

## CHAPTER 6

# ORIGIN OF THE AMNIOTE FEEDING MECHANISM: EXPERIMENTAL ANALYSES OF OUTGROUP CLADES

George V. Lauder  
Gary B. Gillis

## INTRODUCTION

One of the areas of vertebrate structure and function that has received the most attention during the past 20 years is the study of the feeding system. Due to the relatively good fossil record of bones, the many characters within the jaws used for systematic diagnoses, and interest in the mechanisms used by vertebrates to obtain resources from the environment, functional morphologists and paleontologists have devoted considerable effort to analyzing the vertebrate skull (Bels *et al.*, 1994b; Hanken and Hall, 1993). Investigation of skull design has included characterizing historical transformations of structure and functional patterns within major clades. For example, within the last 15 years, a number of reviews have appeared that deal with aspects of mammalian feeding mechanisms (Novacek, 1993; Russell and Thomason, 1993; Weijs, 1994), as well as jaw function in fishes (Frazetta, 1994; Lauder, 1983a; Liem, 1984), amphibians (Lauder and Reilly, 1994; Roth *et al.*, 1990), and lizards (Bels *et al.*, 1994a; Smith,

1993). However, the study of skull design in relation to several key events in vertebrate evolution, such as the origin of terrestrial feeding systems in tetrapods and the origin of amniote skull structure and function, has been less well analyzed.

This chapter will focus on the origin of the amniote feeding mechanism as a key event in the evolution of the vertebrate skull. However, rather than describe feeding systems within various amniote clades which have been reviewed elsewhere, we will center our analysis around a single general theme. We contend that in order to understand amniote feeding mechanisms and their diversification, it is essential first to understand the structure and function of the feeding mechanism in out-group clades. Thus, we will examine the feeding mechanisms of fishes and amphibians as a means of determining which functional traits are likely to have been primitively present in amniotes. Furthermore, based on this analysis of out-group clades, we believe that many functional attributes of the feeding mechanisms of amniotes are most parsimoniously explained as plesiomorphies retained from anamniote ancestors. Hence, it is important to understand aquatic feeding mechanisms in fishes, as well as aquatic and terrestrial feeding mechanisms in amphibians as a basis for assessing function in amniote taxa that are primitively terrestrial, but in some clades, have secondarily returned to the aquatic environment. Finally, we suggest that further experimental studies of extant amniote and anamniote taxa should provide a better understanding of the evolution of amniote and, more generally, vertebrate feeding mechanisms. For example, understanding general principles of divergence between aquatic and terrestrial feeding systems is an essential step in determining the role that environmental constraints have played in the evolution of vertebrate feeding mechanisms

**Figure 1.** Lateral and ventral views of cranial movements during prey capture in *Lepomis macrochirus*. The earthworm prey has been dropped through a tube and can be seen emerging from the bottom opening in the first frame. At time = 0 ms, the gape cycle is just beginning. Note that at peak gape (60 msec) lateral expansion of the head (seen in ventral view) has just begun and the upper jaw is maximally protruded. At 80 msec, the jaws have closed on the prey. Further movements of the prey into the mouth are accomplished by transport movements. Modified from Gillis and Lauder (1995). →





(Bramble and Wake, 1985; Lauder and Reilly, 1994; Lauder and Schaeffer, 1993).

## OUTGROUP PATTERNS: FISHES

The monophyletic clades of extant fishes that form out-group taxa to tetrapods and amniotes are the sharks and relatives (Elasmobranchiomorpha), ray-finned fishes (Actinopterygii), coelacanths (Actinistia), and lungfishes (Dipnoi). The feeding mechanisms of members of all of these taxa have been studied in some form or other during recent years, and a comparative analysis of feeding morphology and function in these clades provides the basis for our subsequent consideration of tetrapod feeding systems.

### *Initial Prey Capture*

Despite the diversity of skull morphology represented by taxa as phylogenetically divergent as sharks, bass, and lungfishes, many common fundamental features of the process of initial prey capture have been observed. Most important is the observation that many taxa capture prey by suction feeding (Grobeck and Pietsch, 1979; Lauder, 1985a; Liem, 1970; Norton and Brainerd, 1993; Nyberg, 1971; Westneat and Wainwright, 1989).

The process of suction feeding involves creating a pressure within the oral cavity that is less than ambient. As shown in figure 1, expansion of oral volume occurs by lateral movement of the suspensoria, elevation of the neurocranium, depression of the lower jaw, and ventral movement of the hyoid region. The result of these movements is a reduction in oral cavity pressure that draws water into the mouth anteriorly carrying the prey toward the gape. The strike may be unsuccessful, in which case the prey escapes; the strike may result in prey being caught between the upper and lower jaws as the mouth closes (as in Fig. 1); or the prey may be completely drawn into the oral cavity. During the time that the mouth is opening, bones covering the gills laterally prevent water influx from the area posterior and lateral to the head and allow an essentially unidirectional flow of water through the mouth from anterior to posterior. Water flows first into the oral cavity, then between and around gill bars and filaments to exit finally in an expanding gap between opercular elements and the



side of the head (Fig. 1). In the absence of an appropriate morphological design, the reduction in oral cavity pressure would be expected to draw in water from both posterior and anterior to the head, reducing the effectiveness of suction directed toward the prey.

Direct measurement of pressure changes simultaneously at several sites within the mouth cavity of ray-finned fishes using suction feeding shows that the branchial apparatus may have a significant influence on the function of the feeding mechanism. Figure 2 illustrates the comparative pressures measured at three sites in the oral cavity of a ray-finned fish during suction feeding. Note that, first, negative pressures may be quite large, reaching nearly 600 cm H<sub>2</sub>O below ambient. Second, pressures measured anteriorly and posteriorly within the oral cavity are essentially equivalent in magnitude. Third, posterior to the gill bars in the opercular cavity the pressure drop is only about one-fifth that in the oral cavity. Experimental studies have shown that this reduced negative pressure is caused by the gill bars themselves, which are adducted to form a high resistance to flow at the posterior limit of the oral cavity as the mouth opens (Lauder, 1983c). The gill bars are then abducted to allow water to pass posteriorly as the mouth closes.

Although many taxa do not generate large negative pressures during suction feeding (Norton and Brainerd, 1993), fishes as phylogenetically divergent as sharks (Frazetta, 1994; Moss, 1977; Motta *et al.*, 1991), lungfishes (Bemis, 1987; Bemis and Lauder, 1986), and coelacanths (inferred by Lauder, 1980b) are capable of using suction during feeding.

A typical pattern of jaw muscle activity used during suction feeding is illustrated in figure 3. The time from the onset of mouth opening to peak gape is called the expansive phase, and muscles active at the start of this phase include the levator operculi, sternohyoideus (rectus cervicis), and epaxial muscles (Fig. 3). These muscles act to depress the lower jaw and hyoid, and to elevate the neurocranium. Muscles connecting the hyoid to the lower jaw (such as the geniohyoideus) and the adductor mandibulae muscles may also be active during this time. In such cases, there is considerable overlap between the activity of mouth closing and opening muscles. As the mouth closes (the compressive phase), activity continues in the

