

Stephen M. Reilly  
George V. Lauder

School of Biological Sciences,  
University of California,  
Irvine, Calif., USA

# Morphology, Behavior, and Evolution: Comparative Kinematics of Aquatic Feeding in Salamanders

## Key Words

Kinematics  
Morphology  
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*Amphiuma*  
*Siren*  
*Ambystoma*  
*Necturus*  
*Dicamptodon*  
*Cryptobranchus*

## Abstract

The kinematics of aquatic prey capture were studied in species representing six salamander families (Ambystomatidae, Amphiumidae, Cryptobranchidae, Dicamptodontidae, Proteidae, and Sirenidae) to test the hypothesis that the process of aquatic prey capture is similar in these families. Seven variables were digitized from high-speed video records of prey capture, and a nested analysis of variance was performed to test for both significant individual within taxon and among taxa effects. The time-to-peak head angle and gape variables showed no taxon effect, while the other five variables exhibited highly significant differences among taxa. *Cryptobranchus* and *Siren* showed the most divergent kinematic pattern from the other taxa in a multivariate analysis of all variables, while *Ambystoma*, *Dicamptodon*, and *Amphiuma* tended to have similar overall patterns of head movement. These results show that kinematic patterns during aquatic feeding are not conserved across salamander taxa, and that phylogenetic differentiation in head morphology has been accompanied by novelties in feeding function. The feeding mechanisms of *Cryptobranchus* and *Amphiuma* have a bidirectional hydrodynamic design with kinematic correlates that are similar to kinematic characteristics of aquatic feeding in turtles and transformed ambystomatid salamanders. A general framework is presented as an aid to understanding the interrelationships among muscle activity patterns, morphology, and behavior (kinematic patterns). By considering the distribution of taxa in three multivariate spaces, corresponding to three of the levels at which one might analyze a behavior (kinematics, morphology, and motor pattern), it is possible to identify patterns of correspondence among the levels, which aid in understanding the evolution of behavior.

## Introduction

Behavior results from the control of morphological systems by motor output from central nervous system circuitry. The study of a behavior (either within a species or across taxa) thus involves understanding at least three levels of variation: motor patterns generated by the central nervous

system, the arrangement of morphological features involved in the behavior, and details of the behavior itself, such as the pattern of bone movement. Variation in the motor pattern may be quantified by comparing patterns of muscle activity in the form of electromyographical signals (EMGs) recorded from muscles. Morphological variation among taxa may be characterized by morphometric anal-

ysis of relevant features of the musculoskeletal system. Behavior may be analyzed by quantifying the kinematics (movements) of those features of the morphology involved in the behavior. In addition, the wiring of central circuits and the modulation of such circuits plays an important role in determining the pattern of motor output to peripheral structures (e.g., Cohen et al., 1988).

A number of papers in the literature have focused on one of these three levels and compared variation across vertebrate taxa. At the level of muscle activity patterns, comparative (interspecific) analyses have used data on muscle function to address evolutionary, ecological, and phylogenetic questions [Liem, 1978, 1979; Emerson and De Jongh, 1980; Liem and Greenwood, 1981; Cundall, 1983; Lauder, 1983; Shaffer and Lauder, 1985a; Wainwright and Lauder, 1986; Jayne, 1988a, b; Sanderson, 1988; 1990; Wainwright, 1989; Wainwright et al., 1989]. Morphometric comparisons among taxa have often been conducted to quantify interspecific differences in structure, either for phylogenetic purposes or for analyses of shape transformation (e.g. Shaffer, 1984; Bookstein et al., 1985; Shea, 1985; Strauss, 1985; Bemis, 1987; Reilly, 1987; Wainwright, 1988; Rohlf and Bookstein, 1990), and numerous interspecific morphological analyses have also been conducted in conjunction with research in descriptive and functional morphology. Finally, many investigations have quantified variation interspecifically at the kinematic level to understand how movement (behavior) varies across taxa [Alexander, 1970; Liem, 1970; Lauder, 1980a, 1985; Hiiemae and Crompton, 1985; Shaffer and Lauder, 1985a; Jayne, 1986; Motta, 1988; Westneat and Wainwright, 1989; Sanford and Lauder, 1990; Sanderson, 1990, 1992].

Although some papers have considered more than one level across taxa to address comparative functional, ecological, or evolutionary questions [e.g., Gans, 1974; Norberg, 1990] usually only a single level is examined in detail, and most attempts to relate patterns of variation among levels are qualitative. However, in order to understand the evolution of behavior, it is necessary to demonstrate quantitative relationships among levels, and to define precisely how patterns of variation map among the three levels of analysis. Exactly how do interspecific patterns of variation in morphology, for example, relate to kinematic variation among taxa? Do taxa with divergent morphologies tend to differ in kinematics from other taxa?

The overall goal of this paper is to present a case study of the feeding mechanism in salamanders that quantitatively integrates two levels of analysis (morphology and kinematics), by describing each level quantitatively. This will pro-

vide the basis for generating predictions about the third level (motor patterns) to be tested in a future study. There are four specific goals of this paper: first, to describe quantitatively the feeding behavior of species representing six families of aquatic salamanders; second, to analyze patterns of variation in feeding kinematics to test the hypothesis that the process of aquatic feeding is similar in these families; third, to relate kinematic patterns to morphological variation among taxa; and fourth, to use these data as the basis for a general discussion of the historical relationship between behavior, morphology, and motor output from the central nervous system.

## Materials and Methods

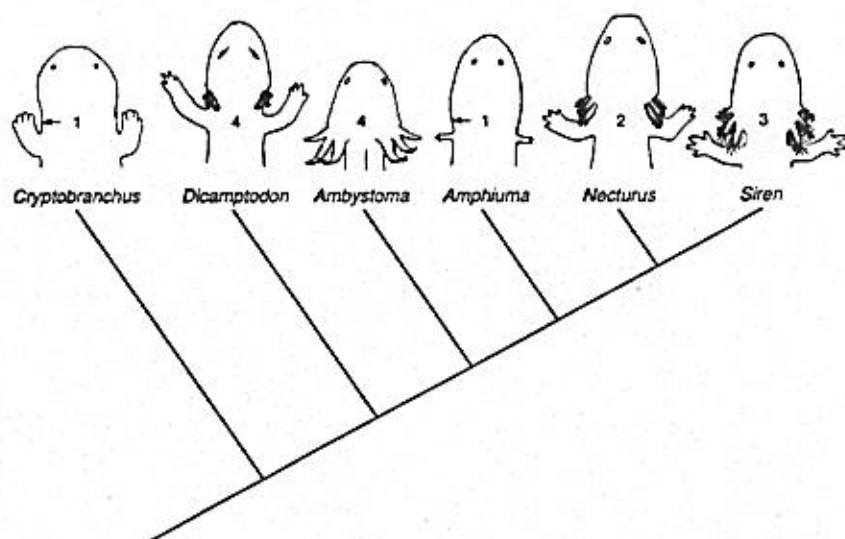
Six species representing six salamander families were used for the analysis of aquatic feeding kinematics: adult *Cryptobranchus alleghe-nienseis* (Cryptobranchidae:  $n=4$ ), larval *Dicamptodon tenebrosus* (Dicamptodontidae:  $n=5$ ), adult *Ambystoma mexicanum* (Ambystomatidae:  $n=5$ ), adult *Amphiuma means* (Amphiumidae:  $n=2$ ), adult *Necturus maculosus* (Proteidae:  $n=3$ ), and adult *Siren intermedia* (Sirenidae:  $n=2$ ). Henceforth, each species will be referred to by its generic name.

These six taxa were chosen because they span the range of both taxonomic and morphological diversity in extant salamander families with representatives that feed aquatically. Representatives were chosen from six of the nine extant salamander families to reflect the range of morphological divergence in both head and body shape within the Caudata. The head morphology (in dorsal view) of the six taxa studied here is illustrated in figure 1 within the context of one hypothesis of salamander phylogenetic relationships [Cloutier, 1992]. These six taxa vary considerably in body shape, head width and length, number of gill slits, extent of external gill structure, and mouth shape. Our choice of these six taxa was also driven in part by the possibility of comparing pairs of species with similar morphological features to see if the kinematics of feeding were similar. For example, *Amphiuma* and *Cryptobranchus* both possess one gill slit, while *Dicamptodon* and *Ambystoma* each possess 4 gill slits. These pairs may be compared to test for kinematic correlates of gill slit number.

Individuals of *Ambystoma*, *Amphiuma*, and *Necturus* were obtained commercially. The specimens of *Siren*, *Cryptobranchus*, and *Dicamptodon* were collected under state scientific collecting permits from southern Illinois, southern Missouri, and northern California, respectively. Animals were maintained in separate aquaria at 21 °C and fed earthworms. The original research reported herein was performed under guidelines established by the Animal Research Committee of the University of California at Irvine.

