

## THE EVOLUTION OF TETRAPOD FEEDING BEHAVIOR: KINEMATIC HOMOLOGIES IN PREY TRANSPORT

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**Abstract.**—One of the major features of the aquatic-to-terrestrial transition in vertebrate evolution was the change in the mechanism used to transport prey from the jaws to the throat. Primarily, vertebrates use hydraulic transport, but the transition to terrestrial life was accompanied by modifications of the hyobranchial apparatus that permit tongue-based transport. Despite an extensive data base on amniote feeding systems and mechanisms of intraoral prey transport, few data are available on the mechanism of prey transport in anamniote tetrapods. Transport cycles of four *Ambystoma tigrinum* (Amphibia) feeding on worms and crickets were filmed at 150 frames per second to produce quantitative profiles of the intraoral transport cycles for the two prey types. During the transport cycle the head and body remain stationary relative to the background; transport in *Ambystoma tigrinum* thus does not involve inertial movements of the head or body. Prey type had little effect on the kinematics of prey transport. The process of prey transport may be divided into four phases: preparatory, fast opening, closing, and recovery. The preparatory phase itself is divided into two parts: an extended segment that may include slight slow opening and a static phase prior to mouth opening where no change in gape occurs. The kinematic profile of transport in terrestrial salamanders is extremely similar to that used by fishes during hydraulic (aquatic) prey transport. We hypothesize that the distinct recovery and preparatory phases in the transport cycle of anamniote tetrapods are together homologous to the slow opening phases of the amniote cycle, and that during the evolution of terrestrial prey processing systems the primitive extended preparatory phase has become greatly compressed and incorporated into the amniote gape cycle.

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The transition from water to land in vertebrate evolution involved a great many morphological and functional changes in the skull and feeding mechanism. Aquatic vertebrates capture their prey primarily by suction feeding in which a current of water, created by intraoral pressure changes, carries the prey into reach of the jaws (Lauder, 1985; Lauder and Reilly, 1988). Water currents created by movements of cranial and hyobranchial bones manipulate prey within the oral cavity, and even fishes that chew their prey extensively after capture, such as lungfishes, use a hydraulic transport system (Bemis and Lauder, 1986). In contrast (and primarily due to the differing densities of water and air) terrestrial vertebrates chiefly rely on movements of the tongue to manipulate prey within the oral cavity (Bramble and Wake, 1985; Hiiemae and Crompton, 1985).

The mechanism of intraoral prey manipulation and transport has been studied in many amniotes (Crompton et al., 1977; Byrd et al., 1978; Throckmorton, 1980; Gorniak and Gans, 1982; Smith, 1984, 1986; Franks et al., 1984; Hiiemae and Crompton, 1985; Crompton, 1989) and the pattern of cranial bone movements is now well characterized

for several taxa. Movement of the jaws, hyoid apparatus, and tongue have been quantified and a general understanding of cyclical motions of the jaws and hyoid during chewing and prey transport has emerged (e.g., Gans et al., 1978; Hiiemae and Crompton, 1985). Bramble and Wake (1985) proposed a model for prey transport in primitive, generalized tetrapods, and other investigators have analyzed patterns of jaw movements relative to different types of food eaten (De Vree and Gans, 1973; Crompton et al., 1977; Weijs and Dantuma, 1981).

In contrast to the numerous studies of amniote feeding systems, there are virtually no data on anamniote tetrapod prey transport mechanisms. Yet, such data are critical both to (1) understanding the origin of terrestrial feeding systems and the historical transformation of primitive hydraulic feeding systems into terrestrial tongue-based prey transport designs, and (2) testing the generality of models of tetrapod feeding.

The aims of this paper are threefold. First, we present kinematic data on prey transport in a terrestrial non-amniote tetrapod, the tiger salamander *Ambystoma tigrinum*. These data serve as a description of the process of intraoral prey transport from the jaws

to the esophagus. Second, we compare these data to previous results on both amniotes and ray-finned fishes, and propose homologies between phases of the transport cycle in *Ambystoma tigrinum* and the prey transport cycles of fishes and amniotes. Third, we examine primitive features of the prey transport system in tetrapods and discuss several hypothesized evolutionary transformations in tetrapod feeding systems.

#### MATERIALS AND METHODS

Kinematic data were obtained from four adult *Ambystoma tigrinum mavortium* (snout-vent lengths 106–112 mm) collected from near Limon, Lincoln County, Colorado. Animals were trained to feed under bright lights (1,200 watts) and filmed with a Redlake Locam camera using Kodak 4X Reversal film at 150 frames per second. During filming, tiger salamanders were placed in an eight-liter glass aquarium with a background marked with a grid of one-cm squares. The temperature in the aquarium during filming was about 20°C, and a cooling system was used while the filming lights were on to keep the air in the aquarium at an approximately constant temperature. Prey (either adult crickets (*Acheta domestica*) or 4–6-cm long earthworm pieces (*Lumbricus*)) were presented to the animal in front of the jaws and filming began at or before the strike and continued until transport of the prey into the mouth and down the esophagus had been completed.

Transport cycles with clear lateral views and no obstruction of landmarks by the prey items were selected for analysis. A total of 20 worm transport cycles (5 from each of four animals) and 22 cricket cycles ( $N = 6, 7, 4, 5$  from the same four animals) were digitized. Films were projected frame by frame onto a Houston Instruments Hipad digitizer where distances and angles describing the positions of the body, head, jaws, hyoid and tongue were measured directly. For each cycle, frame zero was defined as the frame preceding the first frame in which the mouth began to open before prey transport. Thirty-eight frames were analyzed from each cycle using frame zero as a reference: frame -60, -50, -40, -30, -20, -10, -5 to +15 (in one-frame increments), 20, 25, 30, 35, 40, 50, 60, 70, 80, 90, 100.

These points encompass a time from 400 msec before to 667 msec after time zero, and were chosen from a preliminary viewing of the films.

Eight variables were digitized from each of these 38 frames for each transport cycle (Fig. 1). For each animal, two stable and readily identifiable landmarks were located on dorsal spot patterns from which to measure movements relative to the body. Because the body landmarks differed for each individual, the relative change in the angle variable was used (described below). The vertex of the angle of the jaw, where the upper and lower lips intersect, was used to measure head and hyoid positions. Body position (BP, measured in cm), is the horizontal distance from a landmark spot on the body to a fixed line on the background grid (Fig. 1). Head position (HP, measured in cm) is the horizontal distance from a spot near the angle of the jaw to a fixed line on the background grid. Head and body positions quantify horizontal movements of the animal's body and head relative to the background; both head and body positions were measured to determine if the head could be extended anteriorly, independently of the body by extension of the neck. Large parallel changes in these two variables or large changes in head position with no change in body position would indicate that inertial feeding occurs.