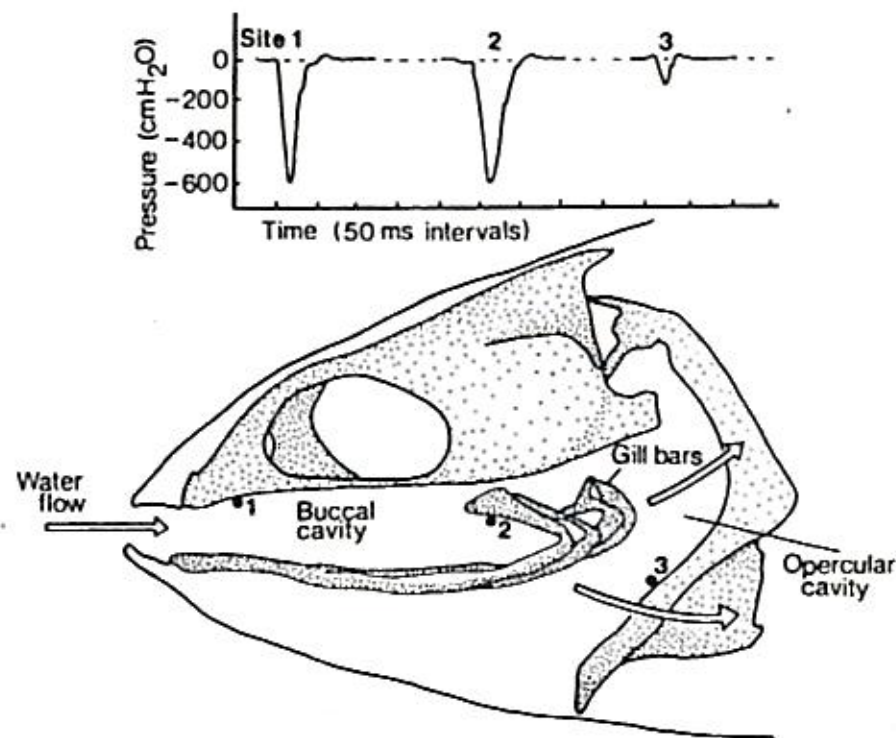
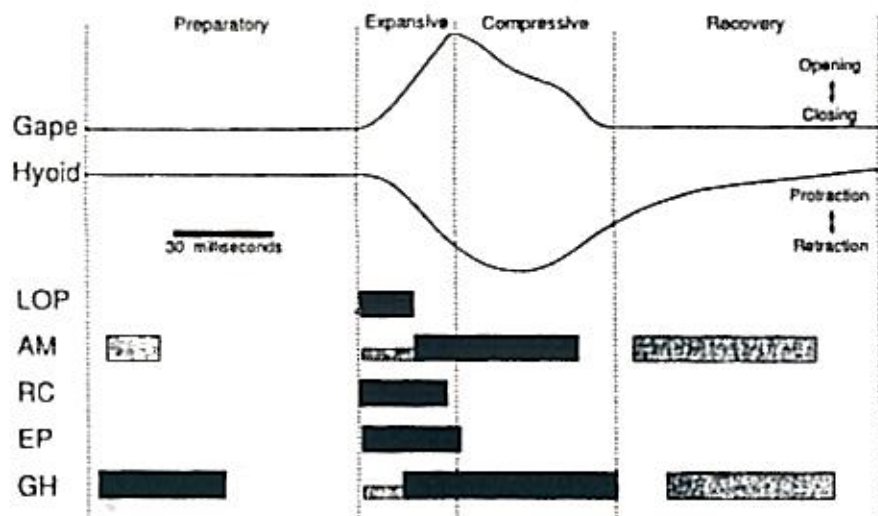


Figure 2. Diagram of the pattern of pressure change in the oral cavity of a percomorph fish during prey capture based on the experimental data from Lauder (1980c; 1983c). Suction feeding is produced by intraoral pressure changes. Note that the negative pressure posterior to the gill bars is greatly reduced compared to both the anterior and posterior sites within the oral cavity (after Lauder 1985c).

adductor mandibulae and geniohyoideus muscles. One consistent kinematic pattern found in almost all teleost fishes studied to date is the peak in hyoid excursion during the compressive phase. This maximal hyoid excursion occurs later than peak gape (Fig. 3) and yet prior to maximal opercular expansion; there is thus an anterior to posterior sequence of peak gape, peak hyoid, and maximum opercular excursion. The recovery phase (defined as the time

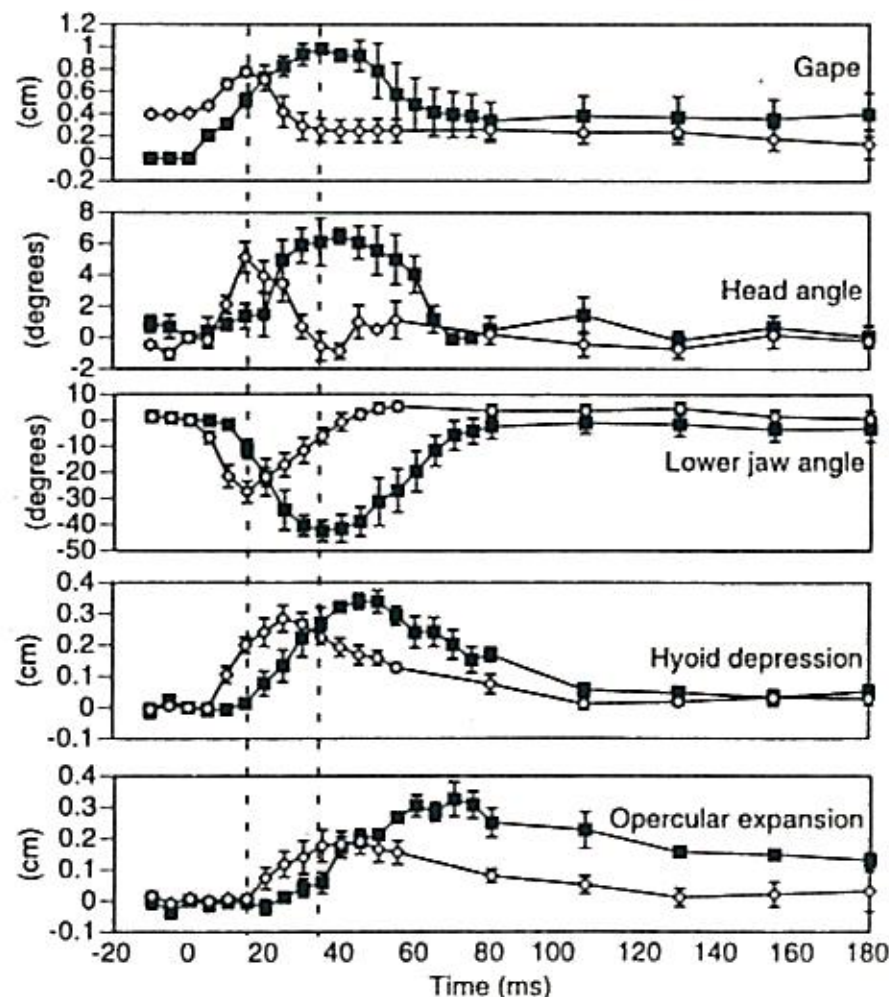


**Figure 3.** Schematic diagram of kinematic and motor patterns common to initial prey capture events in many ray-finned fishes. The names of phases associated with kinematic events are indicated at the top. Note that phase names differ in the fish and tetrapod literature. For example, in tetrapods the compressive phase is referred to as the closing (or fast closing) phase. The preparatory phase has only been observed in a few taxa to date. Black bars indicate times when muscles are consistently active whereas gray bars indicate activity that is only intermittently present. Modified from Lauder and Reilly (1994).

from jaw closure to the return of hyoid, suspensorial, and opercular elements to their initial positions) typically involves activity in the jaw, hyoid, and suspensorial adductor muscles. Finally, in some ray-finned fishes, a preparatory phase occurs prior to mouth opening in which the volume inside the mouth cavity is reduced by activity of jaw and hyoid adductors. This phase has primarily been observed in percomorph ray-finned fishes and has not been found in plesiomorphic taxa (Lauder, 1980a).

#### Intraoral Prey Transport

The process of moving prey from the jaws to the esophagus is referred to as prey transport. In many fishes, the process of transport involves two discrete components: hydraulic transport and pharyngeal



**Figure 4.** Comparison between prey capture and transport kinematics in *Lepomis macrochirus*. Prey transport is indicated by open symbols and initial capture events by solid symbols. The dashed lines indicate peak gape for transports and captures. After Gillis and Lauder (1995).



jaw transport. During pharyngeal jaw transport, fishes use active movements of the gill arches to grasp, manipulate, and move prey from the posterior region of the oral cavity directly to the esophagus (Liem, 1973; Liem and Greenwood, 1981). In order for pharyngeal jaw transport to occur, the prey must be located between the upper and lower pharyngeal jaws (Lauder, 1983b). To transport prey into this location fish utilize suction (hydraulic transport) and create a current of water through the mouth that carries prey from the anterior jaws to the pharyngeal jaws posteriorly. Fishes, such as lungfishes and sharks, that do not have mobile tooth plates on the gill arches to manipulate prey use hydraulic transport exclusively to move prey to the esophagus (Bemis and Lauder, 1986).