### Kinematic Descriptions

Individual animals were trained to feed under lights and filmed at 200 fields per second using a NAC HSV-400 high-speed video system with two synchronized strobes. Salamanders were filmed in lateral view in 8- to 100-liter glass aquaria with a background grid of 1 cm squares. The animals were offered 1-3 cm long earthworm pieces (*Lumbricus*) presented in front of the jaws with a pair of forceps. Prey were standardized across taxa to reduce the possibility of introducing



**Fig. 1.** Phylogenetic relationships of the six salamanders taxa used in this study [cladogram after Cloutier, 1992]. Head outlines (not drawn to scale) are shown for each taxon and the number of open gill slits is given for each species. Arrows point to the location of the gill opening for species without external gills.

kinematic variation by altering the prey stimulus, although previous research has indicated that there is little prey-induced variation in aquatic salamander feeding [Reilly and Lauder, 1989a]. Video sequences of each feeding by each animal were analyzed field by field using a PC-based custom image analysis system and digitizing software to quantify strike kinematics. Five aquatic prey capture sequences were analyzed from each individual.

To quantify basic kinematic patterns for each species three kinematic variables were digitized from video sequences. For each feeding sequence, time zero was defined as the field preceding the first field in which the mouth began to open during the strike. Head angle was measured (in degrees) as the elevation of the head, defined by three points: one at the anterior tip of the upper jaw and two landmark spots on the body. Head angle increases when the head is elevated. Gape distance (in mm) is the linear distance between the anterior tips of the upper and lower jaws. Hyoid depression (in mm) was measured as the vertical distance of the gular region directly below the vertex of the jaw angle. Hyoid depression increases as the hyobranchial apparatus is retracted posteriorly and rotated ventrally during suction feeding, and it decreases to its minimum when the hyoid recycles anterodorsally. Maximum hyoid depression occurs at maximum hyoid retraction. These kinematic measurements capture variation in initial strike kinematics during the gape cycle as the mouth opens and closes: they do not measure head movements that occur following capture of the prey.

Twenty-two video fields were analyzed from each feeding cycle beginning with time zero. This encompasses a range from time zero through 105 milliseconds (ms) after the start of mouth opening, which is approximately twice the length of the gape cycle. In addition, *Necturus* and *Cryptobranchus* feedings were quantified to +200 ms and +720 ms, respectively, to illustrate kinematic differences in hydrodynamic designs.

To quantitatively summarize the kinematics of aquatic prey capture, the movement curves (profiles) for each kinematic variable were averaged for one individual ( $n=5$  feedings) from each species. To do this, the mean was calculated ( $\pm$  standard error) for each field and

plotted against time in milliseconds (5 ms/field). Because of differences in the positions of landmarks used to measure the head angle and hyoid depression, these profiles were transformed to a value of 0 at time 0 before averaging to reflect only the change in angle or excursion. 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 figures 2 and 3 represent averages for one individual from each species. These profiles illustrate general kinematic patterns and should not, therefore, be used to estimate the statistical significance of differences between species.

#### *Morphological Measurements*

To provide a general indication of overall head shape in the six taxa studied kinematically, the number of gill slits and four linear measurements (in mm) measured from each individual were used. Head width was measured at the angle of the jaws. Head length was measured from the snout to the first external gill or gill opening. Lower jaw length was measured from the tip of the lower jaw to the angle of the jaw. Head depth was measured just posterior to the eye as the vertical depth of the head (from the top of the cranium to the bottom of the lower jaw).

#### *Statistical Analyses*

To examine statistically the extent of kinematic variation, seven variables, reflecting maximum excursions and timing of movement (listed in table 1), were digitized from video sequences for each individual aquatic feeding cycle. Three peak-amplitude variables were measured as the difference between the value at time 0 and the maximum value (for head angle and gape distance) or the beginning of a plateau (for hyoid depression) during the feeding cycle. Three time-to-peak duration variables (for head angle, gape distance, and hyoid depression) were measured from time zero to the time of the maximum value. Gape cycle time was measured from time zero (mouth opening) to the field in which the mouth closed. Species means



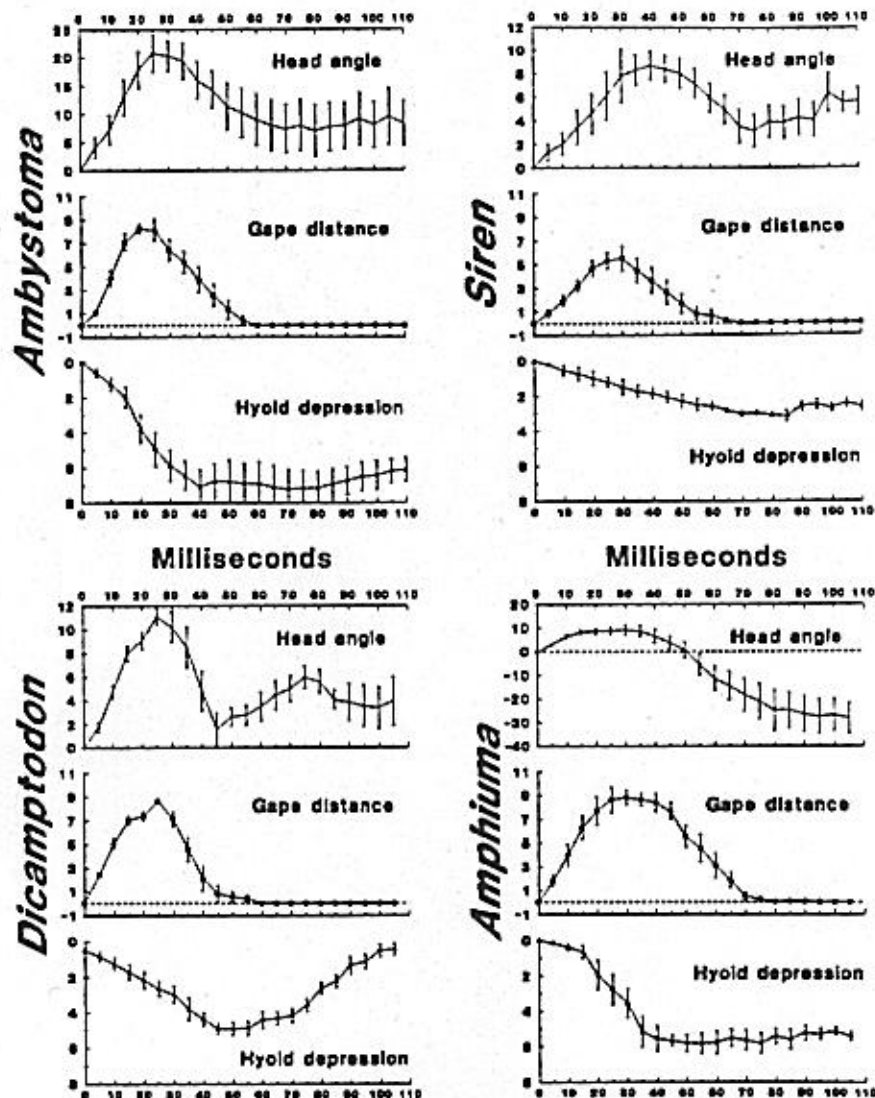


Fig. 2. Mean kinematic profiles for four species of aquatic feeding salamanders. Means ( $\pm$  standard errors) for three kinematic variables plotted against time (in ms) are based on five feedings from one individual of each species. Time 0 is the video field immediately before the onset of mouth opening. Head angle (in degrees) indicates the elevation of the head relative to the body and has different scales for each species. Gape distance (in mm) and hyoid depression (in mm) are plotted with the same scales for all four species. Hyoid depression reflects the ventral expansion of the buccal cavity as the hyobranchial apparatus rotates posteroventrally during suction feeding. Note that *Amphiuma* exhibits a large negative head angle and has a delay in rapid hyoid depression during feeding.

( $\pm$  standard errors) for each kinematic variable were calculated by pooling all feedings for each species.

