

Amphibian Feeding Behavior: Comparative Biomechanics and Evolution

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1 Introduction

The clade Amphibia is critical for our understanding of vertebrate evolution. Because of their position as a basal lineage of tetrapods, nearly all aspects of amphibian biology are of special interest to those interested in the origin of terrestrial life and in the morphological, physiological, ecological, and behavioral changes involved in aquatic to terrestrial transitions. In addition, amphibian taxa illustrate with particular clarity the phenomenon of metamorphosis, allowing the experimental study of aquatic-to-terrestrial transitions on a single individual during ontogeny. Although phylogenetic relationships among the three extant amphibian clades (and among fossil amphibian taxa) are still a matter of debate (Bolt 1977; Carroll and Holmes 1980; Duellman and

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Trueb 1986; Trueb and Cloutier 1991), the relevance of amphibian clades to problems in vertebrate biology is not at issue. Extant amphibian lineages, because of their phylogenetic position near the base of the tetrapod radiation and because of the mosaic nature of character distribution in these taxa (many amphibian taxa retain large numbers of primitive features in the musculoskeletal system, while at the same time displaying numerous derived characteristics), are prime candidates for comparisons to both fish and amniote clades.

One key aspect of a transition (evolutionary or ontogenetic) between an aquatic and a terrestrial environment is the problem of obtaining food. How do animals manage to modify behavioral, morphological, or physiological patterns associated with food acquisition to permit function in both environments? Extant amphibian clades allow this question to be addressed from a number of different perspectives. First, individual amphibians may undergo an ontogenetic transformation from an aquatic feeding mode as a larva to a terrestrial feeding mode after metamorphosis. This provides an experimental opportunity to study directly form and function in the feeding mechanism across environments. Second, some terrestrial amphibians may be induced to feed in the water, providing an opportunity to examine how well a terrestrial feeding mechanism functions biomechanically in an aquatic environment. Third, the three major extant amphibian clades are widely divergent in their cranial morphology, providing an opportunity to examine how different lineages of amphibians have (perhaps independently) solved biomechanical problems (such as terrestrial prey capture using tongue projection). Fourth, many features of larval amphibian feeding mechanisms are very similar to those of outgroup clades such as lungfishes and ray-finned fishes (Actinopterygii), facilitating evolutionary analyses via comparisons of homologous morphologies, functions, and behaviors.

In this chapter, our aim is to summarize the current state of knowledge about amphibian feeding biomechanics, with the general objective of placing the biomechanics of amphibian feeding within the framework of vertebrate evolution. Our specific goals are first, to review the biomechanics of prey capture in outgroup clades to provide historical and phylogenetic background; second, to analyze the biomechanics of feeding in the two extant amphibian lineages for which there are the most complete data (salamanders and frogs); third, to compare feeding mechanisms in fish, amphibian and amniote taxa to search for general historical patterns and relationships; finally, to assess needed future directions for research in the functional morphology of amphibian feeding.

2 Overview of Feeding Mechanics in Fishes

2.1 Initial Prey Capture

We begin our consideration of amphibian feeding biomechanics with an overview of functional patterns that have been established for outgroup clades such as lungfishes and ray-finned fishes. Analyses of tetrapod feeding mechanics have

often proceeded without considering the functional patterns present in outgroup taxa. Biomechanical analyses benefit in many ways from an historical perspective on the evolution of function (Gans 1980; Lauder 1986b, 1990, 1991), and aquatic feeding systems in fishes have much to teach us about both amphibian and amniote feeding patterns. If models of tetrapod feeding behavior are to be properly generated and interpreted, then a firm phylogenetic foundation for hypothesized functional patterns is essential.

A key conclusion from past research on the functional morphology of the feeding mechanism in fishes is that, despite considerable specialization among lineages of fishes [consider the differences between a lungfish (Dipnoi) and a largemouth bass (Actinopterygii: Centrarchidae)], there are many common functional patterns that are of general occurrence (Lauder 1985a, b). This is a fortunate result because it allows us to identify several primitive biomechanical features of fish feeding systems and then to use these as a basis for evaluating amphibian biomechanics. These features are hypothesized to be primitive for tetrapod feeding systems (Lauder 1985a; Reilly and Lauder 1990a; Lauder and Shaffer 1993).

Figure 1 summarizes the pattern of muscle activity and gape and hyoid kinematics common to feeding mechanisms in many species of ray-finned fishes. Similar functional patterns have been noted in lungfishes (Bemis and Lauder

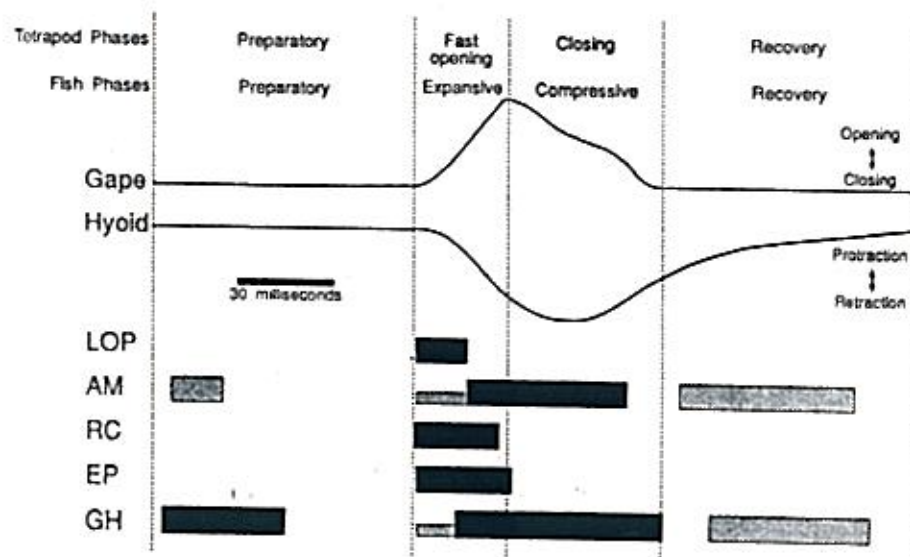


Fig. 1. Generalized feeding pattern for actinopterygian fish and lungfish, hypothesized to represent the primitive condition for tetrapods. The distinct kinematic phases of the strike are labeled at the top of the figure. Black bars indicate muscle activity that is consistently present, gray bars indicate frequent activity, and changes in height of the bars show large-scale changes in the amplitude of muscle activity. AM Adductor mandibulae; EP epaxial; GH geniohyoidus; LOP levator operculi; RC rectus cervicis

1986; Bemis 1987). Although experimental data are currently not available on coelacanth, mechanical linkages hypothesized from anatomical analysis (Lauder 1980a) also suggest that similar patterns existed in the Actinistia.

The process of initial prey capture in fishes was formerly divided into four phases: preparatory, expansive, compressive, and recovery (Lauder 1985a). These terms are similar to those proposed for amphibian (and some amniote) clades: preparatory, fast opening, closing, and recovery, respectively. To be consistent, we will use the tetrapod phase names shown at the top of Fig. 1 throughout this work (see also Reilly and Lauder 1990a). Ray-finned fishes and lungfishes lack a slow opening phase (which is present in many amniote taxa) and thus this phase is not discussed here. Most fishes also lack a preparatory phase. When the preparatory phase is present, the buccal cavity is compressed to force out water and reduce intraoral volume. Activity of the jaw adductor muscles and ventral throat muscles (such as the geniohyoideus) is often seen during this phase.

The preparatory phase ends and the fast opening phase begins with the onset of mouth opening. As the gape increases rapidly at the onset of the strike, the hyoid arch moves posteroventrally from its initial protracted position (Fig. 1). Three main muscles effect these actions: the levator operculi, epaxialis, and rectus cervicis (= sternohyoideus in the ichthyological literature). The rectus cervicis is a major muscle of the fast opening phase and acts to (1) increase the gape via ligamentous connections between the hyoid and mandibular arches, (2) increase mouth cavity volume by moving the floor of the mouth ventrally, and (3) increase mouth cavity volume by forcing the sides of the head (suspensoria) laterally. The epaxialis and levator operculi muscles assist mouth opening by elevating the skull and depressing the mandible.

The fast opening phase ends and the closing phase begins at maximum gape. The closing phase is generally of slightly longer duration than the opening phase, although there is considerable variability among feeding events on a single prey type, among prey types, among individuals, and among species. Closing of the mouth is initiated by activity in the adductor mandibulae muscles. Adductor muscle activity may begin at a low level with the onset of the mouth opening muscles, indicating that antagonistic muscles are synchronously activated with the onset of the fast opening phase (Lauder 1980b, 1983b, 1985a). Peak adductor muscle activity does, however, occur after peak activity in the mouth opening muscles such as the levator operculi and rectus cervicis. During the closing phase, the hyoid reaches peak posteroventral movement due to the action of the rectus cervicis muscle (Fig. 1). The closing phase ends as the gape reaches its minimum value. If the jaws have closed on a prey item, then gape at the end of the closing phase will be greater than the initial gape.

A consistent feature of the timing of gape and hyoid kinematic profiles during initial prey capture in fishes is the delay in peak hyoid excursion relative to peak gape: the hyoid reaches its maximum posteroventral excursion after maximum gape has been reached. In most fishes, lateral opercular expansion reaches its peak after the hyoid, providing an anteroposterior timing in peak excursions:

first maximum gape, then maximum hyoid retraction, and finally maximal opercular abduction.

The fast opening and closing phases together constitute the gape cycle, which in fishes is roughly bell-shaped: no gape cycles have been published which show a plateau during the fast opening phase.

The recovery phase is that phase during which the gape remains relatively constant and the hyoid moves anterodorsally due to synchronous activity in the jaw adductor muscles and ventral mouth musculature such as the geniohyoideus (Fig. 1). The jaw adductor muscles act to stabilize the mandible so that the geniohyoideus muscle, with its origin at the mandibular symphysis, can act to protract the hyoid. Completion of the recovery phase may take up to several seconds, and is frequently interrupted by the onset of transport sequences (or buccal manipulation events) to move prey posteriorly in the oral cavity.