Although the process of hydraulic prey transport is superficially similar to initial prey capture by suction feeding, recent results have shown that there can be substantial kinematic differences between prey capture and transport (Gillis and Lauder, 1995). The kinematics of hydraulic transport are illustrated in figure 4 and compared to the kinematics of prey capture. Prey caught between the jaws following the strike are moved posteriorly by a combination of jaw, hyoid, and opercular movements that are significantly more rapid than the motions used to capture prey initially. For example, the mean duration of prey capture in the *Lepomis macrochirus* studied by Gillis and Lauder (1995) was 65 msec, while hydraulic transport was accomplished in 36 msec. In addition, kinematic excursions during transport tend to be smaller than during prey capture.

The process of hydraulic prey transport is widespread among tetrapod out-group taxa and represents a general biomechanical strategy for manipulating prey in the aquatic medium. By creating patterns of water movement within the oral cavity, prey caught between the jaws may be moved into a position appropriate for swallowing. In this sense, hydraulic transport is the functional analog of the tetrapod tongue, and motor patterns associated with hydraulic manipulation in fishes may have played an important role in the evolution of tongue function in early tetrapods.

## OUTGROUP PATTERNS: AMPHIBIANS

Amphibian taxa represent an important clade for understanding amniote feeding mechanisms. Within the Amphibia are species that exhibit aquatic feeding, terrestrial feeding, and (in some taxa) ontogenetic and/or ecological transitions between these two feeding modes. At first glance, it seems, one could hardly ask for a better out-group clade on which to conduct experimental analyses of feeding mechanisms. By studying aquatic feeding in amphibians, one can hold the environment constant and compare their feeding behaviors to those of fish out-group clades in order to examine which functional attributes in amphibians are likely to have been retained from ancestral patterns in fishes. Additionally, terrestrial feeding in amphibians can be compared to aquatic feeding in amphibians and fishes to better understand how the transition to land influenced feeding morphology and function. Furthermore, a longitudinal analysis of feeding across ontogenetic environmental transitions allows the effects of change in environment to be studied directly in the same individuals. Finally, by comparing terrestrial feeding in amphibians to that in amniotes one should be able to define amniote patterns that have been inherited directly from the terrestrial anamniotic feeding mechanism as well as those that appear to be novel for the clade.

Unfortunately, the promise of the Amphibia has yet to be completely fulfilled. Uncertainties in the phylogenetic relationships among and within the three extant clades (Canatella and Hillis, 1993; Larson and Dimmick, 1993; Trueb and Cloutier, 1991) make it difficult to determine which character states within extant clades are primitive for this group as a whole. This problem is complicated by the existence of numerous early amphibian fossil taxa that bear greatest resemblance in jaw morphology to only one of the three extant clades—salamanders (Carroll and Holmes, 1980). Also, in some amphibian clades such as caecilians, relatively few taxa have been studied functionally although recent results (O'Reilly, 1990; O'Reilly and Deban, 1991) will add considerably to current data. In addition, and despite considerable progress during the last five to six years in the comparative study of feeding in frogs (Anderson, 1993; Deban and Nishikawa, 1992; Gray and Nishikawa, 1995; Nishikawa *et al.*, 1992;



Nishikawa and Canatella, 1991; Nishikawa and Roth, 1991; Trueb and Gans, 1983), salamanders (Beneski *et al.*, 1995; Elwood and Cundall, 1994; Findeis and Bemis, 1990; Larson *et al.*, 1996; Lauder and Reilly, 1990; Lauder and Schaffer, 1988; Maglia and Pyles, 1995; Miller and Larson, 1990; Reilly, 1995; Reilly and Lauder, 1988, 1989, 1990b, 1991a), and caecilians (Bemis *et al.*, 1993; Nussbaum, 1983; O'Reilly, 1990), we still lack data on many aspects of feeding behavior in this diverse taxonomic group. For the Amphibia as a whole, the process of prey transport has only been studied quantitatively in a few species, the metamorphosis of feeding function has received limited attention, and data on electromyographic patterns of muscle function are still very limited. Only in one species, for example, has the function of jaw musculature been studied across metamorphosis as well as during prey transport. Nonetheless, the diversity of taxa for which data are available is growing, and these data provide several important insights relevant to amniote feeding.

#### *Aquatic Prey Capture*

Based upon the phylogenetic distribution of suction feeding in non-tetrapod out-groups [such as Dipnoans (Bemis, 1987; Bemis and Lauder, 1986) and actinistians (Lauder, 1980b)] and on morphological correlates of suction feeding function in early tetrapod fossils (Carroll, 1988; Lauder and Reilly, 1994), it is likely that suction feeding is primitive for the class Amphibia. However, whereas each of the three extant clades of amphibians possess aquatic members, some utilize derived feeding mechanisms distinct from their suction feeding ancestors.

Aquatic and semiaquatic adult anurans are known to use their forelimbs to capture and help manipulate prey under water (O'Reilly and Deban, 1991). In addition, aquatic adult caecilians are not known to generate suction during feeding (O'Reilly, personal communication). Instead, like terrestrial caecilians examined to date, they utilize jaw prehension to capture prey. Interestingly, however, *Typhlonectes natans* (an aquatic South American caecilian) does possess certain kinematic features common to suction feeders (e.g., expansion of the buccal cavity during prey capture). Therefore, perhaps aspects of the ancestral suction feeding pattern have been retained in some adult aquatic caecilians whose derived morphologies

preclude the production of adequate negative pressures to generate useful suction (O'Reilly, 1990; O'Reilly and Deban, 1991).

Although suction feeding is not retained in all aquatic amphibians, it is present within all three of the extant amphibian clades, being widespread among aquatic salamanders (larvae and adults), present in some aquatic anurans, and common to many aquatic larval caecilians (O'Reilly, 1990; personal communication). In addition, some tadpole species are known to use suction feeding (Wassersug and Hoff, 1982).

The most important general distinction to make concerning the diversity of suction feeding in amphibians is that taxa within this clade generally possess one of two fundamentally different feeding mechanisms: unidirectional systems in which water flows from anterior to posterior through the mouth cavity (as in fishes), and bidirectional systems in which water drawn into the mouth by suction during the initial phases of the strike must exit anteriorly as the mouth closes (Lauder and Shaffer, 1986). Among salamanders, this distinction is relevant to species that feed in the water as both larvae (with a unidirectional feeding system) and as adults (bidirectionally), and also to comparative analyses of aquatic adults, which possess only limited gill openings posteriorly. These taxa (e.g., *Cryptobranchus*) possess functionally bidirectional feeding mechanisms, and display features of the jaw movement during the strike that are different from taxa possessing unidirectional mechanisms either as larvae or as adults (Cundall *et al.* 1987; Elwood and Cundall, 1994; Reilly and Lauder, 1992).

Analyses of unidirectional suction feeding in salamanders have revealed many similarities with the suction feeding mechanisms of fishes (Lauder, 1985a). During the expansive phase (or fast opening phase in tetrapod terminology) cranial elevation and lower jaw depression both contribute to the gape, hyoid depression is a major effector of intraoral pressure reduction, and there is a distinct recovery phase that is similar to that of fishes. In addition, the fundamental sequence of peak excursions shown in figures 3 and 4 is retained during aquatic prey capture in salamanders, as is the onset of hyoid depression during the Expansive Phase. Hydraulic transport is used to manipulate prey within the oral cavity (Elwood and Cundall, 1994;



Gillis and Lauder, 1994), and electromyographic patterns of homologous muscles show general similarities to those of fishes (Lauder and Reilly, 1990; Lauder and Shaffer, 1985; Reilly, 1995; Shaffer and Lauder, 1985, 1988; Wainwright *et al.*, 1989). The morphological differences between salamanders and fishes (such as limited lateral suspensorial mobility and the lack of ossified opercular elements in salamanders) do not obviate the many kinematic similarities in the feeding mechanism.