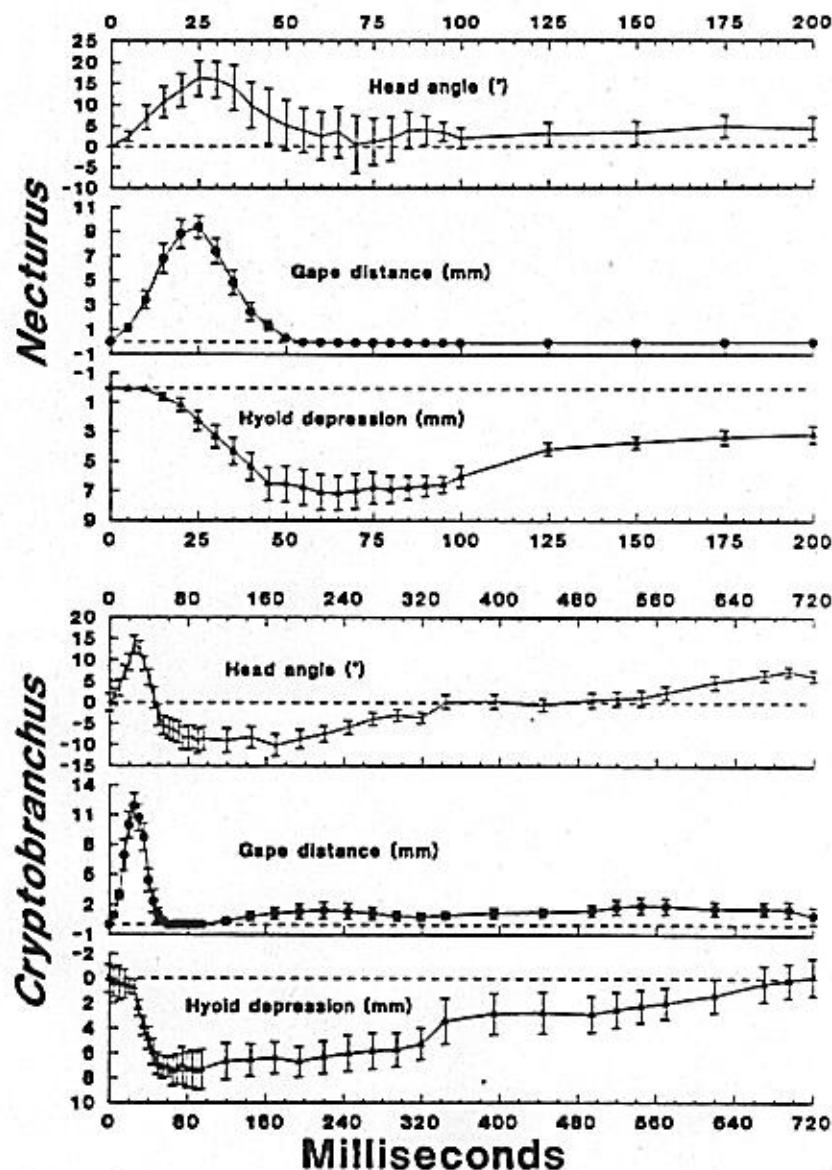
Each variable was analyzed using a two-level nested analysis of variance (ANOVA) design with various numbers of individuals (individual level) nested within each of the six species (taxon level). The taxon level was a fixed effect, and individual level was a random effect. The individual mean-square was used as the denominator in computing the F-ratios for the taxon effect as is customary in nested designs [Sokal and Rohlf, 1981]. F-values for the individual-within-taxon effect were calculated using the error variance as the denominator. Mean differences among species were examined a posteriori using Tukey-Kramer HSD pairwise comparisons of the taxon level variance with a  $p < 0.05$  significance level. Thus, between-species comparisons were not confounded by within species (individual) variance. Estimates of total variance in each kinematic variable were partitioned

into three components: among taxa, within taxa, and within individual (error) following Sokal and Rohlf [1981].

To explore multivariate patterns of variation in aquatic feeding behavior, we conducted a principal components analysis on the seven kinematic variables by using a correlation matrix of untransformed data. We were unable to perform a generalized multivariate analysis of variance (MANOVA) on the complete data set, because the number of independent kinematic variables (seven) exceeds the number of observations in each cell (five). Therefore, we performed our MANOVA on principal component scores from the first two components to test the overall null hypothesis that there is no taxon-level difference in feeding kinematics.

Patterns of multivariate head size and shape among the six species were examined using principal components analysis of the five morphological variables (the four given at the bottom of table 1 and gill

**Fig. 3.** Mean kinematic profiles for aquatic feeding in *Necturus* and *Cryptobranchus*. Means ( $\pm$  standard errors) and variables are plotted as in figure 2, with the curves extended until the onset of prey swallowing behavior. Note that *Cryptobranchus* exhibits a large negative head angle and has a delay in rapid hyoid depression during feeding. *Necturus* exhibits unidirectional feeding kinematics with the gape remaining closed after the strike as the hyoid elevates to expel water through the gill slits. In *Cryptobranchus* periods of mouth opening after the strike are associated with hyoid elevation.



opening number, fig. 1) using a correlation matrix and untransformed data. A second analysis was conducted on a log-transformed data set and showed only very minor differences from untransformed data.

## Results

Results from the video analyses will first be described for each species followed by statistical analyses of interspecific patterns.

### Descriptive Kinematics

Mean kinematic profiles for head angle, gape distance and hyoid depression are presented in figures 2, 3. In all six species the mouth opens rapidly ( $<35$  ms) to a peak and then closes after the prey is engulfed. Except in *Amphiuma* and *Cryptobranchus*, the mouth remains closed after the strike as the hyoid is elevated to expel water from the buccal cavity through the gill slits. The cycle of head elevation coincides roughly with the cycle of mouth opening. Head angle returns nearly to its initial position during mouth clos-

**Table 1.** Mean kinematic and morphological measures (one standard error for each measure given in parentheses) for species representing six families of salamanders. Kinematic means are based on five feedings per individual (n) and morphometric means are based on one measurement per individual. Angles are in degrees, distances are in millimeters, and timing variables are in milliseconds from the onset of mouth opening. Mean differences were determined by post-hoc Tukey-Kramer HSD pairwise comparisons using the taxon level variance for variables with significant taxon effects in the nested ANOVA (see table 2). Means not significantly different from each other at the  $p < 0.05$  level are connected by underlining

Variable	Amphiura (n=2)	Ambystoma (n=5)	Dicamptodon (n=5)	Cryptobranchus (n=4)	Necturus (n=3)	Siren (n=2)
Peak head angle	<u>9.7 (1.1)</u>	19.9 (1.1)	15.4 (0.7)	17.2 (0.9)	<u>13.2 (1.2)</u>	<u>7.1 (1.5)</u>
Time-to-peak head angle	30.5 (3.0)	<u>32.8 (0.9)</u>	33.6 (1.7)	<u>30.4 (1.0)</u>	35.0 (1.9)	32.0 (1.7)
Peak gape distance	<u>8.7 (0.5)</u>	<u>9.4 (0.4)</u>	<u>8.3 (0.3)</u>	15.4 (0.8)	<u>9.3 (0.4)</u>	5.9 (0.3)
Time-to-peak gape distance	31.5 (1.7)	26.4 (1.2)	29.0 (1.4)	30.0 (1.0)	23.0 (1.0)	29.0 (1.7)
Peak hyoid depression	<u>5.7 (0.4)</u>	<u>6.2 (0.4)</u>	<u>4.9 (0.3)</u>	12.5 (1.0)	6.9 (0.7)	<u>3.6 (0.3)</u>
Time-to-peak hyoid depression	<u>50.0 (2.2)</u>	<u>36.0 (1.5)</u>	<u>50.0 (1.5)</u>	<u>56.0 (2.4)</u>	<u>56.7 (1.2)</u>	<u>53.0 (4.2)</u>
Gape cycle time	72.0 (1.86)	<u>59.0 (1.8)</u>	<u>54.4 (2.47)</u>	<u>53.3 (1.1)</u>	51.0 (1.0)	<u>61.0 (2.8)</u>
Head length	65.0 (3.0)	35.9 (2.0)	26.7 (0.3)	51.3 (5.5)	51.7 (1.2)	36.0 (1.0)
Lower jaw length	24.4 (0.8)	10.6 (0.7)	9.9 (0.5)	25.5 (2.7)	19.0 (0.5)	10.9 (0.1)
Head depth	20.8 (0.9)	12.5 (0.7)	10.1 (0.8)	18.0 (1.9)	18.2 (0.9)	11.5 (0.5)
Head width	33.0 (1.0)	25.2 (1.5)	20.0 (0.7)	42.0 (4.1)	32.0 (0.6)	22.5 (0.9)

**Table 2.** Analysis of variation of feeding kinematics in six species of aquatic feeding salamanders. Each variable was analyzed using a nested analysis of variance for taxon effects (individuals nested within each taxon, d.f. = 5, 15) and individual effects (feeding trials nested within each individual, d.f. = 15, 84). For each effect the F-value (F) and P-value (P) are given

Kinematic variable	Analysis of variance		Percent of total variance		
	Taxon effect	Individual effect	Among individuals		Among trials
	F (P)	F (P)	Among taxa	within taxa	within individuals
Peak head angle	6.74 (0.0001)*	3.90 (0.0001)*	45	20	35
Time-to-peak head angle	0.66 (0.663)	2.12 (0.016)	0	18	82
Peak gape distance	13.87 (0.0001)*	4.26 (0.0001)*	65	14	21
Time-to-peak gape distance	1.83 (0.167)	3.10 (0.0001)*	9	27	64
Peak hyoid depression	6.20 (0.003)*	11.46 (0.0001)*	53	32	15
Time-to-peak hyoid depression	6.63 (0.002)*	3.72 (0.0001)*	44	20	36
Gape cycle time	3.80 (0.002)*	3.74 (0.0001)*	47	25	28

\* Significant Bonferroni probability ( $p < 0.007$ ).

ing but remains above 0 degrees except in *Cryptobranchus* and *Amphiura*. In these species the head depresses from maximum elevation through its initial position during the first half of mouth closing and continues to bend ventrally until after the mouth has closed. Rapid hyoid depression begins with the onset of mouth opening in *Dicamptodon*,

*Ambystoma*, and *Siren* and continues to move posteroventrally, reaching a maximum after peak gape. In *Necturus*, the onset of hyoid depression is delayed 10 to 15 ms, but once initiated, the hyoid depresses rapidly and exhibits a profile similar to that of *Dicamptodon*, *Ambystoma*, and *Siren*. In *Cryptobranchus* and *Amphiura* there is a 15 to 25

ms delay from the onset of mouth opening before rapid hyoid depression begins. The delay in peak hyoid depression is so great in *Cryptobranchus* that rapid posteroventral hyoid rotation does not even begin until peak gape is reached. In all taxa, maximum hyoid depression is achieved after maximum gape distance.

