

Derived Life History Characteristics Constrain the Evolution of Aquatic Feeding Behavior in Adult Amphibians

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Abstract

Initial descriptions of aquatic prey capture in adult amphibians only included species that use suction feeding (i.e., capture prey from beyond the jaw tips by generating flow into the buccal cavity). However, later surveys of amphibian feeding found many species that feed in water using alternative methods of prey capture (e.g., jaw or tongue prehension). These contrasting results raise the question of why suction feeding has evolved in the adult stage of some aquatic amphibians but not in others. Here, we propose the hypothesis that the emergence of derived life history patterns can constrain the evolution of aquatic feeding behavior in adults. Specifically, we hypothesize that the loss of characteristics needed for effective suction feeding in larvae appears to lower the probability that suction feeding will subsequently evolve in adults. New data on the aquatic feeding behavior of frogs, salamanders, and caecilians are combined with data and phylogenies from the literature to test this hypothesis. The results of a concentrated changes test and the statistical comparison of multiple independent transitions to aquatic feeding in adults are consistent with the hypothesis. Adults capable of suction feeding have evolved mainly in clades that possess a larval life stage with suction feeding, while clades that lack larvae or that have specialized larval feeding behavior (e.g., suspension feeding or oviductal feeding) are less likely to produce taxa with suction feeding adults. The loss of morphological features rather than the loss of motor patterns associated with suction feeding seems to have driven this evolutionary pattern.

Key words: caecilian, constraint, frog, larval stage, prey capture, salamander, suction feeding.

Introduction

Comparative studies that reach evolutionary conclusions necessarily involve assumptions about the relationships of the included taxa. With this in mind, many biologists advocate the explicit use of phylogenetic hypotheses in all comparative studies (e.g., Lauder, 1981, 1982, 1990; Felsenstein, 1985; Rieppel, 1988). Within an explicit phylogenetic framework, various methods have been proposed for assessing historical hypotheses (e.g., Ridley, 1986; Lauder and Liem, 1989; Maddison, 1990; Harvey and Pagel, 1991; Miles and Dunham, 1993). In comparative studies of functional systems, such historical analyses can provide information about the origins of both behavioral and morphological characteristics and historical factors that may have influenced their evolution. Historical hypotheses that can be tested in the context of a phylogeny include those concerning the presence and influence of constraints (*sensu* Schwenk, 1995). A constraint reduces the probability

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of certain evolutionary outcomes in clades that possess it relative to those that lack it (Lauder and Liem, 1989; Miles and Dunham, 1993). Schwenk and Wagner (2003) conclude that a hypothesis of constraint is best tested in the context of a phylogeny, specifically in an analysis that compares "constrained" and "unconstrained" clades. The presence of a constraint is even more powerfully studied when the suspected constraint evolves independently in many clades. These historical analyses require a null model of how evolution of the focal character or suite of characters is expected to proceed in the absence of the hypothesized constraint (Schwenk, 1995; Schwenk and Wagner, 2003).

The goal of this study is to explore the hypothesis that, within Lissamphibia, the evolution of derived larval feeding behavior has constrained the evolution of feeding behavior in aquatic adults. If the ancestor of Lissamphibia had an adult life history stage that did not forage in water, then aquatic feeding has evolved secondarily numerous times in adult amphibians. Many of these aquatic foraging adults are salamanders that employ suction feeding (Reilly and Lauder, 1992). All of these salamanders possess a larval life history stage that uses suction to capture prey and they have acquired aquatic larval feeding behavior through heterochrony in which larval morphology and function are retained into adulthood. However, not all secondarily aquatic clades have acquired the ability to perform suction feeding. We hypothesize that the lack of suction feeding in secondarily aquatic adults is linked to the loss of suction feeding behavior from the larval stage during amphibian phylogenesis.

There are at least two scenarios in which the presence of derived life history characteristics might eliminate access to suction feeding through heterochrony, and thereby reduces the probability of the evolution of suction feeding in adults. First, the larval stage and larval feeding behavior can be deleted from the ancestral amphibian life history pattern (i.e., direct development). In this case, the potential for acquiring larval characteristics (including suction feeding) in adults via heterochrony is lost. Second, the larval stage may possess derived morphological or behavioral characteristics that no longer facilitate suction feeding. For example, the evolution of viviparity in caecilians is associated with feeding specializations in fetuses that are not generally associated with suction feeding (Parker and Dunn, 1964; M. Wake, 1977, 1978; Wilkinson, 1991). In this second case, the potential for acquiring suction feeding behavior in adults through heterochrony is again lost, even though a distinctive juvenile stage is still present.

When the members of a clade forage in water as adults and do not acquire suction feeding characteristics, either behavioral or morphological, through heterochrony, there are three possible evolutionary outcomes: (1) they may utilize the ancestral adult characteristics that originally evolved for terrestrial foraging; (2) they may evolve novel characteristics that allow them to use suction to capture prey (these might resemble the ancestral larval amphibian characteristics associated with suction feeding); or (3) they may evolve novel characteristics for aquatic prey capture that do not involve suction feeding. These potential outcomes can be identified only in the context of an explicit phylogenetic hypothesis.

We combine the results of previous studies of amphibian feeding kinematics with new data on aquatic feeding behavior in several species of salamanders and frogs. We then map the combined data on various phylogenetic hypotheses from the literature. The combined data set is necessary in order to estimate the sequence and phylogenetic positions of transitions in amphibian feeding behavior. The results of our analysis suggest that many clades of amphibians with diverse life history characteristics have returned independently to aquatic environments to forage as adults. The repeated evolution of secondarily aquatic adults provides a set of "natural experiments" that we use here to test the hypothesis that the loss of a suction-feeding larval stage deters the evolution of suction feeding in adult amphibians.

Materials and Methods

Aquatic feeding behavior of metamorphosed individuals was videotaped for twelve species: the aquatic frogs *Lepidobatrachus llanensis* (n=7), *Xenopus laevis* (n=3), *Pipa pipa* (n=2) and *Hymenochirus sp.* (n=3); the amphibious frogs *Bombina orientalis* (n=3), *Caudiverbera caudiverbera* (n=3) and *Rana catesbeiana* (n=3); the aquatic salamander *Pachytriton brevipes* (n=5); the amphibious salamanders *Pleurodeles waltl* (n=6) and *Salamandrella keyserlingii* (n=1); the amphibious caecilian *Hypogeophis rostratus* (n=2); and the aquatic caecilian *Typhlonectes natans* (n=5).

To investigate the larval origins of adult aquatic feeding behavior, we videotaped feeding in larvae of the salamander *Pleurodeles waltl* (n=2) and larvae of an unidentified species of caecilian of the genus *Epicrionops* (n=4). To examine possible terrestrial origins of aquatic feeding behavior, terrestrial feeding was videotaped in metamorphosed individuals of the amphibious frog *Bombina orientalis* (n=3); the terrestrial frog *Chacophrys pierottii* (n=2); the terrestrial caecilian *Ichthyophis kohtaoensis* (n=5); and the amphibious caecilian *Hypogeophis rostratus* (n=4). The aquatic feeding behavior of adult individuals of the aquatic salamander *Siren intermedia* (n=3) was recorded in order to include the feeding behavior of an aquatic, paedomorphic species in our study and because it appears to represent the most basal clade of living salamanders (Duellman and Trueb, 1986; Larson and Dimmick, 1993). Finally, we videotaped the feeding behavior of an unidentified species of lungfish of the genus *Protopterus* (n=2) in order to provide a comparison to an outgroup of amphibians.