The fundamental patterns described previously for aquatic prey capture in fishes thus are retained in many salamanders that feed in the water. These traits cannot then be considered unique to fishes and when similar traits are discovered in amniotes they cannot be regarded as amniote specializations.

#### *Aquatic Prey Transport*

Aquatic intraoral prey transport has been examined quantitatively in only one amphibian taxon to date—larvae of *Ambystoma tigrinum* (Gillis and Lauder, 1994). Suction-based transport in this larval salamander showed remarkable kinematic similarity to the suction-based transport utilized by bluegill sunfish. Kinematic traits shared by transport behaviors across taxa include similar timings of maximal gape, cranial elevation, and gape cycle duration; these behaviors cluster together in a multivariate analysis based on seven kinematic variables (Gillis and Lauder, 1995). Furthermore, suction-based transport behaviors in both sunfish and tiger salamander larvae, while similar to one another, exhibit consistent differences relative to the suction-based capture behaviors in both of these taxa. We suggest that the similarities between aquatic prey transport behaviors in sunfish and larval *A. tigrinum* reflect the retention of a suction-based transport behavior from a common ancestor, and we contend that the divergence between aquatic capture and transport behaviors may constitute a plesiomorphic feature of vertebrate feeding systems.

#### *Terrestrial Prey Capture*

The transition to land during vertebrate evolution required many substantial changes in the morphological and physiological components of organismal design. As amphibians represent the most

primitive vertebrate class to have succeeded in making such a transition (all three extant clades have terrestrial representatives), they are an excellent group within which to examine terrestrial feeding. By comparing terrestrial feeding mechanisms in amphibians to those in aquatic amphibians and fishes, one can better appreciate the kinds of changes that evolved to facilitate feeding on land.

Due to the lower density and viscosity of air relative to water and prey, movement of the aerial medium itself is not a useful vehicle for bringing prey toward the jaws. Instead, the organism itself (or part of it) must move toward and capture the prey. Hence, terrestrial prey capture in many salamanders and frogs is generally associated with projection of the tongue out of the mouth toward the prey (Findeis and Bemis, 1990; Gans and Gorniak, 1982a,b; Nishikawa and Canatella, 1991; Nishikawa and Roth, 1991; Reilly and Lauder, 1989). Accordingly, concomitant with a transition to land in amphibians (be it developmental, ecological, or evolutionary) many structural components of the feeding mechanism are altered (Duellman and Trueb, 1988; Lauder and Reilly, 1990; Wassersug and Hoff, 1982). Many of these alterations facilitate tongue projection, such as osteological and myological modifications to the skull and associated muscles, the formation of a tongue and its intrinsic musculature, and the remodeling of gill arch elements to support the tongue.

Lingual-based terrestrial feeding in many amphibians thus contrasts sharply with the suction mechanism used during aquatic feeding by actively controlling and utilizing specialized musculature and skeletal designs during the protraction and retraction of a projectile tongue. In addition, in salamanders (Larsen *et al.*, 1996; Miller and Larsen, 1990) and frogs (Gray and Nishikawa, 1995; Nishikawa and Canatella, 1991; O'Reilly and Nishikawa, 1995) that lunge during prey capture (in addition to protracting their tongue), specializations in locomotor function may also be involved in prey capture. Even in terrestrial feeding systems in which prey are approached closely and the jaws are used to catch prey directly (thus obviating the need for tongue projection), as in terrestrial cecilians (Bemis *et al.*, 1983; Nussbaum, 1983; O'Reilly, 1990), specializations such as those of the jaw adduction mechanism can be present.



Interestingly, comparisons of salamander and frog feeding mechanisms suggest that these two clades possess fundamentally different systems of neural control of jaw musculature (Nishikawa *et al.*, 1992; Roth *et al.*, 1990). For example, in salamanders, very little muscle activity is present prior to mouth opening, whereas in *Bufo*, muscles such as the geniohyoideus and intermandibularis may be active for 100 to 200 msec prior to the start of the fast opening phase (Gans and Gorniak, 1982a). Frogs possess extensive sensory feedback mechanisms to modulate movements of the jaws during feeding (Anderson and Nishikawa, 1993; Nishikawa *et al.*, 1992), whereas salamanders appear to lack such mechanisms for altering the strike while it is in progress.

Analyses of frog feeding kinematics have shown that considerable diversity exists among taxa in the kinematic patterns used during prey capture, the underlying musculoskeletal mechanisms involved in prey acquisition, and the neural substrates of prey capture (Gans and Gorniak, 1982a; Gray and Nishikawa, 1995; Nishikawa *et al.*, 1992; Nishikawa and Canatella, 1991; Nishikawa and Roth, 1991; Nishikawa and Gans, 1992; Ritter and Nishikawa, 1995). However, only recently have terrestrial prey capture kinematics in salamanders been shown also to exhibit considerable diversity (Findeis and Bemis, 1990; Larsen and Beneski, 1988; Larson *et al.*, 1989; Lombard and Wake, 1977; Maglia and Pyles, 1995; Miller and Larsen, 1990).

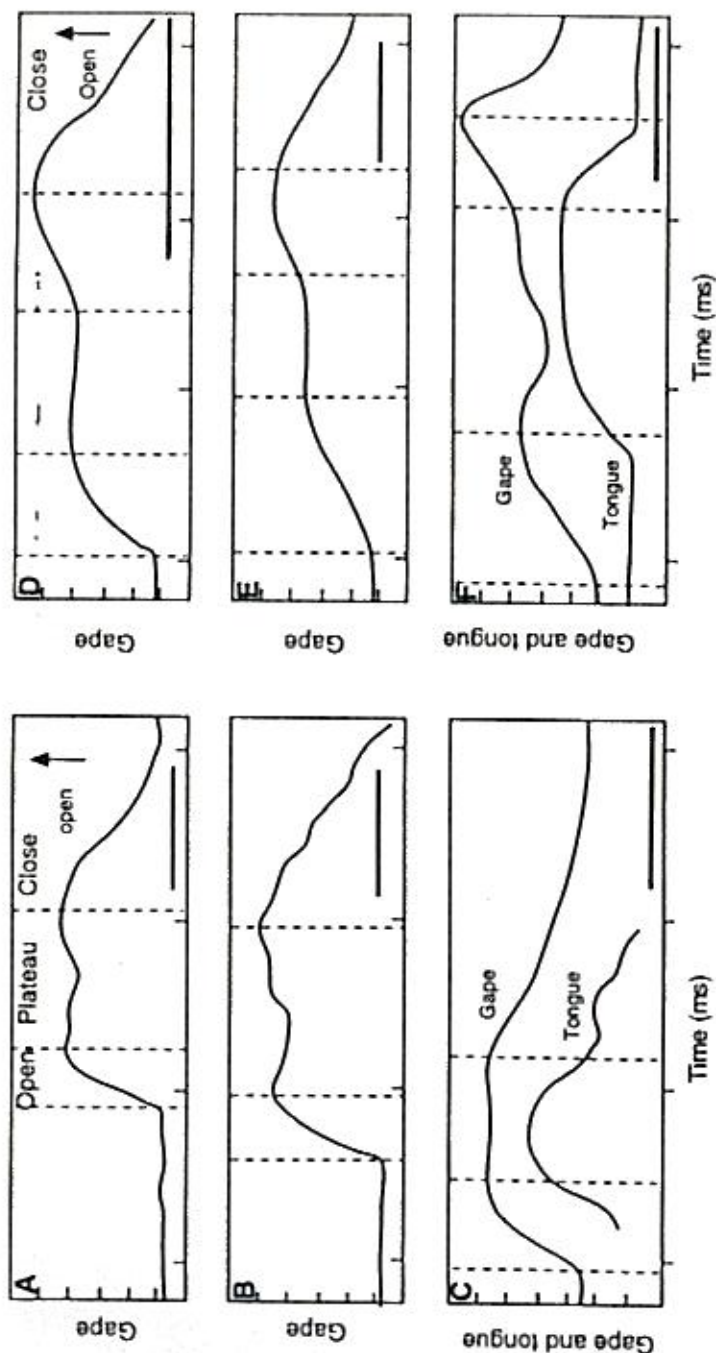
Despite the variation in feeding kinematics, and differences in the neural control of jaw and tongue movements among frogs and salamanders, at least one generalization can be made regarding the kinematics of terrestrial prey capture in these taxa: jaw and tongue movements appear to be coordinated during the gape cycle. As a result, the gape profile of terrestrially feeding salamanders and frogs typically follows one of two general patterns, both of which are distinct from the bell-shaped profile seen during aquatic suction-based feeding (Fig. 3). In the first pattern, which we term a three-phase pattern (after Beneski *et al.*, 1995) the gape cycle consists of three distinct parts: first, there is a period of relatively rapid mouth opening (during which the tongue is raised from the floor of the mouth and begins to be protracted), second, there is a period of a relatively stable or slowly increasing gape (during which the tongue is protracted fully

