# Hyolingual Feeding Systems of the Plethodontidae: Comparative Kinematics of Prey Capture by Salamanders With Free and Attached Tongues

JOHN H. LARSEN, JR., JOHN T. BENESKI, JR., AND DAVID B. WAKE
*Electron Microscopy Center and Department of Zoology, Washington State
University, Pullman, Washington 99164-4210; Department of Biology,
West Chester University, West Chester, Pennsylvania 19383; Museum of
Vertebrate Zoology and Department of Zoology, University of California,
Berkeley, California 94720*

ABSTRACT    High-speed cinematography (500 fps) was used to analyze quantitatively the kinematics of terrestrial prey capture in *Bolitoglossa occidentalis, B. mexicana, Ensatina eschscholtzii, Plethodon glutinosus, Desmognathus quadramaculatus, Hynobius kimurae,* and *H. nebulosus.* The gape cycle of these salamanders is highly stereotyped. In *B. occidentalis* the mouth is opened by a combination of cranial elevation and mandibular depression. The gape increases dramatically during tongue retraction, thus allowing the prey to be delivered to the rear of the oral cavity without being impeded by the marginal teeth. The absence of a feeding function for these teeth apparently has resulted in their reduction and/or morphological alteration in some bolitoglossines. Observed differences in jaw rotation between successful and unsuccessful prey capture attempts appear to be biomechanical phenomena and *not* adjustments by the salamander in response to neural feedback.

Tongue projection is most rapid and highly accurate in the two bolitoglossines and *Ensatina.* The distance to which the tongue can be protracted from the mouth is 7% snout-vent length in *D. quadramaculatus, P. glutinosus, H. kimurae,* and *H. nebulosus* (attached protrusible tongue); 15% in *E. eschscholtzii* (attached projectile tongue); and 30% in *B. occidentalis* (free projectile tongue). Even though tongue protraction is significantly faster in salamanders with projectile tongues than those with protrusible tongues, the range of times for the entire gape cycle is generally similar for all salamanders (ca. 100 ms). However, less derived salamanders spend a shorter period preparing the tongue for firing and more time in its projection than *E. eschscholtzii* and *B. occidentalis.* One obvious advantage for increasing the speed of tongue protraction is that it decreases the prey's available escape time. In the supergenus *Bolitoglossa* prey are limited to small, active invertebrates by a combination of stereotyped feeding behavior, a small tongue pad, and a lightweight hyolingual apparatus that is projected extremely fast.

While all terrestrial salamanders possess the same basic feeding system, the bolitoglossines have evolved an impressive array of unique specializations for capturing small, rapidly moving prey. This suite of characters has enabled the tribe to radiate rapidly into a vast variety of microhabitats.

Approximately 60% of extant species of salamanders are members of the Plethodontidae (Frost '85). Much of the success of this family is related to two key innovations: 1) the loss of lungs, resulting in the elimination of biomechanical and functional constraints associated with use of the hyobranchial apparatus as a force pump to fill the lungs and the subsequent evolution of a structurally and functionally complex prey capture system (Roth and Wake, '85a; Wake, '82); and 2) the phylogenetic disappearance of the aquatic larva from the life cycle of many plethodontid species (Wake, '66). With the loss of this ontogenetic stage, the hyobranchial apparatus was released from its functions in larval gill-support and aquatic feeding and subsequently became increasingly specialized as a mechanism for tongue projection during prey capture (Lombard and Wake, '77; Wake, '82).

The tongue is the primary structure for prehending prey in all terrestrial urodeles; its function in this manner is apparently primitive for the order (Bramble and Wake, '85; Larsen and

Beneski, '88; Larsen and Guthrie, '75). The feeding apparatus of bolitoglossines is modified from the primitive plethodontid condition by an increase in the mass and function of the second ceratobranchials relative to the first ceratobranchials, and by development of very long epibranchials. These and other alterations in the system have led to a more efficient mechanism for folding the hyobranchium and for transmitting force during tongue protraction (Lombard and Wake, '76, '77).

Lombard and Wake ('77, '86) identified and described three functional types of tongue projection systems for the genera of the Plethodontidae: 1) attached protrusible, 2) attached projectile, and 3) free projectile. An attached protrusible tongue is present in the Desmognathinae, *Plethodon,* and *Aneides* and is the presumed ancestral state (Lombard and Wake, '86). An attached projectile tongue evolved at least three times within the family (*Ensatina, Batrachoseps,* and some hemidactyliines; Lombard and Wake, '86). A free projectile tongue evolved at least twice within the tribe Bolitoglossini, once in *Hydromantes,* and once within the supergenus *Bolitoglossa.*

Various aspects of terrestrial feeding in salamanders have been described and discussed by Bramble and Wake ('85), Dalrymple et al. ('85), Druner ('01, '04), Francis ('34), Hinderstein ('71), Lombard and Wake ('76, '77), and Wake ('82). Studies using high-speed cinematography by Dockx and De Vree ('86), Larsen and Beneski ('88), Larsen and Guthrie ('75), and Reilly and Lauder ('88) and low-speed cinematography by Severtsov ('71) have shown that the tongue pad is the structure to make initial contact with the prey during capture. While large prey items, adhering to the sticky pad, are returned to the jaws to be immobilized by the marginal teeth (Larsen and Guthrie; '75), small prey are carried beyond the jaws and deposited at the rear of the oral cavity where they can be held firmly between the tongue and the palatal teeth. Highly efficient and rapid tongue protraction and retraction mechanisms are critical to successful prey capture by terrestrial salamanders.