The function of mouth cavity expansion and the role of cranial muscle activity is to cause a pressure reduction within the oral cavity which draws water and prey into the mouth. This mode of feeding in fishes is called suction feeding because of the negative (or "suction") pressure generated within the mouth cavity. Experimental measurement of these negative pressures (Lauder 1980c, d, 1983a, 1986a; Liem 1980) has established several features of the suction feeding mechanism. First, pressure measurements made simultaneously both anterior and posterior to the gill bars (which are composed of hypobranchial, ceratobranchial, and epibranchial elements supporting the gill filaments) in sunfishes (Centrarchidae) have demonstrated that there is a clear pressure differential across the gill bars, with the pressure anteriorly in the mouth two to six times more negative than the pressure in the opercular cavity. Second, the timing of gill bar, opercular, and hyoid movement effects the predominantly unidirectional flow of water through the mouth cavity (a small reverse flow from the opercular into the buccal cavity may also occur at the onset of the fast opening phase). Third, gill bar adduction is timed so that the gill bars are maximally adducted near the time of peak negative pressure, preventing significant water flow from posterior to anterior into the buccal cavity. Overall, the process of initial prey capture by suction feeding involves the initiation of a rapid (and unsteady) flow of water into the mouth that results from the rapid opening of the mouth and depression of the hyoid.

2.2 Prey Manipulation and Transport

Once the prey has been captured, a series of mouth movements is usually observed that manipulates the prey into a position for swallowing (Liem 1970; Lauder 1979, 1983b). Although many strikes involving suction result in the prey being brought directly into the buccal cavity, unless the prey is very small, buccal manipulation is still employed to position prey for swallowing. Such prey manipulation within the mouth cavity occurs by creating currents of water flow via jaw, hyoid, and opercular movements, and Bemis and Lauder (1986) referred

to this as a hydraulic mechanism of prey transport. Prey are moved anteriorly and posteriorly, as well as mediolaterally, by currents of water. Hydraulic prey transport is accomplished via similar mechanisms to those described above for initial prey transport: prey are moved posteriorly in the mouth toward the pharyngeal jaws by a current of water resulting from mouth opening and delayed hyoid and opercular expansion (Lauder 1980b, 1983b). Anterior flows of water are created by changing the timing of opercular, hyoid, and gape movements, and this results in an altered pressure profile during prey manipulation (Lauder 1980b).

The kinematic patterns involved in prey transport toward the esophagus are very similar to those seen during initial prey capture by suction feeding. The timing of gape and hyoid profiles is similar, with maximal hyoid retraction occurring after peak gape (Bemis and Lauder 1986).

3 Salamander Feeding Mechanics

3.1 Comparative Framework

Due to the variety of possible comparisons that may be made among taxa, behaviors, and between the aquatic and terrestrial environments, it is useful to begin a consideration of the biomechanics of feeding in salamanders with the general comparative scheme outlined in Fig. 2. The two key behaviors of interest are (1) the initial strike in which the prey is first captured and brought into the mouth cavity, and (2) the transport of prey to the esophagus following the initial strike. Given these two behaviors, there are four levels of comparison (Fig. 2).

First, strike and transport behaviors may be compared within each species or clade being studied (Fig. 2: comparison A). Thus, within the species *Ambystoma tigrinum*, measured features of strike and transport skeletal movement and muscle activity patterns may be compared to determine (quantitatively) what differences exist between the two behaviors. Second, the two behaviors may be compared across metamorphosis (Fig. 2: comparison B) to determine how skeletal movement and muscle activity change during ontogeny. Third, post-metamorphic salamanders may be studied feeding in both aquatic and terrestrial environments and the strike and transport behaviors compared (Fig. 2: comparison C). Fourth, strike and transport behaviors in salamander taxa may be compared to outgroup clades to determine which kinematic or motor pattern attributes have a general distribution within lower vertebrates (comparison D). In addition, different clades of salamanders may be compared with each other (not shown in Fig. 2) to determine the extent of phylogenetic variation within salamanders (both aquatic and terrestrial) in kinematic and motor patterns used during both initial prey capture and subsequent prey transport.

The goal of the comparative tests outlined in Fig. 2 is to provide a comprehensive picture of the ontogeny and phylogeny of the feeding mechanism in

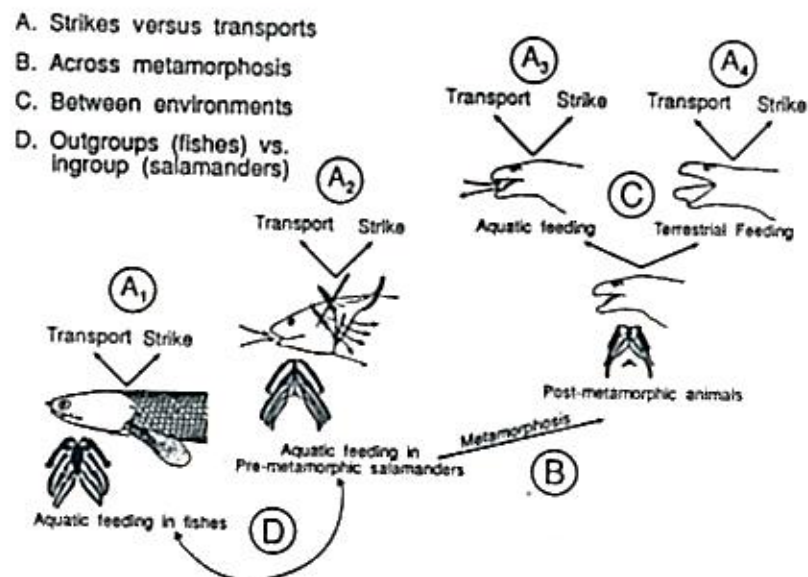


Fig. 2. Chart of the feeding behaviors of fish and salamanders and possible comparisons to be made among taxa, metamorphic conditions, and behaviors. Comparisons A_1 – A_4 contrast strike and transport behaviors within taxa: ray-finned fishes, larval salamanders, and postmetamorphic salamanders feeding in the water and on land. Aquatic feeding in premetamorphic salamanders occurs by suction feeding with unidirectional flow through the mouth cavity (indicated by arrows showing water flow in the mouth and out the gill openings posteriorly in comparison A_2). Aquatic feeding in postmetamorphic salamanders also occurs by suction feeding, but water flow is bidirectional (as indicated by arrows showing water flow in and out of the mouth in comparison A_3). Comparison B compares feeding function across metamorphosis during salamander ontogeny. Comparison C contrasts prey capture (both strikes and transports) in postmetamorphic salamanders feeding in the water and on land. Comparison D compares prey capture (both strikes and transports) in salamanders and outgroup taxa. Another possible comparison contrasts feeding behavior in different salamander taxa (e.g., Reilly and Lauder 1992). Schematic diagrams of the hyobranchial apparatus are shown for outgroup taxa (fishes, *Polypterus*), and for pre- and postmetamorphic salamanders

salamanders. To date, only a few of these comparisons have been conducted, and there are many gaps in our knowledge. Many studies of salamander feeding kinematics have been conducted without considering potentially primitive aspects of feeding kinematics present in fishes, and electromyographic data on muscle function are available only for two species. Furthermore, just one species has been studied across metamorphosis, and limited data are available only for one species comparing strike and transport behaviors quantitatively. A great deal of work remains to be done.

3.2 Initial Prey Capture

3.2.1 Aquatic Feeding

The biomechanics of initial prey capture in the water has been studied most extensively in the genus *Ambystoma*: Lauder and Shaffer (1985) described the morphology of the feeding apparatus in conjunction with high-speed cinematography of prey capture, electromyography, buccal pressure recordings, and impedance measurements of gill bar movement. Despite a number of morphological differences from outgroup taxa, patterns of skeletal movement during prey capture by *Ambystoma* are extremely similar to that of ray-finned fishes: most aquatic salamanders and fishes use a suction feeding mechanism (Lauder 1985a, b; Lauder and Shaffer 1985, 1993, Reilly and Lauder 1989a, 1992). The general pattern of timing of skeletal movements so common in outgroup clades is preserved in *Ambystoma*: peak gape is reached first, followed by maximal hyoid depression, and then by the efflux of water out of the gills.

An impedance recording technique was used to transduce directly the distance between adjacent gill bars and this showed that maximal gape coincides with maximal gill bar adduction which prevents water influx from the region posterior to the head as the mouth opens (Lauder and Shaffer 1985). The gill bars in larval *Ambystoma* possess interlocking gill rakers which form an effective barrier to water flow in a similar manner to the gill bars of fishes. Maximal gill bar adduction coincides also with maximal negative pressure in the mouth cavity. As the mouth closes on the prey, the gill bars are abducted and water flows out posteriorly between the abducted gill bars: water flow during prey capture is unidirectional (from anterior to posterior).

Recordings of muscle activity during prey capture made in conjunction with film records of head movement (at 200 frame/s) show that the mouth opens as a result of combined activity in the epaxialis, depressor mandibulae, rectus cervicis, and geniohyoideus muscles. Activity in anatomical antagonists, the depressor mandibulae, and adductor mandibulae begins simultaneously just prior to the onset of mouth opening, but the depressor mandibulae reaches peak activity (as measured by spike number and amplitude in electromyograms) 5 to 20 ms before the adductor mandibulae.

Comparative data from other salamander taxa are only available for patterns of head movement (Reilly and Lauder 1992); no electromyographic data are available for aquatic feeding to allow comparisons across salamander families. Reilly and Lauder (1992) studied initial prey capture in species in the families Ambystomatidae, Dicamptodontidae, Amphiumidae, Sirenidae, Proteidae, and Cryptobranchidae. By measuring seven variables from high-speed videos of prey capture, they showed that there was highly significant differentiation among these taxa in feeding kinematics. In particular, *Cryptobranchus* and *Siren* showed the most divergent patterns of feeding kinematics from the other taxa. Reilly and Lauder (1992) did find clear kinematic correlates of the reduction in posterior gill openings. In both *Cryptobranchus* and *Amphiuma* (which possess

restricted posterior gill openings for the exit of water during feeding) the angle of the head is depressed well below its starting value. Also, hyoid depression is delayed for up to 15 ms after the start of mouth opening in both taxa. However, despite showing significant quantitative differences in initial prey capture, all taxa showed the general patterns outlined above of the delay in maximum hyoid depression relative to maximum gape. All taxa also showed the characteristic bell-shaped gape profile seen in fish.