Lower jaw angle (LJA, measured in degrees) is the angle of the jaw relative to two landmark spots on the body (Fig. 1). LJA decreases when the jaw is depressed. Head angle (HDA, measured in degrees) is the elevation of the head, defined by three points, one at the anterior tip of the upper jaw and two spot landmarks on the body. HDA increases when the head is elevated (Fig. 1). Gape distance (GD, in cm) is the linear distance between the anterior tips of the upper and lower jaws. Hyoid distance (HYD, in cm) is the vertical distance of the gular region from the vertex of the jaw angle. HYD increases as the hyobranchial apparatus (and tongue) is pulled posteriorly and rotates ventrally during retraction, and decreases to its minimum when the hyoid and tongue recycle anterodorsally. It should be noted that movements of the tongue are mechanically linked to protraction and retrac-

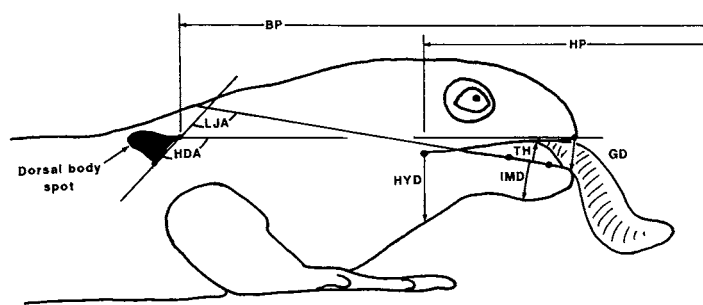


FIG. 1. Kinematic variables measured from film frames of intraoral transport in *Ambystoma tigrinum*. Variables are: BP, body position; GD, gape distance; HDA, head angle; HP, head position; HYD, hyoid distance; IMD, intermandibular distance; LJA, lower jaw angle; TH, tongue height. Both head and body positions were measured with respect to a fixed line on the background grid. HDA and LJA were measured relative to two landmarks on the body, dorsal and posterior to the shoulder girdle. HYD increases as the hyobranchial apparatus and attached tongue move posteroventrally during retraction and decreases when the tongue and hyoid recycle forward. Details regarding measurements of the variables are given in Materials and Methods.

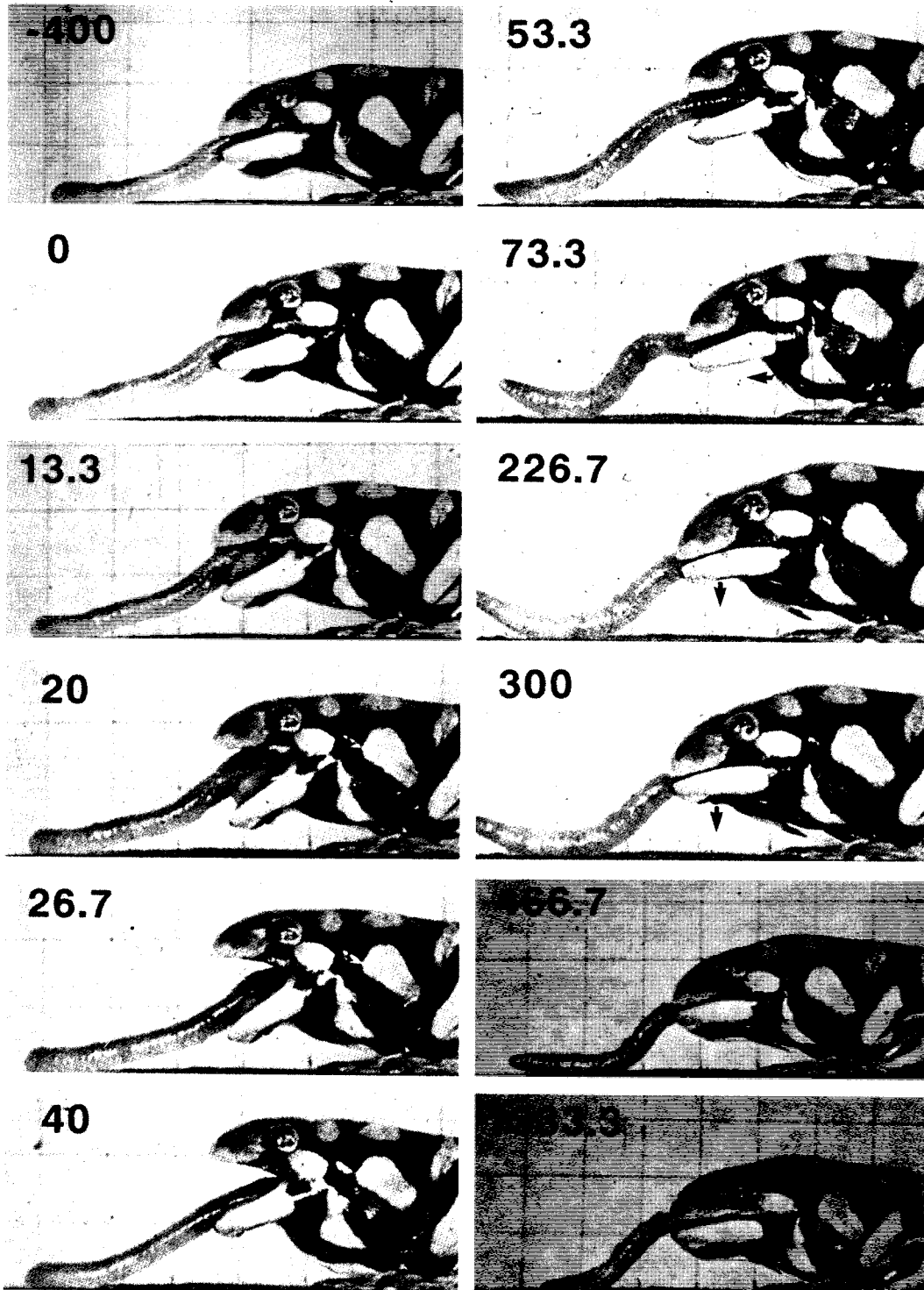
tion of the hyobranchial apparatus by the presence of median skeletal elements (basibranchial and second radials) that lie within the tongue musculature (Reilly and Lauder, 1989a). Maximum HYD occurs at maximum hyoid retraction. Intermandibular distance (IMD, in cm) is the maximum perpendicular distance that the intermandibular area extends ventrally from the lower jaw. IMD increases when the tongue is pushed anteriorly under the prey. Tongue height (TH, in cm) is the greatest perpendicular height of the tongue above the dorsal margin of the lower jaw and is visible only when the jaw is partially open.

To quantitatively summarize the kinematics of prey transport, the movement curves (profiles) for each kinematic variable were averaged across individuals for the two prey types. To do this the mean was calculated ( $\pm$ SE) for each of the 38 frames and plotted against time in milliseconds (6.667 msec/frame). Because of differences in individual spot landmarks used in the angle measurements, the angle profiles were transformed to  $0^\circ$  at time 0 before averaging to reflect change in angle. In other words, each digitized value in a profile received the same transformation necessary to adjust the

value at time 0 to zero. It is important to emphasize that kinematic profiles such as those presented in Figure 3 represent overall averages for all individuals within a prey type and levels of variation are confounded. These values should not, therefore, be used to estimate the statistical significance of differences between the two prey types.

To statistically examine the extent of kinematic modulation attributable solely to the prey type, kinematic profiles for each individual transport cycle were analyzed using a Tektronix 4107 graphics terminal to digitize amplitudes and durations of movement. Thirteen variables (listed in Table 1) were measured from the kinematic profiles for each cycle. Five peak-amplitude variables were measured as the difference between the value at time 0 and the maximum value (for GD, HDA, LJA) or the beginning of a plateau (for HYD, IMD) during the transport cycle. Five time-to-peak duration variables (for GD, HDA, LJA, HYD, IMD) were digitized from time 0 to the time of the maximum. For example, the time from the start of mouth opening to the time of maximum gape was measured as the "time-to-peak gape" variable (Table 1). Three cycle times (for GD, HDA, LJA) were mea-

FIG. 2. Frames from a high-speed film of one feeding sequence depicting an intraoral prey transport cycle in *Ambystoma tigrinum*. The time is indicated on each frame in milliseconds. Time 0 is defined as the frame immediately preceding the frame in which the mouth first starts to open. Arrows indicate the anterior protraction of the hyoid (73.3 msec) causing the intermandibular area to bulge ventrally as the tongue slides under the prey



(226.7–466.7 msec). The beginning of the next transport cycle occurs 800 msec after the last frame shown. Note how the hyobranchial apparatus (with the tongue and attached prey) moves posteroventrally from 13.3 msec to 53.3 msec. This movement pulls the worm into the mouth.

