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Evolution of Motor Patterns: Aquatic Feeding in Salamanders and Ray-Finned Fishes

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Abstract. Patterns of muscle activity (motor patterns) have generally been found to be strongly conserved during the evolution of aquatic feeding behavior within closely related groups of fishes and salamanders. We conducted a test of the generality of motor pattern conservation with a much broader phylogenetic scope than has been done previously. Activity patterns of three cranial muscles were quantified from electromyographic (EMG) recordings made during suction feeding in a salamander (*Ambystoma mexicanum*) and 4 widely divergent species of ray-finned fishes (*Amia calva*, *Notopterus chitala*, *Micropterus salmoides* and *Lepomis macrochirus*). General features of the motor pattern were the same in all species, but multivariate and univariate analyses of variance revealed highly significant differences among the 5 species in the average muscle activity pattern, indicating that the motor pattern has not been precisely conserved among these 5 taxa. Five of eight EMG variables that describe the intensity and timing of muscle activity differed among species. Only the intensity of activity of the adductor mandibulae appears to be a strongly conserved feature of the suction feeding motor pattern in anamniotes. A discriminant function analysis of the 8 EMG variables successfully classified about two thirds of the feeding incidents as belonging to the correct species. In contrast to the results of previous studies of closely related taxa, we found that numerous quantitative differences exist among species, indicating that functionally significant details of suction feeding motor patterns have changed during evolution, whereas several general features of the pattern have been conserved.

Introduction

Fishes and aquatic salamanders exhibit a remarkable diversity of feeding behaviors. The range includes activities such as picking individual plankton from the water column, scraping algae from rock surfaces, luring prey with modified appendages and stunning prey with electrical shocks. Nearly all anamniotes, however, retain the ability to capture prey by suction feeding [Liem, 1984; Motta, 1984; Lauder, 1985]. Suction feeding is primitive for the Osteichthyes (bony fishes) and is by far the most frequently used mode of prey capture among the roughly 24,000 species of aquatic feeding anamniotes [Muller and Osse, 1984; Lauder, 1985]. The pattern of trophic di-

versification within this group has largely been one in which new behaviors and morphological changes have been added to the primitive behavior of suction feeding [e.g. Liem, 1979, 1980; Lauder, 1983; Barel, 1984; Motta, 1988; Norton, 1988; Westneat and Wainwright, in press].

In analyzing the evolution of a behavior, such as suction feeding, it is useful to consider the functional design of the system that is responsible for the behavior [Lauder and Shaffer, 1988]. Independent or concurrent evolutionary change at several levels of design may alter aquatic feeding behavior [Lauder and Shaffer, 1988]. Changes in peripheral morphology, physiological properties of peripheral morphology, patterns of muscle activity (motor pattern), and central

neuronal interconnections and circuits may result in changes in the patterns of movement during suction feeding. Thus, suction feeding behavior can evolve in response to alterations in the size and shape of cranial muscles and bones [Barel, 1983], or the physiological properties of the cranial muscles [e.g. Ono and Kaufman, 1983; Wainwright, 1988] and bones [Muller and Osse, 1984]. Similarly, changes in the patterns of muscle activity can alter the sequence of movements during feeding [e.g. Lauder and Shaffer, 1988], and the organization of circuitry in the central nervous system may determine motor patterns themselves [Roth et al., 1988].

In the present study we assessed evolution at one level of design of the suction feeding mechanism, the level of the motor pattern. We quantitatively compared the motor patterns exhibited by a salamander and 4 widely divergent ray-finned fishes. The common ancestor of tetrapods and ray-finned fishes dates from the Devonian [Schultze, 1977]. This study, therefore, examines the evolution of the suction-feeding motor pattern since the divergence of the tetrapod and ray-finned fish lineages over 400 million years ago.

Several recent studies of feeding behavior in fishes and salamanders have quantitatively compared motor patterns among closely related species [Shaffer and Lauder, 1985; Wainwright and Lauder, 1986; Sanderson, 1988; Wainwright, 1989]. The general conclusion from this body of work is that motor patterns tend to be strongly conserved among closely related taxa. Indeed, motor patterns may be very similar even in the face of considerable morphological evolution in trophic structures [e.g. Sanderson, 1988; Westneat and Wainwright, in press]. Thus, evolutionary changes in suction feeding behavior among closely related species seem rarely to be due to major alterations in the patterns of muscle activity that drive the behavior [see Lauder, 1983, for a counter-example that does not involve suction feeding]. The goal of the present study was to test the generality of motor pattern conservation in a much broader phylogenetic context than has been done previously. We find that, while the qualitative pattern of muscle activity used during suction feeding is similar in all 5 taxa, numerous quantitative differences exist, indicating that functionally significant details of the suction feeding motor pattern have specialized during evolution while several general features of the pattern have been conserved.

Materials and Methods

Specimens

Five species that provide a broad phylogenetic sample of extant aquatic feeding anamniotes were chosen for the analysis of motor pattern evolution (fig. 1): the ambystomatid salamander *Ambystoma mexicanum* ($n = 5$), the primitive ray-finned fish *Amia calva* ($n = 3$), the primitive teleost fish *Notopterus chitala* ($n = 3$) and two members of the perciform fish family Centrarchidae, *Micropterus salmoides* ($n = 7$) and *Lepomis macrochirus* ($n = 4$). The presently accepted genealogical relationships among these 5 species are shown in figure 1A. They vary widely in natural habitat, foraging behavior and feeding habits, but all use suction feeding to capture prey.

All animals were sexually mature adults chosen to minimize intra- and interspecific variation in body size. The effect of body size on motor patterns is not known and, although differences in average body size did exist in our sample of experimental individuals, no obvious effects of body size could be seen in the data set. The *Ambystoma* (mean snout-vent length = 106.5 mm) were obtained from a laboratory colony in Irvine, Calif., USA; *Amia* [mean standard length (SL) = 312 mm] were collected in central North Carolina; *Notopterus* (mean SL = 287 mm) were obtained from commercial pet dealers, and the two centrarchids (*Micropterus*, mean SL = 176 mm; *Lepomis*, mean SL = 158 mm) were collected in northern Illinois and Indiana. Animals were maintained separately in 30- to 100-liter aquaria at 21°C (except *Notopterus* which were held at 25°C) and fed a mixed diet of living fishes (*Carassius*, *Pimephales*, *Poecilia* and *Notemigonis*) and earthworms (*Lumbricus*). Guidelines used for the original research reported herein were established by the Animal Research Committee of the University of California at Irvine.