3.2.2 Terrestrial Feeding

In contrast to aquatic feeding in salamanders, which has just begun to attract attention from experimental zoologists, the process of prey capture by terrestrial salamanders has interested morphologists for nearly a century (Druner 1902, 1904; Francis 1934; Edgeworth 1935; Lombard and Wake 1976, 1977; Reilly and Lauder 1989a). Most functional research on terrestrial feeding has been conducted on the genus *Ambystoma*, although comparative functional data are now available on the families Plethodontidae (Severtsov 1971; Thexton et al. 1977; Larsen et al. 1989) and Salamandridae (Findeis and Bemis 1990; Miller and Larsen 1990).

Terrestrial prey capture occurs by projection of the tongue out of the mouth toward the prey, and involves the coordinated movement of the skull and hyobranchial apparatus. The strike of a terrestrial salamander differs considerably from an aquatic prey capture event. Figure 3 shows five fields from a high-speed video sequence of prey capture in *Ambystoma tigrinum* which illustrate the general sequence of head movements used to capture prey by tongue projection on land.

As the mouth opens (Fig. 3: 0 ms), the hyobranchial apparatus is moved anterodorsally (protracted) and the tongue base lifted. The protracted tongue base serves as a platform from which the tongue flips forward to contact the prey. Twenty-five milliseconds after the start of mouth opening, maximum gape has been almost reached and the plateau phase of the gape cycle begins. Maximal tongue projection is reached at about 35 ms near the middle of the gape plateau, and the tongue then contacts the prey. Peak tongue projection separates the projection and retraction phases of hyobranchial movement (Fig. 3). The retraction phase of tongue movement involves posteroventral hyobranchial movement to pull the base of the tongue back into the mouth with the prey attached. During the closing phase, the gape decreases and the jaws close on the prey (Fig. 3: 90 ms).

The plateau in the gape cycle appears to be a consistent feature of salamanders feeding on land, and may be related to the necessity of projecting the tongue out of the mouth: a near-constant gape occurs while the tongue is extended beyond the plane of the gape toward the prey (Reilly and Lauder 1989a). As a result of the distinct plateau, discrete fast opening and closing phases may be difficult to define. Although a tongue-based feeding system in salamanders

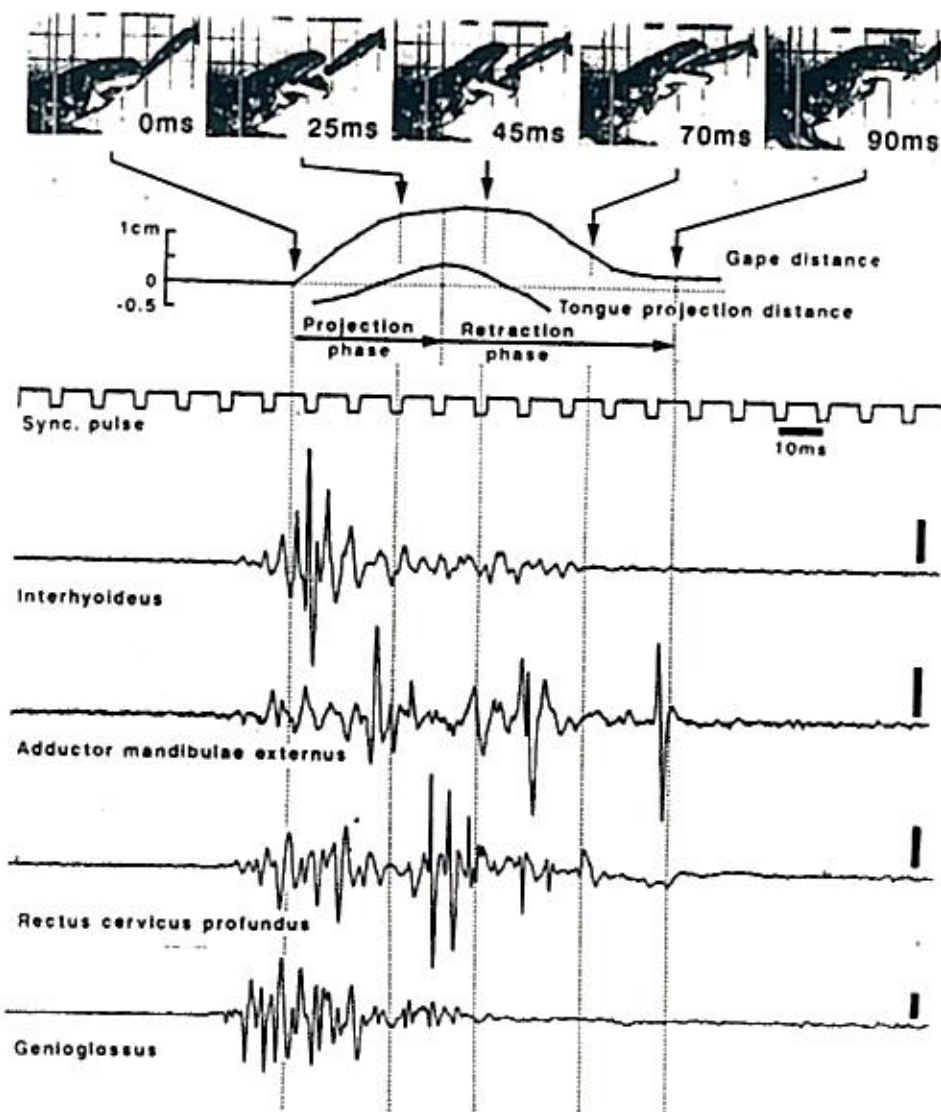


Fig. 3. Synchronized kinematic and electromyographic patterns during the strike with five representative video fields from this feeding sequence illustrated at the top. The time between peaks in the synchronization pulse illustrated below the kinematic plots is 10 ms. Note that activity in the interhyoideus and genioglossus muscles rises rapidly to a peak, while the adductor mandibulae and rectus cervicis profundus peak activity times are delayed until the plateau phase of the gape profile. Electrode positions in the illustrated muscles were confirmed by dissection following the experiment. Vertical bars to the right indicate 0.1 mV. (Reilly and Lauder 1990b)

would appear to function best in a terrestrial setting. Schwenk and Wake (1988) did find a case of a plethodontid salamander that feeds underwater using tongue projection. If nothing else, this illustrates that functional mechanisms thought to work only in one medium can be used elsewhere, and provides rather convincing evidence for the independent evolution of aquatic feeding in this species.

The major morphological components of the feeding system in a transformed tiger salamander (*Ambystoma tigrinum*) are illustrated in Fig. 4. Figure 4A shows the tongue in an elevated position as it is after hyobranchial protraction (roughly the position depicted in Fig. 3: 25 ms). The position of the tongue at rest is shown (equivalent to Fig. 3: 0 ms video frame) in Fig. 4B. The major muscles acting to protract and elevate the hyobranchial apparatus are the geniohyoideus (GH), genioglossus (GG), intermandibularis (IM), and subarcualis rectus one (SAR). These muscles act synergistically to move the branchial apparatus (Fig. 4: horizontal hatching) anterodorsally relative to the hyoid and lower jaw thus protracting the tongue. In particular, the SAR acts to slide the first ceratobranchial element anterior relative to the hyoid which is restrained by its ligamentous attachment to the quadrate bone (Reilly and Lauder 1988b, 1991a;

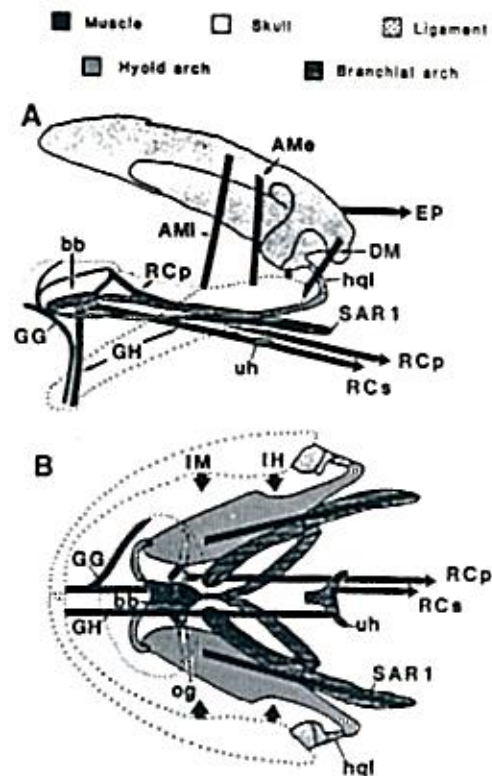


Fig. 4. Schematic diagram of representative muscles used during feeding in transformed salamanders (based on *Ambystoma tigrinum*). A The tongue is shown in a partially projected state, corresponding to the second video field (25 ms) in Fig. 3. The hyobranchial apparatus has been protracted, but the tongue pad is not flipped. A black dot marks the position of the jaw joint. Small dots outline the tongue, while large dots outline the lower jaw. B The tongue, lower jaw, and hyobranchial apparatus are shown in rest position as in the first video field of Fig. 3. AMe Adductor mandibulae externus; AMI adductor mandibulae internus; bb basibranchial; DM depressor mandibulae; EP epaxial; GG genio glossus; GH geniohyoideus; hql hyoquadrate ligament; IH interhyoideus; IM intermandibularis; og otoglossal cartilage; RCs rectus cervicis superficialis; RCp rectus cervicis profundus; SAR subarcualis rectus one; uh urohyal

Fig. 4). As the branchial apparatus is protracted, the tongue is also flipped forward by contraction of the genioglossus muscle fibers which reach up into the tongue pad. The flipping action of the tongue extends the tip of the tongue forward to contact the prey (Reilly and Lauder 1989a, 1990b).