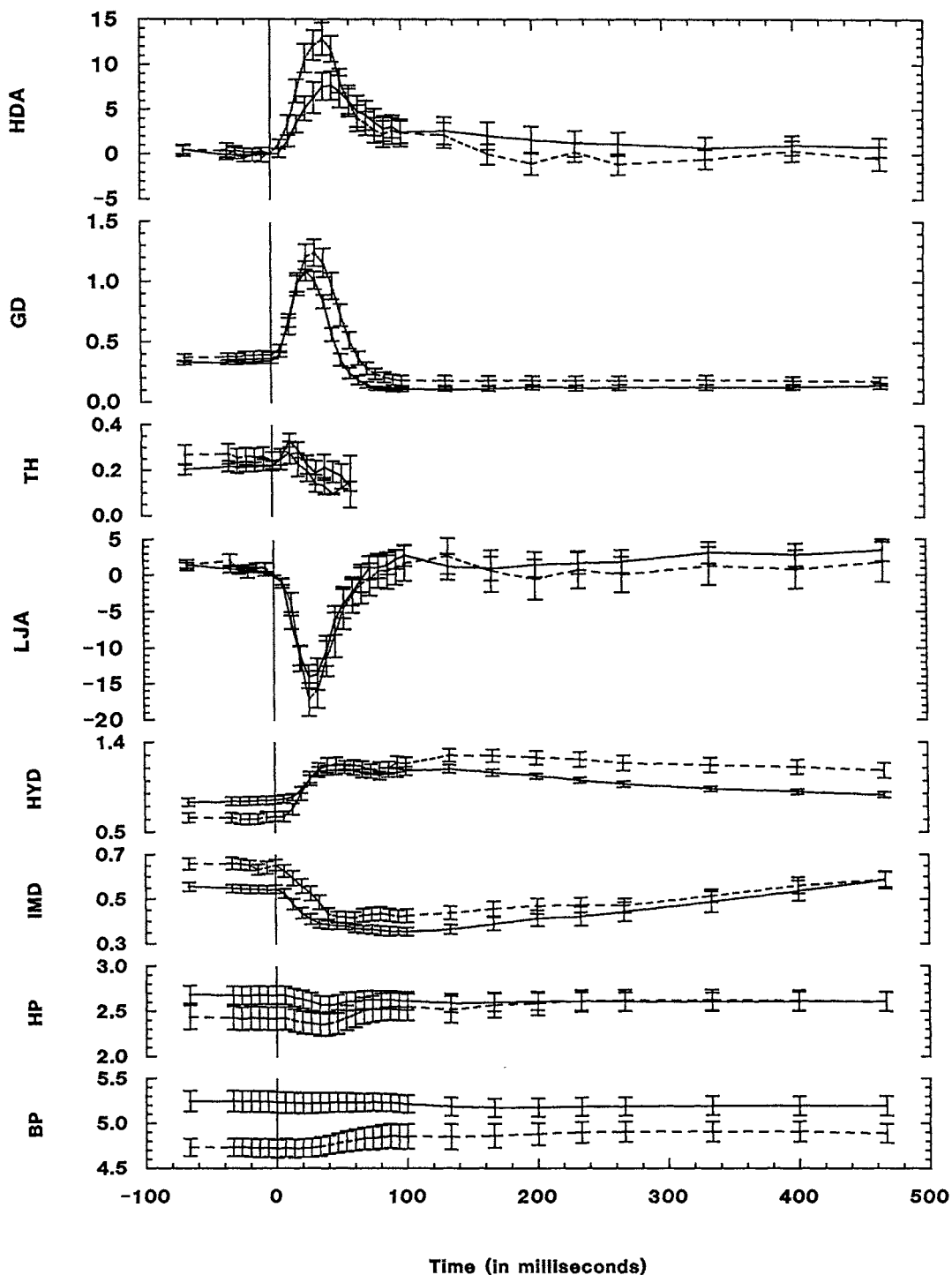


FIG. 3. Quantitative profiles for eight variables describing the kinematics of intraoral prey transport in *Ambystoma tigrinum*. Mean profiles ( $\pm$  standard errors) for worm (solid line,  $N = 22$ ) and cricket (dashed line,  $N = 20$ ) transport cycles are plotted against time for each variable (distances in cm, angles in degrees). Angle variables have been scaled to a value of zero degrees at time 0 to allow averaging of cycles with different initial head angles. The tongue height variable (TH) is not measurable after 60 msec. Note that there is little variation

TABLE 1. Mean and statistical differences of kinematic variables describing the intraoral transport cycle for *Ambystoma tigrinum* feeding on two prey types.

Variable <sup>1</sup>	Mean $\pm$ standard error		Analysis of variance tests <sup>2</sup> for		
	Worms (N = 22)	Crickets (N = 20)	Prey type	Individual	Interaction
Peak gape distance	0.8 $\pm$ 0.07	1.0 $\pm$ 0.11	ns	ns	ns
Time to peak gape	19.9 $\pm$ 1.1	22.8 $\pm$ 1.2	ns	ns	ns
Gape cycle time	53.6 $\pm$ 2.3	60.8 $\pm$ 2.6	ns	ns	ns
Peak head angle	12.8 $\pm$ 1.4	16.1 $\pm$ 1.7	ns	ns	ns
Time to peak head angle	26.0 $\pm$ 1.7	26.3 $\pm$ 1.7	ns	0.000	0.000
Head cycle time	51.6 $\pm$ 2.5	53.0 $\pm$ 2.3	ns	0.000	ns
Peak lower jaw angle	19.8 $\pm$ 1.5	21.3 $\pm$ 2.4	ns	ns	ns
Time to peak lower jaw angle	19.7 $\pm$ 1.1	22.0 $\pm$ 1.4	ns	ns	ns
Lower jaw cycle time	45.6 $\pm$ 2.0	49.6 $\pm$ 2.3	ns	ns	ns
Peak hyoid distance	0.4 $\pm$ 0.04	0.5 $\pm$ 0.04	ns	ns	ns
Time to peak hyoid distance	28.7 $\pm$ 1.9	33.7 $\pm$ 2.2	ns	ns	ns
Peak intermandibular distance	0.2 $\pm$ 0.02	0.3 $\pm$ 0.02	ns	ns	ns
Time to peak intermandibular distance	27.1 $\pm$ 2.7	34.1 $\pm$ 2.2	ns	ns	ns

<sup>1</sup> Time = milliseconds, distances = centimeters, angles = degrees.

<sup>2</sup> P values with degrees of freedom: prey type = 1, 3; individual, interaction = 3, 34; ns =  $P > 0.0013$ .

sured from time 0 to the beginning of a plateau at the end of the transport cycle and provide an indication of the total duration of movement.