Feeding trials were conducted with the 4 fish taxa by introducing 3- to 4-cm-long fishes (*Pimephales* or *Carassius*) into the aquarium with the experimental individual. All *Ambystoma* were fed 2- to 3-cm pieces of earthworm. Many fishes can alter the motor pattern used during suction feeding in response to different prey [Liem, 1979; Wainwright and Lauder, 1986; Sanderson, 1988], so it was important to base comparisons among fish species on data from feedings with the same prey type. Unlike fishes, however, *A. mexicanum* exhibits a stereotyped motor pattern that does not vary with prey type [Reilly and Lauder, 1989]. Thus, prey type effects could be eliminated as a potential source of variance in the motor pattern comparisons among *Ambystoma* and the 4 fish species.

Myology

In all experiments, electromyographic (EMG) recordings were made from three muscles that were selected on the basis of two primary criteria: all three muscles (1) are functionally prominent in the feeding mechanism of aquatic anamniotes, and (2) are believed to be homologous across the 5 taxa. The functional morphology of aquatic feeding in fishes and salamanders has been described in detail elsewhere [Lauder, 1981, 1985; Lauder and Shaffer, 1985], only a brief account of the relevant muscles and their functions will be presented here.

Three muscles were examined, the anterior portion of the epaxialis (EP), which elevates the head during the strike; the sternohyoideus (SH), which effects the primary suction-generating movement of depressing the hyoid bar and thus the floor of the mouth

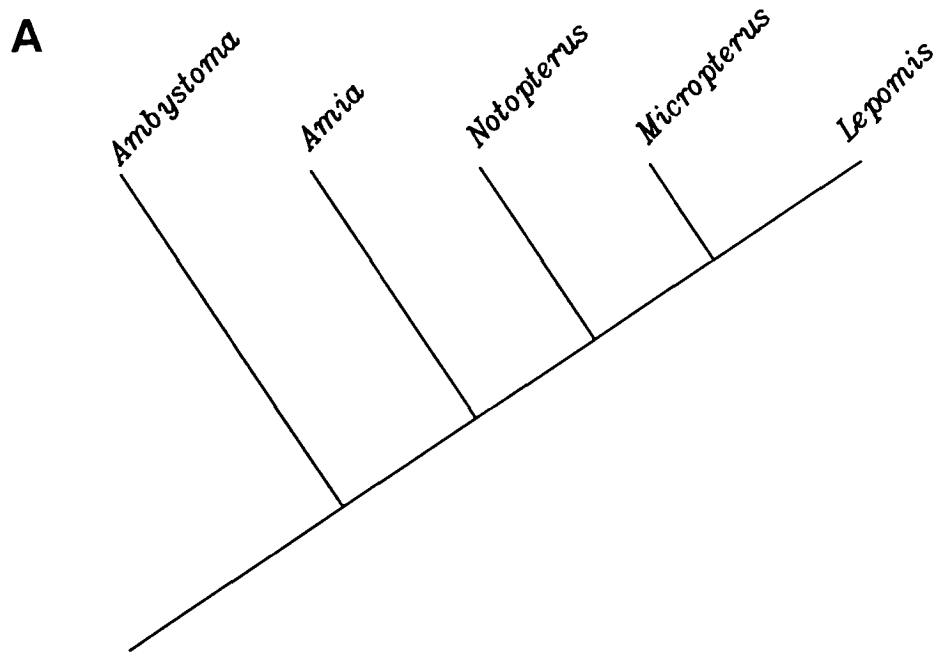


Fig. 1. Currently accepted phylogenetic relationships of the salamander and 4 ray-finned fish species that were compared in the present study [Lauder and Liem, 1983]: *A. mexicanum*, *A. calva*, *N. chitala*, *M. salmoides* and *L. macrochirus*. **B** Diagram of the nested ANOVA experimental design used to compare the suction feeding motor patterns exhibited by the 5 study taxa. Nested within each species were various numbers of individuals (the exact numbers are indicated) and several replicate feedings were obtained from each individual (numbers in figure are the average number of replicate feedings for each species).

B

AMBYSTOMA					AMIA			NOTOPT.			MICROPTERUS				LEPOMIS			
1	2	...	5		1	2	3	1	2	3	1	2	...	7	1	2	3	4
1					1			1			1				1			
2					2			2			2				2			
⋮		...			⋮			⋮			⋮		...		⋮			
9					11			7			9				9			

(the homologue of this muscle in salamanders is called the rectus cervicis [Lauder and Shaffer, 1985]), and the adductor mandibulae (AM), which is the primary jaw adductor in all 5 taxa. A fourth muscle that does not occur in salamanders, the levator operculi (LOP), was recorded from in experiments with the 4 fish species. This muscle functions in depressing the lower jaw through the opercular series coupling to the mandible. All recordings were made from the left member of these bilaterally paired muscles.

Electromyography

EMG recordings were made following a previously described protocol [Shaffer and Lauder, 1985; Wainwright, 1989]. Bipolar fine-wire electrodes were implanted percutaneously into the muscles of anesthetized animals (methane tricaine sulfonate anesthesia). Electrodes were constructed by threading two 75-cm pieces of

polyethylene-coated stainless-steel wire (0.051 mm in diameter) through a 26-gauge hypodermic needle. The first 15 cm of the two wires were glued together with a cyanoacrylate adhesive [Jayne, 1988], 0.5-mm wire tips were cleanly exposed using a razor blade under a dissecting microscope, and 1.5 mm of the paired wire was bent back against the barrel of the needle. The hooked tips served to anchor the electrodes in the muscle, holding them firm, both while the needle barrel was being withdrawn and during the feeding trials. The electrodes were glued together into a common cable that was tied to a mid-dorsal suture behind the animal's head. In some experiments additional sutures were used to anchor electrodes more proximal to their target muscle.