Electromyographic recordings during prey capture reveal a complex pattern of activity in head muscles (Lauder and Shaffer 1988; Reilly and Lauder 1990b). Nearly all muscles are synchronously active (Fig. 5A), but display different patterns of amplitude and spike frequency following initial activity. Onset times alone reveal very little about muscle function, and it is important to consider the pattern of activity *within* the muscle burst. The depressor mandibulae, genioglossus, interhyoideus, rectus cervicis superficialis, and geniohyoideus all show a rapid rise to a single dominant peak in activity within 25 ms from the start of mouth opening (Reilly and Lauder 1990b). The adductor mandibulae muscles tend to peak later, but show some variability both among muscle divisions and among feedings and individuals in the precise timing of peak activity. The SAR and epaxial muscles show a double-peak pattern with the first period of activity reaching a maximum at 5 to 10 ms after the mouth starts to open, and a second period of intense activity at 60 to 80 ms.

The process of prey capture in terrestrial tiger salamanders appears to be a relatively stereotyped one based on comparisons of successful and unsuccessful strikes at prey. Reilly and Lauder (1990b) found that 66 out of 77 variables measured from 11 cranial muscle electromyograms did not differ with success or failure of the strike. Successful and unsuccessful strikes also had indistinguishable times to tongue contact with the prey and gape cycle times (the tongue did contact the prey in all strikes, but failed to adhere in unsuccessful strikes).

The distinctive nature of the terrestrial strike invites hypotheses on the evolutionary origin of the tongue projection behavior. In *Ambystoma* larvae, the hyobranchial apparatus functions to open and close the gill slits (controlling water flow through the mouth), to contribute to intraoral volume changes during suction feeding, and to compress prey against the roof of the buccal cavity during prey manipulation after capture (Reilly and Lauder 1989a). This latter role involves strong anterodorsal movements of the hyobranchial apparatus. After metamorphosis when terrestrial feeding occurs, the hyobranchial apparatus no longer functions to move water, and buccal volume changes play an important role during respiration. However, anterodorsal movement of the branchial apparatus is used during tongue projection, and hyobranchial motion during aquatic intraoral prey manipulation and the early phases of terrestrial tongue projection are similar. Regal (1966) proposed the hypothesis that feeding by terrestrial tongue projection evolved from a manipulative function of the hyobranchial apparatus, and Reilly and Lauder (1989a) elaborated on Regal's suggestion. We suggest that elevation of the hyobranchial apparatus during the early stages of the strike on land may be homologous to the dorsal elevation of the tongue during larval prey manipulation within the mouth. Novel functional aspects of tongue projection during the terrestrial strike (such as flipping of the tongue and protraction of the ceratobranchial relative to the ceratohyal) are a

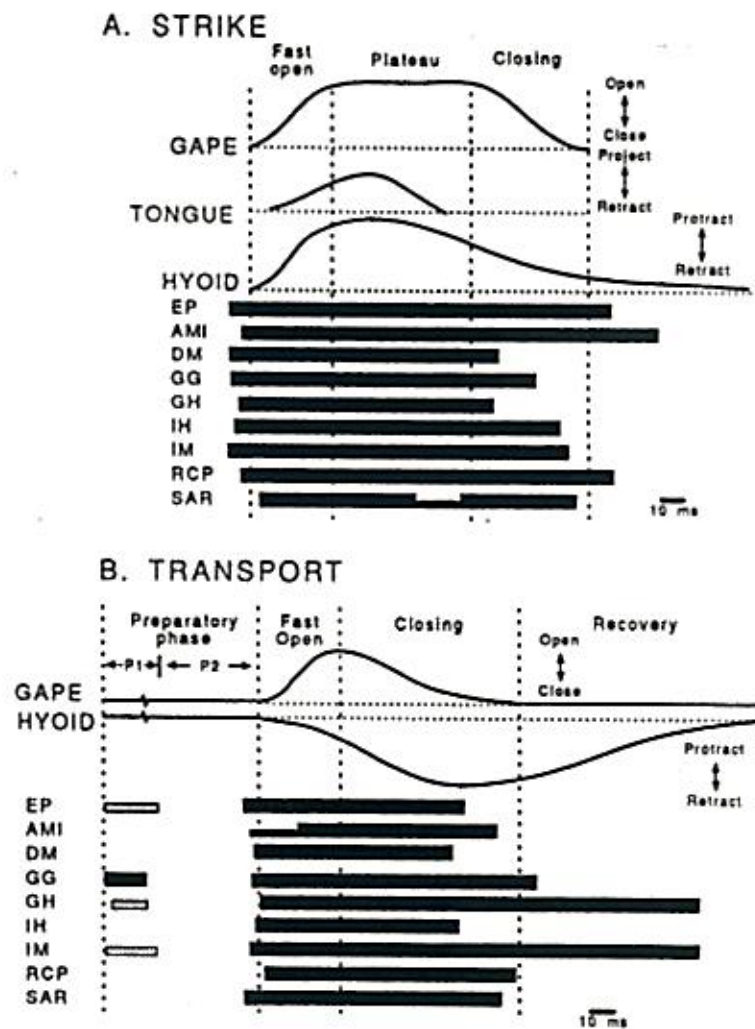


Fig. 5. Generalized terrestrial salamander feeding patterns during A the strike and B prey transport. Kinematic patterns for the gape and hyoid are shown for each behavior and a summary of the motor pattern is illustrated below: black bars indicate the time during which each muscle is active, gray bars indicate occasional activity, and changes in bar height reflect consistent patterns of amplitude variation. In B (transport), the duration of the P1 and P2 portions of the preparatory phase are shortened in this schematic figure from their real durations. P1 may last up to 5 s, while P2 generally is of 100 to 150 ms duration. During most of P2, there is no muscle activity until about 10 ms before the mouth begins to open. Note the presence of a plateau in the gape profile during the strike, but the lack of such a plateau during prey transport, and the similarities between transport kinematics and the strike kinematics for fish are shown in Fig. 1. Data for this figure were taken from Reilly and Lauder (1990b, 1991b)

consequence of novel morphological features acquired at metamorphosis. Thus, the terrestrial strike may have evolved via the addition of morphological and functional novelties at metamorphosis onto a primitive pattern of hyobranchial elevation present in larvae.

The most comprehensive comparative data on feeding kinematics in salamanders are available for the families Salamandridae and Plethodontidae. In salamandrids, Findeis and Bemis (1990) studied *Taricha* in detail and found that the lack of a mandibulohyoid ligament allows the ceratohyal to move anteriorly during tongue projection. These authors suggest that salamandrids may have a derived mode of tongue projection as compared to the primitive mechanism in which the hyoid arch is relatively stable during tongue projection. Another interesting feature of the strike in *Taricha* is the long gape cycle (on the order of 200 ms).

In the family Plethodontidae, Larsen et al. (1989) have analyzed data from *Bolitoglossa*, *Ensatina*, *Plethodon*, and *Desmognathus*. Their data show that gape cycles in this family are about 100 ms long and that peak gape occurs near the end of tongue retraction into the mouth. These authors also note that in *Bolitoglossa occidentalis* there is no forward body movement during the strike, which they explain as an adaptation to arboreal feeding, noting that "...a sudden forward lunge could cause it to fall to the ground". However, *Ambystoma tigrinum* also remains stationary during both the strike and prey transport behaviors (Reilly and Lauder 1989a, 1990a) and the lack of body movement may have nothing to do with an arboreal feeding mode.

3.2.3 Metamorphosis of Feeding Function

Metamorphosis of feeding function has been studied in *Ambystoma tigrinum* by Lauder and Shaffer (1986, 1988) and Shaffer and Lauder (1988), and morphological changes in the head at metamorphosis in this species have been analyzed by Reilly and Lauder (1990c) and Lauder and Reilly (1990).

A useful starting point for analyses of metamorphosis and the functional changes that take place is to consider three "stages" of ontogeny: larvae, metamorphosed salamanders feeding on land, and metamorphosed salamanders feeding in the water. By comparing feeding function in larvae (which feed in the water) to metamorphosed animals feeding in the water, the effect of changes in morphology across metamorphosis may be analyzed: the environment is held constant. By comparing feeding function of salamanders after metamorphosis in the water and on land, the effect of the environment alone may be seen: morphology is held constant (e.g., Fig. 2, comparison C). For analyses of the ontogeny of function in salamanders, it is vital to be able to separate the effects of environment and morphology.

The major conclusion of the studies of Lauder and Shaffer (1986, 1988) and Shaffer and Lauder (1988) is that the process of metamorphosis does not carry with it obligatory changes in muscle activity patterns. Measurements of muscle

activity patterns in larvae and metamorphosed *Ambystoma* feeding in the water showed that there was no difference in motor output (Lauder and Shaffer 1988). However, there is a dramatic drop in feeding performance after metamorphosis that appears to be due to a decrease in the mass of cranial muscles that power the fast opening phase (depressor mandibulae and rectus cervicis; Lauder and Reilly 1990) and the change from a unidirectional feeding mode in larvae to a bidirectional mode after metamorphosis (Lauder and Reilly 1988). The capture of elusive prey is less effective when water must reverse course and exit from the mouth anteriorly during the closing phase (Lauder and Shaffer 1986; Reilly and Lauder 1988a).

Feedings in the water by both larvae and metamorphosed individuals showed a characteristic bell-shaped gape profile with no plateau phase. Only minimal and occasional tongue elevation was observed in metamorphosed animals when feeding in the water.

Both muscle activity and kinematic aspects of feeding differed significantly between metamorphosed tiger salamanders feeding in the water and on land (Lauder and Shaffer 1988; Shaffer and Lauder 1988). On land, feedings showed a characteristic plateau in the gape profile and muscle activity durations tended to be longer than during aquatic feedings. Terrestrial feedings also involve tongue projection toward the prey and concomitant kinematic and motor pattern novelties in those muscles that arise at metamorphosis.

3.3 Prey Transport

Although nearly all studies of head function in salamanders have focused on the initial strike, a second vital function of head muscles and skeletal elements is the manipulation and transport of prey from the mouth to the esophagus and stomach after prey are captured. Quantitative studies of prey transport behavior have been conducted only for terrestrial feedings in *Ambystoma tigrinum*, and yet some intriguing patterns have been found. The study of prey transport is an area very much in need of further investigation, especially in nonamniote tetrapod taxa.