All animals were purchased from commercial suppliers, except for the *Epicrionops* larvae and the *Hypogeophis*, which were collected by R. A. Nussbaum in Ecuador and the Seychelles Islands respectively, the *Pleurodeles* that were obtained from a captive colony at the Brain Research Institute at the University of Bremen, Germany, and the *Salamandrella* which was provided by Paul Griffin. *Protopterus* were housed in 40 liter aquaria and maintained on a diet of earthworms (*Lumbricus*), goldfish (*Carassius*) and snails. *Caudiverbera* and *Lepidobatrachus* were housed in 10 x 20 x 5 cm plastic boxes filled with 4 cm of water and maintained on a diet of goldfish and newborn mice (*Mus*). *Xenopus* and *Pipa* were housed individually in subdivided 40 liter aquaria and kept on a diet of earthworms. *Hymenochirus* were housed in 10 x 20 x 5 cm plastic boxes with 5 cm of water and were maintained on small earthworm pieces and *Tubifex*. *Bombina*, *Chacophrys* and the terrestrial caecilians were housed in the same type of plastic box but with a damp paper towel substrate. *Bombina* and *Chacophrys* were fed crickets (*Acheta*) and waxworms (*Galleria* larvae). Terrestrial caecilians were kept on the same diet with the addition of earthworms. *Rana* were housed in tilted 40 liter aquaria with water at one end and maintained on a diet of waxworms, crickets and earthworms. *Typhlonectes* were housed in 20 liter aquaria with pea-sized gravel substrates and inverted clay dishes for cover. The *Typhlonectes* were kept on a diet of earthworms. *Siren*, *Pleurodeles* and *Pachytriton* were housed individually in subdivided 40 liter aquaria and maintained on earthworm pieces. *Typhlonectes* were maintained at 29°C. All other species were maintained at room temperature (20-27°C).

Qualitative observations of feeding behavior

Protopterus, *Hymenochirus*, *Xenopus*, *Siren*, *Salamandrella*, *Pachytriton*, *Pleurodeles* (both larval and post-metamorphic), *Typhlonectes* and larval *Epicrionops* were videotaped under water. All were videotaped while eating pieces of earthworm, except *Hymenochirus*, which were fed *Tubifex* in addition to earthworms. *Bombina*, *Lepidobatrachus*, *Caudiverbera* and *Rana* were videotaped in shallow water. *Lepidobatrachus* and *Caudiverbera* were fed goldfish. *Bombina* and *Rana* were fed earthworms. *Bombina*, *Ichthyophis* and *Hypogeophis* were fed out of water on a wet paper towel. Caecilians were fed pieces of earthworm. *Bombina* and *Chacophrys* were fed waxworms. Animals videotaped eating earthworms were fed pieces that were small enough not to obstruct the view of their heads. Feeding

sequences were videotaped at room temperature, except for *Typhlonectes* that were filmed at 29°C. All sequences were recorded with a Display Integration Technologies model 660 high-speed, multiframe video camera and a Panasonic AG-6300 VCR at a rate of 60 or 120 fields per second. A synchronized strobe was used for illumination.

Feeding sequences of all species were observed frame by frame and qualitative descriptions of feeding behavior for each species were compiled. The initial position of the prey item was marked on the video screen and movement of the prey item relative to the head of the predator was carefully observed. We followed the criterion of Lauder and Liem (1981), Norton and Brainerd (1993) and Summers et al. (1998) to determine if suction feeding was present or absent in each species. Species were classified as suction feeders only if bucco-pharyngeal expansion generates a rearward flow that accelerates the prey towards the mouth relative to a stationary reference point before the leading edge of the prey item crosses the threshold of the jaws (ram-suction index value greater than -1, Norton and Brainerd, 1993). It is important to note that ram feeding also may include "compensatory suction" which absorbs the bow wave generated by forward head movement but does not accelerate the prey item towards the mouth before it is overtaken by the jaws (Van Damme and Aerts, 1997). Thus, by our somewhat restrictive definition, animals that can generate suction in the buccal cavity may still not be capable of suction feeding. Likewise, by our definition, the use of rhythmic buccal pumping to filter relatively small particles from the water (as is seen in most anuran larvae) is not considered to be suction feeding (see discussion). Although our operational definition permits us to classify suction feeding as either present or absent, we acknowledge that the ability to generate flow using buccopharyngeal expansion varies continuously among aquatic feeding organisms.

Feeding behavior inferred from morphology

The number of taxa included in the phylogenetic analysis was expanded by inferring feeding behavior from two morphological characteristics. For the phylogenetic analysis, we coded taxa as suction feeders if they possessed both labial lobes and a hyobranchial apparatus composed of a rigid system arranged in a four-bar linkage that converts caudally directed contraction of the rectus cervicis into forceful ventral expansion of the buccal cavity (Van Damme and Aerts, 1997; Deban and Wake, 2000). The available kinematic data indicate that, without exception, all amphibian taxa that possess both labial lobes and a hyobranchial apparatus arranged as a four-bar linkage system are capable of suction feeding.

Larvae for which morphology was examined included 3 *Ichthyophis bannanicus*, 5 *Praslinia cooperi*, 7 *Hynobius leechi*, 3 *Salamandrella keyserlingii*, 3 *Onychodactylus fischeri*, 1 *Batrachuperus longdongensis*, 3 *B. tibetanus*, 6 *Rhyacotriton cascadae*, 5 *R. kezeri*, 4 *R. olympicus*, 5 *Taricha torosa*, 3 *Triturus alpestris*, 4 *Cynops* sp., 5 *Ambystoma gracile*, 5 *A. talpoideum*, 3 *A. texanum*, 11 *A. macrodactylum*, 2 *Typhlotriton spelaeus*, 4 *Eurycea junaluska*, 2 *Pseudotriton montanus*, 5 *Agalychnis callidryas*, 5 *Ascaphus truei*, 3 *Bombina orientalis*, 4 *Ceratophrys ornata*, 5 *Hemisus guttatum*, 5 *Megophrys* sp., 5 *Phyllomedusa vaillanti*, 5 *Rhinophryne dorsalis*, and 5 *Spea multiplicata*.