Electrical signals were amplified 10,000 times (Grass P511J preamplifiers) with a bandpass of 100–3,000 Hz and recorded on a Bell and Howell 4020A FM tape recorder at 19 or 38 cm/s tape

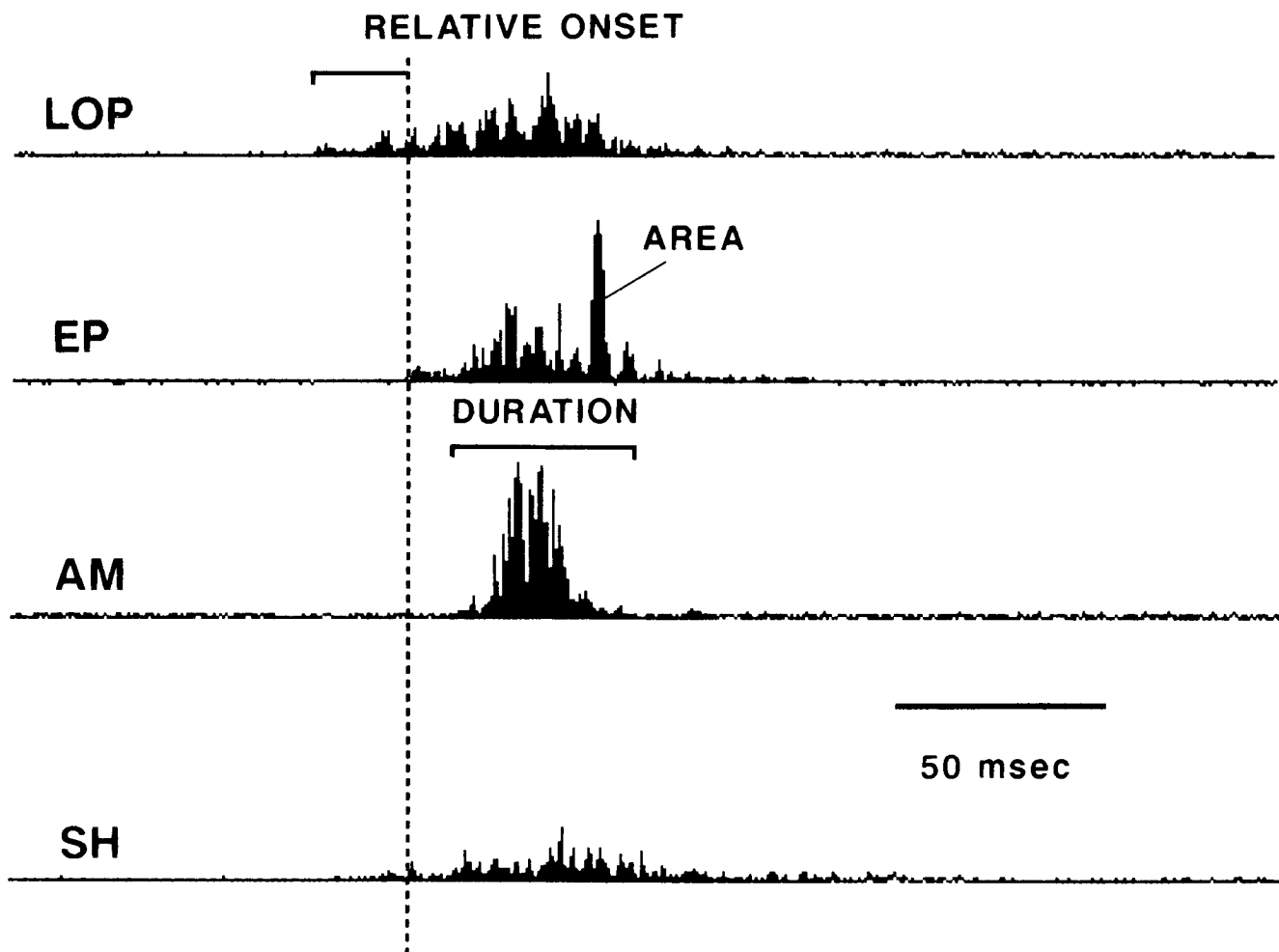


Fig. 2. Sample rectified EMG, recorded during prey capture by *N. chitala*, to illustrate the three types of variables that were measured. See text for detailed descriptions. The vertical dashed line indicates the onset of activity of the epaxialis muscle, which was used as the reference time in measuring relative onset time variables. Integrated areas of muscle activity were measured as the shaded area under each rectified signal, and activity durations were measured as the time, in milliseconds, of each activity burst.

speed. The 60-Hz notch filter was always used. The tape recording of each feeding was later digitized at a sample rate of 2,100 Hz using a Keithley DAS12-bit analogue-to-digital converter and stored on an IBM AT microcomputer. A hard copy, for visual inspection, was made from the digital file of each feeding on a Gould 260 chart recorder.

EMGs were later played into a Tektronix 4107 color graphics terminal, and a computer program was used to rectify the EMGs and aided in measuring several variables that quantified the motor pattern recorded during the strike (fig. 2). For each muscle the duration of the activity burst was measured in milliseconds (EP-DUR, SH-DUR, AM-DUR, LOP-DUR), and the area under the rectified myogram was calculated in millivolts \times milliseconds (EP-AREA, SH-AREA, AM-AREA, LOP-AREA). Also, using the onset of activity of the epaxial muscle as a reference time, the time to the onset

of activity in each of the other muscles was measured in milliseconds (EP-SH, EP-AM, EP-LOP). The choice of the epaxialis as the reference muscle was based on the fact that, unlike the other muscles, it was active in all feedings. Overall, 8 variables were measured from each *Ambystoma* feeding and 11 from each fish feeding that quantified the overall timing and intensity of muscle activity at the strike.