Terrestrial prey transport in *Ambystoma tigrinum* involves repeated cycles of jaw and hyoid motion that move the prey toward the esophagus. There is little "chewing" or reduction of the prey and captured food is usually swallowed whole. Distinct preparatory, fast opening, closing, and recovery phases are present. Reilly and Lauder (1990a, 1991b) have divided the preparatory phase in *Ambystoma tigrinum* into two parts: P1 and P2. During the first part of the preparatory phase (P1) which may last up to 5 s (Fig. 5B: P1), the mouth is closed (gape distance is zero or nearly so), and the hyobranchial apparatus is elevated pressing the prey against the roof of the mouth. Muscles that may be active during this phase include the genioglossus, interhyoideus, geniohyoideus, adductor mandibulae externus, and epaxial muscles (Reilly and Lauder 1991b). The subarcualis rectus one, rectus cervicis, and depressor mandibulae muscles

are all silent. Activity in the genioglossus and buccal elevating muscles acts to press the prey against the roof of the mouth during this phase. During some prey transport sequences, the gape opens slightly (about 1 mm) during P1 phase, but this is a variable occurrence.

During the P2 phase, all muscles are silent until the last 10 to 15 ms prior to the onset of the fast opening phase, and the gape remains constant. The fast opening phase begins with the onset of gape increase due to a rapid rise in activity of the depressor mandibulae, epaxial muscles, and rectus cervicis. Interestingly, the subarcualis rectus one muscle is strongly active during prey transport even though the tongue is not projected from the mouth (Reilly and Lauder 1991b). This muscle has been thought to function primarily in tongue projection, but electromyographic data indicate that it is strongly active during the fast opening phase of prey transport. During this phase, the hyobranchial apparatus moves posteroventrally, pulling the tongue and the attached prey into the oral cavity (Fig. 5B: hyoid curve). Hyoid movement continues into the closing phase, reaching a peak as the gape closes. Thus, it is the posteroventral movement of the hyoid, tongue, and attached prey that mechanically pulls the food posteriorly.

Activity of the epaxial muscles, adductor mandibulae, rectus cervicis, genioglossus, geniohyoideus, and intermandibularis continues through the fast opening phase and into the closing phase (Fig. 5B). Activity in the subarcualis rectus one and interhyoideus is usually completed by the end of the closing phase.

Kinematic analyses of prey transport show that the gape profile (Fig. 5B) is bell-shaped and does not have a plateau (Reilly and Lauder 1990a). In addition, *Ambystoma tigrinum* does not appear to use inertial transport to any significant extent, as the position of the body relative to a fixed background remains nearly constant throughout prey transport. Posteroventral hyobranchial movement during each transport cycle (defined as the time between P1 onset times) moves the prey from 4 to 8 mm toward the esophagus. A number of transport cycles are thus necessary for prey to be completely swallowed.

The recovery phase is characterized by a closed gape with continued muscle activity in the geniohyoideus, intermandibularis, genioglossus, and low level activity in the jaw adductor muscles. During the recovery phase, the tongue and hyobranchial apparatus move anteriorly to a new position under the prey, "resetting" the hyoid for another event. A new transport cycle may then begin with the onset of the P1 phase.

The transport of prey to the esophagus during aquatic feedings has not yet been analyzed in detail. High-speed video records of aquatic prey transport show that the captured prey are moved posteriorly within the buccal cavity toward the esophagus by an anterior-to-posterior flow of water. This water flow is created by rapid jaw movements similar to those used during the initial aquatic strike. Fast opening, closing, and recovery phases are all present, and the relative timing of peak bone excursions is the same as during the strike. Quantitative comparisons between aquatic strike and transport behaviors remain to be conducted.

3.4 Comparisons Among Behaviors in Salamanders

Analyses of the process of initial prey capture and transport both in the water and on land provide data for an overall hypothesis about the phylogenetic and ontogenetic relationships among these behaviors and their underlying physiological mechanisms (Fig. 2). We propose the hypothesis that the terrestrial transport and aquatic prey capture behaviors together are distinct from initial prey capture on land, and that the kinematic and motor patterns used during terrestrial prey transport are derived from and are homologous to the process of prey transport in the water. Specifically, we suggest that when homologous muscles are considered, motor output during terrestrial prey capture will be significantly different from aquatic prey capture, aquatic transport, and terrestrial transport. In addition, the kinematic patterns associated with these three behaviors will be more similar to each other than to the kinematics of terrestrial strikes.

There are some data to support the above hypothesis. Kinematically, only terrestrial strikes possess a plateau in the gape cycle, while the gape cycles of aquatic capture and transport are similar both to each other and to terrestrial transport. The timing and pattern of hyoid movement are similar in the two transport behaviors and in aquatic strikes. Only during terrestrial strikes is the hyobranchial apparatus protracted and elevated during fast opening to serve as a platform from which the tongue is projected. Tongue projection from the mouth may also explain the gape plateau: the mouth must be held open as the tongue moves out and then back into the mouth.

Although there are few quantitative data, initial prey capture in the water and the process of prey transport both in the water and on land appear to be similar in many ways. As noted by Reilly and Lauder (1991b), these behaviors share similar profiles and timings of jaw bone movements, similar sequences of muscle activity, similar durations (aquatic strikes and both transport behaviors show relatively short duration bursts), and similar electromyographic activity profiles of muscles such as the depressor mandibulae (which shows a single peak during aquatic strikes and transports in both environments).

This hypothesis would benefit from an explicit quantitative test among all four behaviors. To date, only the terrestrial strikes and transports have been compared (Reilly and Lauder 1991b), and this comparison revealed many differences between the two behaviors in muscle activity pattern.

The similarity of terrestrial prey transport in *Ambystoma tigrinum* to aquatic feeding strikes and transports in fishes led Reilly and Lauder (1990a) to propose the hypothesis that many features of the terrestrial prey transport cycle in salamanders may be primitive characters retained from nontetrapods and to suggest homologies between the phases of the gape cycle observed in *Ambystoma tigrinum* with those proposed previously for amniote gape cycles. In amniotes, salamanders (aquatic feedings, prey transport in both environments), and fishes, the hyoid undergoes posteroventral excursions during the fast opening phase. During the closing phase, hyoid retraction reaches a peak. In amniotes, hyoid

protraction occurs during the slow opening phase, a time that corresponds to the recovery and preparatory phases in salamanders and fishes. Thus, one possible hypothesis is that the preparatory and recovery phases of fishes and salamanders are together homologous with the slow opening phase in the amniote transport cycle.

According to this view, the relationship between gape and hyoid cycles during the fast opening and closing phases in amniotes is a primitive and complex functional character that has been retained from outgroup taxa such as ray-finned fishes and lungfishes (Bemis and Lauder 1986). These features of the transport cycle have thus been little modified with the origin of terrestrial vertebrate life. On the other hand, the transformation of the recovery and preparatory phases in salamanders into a slow opening phase in amniotes represents a significant functional shift that may represent a key novelty in amniote feeding systems.

4 Frog Feeding Mechanics

4.1 Background

The mechanism by which frogs capture their prey has been the subject of speculation since the 1820s (Gans and Gorniak 1982a). The most obvious feature of the frog prey capture system, tongue projection from the mouth, has been the focus of several divergent hypotheses purporting to provide a mechanical explanation for observed movements. As Gans and Gorniak (1982a) note in their comprehensive review of the history of prey capture mechanisms in frogs, proposals for the cause of tongue projection have ranged from elevated pressure in the lymphatic sublingual sinus to various hypotheses about muscular mechanisms of tongue projection. One possible reason for the number of divergent hypotheses is the considerable phylogenetic diversity that exists in feeding behavior and morphology in anurans (Trueb 1973; Emerson 1976; Regal and Gans 1976; Gans and Gorniak 1982a; Horton 1982; Trueb and Gans 1983).

In 1977, Emerson proposed a hypothesis for projection of the tongue in *Bufo marinus* that involved the hyoid apparatus, intrinsic tongue muscles such as the genioglossus, and the geniohyoideus muscles. Emerson proposed that the hyoid moves anteriorly during mouth opening as a result of relaxation of the sternohyoideus muscle, which contracts to hold the hyoid in place during initial mouth opening. Anterior movement of the hyoid during subsequent mouth opening then assists in anterior movement of the tongue out of the mouth. This hypothesis was tested by Gans and Gorniak (1982a, b), who conducted both high-speed filming and electromyographic studies of prey capture in *Bufo marinus*. They concluded that anterior hyoid movement does not play a role in tongue projection by *Bufo*.

The Gans and Gorniak papers proposed another mechanical hypothesis for tongue projection. They suggested that the submentalis muscle contracts to depress the symphysis of the mandible and to adduct the dentary bones. Contraction of the genioglossus medialis muscle causes the tongue to stiffen into a rigid rod that is then rotated anteriorly by the rising wedge formed by the submentalis and genioglossus basalis. The work of Gans and Gorniak corroborated the notion that muscle activity (and not hydraulic pressure) is responsible for tongue projection in *Bufo*, and showed that the hyoid probably plays only a minor role in tongue projection.

The Gans and Gorniak papers have stimulated new research on frog feeding systems in the 10 years since their publication, and data on the neural control and phylogenetic diversity of anuran feeding behavior are beginning to appear (Trueb and Gans 1983; Ewert 1984; Grobstein et al. 1985; Matsushima et al. 1985; Anderson 1990; Deban and Nishikawa 1990; Nishikawa and Gans 1990; Nishikawa and Cannatella 1991; Nishikawa and Roth 1991; Nishikawa et al. 1991). Earlier seminal studies include those by Comer and Grobstein (1978, 1981) and Ingle (1968).

4.2 Data and Current Hypotheses

The morphology of the feeding system in anurans differs considerably from that of the salamanders analyzed above. Although there is also a great deal of variation among anurans in morphology, Fig. 6 presents some basic features of the feeding mechanism in an anuran such as *Bufo* as a general basis for comparison to salamander feeding systems (Fig. 4) and as an aid to understanding the kinematic patterns of prey capture discussed below in frogs. Both mandibular depressor and adductor muscles are present, originate on the skull, and insert on the lower jaw (Fig. 6A; Duellman and Trueb 1986). The intermandibularis posterior muscle forms a sheet extending broadly between the mandibular rami (this is a primitive feature of gnathostomes; Lauder 1980b), while the submentalis muscle extends between the mandibular rami just posterior to the mentomeckelian bones at the symphysis (Fig. 6B). The geniohyoideus medialis muscle extends posteriorly from its origin at the symphysis to insert near the laryngeal cartilages (Gans and Gorniak 1982a). Dorsal to this muscle, the complicated genioglossus muscle, with many separate slips, extends from the tip of the mandible into the tongue. Many other muscles involved in the anuran feeding mechanism are described by Gans and Gorniak (1982a) and Duellman and Trueb (1986).