Each variable was analyzed using a two-way analysis of variance design with prey type as a fixed effect and individuals as a random effect. Thus, the interaction mean square was substituted for the error mean square as the denominator in computing the F-ratios for the prey type effect (Sokal and Rohlf, 1981). The Bonferroni corrected level of significance ( $0.05/39 = 0.0013$ ) was chosen because multiple univariate comparisons were being conducted (Sokal and Rohlf, 1981). In a few multiple transport sequences some evidence was obtained that peak mouth and hyoid excursions varied systematically as the swallowing sequence progressed, but most of the sequences digitized consisted of only one or two cycles. In these data there was little evidence of autocorrelation among cycles within a sequence and each transport cycle was treated as independent for statistical analysis.

Prey characteristics were compared by measuring diameters and weights of the worm pieces and crickets fed to the animals during filming. The crickets were significantly greater in diameter ( $P < 0.001$ ) by 2 mm on average, and weighed significantly less ( $P < 0.001$ ), about half that of the worm pieces. Crickets were consumed in 1–3 transport cycles while worms were consumed in 3–7 cycles.

## RESULTS

Figure 2 shows a typical pattern of movement during intraoral prey transport in *Ambystoma tigrinum*. Prey transport involves repeated cycles of jaw and hyoid movement that advance the prey through the oral cavity and into the esophagus. Chewing or maceration of the prey does not take place and the major actions of the jaws and hyoid (with tongue attached) are to hold and move prey posteriorly. At time 0, the hyobranchial apparatus is pressed dorsally against the prey and has moved into this position in the time since the previous gape cycle. From  $-400$

←

in the profiles due to prey type, and that no change in body or head position occurs during transport indicating that inertial feeding is not being used. Because several levels of variation are confounded in the means plotted here, these data should not be used to make statistical comparisons but rather they should be used as a guide to the pattern of movement. For exact means of kinematic events by prey type see Table 1. Abbreviations: BP, body position (in cm); GD, gape distance (in cm); HDA, head angle (in degrees); HP, head position (in cm); HYD, hyoid position (in cm); IMD, intermandibular distance (in cm); LJA, lower jaw angle (in degrees); TH, tongue height (in cm).

to 0 msec (Fig. 2) a decrease in IMD and a slight increase in gape can be seen. From time 0 to 26.7 msec the tongue remains adhered to the prey as the mouth opens. Between 26.7 and 73.3 msec prey transport occurs: the mouth is open, the hyobranchial apparatus (with the attached prey) is rapidly moved posteroventrally thus drawing the prey into the oral cavity, and the jaws then close on the prey. Typically, an earthworm such as that shown in Figure 2 will move from 4 to 8 mm into the mouth with each transport cycle. After the jaws close on the prey the hyobranchial apparatus begins to move anteriorly (Fig. 2: 73.3 msec, arrow) and slides under the prey causing a depression of the buccal floor (Fig. 2: 226.7 and 300 msec, arrows).

Mean kinematic profiles of worm and cricket transport cycles are shown in Figure 3. Mouth opening is accomplished by simultaneous elevation of the head and depression of the lower jaw (Fig. 3: HDA, LJA). The gape distance is constant for 100 msec prior to mouth opening and constant but smaller for about 400 msec after mouth closure. Hyoid distance (HYD) rapidly increases during mouth opening and then gradually decreases for over 400 msec after the mouth has closed. Intermandibular distance (IMD) exhibits the opposite profile as HYD reflecting the retraction and subsequent gradual protraction of the hyoid. Head and body positions remain stationary throughout the transport behavior (Fig. 3: HP, BP) indicating that neither the head nor the body moves anteriorly as the prey is transported posteriorly.

Mean and statistical prey type comparisons for kinematic variables digitized from individual profiles are given in Table 1. Means for cricket cycles were not significantly different from worms for any of the variables measured. Gape and head cycle time and time-to-peak head angle were the only variables exhibiting an individual effect. From these data the kinematics of prey transport can be described quantitatively from the reference point of time 0. When transporting worms the peak gape distance averaged 8 mm. Lower jaw depression (19.9°) contributes more to mouth opening than head elevation (12.8°). Lower jaw angle peaks (19.7 msec) with maximum gape (19.9

msec) but head angle peaks later (26.0 msec) coinciding with maximum hyoid depression (28.7 msec) and minimum intermandibular distance (27.1 msec). Prior to mouth opening the intermandibular distance peaks at 2 mm and during prey transport the hyoid is depressed 4 mm. Lower jaw angle returns to its initial position at about 45.6 msec, before both head (51.6 msec) and gape (53.6 msec) cycle times are completed.

The digitized profile for GD, HYD, and IMD during six consecutive transport cycles from a single individual is presented in Figure 4. Transport of 4 cm of earthworm took approximately 17 seconds with up to 5 seconds between gape cycles. Maximum gape and maximum hyoid depression tend to decrease with time while the amount of intermandibular depression is similar in each transport cycle (Fig. 4: IMD). Film sequences between these transport cycles indicate that straight lines connecting the digitized points are representative of the intercycle movements of these variables (except between cycles 2 and 3 where IMD continues to increase slightly beyond 667 msec). The slow increase in gape from one cycle to the next is most pronounced during the early stages of feeding, although feeding sequences often do not show an increase in gape between transport cycles. The gradual, small increase in gape noted in Figure 4 between gape cycles tends to stop about 100 msec prior to the subsequent gape cycle, thus the gape distance remains constant just prior to the onset of the gape cycle (Fig. 3: GD).

## DISCUSSION

### *Kinematics of Prey Transport*

Prey transport behavior in *Ambystoma tigrinum* is composed of four phases that may be defined by gape and hyoid kinematic patterns: preparatory, fast opening, closing, and recovery. The long preparatory phase (Fig. 4: open bars) begins at the time the hyoid has recovered from its posteroventral depression (after the mouth has closed) when the rapid decrease in the HYD variable ends (e.g., Fig. 4: cycle 2). The end of the preparatory phase is marked by the onset of rapid increase in gape as the mouth opens during prey transport (Figs. 3, 4: GD). It is divided into two parts. During the first part

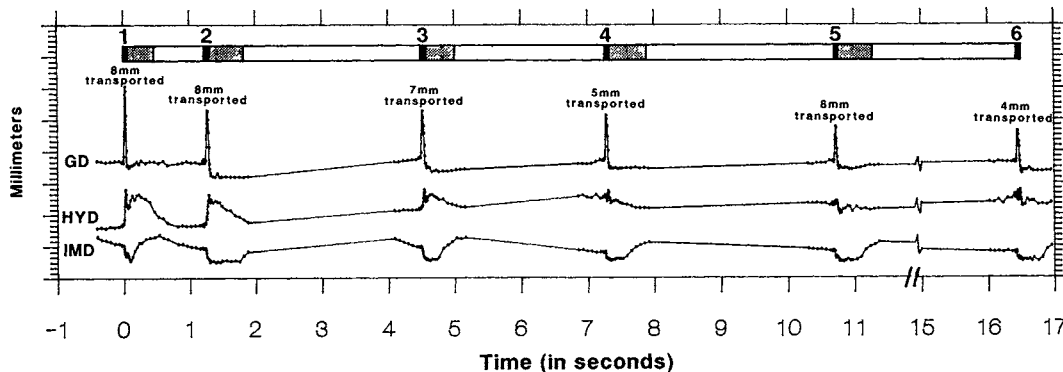


FIG. 4. Intraoral transport of a 5-cm-long earthworm in *Ambystoma tigrinum*. Approximately 1 cm of the worm was pulled into the mouth during initial prey capture. The remaining 4 cm was transported during the six cycles shown. Digitized points for each cycle (indicated by dots) are from 400 msec before to 667 msec after initiation of mouth opening. The straight lines connect distances between the digitized ends of one cycle and the onset of the succeeding cycle and indicate the extent of change in distance of each variable in the intervening time as verified by viewing of the films. The numbered black bars indicate transport gape cycles. Stippled bars indicate the period of gradual increase in IMD and decrease in HYD as the tongue slides anteriorly under the prey (the recovery phase). Open bars demark the extended preparatory phase during which gape may slowly increase (by about 1 mm) and the prey is compressed. The approximate length of worm transported during each cycle is indicated. Photographs of film frames of transport cycle 1 are presented in Figure 2.