Statistical Analyses

The overall experimental design was a two-level nested analysis of variance (ANOVA), with various numbers of individuals nested within each of the 5 species (fig. 1B). The replication of individuals within species is particularly important because high levels of variation in EMG variables among individuals have previously been reported in these and other aquatic feeding vertebrates [Shaffer and

Lauder, 1985; Bemis and Lauder, 1986; Wainwright and Lauder, 1986; Sanderson, 1988], underscoring the need for comparisons among species to be based on adequate estimates of within-species variance [see discussions in Shaffer and Lauder, 1985; Wainwright, 1989]. Between 7 and 12 replicate feedings from each individual (mean = 9.2) constituted the contents of a single cell in this design (fig. 1B), for a total of 202 feedings that were analyzed.

This data matrix of 8 EMG variables by 202 feedings (1,616 entries) contained 16 missing entries, scattered throughout all 5 taxa. Missing data came about for two reasons. First, in 11 cases a muscle was not active during a particular feeding, and hence the relative onset time variable for that muscle could not be measured. Second, no variables could be measured from 5 myograms which were superimposed on low-frequency motion artifacts. When performing multivariate statistical analyses on a data set with empty cells, a single missing entry causes the entire feeding to be omitted from the computations. To avoid the loss of information in this manner we replaced each of the 16 missing values in our data matrix with the mean calculated for that variable and the individual animal from which the feeding was recorded. No differences were found between the results of univariate ANOVAs run on this modified data set and the original data. All subsequent analyses were performed on the modified data set.

To test the null hypothesis that the motor pattern was the same in all 5 taxa, an overall multivariate analysis of variance (MANOVA) was performed on the 8 EMG variables common to *Ambystoma* and the 4 fish taxa. Univariate ANOVAs were then run to examine the patterns of variation in each variable separately. In all tests of the species effect, the F ratios were constructed with the mean squares for the individual factor in the denominator [Sokal and Rohlf, 1981]. Significant tests of the species effect indicated which aspects of the motor pattern were not the same in all species.

To further examine the distinctiveness of each species' motor pattern, a discriminant analysis was performed on the 8 EMG variables shared among the 5 taxa. This discriminant analysis revealed the linear combinations of the 8 EMG variables which best distinguished the muscle activity patterns of the 5 species, permitting an assessment of the certainty with which feedings can be attributed to each species. Raw data visually met the distributional assumptions of parametric statistics, so all computations were performed with untransformed data using Systat [Wilkinson, 1986] on a microcomputer.

Results

Several aspects of muscle activity exhibited during suction feeding were similar in all 5 taxa (fig. 3). On average, each muscle shows a single, intense burst of activity that lasts between 30 and 110 ms, and all muscles show a high degree of overlap in activity (fig. 2, 3). The onset of activity of the adductor mandibulae muscle follows that of the epaxialis, sternohyoideus and levator operculi muscles by about 5–20 ms. The levator operculi muscle always begins activity before the other three muscles. Qualitatively, the activity patterns in the 5 species were similar to those seen in

other aquatic feeding amphibians and fishes [Liem, 1979; Lauder, 1981; Lauder and Shaffer, 1985; Bemis and Lauder, 1986; Wainwright and Lauder, 1986].

Some differences among species are, however, conspicuous. The mean durations of activity in the epaxialis, sternohyoideus and levator operculi muscles were longer in *Amia* than in the other 4 taxa (fig. 3; EP, SH, LOP). The epaxialis and sternohyoideus also exhibited greater integrated areas in *Amia* (table 1; EP-AREA, SH-AREA). In addition, the relative onset time of the adductor mandibulae was longer in *Micropterus* and *Lepomis* than in the other 3 taxa (fig. 3, AM).

Quantitative Comparisons among all Species

The overall MANOVA revealed a highly significant overall species effect (table 2). Thus, the motor pattern is not the same across the 5 taxa. Five of the eight EMG variables showed a significant species effect in the univariate ANOVAs (table 3). As suggested by a visual inspection of the average motor patterns (fig. 3), both the duration of activity and the integrated area of activity of the epaxialis and the sternohyoideus were significantly different among species (table 3; EP-DUR, EP-AREA, SH-DUR, SH-AREA). Neither duration nor integrated areas of the adductor mandibulae differed significantly among species. Of the 2 relative onset variables, only the adductor mandibulae showed a significant species effect.

There was a highly significant multivariate difference among individuals within species, and all 8 variables showed significant univariate differences among individuals within species (tables 2, 3).

The discriminant function analysis used 4 canonical factors to correctly classify 132 of the 202 feedings for an overall accuracy of 65.3% (table 4). *Amia* exhibited the most distinctive motor pattern, with 88% of its feedings (29 of 33) correctly classified, while only 47% of the *Micropterus* feedings were correctly classified. About one third (29.7%) of the *Micropterus* feedings were incorrectly identified as belonging to *Lepomis*, indicating that these 2 taxa have similar motor patterns. About two thirds of the feedings from *Ambystoma*, *Notopterus* and *Lepomis* were correctly identified (table 2). The only 2 species that were completely separable were *Amia* and *Ambystoma* (table 4, fig. 4).