The present study is a quantitative analysis of feeding kinematics in *Bolitoglossa occidentalis,* a species with a free projectile tongue (Lombard and Wake, '77, '86), and it compares this prey-capture system with that of *Desmognathus, Plethodon,* and *Hynobius* (attached protrusible tongue), and *Ensatina* (attached projectile tongue).

## MATERIALS AND METHODS

Ten adult *Bolitoglossa occidentalis* (28–41 mm snout-vent length, SVL) were filmed feeding on *Drosophila* sp.; all prey capture sequences were recorded cinematically at 500 fps on Kodak 7222 and/or 7224 negative film, as described by Larsen and Beneski ('88). The prey were suspended from forceps directly in front of each salamander. A total of 17 feeding sequences (7 successful strikes and 10 unsuccessful strikes) were filmed from either a lateral (N = 14) or frontal (N = 3) view.

All recorded sequences were examined with a Selecta Frame IV motion analyzer; eight lateral views (4 successful strikes and 4 unsuccessful strikes) were analyzed quantitatively and standardized according to procedures outlined by Larsen and Beneski ('88). Briefly, the position of the cranium, mandible, and tongue pad were digitized (frame by frame) and the data were used to compute 1) horizontal and vertical displacements by the anterior tip of the snout and by the mandibular symphysis, 2) the angular rotation of the cranium and mandible relative to the horizontal plane, and 3) the distance that the tongue pad extended beyond the mandibular symphysis. All linear measurements are expressed as a percentage of head length (% HL) which was determined from the films as twice the distance from the anterior tip of the snout to the posterior corner of the eye or as a percentage of snout-vent length (% SVL) which was determined from preserved specimens; all angular measurements are expressed in degrees (°), and all times are expressed in milliseconds (ms). Because of their slightly oblique or frontal views, the remaining nine sequences were analyzed for temporal and qualitative data, but not for linear displacements or angular measurements.

For comparative purposes, films of 47 feeding sequences by five additional species of urodeles were analyzed. These include: *Bolitoglossa mexicana* (N = 2), *Hynobius kimurae* (N = 20), *H. nebulosus* (N = 13), *Desmognathus quadramaculatus* (N = 3), *Plethodon glutinosus* (N = 7), and *Ensatina eschscholtzii* (N = 2).

## RESULTS

Prey capture by *Bolitoglossa occidentalis* (Fig. 1) involves two distinct but interrelated activities—a gape cycle and a tongue cycle. As in *Desmognathus* (Larsen and Beneski, '88), the gape cycle is described by four phases: phase I, or initial gape; phase II, or intermediate gape/tongue
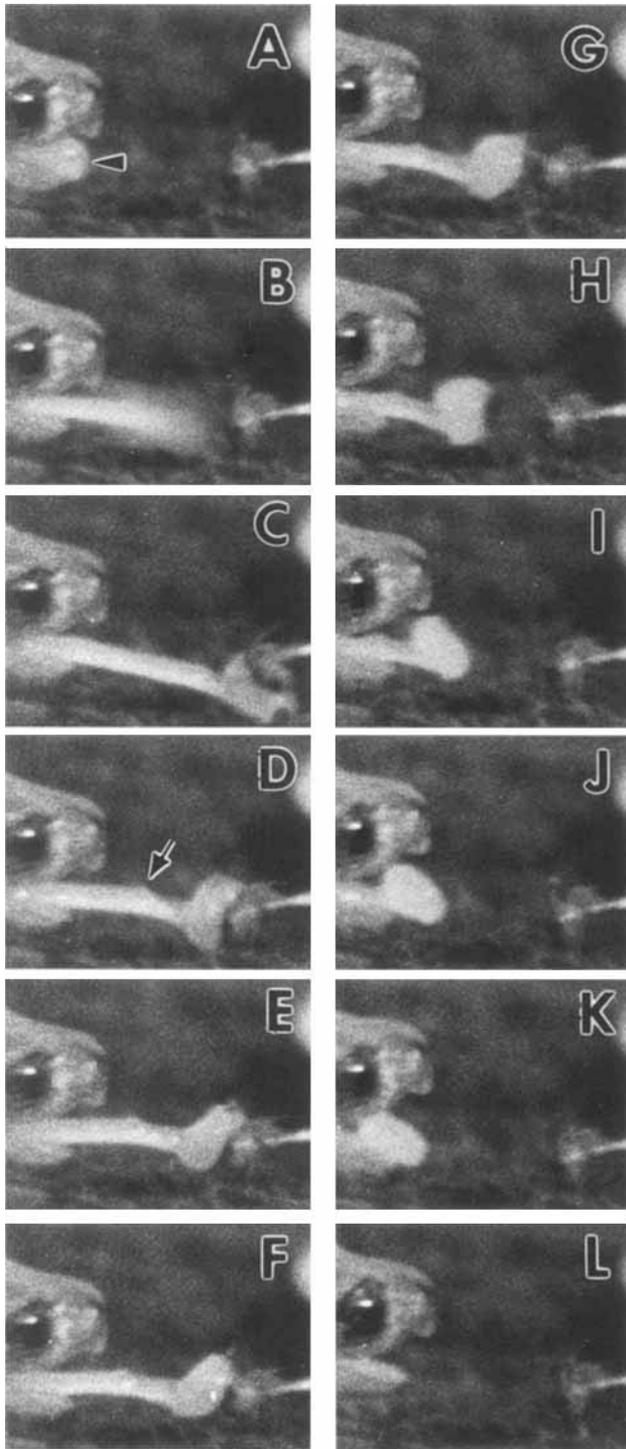
Fig. 1. Cinematic frames (1, 2, 3, 5, 6, 7, 8, 9, 10, 11, 12, 21) of a *Bolitoglossa occidentalis* tongue projection-return cycle at 500 fps. In **A** tongue pad (arrowhead) is at front of mouth on mandibular symphysis. Note joints between ceratobranchials II and basibranchial (arrow) in **D**. In **L** tongue pad has returned to the back of the oral cavity but mouth is still open. Note that actual tongue protraction is so rapid, 500 fps does not stop action (**B**).