Specimens representing perennibranchiate (neotenic) species for which morphology was examined included 11 *Amphiuma means*, 3 *Necturus maculosus*, 7 *N. alabamensis*, 17 *E. nana*, 5 *E. neotenes*, 3 *E. tynerensis*, 1 *E. rathbuni* (also examined by Rose, 1995a), 1 *Gyrinophilus pallidus*, and 2 *G. porphyriticus* neotenes. Metamorphosed adults for which morphology was examined included 4 *Onychodactylus japonicus*, 4 *O. fischeri*, 5 *Batrachuperus tibetanus*, 4 *B. karlschmidti*, 3 *B. longdongensis*, 2 *B. yenyuanensis*, 3 *Ambystoma talpoideum*, 3 *A. maculatum*, 3 *A. texanum*, 2 *A. macrodactylum*, and 2 *Pseudotriton montanus*. Museum catalog numbers of specimens examined are listed in Appendix 1.

Neotenic specimens were generally not classified as adults or larvae. As wide a size range of specimens was examined as possible, however, to include both adults and juveniles. The

morphology of large and small perennibranchiates (neotenes) of a species was essentially the same; in all cases they have the morphological attributes of suction feeders. Thus, all perennibranchiates were classified as suction feeders as both "adults" and "larvae" (Appendix 2).

Phylogenetic analysis

The data gathered by us and the data available from the literature were mapped as discrete characters onto current hypotheses of amphibian relationships (Wake, 1966; Wake and Özeti, 1969; Cannatella, 1985; Duellman and Trueb, 1986; Lombard and Wake, 1986; Maxson and Ruibal, 1988; Cannatella and Trueb, 1988a, 1988b; Shaffer et al., 1991; Ford and Cannatella, 1993; Larson and Dimmick, 1993; Hedges and Maxson, 1993; Hedges et al., 1993; Hass et al., 1993; Sever, 1994; Hay et al., 1995; Ruvinsky and Maxson, 1996; Titus and Larson, 1996; Wilkinson and Nussbaum, 1999; Chippindale et al., 2000; Emerson et al., 2000; Vences et al., 2000; Hillis et al., 2001; Maglia et al., 2001). Some of these hypotheses are based on morphology, some are based on molecules, and some used both types of data.

The phylogenies proposed for salamanders and caecilians are largely in agreement. However, three very different arrangements of basal anurans have been proposed in the past ten years (Ford and Cannatella, 1993; Hay et al., 1995; Maglia et al., 2001). Therefore, we mapped our characters onto the three different proposed arrangements of basal frogs to determine how this would influence the outcome of our analyses. The most parsimonious number of transitions of larval feeding behavior and adult feeding behavior on these phylogenies was determined using MacClade version 3.06 and a Macintosh G4 computer.

When mapping characters, caecilians, salamanders and frogs were each analyzed independently. Some taxa (e.g., hynobiid salamander genus *Ranodon*) were not included in the analyses because they were not included in any of the published phylogenetic hypotheses we examined. Other taxa were pruned from the trees to simplify the analysis (e.g., large clades with a single set of character states, such as bolitoglossine plethodontid salamanders, were condensed into single taxa.). For the purposes of our analyses, terminal taxa that are known to have aquatic neotenic populations were split into a pair of sister taxa: a neotenic taxon and a metamorphosing taxon. The neotenic "taxon" was coded as having a suction feeding "larval" stage and an aquatic suction feeding "adult" stage. The metamorphosing "taxon" was coded as having a suction feeding larval stage with the adult stage being coded depending on the known habits of metamorphosing populations. A single, most parsimonious scenario was generated for the larval life stage of all three groups and for the adult stage of caecilians. This single larval tree was generated using parsimony combined with the following assumptions: 1) the ancestor of desmognathine plethodontid salamanders had a free-living, suction-feeding larval stage; and 2) the larval stage of all living caecilians is homologous (i.e., all species with a larval life history stage inherited this life history from a common ancestor). Depending on the assumed ancestral adult character states for each tree (i.e., terrestrial, aquatic or suction feeding), the character states of several internal branches on the phylogenies of adult frogs and salamanders were equivocal. For salamanders, we generated every possible fully unequivocal tree that required five or fewer additional manually fixed branches (i.e., additional assumptions) by using the paintbrush tool in MacClade to fix the character state of various combinations of equivocal branches. We followed the same procedure for frogs but only generated the trees that required three or fewer additional manually fixed branches. This process allowed us to explore the robustness of our conclusions by determining the consequences of assuming both different ancestral states for the salamander and frog trees and different states for the resulting equivocal branches within each tree.

We performed two different analyses in order to test the constraint hypothesis. In both analyses, the null hypothesis was that there is no association between having a suction feeding larval life

history stage and the appearance of suction feeding in secondarily aquatic adults. Therefore, we would commit a Type I error if we were to accept the constraint hypothesis when it was really false or a Type II error if we were to reject the constraint hypothesis when it was really true.

In the first analysis, we modified the approach of Ridley (1983, 1986) to determine if there was an association between the presence or absence of a suction feeding larval stage and the appearance of suction feeding in secondarily aquatic adults. For each combination of our larval scenario and the various adult scenarios, we used parsimony to infer where during amphibian phylogenesis adults had shifted from terrestrial to aquatic feeding and the most likely condition of larval feeding behavior at that transition. For each independent adult transition from terrestrial to aquatic feeding behavior, suction feeding in larvae was scored as present or absent. If suction feeding appeared in any of the adults of any taxon beyond the transition, the transition was scored as suction feeding present in adults (see results). Each transition to aquatic feeding in adults was treated as an independent evolutionary event and a single data point, because including each taxon with aquatic feeding in adults clearly would have violated the assumption of independence of data points in the statistical analysis (see Ridley, 1983). There were four possible ways each transition could be scored: A) suction feeding present in both larvae and adults; B) suction feeding present in larvae but not in adults; C) suction feeding not present in larvae but present in adults; or D) suction feeding present in neither larvae nor adults. We then calculated the ratio of the number of transitions in which larval and adult behavior were consistent with one another (A+D) to the total number of transitions (A+B+C+D) and determined the probability that this "transition ratio" belongs to a binomial distribution with a mean of 0.5 (0.5 is the expected ratio, i.e., half of the transitions will be of type A or D). Our hypothesis does not require that suction feeding replaces terrestrial feeding behavior patterns, so taxa that display suction feeding and perform other behavior patterns (as in the newt *Pleurodeles*) were simply coded as using suction feeding. In only one case, pipid frogs, did larval feeding behavior appear to have changed character states after an adult transition to aquatic foraging behavior. In this case, we scored the transition in the most conservative manner possible (suction feeding not present in larvae but present in adults).

