The ontogeny of feeding kinematics in a giant salamander *Cryptobranchus alleganiensis*: Does current function or phylogenetic relatedness predict the scaling patterns of movement?

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Abstract

Studies of the scaling of feeding movements in vertebrates have included three species that display both near-geometric growth and isometry of kinematic variables. These scaling characteristics allow one to examine the "pure" relationship of growth and movement. Despite similar growth patterns, the feeding movements of toads (*Bufo*) slow down more with increasing body size than those of bass (*Micropterus*), and sharks (*Ginglymostoma*). This variation might be due to major differences in the mechanism of prey capture; the bass and sharks use suction to capture prey in water, while the toad uses tongue prehension to capture prey on land. To investigate whether or not these different scaling patterns are correlated with differences in feeding mechanics, we examined the ontogenetic scaling of prey capture movements in the hellbender salamander (*Cryptobranchus alleganiensis*), which also has near-geometric growth. The hellbender suction feeds in the same general manner as the teleosts and shark, but is much more closely related to the toad. The feeding movements of the hellbender scale more similarly to the feeding movements of toads than to those of fishes or sharks, indicating that phylogenetic relatedness rather than biomechanical similarity predicts ontogenetic scaling patterns of movement.
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Introduction

The effect of body size on the manner and speed of movement has long been a focal point of studies on animal locomotion (e.g., Rand and Rand, 1966; Pennycuick, 1975, 1990; Emerson, 1977; Biewener, 1983; Schmidt-Nielsen, 1984; Wilson et al., 2000). Changes in absolute size (i.e., mass or body length) are correlated with changes in many locomotor variables. For example, mammals of small body mass tend to have a more crouched posture than larger animals when performing the same gait (Biewener, 1989) and the stride frequency tends to decrease with increasing body mass (Heglund et al., 1974). Body dimensions also profoundly

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influence many aspects of locomotor performance, such as top speed, cost of transport and maximum jumping distance (McMahon, 1975; Pedley, 1977; Garland, 1983; Lindstedt and Thomas, 1994; Toro et al., 2003). Studies on the scaling of various aspects of locomotion have provided key insights into the evolution of diverse locomotor designs.

In contrast to locomotion, studies exploring the scaling of feeding movements are uncommon. There is a substantial literature on feeding behavior in ana-mniotes and interspecific and evolutionary comparisons have been the focus of several papers and book chapters (e.g., Lauder, 1985; Muller and Osse, 1984; Reilly and Lauder, 1992). However, ontogenetic scaling data have been gathered for only a handful of species including largemouth bass, *Micropterus salmoides* (Richard and Wainwright, 1995; Wainwright and Shaw, 1999), spotted sunfish, *Lepomis punctatus*, bluegill sunfish, *L. macrochirus* (Wainwright and Shaw, 1999), zebrafish, *Danio rerio* (Hernandez, 2000), nurse sharks, *Ginglymostoma cirratum* (Robinson and Motta, 2002), fire salamanders, *Salamandra salamandra* (Reilly, 1995), Sonoran Desert toads, *Bufo alvarius*, (O'Reilly, 1998) and spiny lizards, *Sceloporus undulatus* and *Sceloporus magister* (Meyers et al., 2002).

While the durations of feeding movements in most of the species described to date are positively correlated with changing head dimensions, those of toads increase more radically than the rest. The durations of feeding movements of aquatic sharks and teleost fishes display positive scaling coefficients[2] ranging from 0.16 to 0.59 (i.e., duration scales as $L^{0.16}$ to $L^{0.59}$) for jaw and hyobranchial movements (Richard and Wainwright, 1995; Wainwright and Shaw, 1999; Hernandez, 2000; Robinson and Motta, 2002). In aquatic larval salamanders, the timing of jaw and hyoid movements during feeding is independent of body dimensions (Reilly, 1995). In the terrestrial lizard *Sceloporus*, the durations of jaw and tongue movements are also largely independent of body size (Meyers et al., 2002). In contrast, the durations of similar feeding movements increase with increasing size in toads with scaling coefficients ranging from 0.73 to 1.01, a condition that appears to be derived among vertebrates.

The evolution of a divergent scaling pattern in toads may have been driven by the biomechanics of ballistic tongue projection and its associated neurological specializations. Toads use a relatively elaborate mechanism to protract their tongues that involves tight coordination of jaw and tongue movements via a unique sensory feedback system (Nishikawa and Gans, 1996; Deban et al., 2001). Alternatively, the higher scaling coefficients observed in toads might be a more general characteristic of amphibians that is not tied to any particular functional characteristics.

To begin to address this issue, we quantified the feeding movements of hellbenders, *Cryptobranchus alleganiensis*, of a wide range of body sizes. Hellbenders are large (over 70 cm total length when fully grown), completely aquatic salamanders found in mountainous regions of the eastern United States (Conant and Collins, 1991; Nickerson and Mays, 1973). Belonging to the Lissamphibia, they are much more closely related to *Bufo* than they are to sharks and teleost fishes (Fig. 1), but like the sharks and fishes for which scaling data are available, they use suction to capture prey that is often very large relative to themselves (Elwood and Cundall, 1994). If natural selection on behavior in response to the evolution of feeding biomechanics is the predominant factor driving the evolution of the steeper scaling coefficients in *Bufo*, the scaling pattern in *Cryptobranchus* should be more similar to other suction feeding vertebrates than to *Bufo*. On the other hand, if phylogenetic affinity determines the relationship between feeding movements and body size, the movements of *Cryptobranchus* should scale like those of *Bufo* and not like those of sharks and teleost fishes (Fig. 1). The goals of this study are (1) to
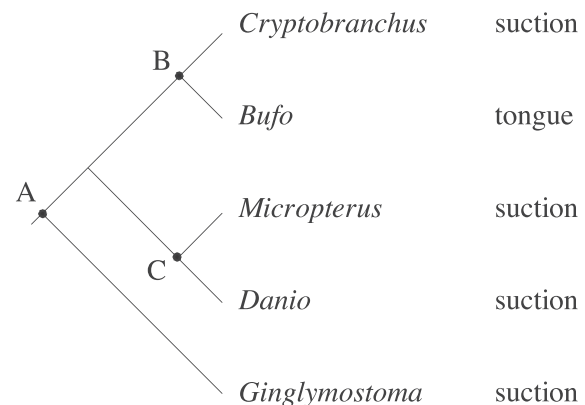
Fig. 1. Phylogenetic relationships of taxa discussed in this study. Node A indicates a more distant common ancestor of the fishes *Micropterus*, *Danio* and *Ginglymostoma*, compared to node B, the recent shared ancestor of the amphibians *Cryptobranchus* and *Bufo*. The comparison of scaling relationships between *Cryptobranchus*, *Bufo*, *Micropterus* and *Ginglymostoma* allows us to determine whether phylogeny or biomechanics predicts scaling patterns, because the taxa above node B represent both a divergence in biomechanics and recent shared ancestry. Comparison of taxa above node C, on the other hand, while representing a relatively recent shared ancestry, have not diverged in biomechanics and therefore would not be a good test of the hypothesis. Feeding modes are shown next to taxon names.