Canonical factor 1 of the discriminant analysis was most highly correlated with the duration of activity

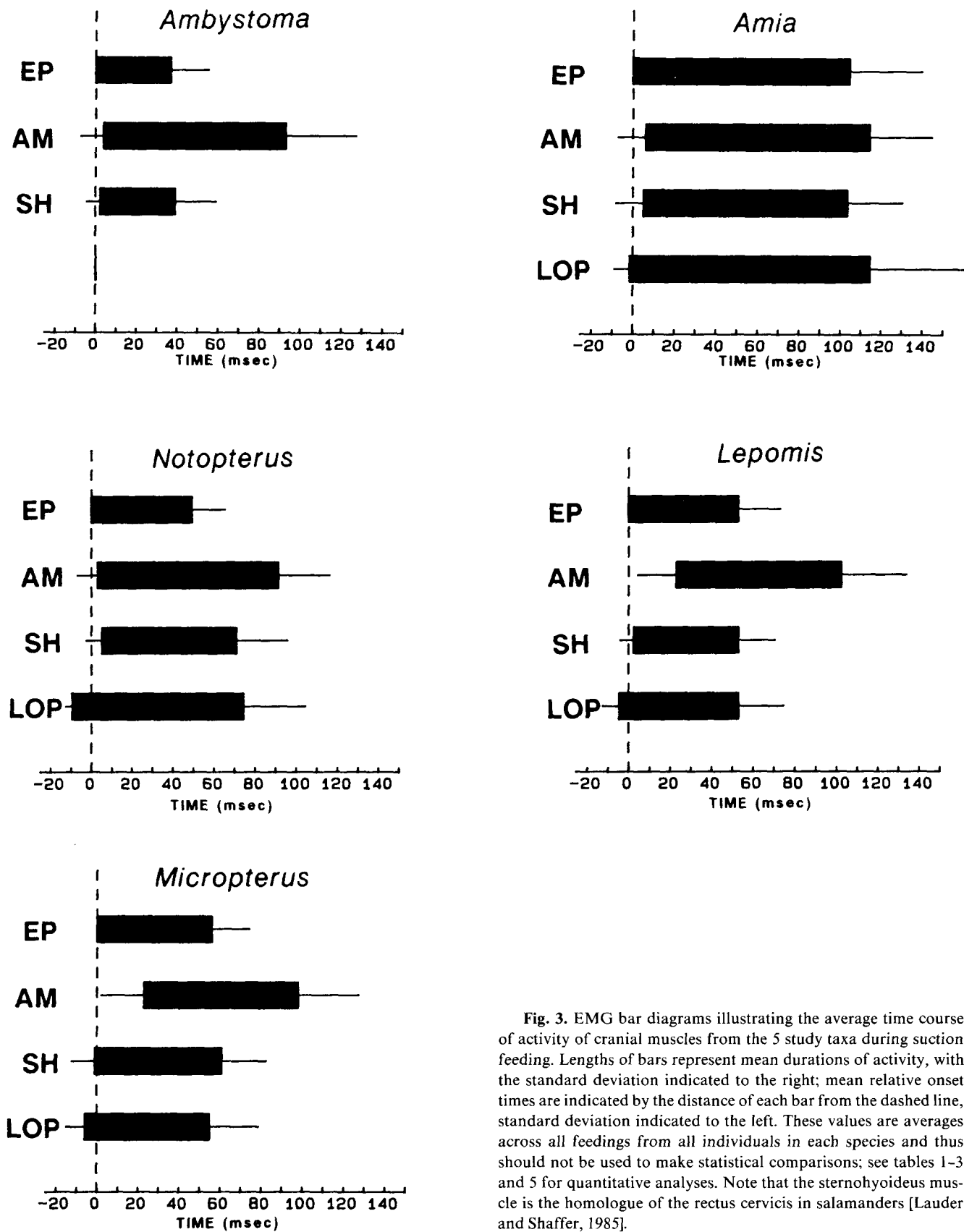


Fig. 3. EMG bar diagrams illustrating the average time course of activity of cranial muscles from the 5 study taxa during suction feeding. Lengths of bars represent mean durations of activity, with the standard deviation indicated to the right; mean relative onset times are indicated by the distance of each bar from the dashed line, standard deviation indicated to the left. These values are averages across all feedings from all individuals in each species and thus should not be used to make statistical comparisons; see tables 1-3 and 5 for quantitative analyses. Note that the sternohyoideus muscle is the homologue of the rectus cervicis in salamanders [Lauder and Shaffer, 1985].

Table 1. Mean (\pm standard deviation) for the integrated area variables (in units of millivolts \times milliseconds) measured from activity bursts of four muscles (levator operculi, epaxialis, sternohyoideus, adductor mandibulae) at the suction feeding strike in 5 species

Species	Variable			
	LOP-AREA	EP-AREA	SH-AREA	AM-AREA
<i>Ambystoma</i> (n = 47)	-	32.8 \pm 14.3	22.98 \pm 14.6	28.0 \pm 19.3
<i>Amia</i> (n = 35)	59.5 \pm 39.2	139.8 \pm 99.4	147.4 \pm 83.9	64.8 \pm 51.6
<i>Notopterus</i> (n = 21)	66.6 \pm 46.2	49.1 \pm 36.0	58.8 \pm 47.8	56.5 \pm 54.2
<i>Micropterus</i> (n = 64)	44.6 \pm 29.7	46.2 \pm 29.4	71.7 \pm 43.7	64.5 \pm 55.1
<i>Lepomis</i> (n = 41)	44.9 \pm 39.2	45.8 \pm 33.7	47.5 \pm 31.7	67.4 \pm 33.3

Means were calculated for all feedings from all individuals in each species, and therefore, should not be used for statistical comparisons. See tables 2, 3 and 6 for statistical comparisons. *Ambystoma* has no levator operculi muscle.

Table 2. Results of overall MANOVA on 8 EMG variables recorded during feeding from 5 species of aquatic vertebrates

Factor	d.f.	Wilks' λ	F ratio	Probability
Species	32, 38	0.003	4.5	p < 0.001
Individuals	136, 1,274	0.019	6.8	p < 0.001

See figure 1 and Materials and Methods for a discussion of the experimental design. d.f. = Degrees of freedom.

Table 3. F ratios from univariate ANOVA contrasting the motor patterns used during aquatic feeding in 5 species of anamniotic vertebrates: *A. mexicanum*, *A. calva*, *N. chitala*, *M. salmoides* and *L. macrochirus*

Variable	Factor	
	species (d.f. = 4,17)	individuals (d.f. = 17,180)
EP-DUR	13.5**	5.1**
SH-DUR	12.8**	4.0**
AM-DUR	0.5	10.6**
EP-AREA	4.6*	16.3**
SH-AREA	8.1**	6.4**
AM-AREA	1.0	12.3**
EP-SH	0.7	7.7**
EP-AM	4.5*	3.6**

* p < 0.05; ** p < 0.01. d.f. = Degrees of freedom.