protraction; phase III, or final gape/tongue retraction; and phase IV, or final mouth closure (Table 1). The tongue is active during all four phases of the gape cycle; however, the tongue extends beyond the mandibular symphysis only during phase II and the beginning of phase III (i.e., phase IIIA). The tongue can be projected laterally at an angle of up to 45° from the main axis of the head.

### Gape cycle

Kinematic analyses reveal that the general pattern and duration of the gape cycle of *Bolitoglossa occidentalis* are relatively stereotyped (Fig. 2). Immediately prior to the start of prey capture, the salamander is stationary, its head is oriented towards the prey, and its mouth is closed (gape angle = 0°). During initial gape (phase I) the mouth is opened by a combination of ventral depression of the mandible and dorsal elevation of the cranium. Phase I is usually the longest phase of the gape cycle (Table 1); at the end of phase I, mean gape angle is approximately 23° (Fig. 3) and the tongue pad is repositioned at or near the mandibular symphysis.

Intermediate gape/tongue protraction (phase II) is always the shortest phase of the gape cycle (Table 1). Similar projection speeds (3–5) ms) were recorded by Thexton et al. ('77). As the tongue is protracted beyond the mandibular symphysis, only a slight increase occurs in the gape angle; mean gape angle at the end of phase II is approximately 25° (Fig. 3).

During final gape/tongue retraction (phase III) the gape angle continues to widen; as the tongue pad is returned to the oral cavity, the gape angle increases dramatically to its maximum value (mean maximum gape angle = 50°) (Fig. 3). Maximum gape angle is achieved by the continued movements of the cranium and mandible: during the phase I–III interval (i.e., from the start of the prey capture sequence to maximum gape angle), the anterior tip of the snout is elevated an average of +41% HL and the mandibular symphysis is depressed an average of −9% HL. Despite this difference in their vertical displacements, the angular rotation of the cranium and mandible during this same interval are nearly equivalent (cranium = +24°; mandible = −26°). The similarity in the amount of angular rotation by the cranium and mandible, but dissimilarity in the amount of vertical displacement by the snout and mandibular symphysis demonstrate that the entire head is elevated as the jaws open during the phase I–III interval (Fig. 4).

TABLE 1. Comparison of successful and unsuccessful prey capture kinematics for Bolitoglossa occidentalis[1]

| Behavior | PI | PII | PIIIA | Time (ms) PIII | PIV | GC | TEC | %HL MTE | Degrees MGA |
|---|---|---|---|---|---|---|---|---|---|
| Successful capture X̄ | 35.0 | 7.0 | 19.0 | 31.0 | 24.3 | 99.4 | 26.0 | 83.0 | 51.8 |
| SE | 2.6 | 0.7 | 1.4 | 1.2 | 1.7 | 2.2 | 1.5 | 6.5 | 5.0 |
| Unsuccessful capture X̄ | 34.7 | 8.3 | 23.0* | 30.7 | 26.7 | 99.6 | 31.3* | 102.1 | 48.0 |
| SE | 2.4 | 1.5 | 1.0 | 0.9 | 1.6 | 2.5 | 1.9 | 12.5 | 3.5 |

[1]PI–PIV = phase I–phase IV; GC = gape cycle; TEC = tongue extension cycle; MTE = maximum tongue extension; MGA = maximum gape angle; X̄ = mean; SE = standard error.
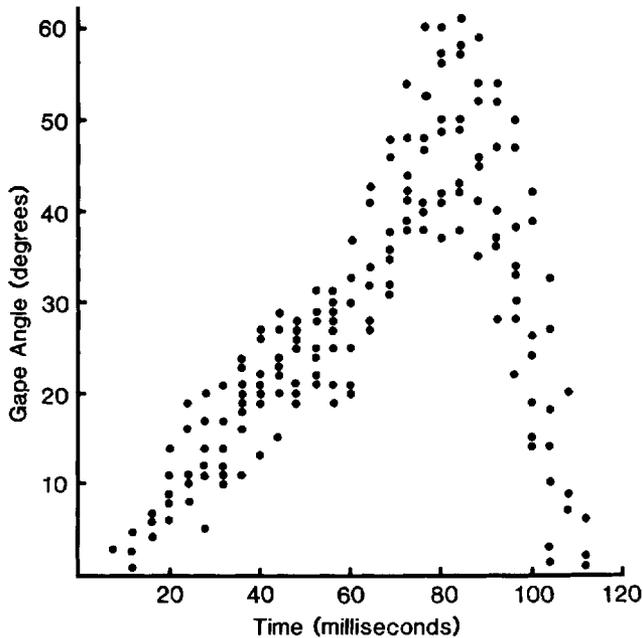*$P < 0.05$.