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[2]Scaling coefficients presented here are from the allometric equation: $y = \log a + b \log L$, where y is the kinematic variable plotted versus body length, L, a is the y-intercept of the regression line, and b is the slope of the regression line or the scaling coefficient. A scaling coefficient of $b = 1.00$ for a variable, y, indicates that y increases in direct proportion to body length, or $y \propto L^{1.00}$.

characterize the scaling of body dimensions and feeding movements in *Cryptobranchus*, and (2) to determine whether *Cryptobranchus* more closely resembles toads or fishes in the scaling of their feeding movements.

Materials and methods

The *C. alleganiensis* Leuckart, 1821 used in this study were collected from wild populations in western North Carolina and maintained on a diet of earthworms (*Lumbricus*), tubifex worms (*Tubifex*), and goldfish (*Carassius*). Salamanders were housed individually in filtered tap water at 12 °C, on a local (Berkeley, CA) light cycle. The ten animals from which data were collected ranged in size from 43 to 370 mm snout-vent length (SVL) and 1.3–850 g body mass (Table 1). The three smallest animals were larvae and retained external gills, while the remaining animals were metamorphosed.

Five morphological measurements were made of each individual: (1) SVL, measured from the tip of the snout to the posterior angle of the vent, (2) total length, (3) head width, measured at the jaw joint, (4) head length, measured from the tip of the snout to the rear edge of the angular ossification of the lower jaw, and (5) body mass. Total length was omitted for one individual whose tail was incomplete.

Feeding behavior was videotaped at 180–400 fields s^{-1} in lateral view with a Display Integration Technologies HSC 300 high-speed video camera with synchronized stroboscopic illumination or a J.C. Labs 250-Plus high-speed video camera with electronic shutter and flood lamp illumination. Animals were videotaped in lateral view feeding on goldfish, earthworms, or tubifex worms against a background grid to provide scaling factors and aspect-ratio correction. Several feedings were recorded for each individual, but only those in which the jaws and throat were visible throughout the sequence, and in which the salamander remained in lateral or rostrolat-

eral view were used for kinematic analysis. Sequences in which the animal twisted along its body axis, which were common, were excluded from the analysis. A total of 28 feeding sequences were analyzed.

Videography and kinematic analysis

Video sequences were captured and analyzed using NIH Image version 1.61 and Microsoft Excel version 5.0 software. The x, y coordinates of four points on the salamander were recorded from each field of the video sequence: (1) tip of upper jaw; (2) tip of lower jaw; (3) nape, the point of flexion at the head–neck joint; and (4) the ventral-most point on the throat, where the hyobranchial apparatus was visible as a bulge through the skin. These x, y coordinate data were used to calculate kinematic variables that describe the timing and extent of movements of head and jaws of the salamanders. Distances were calculated in mm. Duration and timing variables were calculated in milliseconds (ms) relative to the start of movement at time zero. Times were converted from frames to ms by multiplying the frame of the event (or frames of the duration) by the time interval between frames.

Two linear distances were calculated for each field directly from the x, y coordinate data: (a) gape distance, the distance between the upper jaw tip and the lower jaw tip, and (b) hyobranchial depression distance, the distance between the nape and the ventral-most point on the throat, normalized by subtracting the resting hyobranchial depression distance taken the first frame of the feeding sequence (Fig. 2). In addition, gape angle was calculated as the vertex angle of an isosceles triangle with gape distance as the base and mandible lengths as the sides for each field of the feeding sequences. Maximum values of gape distance and hyobranchial depression and the time needed until these values were

Table 1. Morphological measurements of experimental animals

SVL (mm)	Total length (mm)	Head length (mm)	Head width (mm)	Mass (g)
43	57	12	9	1.3
75	—	17	13	6.1
76	114	17	13	7.7
135	201	27	22	24.3
165	247	33	25	52
189	292	38	32	82
284	415	64	55	283
342	530	72	75	850
352	553	78	70	736
370	530	77	74	848
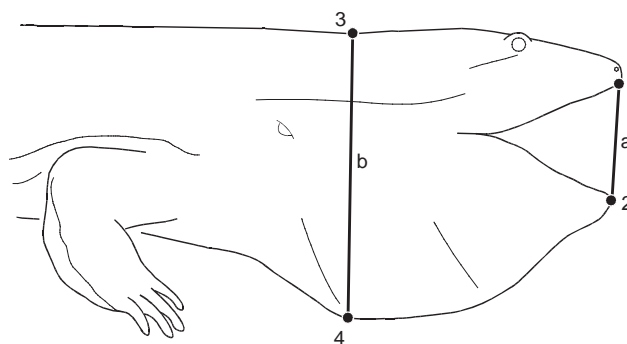
Fig. 2. Points used in kinematic analysis are (1) upper jaw tip, (2) lower jaw tip, (3) nape, and (4) hyobranchial apparatus. Distances are (a) gape distance and (b) hyobranchial depression distance.

reached were used to calculate durations and velocities of movement.

Four durations were calculated: (1) duration of mouth opening, the time between the start of mouth opening and maximum gape; (2) duration of mouth closing, the time between the start of mouth closing and the completion of mouth closing; (3) duration of the gape cycle, the time between the start of mouth opening and the completion of mouth closing, or the sum of durations 1 and 2; (4) duration of hyobranchial depression, the time between the start of hyobranchial depression and maximum hyobranchial depression.