#### Statistical Analysis

Means for kinematic variables for each species are presented in table 1. Analysis of variance on the seven kinematic variables (table 2) revealed significant variation both among and within taxa for most variables. Time-to-peak head angle was the only variable that had no significant variation among or within species. Time-to-peak gape distance had significant within-species variation but did not show a significant taxon effect. The remaining variables showed significant differences, both among species and among individuals within species. Statistical similarity among species means for kinematic variables (tested on the taxon level variance) is indicated by underlining in table 1.

Time-to-peak head angle showed little variation across all six species, and species means only ranged from 30.4 to 35.0 ms. However, peak head angle did show a significant taxon effect, and species means were evenly spaced in a range from 19.9° in *Cryptobranchus* to 7.1° in *Siren* (table 1). Four species had similar mean peak gape distances between 8.3 and 9.3 mm, while *Cryptobranchus* (15.4 mm) and *Siren* (5.9 mm) were significantly higher and lower, respectively. Five of the species shared nearly identical time-to-peak gape distance (23.0–31.5 ms). The amount of peak hyoid depression in *Cryptobranchus* (12.5 mm) was significantly greater than the means for the other five species, which ranged from 3.6 to 6.2 mm. Time-to-peak hyoid depression was nearly identical for all species (50.0 to 56.7 ms), except for *Ambystoma* in which the hyoid peaked significantly earlier (36.0 ms). Gape cycle time ranged from 51 ms in *Necturus* to 61 ms in *Siren* with *Amphiuma* having a significantly longer gape cycle of 72 ms duration.

Peak head angle is coincident with peak gape, and thus head elevation is tightly coupled with mouth opening (except in *Necturus* where peak gape occurs an average of 12 ms prior to peak head angle). Hyoid depression peaks during or near the end of mouth closing, at about 10 to 26 ms after peak gape. The mouth opening and mouth closing phases each comprise about half (44–56%) of the gape cycle.

Multivariate patterns of aquatic feeding behavior are illustrated by principal components analysis of the seven kinematic variables (fig. 4). Principal component 1 distinguishes *Siren* and *Cryptobranchus* from the rest of the spe-

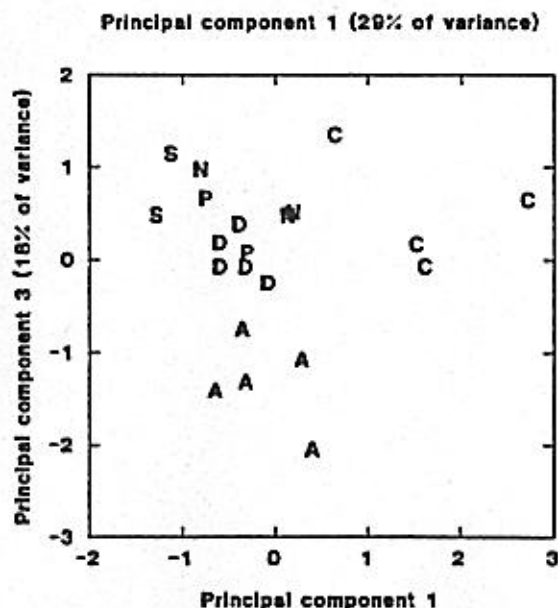
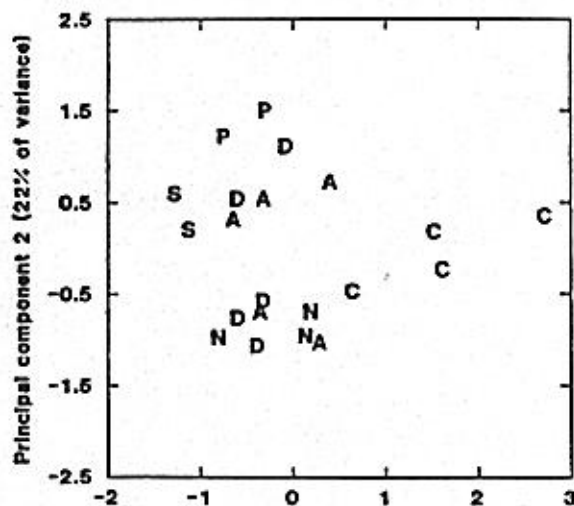


Fig. 4. Principal components analysis of aquatic feeding behavior based on seven kinematic variables in six species of salamanders. Each symbol is the mean score for five feedings from a single individual. Multivariate kinematic differences among species are indicated by the major contributions of the original variables to principal components 1 (peak gape distance and peak hyoid depression), 2 (gape cycle time and time-to-peak gape) and 3 (time-to-peak hyoid depression). Note that *Siren* and *Cryptobranchus* represent the extremes on principal component 1, while *Ambystoma* falls below the other species on principal component 3. Abbreviations: A, *Ambystoma*; C, *Cryptobranchus*; D, *Dicamptodon*; N, *Necturus*; P, *Amphiuma*; S, *Siren*.



cies primarily on the basis of peak gape distance and peak hyoid depression. Principal component 2, on which gape cycle time and time-to-peak gape loaded highly, separates *Amphiuma* and *Necturus* from each other but not from the other species. Time-to-peak hyoid depression loads highly on principal component 3, which separates *Ambystoma* from the other species. The MANOVA performed on principal component one and two scores showed a highly significant effect of taxon (Wilks' Lambda = 0.188; df = 10, 196;  $p < 0.0001$ ), indicating that taxon means are different when many kinematic variables are considered simultaneously.

Species means for four head measurements are presented in table 1. Principal components analysis of the morphological measures of the 21 individuals used in this study (fig. 5) revealed that nearly all the morphological variance (95.4%) was accounted for by the first two principal components. Each of the species occupies a separate region of morphospace on the basis of these two components although *Ambystoma*, *Siren*, and *Dicamptodon* all cluster closely together. The morphological distance measures had high positive correlations ( $R \geq 0.94$ ) with the first principal component. Gill slit number had a high negative correlation ( $R = -0.93$ ) with the first principal component. All five variables had low correlations with principal component 2.

## Discussion

The six species of aquatic salamanders are similar in some general aspects of their feeding behavior, but several significant differences in head movement and timing were found among species. For purposes of discussion the basic patterns of aquatic feeding kinematics based on the general similarities observed among the six species will be described first, and then specific species differences will be discussed. This will be followed by discussion of the effects of head size and shape on kinematic patterns and of general issues in the study of kinematics, morphology, and underlying muscle activity patterns.

### General Kinematics of Aquatic Feeding in Salamanders

Aquatic feeding in all six species involves rapid opening and closing of the mouth with the opening and closing phases of approximately equal duration. The head is rapidly elevated during mouth opening and peaks in elevation at about the same time as peak gape (30–35 ms). Peak gape is reached approximately 30 ms from the onset of mouth opening. Hyoid depression begins with mouth opening and

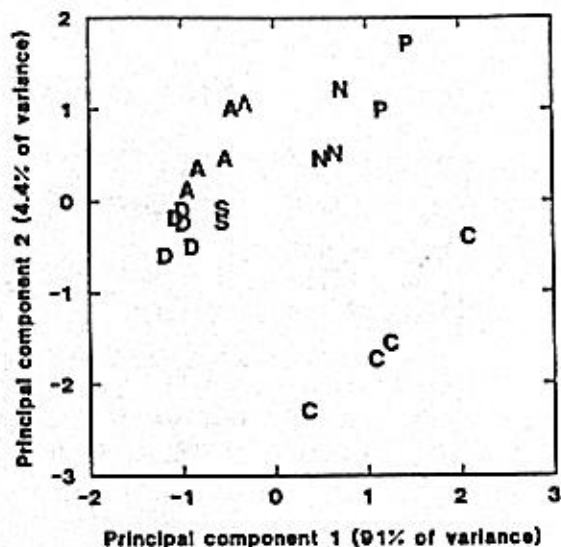


Fig. 5. Principal component analysis (PCA) of external head morphology in six species of salamanders. Symbols represent individuals for each species. This PCA was calculated from five variables: the four morphological measures given at the bottom of table 1, and gill opening number. Because morphological distance measures were highly and positively correlated with principal component 1 and only weakly correlated with principal component 2, the first axis is interpreted as size and gill opening number and the second axis as shape. Symbols as in figure 4.

reaches its maximum in about 50 to 56 ms, which is just before or coincident with mouth closing. In all species, peak hyoid depression is reached consistently after peak gape, and the hyoid remains depressed well past closure of the jaws.