of the preparatory phase there is a decrease in the intermandibular distance and a long, gradual increase in gape (<1 mm) may occur (Fig. 2: 466.7–1,333.3 msec; Fig. 4). The second part of the preparatory phase, which occurs just prior to the rapid mouth opening phase, is a static period during which gape and hyoid position are constant (Fig. 3). As can be seen by the pattern in the GD, HYD and IMD variables (Figs. 3, 4), no change in distance occurs in the 100 msec preceding mouth opening. The entire preparatory phase may last from 2 to 5 seconds, and may be shorter if two transport cycles follow closely in time (as in cycles 1 and 2 in Fig. 4).

During the preparatory phase, antero-dorsal pressure of the tongue and hyoid and gular musculature appear to gradually increase compressive loading on the prey (perhaps against the vomerine teeth), often forcing the gape to increase, followed by a static period prior to the next gape cycle. The major muscles with appropriate lines of action to cause dorsal pressure on the prey are the subarcualis rectus 1, genioglossus, geniohyoideus, interhyoideus, and intermandibularis (Reilly and Lauder, 1989a). Electromyographic data (Reilly and Lauder, in prep.) indicate that the intermandibularis,

interhyoideus and geniohyoideus exhibit some activity during the first part of the preparatory phase but that none of these muscles or the jaw adductors or depressors are active during the second part.

Prey transport occurs during the relatively rapid cycle of mouth opening and closing termed the gape cycle (Fig. 4, black bars). The fast opening phase, representing the first part of the gape cycle, is associated with hyoid retraction. Fast opening extends from the start of mouth opening to maximum gape (Table 1; Fig. 2, 0–26.7 msec) and typically lasts for about 20 msec. Divergence of the profiles for HYD and IMD during mouth opening (Figs. 2, 4) indicates that the hyobranchial apparatus has been retracted posteroventrally (increase in HYD) and that the tongue has moved up and back into the oral cavity relative to the lower jaw (decrease in IMD). During the fast opening phase the lower jaw is rapidly depressed and maximum lower jaw angle coincides with maximum gape (Table 1).

The closing phase lasts from maximum gape to the closure of the jaws and is nearly twice as long as the fast opening phase (Table 1). During the closing phase maximum hyoid retraction occurs as indicated by the peak in hyoid depression (HYD) and min-



imum intermandibular distance (IMD). Maximum head elevation occurs during the closing phase and is synchronous with maximum hyoid retraction (Table 1).

The recovery phase occurs as the tongue is returned anteriorly to its initial position under the prey, apparently pressing the prey into the vomerine teeth (Fig. 2: arrows; Fig. 3). This phase begins after the jaws have closed with the first anterior movement of the hyoid after retraction (indicated by the convergence of the IMD and HYD curves after the mouth has closed; Figs. 3, 4). The recovery phase ends when the hyoid and intermandibular area return to their initial positions before the preparatory phase (IMD and HYD plateau; Figs. 3, 4). The gape remains constant during the recovery phase. The recovery phase has also been reported in *Desmognathus* (Larsen and Beneski, 1988).

The horizontal positions of the body and head relative to the substrate on which the salamander is standing remain constant throughout the entire transport cycle (Fig. 3: BP, HP). Thus, the head and body remain stationary during transport of the prey demonstrating that inertial movements of the head and body are not used to aid in prey transport.

Prey transport in *Ambystoma tigrinum* appears to be a stereotyped behavior. Stereotypy is indicated by the analysis of variance of variables describing intraoral prey transport. Table 1 shows that there is no statistical difference in kinematics for the two prey types. Although cricket and worm gape cycles were not significantly different, the cricket transport cycles did tend to have higher values for many of the variables. The slight increase in kinematic means may be due to the larger size of the crickets, which were statistically greater in diameter than the worms. Excursions of the mouth and hyoid were also seen to decrease slightly (but not significantly) in sequential cycles on the same worm (Fig. 4). Perhaps as more and more of the worm has been moved down the esophagus, submaximal kinematic cycles are needed to transport the prey because esophageal muscles are contributing to prey transport.

In *Ambystoma tigrinum*, transport cycles follow immediately after successful prey

capture and continue until the entire prey is moved into the esophagus. At the end of the last transport sequence, a distinct swallowing action is observed. Comparison of prey transport with terrestrial prey capture for worm prey (Reilly and Lauder, 1989a) reveals several striking differences in kinematic profiles. The gape cycle during transport lasts approximately one third the duration of the gape cycle during terrestrial prey capture. Much of the longer gape cycle during initial prey capture is associated with a plateau in maximum gape during which tongue projection and retraction occur (Reilly and Lauder, 1989a). Maximum gape during transport is about the same as during tongue projection (8–9 mm).

Timing of lower jaw movement differs considerably between prey capture and transport. During transport, the lower jaw angle peaks with maximum gape and returns to its initial position at about the same time that the mouth closes on the prey (45.6 msec and 53.6 msec, respectively). During the strike, lower jaw depression peaks during fast opening and returns to resting position by maximum gape, about 100 msec before mouth closing (Reilly and Lauder, 1989a). Thus, head elevation is greater and contributes more to the gape cycle during tongue projection while lower jaw depression is an equal contributor in prey transport cycles.

Transformed *Ambystoma tigrinum* are known to spend time in aquatic habitats where they use suction feeding to capture (Miller and Larsen, 1986; Lauder and Shaffer, 1988) and manipulate (Regal, 1966) prey. In general the kinematics of aquatic suction feeding by transformed adults (Shaffer and Lauder, 1988; Reilly and Lauder, 1989a) are very similar to terrestrial prey transport kinematics. Although the duration of suction feeding is nearly twice as long as a transport cycle, the shapes of the profiles are similar. The gape, head angle, and lower jaw profiles have the same general shape as transport profiles with a rapid peak and decline in the gape: no plateau is present in the gape profile as in terrestrial prey capture by tongue projection (Reilly and Lauder, 1989a). In both prey transport and suction feeding the hyoid is rapidly retracted early in the fast opening phase. This pos-

terior movement of the hyoid causes tongue retraction when the mouth is closed during terrestrial prey transport, and generates negative pressure to draw water into the mouth during suction feeding. Protraction of the hyoid also is similar in the two behaviors, and occurs during the recovery phase after the mouth has closed.