While recent research has shown that there may be differences in the feeding mechanisms of neobatrachian frogs and more plesiomorphic taxa (Nishikawa and Gans 1990; Nishikawa and Roth 1991; Smith and Nishikawa 1991), the overall kinematics of prey capture are qualitatively similar among the taxa studied to date. Figure 7 illustrates gape and tongue profiles measured from prey

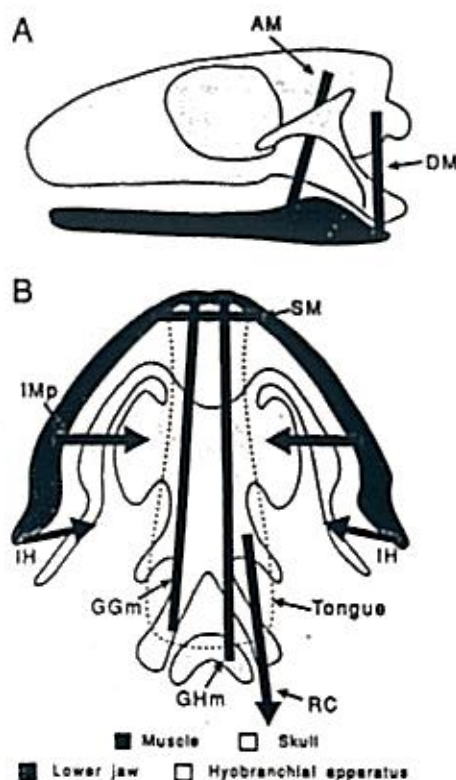


Fig. 6. Schematic diagram of representative muscles used during feeding in frogs (based on *Bufo*) in A lateral view and B ventral view. Note the expanded hyobranchial plate that contrasts with salamanders which possess separately articulating ceratobranchials. Several muscles are not shown for clarity (see Gans and Gorniak 1982a). These include the genioglossus basalis located deep to the submentalis, the hyoglossus, and the geniohyoideus lateralis. Note that the genioglossus medialis passes beneath the hyoid and into the tongue (dotted outline) in this view. AM Jaw adductor complex; DM depressor mandibulae; FFm genioglossus medialis; GHm geniohyoideus medialis; IH interhyoideus; IMP intermandibularis posterior; RC rectus cervicis or sternohyoideus; SM submentalis

capture sequences in *Ascaphus*, *Discoglossus*, and *Bufo* (Gans and Gorniak 1982a, b; Nishikawa and Cannatella 1991; Nishikawa and Roth 1991). The gape profile may exhibit considerable variation from feeding to feeding (Nishikawa and Cannatella 1991), but peak tongue projection usually occurs during the plateau phase of the gape cycle. Gape cycles are often bimodal and the valley between the two peaks roughly corresponds to the time of peak tongue projection.

The gape cycle may vary in duration from 80 to over 300 ms (Nishikawa and Cannatella 1991). In primitive anurans (e.g., *Discoglossus*, *Ascaphus*; Nishikawa and Cannatella 1991; Nishikawa and Roth 1991), the tongue is projected only about 3 mm beyond the margin of the lower jaw. Key characteristics of the feeding mechanism in primitive anurans are (1) forward movement of the body which begins at or before the mouth starts to open and reaches a peak near maximum gape, which moves the head (and tongue) closer to the prey, (2) ventral bending of the mandible at the mentomeckelian joint as the mouth opens, and (3) considerable variation in feeding kinematics depending on the success of the strike.

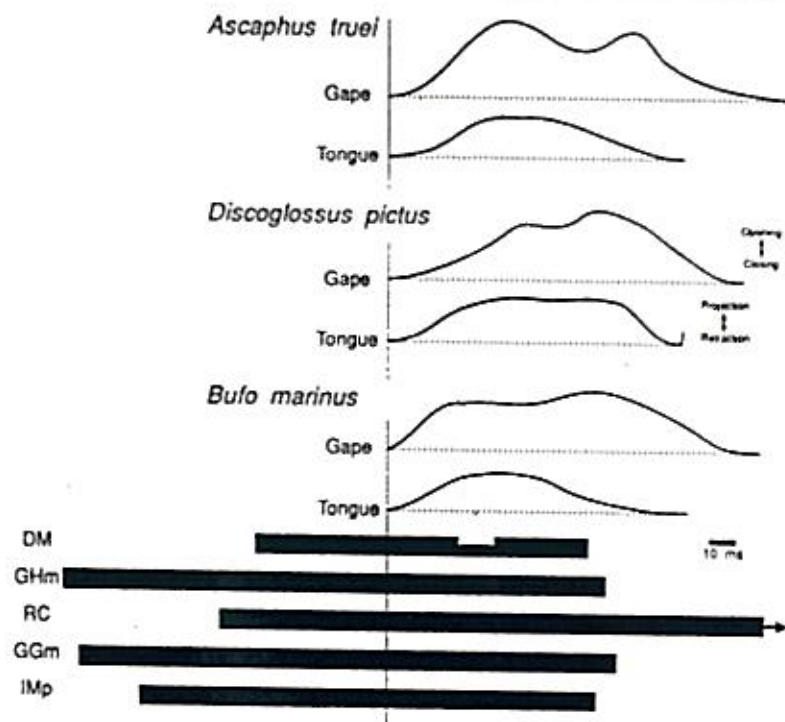


Fig. 7. Generalized anuran feeding patterns during the strike. Gape, hyoid profiles and muscle activity patterns were constructed from the data in Nishikawa and Cannatella (1991), Nishikawa and Roth (1991), and Gans and Gorniak (1982a, b). Black bars indicate the duration of muscle activity in *Bufo marinus* based on data in Gans and Gorniak (1982a). Note the variability in gape profiles among taxa; each taxon also shows considerable intraspecific variability (not shown)

As described for *Ascaphus* by Nishikawa and Cannatella (1991), the mouth opens and the tongue pad rotates anteriorly around the mandibular symphysis from an initial dorsal position to a ventral position at peak tongue extension. In this position, prey contact is made, and forward body and head movement continues past the prey as the tongue adheres to the prey item. Retraction of the tongue with the prey attached begins after peak gape and is completed as the mouth closes (Fig. 7).

Nishikawa and Roth (1991) conducted an experiment on the feeding system of *Discoglossus* to examine the hypothesis that the submentalis muscle is an important part of the tongue projection mechanism. As proposed by Gans and Gorniak (1982a), the submentalis muscle acts as an elevating wedge when it contracts, and forms a fulcrum around which the stiffened genioglossus muscle can rotate with the tongue. In *Discoglossus*, denervation of the submentalis

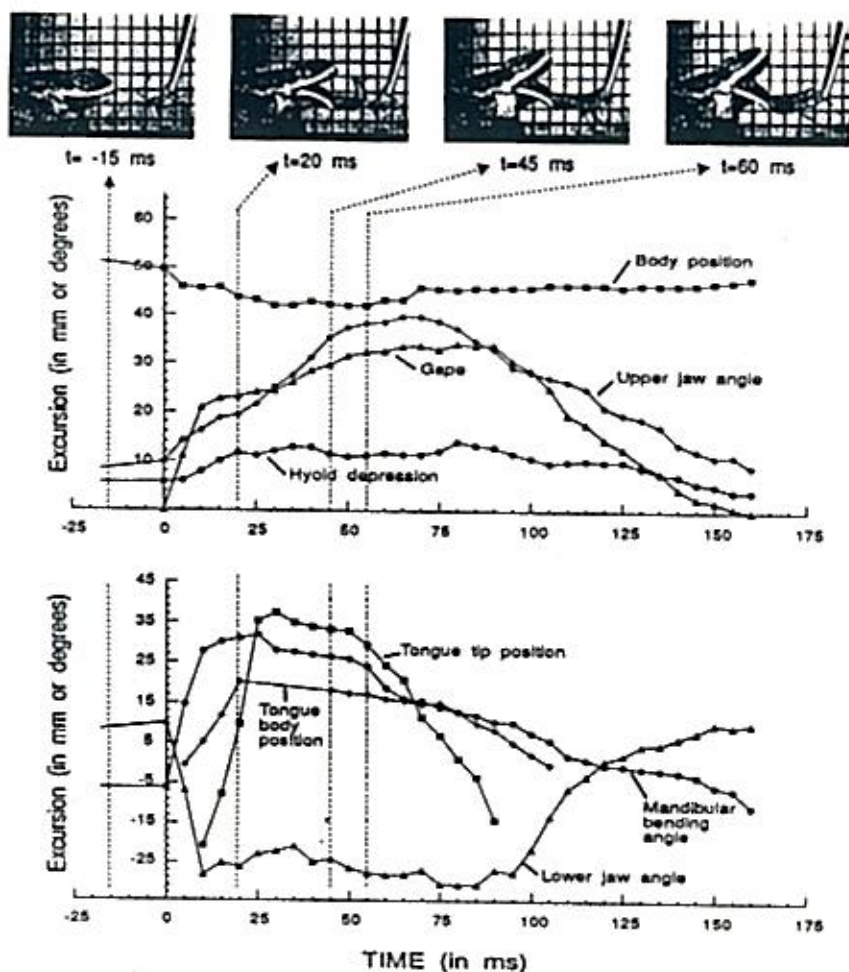


Fig. 8. Graphs of feeding kinematics in *Bufo cognatus*, with four representative video fields from this sequence shown at the top for reference. The video fields were obtained with a NAC HSV-400 high-speed video system in a manner similar to that described in Reilly and Lauder (1990b, 1991b, 1992). The top graph shows gape distance (triangles, in mm) measured between the tips of the upper and lower jaw; body position (squares, in mm) relative to a fixed reference line in the background located in front of the head; upper jaw angle (diamonds, in degrees) measured relative to a fixed external horizontal line; and hyoid depression (circles, in mm) measured as the distance from the angle of the jaw to the ventral-most buccal depression below the mandible. The bottom graph shows lower jaw angle (triangles, in degrees) measured relative to a fixed external horizontal line, mandibular bending angle (circles, in degrees) measured along the ventral margin of the mandible; tongue tip position (squares, in mm; negative values indicate that the tip of the tongue is located inside the plane of the gape, positive values show that the tongue has moved out of the mouth); and tongue body position (diamonds, in mm), a measurement that tracks the anterior position of the rigid body of the tongue. Note that positive angles indicate that the bone is elevated above the horizontal, while negative angles indicate that the bone is angled below the horizontal. The four video fields at the top of the

eliminated mandibular bending, but did not affect tongue projection. Denervation of the genioglossus muscle did significantly affect tongue morphology and projection during the strike, indicating that this muscle is critical to successful tongue protrusion. Similar results have been obtained in *Hyla cinerea* (Deban and Nishikawa 1990). However, denervation of the submentalis in *Spea* had little effect on either tongue protrusion or mandibular bending during feeding, and both the geniohyoideus and genioglossus appear to be necessary for tongue protrusion in this genus (Smith and Nishikawa 1991).