This kinematic pattern conforms exactly to the general pattern of aquatic feeding defined as being primitive for jawed vertebrates [Lauder, 1980a, 1985; Reilly and Lauder, 1990]. Maximal hyoid depression following maximum gape is a functional characteristic shared by many ray-finned fishes [Lauder 1980a, b] and lungfishes [Bemis and Lauder, 1986], and it may be a general feature of prey capture in the aquatic environment [Lauder, 1985; Reilly and Lauder, 1990; Lauder and Shaffer, 1992]. Prey capture using this general kinematic pattern is usually referred to as suction feeding [Liem, 1970; Lauder, 1985], in which a rapid pressure reduction within the oral cavity (resulting from head elevation and lower jaw and hyoid depression) causes a flow of water into the mouth. Suction feeding in



fishes and salamanders appears to be broadly similar among all taxa that have been studied to date. The diversity of head morphologies exhibited by the six salamander taxa studied here illustrates that even considerable difference in head size, shape, and number of gill openings among taxa does not affect the basic pattern of aquatic suction feeding so widely distributed among fishes and amphibians.

#### *Statistical Differences Among and Within Species*

Despite the presence of considerable overall similarity in the kinematic profiles of the six taxa, there are several important quantitative differences. *Dicamptodon* exhibits feeding kinematics that fit the general kinematic pattern described above. Four other species differed significantly from the general kinematic pattern in at least one kinematic variable as indicated by comparisons of species means for kinematic variables (tables 1, 2) and the multivariate kinematic patterns (fig. 4). *Amphiuma* fit the general pattern well except for having a significantly longer gape cycle time (72 ms). *Cryptobranchus* and *Siren* differed from the others on the basis of the magnitude of gape and hyoid depression, as reflected by their positions on principal component 1 (fig. 4). *Cryptobranchus* had significantly greater peak gape (15.4 mm) and hyoid depression (12.5 mm), while *Siren* had significantly smaller peak gape (5.9 mm) and the smallest hyoid depression (3.6 mm). *Ambystoma* had a significantly shorter time-to-peak hyoid depression (table 1), which is reflected in its separation from the others on principal component 3 (fig. 4).

These quantitative differences in feeding kinematics reflect taxonomic differentiation in head function and may be compared to the differences noted in a previous study of feeding kinematics within the genus *Ambystoma* [Shaffer and Lauder, 1985b]. Although time-to-peak head angle was not measured in that study, Shaffer and Lauder [1985b] found that the variables describing hyoid movement were most different among species within *Ambystoma* and provided the best kinematic discrimination among species. This finding was of interest in part because hyoid movement is a key contributor to suction feeding performance [Lauder, 1985], and differences in hyoid kinematics may reflect differing suction abilities of *Ambystoma* species. In contrast to that finding, in this study no one group of variables can be identified as being particularly useful in separating the six taxa kinematically. As shown both by tables 1 and 2 and the principal component analysis (fig. 4), each kinematic variable shows a different pattern of interspecific variation. The species most kinematically distinct from the

others, *Siren* and *Cryptobranchus*, are best distinguished by a combination of kinematic variables illustrated by the principal component analysis (fig. 4). Hyoid depression certainly is an important component of the separation of *Cryptobranchus* in multivariate kinematic space, but other kinematic variables contribute as well.

Shaffer and Lauder [1985b] also found that the variable most similar among species of *Ambystoma* was maximum cranial elevation angle. This result differs from that obtained in the present study (tables 1, 2), where peak head angle varies significantly among species. Thus, there appears to be little relationship between the patterns of variation in feeding kinematics seen within the genus *Ambystoma* and variation seen among more distantly related taxa.

#### *Head Size and Shape*

The principal components analysis of head measurements reveals patterns of variation in head size and shape (fig. 5). Because the morphological variables had high and positive correlations with principal component 1 and very low correlations with principal component 2, the first component may be interpreted as an overall head size axis and the second component as an overall shape axis [Bookstein et al., 1985; Strauss, 1985].

Pairwise species comparisons based on size and shape using ANOVA's on principal component 1 and principal component 2 scores (fig. 5) reveal that *Cryptobranchus* is distinct from all other species, *Necturus* and *Amphiuma* form another group, and *Siren*, *Dicamptodon*, and *Ambystoma* form a third distinct cluster. Examination of the differences in the seven kinematic variables (table 1) among these species groups revealed no patterns in the types or number of variables that differed when size, shape, both or neither were different; each group differed in several kinematic variables from the other groups. In addition, *Siren* and *Ambystoma*, which share a similar region of the head morphospace, had four kinematic variables that differed and were completely distinguishable in kinematic principal component space. Thus, in addition to the rather considerable external morphological differences in head structure (fig. 1), each taxon appears to have a number of kinematically unique features which distinguish it from other taxa.

Comparisons of individual morphological and kinematic variables (table 1) reveal that kinematic durations and excursions are not explained simply by greater head size alone causing greater excursions and movement durations.

Three examples illustrate this point. First, the six species, ranging in head length from 26 to 65 mm and peak head angle excursions of 7 to 20°, had no significant differences in the time-to-peak head angle or time-to-peak gape distance (table 2). Second, *Ambystoma* which has about half the head length and depth of *Amphiuma* has the same peak gape and hyoid depression distances but greater peak head elevation. Third, *Cryptobranchus*, which has similar head size to *Amphiuma*, has twice the peak gape and hyoid depression and yet a 20 ms shorter gape cycle time. Thus, greater head size alone does not directly influence the excursion or timing of feeding movements and does not explain the observed pattern of kinematic variation. A similar result was found for the feeding kinematics of fishes [Sanford and Lauder, 1990].

#### *Unidirectional and Bidirectional Feeding Designs*

Despite the lack of a simple relationship between external morphological characteristics and strike kinematics as noted above, there is one key morphological aspect that does show clear kinematic correlates *following the strike*: the basic hydrodynamic design of the feeding mechanism. In most ray-finned fishes and larval ontogenetic stages of salamanders that feed in the water, the pattern of water flow through the mouth is unidirectional [Lauder, 1985; Lauder and Shaffer, 1986]. That is, water drawn into the mouth during prey capture passes through the oral cavity and out between gill supports posteriorly during the strike. *Siren*, *Necturus*, *Ambystoma*, and *Dicamptodon* show this pattern, and each of these taxa possesses two or more gill slits (fig. 1) through which water passes during the compressive phase of suction feeding. However, both *Cryptobranchus* and *Amphiuma* have only one gill opening, and the space available for water to exit posteriorly has been greatly reduced by the nearly complete closure of most gill slits. These taxa appear to possess a bidirectional feeding system [Lauder, 1980c; Lauder and Shaffer, 1986] similar in character to that of post-metamorphic *Ambystoma*, which feed in the water. During bidirectional feeding, water drawn into the mouth during suction feeding passes back out of the mouth anteriorly after the prey has been caught.

In both *Amphiuma* and *Cryptobranchus* (fig. 3), the mouth opens again after initial mouth closure, and water can be seen emerging from the mouth. This occurs as the hyoid is protracted (fig. 3). These two taxa with the bidirectional flow design of the feeding mechanism also share two other kinematic characteristics not possessed by other taxa (in addition to the modified gape profile). First, in

*Amphiuma* and *Cryptobranchus*, head angle passes the initial value of zero at the start of the strike to become strongly depressed (between 10 and 30°), beginning during the late stages of mouth closure and continuing well past gape closure after the strike. This indicates that the head is being bent ventrally on the vertebral column in these two taxa and is contributing to gape closure, together with elevation of the lower jaw. Secondly, there is a delay in the onset of rapid hyoid depression in *Amphiuma* and *Cryptobranchus* of more than 15 ms such that peak hyoid velocity is delayed until late in the opening phase of the strike and almost to peak gape. *Necturus* shows some tendency to exhibit this pattern of hyoid movement, although the delay in hyoid depression is not as great as in *Amphiuma* or *Cryptobranchus*.

Although there is a greatly reduced set of gill openings posteriorly in *Amphiuma* and *Cryptobranchus*, some water flow does emerge from the reduced gill openings after the jaws have closed. Most of the water drawn into the mouth during feeding by *Cryptobranchus* emerges anteriorly from the mouth [as shown by dye injection studies, Lauder and Reilly, unpubl.] but some water also flows out posteriorly. Feeding is thus largely bidirectional with a small unidirectional flow. The key characteristic of unidirectional feeders is the start of water exit from posterior gill openings during the closing phase of the strike, before the jaws have closed completely.

It is intriguing that an independent kinematic study of bidirectional feeding in the snapping turtle, *Chelydra serpentina* [Lauder and Prendergast, 1992] reveals similar kinematic correlates to those found here for bidirectionally feeding salamanders. In the snapping turtle, the gape opens again after initial closing to allow water drawn into the mouth to exit anteriorly. The head angle is depressed considerably below the initial starting value, and rapid hyoid depression does not begin until 20 ms or more after the mouth starts to open.

It is also noteworthy that post-metamorphic tiger salamanders (*Ambystoma tigrinum*) feeding in the water show these same patterns [Lauder and Reilly, 1989b]: depression of head angle below the initial value, and a delay in hyoid depression. Thus, snapping turtles, post-metamorphic tiger salamanders, and bidirectional aquatic salamanders such as *Cryptobranchus* and *Amphiuma* all show very similar kinematic correlates of a bidirectional feeding design.