In the second analysis, we used the approach of Maddison (1990) and performed a concentrated changes correlation test using MacClade version 3.06 on a Macintosh G4 computer. The concentrated changes test determines the probability that the number of transitions observed in a character would fall in the clades of interest by chance alone when randomly placed on a preexisting phylogenetic scenario (Maddison, 1990). The outcome of this test was biased by the fact that we condensed some large clades to single taxa (Sillén-Tullberg, 1993). However, this bias was against the constraint hypothesis, only making the test more conservative. Anywhere from 9 to 16 transitions to adult suction feeding were inferred depending on which ancestral state was assumed for adult frogs and salamanders and how the equivocal branches of their respective adult trees were fixed. Our single preferred scenario for the evolution of larval feeding behavior included several soft polytomies including the unresolved relationships between frogs, salamanders and caecilians. A concentrated changes test can only be used on a fully resolved tree. Therefore, in MacClade 3.06, we generated 10 randomly resolved trees and used parsimony and the assumption that larvae have been retained from a common ancestor in salamanders and caecilians to infer the character states (suction feeding larvae present or absent) of the internal branches of these trees. For each tree, we then determined the probability that from 3 to 16 transitions to adult suction feeding randomly occurred in clades with suction feeding larvae, using 10,000 replicates in each simulation (Maddison and Maddison, 1992).

Results

Observations of feeding behavior

The lungfish *Protopterus* used suction feeding to capture prey. The majority of the lateral gape was occluded by labial lobes, large overlapping flaps originating on both the upper and lower jaws. Prey items were moved quickly into the mouth with little or no forward body movement. *Protopterus* displayed some variation in behavior in response to prey type; their movements when capturing earthworms appeared sluggish relative to their movements when capturing active prey such as goldfish. More detailed descriptions and cinematic sequences of feeding in lungfish can be found in Bemis and Lauder (1986, *Lepidosiren*) and Bemis (1987, *Protopterus*).

The salamanders *Siren*, *Pleurodeles*, and *Pachytriton* also used suction to capture prey, but displayed no obvious variation in behavior with prey type. All of three of these salamanders approached food very closely and often touched it with their snouts. Rapid hyobranchial depression was used to accelerate prey into the oral cavity. As the hyobranchial apparatus struck the substrate, the head and trunk were often jolted upward. Like *Protopterus*, all three salamanders have labial lobes that restrict the flow of incoming water to the

most anterior portion of the gape during feeding (Figs. 1 and 2). Unlike *Protopterus*, their movements were very rapid even with slow-moving prey such as earthworm pieces. In *Siren* and larval *Pleurodeles*, most of the water taken into the oral cavity during prey capture was expelled rapidly through the gill slits, but metamorphosed *Pleurodeles* and *Pachytriton* lack gill slits and expelled water slowly through their mouths. *Salamandrella* used jaw prehension to capture earthworms in water and did not exhibit hyobranchial depression or any ability to accelerate prey towards the jaws.

The larval caecilians observed in this study fed in much the same way as aquatic salamanders. The larvae of *Epicrionops* approached prey closely before rapidly sucking it into their mouths. Like salamanders, feeding movements were relatively rapid with both evasive and slow-moving prey. Like both *Protopterus* and the salamanders we observed, *Epicrionops* larvae possess labial lobes that occlude the lateral gape during feeding.

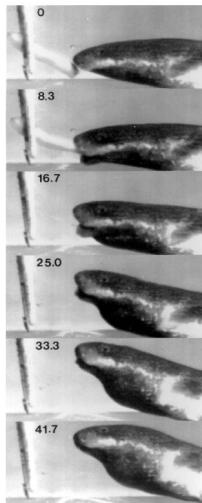


Figure 1. Sequential frames of suction feeding in *Siren intermedia*, an aquatic, paedomorphic salamander. Note the lack of forward movement of the body, the acceleration of the prey into the oral cavity, and the occluded lateral gape.

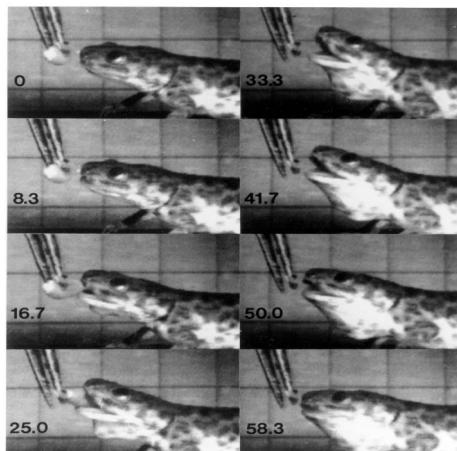


Figure 2. Sequential frames of suction feeding in *Pleurodeles waltl*, an aquatic, metamorphosed salamander. Note the lack of forward movement of the body, the acceleration of the prey into the oral cavity, and the occluded lateral gape.

Despite the presence of a single external gill slit, or spiracle, the movement of debris in the water indicated that most of the water taken into the mouth during feeding was expelled through the mouth.

Metamorphosed caecilians all used jaw prehension to capture prey, whether feeding on land or in water. They pinned their prey against the substrate while slowly lunging forward. Prey were then subdued and swallowed in a struggle that, in the case of earthworms, lasted up to several minutes. The amphibious *Hypogeophis* used jaw prehension both on land and in water. Aquatic adult *Typhlonectes* captured prey in essentially the same manner as terrestrial species, with the addition of substantial hyobranchial depression during mouth closing. However, among more than 100 feeding sequences, *Typhlonectes* was never observed to perform suction feeding. *Typhlonectes* and *Hypogeophis*, like terrestrial caecilians, have an unoccluded lateral gape, a morphological feature that is rarely present in suction feeders.

The frogs displayed the greatest diversity of prey capture behavior. When feeding on land, *Bombina* and *Chacophrys* used tongue prehension to capture waxworms. They lunged and opened their mouths while bending their lower jaws to expose fleshy tongues to their prey. After contact, waxworms were pulled between their closing jaws by their tongues. When feeding in shallow water, *Bombina* used jaw prehension to capture earthworms. If the worm came into contact with a forelimb, it was scooped into the mouth using one or both front feet. *Caudiverbera* and *Lepidobatrachus* sat in shallow water with their forelimbs outstretched. When goldfish swam over their forelimbs, they simultaneously pulled their forelimbs upwards and lunged forward with their mouths open. The fish were then scooped into their jaws (Fig. 3).

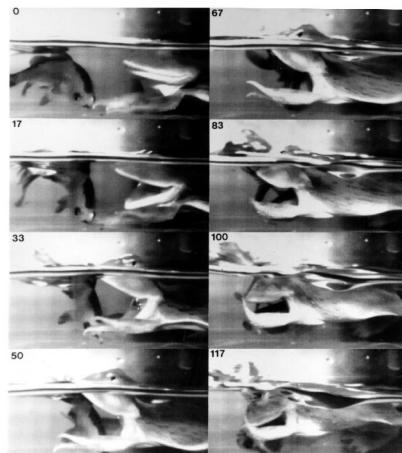


Figure 3. Sequential frames of ram feeding aided by forearm scooping in *Lepidobatrachus llanensis*, an aquatic frog. Note the lunge forward and lack of occlusion of the lateral part of the gape (in contrast to Figures 1 and 2) and the use of the forearms to scoop the fish into the mouth.

Although both of these species protruded their tongues during terrestrial feeding, tongue protrusion was not always observed during aquatic feeding in *Caudiverbera*, and tongue protrusion was never observed during aquatic feeding in *Bombina* or *Lepidobatrachus*. When feeding in shallow water, *Rana* flipped its tongue at submerged earthworms but retracted the tongue after it hit the surface of the

water and captured the worms using jaw prehension and forearm scooping. About half of the feeding attempts of *Rana* did not include forearm scooping.