Three average linear velocities and two average angular velocities were calculated from the position and duration variables: (1) average velocity of mouth opening, maximum gape divided by the duration of mouth opening; (2) average velocity of mouth closing, maximum gape divided by the duration of mouth closing; (3) average velocity of hyobranchial depression, maximum hyobranchial depression divided by the duration of hyobranchial depression; (4) average angular velocity of mouth opening, maximum gape angle divided by the duration of mouth opening; and (5) average angular velocity of mouth closing, maximum gape angle divided by the duration of mouth closing. Average velocities are reported in $m s^{-1}$ and average angular velocities are reported in $deg s^{-1}$.

Statistical analyses

The 12 kinematic variables and four of the five morphological variables were $\log_{10}$ transformed and the average for each individual and the greatest value for each variable from each individual was plotted against the $\log_{10}$ of SVL. The resulting scatter of each variable was fitted by linear regression using the least-squares (LS) method. The LS regression was used because kinematic variables have greater associated error than the morphological variable against which they are regressed (SVL), and because previous studies on the scaling of movement have used LS regressions. We also analyzed the morphological data using reduced major axis (RMA) regression (see methods of Robinson and Motta, 2002 for cogent discussion of appropriate use of different types of regression in scaling studies). The RMA slopes were within 0.01 of the LS slopes, therefore only LS slopes are discussed further.

The 95% confidence intervals of the slope of each regression line were used to determine (1) whether or not the *C. alleganiensis* used in this study are growing geometrically in morphological dimensions, and (2) if the observed kinematic data are consistent with the model of kinematic growth (discussed below) that is based on the premise of geometric growth of morphol-

ogy. In other words, if the slope of the growth line (i.e., the scaling coefficient) predicted by the model fell within the confidence intervals of the observed slope (scaling coefficient), we would fail to reject the kinematic growth model.

Among the scaling data in the literature, only those data from sharks (Robinson and Motta, 2002), bass (Richard and Wainwright, 1995) and toads (O'Reilly, 1998) are suitable for direct statistical comparison to the data from *Cryptobranchus*. The data from fire salamanders (*Salamandra*) encompass only a doubling of body length of very young individuals (Reilly, 1995; see *Discussion*), sunfish (*Lepomis*) and zebrafish (*Danio*) display significant morphological allometry during ontogeny (Wainwright and Shaw, 1999; Hernandez, 2000), zebrafish and spiny lizards (*Sceloporus*) display significant kinematic allometry in excursions with increasing body size (Hernandez, 2000; Meyers et al., 2002), and the data from *Lepomis* do not include variables describing linear or angular excursions (Wainwright and Shaw, 1999). In addition, the kinematic data from *Sceloporus* were analyzed using RMA regression (Meyers et al., 2002), which precludes the direct comparison to the results of our LS regressions.

We determined if the kinematics of *Cryptobranchus* scale more similarly to those of toads, those of bass, or those of sharks, by statistically comparing the scaling coefficient of each kinematic variable from *Cryptobranchus* to the scaling coefficients of the same variable from toad, bass, and shark. Because toads use tongue protraction and *Cryptobranchus* use suction, we could not compare hyobranchial depression kinematics between these two species, and we focused only on jaw movements (9 of 12 kinematic variables). Data for toad variables were taken from O'Reilly (1998), data for bass were taken from Richard and Wainwright (1995) and data for sharks were taken from Robinson and Motta (2002). Values that were not included in the published reports (e.g. standard errors of slopes for sharks and angular velocities for toads) were computed from the original raw data used in those studies, courtesy of the authors. Not all variables were measured in all species. LS regression analyses of kinematic and morphological data in *Cryptobranchus* were performed using StatView version 5.0, and RMA regression analyses on morphological data were performed using JMP 5.1. The comparisons of scaling coefficients between taxa were performed with Microsoft Excel 2004. If zero fell within the 95% confidence limits of the mean difference (between species) of the scaling coefficients for each variable, we could not reject the hypothesis that the scaling coefficients are the same, and concluded that the two species scale similarly in that variable (Bailey, 1995). Scatterplots for figures were created in SigmaPlot 8.0.

Results

Morphology

The animals used in this study grow geometrically in the four morphological variables measured (Fig. 3). Least-squares regression with SVL as the independent variable showed that total length has a scaling coefficient of 1.04, head length has a coefficient of 0.92, and head width 1.04. None of these is significantly different from 1.00, which describes geometric similarity (Table 2). Mass has a coefficient of 3.03 when regressed against SVL, which is not significantly different from the 3.00 predicted by geometric similarity. (SVL has a coefficient of 0.33 when regressed against body mass, not significantly different from the 0.33 that represents geometric similarity.)

Kinematics

The feeding movements of *Cryptobranchus* are typical for a suction feeding salamander, and similar to those of suction feeding fishes (Muller and Osse, 1984; Richard and Wainwright, 1995). Mouth opening and closing were of approximately the same duration, and peak hyobranchial depression occurred after peak gape (Fig. 4).