In order to depict the overall kinematic pattern during the strike in anurans in a manner similar to that which we have previously used on ambystomatid salamanders, we present in Fig. 8 an analysis of a prey capture sequence in *Bufo*. These data were obtained from high-speed video sequences (200 fields/s) of prey capture in *Bufo cognatus*. Four representative video fields are reproduced at the top of Fig. 8 and correspond to four times during the strike. These video fields may be compared to similar high-speed video data for ambystomatid salamanders shown in Fig. 3.

The data presented in Fig. 8 reveal that the mouth opens rapidly for 10 ms and then the rate of gape increase declines as the gape increases to its peak at 80 ms after the time when the mouth first begins to open. Gape velocity thus varies considerably within the fast opening phase (time 0 to peak gape), and the fast opening phase is longer than the closing phase. The gape increase is achieved both by elevation of the head (and thus the upper jaw) and by depression of the mandible. Lower jaw angle (Fig. 8) declines precipitously during the first 10 ms of the feeding, and remains at an extended plateau throughout the rest of the fast opening phase and the beginning of the closing phase. Comparison of the gape, lower jaw, and upper jaw profiles in Fig. 8 shows that the initial rapid increase in gape is due mostly to depression of the lower jaw. For the remainder of the fast opening phase, the increase in gape is due to elevation of the head and thus the upper jaw. During the closing phase, both the lower jaw and head move to close the gape distance. During the first 10 ms of the fast opening phase, the mandible bends dramatically as the lower jaw is depressed (Fig. 8) and the peak in mandibular bending occurs only 25 ms into the strike. Mandibular bending decreases steadily during the last two-thirds of the fast opening phase and throughout the closing phase.

Forward body movement increases as the mouth begins to open and maximal forward movement occurs during the fast opening phase. Body position remains relatively stable during the closing phase. Ventral hyoid movement also begins with the onset of mouth opening, and peaks at maximum gape, before returning to the initial rest position at the end of the closing phase.

Fig. 8. Cont.

figure correspond to the positions on the graphs indicated by the dashed lines. Note that the video field at $t = 20$ ms shows the tongue being flipped out of the mouth. The stiff body of the tongue is held nearly horizontal in this field, while the more flexible distal portion is nearly vertical as it rotates over the base of the tongue toward the prey. Time = 0 ms indicates the field before the mouth first begins to rapidly open; prior to time 0, the gape distance is 0

The tip of the tongue, first visible within the opening mouth 10 ms after time 0 (Fig. 8), moves rapidly out of the mouth during the fast opening phase: peak tongue tip extension occurs at 30 ms in this feeding, and has returned to nearly its initial position by the onset of the closing phase. The position of the anterior extent of the stiffened body of the tongue follows a similar course, with a rapid anterior movement followed by a slow return during the last half of the fast opening phase.

There are very few comparative electromyographic data on anurans to correlate with the kinematic patterns described above, although the studies of Gans and Gorniak (1982a, b) provide excellent data on *Bufo*. Matsushima et al. (1985) do present electromyographic data on *Bufo* that resulted from snapping behavior elicited by brain stimulation. However, we believe that these data should be treated with considerable caution until quantitative kinematic analyses show that the "snapping" behavior is the same as unrestrained strikes at live prey.

Some of the electromyographic data presented by Gans and Gorniak (1982a, b) are summarized in Fig. 7 for muscles that are comparable to those of salamanders. A key feature of the strike in *Bufo* is the early onset of muscle activity relative to the onset of mouth opening. During the equivalent of the salamander preparatory phase 2 (100 ms immediately preceding the onset of mouth opening), many muscles are active in *Bufo*. The depressor mandibulae muscle shows a tendency toward a double burst pattern (or at least a bimodal spike amplitude distribution) with the second burst occurring during the plateau or dip in the gape profile.

5 Comparative Analysis of Amphibian Feeding

The data available to date on the feeding systems of anurans and salamanders, although limited in comparative scope, do point strongly to substantial differences in the physiological mechanisms underlying feeding behavior in these two clades of amphibians (Roth et al. 1990). The comparative morphological and neurobiological data, however, are of much greater comparative breadth than functional data. Kinematic patterns are just now becoming available from a variety of salamander and anuran taxa to permit quantitative comparative analyses (Erdman and Cundall 1984; Cundall et al. 1987; Larsen et al. 1989; Reilly and Lauder 1989a, 1990b, 1992; Findeis and Bemis 1990; Nishikawa and Cannatella 1991; Nishikawa and Roth 1991). Quantitative electromyographic data are only available for two taxa: *Bufo marinus* (Gans and Gorniak 1982a, b) and *Ambystoma tigrinum* (Lauder and Shaffer 1985, 1988; Shaffer and Lauder 1985b; Reilly and Lauder 1989b, 1990b, 1991b), and this greatly restricts the generality of comparisons between anurans and salamanders.

Even with the limited comparative data now available, there appear to be two key differences between anurans and salamanders in feeding function. First, if

electromyographic data on *Bufo* are corroborated by future studies, then anurans would appear to use a fundamentally different motor pattern during feeding than salamanders (also see Roth et al. 1990). Second, although there may be a diversity of feeding systems within anurans, the role of the hyoid in the feeding mechanism seems to differ substantially between salamanders and anurans. The salamander feeding system is fundamentally hyoid-based. This is true for both aquatic and terrestrial feedings, as well as for strike and transport behaviors. In most species of anurans, the hyoid appears to play a relatively small role in tongue projection, and this may be related to larval specializations in feeding behavior.

An overall hypothesis of historical patterns to the major functional features of the feeding mechanism in amphibians is presented in Fig. 9 within the phylogenetic context of other vertebrate clades. Three key conclusions emerge from this analysis, and each will be considered seriatim.

First, many features of the feeding mechanism of amphibians are primitive characteristics that are retained from nontetrapod taxa. The extent to which both amphibian and amniote feeding kinematics retain primitive functions from nontetrapods has not been widely recognized, and yet some characters are conserved throughout many vertebrate clades. A prime example of functional conservatism is hyoid retraction during the fast opening phase (Fig. 9). Movement of the hyobranchial apparatus in a posteroventral direction occurs during the time in which the gape is rapidly increasing in a wide diversity of vertebrates during either the initial strike, prey transport within the mouth cavity, or both. Thus, taxa as divergent as turtles, mammals, lizards, salamanders, lungfishes, and sunfishes all exhibit hyoid retraction during the fast opening phase of prey transport.

Second, the functional patterns (both kinematic and electromyographic) involved in prey capture by amphibians do not fit the general pattern proposed for tetrapods by Bramble and Wake (1985). Bramble and Wake (1985) proposed a generalized model of jaw function during prey transport in lower tetrapods. This model predicts four distinct components of the gape cycle and associated muscle activities.

However, results from experimental studies in salamanders (Reilly and Lauder 1991b) have revealed neither the predicted muscle activity patterns nor the predicted kinematic features of the gape cycle. Rather than a single "generalized feeding cycle", tetrapods appear both to have retained primitive features from fishes and to have acquired distinct functional novelties at several phylogenetic levels (Fig. 9). In particular, amniote feeding systems possess several novelties in feeding function (Fig. 9) including extensive intraoral food processing, the presence of a slow opening phase in the gape cycle (Crompton 1989; Schwenk and Throckmorton 1989), and the common use of inertial feeding. These attributes are primitively lacking in nonamniote taxa. Specifically, salamanders and frogs lack a slow opening phase of the gape cycle and this is a primitive character inherited from nontetrapod ancestors. Indeed the slow opening phase of amniotes appears to be homologous to the preparatory and

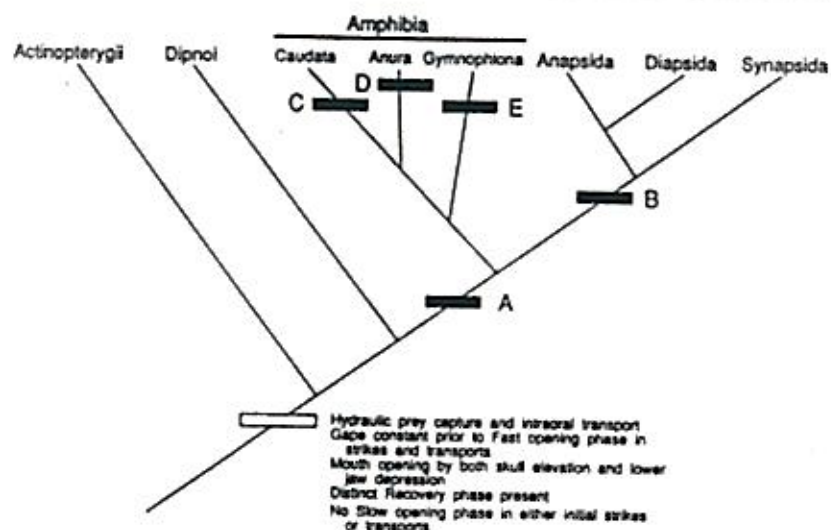


Fig. 9. Tetrapod phylogeny [with representative outgroups: ray-finned fishes (Actinopterygii) and lungfishes (Dipnoi)] to show one hypothesized historical pattern to the transformation of functional characteristics in the feeding mechanism. This figure is a modification and expansion of the hypothesis presented in Reilly and Lauder (1990a; Fig. 6). Features described next to the open bar at the stem of the phylogeny reflect functional characters as follows. (Note that due to the scarcity of comparative data, functional characteristics of the feeding mechanism proposed to be primitive for the entire clade. Letters next to black bars indicate groups of functional characters as follows. (Note that due to the scarcity of comparative data, functional characteristics listed here may turn out to be restricted to a derived set of taxa within the clade or may be more general and thus primitive for salamanders and frogs together or even for the Amphibia.) A Long preparatory phase prior to fast opening, tongue-based terrestrial intraoral prey capture and transport; B extensive intraoral food processing, inertial feeding present, recovery phase compressed into gape cycle, gape increase mostly by lower jaw depression, short slow opening phase just prior to fast opening; C tongue projection based on a mechanism involving the branchial skeleton and the subarcualis rectus one muscle, relatively little influence of sensory feedback on the feeding motor pattern; D submentalis muscle present, mandibular bending present, extensive modulation of the feeding kinematic pattern, novel strike motor pattern with jaw muscle activity in several muscles beginning well before the onset of mouth opening, lack of a distinct recovery phase; E novel jaw closing mechanism involving the interhyoideus posterior muscle

recovery phases together of amniotes (Reilly and Lauder 1990a, b, 1991b), a time when the hyoid is protracting (moving anterodorsally).