The three pipids included in the study displayed very different feeding behavior patterns. *Pipa* always used its forearms to scoop prey into its mouth while *Xenopus* used its forelimbs when capturing relatively large prey. Lateral and ventral views of *Xenopus* feeding on small pieces of earthworm showed that prey were overcome by rapid forward movement rather than acceleration of prey toward the frog. Although suction appears to play little or no role in the initial effort of *Xenopus* to get prey between their jaws, the distal ends of longer pieces of worm are accelerated toward the mouth after the proximal ends enter the buccal cavity, indicating that suction is involved in prey transport following initial capture. Compensatory suction (*sensu* Van Damme and Aerts, 1997) may also play an important role when *Xenopus* lunges towards prey. In contrast, *Hymenochirus*

was never observed to use its forelimbs to acquire prey. They always used suction to accelerate prey items into their mouths (Fig. 4). Even in sequences in which they lunge a great distance toward prey, *Hymenochirus* always stop short of overtaking it. All of the frogs have unoccluded lateral gapes, with the exception of *Hymenochirus*, which has flaps of tissue inside the oral cavity that can be seen during mouth opening. Combined with jaw bending, these oral flaps substantially occlude the lateral gape during feeding, acting analogously to the labial lobes of salamanders.

In summary, lungfish, larval caecilians, larval and adult salamanders, and adult *Hymenochirus* are capable of capturing food from beyond the tips of their jaws and can be classified as suction feeders. In contrast, adult caecilians and adult frogs with the exception of *Hymenochirus* were never observed to utilize suction feeding, and appear to lack the ability to draw in prey from beyond their jaw tips. Those taxa that use suction possess structures that occlude much of the lateral part of the gape when the mouth is open, while those taxa that do not use suction tend to have open lateral gapes.

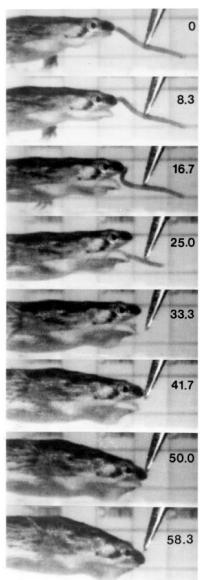


Figure 4. Sequential frames of suction feeding in *Hymenochirus*, an aquatic frog. Note the lunge falling short of the prey, the jaw bending, the acceleration of the prey into the oral cavity, and the lack of forearm scooping (in contrast to Figure 3).

Character mapping

Among living amphibians, the current distribution of life histories that include a free-living larval stage could be interpreted as evidence that a larval stage is primitive for each of the three major groups. It is possible that a larval stage may have re-evolved twice among amphibians; once in *Desmognathus* and once in the clade of caecilians native to the Seychelles (*Praslinia*, *Grandisonia* and *Hypogeophis*). Convergent evolution of the larval stage seem unlikely, however, because it would require the convergent evolution of a suite of complex morphological characteristics (e.g., the structure of the hyobranchial apparatus and the lateral line system). Unless new evidence comes to light that would lend support to the idea of the convergent evolution of larvae during amphibian phylogenesis, we favor the "single homologous larvae" scenario. This scenario was used in all of our comparative analyses.

If we accept the assumption that larvae, when present, were retained from a common ancestor in salamanders and caecilians, character mapping using MacClade 3.06 supports a single scenario regarding the evolution of larval suction feeding within the taxa sampled in this study. Among caecilians, larval suction feeding was lost at least twice (Fig. 5).

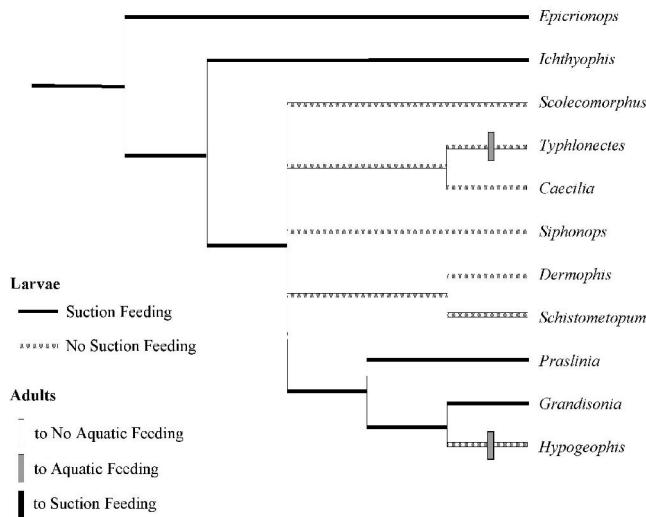


Figure 5. The evolution of larval and adult feeding behavior in caecilians. It is assumed that all caecilian larvae are homologous to one another. In order to perform the concentrated changes test, the soft polytomy was resolved randomly using MacClade 3.06. It is assumed that direct development evolved before aquatic foraging in *Hypogeophis* (see text). Phylogeny modified from Hedges et al. (1993) and Wilkinson and Nussbaum (1999). For coding of feeding behavior in terminal taxa see Appendix 2.

Among larval salamanders, suction feeding was lost four times (Figs. 6-8). Among the Anura, suction feeding in larvae was lost in a common ancestor and has re-evolved twice, in *Hymenochirus* and *Lepidobatrachus* (Figs. 9-11). This single scenario for the sequence of changes in larval feeding behavior is the same regardless of how the polytomies of these trees are resolved or which arrangement of basal anuran clades is preferred among those proposed by Ford and Cannatella (1993), Hay et al. (1995), and Maglia et al. (2001).

The phylogenetic analysis of adult caecilian feeding behavior produces a single scenario in which aquatic feeding evolved at least twice in adults (Fig. 5). Because the relationships among the majority of "higher" caecilian clades (*sensu* Wilkinson and Nussbaum, 1996) have yet to be resolved, larval suction feeding may have been lost more than twice. However, unless future analyses radically rearrange the currently accepted phylogenetic hypotheses, the independent emergence of aquatic foraging in *Hypogeophis* and *Typhlonectes* is unambiguous.

The analysis of adult salamander character states resulted in several equivocal internal branches. Depending on how the character states at these branches are fixed (i.e., the additional assumptions added to the analysis), several different scenarios emerge. Three possible scenarios, including those resulting from the most extreme application of assumptions that favor or counter our hypothesis of constraint, are presented in Figures 6, 7 and 8.

In scenario A (Fig. 6), the adult phase of the common ancestor was terrestrial, with aquatic feeding in the adult phase evolving 13 times independently in *Siren*, *Cryptobranchoidea*, *Amphiuma*, *Desmognathus*, *Hemidactylini* (excluding *Hemidactylum*), *Rhyacotriton*, *Necturus*, *Pleurodeles*, other Salamandridae, *Dicamptodon copei*, *Ambystoma tigrinum*, *A. talpoideum*, and *A. gracile*. Suction feeding evolved subsequent to 11 of these transitions to aquatic feeding and evolved 15 times independently all together.