Fig. 2. Scatterplot of gape angle versus time for 8 feeding sequences by Bolitoglossa occidentalis. The start-time of each sequence is adjusted such that maximum gape angle occurs at 84 ms in all sequences. The adjusted start-times are 0 ms (N = 2), 8 ms (N = 5), and 20 ms (N = 1).
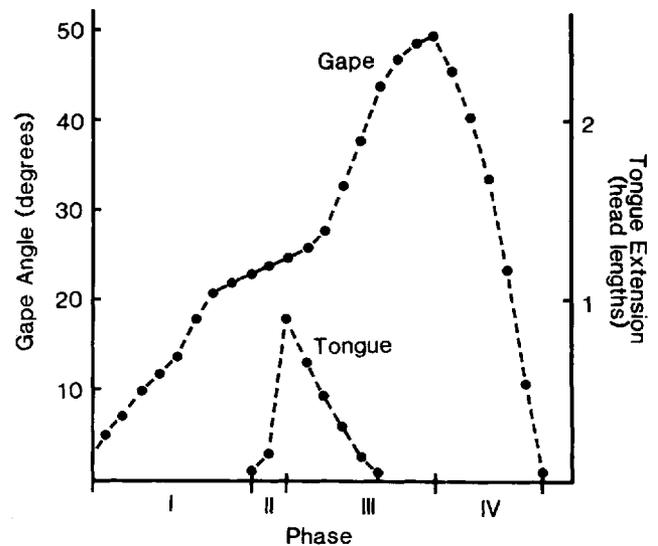


Fig. 3. Graph depicting the relationship between mean gape angle and mean tongue extension distance throughout the four phases of prey capture by Bolitoglossa occidentalis (N = 8).

During phase IV the mouth closes rapidly (26 ms). Mouth closure results from the combined movements of the cranium and mandible. The snout is lowered (− 23% HL) as the cranium rotates ventrally (− 22°), and concomitantly, the mandibular symphysis is elevated (+ 24% HL) as the mandible rotates dorsally (+ 28°). The similarity of both rotation (− 22° vs. + 28°) and vertical displacement (− 23% HL vs. + 24% HL) by the cranium and mandible indicate that the vertical position of the head does not change during phase
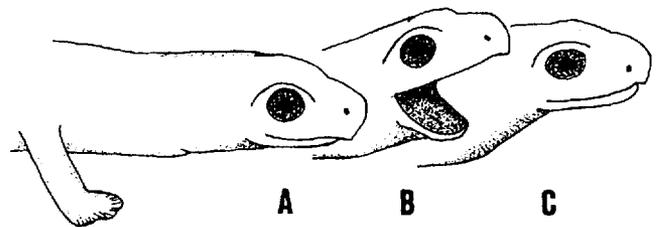


Fig. 4. Line tracings of selected cinematic frames (500 fps) from a feeding sequence by Bolitoglossa occidentalis demonstrating relative changes in the rotation, elevation, and depression of the mandible. A: Head position at the start of phase I. B: Head position at the end of phase III. C: Head position at the end of phase IV. Because the head does not move forward during prey capture by this species, successive drawings are offset horizontally only to facilitate comparison of vertical and angular changes.

IV (Fig. 4). Once the jaws have closed completely, the head is bent downward; during subsequent deglutition, the eyes are depressed into the head presumably by contractions of the retractor bulbi muscles.

The forward surge of the head and body that is a major characteristic of prey capture by desmognathine salamanders (Larsen and Beneski, '88) is negligible in *Bolitoglossa occidentalis*. In the latter species, delivery of the prey to the oral cavity is due entirely to tongue retraction rather than to a combination of tongue retraction and head surge as in *Desmognathus* (Larsen and Beneski, '88). Mean maximum head surge for *B. occidentalis* was only 3% HL (range 1% to 8%) as compared to 31% HL (range 22% to 36%) for *D. quadramaculatus*.

### Tongue cycle

As initial gape forms during phase I, the tongue pad is lifted from the floor of the mouth, and brought forward slowly to the level of the mandibular symphysis. During phase II, the tongue is projected rapidly to its maximum protraction distance (Fig. 3) until it extends well beyond the mandibular symphysis (mean maximum tongue extension: 93% HL; range 71% to 137% HL; 27% to 30% SVL). As it travels forward, the glandular dorsal surface of the tongue pad rotates anteroventrally so that it is redirected towards the prey. The prey usually is struck by the pad prior to maximum tongue extension (Fig. 1). Upon impact with the prey, the tongue pad rotates as a result of the biomechanics of projection (Lombard and Wake, '77) and in response to prey inertia. In no case does the tongue pad strike the forceps. Maximum total anteroventral rotation is approximately 180°.

Almost immediately upon reaching its maximum extension, the tongue begins to return to the oral cavity (Fig. 3). During its return, the glandular dorsal surface of the tongue pad rotates posterodorsally (Fig. 1) such that by the time it reaches the mandibular symphysis, it is oriented vertically (90°); as the tongue pad crosses the mandibular symphysis, it quickly rotates from 90° to approximately 0°, then continues to move deep into the oral cavity. Maximum gape is achieved during the final period of posterior tongue displacement that occurs after the pad has reentered the oral cavity (Fig. 3). Once the tongue is positioned deep within the throat, the jaws quickly close.

Tongue extension beyond the mandibular symphysis is limited to phase II and phase IIIA. On average, the tongue extension cycle (phase II + phase IIIA) lasts 28.7 ms, or 29% of the entire gape cycle. Notably, the time required for protraction of the tongue pad (phase II) is only 8% of the gape cycle (7.7 ms).