However, these kinematic similarities occur after the gape cycle is complete, and thus are not reflected in the variables chosen here to analyze the gape cycle itself (mouth opening and closing during the strike). During the gape cycle, *Amphiuma* and *Cryptobranchus* show clear dif-



ferences in feeding behavior (reflected in their different positions in fig. 6) despite some similarities in subsequent kinematic patterns (due to the bidirectional design) after the jaws have closed. These two taxa also differ considerably in morphology (fig. 6).

The similarity of head movement among bidirectionally feeding taxa may reflect hydrodynamic constraints of capturing prey in the water with a mouth that is essentially closed posteriorly. *Amphiuma*, *Cryptobranchus*, and *Chelydra* appear to have very large buccal capacities to accommodate water flowing into the mouth during the strike; this water would exit through the rear of the head in unidirectional feeders. Thus, feeding appears to be unidirectional during most of the gape cycle; then water is expelled slowly back out through the mouth in a controlled manner after gape closing. In addition, each of these taxa appears to have derived features to enhance prey holding during the expulsion phase. *Amphiuma* has large recurved teeth on the jaws and palate and labial folds occluding the side of the mouth. *Cryptobranchus* has a flexible mandibular symphysis and asymmetrical control of the jaw closing [Cundall et al., 1987] and can hold the prey with one side of the jaw and open the other side for water expulsion. *Chelydra* has a 'beak' on the upper jaw which can hold prey while water flows through the angle of the jaws [Lauder and Prendergast, 1992]. Similarity of kinematic features across taxa as divergent as *Amphiuma*, *Cryptobranchus*, and *Chelydra* argues for an explanation of observed kinematic similarity as convergence based on the physical demands of bidirectional feeding, not on common ancestral feeding traits.

### Morphology and Behavior

Although univariate comparisons are useful for evaluating particular differences among taxa, it is difficult to appreciate interspecific patterns of differentiation in kinematic (behavioral) and morphological features from univariate analyses alone. In addition, the relationship between interspecific patterns across levels is best appreciated by considering both levels together. One approach to understanding the relationship of morphology to behavior is to compare species associations in morphological space to the pattern of interspecific association in a kinematic (or behavioral) space. This abstract notion may be made more concrete if we consider the principal component analyses for the morphological and kinematic variables presented here as representing two multidimensional spaces in which each taxon is located (fig. 6). This visualization of the patterns of morphological and kinematic variation for all six

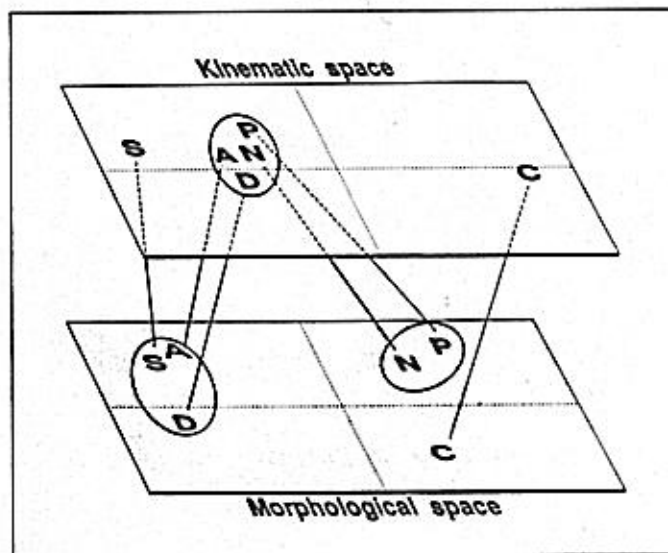


Fig. 6. Relationship between morphology and kinematics in the six salamander taxa studied here. Each plane represents a two-dimensional space based on the multivariate patterns of morphological and kinematic dispersion of the six species from the corresponding principal components analyses (principal components 1 vs 2 from figures 4 and 6). The morphological principal components analysis may be interpreted as a morphological space and the kinematic principal components analysis as a kinematic space. Circled taxa indicate similarity in either kinematics or morphology as revealed by a MANOVA on the PC1 and PC2 scores. Lines show the correspondence between these two levels of analysis. Note that *Cryptobranchus* is divergent in both morphology and kinematics. Abbreviations for species means: A, *Ambystoma*; C, *Cryptobranchus*; D, *Dicamptodon*; N, *Necturus*; P, *Amphiuma*; S, *Siren*.

taxa together allows us to consider the extent to which morphological variation may be viewed as explaining patterns of kinematic variation. For example, if taxa that cluster together on morphological criteria share kinematic features, then perhaps the shared behavioral traits are a consequence of shared morphological features (such as a wide head, reduced gill openings, large muscle mass, long muscle lever arm, large buccal volume, etc.). If two species share a characteristic such as large mass of the depressor mandibulae muscle, for example, then that may explain why the time-to-peak gape is shorter in those taxa.

In any attempt to compare the relative positions of taxa across levels (as in fig. 6) the choice of variables that go into the analysis at each level is critical. If causal connections are to be made across levels, then the morphological variables chosen must be ones which play a causal role in generating



behavior. For example, the bones measured to produce the pattern of variation at the morphological level in figure 6 should be those involved in producing the behaviors quantified at the kinematic level of figure 6. If feeding behavior and morphology of the hindlimb were measured to generate a diagram such as that in figure 6, then causal connections would be difficult to draw despite the possible presence of observed correlations among levels: we have no reason to suspect a causal connection between limb bone morphology and kinematic patterns of head bones during feeding in aquatic salamanders. For meaningful conclusions to be drawn across levels, it is important to choose variables based on *a priori* biomechanical analyses that serve to establish a causal link between the morphological and behavioral features of interest.

For our data, figure 6 depicts the relative positions of the six taxa studied in morphological and kinematic space. Four of the taxa (*Ambystoma*, *Dicamptodon*, *Necturus*, and *Amphiuma*) share a number of kinematic traits and cluster together in multivariate kinematic space. Both *Siren* and *Cryptobranchus* are divergent kinematically from the other taxa. Only *Cryptobranchus* is substantially distinct in both kinematic and morphological space. The overall pattern of variation among the six taxa studied shows some of the possible combinations of relationships between the two levels. For example, taxa with dissimilar morphologies may show similar overall kinematics (*Dicamptodon* and *Necturus*), taxa with similar morphology may show dissimilar kinematics (*Siren* and *Ambystoma*), and taxa that are divergent morphologically may show divergent feeding kinematics (*Cryptobranchus*).

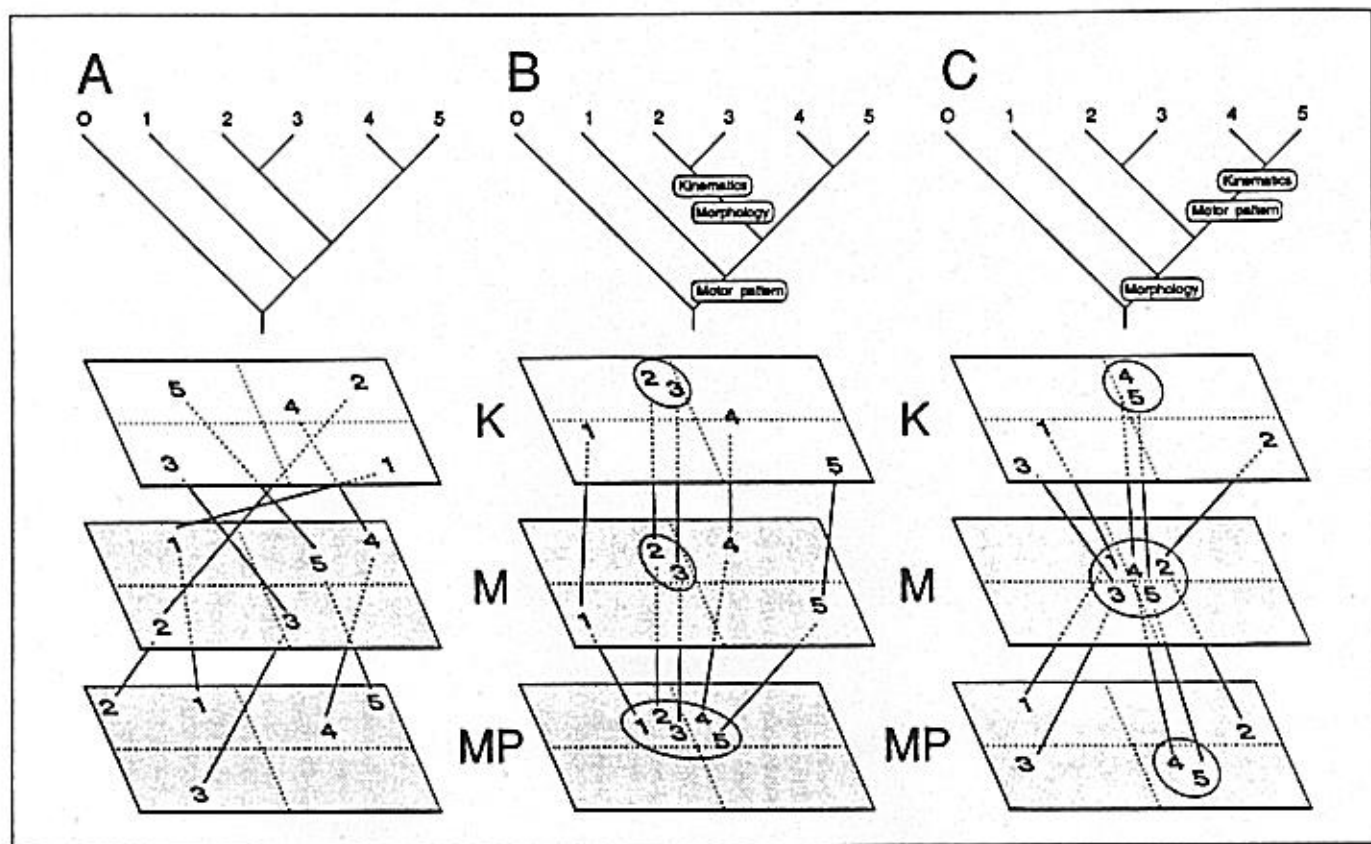
Based on the data presented here, the measured morphological features may be causally related to the distributions of three taxa at the kinematic level (fig. 6). Larval *Ambystoma* and *Dicamptodon* both share similar morphology of the head and similar kinematic patterns of prey capture. *Cryptobranchus* is divergent both morphologically and kinematically, and the divergent kinematic pattern may be due in part to the large head and consequently increased buccal volume involved in suction feeding. While the presence of reduced posterior gill openings does have clear kinematic correlates in *Amphiuma* and *Cryptobranchus* (as well as in *Chelydra* and post-metamorphic *Ambystoma*) these kinematic features are not prominent features of the gape cycle itself: they occur after the jaws have closed. Morphological features such as gill opening number, jaw length, and head width (expected *a priori* to be related to suction feeding based on previous biomechanical analyses; Lauder and Shaffer [1986], Lauder and Reilly [1988, 1990]), do not show any clear relationship to pat-