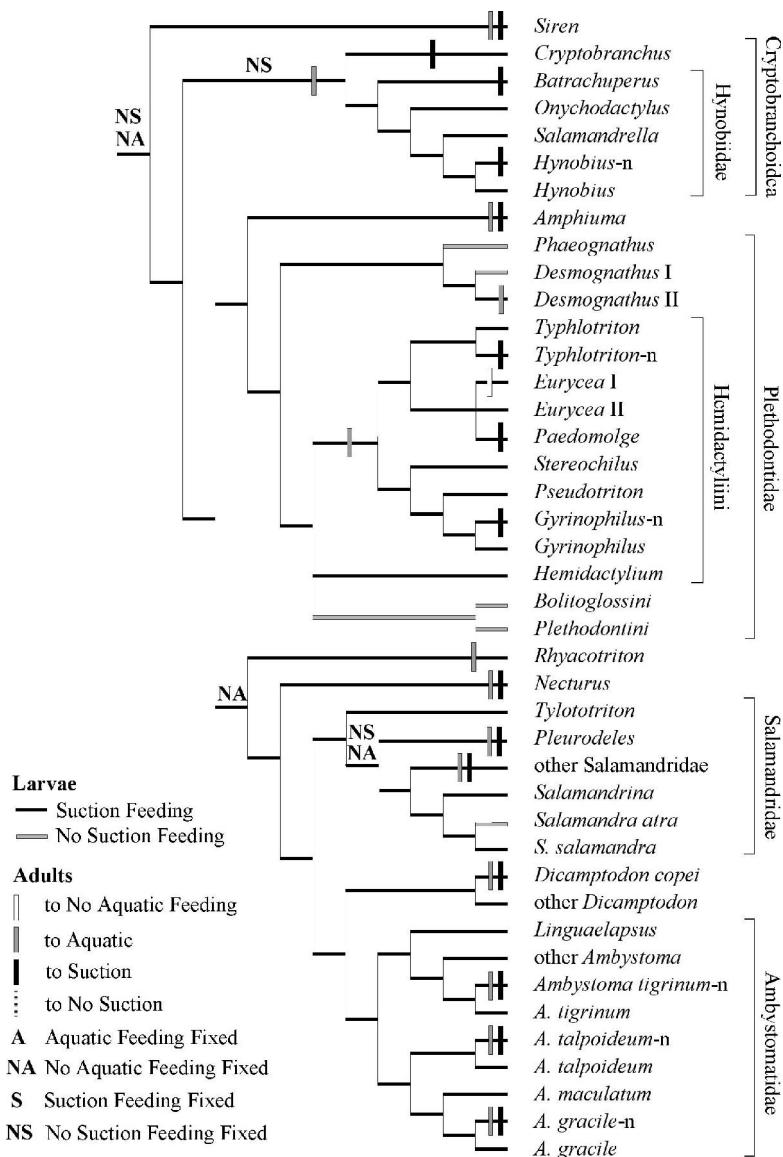


Figure 6. In this scenario (A) for the evolution of larval and adult feeding behavior in salamanders, it is assumed: 1) that all salamander larvae are homologous, and 2) that salamanders ancestrally were terrestrial and were not capable of suction feeding. Thus, aquatic feeding evolved 13 times independently. Suction feeding evolved subsequent to 11 of these 13 transitions to aquatic feeding, and 15 times altogether. Note that many terrestrial clades are collapsed to single taxa, while aquatic taxa are shown in greater detail. Phylogeny modified from Wake (1966), Wake and Özeti (1969), Lombard and Wake (1986), Shaffer et al. (1991), Larson and Dimmick (1993), Sever (1994), Titus and Larson (1996), Chippindale et al. (2000) and Hillis et al. (2001). For coding of feeding behavior in terminal taxa, see Appendix 2.

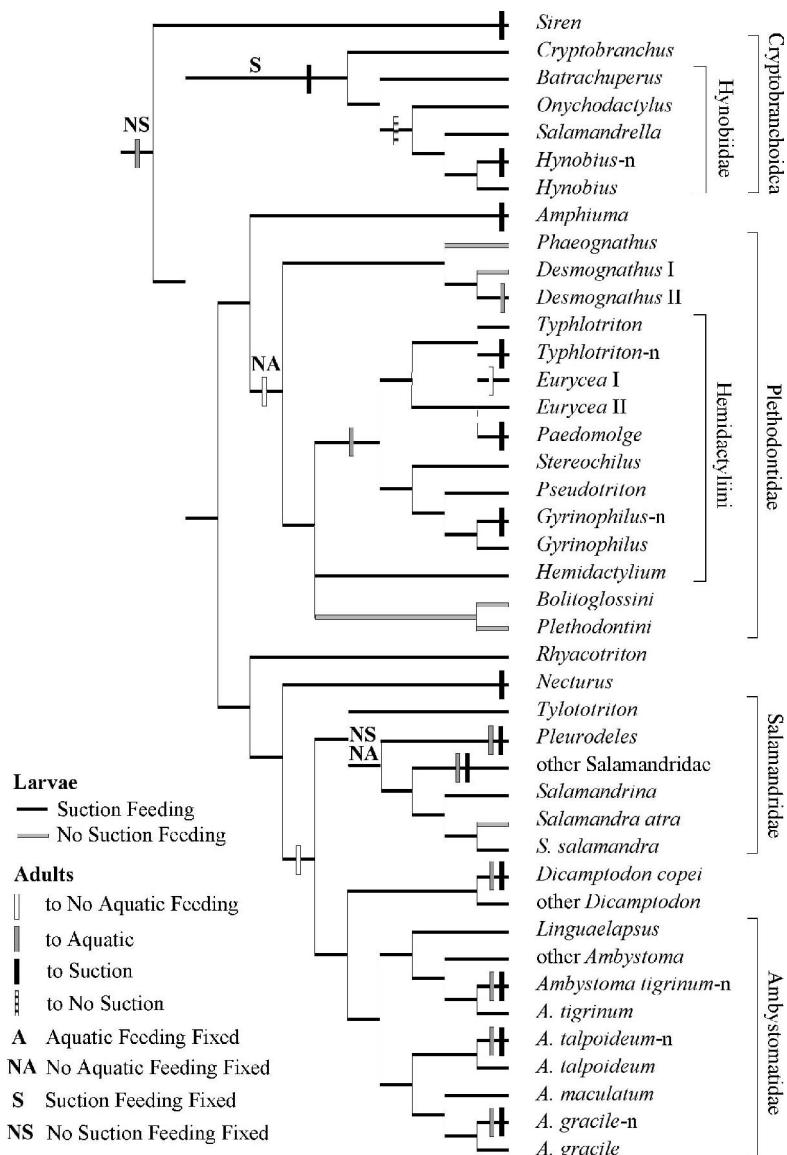


Figure 7. In this scenario (B) for the evolution of larval and adult feeding behavior in salamanders, it is assumed that the common ancestor of salamanders fed in water but did not utilize suction feeding. Aquatic feeding evolved only 9 times independently. Suction feeding evolved subsequent to 8 of these transitions, and 15 times altogether. Phylogeny as in Figure 6.