Third, frogs and salamanders appear to have acquired many novelties in the feeding mechanism, both morphological and functional, that reflect both the biomechanical requirements of terrestrial feeding and phylogenetic diversification into distinct feeding systems. As emphasized by Roth et al. (1990), frogs appear to exhibit considerable diversification in feeding function, with several different methods of tongue projection used within the Anura (Trueb and Gans 1983; Roth et al. 1990; Nishikawa and Roth 1991; Smith and Nishikawa 1991).

The anuran feeding mechanism displays much more extensive diversification in function of the hyobranchial apparatus, variability in the feeding mechanism (Anderson 1990; Nishikawa and Cannatella 1991; Nishikawa and Roth 1991), and involvement in sensory feedback pathways (Nishikawa and Gans 1990) than do salamander taxa that have been studied so far. Indeed, the salamander feeding system seems to retain many more primitive (nontetrapod) morphological and functional features than the anuran feeding system which has acquired numerous functional and morphological apomorphies.

Comparison of the data presented here for salamanders (Figs. 4 and 5) and frogs (Figs. 6, 7, and 8) illustrates the many differences between these two taxa. Most larval salamanders retain the basic morphological configuration of the nontetrapod feeding mechanism with a hyoid arch, branchial elements, and associated muscles, as well as a large number of functional similarities in motor pattern and kinematics to outgroup taxa (Lauder and Shaffer 1985; Lauder and Reilly 1988). Even transformed salamanders, while acquiring both morphological and functional novelties at metamorphosis for terrestrial tongue projection (Lauder and Shaffer 1988, 1993), retain outgroup functional characteristics during prey transport behaviors (Reilly and Lauder 1990a, 1991b). Thus, the gape cycle during prey transport lacks the plateau phase, and is similar to the gape cycle of larval salamanders, transformed salamanders feeding in the water, and outgroup taxa like lungfishes and ray-finned fishes. In addition, analyses of variation in the feeding mechanism of ambystomatid salamanders have shown that, while there is often significant variation among individuals, there is very little variation in either kinematic or electromyographic patterns within an individual when different prey are caught or if prey are captured or missed (Shaffer and Lauder 1985a, b; Reilly and Lauder 1989b, 1990a, 1991b).

When compared to both salamanders and outgroup taxa (Fig. 9), frogs possess a highly modified hyoid apparatus, jaws and skull, novel features of the buccal musculature (such as the submentalis muscle), relatively variable strike kinematics that are altered based on strike success and prey size, and many novel features of the kinematic pattern of the strike. In addition, frogs also possess a highly modified larval stage with a feeding mechanism that also exhibits a large number of novel features and considerable diversity across taxa (De Jongh 1968; Wassersug and Hoff 1979; Ruibal and Thomas 1988).

Bone movement and muscle function in frogs differ from salamanders and nontetrapod outgroups in at least four major attributes evident from currently available data. First, there is no recovery phase (this may be due in part to the many morphological, behavioral, and ecological novelties in anuran larvae). In *Bufo* for example (Fig. 8), hyoid depression and tongue projection return to their initial rest positions by the end of the closing phase. Data for *Ascaphus* and *Discoglossus* (Nishikawa and Cannatella 1991; Nishikawa and Roth 1991) also show that these taxa lack a recovery phase comparable to the plesiomorphic condition for tetrapods (Fig. 9). Second, patterns of hyoid movement during the strike are quite different in both fish (in which the hyoid moves posteroventrally) and terrestrial salamanders (in which the hyobranchial apparatus is protracted).

Third, the patterns of jaw movement in frogs may be considerably different from outgroup taxa. For example, in *Bufo* (Fig. 8), the lower jaw drops rapidly as the mouth opens, and maintains a plateau until the start of the closing phase. Not all frogs show this specific pattern (Nishikawa and Roth 1991) and many frog species show considerable intraspecific (as well as interspecific) variation in upper and lower jaw kinematics not found in outgroup clades. Fourth, the electromyographic patterns at the strike in frogs appear to differ (for homologous muscles) from those in salamanders. Jaw muscles in frogs may be active for a significant period of time prior to the onset of mouth opening, something not yet seen in salamanders.

In salamanders, quantitative analyses of electromyographic patterns at the strike are only available for *Ambystoma tigrinum* (larvae: Lauder and Shaffer 1985, 1988; transformed individuals: Lauder and Shaffer 1988; Reilly and Lauder 1990b, 1991b, in prep.), and these data show that the onset of muscle activity is indeed nearly synchronous (within 5 ms, even for antagonistic muscles). Reilly and Lauder (1990b) also showed that each muscle in the feeding mechanism possesses a distinctive pattern of activation and amplitude variation during the strike.

Although this discussion has focused on anurans and salamanders, caecilians form a third clade that is important to future discussions of the evolution of form and function in the amphibian feeding mechanism. As yet, the only data available on caecilians are those of Bemis et al. (1983) who studied prey transport, Nussbaum (1983), O'Reilly (1990), and O'Reilly and Deban (1991). Bemis et al. (1983) and Nussbaum (1983) showed that caecilians possess many novelties in the feeding mechanism, including a new mechanism of jaw closing, and involving the interhyoideus posterior muscle. Further data on all aspects of caecilian feeding mechanisms (initial strike and transports in both aquatic and terrestrial environments) are badly needed.

6 Recommendations and Future Directions

In describing and comparing feeding mechanisms of anurans and salamanders, several directions for future research have become apparent. In addition, we would like to make a number of recommendations to facilitate comparative analyses among amphibian taxa.

Our first recommendation is that a standard set of terminology be developed for comparing feeding function that is phylogenetically based. We suggest, therefore, that the terminology used to describe the plesiomorphic feeding pattern for tetrapods be extended to all amphibian taxa as the basis for initial descriptions of feeding behavior. Thus, the preparatory, fast opening, closing, and recovery phases with their associated definitions based on gape and hyoid cycles (Reilly and Lauder 1990a, b; Lauder and Prendergast 1992) could be used as a foundation of primitive kinematic features present in outgroups. Not all

taxa will possess all these phases (e.g., frogs appear to lack a recovery phase), and new kinematic features will certainly be described that require new terms (the frog fast opening phase may need to be subdivided into distinct parts). These apomorphic behaviors should be given apomorphic terms, and not be confusingly described using terminology with well-established meanings in plesiomorphic taxa. Additional descriptive terms for tongue movements should be agreed on so that kinematic phases such as projection, protraction, and retraction have accepted meanings to all workers. The precise definition of all kinematic terms will be of considerable value when studies of the feeding motor pattern are expanded to include more taxa.

Our second recommendation stems from the unfortunate tendency of workers investigating one amphibian taxon to proceed independently from functional research being done on other taxa. We suggest that specific collaborative research utilizing frogs, salamanders, and caecilians be conducted to permit direct, quantitative, statistical comparisons in feeding system function across taxa. Functional research on amphibian feeding mechanisms has proceeded to date via analyses of behavior within each major amphibian clade. This is appropriate to establish a baseline of data, but does not encourage quantitative comparisons of feeding systems across taxa.

Third, we suggest that when comparisons among major amphibian clades are conducted, that homologous morphological and functional components be compared using quantitative statistical methods. It is all too easy to make qualitative generalizations based only on a few species and on the analysis of a limited number of variables. Analyses of motor patterns, for example, should involve appropriate signal filtering, quantification, and statistical analysis of measured variables before conclusions regarding differences among taxa are announced. While uncertainties in the homology of morphological features across taxa may limit the breadth of functional comparisons, there are a number of muscles (such as the intermandibularis, geniohyoideus, and depressor mandibulae) which may be suitable subjects for comparative studies.

Based on the research described in this chapter, there are three areas which we view as being in particular need of investigation. First, there are currently no data on prey transport in anurans. Transport behaviors are of special importance because they may provide evidence that primitive motor and kinematic patterns, thought to be absent when only the initial strike is studied, are in fact present. Second, functional data on caecilians are lacking and, in particular, comparative analyses of aquatic and terrestrial prey capture will be of interest to contrast with currently available data on salamanders. Third, a broadly quantitative comparison among strike and transport behaviors in all three major clades of amphibians and nontetrapod outgroups will test the extent of phylogenetic conservatism in both strike and transport behaviors. It is somewhat shocking to discover, given the rather large number of published generalizations about amphibian feeding behavior, that quantitative data on muscle function are available only for two species of Amphibia. We suggest that further generalizations should await the production of experimental data on which to

base functional and historical hypotheses. Such comparative functional data will also contribute to our understanding of the patterns of diversification in amphibian feeding mechanisms, a key theme especially in the Anura.

The feeding system of amphibians offers an excellent study system within which to investigate problems of structural and functional evolution. The three major clades of extant amphibians have diversified structurally to a remarkable extent, ecologically, environmentally, and morphologically. The examination of how functional patterns have been transformed in this clade will be of great assistance in our attempts to understand major features of vertebrate evolution such as the transition from water to land, and the nature of historical patterns to functional characters.

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