and begins to be retracted), and third, there is a period of rapid mouth closing (during which the tongue is brought back into the mouth while the jaws close on the prey item). This three phase gape cycle can be seen in figure 5 (panels A, B, and C) and is common to terrestrially feeding ambystomatid salamanders as well as many frogs studied to date (Beneski *et al.*, 1995; Deban and Nishikawa, 1992; Nishikawa and Canatella, 1991; Reilly and Lauder, 1989). In the four phase gape cycle pattern (Beneski *et al.*, 1995) (Fig. 5D-F), a second period of rapid mouth opening is inserted between the period of relatively stable or slowly increasing gape and the period of rapid mouth closing seen in the three-phase pattern. This second period of further gape opening occurs during tongue retraction and appears to accommodate the prey item being returned to the mouth. This four-phase gape cycle is exhibited by many terrestrial salamander clades examined to date (Findeis and Bemis, 1990; Larsen *et al.*, 1989; Miller and Larsen, 1990), including members of the most primitive terrestrial family, the Hynobiidae (Larsen *et al.*, 1996). Hence, the three-phase gape cycle during prey capture seen in ambystomatids is quite possibly a derived kinematic pattern for terrestrial salamanders, whereas the four-phase cycle is likely to be the primitive condition (Beneski *et al.*, 1995). Additionally, forward body lunges appear to be common to many terrestrially feeding frogs and salamanders (although not to ambystomatid salamanders), and this behavior is probably also primitive for terrestrial frogs and salamanders (e.g. Gray and Nishikawa, 1995).

To summarize briefly, projection of the tongue is nearly ubiquitous during prey capture in terrestrial frogs and salamanders. Although variability exists in the feeding mechanisms within and

**Figure 5.** Representative gape profiles from amphibian taxa showing the distinction between three-phase profiles (A-C) and four-phase profiles (D-F). Tongue protrusion is shown in relation to gape in panels C and F. A, *Hyla cinerea*, modified from Deban and Nishikawa (1992); B, *Spea multiplicata*, modified from O'Reilly and Nishikawa (1995); C, *Ambystoma tigrinum*, modified from Reilly and Lauder (1989); D, *Hynobius kimurae*, modified from Larsen *et al.* (1996); E, *Taricha torosa*, modified from Findeis and Bemis (1990); F, *Desmognathus fuscus*, modified from Larsen and Beneski (1988). Vertical dashed lines delimit the phases indicated in panels A and D. The scale bars indicate a time of 50 msec. →



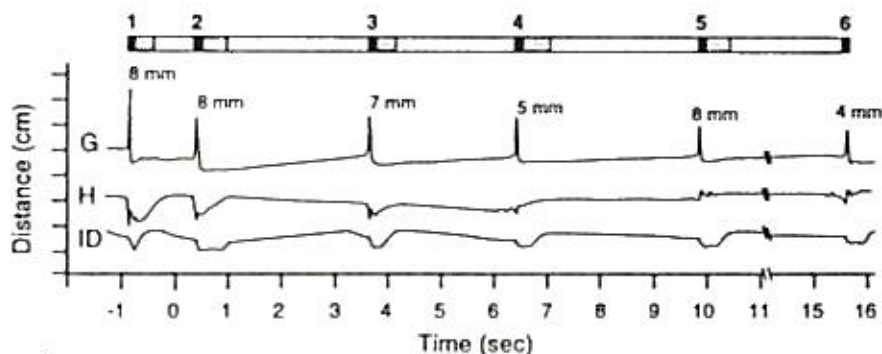


among these taxa, lingual-based terrestrial prey capture shares several general patterns among amphibians, that distinguish it from the aquatic feeding behaviors present in aquatic ancestors. First, projection of the tongue during mouth opening involves protraction of the hyoid apparatus during this portion of the gape cycle, whereas during suction feeding the hyoid begins to be retracted during mouth opening in order to enlarge and reduce the pressure within the buccal cavity (Fig. 3). Second, a period of relatively stable or slowly increasing gape is present during tongue projection (the lack of lower jaw movement during this period presumably provides a more stable platform from which to project the tongue), whereas during suction-based aquatic feeding the gape profile is more bell shaped, lacking a relatively stable (plateau) phase (Fig. 3). Third, although movement of the hyoid apparatus has not generally been explicitly measured during terrestrial feeding in amphibians, in cases in which it has been quantified in terrestrial salamanders (Reilly and Lauder 1989; Findeis and Bemis, 1990), retraction of the hyoid continues through the mouth closing portion of the gape cycle (even after the tongue has been retracted fully back into the mouth), as well as after the mouth is closed. This contrasts with suction feeding wherein the hyoid is being protracted during the recovery phase of the gape cycle (Fig. 3).

#### Terrestrial Intraoral Prey Transport

Amphibians do not process their food intraorally in any significant manner beyond crushing or biting prey between the jaws following capture (Bemis *et al.*, 1983; DeVree and Gans, 1994; Elwood and Cundall, 1994; Erdman and Cundall, 1984; Schwenk and Wake, 1983). Prey held in the mouth may be pressed against vomerine teeth, but extensive processing or reduction of food into smaller pieces does not occur. A major function of the tongue following capture of prey is to transport food from the jaws to the esophagus, and use of the tongue in this manner has been documented in caecilians (Bemis *et al.*, 1983) and salamanders (Reilly and Lauder, 1990a). As is the case with initial prey capture in a terrestrial environment, prey that are much denser than the surrounding fluid require a non-medium dependent transport mechanism. As amphibians use their tongue to transport prey and are the most plesiomorphic clade of tetrapods, they represent an important clade for understanding the





**Figure 6.** Gape and hyoid kinematic profiles for terrestrial prey transport in *Ambystoma tigrinum*. Six transport cycles following capture of an earthworm are shown, and at each cycle the prey is moved posteriorly toward the esophagus. Open bars at the top indicate the duration of the preparatory phase, black bars the transport gape cycles, and shaded bars the recovery phase. Distances shown above each gape cycle indicate the amount of prey transported posteriorly. Abbreviations: G, gape distance; H, hyoid depression; ID, intermandibular distance, which reflects movement of the tongue anteriorly between the mandibular rami. Modified from Reilly and Lauder (1990a).

use of tongue-based mechanisms for intraoral prey movement in amniotes.