### Comparative kinematics

Kinematic stereotypy of the *Bolitoglossa occidentalis* gape cycle is demonstrated further by comparison of successful and unsuccessful prey capture attempts. Except for a slight difference in the durations of phase IIIA (and consequently the tongue extension cycles), no statistically significant differences were observed between the durations and partitioning of the gape cycle, maximum tongue extensions, or maximum gape angles of successful versus unsuccessful prey capture sequences (Table 1). The success of the prey capture attempt, however, did influence the kinematics of jaw rotation. When prey capture was successful, there was a significant increase in mandibular rotation during mouth opening and closing compared to when prey capture was unsuccessful (31° vs. 22°; t = 2.474; P < 0.05).

In order to examine the relationship between the three functional categories of tongue projection proposed by Lombard and Wake ('77, '86; see below) and prey capture kinematics, the gape cycle of *Bolitoglossa occidentalis* (which has a free projectile tongue) was compared to the gape cycles of plethodontid salamanders having a 1) free projectile tongue (*B. mexicana*), 2) attached projectile tongue (*Ensatina eschscholtzii*), and 3) attached protrusible tongue (*Plethodon glutinosus* and *Desmognathus quadramaculatus*). The gape cycle of *B. occidentalis* also was compared to those of two species of the Hynobiidae (*Hynobius nebulosus* and *H. kimurae*) which also have attached protrusible tongues.

With the exception of phase IV, the gape cycle of *Bolitoglossa occidentalis* is not significantly different than that of *B. mexicana* (Table 2). However, several important kinematic differences are present between the gape cycle of *B. occidentalis* and those of the species with more primitive and less specialized methods of tongue projection (Table 2; Fig. 5). The most consistent differences involve the parameters associated with tongue projection: *Hynobius kimurae, H. nebulosus, Desmognathus quadramaculatus, Plethodon glutinosus*, and *Ensatina eschscholtzii* spend significantly less time preparing the tongue for projection (phase I), and all but *E. eschscholtzii*

*TABLE 2. Comparative kinematics of prey capture*[1]

| Species | | PI | PII | PIIIA | PIII | PIV | GC | TEC |
|---|---|---|---|---|---|---|---|---|
| | | | | | Time (ms) | | | |
| B. occidentalis | $\bar{X}$ | 34.8 | 7.7 | 21.0 | 30.8 | 25.5 | 99.6 | 28.7 |
| | SE | 1.7 | 0.8 | 1.0 | 0.7 | 1.2 | 1.4 | 1.4 |
| B. mexicana | $\bar{X}$ | 37.0 | 5.0 | 20.0 | 27.0 | 39.0* | 108.0 | 25.0 |
| | SE | 3.0 | 1.0 | <0.1 | 1.0 | 5.0 | 2.0 | 1.0 |
| E. eschscholtzii | $\bar{X}$ | 6.7** | 11.6 | 26.4[2] | 39.6* | 29.7 | 87.4* | 38.0[2] |
| | SE | <0.1 | 1.6 | — | 3.3 | 9.9 | 4.9 | — |
| P. glutinosus | $\bar{X}$ | 21.3** | 19.3** | 25.5* | 30.3 | 25.3 | 96.3 | 44.0** |
| | SE | 1.3 | 2.7 | 1.6 | 2.1 | 4.4 | 6.3 | 2.9 |
| D. quadramaculatus | $\bar{X}$ | 19.8** | 37.3** | 23.1 | 23.1** | 29.7 | 109.9** | 60.4** |
| | SE | 1.9 | 10.5 | 1.9 | 3.3 | 8.3 | 1.1 | 11.5 |
| H. nebulosus | $\bar{X}$ | 17.7** | 36.0** | 26.3 | 32.9 | 29.1 | 115.7* | 62.3** |
| | SE | 1.7 | 2.6 | 2.5 | 2.5 | 1.9 | 7.2 | 4.5 |
| H. kimurae | $\bar{X}$ | 15.1** | 27.4** | 16.1* | 22.0** | 29.8 | 94.4 | 43.9** |
| | SE | 1.1 | 2.4 | 1.5 | 2.0 | 1.9 | 5.7 | 3.5 |

[1] Levels of significance are for pairwise t-tests between *Bolitoglossa occidentalis* and each of the additional species listed. Refer to Table 1 for an explanation of abbreviations. $\bar{X}$ = mean; SE = standard error.
[2] N = 1.
*P < 0.05.
**P < 0.01.

expend significantly more time actually projecting the tongue pad (phase II) than *B. occidentalis* (Table 2). In addition, the tongue is extended beyond the mandibular symphysis a maximum of 30% SVL by *B. occidentalis* (Fig. 1), 15% SVL by *E. eschscholtzii*, but only 7% SVL by *H. kimurae*, *H. nebulosus*, *D. quadramaculatus*, and *Plethodon glutinosus* (Fig. 5). These differences in phase II also yield significantly different times for the tongue extension cycles of these species (TEC; Table 2). Despite the differences in phase I and phase II, all five of the less specialized species spend nearly an equivalent amount of time on final mouth closure (phase IV) as does *B. occidentalis*. Furthermore, the range of times for the entire gape cycle (GC; Table 2) is remarkably narrow for all species investigated.