When average values for kinematic variables are plotted against SVL, the maximum excursions of the jaws and hyobranchial apparatus are directly proportional to body size (Fig. 5). Maximum gape distance scales with a coefficient of 0.91 and maximum hyobranchial depression with 0.77, neither significantly different from 1.00 (Table 2). Maximum gape angle scales with a coefficient of 0.02, which is not significantly different from 0.00. Duration of mouth opening scales as 0.96, duration of mouth closing as 0.98, duration of the gape cycle as 0.98, and duration of hyobranchial depression as 0.87; none were significantly different from 1.00, given the 95% confidence intervals of the slopes (Fig. 6). Linear velocities scale with slopes not significantly different from 0.00: velocity of mouth opening scales as 0.00, velocity of mouth closing as 0.05, and velocity of hyobranchial depression as 0.13 (Fig. 7). Angular velocity of mouth opening scales as 0.92 and angular velocity of mouth closing as 0.97, which were not significantly different from 1.00 (Fig. 7).
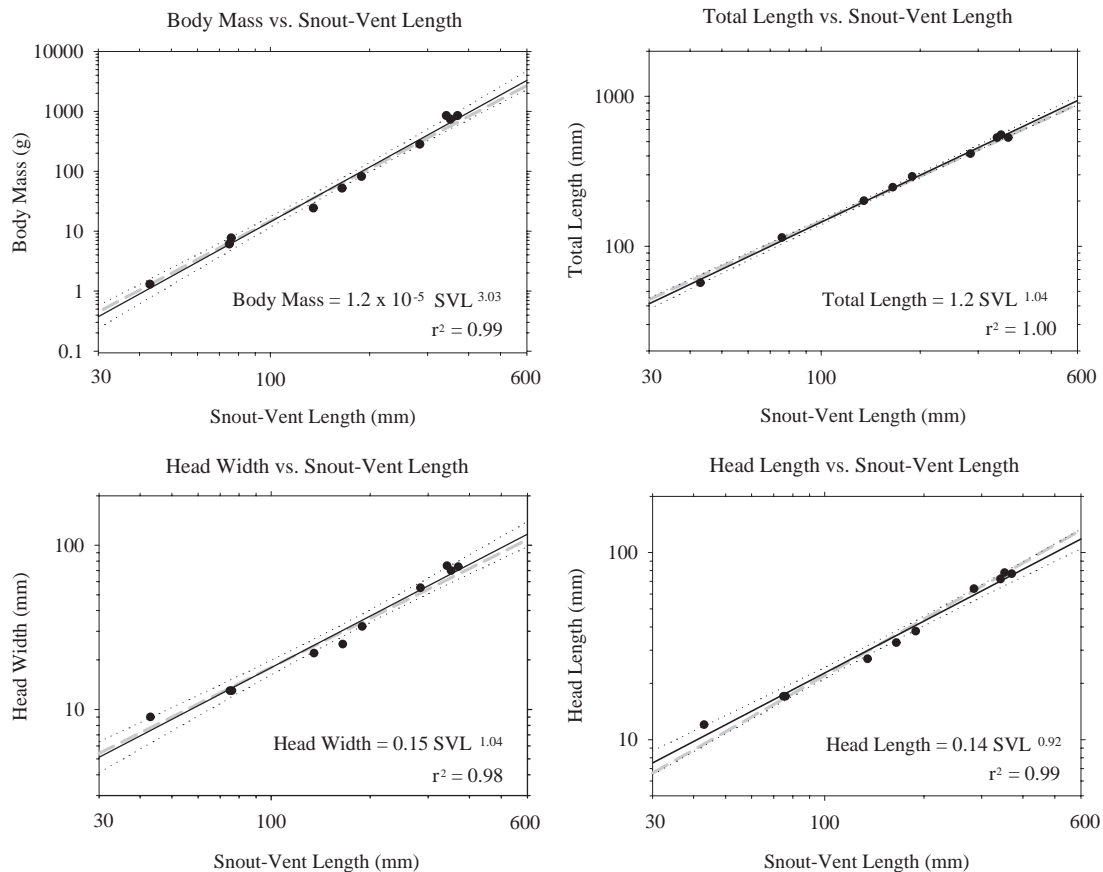
Fig. 3. Plots of morphological variables on log–log scales, showing slopes (exponents) of regression lines and r^2. All variables are regressed on snout-vent length. Slopes indicate near-geometric similarity.

Table 2. Expected and observed slopes of least-squares regression lines of the log of the average of each variable for each individual of *Cryptobranchus* as a function of log snout-vent length (SVL) (95% confidence intervals and standard errors of the slope of each regression are also shown)

Variable	Number of individuals	Expected slope	LS observed slope	Lower CI	Upper CI	Standard error of slope
Total length	9	1	1.04	0.99	1.09	0.02
Head length	10	1	0.92	0.84	1.01	0.04
Head width	10	1	1.04	0.92	1.17	0.05
Body mass	10	3	3.03	2.78	3.29	0.11
Maximum gape distance	10	1	0.91	0.62	1.20	0.13
Maximum gape angle	10	0	0.02	0.25	0.22	0.10
Maximum hyo. depression dist.	10	1	0.77	0.37	1.18	0.18
Duration of mouth opening	10	1	0.96	0.72	1.20	0.10
Duration of mouth closing	10	1	0.98	0.58	1.37	0.17
Duration of gape cycle	10	1	0.98	0.65	1.30	0.14
Duration of hyobranchial depression	10	1	0.87	0.47	1.26	0.17
Velocity of mouth opening	10	0	0.00	0.30	0.30	0.13
Velocity of mouth closing	10	0	0.05	0.45	0.35	0.17
Velocity of hyobranchial depression	10	0	0.13	0.61	0.35	0.21
Angular velocity of mouth opening	10	1	0.92	1.18	0.67	0.11
Angular velocity of mouth closing	10	1	0.97	1.34	0.60	0.16

Expected slope falls within 95% confidence intervals of observed slope for all variables.
Distances are in mm, velocities in m s^{-1}, angles in deg and angular velocities in deg s^{-1}.

When the greatest values for each variable from each individual are plotted against SVL to examine feedings of maximal effort, essentially the same results are obtained. Maximum excursions scale with slopes not significantly different from 1.00: maximum gape distance scales as 0.84 and maximum hyobranchial depression as 0.65. Maximum gape angle scales with a slope of 0.08, which was not significantly different from 0.00, given the confidence intervals. Durations also scale with slopes not significantly different from 1.00: duration of mouth opening scales as 1.04, duration of mouth closing as 1.07, duration of gape cycle as 1.02, and duration of hyobranchial depression as 0.81. Linear velocities scale with slopes not significantly different from 0.00: velocity of mouth opening scales as 0.02, velocity of mouth closing as 0.04 and velocity of hyobranchial depression as 0.20. Angular velocity of mouth opening scales as 0.90, and velocity of closing as 0.98, which did not differ significantly from 1.00 (Table 3).