Unfortunately, quantitative analyses of terrestrial prey transport have only been performed for one amphibian, *Ambystoma tigrinum*. An entire sequence of prey transport following capture of an earthworm is shown for *A. tigrinum* in figure 6. About 1 cm of a 5 cm long earthworm was captured between the jaws at the strike, and the remaining 4 cm was transported into the oral cavity and esophagus in a series of six transport cycles. The gape cycle of lingual-based prey transport closely resembles that of hydraulic transport in fishes and larval salamanders. Each cycle involves rapid mouth opening in a fast opening phase, followed by a closing phase, and between 4 and 8 mm of the prey is transported posteriorly with each cycle. Unlike the

gape cycle of the initial strike, the gape profile of a transport is bell shaped (Fig. 7) with no plateau maintaining a near constant gape opening. The hyoid moves rapidly in a posteroventral direction during the fast opening phase, and this movement draws prey attached to the tongue posteriorly. During the recovery phase, the tongue is protracted anterodorsally sliding under the prey prior to the next transport cycle.

One key feature of the prey transport cycle is the extended preparatory phase which may last several seconds and has been divided into two parts (Reilly and Lauder, 1990a). During the first part (P1) the gape slowly increases by about 1 mm and the prey is compressed against the roof of the mouth by elevation and protraction of the hyoid. The second part of the preparatory phase (P2) is shorter and during this time just prior to the fast opening phase the gape is held constant. During prey transport in *A. tigrinum* the head and body do not move horizontally, and there is thus no inertial component of body movement relative to the prey: Posterior prey movement is entirely a consequence of posterior tongue movement.

Electromyographic analysis of jaw muscle function during prey transport (Fig. 7) has shown that muscle activity patterns used for prey transport differ significantly from those used to capture prey initially (Reilly and Lauder, 1991b). During prey transport, durations of muscle bursts tend to be shorter, intrinsic tongue muscles such as the genioglossus show very little activity, and the adductor mandibulae internus muscle reaches peak activity much earlier than during initial prey capture. Most surprisingly, the subarcualis rectus one muscle, the major tongue protractor, is strongly active in a single burst despite the lack of observed tongue projection during transport (Fig. 7).

Based on the general similarities of gape and hyoid kinematic profiles in terrestrial transport by *Ambystoma tigrinum* and hydraulic transport by fishes, Lauder and Reilly (1994; also see Reilly and Lauder, 1990a) hypothesized that these two behaviors are distinct from the process of terrestrial prey capture and that the kinematic and motor patterns used during terrestrial transport are derived from the plesiomorphic pattern used for hydraulic transport. Gillis and Lauder (1994) tested this hypothesis explicitly by comparing statistically the kinematic patterns of four behaviors in *A. tigrinum*: aquatic capture



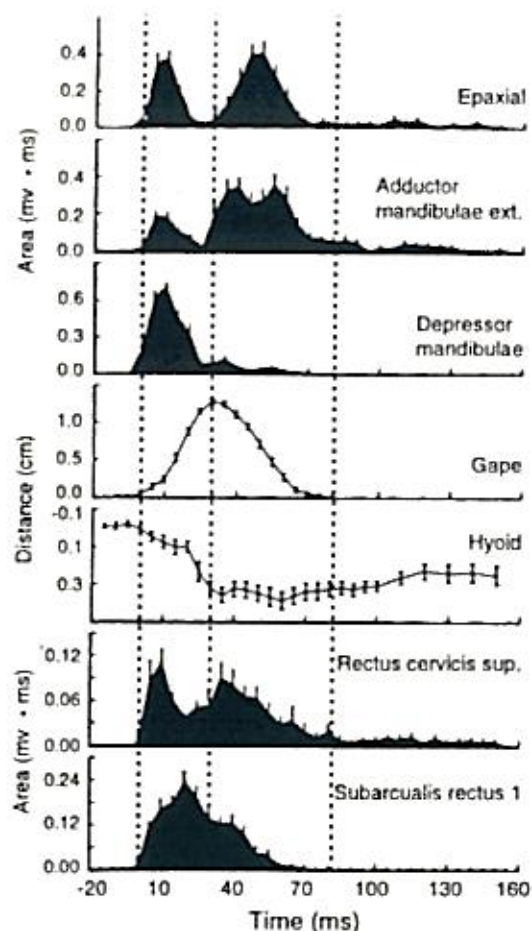


Figure 7. Kinematic and muscle activity profiles during prey transport in *Ambystoma tigrinum*. Solid curves represent the mean rectified integrated area at each time interval for each muscle. Short vertical lines indicate standard errors for all curves which are the mean of 17 transport events. All data were recorded simultaneously. Dashed vertical lines indicate the onset of mouth opening, peak gape, and mouth closing from left to right. Modified from Reilly and Lauder (1991b).

and transport and terrestrial capture and transport. Transport behaviors are indeed similar to one another and distinct from capture behaviors in that they occur significantly more rapidly and involve reduced

excursions relative to prey capture. This suggests that many aspects of the lingual-based transport behavior seen in amphibians may have been inherited directly from the suction-based aquatic transport behaviors of aquatic ancestors. Further studies of prey transport in other amphibians are needed before such an hypothesis can be further supported.

## SUMMARY OF OUTGROUP DATA

Based on these experimental results from extant out-group clades, ten key features of the tetrapod feeding mechanism can be hypothesized as having been present in the terrestrial anamniotic ancestors of amniotes. (1) Prior to the onset of the mouth opening, gape was held constant with the jaws closed or nearly so prior to initial prey capture, or held at a constant low value before mouth opening begins during the prey transport cycle. (2) Mouth opening occurred as a result of both cranial elevation (the product of epaxial muscle activity) and lower jaw depression (caused by activity in the rectus cervicis and depressor mandibulae muscles). (3) The presence of a fleshy tongue permitted lingual-based prey capture and transport. (4) During prey capture, protraction of the hyoid apparatus was used to project the tongue, and occurred as the mouth was opening, or during a period of relatively stable gape. (5) Retraction of the hyoid apparatus during prey capture returned the tongue to the mouth and continued even after the mouth was closed. (6) The prey capture gape cycle was characterized by four phases—a period of mouth opening, a period of stable or slowly increasing gape, a second period of further mouth opening, and a period of rapid mouth closing. (7) A forward lunge occurred concomitant with the prey capture gape cycle. (8) Terrestrial prey transports exhibited a bell-shaped gape profile and were distinct kinematically and electromyographically from the initial capture of prey. (9) Transport of prey within the mouth occurred by posteroventral movements of the hyoid apparatus during mouth opening (in a manner similar to aquatic prey transport). (10) During transport, the hyoid apparatus was protracted (moved anterodorsally) during a Recovery Phase, after the mouth was closed.

Several of these plesiomorphic patterns are modified significantly within amniotes, and yet without an understanding of the

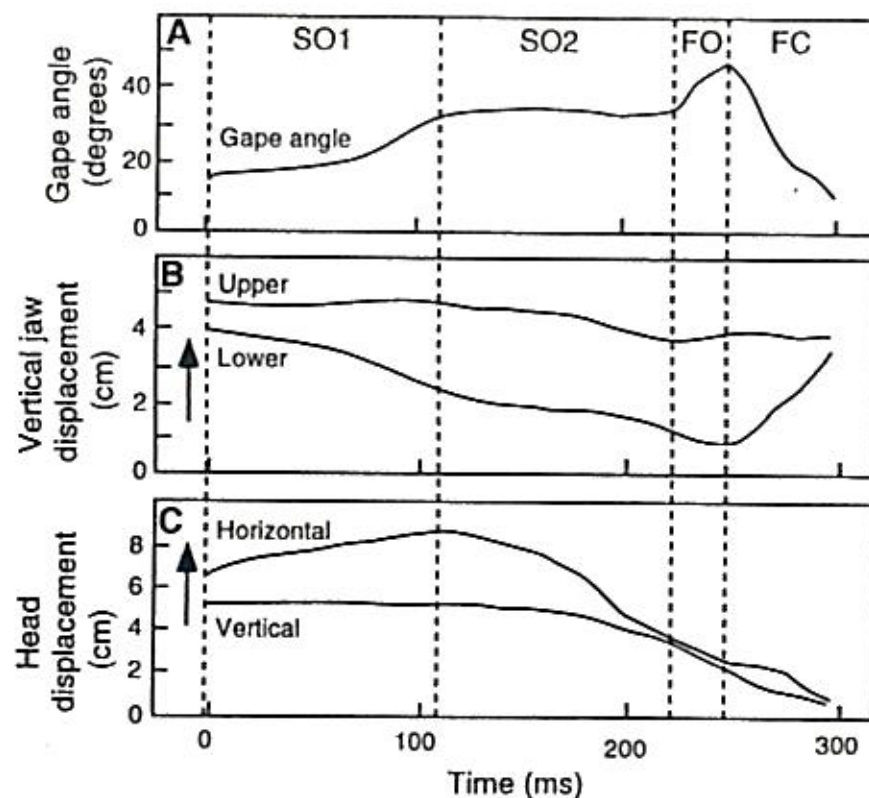


historical origin of amniote functional traits we would be unable to identify sequences of historical transformation in feeding function or to identify homologous functional attributes of feeding systems among tetrapods.