## DISCUSSION

As in *Desmognathus* (Larsen and Beneski, '88), the gape cycle of *Bolitoglossa* begins with the mouth being opened by a combination of dorsal elevation of the cranium and ventral depression of the mandible. The cycle is highly stereotypic in *B. occidentalis* as indicated by both successful and unsuccessful prey capture attempts. The only major intraspecific difference is more mandibular rotation during mouth opening and final closure when a capture attempt is successful. This increase in mandibular rotation could be related to the additional mass (prey) at the tip of the tongue and/or possibly "recoil" from the tongue pad striking the prey; in either case, the additional force may be transmitted from the tongue pad, through the stalk to the lower jaw, causing the jaw to rotate further. Thus, the observed differences in jaw rotation between successful and unsuccessful prey capture attempts appear to be strictly biomechanical and *not* adjustments by the salamander in response to neural feedback. The less derived plethodontids, as well as terrestrial hynobiids, ambystomatids, and many salamandrids exhibit a similar degree of gape cycle stereotypy (Larsen and Beneski, '88; Larsen and Guthrie, '75; Lombard and Wake, '76, '77; Roth, '76, '87) (Larsen, Beneski, and Miller, unpublished data). In the bolitoglossines the combination of highly stereotypic prey capture behavior and a relatively small lingual pad, seems to limit the size and type of prey that they can successfully capture to small, often moving, arthropods (Lombard and Wake, '77; Wake, '87); such specializations apparently enabled them to exploit "niches" which otherwise would have been unavailable.

An important component of the prey capture cycle appears to be phase II, tongue projection (Table 2). Of all terrestrial salamanders examined, this phase is most rapid in *Bolitoglossa occidentalis*, *B. mexicana*, and *Ensatina*. Even though the length of time required for tongue protraction is significantly shorter in *Bolitoglossa* than in salamanders with attached protrusible
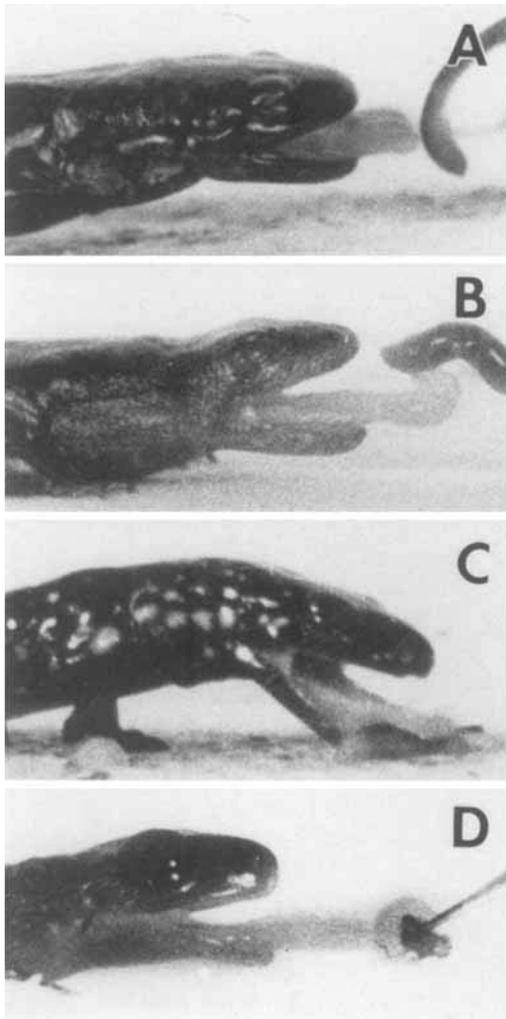
Fig. 5. Cinematic frames of salamanders with their tongues fully protracted and the pad in contact with prey (*Lumbricus* sp.—A–C; *Drosophila* sp.—D). **A:** *Hynobius kimurae* (protrusible tongue). **B:** *Desmognathus quadramaculatus* (protrusible tongue). **C:** *Plethodon glutinosus* (protrusible tongue). **D:** *Ensatina eschscholtzii* (attached projectile tongue).

tongues, the range of times for the entire gape cycle is generally similar for all salamanders analyzed in this study (Table 2). One possible adaptive advantage of rapid tongue extension is that it decreases the prey's available escape time. Thus, even small moving insects are vulnerable to the prey-capture system of the bolitoglossines (Wake, '87). Most other terrestrial salamanders take larger prey that are delivered into the oral cavity by a short, often massive and usually bulbous tongue. Such prey, because of their large size, make contact with and are restrained by the marginal dentition. The smaller bolitoglossine tongue

pad, however, carries the entire small prey item to the posterior region of the mouth. In these salamanders marginal teeth play little or no role in prey capture; usually only the palatal teeth are involved. The apparent absence of a function in feeding for the marginal teeth has resulted in a reduction in their number and/or an alteration to their morphology in some bolitoglossines including species of *Thorius* and *B. rufescens* and *B. colonnea* (Wake, unpublished data).

While most terrestrial salamanders combine a forward head/body surge with tongue projection (Dalrymple et al., '85; Larsen and Beneski, '88), *Bolitoglossa occidentalis* does not (Roth and Wake, 85b). It has been suggested by Roth and Wake ('85a) and Wake et al. ('88) that by remaining immobile, except for tongue thrusts during prey capture attempts, bolitoglossine species are less likely to attract the attention of predators or frighten prey. However, the absence of a head/body surge by *B. occidentalis* also appears to be related to this salamander's arboreality among bromeliad and banana leaves. Because the species is a leaf axil specialist a sudden forward lunge could cause it to fall to the ground. Investigations on the distribution of tropical plethodontids by Wake and Brame ('69) and Wake and Lynch ('76) demonstrated a correlation between arboreality and a fully webbed manus and pes. Thus, the combination of foot specializations, small body size (Alberch, '81), and a behavior pattern that lacks a head/body surge, as occurs in *B. occidentalis*, appears to be highly adaptive for safely moving about and maintaining position on a swaying platform (large smooth leaf) during prey capture. The head/body surge in other genera may increase the force of contact with and extend the distance at which prey can be taken. In bolitoglossines these functions are accomplished almost entirely by the tongue mechanism. The maximum strike range that we observed for *B. occidentalis* was 143% HL compared to only 64% HL for *Desmognathus quadramaculatus*. Head/body surge is apparently an important component of deglutition in most terrestrial salamanders (Dalrymple et al., '85; Larsen and Beneski, '88; Larsen and Guthrie, '75), but it is absent from this stage of the feeding cycle in *B. occidentalis*, probably for the reasons cited above.