Cryptobranchus differed significantly from *Micropterus* (Richard and Wainwright, 1995) in 10 of the 12 scaling coefficients (Table 4). Only maximum gape distance and maximum gape angle were the same in these two species. *Cryptobranchus* differed significantly from *Bufo* in none of the 9 scaling coefficients (Table 5). Finally, *Cryptobranchus* differed significantly from *Ginglymostoma* in only two of six coefficients: duration of mouth opening and duration of gape cycle (Table 6).
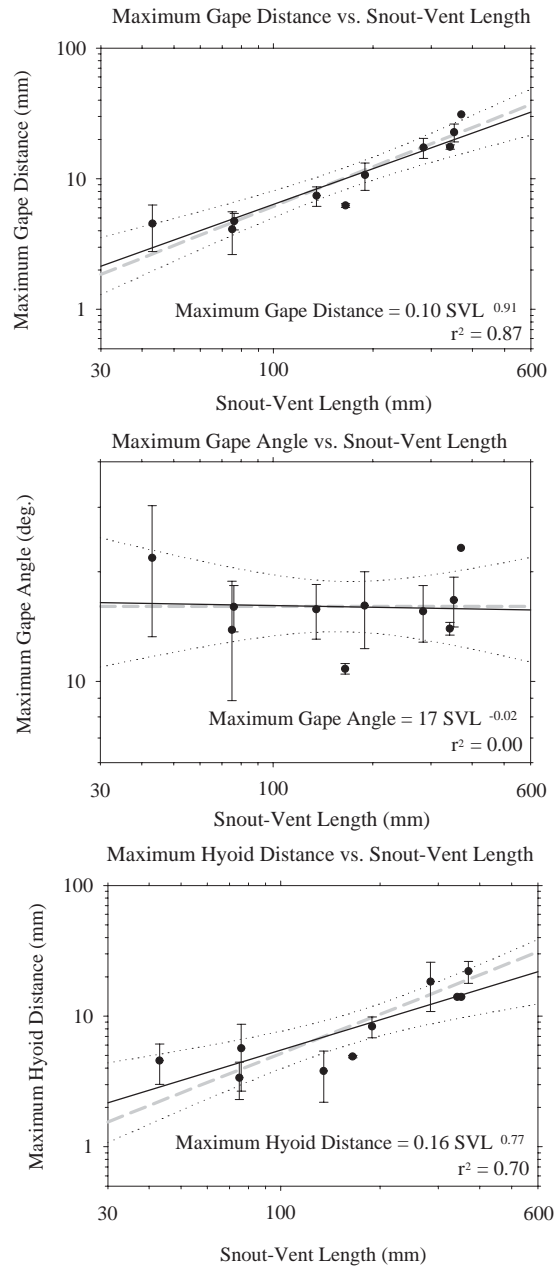
Discussion

Hill (1950) articulated the first quantitative model of the scaling of movement in vertebrates. Extrapolating from his in vitro data describing the contractile properties of vertebrate muscle (Hill, 1938), he concluded that the durations of similar movements should scale in proportion to length in vertebrate biomechanical systems. Specifically, Hill calculated that in geometrically similar vertebrates performing similar movements such as striding locomotion, with similar effort, stride frequency should scale inversely to limb length, while stride length should increase in direct proportion to limb length. The scaling of frequency and stride length would then cancel one another out and the maximum running velocity of animals would be independent of body dimensions. Hill's model has been the basis of all subsequent studies of the scaling of movement in vertebrates.
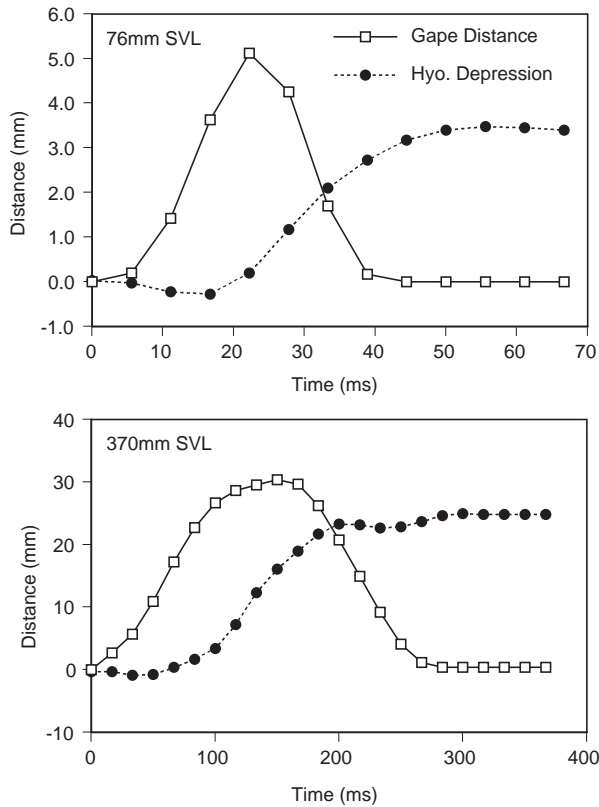
Fig. 4. Representative kinematic profiles of gape distance and hyobranchial depression of a 76 mm SVL *Cryptobranchus* compared to a 370 mm SVL *Cryptobranchus* showing similar movements of jaw and hyobranchial apparatus at two different time scales. The pattern of peak hyobranchial depression occurring after peak gape is typical of suction feeders and is very similar to the pattern observed in *Micropterus*.

Fig. 5. Plots of excursion distances and gape angle versus snout-vent length on log scales, showing slopes of regression lines and r^2. The slopes for gape and hyoid distance are not significantly different from 1, and the slope for gape angle is not significantly different from 0. Expected slopes are shown in thick gray lines. Ninety-five percent confidence intervals of observed slopes are shown as dotted lines. Standard deviations are shown as black bars.

Efforts to test Hill's hypothesis have been frustrated by the difficulty of finding an animal system in which growth is geometric across a large range of body sizes (Emerson, 1977). Hill's prediction that top running speed should scale independently of body mass has been found to hold for a 50-fold range of body mass in ungulates (e.g., Alexander et al., 1977) and for mammals ranging in size from dogs to horses (Hill, 1950). The prediction fails at extreme sizes, however, possibly due to allometric scaling in morphology; both larger and smaller mammals are slower than predicted (Pennycuick, 1992). Recent studies have focused on feeding in ectothermic vertebrates because these systems appear, at least superficially, to grow with geometric similarity; that is, they appear to meet more closely the requirements of Hill's model. Ectotherms also have the advantage of growing through enormous body size ranges in ontogeny, allowing us to determine intraspecific scaling relationships.