## PRIMITIVE AMNIOTE FEEDING MECHANISMS

Although amniote taxa display considerable diversity in their feeding mechanisms, a number of authors have abstracted from the large base of comparative data several general features of amniote jaw function that are believed to be primitive for the clade as a whole (Bels *et al.*, 1994a; Bramble and Wake, 1985; Delheusy and Bels, 1992; Hiiemae and Crompton, 1985; Reilly and Lauder, 1990a; Schwenk and Throckmorton, 1989). Many of these characteristics of amniote feeding are well illustrated by the feeding systems in lizards that primitively use lingual prehension to capture prey (Herrel *et al.*, 1995; Schwenk and Throckmorton, 1989; Smith, 1984, 1988). Here we focus on lizard prey capture and manipulation as exemplifying many traits that may be representative of primitive amniote feeding mechanisms.

The transition to amniote feeding involves several significant morphological and functional changes from feeding systems described previously in amphibians and fishes. The gill arch elements that feature so prominently in fish and salamander feeding have been modified and greatly reduced. The tongue and supporting skeletal elements have become elaborated (Delheusy *et al.*, 1994; Smith, 1986), and the skull has a smaller number of independently mobile elements [the presence of various types of cranial kinesis notwithstanding (Frazetta, 1962; Smith and Hylander, 1985)]. Many amniote taxa utilize extensive intraoral food processing prior to swallowing prey, and several distinct behaviors associated with such prey manipulation have been described: for example, inertial feeding, "cleaning of teeth," chewing or reduction of prey, and pharyngeal packing. Here our focus will be on describing the function of the feeding mechanism during prey capture and transport, with the overall aim of assessing functional traits that might be primitive for the Amniota.



**Figure 8.** Gape distance (A) and vertical (B) and horizontal (C) jaw and head displacement plotted for prey capture in *Oplurus cuvieri*. Note the presence of a slow opening phase in the gape profile (SO1) and the relative lack of upper jaw movement. Arrows in B and C indicate dorsal and posterior movement respectively. Modified from Delheusy and Bels (1992).

### Terrestrial Prey Capture

The gape profile of initial prey capture is illustrated for the iguanid lizard *Oplurus cuvieri* in figure 8 (Delheusy and Bels, 1992). The gape profile is divided into four distinct phases: an initial phase of slow opening (SO1), a plateau of relatively constant gape (SO2), fast opening (FO), and a fast closing phase (FC). This is somewhat similar to the four-phase cycle seen in many terrestrial salamanders, although the initial phase of opening in these out-group taxa is relatively rapid,



whereas in lizards it can be quite slow. The skull moves posteriorly slightly during SO1 and reaches maximal posterior movement during the transition to SO2 (Figure 8) before moving anteriorly substantially during SO2, FO, and FC. Vertical motion of the skull is minimal during the SO1, but ventral movement begins during SO2 and continues through both the FO and FC phases. Gape is the result of movement of both the upper and lower jaws, however, the lower jaw tends to account for most of the gape changes observed during the gape cycle. For example, the gape increase during SO1 and FO is due mostly to lower jaw movement and much of the change in gape during Fast Close is due to elevation of the lower jaw while the upper jaw remains relatively immobile [Figure 2; (Delheusy and Bels, 1992)].

Anterior movement of the tongue begins during the SO1 phase but accelerates rapidly during SO2 as the tongue is extended toward the prey. Prey contact occurs at the end of SO2 (Delheusy and Bels, 1992), and during the FO phase the tongue and hyoid move posteroventrally to bring prey into the mouth. The kinematic pattern at this time is quite similar to that seen in terrestrial salamanders with a four-phase feeding cycle (Fig. 5).

Although the slow opening phases have been observed in prey capture events from taxa in all three major lineages of iguanid lizards (Herrel *et al.*, 1995; Schwenk and Throckmorton, 1989; Wainwright *et al.*, 1991), not all species show both these phases, and the occurrence of the SO phases may also depend on prey type (Bels and Grosse, 1990; Gorniak *et al.*, 1982; Urbani and Bels, 1995). *Anolis equestris*, for example, shows only a single SO phase with no distinct plateau (SO2) phase during prey acquisition (Bels and Delheusy, 1992). In addition, analysis of aquatic prey capture kinematics in amniotes such as the snapping turtle (*Chelydra serpentina*) show that there is no slow opening phase of the gape cycle (Lauder and Pendergast, 1992). Kinematic profiles during mouth opening resemble those of aquatic prey capture in aquatic amniote ancestors.

Electromyographic studies of jaw muscle function during initial prey capture have shown that during the slow opening phases there is considerable activity in the hyoid and intrinsic tongue muscles (Herrel *et al.*, 1995) that continues into the fast opening phase. The onset of activity in the depressor mandibulae is coincident with the

start of Fast Opening while the sternohyoideus muscle is active during fast opening and again during the closing phase [which consists of both fast close and slow close phases in *Agama*; (Herrel *et al.*, 1995)]. The adductor and pterygoid muscles are strongly active during the fast opening and closing phases.

As noted by Herrel *et al.* (1995), jaw muscle activity patterns in *Agama* are very similar to those described previously for chameleons (Wainwright and Bennett, 1992), whereas there are significant differences with jaw motor patterns reported for *Sphenodon* (Gorniak *et al.*, 1982). However, given the paucity of comparative data on motor patterns during initial prey capture in lizards it is difficult to generalize on the causal bases for these differences.

#### Terrestrial Prey Transport

Following prey capture, lizards display a number of intraoral manipulatory behaviors including chewing, repositioning of prey, pharyngeal packing, cleaning, and transport (e.g. Deheusy and Bels, 1992; Kraklau, 1991; Smith, 1984, 1988). In order to make comparisons with nonamniote taxa it is important to base comparative analyses and evolutionary hypotheses on appropriate behavioral comparisons; in some cases it is difficult to discern from published figures which behavior is being analyzed, and without detailed kinematic studies or x-ray cinematography it is often difficult to know exactly how prey are being moved within the oral cavity. In an effort to describe comparable data for amniotes and anamniotes we will focus on terrestrial prey transport behavior, recognizing that jaw function in amniotes is associated with a wide diversity of postcapture behaviors.