#### *Intraoral Transport in Primitive Tetrapods*

The stereotyped kinematics of prey transport in *Ambystoma tigrinum* represent a reasonable basis for a model of intraoral prey transport in primitive generalized tetrapods. We make this statement because (1) the Caudata retain many plesiomorphic features of the feeding mechanism of primitive tetrapods (Schmalhausen, 1968; Carroll and Holmes, 1980; Jarvik, 1980; Duellman and Trueb, 1986), and (2) this species is a member of the generalized caudate family, Ambystomatidae, in which the feeding mechanism has been conservative in evolution (Regal, 1966; Wake, 1982; Bramble and Wake, 1985). We emphasize that we are not using *Ambystoma tigrinum* as a representative of the "ancestral" caudate or tetrapod. Rather, we use tiger salamanders as a model anamniote system, which retains many primitive tetrapod characters in the feeding mechanism to provide data that may be used for comparison to the well-described feeding cycles of fishes (Liem, 1970; Lauder, 1980a, 1980b, 1985), the hypothetical model of the primitive, generalized tetrapod prey transport cycle of Bramble and Wake (1985), and the chewing and transport cycles of amniotes (Crompton et al., 1977; Franks et al., 1984; Bramble and Wake, 1985; Gans et al., 1978). The kinematic pattern described here for *Ambystoma tigrinum* is abstracted into a general kinematic profile in Figure 5B and is compared with outgroups (Fig. 5A) and the amniote pattern illustrated in Figure 5C.

In aquatic salamanders and outgroups (actinopterygian fishes and lungfishes), the kinematics of aquatic prey capture and hydraulic intraoral prey manipulations are very similar and three kinematic phases have been demonstrated in the generalized feeding cycle (Fig. 5A): fast opening, closing and recovery (Liem, 1970, 1978; Lauder, 1980a,

1980b, 1985; Lauder and Shaffer, 1985; Bemis and Lauder, 1986). The fast opening phases in *Ambystoma tigrinum* (Fig. 5B) and fishes (Fig. 5A) are similar in involving rapid posteroventral hyoid retraction. The recovery phase in both fishes and salamanders involves the resetting of the hyoid to nearly its initial position during a relatively long period prior to the next gape cycle.

We hypothesize that the prey transport cycle in primitive tetrapods (Fig. 5B) includes a lengthy preparatory phase that is subdivided into two phases, P1 (preparatory phase 1), and P2 (preparatory phase 2). The P1 phase is a long period, encompassing most of the transport cycle (1 to 5 seconds), when the hyoid and gape remain relatively stable, but some slow opening may occur (up to 10% of maximum gape). It is followed by the second shorter part of the preparatory phase (P2) prior to fast opening when the gape, hyoid, and tongue remain static. These two phases compress the tongue into the prey in preparation for the actual transport of prey into the oral cavity. The prey is transported into the pharynx during the fast opening and closing phases (Fig. 5: FO, C) as the tongue and hyoid move posteroventrally with the prey attached. The rapid increase in gape at the end of P2 initiates the fast open phase, so named for its similarity to the rapid mouth opening that characterizes this portion of the gape cycle in amniotes. Hyoid retraction begins with fast mouth opening and peaks before the end of the closing phase: the hyoid is held maximally retracted until the mouth is closed. The recovery phase follows as the hyoid is slowly protracted anteriorly under the prey while the mouth is held tightly closed (Fig. 5B). Key features of these phases and proposed homologies to kinematic phases in fishes and amniotes are presented in Table 2.

In amniotes, the gape cycle includes the slow opening phase. Intraoral transport has been studied in many mammals, including rodents, carnivores, herbivores, primates, and marsupials (Weijjs, 1975; Crompton et al., 1977; Byrd et al., 1978; Gans et al., 1978; Hiiemae et al., 1979; Gorniak and Gans, 1980; Franks et al., 1984; Greet and De Vree, 1984; Hylander et al., 1987), in a few lizards (Throckmorton, 1980; Smith,