Previous studies of the scaling of feeding movements in largemouth bass (*M. salmoides*) and the nurse shark (*G. cirratum*) reveal scaling patterns that are very different from those predicted by Hill (1950). Bass grow geometrically and the linear excursions of the jaws and
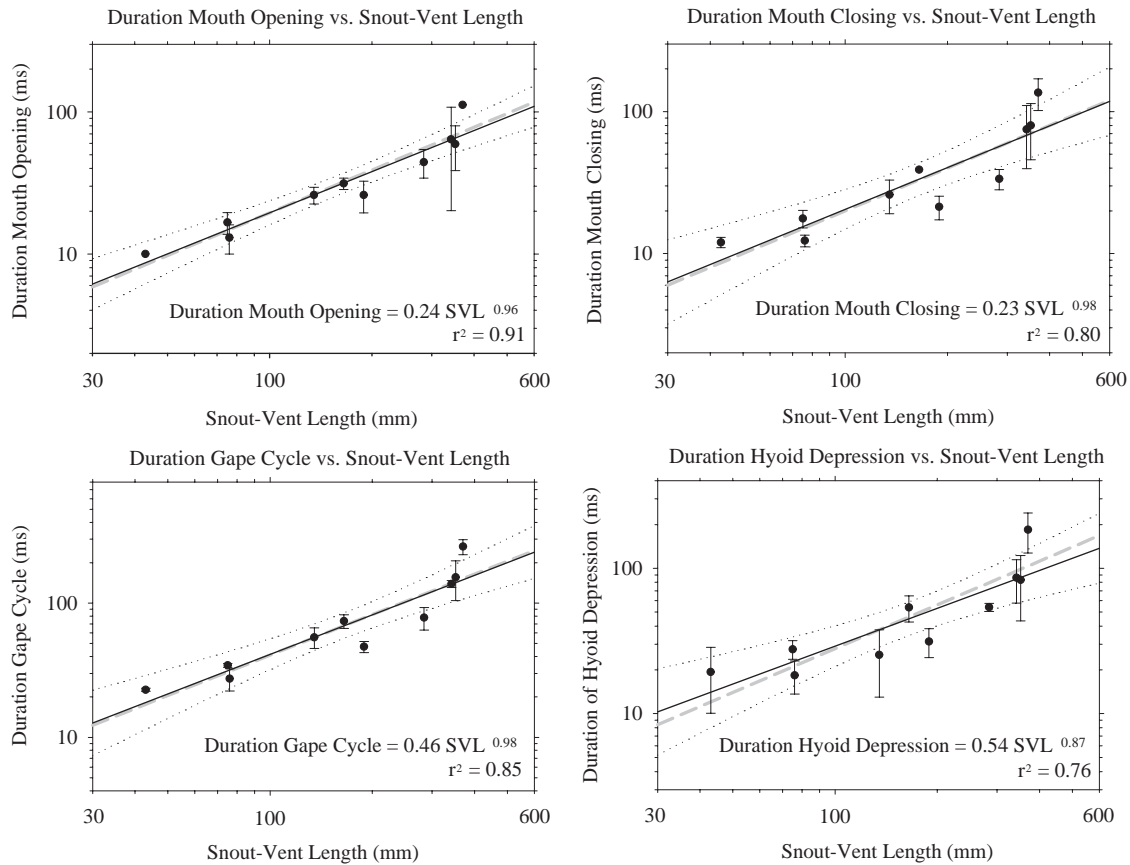
Fig. 6. Plots of duration variables versus snout-vent length on log scales. Slopes are not significantly different from 1, in agreement with Hill's predictions. Expected slopes are shown in thick grey lines. Ninety-five percent confidence intervals of observed slopes are shown as dotted lines. Standard deviations are shown as black bars.

hyoid scale in proportion to standard body length. However, the durations of jaw and hyoid movements scale to body length with slopes much lower (0.31–0.58) than the predicted slope of 1.00 (Richard and Wainwright, 1995; Wainwright and Shaw, 1999). Nurse sharks also meet the assumptions of the Hill-model and display movement durations that scale to body length with shallow slopes ranging from 0.24 to 0.48 (Robinson and Motta, 2002). Thus, as they grow, both bass and sharks show positive allometry of velocity of homologous morphological points during feeding rather than the isometry that Hill predicted.

In contrast to bass and sharks, the feeding movements of the Sonoran Desert toad (*B. alvarius*) are consistent with Hill's predictions. The scaling of the linear dimensions of the head and body of toads are very close to geometric and the linear and angular excursions also scale geometrically as toads increase in body size. The durations of feeding movements, such as mouth opening and tongue protraction, scale with slopes that are not significantly different from the predicted slope of 1.00 (O'Reilly, 1998; Table 5). Homologous anatomical

points on the toads therefore travel at the same average velocity regardless of body size and the time to complete a movement is directly proportional to the linear dimensions of the animal.

Based on morphological and kinematic measurements, *Cryptobranchus* appears to meet the assumptions of Hill's model. The morphological analysis confirms that *Cryptobranchus* is growing with near-geometric similarity (Fig. 3; Table 2). External linear dimensions scale with slopes of 0.92–1.04, and mass scales with a slope of 3.03 when regressed against SVL. As indicated from the scaling of linear and angular excursions, regardless of whether one uses average (Table 2) or maximum (Table 3) values, the feeding movements of *Cryptobranchus* are also similar throughout ontogeny. The timing data from *Cryptobranchus* should therefore be directly comparable to the previously reported data from bass, sharks and toads.