terns of interspecific kinematic divergence (fig. 6). Only *Cryptobranchus* is divergent kinematically and morphologically. The general pattern of non-concordance between the two levels may be explained in one of two ways. First, the morphological variables chosen for analysis may have failed to adequately capture the relevant variation necessary to explain feeding kinematics. Second, information at an additional level (not included in this analysis) may be critical to understanding the relationships among levels. Patterns of muscle activity are likely to be interspecifically variable and may well explain patterns observed between the kinematic and morphological levels. *Dicamptodon* and *Necturus* may share similar kinematic patterns (despite morphological differences) because they both possess different muscle activity patterns during feeding that, combined with differences in morphology, result in similar behaviors.

#### Evolution of Behavior

Therefore, in considering the broader question of the possible relationships between morphology and behavior, it is important to consider an additional level of variation which may also influence how morphology is used during the generation of behavior: the level of muscle activity (motor patterns). Behavioral variation among taxa is certainly influenced by morphological differences, but the pattern of muscle activity may also be a significant variable [Lauder, 1990]: even taxa with similar morphologies may show divergent kinematic patterns if underlying motor output is different.

Figure 7 shows a general scheme in which the relationship among motor patterns, morphology, and behavior (kinematics) may be considered. Three possible patterns are shown for five hypothetical taxa (numbered 1 to 5, with a phylogenetic outgroup taxon, 0), with a corresponding phylogenetic interpretation at the top. Panel A illustrates a pattern in which the five taxa show no consistent positional interrelationships among the three levels: each level has a unique pattern of among-taxon variation, and all taxa are different from each other at each level. A phylogenetic interpretation of this pattern would be that each of the five taxa possesses apomorphic (derived) characteristics of motor pattern, morphology, and behavior. In panel B, the five taxa share a similar motor pattern but are divergent in both morphology and behavior. In this scenario, differences in behavior among taxa may be attributed to differences in morphology but not to differences in muscle activity pattern. Phylogenetically, the motor pattern is a prim-



**Fig. 7.** Visualization of one scheme that may be used to understand the relationships among muscle activity patterns (motor patterns: MP), morphology (M), and behavior (kinematics: K) for five taxa (1 to 5, with a phylogenetic outgroup, 0). The phylogenetic relationships among the three taxa are indicated above each three-level diagram. Although other possibilities certainly exist, three panels (A, B, and C) are shown to indicate the range of interrelationships that may exist when kinematic, morphological, and motor patterns are considered together. The location of each number indicates the mean species value for that taxon. Circled taxa indicate those not significantly different from each other at each level; taxa *not* circled thus are significantly different from each other.

itive character, and taxa 2 and 3 share a derived morphology and behavior. In panel C, the five taxa are all similar in morphology, yet they possess divergent behaviors that appear to correspond to differences at the level of muscle activity patterns. Phylogenetically, the shared morphological characteristics are primitive for the clade, while derived motor patterns and behaviors characterize taxa 4 and 5.

To date, we are not aware of any studies that encompass all three of these levels for a monophyletic clade and that present data interpretable within this framework. Several papers have quantitatively addressed portions of this

In panel A, there is no clear relationship among levels: all taxa are significantly different at each of the three levels. Each taxon thus possesses unique evolutionary novelties in motor pattern, morphology, and kinematics. In panel B, the five taxa share a phylogenetically similar muscle activity pattern but possess divergent morphological and kinematic patterns (taxa 2 and 3 share similarities at both these levels). In panel C, the five taxa share similar morphologies but divergent motor patterns and kinematics (taxa 4 and 5 share similarities at these two levels).

scheme and suggest that future three-level studies are likely to reveal cases that match each of the three panels in figure 7 (and, perhaps, combinations of those patterns). For example, sunfishes (family Centrarchidae) show similar muscle activity patterns during prey capture [Wainwright and Lauder, 1986; Wainwright and Lauder, 1992], but are morphologically diverse in head shape, perhaps corresponding to panel B in figure 7. However, the morphological differences among taxa have not been quantified, and the behavioral level has not been analyzed. In another example, Sanderson [1990, 1992] used a quantitative kine-

matic analysis to show that fish species qualitatively different in morphology may have similar feeding behaviors. In this case morphological differences were not quantified, and patterns of muscle activity are unknown.

The multi-level approach (fig. 7) is useful in focusing attention on the relationship among three levels of analysis helpful in understanding the evolution of behavior [Lauder, 1990] and in emphasizing the relative positions of taxa at each of these levels. This visualization could easily be extended to include a level representing neuronal circuitry, but comparative data on variation in central connections among taxa may be even rarer than comparative motor pattern data.

The three-level scheme also suggests that predictions from analyses at one level may be useful in guiding future research at other levels. For example, the data obtained here at the morphological and behavioral levels (fig. 6), suggest that it would be useful to compare the motor patterns of *Cryptobranchus* and *Siren* to other taxa. Because *Cryptobranchus* and *Siren* differ at the morphological and kinematic levels (fig. 6) one might predict that differences will also exist at the motor pattern level, although this need not be the case if kinematic divergence is causally related to morphological divergence. If the motor patterns used during feeding are conservative during phylogeny, then we would expect the motor pattern level to resemble that of panel B in figure 7 for these taxa. On the other hand, if the divergences in kinematics are mirrored by muscle activity

pattern differences, then a situation resembling panel C would be revealed. Also, the patterns shown in figure 6 suggest that the motor patterns for *Dicamptodon* and *Ambystoma* should be similar to each other, and the motor patterns for *Necturus* and *Amphiuma* should be similar to each other: both pairs of taxa share morphological and kinematic novelties (fig. 6). A final prediction from the morphological and kinematic patterns of figure 6 is that *Siren* should show divergent motor output from *Dicamptodon* and *Ambystoma*: variation at the motor pattern level may explain the divergent feeding kinematics of *Siren* despite the morphological similarity of this taxon to *Dicamptodon* and *Ambystoma*.

A key goal of future research will be the development of a case study in which all three levels of analysis are represented for a monophyletic clade to provide a basis for understanding the evolution of behavior.

