an experimental analysis. – *J. Exp. Biol.* 88, 49–72 (1980c).
- Lauder, G.V.: Patterns of evolution in the feeding mechanism of actinopterygian fishes. – *Amer. Zool.* 22, 275–285 (1982).
- Lauder, G.V.: Prey capture hydrodynamics in fishes: experimental tests of two models. – *J. Exp. Biol.* 104, 1–13 (1983).
- Liem, K.F.: Comparative functional anatomy of the Nandidae (Pisces: Teleostei). – *Fieldiana Zoology* 56, 1–166 (1970).
- Liem, K.F.: Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes I. Piscivores. – *J. Morph.* 158, 323–360 (1978).
- Lombard, R.E., Wake, D.B.: Tongue evolution in the lungless salamanders, Family Plethodontidae. II. Function and evolutionary diversity. – *J. Morph.* 153, 39–80 (1977).
- Matthes, E.: Bau und Funktion der Lippensaume wasserlebender Urodelen. – *Z. Morph. Okol. Tiere*, 28, 155–169 (1934).
- Muller, M., Osse, J., Verhagen, J.: A quantitative hydrodynamical model of suction feeding in fish. – *J. Theor. Biol.* 95, 49–79 (1982).
- Owen, R.: The principal forms of the skeleton and teeth. – Blanchard and Lea (Philadelphia 1854).
- Panchen, A.L. (Ed.): The terrestrial environment and the origin of land vertebrates. – Academic Press (New York 1980).
- Shaffer, H.B., Lauder, G.V.: Aquatic prey capture in ambystomatid salamanders: patterns of variation in muscle activity. *J. Morph.* (in press) (1985).
- Szarski, H.: Sarcopterygii and the origin of tetrapods. In: *Major Patterns in Vertebrate Evolution*, 517–540. Ed.: Hecht, M.K.; Plenum Publishers (New York, 1976).
- Thomson, K.S.: Mechanisms of intracranial kinetics in fossil rhipidistian fishes (Crossopterygii) and their relatives. – *J. Linn. Soc. Lond.* 178, 223–253 (1967).
- Thomson, K.S.: The biology of lobe-finned fishes. – *Biol. Rev.* 44, 91–154 (1969).
- Weisgram, J.: *Claudius angustatus* (Kinosternidae) – Nahrungsaufnahme. – *Wiss. Film Fr.* 28, 28–35 (1982).
- Westoll, T.S.: Ancestry of tetrapods. – *Nature* 141, 127–128 (1938).
- Westoll, T.S.: The origin of tetrapods. – *Biol. Rev.* 18, 78–89 (1943).