Table 4. Results of a discriminant analysis of 8 EMG variables from 5 species of aquatic feeding vertebrates

	<i>Ambystoma</i>	<i>Amia</i>	<i>Notopterus</i>	<i>Micropterus</i>	<i>Lepomis</i>	Total
<i>Ambystoma</i>	32	0	12	0	3	32/47
<i>Amia</i>	0	29	1	3	0	24/33
<i>Notopterus</i>	3	1	15	0	2	15/21
<i>Micropterus</i>	6	2	7	30	19	30/64
<i>Lepomis</i>	4	2	0	5	26	26/37

Rows represent the feedings from each species, and columns are the predicted identity of feedings based on the discriminant analysis. Total feedings = 202.

Table 5. Canonical loadings (correlations between EMG variables and the canonical factors) for the first 2 canonical factors from a discriminant analysis of motor pattern variables from 5 species of anamniotic vertebrates

Variable	Factor 1	Factor 2
EP-DUR	0.70	0.30
SH-DUR	0.59	0.30
AM-DUR	0.20	-0.11
EP-AREA	0.76	0.03
SH-AREA	0.59	0.35
AM-AREA	0.13	0.43
EP-SH	0.11	-0.21
EP-AM	-0.15	0.51

Scores of feedings on the first 2 canonical factors are plotted in figure 4.

and the integrated area of activity in both the epaxialis and sternohyoideus muscles (table 5; EP-DUR, EP-AREA, SH-DUR, SH-AREA). Canonical factor 2 was most highly correlated with the relative onset time of the adductor mandibulae (table 5; EP-AM). A plot of the scores of all feedings on canonical factors 1 and 2 (fig. 4) shows that factor 1 tends to separate *Amia* feedings from the rest, while factor 2 results in some polarization of the two centrarchids against *Ambystoma*. The two centrarchids and *Notopterus* (all members of the Teleostei) overlap extensively in discriminant space. The range of canonical scores for feedings within each species (i.e. the areas enclosed by the polygons in figure 3) is quite high, indicating that the motor pattern varies considerably from feeding to feeding, resulting in overlap among species (fig. 4).

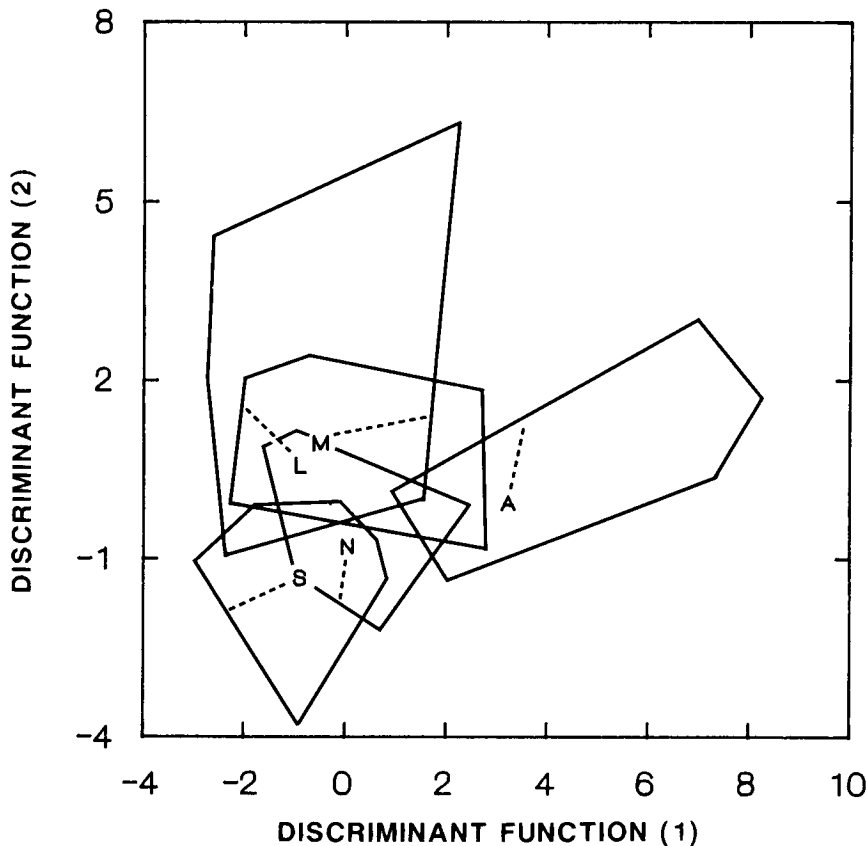


Fig. 4. Species scores on the first 2 canonical axes from a discriminant analysis of 8 EMG motor pattern variables from 5 species of aquatic vertebrates. Letters indicate species mean scores, and polygons enclose all scores for each species. Note that only *Amia* and *Ambystoma* are completely non-overlapping. See text for sample sizes. Species key: A = *A. calva*; L = *L. macrochirus*; M = *M. salmoides*; N = *N. chitala*; S = *A. mexicanum*.

The results of these analyses suggest that *Amia* may be driving the significance of the overall species effect by virtue of its particularly distinct motor pattern. To examine this possibility, a second MANOVA was run in which the data from *Amia* were excluded. Even without *Amia* there was a significant species effect (MANOVA:degrees of freedom = 24,23; Wilks' λ = 0.029; F ratio = 2.36; $p < 0.02$), and 4 of the 8 EMG variables (EP-DUR, SH-DUR, SH-AREA, EP-AM) exhibited a significant species effect in univariate ANOVAs ($p < 0.05$).

Quantitative Comparisons among Fishes

An overall MANOVA on the 11 variables shared by the 4 fish taxa showed a highly significant overall species effect (table 6). Six of the eleven EMG variables were significantly different ($p < 0.05$) among species in univariate ANOVAs. Of the 3 variables introduced by the presence of the levator operculi muscle, only the duration of its activity showed a significant species effect (table 6; LOP-DUR). Thus, no qualitative differences were seen between the analyses performed on all species and those conducted on the 11 variables shared by the 4 fish taxa.