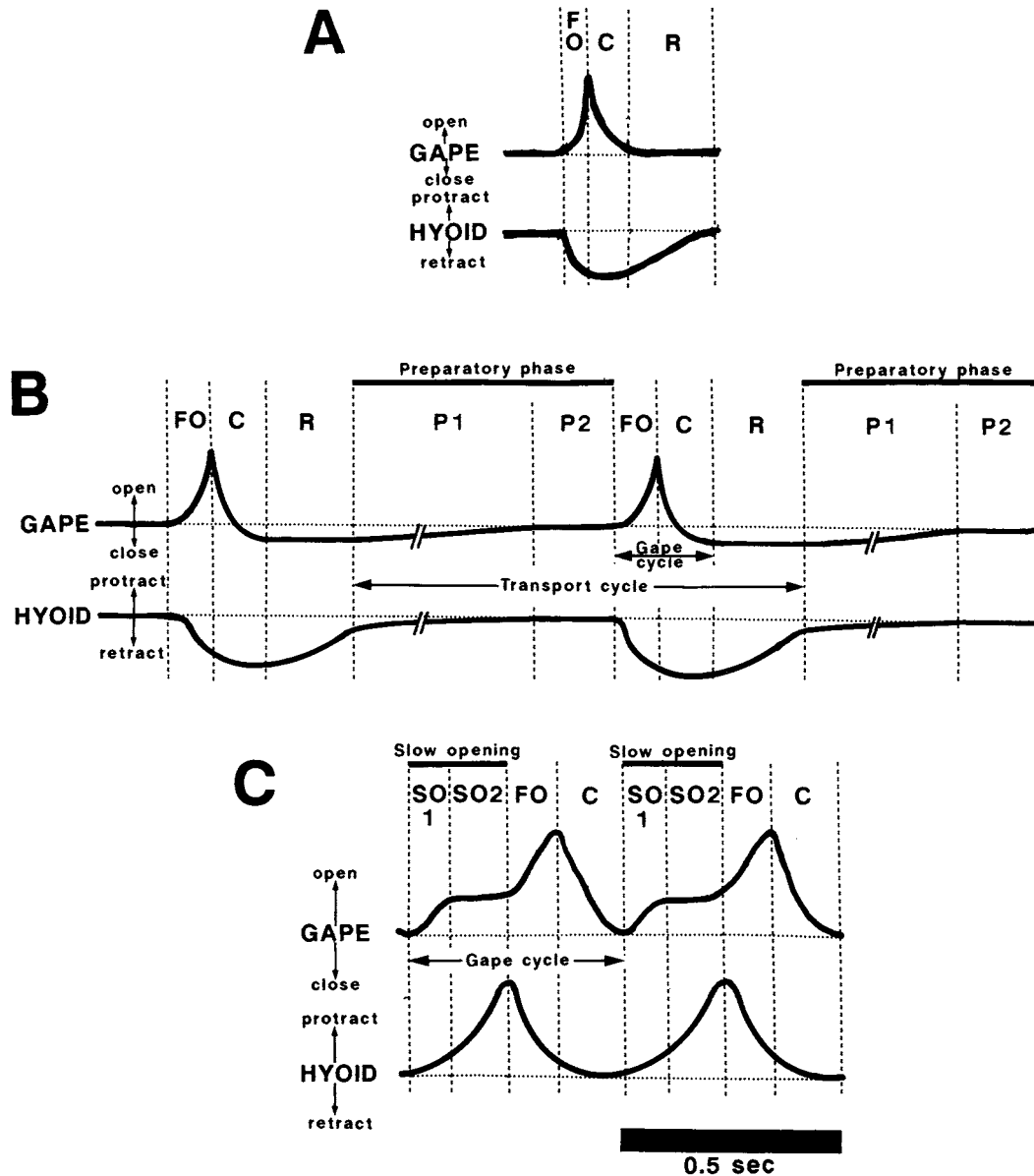


FIG. 5. Comparison of generalized kinematic profiles of suction feeding and hydraulic prey manipulation in an actinopterygian fish (A, based on Liem, 1970; Lauder, 1980a, 1980b, 1985), intraoral transport in a primitive tetrapod (B, based on the kinematics of *Ambystoma tigrinum*; Figs. 2, 3, 4) and intraoral food transport in an amniote (C, based primarily on data from mammals and reptiles; Hiiemae and Crompton, 1985). The time scale given below panel C applies to all three parts of the figure. The kinematic profile in primitive tetrapods (panel B) shares many plesiomorphic similarities with feeding kinematics in actinopterygian fishes (panel A), including the shape and extremely short duration of the gape profile and the presence of a distinct recovery phase during which the hyobranchial apparatus moves anterodorsally. Also, in A and B note similarity of posteroventral hyoid movements during mouth opening. In B, at the end of the preparatory phase the tongue is pressing the prey dorsally against the base of the skull. The preparatory phase is divided into two parts (P1 and P2). Hatch marks in B indicate that the P1 phase may last several seconds. During P2 there is no change in gape or hyoid position. In amniotes, there is often a slow opening phase that is part of the gape cycle (SO1 and SO2). There is no separate recovery phase. We hypothesize that the extended recovery and preparatory phases of primitive tetrapods are together homologous to the slow opening phase of amniotes (see text for further discussion). Abbreviations; C, mouth closing phase; FO, fast open phase; P, preparatory phase in anamniote tetrapods; R, recovery phase; SO1 and SO2, slow open 1 and 2 phases in amniotes.

TABLE 2. Key features of kinematic phases in salamanders and proposed functional homologies with established kinematic phases in amniotes and fishes.

Salamander phase	Key features of		Transport homologies in	
	Gape	Hyoid	Amniotes <sup>1</sup>	Fishes <sup>2</sup>
Fast opening (FO)	rapid increase	rapid retraction	Fast opening (FO)	Opening (O), or expansive phase
Closing (C)	rapid decrease	maximum retraction	Closing (C)	Closing (C), or compressive phase
Recovery (R)	constant	majority of protraction	Compressed into Slow Opening (SO)	Recovery (R)
Preparatory (P)	slight increase	slight protraction	Compressed into Slow Opening (SO)	None <sup>3</sup>
P1	may increase to 10% of maximum	slight protraction	Compressed into Slow Opening (SO)	None <sup>3</sup>
P2	constant	constant	Compressed into Slow Opening (SO)	None <sup>3</sup>

<sup>1</sup> Hiiemae and Crompton, 1985.

<sup>2</sup> Lauder, 1985.

<sup>3</sup> There does not appear to be a preparatory phase during transport in primitive ray-finned fishes and lungfishes (Lauder, 1980a, 1985; Bemis and Lauder, 1986), although this question has yet to be addressed in detail.

1982, 1984, 1986, 1988; Schwenk and Throckmorton, 1989; Bels, 1989; Cleuren et al., 1989), a crocodile (Timmerman et al., 1989), and a Rhynchocephalian (Gorniak and Gans, 1982). These studies indicate that amniotes exhibit a complex intermingling of crushing, repositioning, orientation, reduction, mastication, transport, packing and swallowing behaviors and show great variation in mastication kinematics with different foods (Hiiemae and Crompton, 1985; Crompton, 1989). This contrasts greatly with amphibians, which typically exhibit stereotyped transport behavior that does not involve mastication (chewing, prey reduction) or prey processing (crushing, orientation, repositioning) (Noble, 1931; Thexton et al., 1977; Bemis et al., 1983; Hairston, 1987; Reilly and Lauder, 1989b).

A generalized model for the kinematics of the feeding cycle in amniotes which we can compare with the hypothesized pattern for primitive tetrapods (Fig. 5B) has been described by Bramble and Wake (1985) and Hiiemae and Crompton (1985). This pattern is summarized in Figure 5C. Amniote transport cycles typically have a slow opening phase (often divided into two parts, SO1 and SO2) during which the hyoid is protracted under the food. During slow open 1 (Fig. 5C: SO1) the hyoid begins to protract

and the mouth opens to about 30% or more of maximum gape. Then, during slow open 2 (SO2), which is often absent, the gape remains nearly constant as the hyoid continues to protract. The phase called fast open (Fig. 5C: FO) follows as the gape rapidly increases and the hyoid retracts. Posteroventral motion of the hyoid continues until it reaches a maximum at the end of the closing phase. Often a slowing of gape closing (or power stroke) related to tooth-food-tooth contact is included in the closing phase (Crompton, 1989). This overall cycle of hyoid protraction and retraction during the gape cycle is repeated, with various masticatory and processing cycles inserted, as food is processed, moved to the pharynx, and swallowed. In addition, as noted by Smith (1984) and Throckmorton (1980) there may be a stationary phase in lizards after fast closing during which gape changes little and the hyoid begins to recycle anterodorsally.

Interesting similarities and differences are evident in a comparison of the generalized kinematic cycles of the outgroups, salamanders, and amniotes (Table 2; Fig. 5). In all three cases, hyoid retraction (and therefore prey transport) occurs during the fast opening (FO) and closing phases (C). In the primitive tetrapod pattern (Fig. 5B), as in actinopterygian fishes, transport is followed by

a long recovery phase (R) during which the hyoid slowly recycles anteriorly to its initial position under the prey while the gape is held closed. This contrasts with the amniote pattern in which during transport there is no period of static gape and rapid hyoid protraction following the closing phase.

Fishes lack a slow opening phase but both tetrapod models (Fig. 5B and C) have two phases during which the mouth tends to slowly open then remains constant just prior to fast opening. Preparatory phases in primitive tetrapods (P1 and P2) occur during the long period between hyoid recovery and fast opening and may involve a gradual and small increase in gape. In amniotes, the slow opening phases (SO1 and SO2) occur immediately prior to fast opening as part of the gape cycle and the gape increases to nearly a third of maximum gape during SO1. Hyoid recovery in amniotes occurs during the slow opening phases of the following cycle (Fig. 5C).

We hypothesize that the recovery phase and preparatory phases of primitive tetrapods are together homologous with the slow opening phase of amniotes. This hypothesis is based on the similarity in hyoid and gape kinematic patterns: after closing and prior to fast opening the gape increases slightly while the hyoid is protracted. Because actinopterygian fishes and lungfishes possess a recovery phase (Bemis and Lauder, 1986; Lauder, 1985), we suggest that the recovery phase is retained in primitive tetrapods as a primitive osteichthyan character that was lost (as a distinct phase) in amniotes by compression into the gape cycle. If this hypothesis is corroborated, then one of the major changes that has occurred during the evolution of terrestrial feeding systems is the elimination of separate recovery and preparatory phases by their condensation into the gape cycle itself. As a comparison of Fig. 5B and C shows, slow opening phases, when the hyoid cycles anterodorsally, are part of the gape cycle itself in amniotes while the preparatory and fast opening phases are distinct in the primitive tetrapod pattern.