Transport of prey from the anterior region of the oral cavity into the posterior portion for swallowing has been described for several taxa of lizards (e.g. Deheusy and Bels, 1992; Schwenk and Throckmorton, 1989; Smith, 1984; So *et al.*, 1992). Delheusy and Bels (1992) illustrate successive transport cycles in *Oplurus* and show that many of the phases of the gape cycle present during initial capture are also present during transport. The main consistent exception is the SO2 phase, which is absent. Similar results were obtained by So *et al.* (1992) (Fig. 9). Examination of transport gape profiles suggests that even the recognition of an SO phase in any form may be problematic



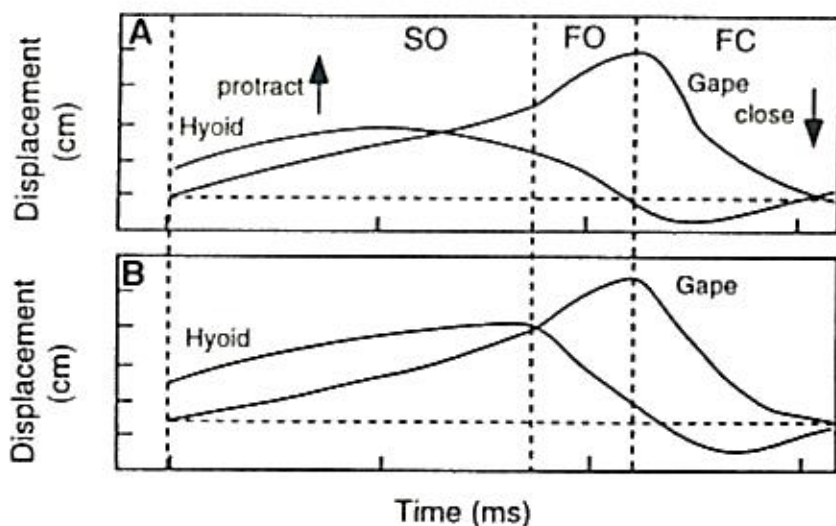


Figure 9. Schematic diagram of gape and hyoid kinematic profiles during prey transport in (A) *Chamaeleo jacksonii*, and (B) *Ctenosaura similis*. Note that the hyoid is protracted during the SO phase and retracted during FO. Modified from So *et al.* (1992); panel B after Smith (1984).

in many gape cycles, as there is only a slight change in slope of gape distance versus time (Fig. 9). Given that any increase in gape is likely to begin slowly, accelerate to a maximum rate of change, and finally decrease toward a maximum excursion, there must mathematically be an inflection point in the gape curve that could be identified as the end of slow opening and the start of fast opening. The existence of this inflection point need not be a reflection of any active neurological control or biomechanical feature of the feeding mechanism. The presence and extent of the SO phase is clearly highly variable both among transport cycles, among manipulatory behaviors, and among taxa.

Transport of prey following capture involves repeated cycles of hyoid protraction and retraction that move prey toward the esophagus. During the slow opening phase of the gape cycle the hyoid is protracted (Fig. 9). Retraction begins either just prior to or during fast opening and continues through the closing phase. This general pattern of gape and hyoid movements is superficially similar to that seen

during the four-phase prey capture cycle seen in most terrestrial salamanders but contrasts substantially with that seen during prey transport in the only terrestrial salamander in which transport has been examined, *Ambystoma tigrinum*. In *A. tigrinum*, recall that the hyoid is retracted over the first portion of the gape cycle (during mouth opening) and protracted during a recovery phase after the gape cycle is finished (after mouth closing). Without further examination of terrestrial prey transport in other amniotes, it will be hard to determine to what extent transport behavior in amniotes has diverged relative to that in terrestrial anamniotic ancestors.

Delheusy and Bels (1992) have conducted quantitative statistical analyses of transport behavior and compared kinematic transport patterns to jaw movements during chewing, initial capture, and cleaning. An analysis of variance showed chewing and transport cycles to differ significantly in duration and time to maximal lower jaw depression, and So *et al.* (1992) also found numerous significant differences between transport and chewing cycles in chameleons. A principal component analysis of these behaviors in *Oplurus* shows that cleaning behavior is the most distinctive and that there is considerable overlap between initial capture, transport, and reduction behaviors. These behaviors, although statistically distinct, nonetheless share a number of common kinematic patterns.

## PLESIOMORPHIC AMNIOTE FUNCTIONAL TRAITS

Comparison of functional patterns in squamates to those described previously for amphibians and fishes suggests that several of the traits observed in amniotes are novel features of the feeding mechanism that are likely to have been present at the base of the amniote radiation. The diversity of intraoral processing behaviors in which the jaws, tongue, and hyoid are all involved (e.g., chewing, repositioning of prey, and cleaning) is a novel feature of the amniote feeding mechanism. In addition, the presence of a slow opening phase in which gape distance increases relatively slowly at the start of the gape cycle is an amniote trait. Associated with slow opening are seemingly unique patterns of hyoid muscle activity that result in hyoid



and tongue protraction during slow opening. However, without further electromyographic studies of terrestrial prey capture in salamanders that utilize a four-phase cycle of feeding, it will be hard to determine whether these patterns of muscle activity are really unique to amniotes or are simply not present in the ambystomatid salamanders (which have a three-phase cycle of prey capture) that have been studied to date.

It is tempting to view experimental data from amniotes as supporting the idea that a SO phase is required for the tongue-based feeding systems that characterize so many squamates. However, ambystomatid salamanders and many frogs possess well-developed tongue-based feeding systems that lack a SO phase.

### SYNTHESIS: CONCLUSIONS AND UNRESOLVED ISSUES

Bramble and Wake (1985) presented a general model of kinematic and electromyographic patterns for tetrapod feeding mechanisms. This model has been of important heuristic value because it has provided a hypothesis against which empirical data from extant tetrapods can be tested. At present, Bramble and Wake's model has received some support (see, for example, Schwenk and Throckmorton, 1989). However, this model has also come under review where experimental results do not match predictions. Based on the results from analyses of individual taxa, various authors have examined specific predictions of this model (Deheusy and Bels, 1992; Reilly and Lauder, 1990a, 1991b; So *et al.*, 1992).

Although there is no doubt that, in amniotes, several general characteristics of the Bramble and Wake model do describe features of jaw function common to many amniote clades, the experimental results summarized above for amniotes and anamniote tetrapods also point out a number of complications that render their description of a "generalized tetrapod" functional pattern problematic.

First, the pattern of jaw movement and muscle function during prey transport in ambystomatid salamanders (the only anamniote taxon for which quantitative data are available on prey transport) is quite different than expected under the general tetrapod model. For

example, there is no slow opening phase, hyoid protraction thus does not immediately precede fast opening, motion of the head and neck does not occur in the predicted manner (there is often very little horizontal skull movement), and there is no electrical activity in the depressor mandibulae and hyoid muscles just prior to the fast opening phase. In fact, many features of ambystomatid transport systems instead appear to be primitive traits inherited from aquatic ancestors. However, recall that ambystomatids show relatively distinct kinematic patterns during prey capture relative to most other salamanders, and it is indeed possible that this is true of their transport behavior as well. Further examination of transport behaviors in other urodeles is required before the accuracy of Bramble and Wake's model can be assessed relative to such primitive tetrapods.

Second, results from a variety of amniote taxa also suggest that kinematic and electromyographic data do not tightly fit predicted patterns. For example, in many transport and manipulation cycles there is no clear SO phase, and electromyographic patterns in the depressor mandibulae, sternohyoideus, adductor mandibulae, and pterygoideus show unpredicted patterns (Herrel *et al.*, 1995). In addition, comparing prey capture in iguanians to the proposed model has been done by several investigators (e.g. Kraklau, 1991; Schwenk and Throckmorton, 1989), and Delheusy and Bels (1992: p. 184) summarize their results by noting that "Our data do not support the model of Bramble and Wake or their speculation about the relationship between SO II duration and the size of the prey."

Given the limited experimental data available in 1985, it is perhaps not surprising that more recent results have called many of our previous concepts of amniote jaw function into question. However, even these additional data are insufficient to do more than suggest the outlines of a new view of amniote feeding function. Given the diversity of both anamniote and amniote taxa, the number of taxa for which we have both kinematic and electromyographic data is surprisingly few. We probably do not have a complete set of kinematic and electromyographic data for more than ten taxa of anamniote tetrapods and squamates. Furthermore, such data are rarely available for the full range of behavioral diversity exhibited by the feeding mechanism. In order to evaluate biomechanical models of jaw



function and to produce evolutionary hypotheses of functional transformation, a much larger data set is needed. Such experimental data will permit a more quantitative assessment of the diversity of feeding system function in primitive amniotes and provide a better understanding of how plesiomorphic functional traits combined with novel features to form the basal amniote feeding mechanism.

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