Discussion

Our comparisons of suction feeding behavior in *Ambystoma* and the 4 fish taxa allow us to make two primary conclusions regarding the evolution of the motor pattern within these phylogenetically diverse groups: (1) several general features of the motor pattern are retained in all 5 species, and (2) in spite of this conservation of the basic motor pattern, numerous quantitative changes have occurred. Below, we consider whether the changes that were observed have significant functional consequences for the feeding mechanism and discuss our results as they relate to the evolution of feeding behavior in anamniotic vertebrates.

Conservation of General Features

There are at least two basic features of the suction feeding motor pattern that are shared by all of the species examined in this study. First, all muscles are active during suction feeding, typically in bursts lasting 30–110 ms (fig. 2, 3). Suction feeding on elusive prey involved strong, nearly simultaneous bursts of activity in all cranial muscles that were examined. Second,

Table 6. F ratios from the ANOVAs and MANOVA comparing 11 EMG variables among 4 ray-finned fish taxa: *Amia*, *Notopterus*, *Micropterus* and *Lepomis*

Variable	Factor	
	species (d.f. = 3,13)	individuals (d.f. = 13,138)
EP-DUR	11.6**	5.3**
LOP-DUR	7.1**	4.1**
SH-DUR	10.3**	3.7**
AM-DUR	1.8	5.0**
EP-AREA	4.1*	16.9**
LOP-AREA	1.0	5.7**
SH-AREA	5.4*	6.3**
AM-AREA	0.1	13.1**
EP-LOP	3.2	1.2
EP-SH	0.7	7.8**
EP-AM	5.1*	2.7**

MANOVA for species factor: degrees of freedom (d.f.) = 33, 18; Wilks' λ = 0.002; F ratio = 5.6; $p < 0.001$; * $p < 0.05$; ** $p < 0.01$

the overall sequence of muscle activity does not vary among species (fig. 3). That is, muscles become active in virtually the same order in all species. The levator operculi begins activity shortly before the epaxialis and sternohyoideus, which are active nearly simultaneously, and these are followed by the onset of the adductor mandibulae muscle (fig. 2, 3). Both of these are general features that have been widely observed in aquatic feeding amphibians and fishes [Osse, 1969; Elshoud-Oldenhav and Osse, 1976; Liem, 1978; Elshoud-Oldenhav, 1979; Lauder and Norton, 1979; Lauder, 1980a, 1981; Lauder and Liem, 1980; Bemis and Lauder, 1986; Wainwright, 1986, 1989; Wainwright and Lauder, 1986; Sanderson, 1988].

General features of the kinematics and the morphological basis of suction feeding have also been conserved in our sample of species [Lauder, 1979, 1980a, b; Lauder and Shaffer, 1985]. In all taxa the feeding sequence begins with cranial elevation and lower jaw depression to open the mouth. This is followed by the primary suction-generating movement of hyoid bar depression, and finally, mouth closing. This kinematic profile is retained across a broad range of anamniotic vertebrates [Lauder, 1985]. It is perhaps not surprising that this conserved sequence of events (jaw opening, hyoid depression and mouth

closing) is produced by the same sequence of muscle activity. Retention of the basic sequence of muscle activity that drives this pattern of movements in *Ambystoma* and the 4 fish taxa provides further evidence that general features of the feeding mechanism in anamniotes have been conserved for at least 400 million years, since actinopterygian fishes diverged from the tetrapod lineage.

Evolution of Quantitative Features

In spite of the tendency for some aspects of the motor pattern to be conserved among the 5 taxa examined, our analyses do show extensive quantitative changes in muscle activity. The overall MANOVA revealed significant differences among the 5 species in their average motor pattern (tables 2, 6). The univariate ANOVAs demonstrated that 5 of the 8 EMG variables differ among species (table 3, 6). Only the duration and the integrated area of activity of the adductor mandibulae and the relative onset time of the sternohyoideus are conserved across all 5 taxa. There are significant differences among species in the duration and integrated area of activity of the epaxialis and sternohyoideus muscles and the relative onset time of the adductor mandibulae (table 3). Of these differences, the most conspicuous are: (1) longer durations and greater integrated areas of activity in the epaxialis and sternohyoideus muscles in *Amia* relative to the other taxa (fig. 3, table 1), and (2) a longer relative onset time of the adductor mandibulae muscle in the two centrarchids, *Micropterus* and *Lepomis* (fig. 3).

Our analyses show that there are numerous statistically significant changes in the motor patterns of these 5 species, but do these changes have significant biological consequences? It could be that the changes in intensity and timing of muscle activity, although statistically significant, are not great enough in magnitude to produce meaningful changes in the mechanical output of the muscles or the bone movements that the muscles effect. How might the observed changes in motor pattern seen in *Amia* and the two centrarchids be expected to influence the functional morphology of the feeding mechanism?

The duration of activity and integrated areas of the epaxialis and the sternohyoideus muscles seen in *Amia* are between 2 and 8 times greater than those exhibited by the other taxa (table 1, fig. 3). Electrical activity of vertebrate muscles, as measured by integrated areas of EMGs, is positively correlated with tension developed by the muscle [Bigland and Lip-

pold, 1954; Walmsley et al., 1978; Ringelberg, 1985]. A positive correlation also exists in centrarchids between activity of the epaxialis and sternohyoideus and the magnitude of negative pressure generated during suction feeding [Lauder et al., 1986]. Thus, all other factors being equal, the motor pattern employed by *Amia* should result in increased muscular tension and greater buccal pressure during feeding, compared to what would be observed if *Amia* used the muscle activity patterns exhibited by any of the other 4 species.