#### *Evolution of Tetrapod Transport Systems*

A key point to emerge from this analysis is that the kinematic profile for the gape and

hyoid during prey transport in terrestrial salamanders is extremely similar to that used during hydraulic prey transport by fishes (compare panels A and B in Fig. 5). Based on our data from *Ambystoma tigrinum* and on the comparison of the three transport patterns illustrated in Figure 5, we propose five characteristics of prey transport to be primitive to the Tetrapoda and its two outgroups (Fig. 6: open bar). (1) Hydraulic prey transport is used to move prey within the oral cavity. (2) Gape is constant prior to fast opening. (3) Mouth opening is attained by both head elevation and lower jaw depression. (4) A recovery phase is present after prey transport during which the hyoid is slowly protracted under the prey while the mouth is held closed. (5) Hyoid retraction is coincident with the fast open phase.

Out of these five characters, only No. 5 remains unchanged throughout tetrapods: hyoid retraction is coincident with fast opening and this is the period of actual prey transport (Fig. 6). Two characters (1 and 2) are transformed into synapomorphies for the Tetrapoda: (1a) Tongue-based terrestrial intraoral prey transport appears in tetrapods facilitating the movement of prey from the jaws to the throat on land. (2a) Between the recovery phase and fast opening there is a long preparatory period of prey compression during which the mouth may gradually open (P1) then remains stable (P2).

Characters 2–4 are transformed and the derived state characterizes the Amniota (Fig. 6): (2b) A short period of slow increase in gape (slow opening) occurs immediately prior to fast opening. Gape is opened to 33% or more of maximum while the hyoid moves anterodorsally from its point of maximum retraction. (3a) Lower jaw movements produce most of mouth opening (Gorniak and Gans, 1982; Smith, 1984; Bramble and Wake, 1985). (4a) Kinematics of the primitive recovery and preparatory phases (R and P) are temporally compressed into the slow opening phases in amniotes (SO1 and SO2). This results in a shift in the timing of gape and hyoid kinematics to recycle the hyoid anterodorsally during a short period just prior to fast opening. Thus, the short contiguously repeated cycles of gape activity in amniotes encompass the entire primitive tetrapod transport cycle, including the

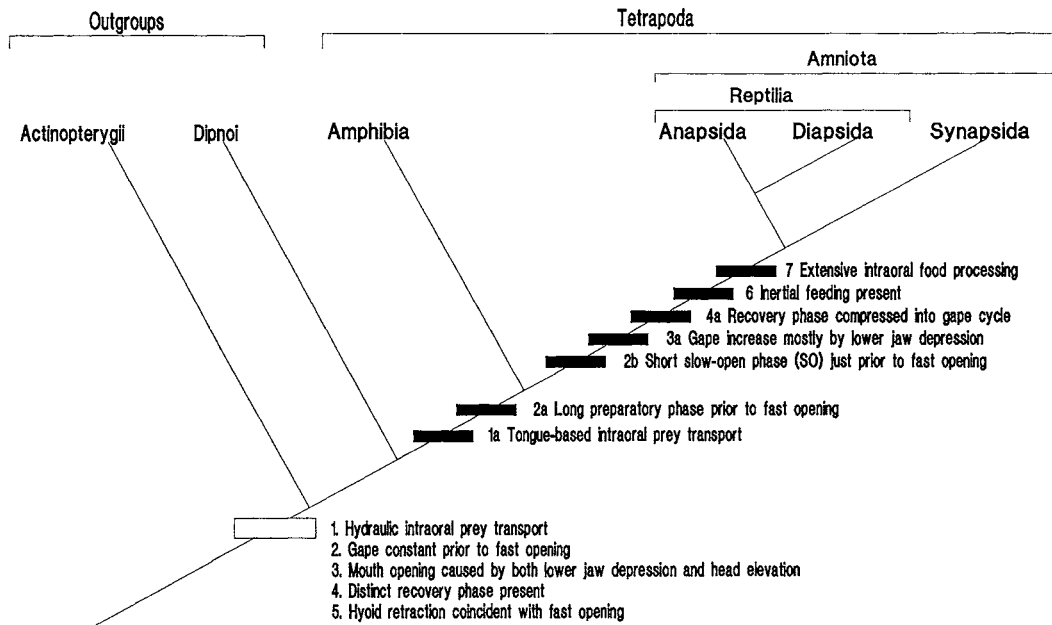


FIG. 6. Simplified phylogeny of tetrapods (based on Gauthier et al., 1988) and selected outgroup taxa (Lauder and Liem, 1983) to illustrate our hypothesis of the evolution of major features of the feeding system in basal clades. We propose that five features of the intraoral prey transport cycle, also present in outgroups, are primitive for tetrapods (open bar: characters 1–5). Two characters (1a, 2a) are common to tetrapods and five features are found in amniote transport and feeding systems (characters: 2b, 3a, 4a, 6, 7). The open bar indicates that the five features listed are plesiomorphic for the outgroups shown; thus, sharks may possess many of these primitive features, too. Some clades within the Amphibia and Reptilia show divergent feeding systems and novel specializations in the jaws and so may not conform to this general scheme when the kinematics are studied in detail. For example, inertial transport may be present in some amphibians (personal obs.). However, the data from *Ambystoma tigrinum* clearly show the presence of a recovery phase and an extended preparatory phase that are substantially modified in amniote feeding systems. In addition, clades such as lungfishes show specialized chewing systems, but retain the primitive hydraulic mode of prey transport.

lengthy hyoid recovery and preparatory protraction phases.

Two kinematic novelties appear in amniotes: (6) Inertial feeding is used (Gans et al., 1978; Smith, 1984, 1986), and (7) extensive masticatory, manipulative, packing, and other behaviors are used in processing ingested food (Crompton, 1989). Some amphibians appear to use inertial movements during prey transport, but comparative data are presently scarce. This character may thus turn out to be present in many amphibians too.

Primitive tetrapods eat intact active prey and efficient intraoral transport of active prey from the jaws to the esophagus is of major importance in terrestrial energy procurement. The initial role of the fleshy tongue in tetrapods may have been to facilitate prey adhesion during intraoral trans-

port (in contrast to possible use during initial prey capture) using primitive transport kinematics similar to the movement profile in ray-finned fishes or lungfishes (Bemis and Lauder, 1986). Furthermore, Regal (1966) and Ozeti and Wake (1969) have hypothesized that prey capture via tongue projection may have evolved from a tongue of manipulative function, and a functional model for the behavioral extension of the prey transport mechanism to produce tongue projection in *Ambystoma tigrinum* supports this hypothesis (Reilly and Lauder, 1989a).

In amniotes the feeding mechanism is generally not used to simply transport large whole prey to the esophagus but rather is used to physically reduce, bite, align, masticate, pack and transport pieces of food using complex patterns of jaw movement. The slow opening phase is associated with hyoid

recovery and anterior movement of the tongue under the food before transport occurs. The slow opening phase varies considerably among amniotes and may even be absent depending on the feeding behavior (initial prey capture, transport, mastication, lapping, puncture-crushing, bilateral transfer, etc.) that occurs during a given gape cycle. Prey transport in amniotes is associated with moving prey items or small amounts of processed food to the pharynx. Although purely transport behaviors in amniotes have not been adequately studied, variability or absence of the slow opening phase during transport is associated with a wide range of intraoral processing behaviors. In contrast, the transport of whole prey is a major function of the hyobranchial apparatus in primitive tetrapods and distinct recovery and preparatory phases are present. The transition from a stereotyped and temporally dominant preparatory phase in primitive tetrapods to a highly variable slow opening phase in amniotes appears to have been one of the major steps in the evolution of tetrapod feeding systems.

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