During phase III the gape angle of *Bolitoglossa occidentalis* and *B. mexicana* increases dramatically to accommodate the prey being returned with the retracting tongue. This increase in the size of the gape also enables the hyolingual sys-

tem to deliver the prey far back into the oral cavity thus reducing the possibility of the prey escaping. Not only does the gape increase during phases I–III, but the head is elevated to facilitate the process of aiming the tongue. Since aiming the free projectile tongue is largely a visual process (Roth, '87), at no time are the eyes retracted by the retractor bulbi muscle as is the case during attempted prey capture by *Desmognathus* (Larsen and Beneski, '88) and *Ambystoma tigrinum* (Larsen and Guthrie, '75). In no recorded feeding sequence did *B. occidentalis* fail to hit the prey with its tongue pad. All unsuccessful capture attempts were caused by a failure of the prey to adhere to the tongue pad, apparently as a result of the prey being presented too close to the salamander.

The distance to which the tongue can be protracted from the mouth ranges from 7% SVL in *Desmognathus quadramaculatus, Plethodon glutinosus, Hynobius kimurae,* and *H. nebulosus* (attached protrusible tongue); through 15% SVL in *Ensatina eschscholtzii* (attached projectile tongue); to as much as 30% SVL in *Bolitoglossa occidentalis* (free projectile tongue). Thexton et al. ('77) reported that maximum tongue projection approximated 44% SVL in *B. occidentalis* with a velocity of 3–5 m/sec. Tongue protraction by the plethodontid *Hydromantes italicus* is apparently relatively and absolutely much greater in distance, but the speed is markedly slower than in species of the tropical supergenus *Bolitoglossa* (Roth '76).

The degree of tongue protraction in salamanders is limited by the length and location of origin and insertion of the genioglossus muscle. According to Lombard and Wake ('77), this muscle exhibits a small increase in length in the desmognathines, *Plethodon* and *Aneides,* relative to species of the other families. It is moderately to extensively elongate in *Ensatina, Hemidactylium* (Lombard and Wake, '77) and *Batrachoseps* (Piatt, '35) respectively. In the hemidactyliine genera *Typhlotriton* and *Stereochilus* it "is reduced to a few fibers or is absent" (Roth and Wake, '85a) and in *Bolitoglossa* it is always absent (Lombard and Wake, '77). Apparently the relatively longer genioglossus muscles of some plethodontid lineages permit greater tongue projection distances. However, when this muscle is absent, as is true in *Bolitoglossa,* it obviously plays no role in restricting the tongue during projection. Possibly, the evolutionary pathway leading to the presently configured free projectile tongue of the supergenus *Bolitoglossa* extended from a short genioglossus to a relatively long one; the muscle then may have become "reduced to a few fibers" (Roth and Wake, '85a) before it eventually disappeared as is the case in some hemidactyliines. Alternatively, the free projectile tongue of *Bolitoglossa* and the attached projectile tongue of *Batrachoseps* may represent divergent structural-functional pathways from an ancestral condition in which a short genioglossus was lost, and elaborated, respectively. Its absence from *B. occidentalis* is in part responsible for this salamander's ability to project the tongue and the entire hyolingual system, except for the epibranchials, from the mouth (Fig. 1), thus providing a relatively greater strike range than is available to salamanders with attached tongues.

The basic gape cycle of *Bolitoglossa occidentalis* is not significantly different from that of most other terrestrial urodeles (Larsen and Beneski, '88; Larsen and Guthrie, '75) and the range of times from start to completion of the cycle is remarkably similar for all salamanders examined. However, two intracyclic differences are significant. The less derived salamanders spend less time preparing the tongue for firing and more time in its projection than *Bolitoglossa* and *Ensatina* (Table 2). This factor apparently is related to the configuration of the bolitoglossine hyolingual system which, because of its complexity, requires greater time for modulation compared to the slower, less protractable mechanisms of the other species investigated. In addition, the latter species probably can open the mouth and commence protraction of the tongue concomitantly. *Bolitoglossa,* on the other hand, fires the tongue so quickly that 1) the mouth must be opened widely before "firing" occurs so that the projecting tongue clears the jaws, and 2) the position of the cranium and jaws must be stabilized to provide a stationary platform for accurate aiming/firing of the tongue.

All terrestrial salamanders possess the same basic prey capture system (Larsen and Guthrie, '75; Larsen and Beneski, '88): a sticky tongue pad for ensnaring prey that can be deployed from the mouth by the hyolingual apparatus. However, within the order Urodela generally, and among the plethodontid groups, specifically, an impressive assortment of unique specializations have evolved from this basic plan. The success of the bolitoglossini in their invasion of diverse tropical habitats and the accompanying adaptive radiation of this tribe (Wake, '87) has been facilitated

by the hyolingual feeding system. This versatile system, which permits the salamanders to capture relatively small active prey rapidly and effectively without calling themselves to the attention of predators, functions in a vast array of microhabits, and may have been of critical importance in both origin and continued evolution of the group.