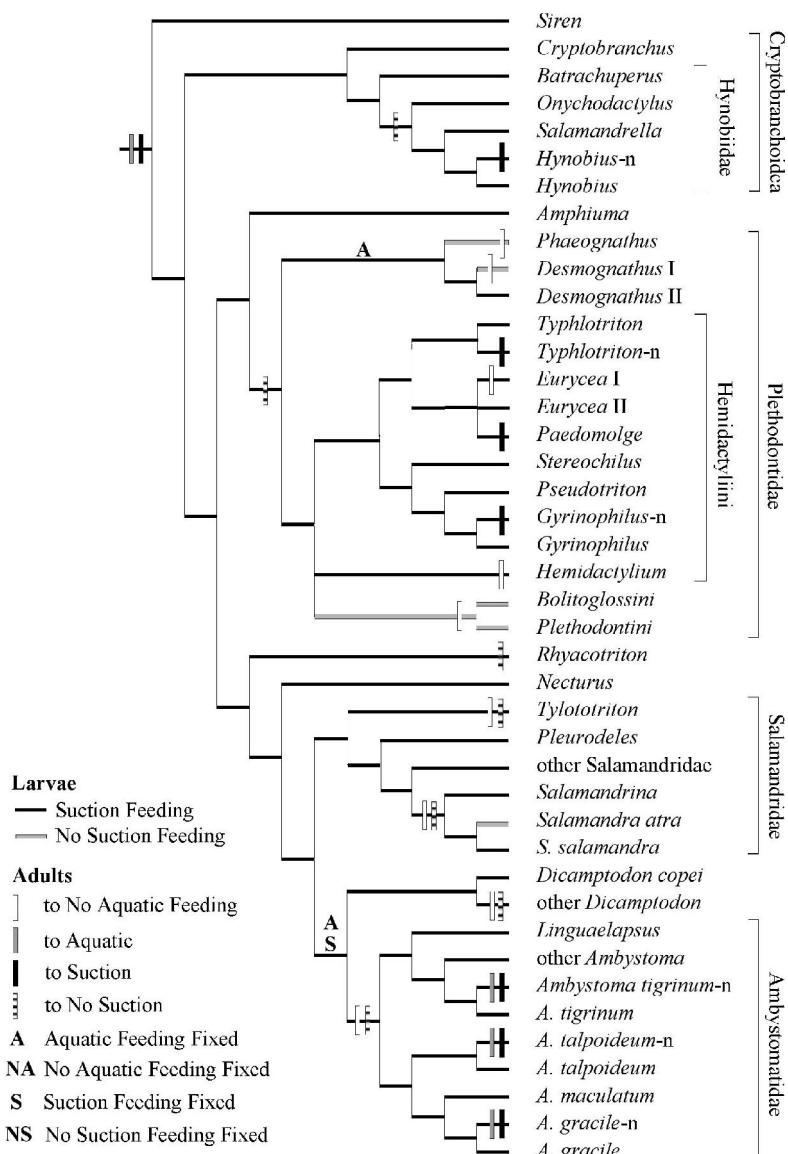


Figure 8. In this scenario (C) for the evolution of larval and adult feeding behavior in salamanders, it is assumed that the common ancestor of salamanders foraged in water and utilized aquatic suction feeding. Thus, in most salamanders, adult aquatic feeding was inherited from a common ancestor. Aquatic feeding evolved only four times independently in adults. Suction feeding evolved subsequent to all four transitions to aquatic feeding, and 8 times altogether. Phylogeny as in Figure 6.

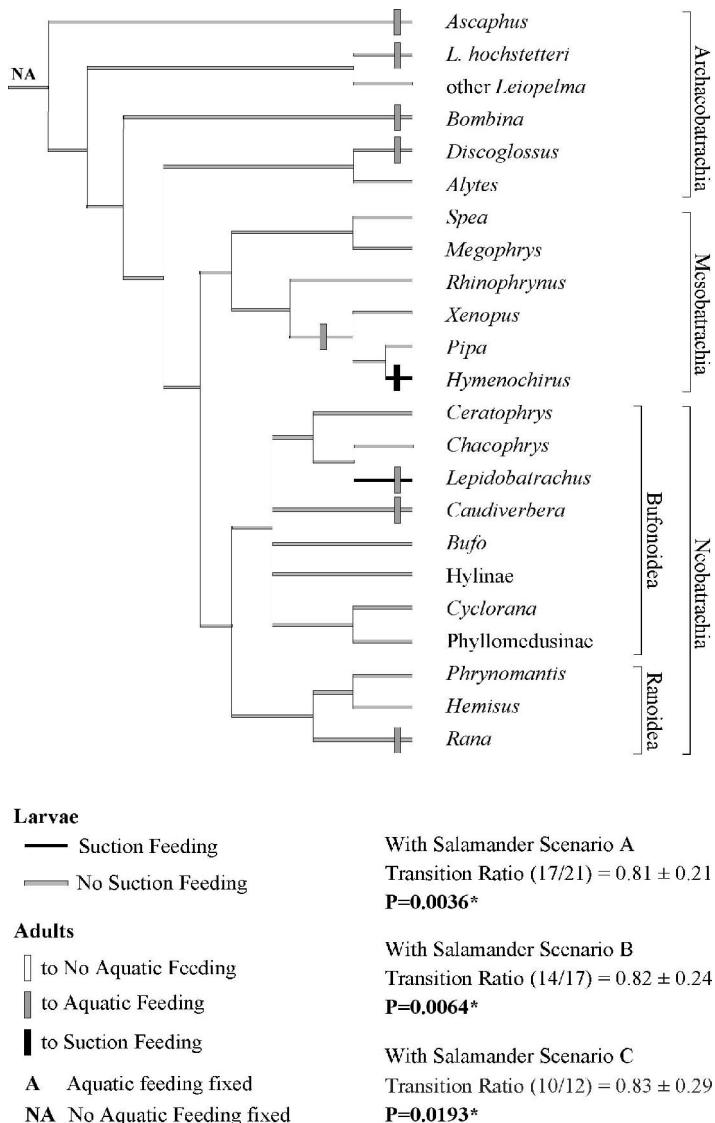
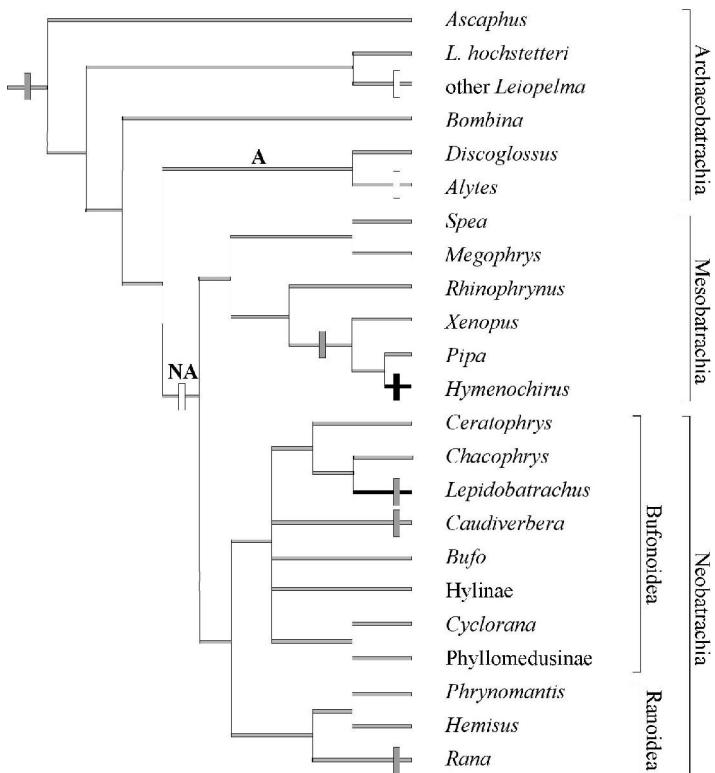