The functional implications of the longer relative onset time of the adductor mandibulae seen in the two centrarchids are not as clear. Within species, an increased relative onset time of the adductor mandibulae is typically associated with suction feeding on immobile prey, rather than feedings on evasive prey like small fishes [Liem, 1978; Wainwright, 1986; Wainwright and Lauder, 1986; Sanderson, 1988]. Since small fishes were the experimental prey in the present study, the relative onset times of the adductor mandibulae were apparently near the shortest values that these centrarchids employ [Wainwright and Lauder, 1986], in spite of the fact that they were *longer* than those seen in the other fishes and *Ambystoma*. One prominent feature of the feeding apparatus in centrarchids that is not present in the other taxa is a protrusible upper jaw. Prey capture kinematics in centrarchids, and many other teleosts, involves considerable anterior excursions of the upper jaw [Motta, 1984]. These movements are generally mediated by the lower jaw, which connects ligamentously to the distal elements of the upper jaw [Motta, 1984]. The adductor mandibulae inserts on the lower jaw, and, thus, the timing of retraction of the upper jaws will be coupled to activity of this muscle. It is noteworthy that other jaw-protruding teleosts, when feeding on fish, exhibit a long average relative onset time of the adductor mandibulae (20–30 ms), compared to the 2–5 ms seen in the other taxa of the present study [e.g. Liem, 1978; Elshoud-Oldenhave, 1979; Sanderson, 1988]. It is possible that long relative onset times of the adductor mandibulae are linked to the added kinematic event of upper jaw protrusion. One aim of future work on the evolution of aquatic feeding behavior will be to explore the effects of upper jaw protrusion, and other key functional innovations, on the motor pattern of suction feeding.

We therefore hypothesize that at least the major differences among species in our EMG data can be

expected to have significant functional consequences. Our interpretation of the consequences of the changes seen in *Amia* could be tested by examining the kinematic and buccal pressure profile correlates of intraspecific variation in muscle activity [i.e. Lauder et al., 1986]. Does negative buccal pressure correlate positively with the integrated area of activity of the SH and EP muscles in *Amia*? While the *average* motor patterns of each species in our study were distinct, there was much variation within species (fig. 4). Overlap between species was extensive enough that even a multivariate discriminant function could only correctly classify about two thirds of the feedings (table 4). Such high intraspecific variation is potentially a powerful tool in testing hypotheses about the functional consequences of motor patterns.

Evolution of Motor Patterns

A considerable body of literature now exists on the evolution of suction feeding motor patterns in aquatic feeding salamanders and fishes [Liem, 1978, 1979, 1980; Lauder and Shaffer, 1985, 1988; Shaffer and Lauder, 1985; Bemis and Lauder, 1986; Wainwright and Lauder, 1986; Sanderson, 1988; Westneat and Wainwright, in press]. Quantitative comparisons of muscle activity have been made across ontogenetic stages within species [Lauder and Shaffer, 1988; Reilly and Lauder, 1989a], among closely related species [e.g. Shaffer and Lauder, 1985; Wainwright and Lauder, 1986; Sanderson, 1988] and in the present study across a broad phylogenetic range of taxa. These studies quantified motor patterns from EMGs by measuring durations and relative timings of muscle activity and, frequently, some indication of the intensity of muscle activity, such as peak amplitude or integrated area under a rectified myogram. The main conclusion that can be drawn from this data base is that, among closely related groups, the suction feeding motor pattern is a highly conserved feature of feeding behavior in aquatic anamniotes, although we show here that it can evolve in functionally significant ways.

Liem's classic, though nonquantitative work on African cichlids [Liem, 1978, 1979, 1980] is the only case study which found differences among closely related species (congeneric or confamilial) in the motor patterns of the oral jaws. Liem [1979, 1980] proposed that the frequent correlations he observed between novel trophic habits and novel motor patterns are a key attribute of cichlids that may have played an im-

portant role in their extraordinary success in the African rift lakes [Freyer and Iles, 1972]. The trend suggested by more recent research, that motor patterns are usually highly conserved, supports Liem's suggestion that cichlids exhibit an unusual propensity for modifications of neuromuscular patterns.

Despite the work on cichlid fishes, quantitative analyses have repeatedly found the suction feeding motor pattern to be strongly conserved during evolution [Shaffer and Lauder, 1985; Wainwright and Lauder, 1986; Sanderson, 1988]. Indeed, the present study is the first *quantitative* analysis to demonstrate multivariate differences among taxa in the average muscle activity pattern used during suction feeding. We have shown that numerous aspects of the motor pattern have changed within a selection of 5 widely divergent taxa. While the general features of the suction feeding motor pattern are the same in our study taxa, the tendency toward conservation of quantitative aspects within genera and families breaks down in this broader phylogenetic context.

The issue of evolutionary conservation of motor patterns has been addressed in other vertebrate behaviors. For example, certain aspects of muscle activity patterns in the shoulder during locomotion can be shown to have been conserved in a reptile (*Varanus*), a mammal (*Didelphus*) and a bird (*Columba*), in spite of major changes in the function of some muscles [Goslow et al., 1989]. In contrast, mammalian suckling motor patterns appear to vary significantly among species [Gordon and Herring, 1987]. Although several striking examples exist of motor pattern conservation [e.g. Wainwright and Lauder, 1986; Lauder and Shaffer, 1988; Goslow et al., 1989], there are also numerous examples of evolutionary transformations in muscle activity [e.g. Lauder, 1983; Gordon and Herring, 1987; and present study]. Motor patterns, therefore, do not appear to be subject to universally strong constraints on their design. The extent of variation within species supports this conclusion. In the present study, nearly all 5 species exhibited considerable overlap in their motor patterns. Thus, in the discriminant analysis, some feedings of each species were confused with feedings of other species. Muscle activity patterns show high levels of variation among individuals within species and within individuals [Shaffer and Lauder, 1985; Wainwright, 1989]. One goal of future research will be to identify the factors that limit the evolutionary plasticity of motor patterns.

closing) is produced by the same sequence of muscle activity. Retention of the basic sequence of muscle activity that drives this pattern of movements in *Ambystoma* and the 4 fish taxa provides further evidence that general features of the feeding mechanism in anamniotes have been conserved for at least 400 million years, since actinopterygian fishes diverged from the tetrapod lineage.

Evolution of Quantitative Features

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