The results reveal that the scaling of the timing of feeding movements in *Cryptobranchus* are the same as those seen in *Bufo* and very different from *Micropterus* or *Ginglymostoma* (Tables 4–6). None of the 7 scaling
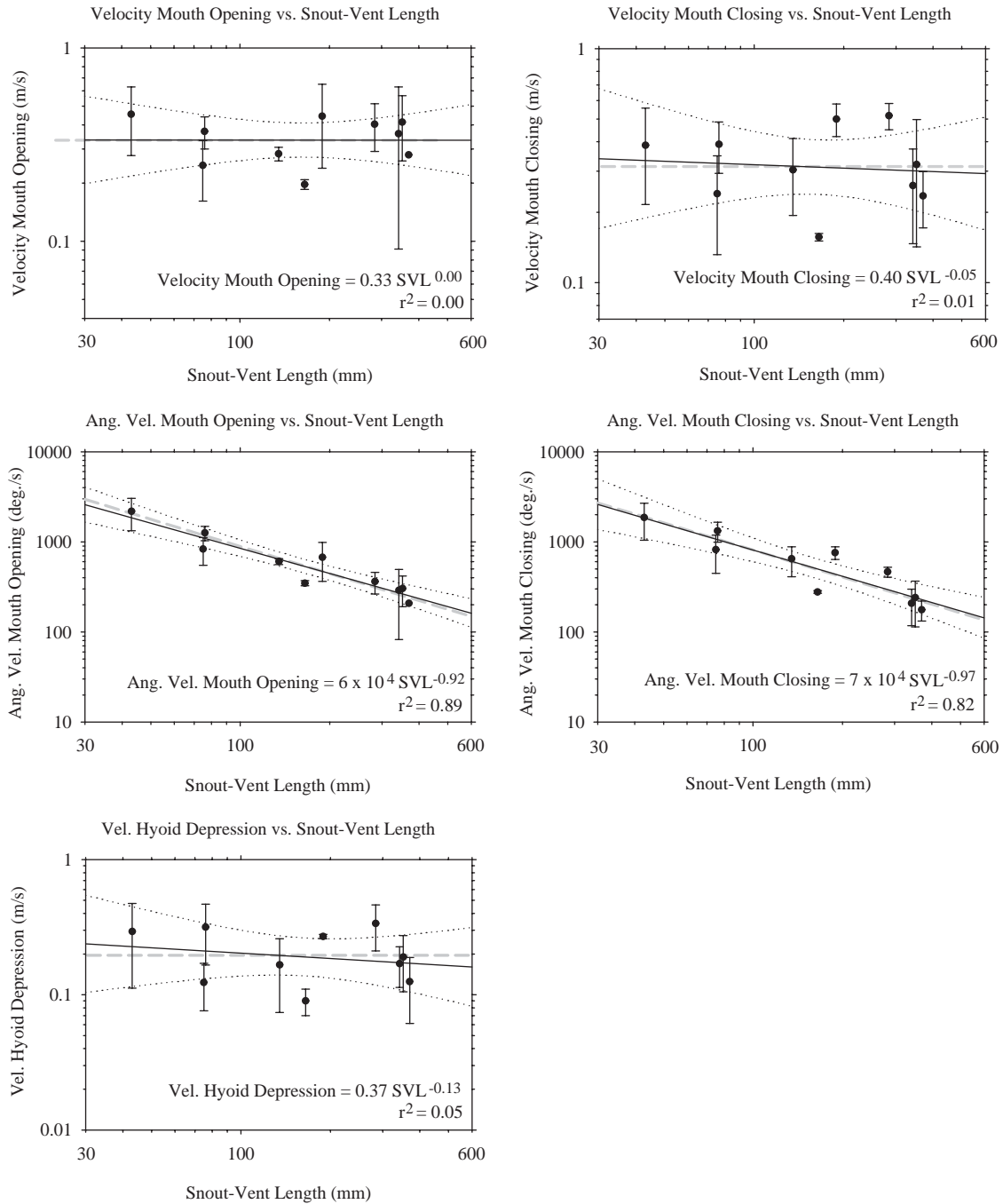
Fig. 7. Plots of linear and angular velocities versus snout-vent length on log scales. Note that slopes of the velocities are not significantly different from 0, and angular velocities are not significantly different from −1, in accordance with the predictions of Hill's model. Expected slopes are shown in thick grey lines. Ninety-five percent confidence intervals of observed slopes are shown as dotted lines. Standard deviations are shown as black bars.

coefficients for the time related variables of *Bufo* were significantly different from those of *Cryptobranchus*, while 9 of the 9 scaling coefficients of time related variables were significantly different from *Micropterus*. In comparison to *Ginglymostoma*, for which fewer variables were available for comparison, 3 of the 3

coefficients of time-related variables were significantly different from *Cryptobranchus*.

The unambiguous statistical results lead us to reject the hypothesis that the biomechanical regime of feeding (aquatic suction versus terrestrial tongue prehension) is at the root of differences in the scaling

Table 3. Expected and observed slopes of least-squares regression lines of the log of the greatest value of each variable for each individual of *Cryptobranchus* as a function of log snout-vent length (SVL) (95% confidence intervals and standard errors of the slope of each regression are also shown)

Variable	Number of individuals	Expected slope	LS observed slope	Lower CI	Upper CI	Standard error of slope
Maximum gape distance	10	1	0.84	0.53	1.15	0.13
Maximum gape angle	10	0	0.08	0.34	0.17	0.11
Maximum hyo. depression dist.	10	1	0.65	0.17	1.13	0.21
Duration of mouth opening	10	1	1.04	0.86	1.23	0.08
Duration of mouth closing	10	1	1.07	0.65	1.48	0.19
Duration of gape cycle	10	1	1.02	0.70	1.33	0.14
Duration of hyo. depression	10	1	0.81	0.40	1.23	0.18
Velocity of mouth opening	10	0	0.02	0.40	0.43	0.18
Velocity of mouth closing	10	0	0.04	0.47	0.40	0.19
Velocity of hyo. depression	10	0	0.20	0.71	0.31	0.22
Angular velocity of mouth opening	10	1	0.90	1.27	0.53	0.16
Angular velocity of mouth closing	10	1	0.98	1.38	0.57	0.18

Expected slope falls within 95% confidence intervals of observed slope for all variables.
Distances are in mm, velocities in m s^{-1}, angles in deg and angular velocities in deg s^{-1}.

of the timing of feeding movements in toads relative to bass and sharks. The previously reported differences between scaling of prey capture movements in bass and nurse sharks on the one hand and toads on the other suggested the logical hypothesis that the different biomechanics of suction feeding and tongue protraction led to the evolution of different ontogenetic scaling patterns. If different scaling patterns were related to biomechanical differences, the movements of a suction feeder should scale similarly to the bass and shark (or another animal using ballistic tongue protraction should scale like the toad). However, the current data demonstrate that the feeding movements of the hellbender scale like those of the toad, despite the fact that it uses the same general mechanism of prey capture as bass and sharks. The scaling of movement patterns is not tightly constrained by the functional characteristics of a given system and can vary considerably without significantly impacting performance. If this is true, then phylogenetic affinity will be a better predictor of scaling

Table 4. Slopes and standard errors for 12 kinematic variables for *Micropterus* and mean differences of slopes comparing *Cryptobranchus* and *Micropterus* with upper and lower 95% confidence intervals of mean differences