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### References

- Alexander, R. McN. (1970) Mechanics of the feeding action of various teleost fishes. *J. Zool. Lond.*, 162: 145-156.
- Bemis, W.E. (1987) Feeding systems of living Dipnoi: anatomy and function. *J. Morphol. Suppl.*, 1: 249-275.
- Bemis, W.E., and G.V. Lauder (1986) Morphology and function of the feeding apparatus of the lungfish, *Lepidosiren paradoxa* (Dipnoi). *J. Morphol.*, 187: 81-108.
- Bookstein, F., B. Chernoff, R. Elder, J. Humphries, G. Smith, and R. Strauss (1985) Morphometrics in Evolutionary Biology. Spec. Publ. 15. Acad. Nat. Sci. Philadelphia.
- Cloutier, R. (1992) Cladistic relationships among the major groups of salamanders. In *Amphibian Relationships* (ed. by D. Hillis and D. Cannatella). Herpetol. Monogr. (in press).
- Cohen, A.H., S. Rossignol, and S. Grillner (1988) Neural Control of Rhythmic Movements in Vertebrates. Wiley and Sons, New York.
- Cundall, D. (1983) Activity in head muscles during feeding by snakes: a comparative study. *Amer. Zool.*, 23: 383-396.
- Cundall, D., J. Lorenz-Elwood, and J.D. Groves (1987) Asymmetric suction feeding in primitive salamanders. *Experientia*, 43: 1229-1231.
- Emerson, S.B., and H.J. De Jongh (1980) Muscle activity at the ilio-sacral articulation of frogs. *J. Morphol.*, 166: 129-144.
- Gans, C. (1974) Biomechanics. An Approach to Vertebrate Biology. J.P. Lippincott, Philadelphia.
- Hilemae, K.M., and A.W. Crompton (1985) Mastication, food transport and swallowing. In *Functional Vertebrate Morphology* (ed. by M. Hildebrand, D.M. Bramble, K.F. Liem, and D.B. Wake). Harvard University Press, Cambridge. pp. 262-290.
- Jayne, B.C. (1986) Kinematics of terrestrial snake locomotion. *Copeia*, 1986: 915-927.
- Jayne, B.C. (1988a) Muscular mechanisms of snake locomotion I: an electromyographic study of lateral undulation of the Florida banded water snake (*Nerodia fasciata*) and the yellow rat snake (*Elaphe obsoleta*). *J. Morphol.*, 197: 159-181.
- Jayne, B.C. (1988b) Muscular mechanisms of snake locomotion: an electromyographic study of the sidewinding and concertina modes of *Crotalus cerastes*, *Nerodia fasciata* and *Elaphe obsoleta*. *J. Exp. Biol.*, 140: 1-33.
- Lauder, G.V. (1980a) Evolution of the feeding mechanism in primitive actinopterygian fishes: a functional anatomical analysis of *Polypterus*, *Lepisosteus*, and *Amia*. *J. Morphol.*, 163: 283-317.
- Lauder, G.V. (1980b) The suction feeding mechanism in sunfishes (*Lepomis*): an experimental analysis. *J. Exp. Biol.*, 88: 49-72.
- Lauder, G.V. (1980c) Hydrodynamics of prey capture in teleost fishes. In *Biofluid Mechanics*, vol. 2 (ed. by D. Schenck). Plenum Press, New York. pp. 161-181.



- Lauder, G.V. (1983) Functional design and evolution of the pharyngeal jaw apparatus in euteleostean fishes. *Zool. J. Linn. Soc.*, 77: 1-38.
- Lauder, G.V. (1985) Aquatic feeding in lower tetrapods. In *Functional Vertebrate Morphology* (ed. by M. Hildebrand, D.M. Bramble, K.F. Liem, and D.B. Wake). Harvard University Press, Cambridge, pp. 230-261.
- Lauder, G.V. (1990) Functional morphology and systematics: studying functional patterns in an historical context. *Annu. Rev. Ecol. Syst.*, 21: 317-340.
- Lauder, G.V., and T. Prendergast (1992) Kinematics of aquatic prey capture in the snapping turtle, *Chelydra serpentina*. *J. Exp. Biol.* 164: 55-78.
- Lauder, G.V., and S.M. Reilly (1988) Functional design of the feeding mechanism in salamanders: causal bases of ontogenetic changes in function. *J. Exp. Biol.*, 134: 219-233.
- Lauder, G.V., and S.M. Reilly (1990) Metamorphosis of the feeding mechanism in tiger salamanders (*Ambystoma tigrinum*): the ontogeny of cranial muscle mass. *J. Zool., Lond.*, 222: 59-74.
- Lauder, G.V., and H.B. Shaffer (1986) Functional design of the feeding mechanism in lower vertebrates: unidirectional vs. bidirectional flow systems in the tiger salamander. *Zool. J. Linn. Soc.*, 88: 227-290.
- Lauder, G.V., and H.B. Shaffer (1992) Design of the aquatic vertebrate skull: major patterns and their evolutionary interpretations. In *The Vertebrate Skull* (ed. by J. Hanken and B. Hall). University of Chicago Press, Chicago (in press).
- Liem, K.F. (1970) Comparative functional anatomy of the Nandidae (Pisces: Teleostei). *Feldiana Zool.*, 56: 1-166.
- Liem, K.F. (1978) Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlids. I. Piscivores. *J. Morphol.*, 158: 323-360.
- Liem, K.F. (1979) Modulatory multiplicity in the feeding mechanism of cichlids, as exemplified by the invertebrate pickers of lake Tanganyika. *J. Zool., Lond.*, 189: 93-125.
- Liem, K.F., and P.H. Greenwood (1981) A functional approach to the phylogeny of the pharyngognath teleosts. *Amer. Zool.*, 21: 83-101.
- Motta, P.J. (1988) Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes: Chaetodontidae): an ecomorphological approach. *Env. Biol. Fish.*, 22: 39-67.
- Norberg, U.M. (1990) *Vertebrate Flight*. Springer, Berlin.
- Reilly, S.M. (1987) Ontogeny of the hyobranchial apparatus in the salamanders *Ambystoma talpoideum* (Ambystomatidae) and *Notophthalmus viridescens* (Salamandridae): the ecological morphology of two neotenic strategies. *J. Morphol.*, 191: 205-214.
- Reilly, S.M., and G.V. Lauder (1989a) Physiological bases of feeding behavior in salamanders: do motor patterns vary with prey type? *J. Exp. Biol.*, 141: 343-358.
- Reilly, S.M., and G.V. Lauder (1989b) Kinetics of tongue projection in *Ambystoma tigrinum*: quantitative kinematics, muscle function, and evolutionary hypotheses. *J. Morphol.*, 199: 223-243.
- Reilly, S.M., and G.V. Lauder (1990) The evolution of tetrapod feeding behavior: kinematic homologies in prey transport. *Evolution*, 44: 1542-1557.
- Rohlf, F.J., and F.L. Bookstein (1990) Proceedings of the Michigan Morphometrics Workshop. Univ. Michigan Mus. Zool. Spec. Publ. No. 2.
- Sanderson, S.L. (1988) Variation in neuromuscular activity during prey capture by trophic specialists and generalists (Pisces: Labridae). *Brain Behav. Evol.*, 32: 257-268.
- Sanderson, S.L. (1990) Versatility and specialization in labrid fishes: ecomorphological implications. *Oecologia*, 84: 272-279.
- Sanderson, S.L. (1992) Functional stereotypy and feeding performance in a trophic specialist. *Funct. Ecol.*, (in press).
- Sanford, C.P., and G.V. Lauder (1990) Kinematics of the tongue-bite apparatus in osteoglossomorph fishes. *J. Exp. Biol.*, 154: 137-162.
- Shaffer, H.B. (1984) Evolution in a paedomorphic lineage. II. Allometry and form in the Mexican Ambystomatidae. *Evolution*, 38: 1194-1206.
- Shaffer, H.B., and G.V. Lauder (1985a) Aquatic prey capture in ambystomatid salamanders: patterns of variation in muscle activity. *J. Morphol.*, 183: 273-284.
- Shaffer, H.B., and G.V. Lauder (1985b) Patterns of variation in aquatic ambystomatid salamanders: kinematics of the feeding mechanism. *Evolution*, 39: 83-92.
- Shea, B.T. (1985) Ontogenetic allometry and scaling: a discussion based on the growth and form of the skull in African apes. In *Size and Scaling in Primate Biology* (ed. by W. Jungers). Plenum Press, New York, pp. 175-405.
- Sokal, R.R., and F.J. Rohlf (1981) *Biometry*. Freeman Press, New York.
- Strauss, R.E. (1985) Evolutionary allometry and variation in body form in the South American catfish genus *Corydoras* (Callichthyidae). *Syst. Zool.*, 34: 381-396.
- Wainwright, P. (1988) Morphology and ecology: functional basis of feeding constraints in Caribbean labrid fishes. *Ecology*, 69: 635-645.
- Wainwright, P. (1989) Prey processing in haemulid fishes: patterns of variation in pharyngeal jaw muscle activity. *J. Exp. Biol.*, 141: 359-375.
- Wainwright, P.C., and G.V. Lauder (1986) Feeding biology of sunfishes: patterns of variation in prey capture. *Zool. J. Linn. Soc. Lond.*, 88: 217-228.
- Wainwright, P.C., and Lauder, G.V. (1992) The evolution of feeding biology in sunfishes (Centrarchidae). In *Systematics, Historical Ecology and North American Fishes* (ed. by R. Mayden). Stanford University Press, Stanford (in press).
- Wainwright, P.C., C.P. Sanford, S.M. Reilly, and G.V. Lauder (1989) Evolution of motor patterns: aquatic feeding in salamanders and ray-finned fishes. *Brain Behav. Evol.*, 34: 329-341.
- Westneat, M.W., and P.C. Wainwright (1989) Feeding mechanism of *Epibulus insidiator* (Labridae: Teleostei): evolution of a novel functional system. *J. Morphol.*, 202: 129-150.