## ACKNOWLEDGMENTS

## LITERATURE CITED

Alberch, P. (1981) Convergence and parallelism in foot morphology in the neotropical salamander genus *Bolitoglossa.* I. Function. Evolution, *35:*84–100.

Bramble, D.M., and D.B. Wake (1985) Feeding mechanisms of lower tetrapods. In: Functional Vertebrate Morphology. M. Hildebrand, D.M. Bramble, K.F. Liem, and D.B. Wake, eds. Univ. Harvard Press, Cambridge, pp. 230–404.

Dalrymple, G.H., J.E. Jutterbock, and A.L. LaValley (1985) Function of the atlanto-mandibular ligaments of desmognathine salamanders. Copeia, *1985:*254–257.

Dockx, P., and F. De Vree (1986) Prey capture and intra-oral food transport in terrestrial salamanders. In: Studies in Herpetology. Z. Rocek, ed. Charles Univ. Press, Prague, pp. 521–524.

Druner, L. (1901) Studien zur Anatomie der Zungenbein-, Kiemenbogen- und Kehlkopfmuskelen der Urodelen. I. Theil, Zool. Jahrb. Abteil. Anat., *15:*435–622.

Druner, L. (1904) Studien zur Anatomie der Zungenbein-, Kiemenbogen- und Kehlkopfmuskelen der Urodelen. II. Theil, Zool. Jahrb. Abteil. Anat., *19:*361–690.

Francis, E.T. (1934) The Anatomy of the Salamander. Oxford Univ. Press, London, 381 pp.

Frost, D.R. (1985) Amphibian Species of the World. Allen Press, Lawrence, Kansas, 732 pp.

Hinderstein, B. (1971) The desmognathine jaw mechanism (Amphibia: Caudata: Plethodontidae). Herpetologica, *27:* 467–476.

Larsen, J.H., Jr., and J.T. Beneski, Jr. (1988) Quantitative analysis of feeding kinematics in dusky salamanders (*Desmognathus*). Can. J. Zool., *66:*1309–1317.

Larsen, J.H., Jr., and D.J. Guthrie (1975) The feeding system of terrestrial tiger salamanders (*Ambystoma tigrinum melanostictum* Baird). J. Morphol., *147:*137–154.

Lombard, R.E., and D.B. Wake (1976) Tongue evolution in the lungless salamanders, family Plethodontidae. I. Introduction, theory and a general model of dynamics. J. Morphol., *148:*265–286.

Lombard, R.E., and D.B. Wake (1977) Tongue evolution in the lungless salamanders, family Plethodontidae. II. Function and evolutionary diversity. J. Morphol., *153:*39–80.

Lombard, R.E., and D.B. Wake (1986) Tongue evolution in the lungless salamanders, family Plethodontidae. IV. Phylogeny of plethodontid salamanders and the evolution of feeding dynamics. Syst. Zool., *35:*532–551.

Piatt, J. (1935) A comparative study of the hyobranchial apparatus and throat musculature of the Plethodontidae. J. Morphol., *57:*213–251.

Reilly, S.M., and G.V. Lauder (1988) Kinetics of tongue projection in *Ambystoma tigrinum:* Quantitative kinematics, muscle function and evolutionary hypotheses. J. Morphol., *199:*223–243.

Roth, G. (1976) Experimental analysis of the prey catching behavior of *Hydromantes italicus* Dunn (Amphibia, Plethodontidae). J. Comp. Physiol., *109:*47–58.

Roth, G. (1987) Studies of Brain Function: Visual Behavior in Salamanders. Springer-Verlag, New York, 301 pp.

Roth G., and D.B. Wake (1985a) Trends in the functional morphology and sensorimotor control of feeding behavior in salamanders: An example of the role of internal dynamics in evolution. Acta Biotheor. (Leiden), *34:*175–192.

Roth, G., and D.B. Wake (1985b) The structure of the brainstem and cervical spinal cord in lungless salamanders (family Plethodontidae) and its relation to feeding. J. Comp. Neurol., *241:*99–110.

Severtsov, A.S. (1971) The mechanism of food capture in tailed amphibians. Dokl. Akad. Nauk SSSR (transl.), *197:*185–187.

Thexton, A.J., D.B. Wake, and M.H. Wake (1977) Tongue function in the salamander *Bolitoglossa occidentalis.* Arch. Oral Biol., *22:*361–366.

Wake, D.B. (1966) Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. Mem. So. Calif. Acad. Sci., *4:*1–111.

Wake, D.B. (1982) Functional and developmental constraints and opportunities in the evolution of feeding systems in urodeles. In: Environmental Adaptation and Evolution. D. Mossakowski and G. Roth, eds. Gustav Fischer, New York, pp. 51–66.

Wake, D.B. (1987) Adaptive radiation of salamanders in middle American cloud forests. Ann. Missouri Bot. Gard., *74:*242–264.

Wake, D.B., and A.H. Brame, Jr. (1969) Systematics and evolution of neotropical salamanders of the *Bolitoglossa helmrichi* group. Contrib. Sci. Nat. Hist. Mus. Los Angeles Co., *175:*1–40.

Wake, D.B., and J.F. Lynch (1976) The distribution, ecology and evolutionary history of plethodontid salamanders in tropical America. Nat. Hist. Mus. Los Angeles Co. Sci. Bull., *25:*1–65.

Wake, D.B., K.C. Nishikawa, U. Dicke, and G. Roth (1988) Organization of the motor nuclei in the cervical spinal cord of salamanders. J. Comp. Neurol., *278:*195–208.