Variable	Slope[a]	Standard error[a]	Mean difference	Upper 95% CI	Lower 95% CI
Maximum gape distance	1.01	0.08	0.190 NS	0.481	0.101
Maximum gape angle	0.01	0.06	0.030 NS	0.262	0.202
Maximum hyo. depression dist.	1.19	0.06	0.420*	0.784	0.056
Duration mouth opening	0.31	0.07	0.650*	0.896	0.404
Duration mouth closing	0.58	0.09	0.400*	0.779	0.021
Duration gape cycle	0.43	0.07	0.550*	0.859	0.241
Duration hyobranchial depression	0.31	0.06	0.560*	0.915	0.205
Velocity mouth opening	0.76	0.09	0.760*	1.072	0.448
Velocity mouth closing	0.64	0.05	0.690*	1.041	0.339
Velocity hyobranchial depression	0.75	0.10	0.880*	1.331	0.429
Angular velocity mouth opening	0.33	0.07	0.590*	0.849	0.331
Angular velocity mouth closing	0.50	0.07	0.470*	0.814	0.126

Asterisks indicate significant differences in means from *Cryptobranchus* and *Micropterus*, indicated by the confidence intervals of mean difference failing to encompass zero.
NS indicates confidence intervals of the mean difference encompassing zero, so the hypothesis that the means differ is not rejected.
[a]Data from Richard and Wainwright (1995).

Table 5. Slopes and standard errors for nine kinematic variables for *Bufo* and mean differences of slopes comparing *Cryptobranchus* and *Bufo* with upper and lower 95% confidence intervals of mean differences

Variable	Slope[a]	Standard error[a]	Mean difference	Upper 95% CI	Lower 95% CI
Maximum gape distance	1.08	0.07	0.174 NS	0.453	0.105
Maximum gape angle	0.01	0.10	0.030 NS	0.310	0.250
Duration mouth opening	0.95	0.14	0.009 NS	0.346	0.328
Duration mouth closing	0.55	0.16	0.430 NS	0.882	0.022
Duration gape cycle	0.72	0.13	0.260 NS	0.629	0.109
Velocity mouth opening	0.13	0.13	0.134 NS	0.489	0.221
Velocity mouth closing	0.32	0.18	0.370 NS	0.852	0.112
Angular velocity mouth opening	0.96	0.17	0.040 NS	0.437	0.357
Angular velocity mouth closing	0.52	0.18	0.450 NS	0.918	0.018

Asterisks indicate significant differences in means from *Cryptobranchus* and *Bufo*, indicated by the confidence intervals of mean difference failing to encompass zero.
NS indicates confidence intervals of the mean difference encompassing zero, so the hypothesis that the means differ is not rejected.
[a]Data from O'Reilly (1998).

patterns than any functional similarities for vertebrates as a whole.

The data in this and other studies illustrate the importance of working with species that grow across at least two or three orders of magnitude in body mass when attempting to quantify the scaling of movement patterns. Reilly (1995) quantified prey capture behavior in eight larval *Salamandra salamandra* at two sizes covering a doubling of body length (approximately a 10-fold increase in body mass), and found that kinematics were identical at both sizes (i.e., the timing of feeding did not change). This result appears superficially to be at odds with ours, however, the three smallest animals in our study span a similar range of body lengths and display no obvious trend in the durations of jaw or hyoid movements (Fig. 6). Similarly, the smallest toads studied by O'Reilly (1998) show negative allometry of the durations of jaw movements (e.g., duration of jaw opening decreased) across a similar size range and 6 individuals. It is possible that these "flattened" patterns in early ontogeny are literally "learning curves", a hypothesis supported by the fact

that small adult toads (*B. quercicus*) feed more rapidly than recently metamorphosed *B. alvarius* of a similar size (O'Reilly, 1998). Regardless, while Reilly (1995) studied the widest range of sizes possible for larvae of *Salamandra* (i.e., birth to metamorphosis), it is an insufficient size range to reject the hypothesis that the feeding movements of this species scale in a similar manner to toads and hellbenders.

All of the data currently available suggest there may be a strong phylogenetic signal in the scaling of feeding movements in vertebrates. Our working hypothesis is that relatively shallow scaling patterns ($L^{0.16}$–$L^{0.59}$) are primitive for gnathostomes and that the steeper scaling lines observed in salamanders and anurans represent a shared, derived characteristic of amphibians. The one scaling study of feeding movements in an amniote (Meyers et al., 2002) suggests yet a third pattern, as the lizards studied (*Sceloporus*) showed little change in the timing of feeding movements over a 5-fold range in SVL. Examination of many additional taxa is needed to determine if this apparent phylogenetic signal is supported.

Table 6. Slopes and standard errors for six kinematic variables for *Ginglymostoma* and mean differences of slopes comparing *Cryptobranchus* and *Ginglymostoma* with upper and lower 95% confidence intervals of mean differences

Variable	Slope[a]	Standard error[a]	Mean difference	Upper 95% CI	Lower 95% CI
Maximum gape distance	0.75	0.15	0.157 NS	0.540	0.226
Maximum hyo. depression dist.	0.87	0.15	0.100 NS	0.553	0.353
Maximum gape angle	0.12	0.15	0.098 NS	0.454	0.258
Duration mouth opening	0.33	0.14	0.627*	0.972	0.282
Duration gape cycle	0.24	0.11	0.739*	1.086	0.392
Duration hyo. depression	0.41	0.18	0.465 NS	0.953	0.023

Asterisks indicate significant differences in means from *Cryptobranchus* and *Ginglymostoma*, indicated by the confidence intervals of mean difference failing to encompass zero.
NS indicates confidence intervals of the mean difference encompassing zero, so the hypothesis that the means differ is not rejected.
[a]Data from Robinson and Motta (2002).

In addition to gathering kinematic data from additional taxa, a deeper understanding of the physiological basis of the scaling patterns observed thus far would be extremely useful. A more detailed analysis of the scaling of morphology in *Bufo* and *Cryptobranchus* would allow comparisons to existing data sets describing the scaling of lever ratios in *Micropterus* (Richard and Wainwright, 1995; Wainwright and Shaw, 1999) and *Sceloporus* (Meyers et al., 2002) and comparisons of the scaling of muscle dimensions and possible ontogenetic changes in muscle architecture (e.g. fiber angles). Another logical next step would be to collect data sets on the motor patterns underlying these movements comparable to the available data on bass (Wainwright and Richard, 1995). A final vital set of data would be a comparison of the contractile properties of the muscles powering feeding movements. In its entirety, such data would allow us to determine if the differences observed in scaling patterns stem from underlying variation in the scaling of motor patterns, muscle architecture, muscle contractile properties or a combination of these factors.

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