Figure 9. In this scenario (A) for the evolution of larval and adult feeding behavior in frogs, it is assumed that the adult stage of a common ancestor of living frogs did not forage in water. In this case, aquatic feeding evolved 8 times independently among adult frogs. Only one of these transitions (in *Hymenochirus*) was associated with the subsequent evolution of suction feeding. Phylogeny modified from Ford and Cannatella (1993), Ruvinsky and Maxson (1996) and Emerson et al. (2000). For statistical analysis, this scenario was combined with the scenario in Figure 5 and with each of the three scenarios proposed in Figures 6 - 8. The transition ratios used in each test are shown \pm 95% confidence intervals. Analyses with similar results were also performed using hypotheses of the arrangement of basal frogs proposed by Hay et al. (1983) and Maglia et al. (2001). For coding of feeding behavior in terminal taxa, see Appendix 2.

**Larvae**

- Suction Feeding
- No Suction Feeding

With Salamander Scenario A
Transition Ratio (16/20) = 0.80 ± 0.22
P=0.0059*

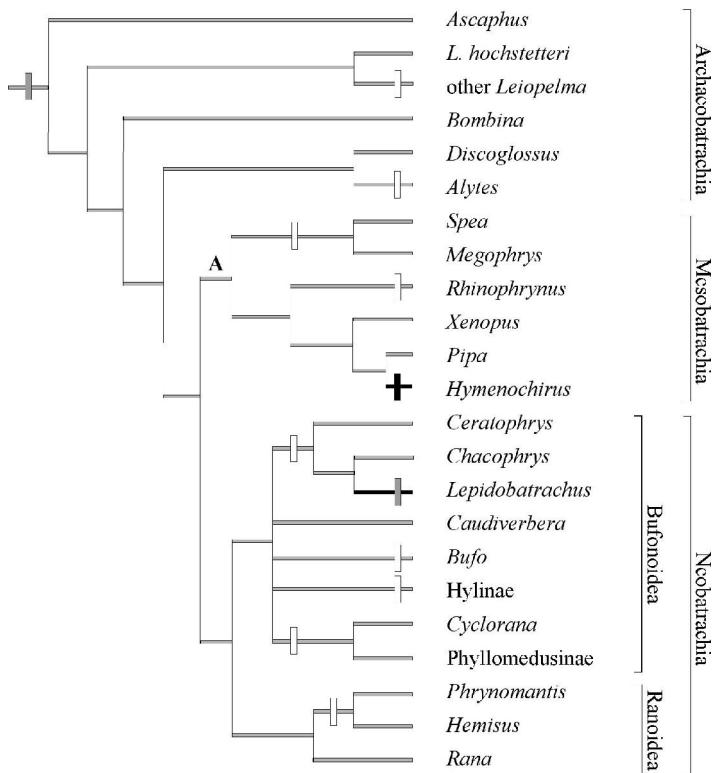
Adults

- || to No Aquatic Feeding
- || to Aquatic Feeding
- to Suction Feeding
- A Aquatic feeding fixed
- NA No Aquatic Feeding fixed

With Salamander Scenario B
Transition Ratio (13/16) = 0.81 ± 0.25
P=0.0106*

With Salamander Scenario C
Transition Ratio (9/11) = 0.82 ± 0.29
P=0.0327*

Figure 10. In this scenario (B) for the evolution of larval and adult feeding behavior in frogs, it is assumed that the common ancestor of Anura foraged in water but did not suction feed and that the common ancestor of Mesobatrachia did not forage in water. Under these assumptions, aquatic foraging evolved five times independently among adult frogs, but suction feeding evolved subsequently only once (in Hymenochirus). Phylogeny and statistical analysis as in Figure 9.

**Larvae**

— Suction Feeding
— No Suction Feeding

With Salamander Scenario A
Transition Ratio (13/17) = 0.76 ± 0.24
P=0.0245*

Adults

|| to No Aquatic Feeding
|| to Aquatic Feeding
| to Suction Feeding

With Salamander Scenario B
Transition Ratio (10/13) = 0.77 ± 0.27
P=0.0461*

A Aquatic feeding fixed
NA No Aquatic Feeding fixed

With Salamander Scenario C
Transition Ratio (6/8) = 0.75 ± 0.26
P=0.1445 NS

Figure 11. In this scenario (C) for the evolution of larval and adult feeding behavior in frogs, it is assumed that both the common ancestor of Anura and the common ancestor of Mesobatrachia foraged in water. In this case, aquatic feeding evolved only twice independently. Phylogeny and statistical analysis as in Figure 9.

This scenario requires six assumptions in addition to the tree topology: 1) the common ancestor of all salamanders was terrestrial; 2) the common ancestor of all salamanders was not capable of suction feeding; 3) the common ancestor of Cryptobranchoidea was not capable of suction feeding; 4) the common ancestor of *Rhyacotriton* and its unnamed sister taxon was terrestrial; 5) the ancestor of salamandrids excluding *Tylototriton* was terrestrial; and 6) the ancestor of salamandrids excluding *Tylototriton* was not capable of aquatic suction feeding.

In scenario B (Fig. 7), the adults of the common ancestor foraged in water, but were not suction feeders. Aquatic feeding in adults evolved nine times independently in Caudata, *Desmognathus*, Hemidactyliini (excluding *Hemidactylum*), *Pleurodeles*, other Salamandridae, *Dicamptodon copei*, *Ambystoma tigrinum*, *A. talpoideum*, and *A. gracile*. Suction feeding evolved subsequently to eight of these transitions and evolved 15 times in total. This scenario requires five assumptions in addition to the tree topology: 1) the adult phase of the ancestor of all salamanders was not capable of suction feeding; 2) the adult ancestor of Cryptobranchoidea was an aquatic suction feeder; 3) the ancestor of salamandrids excluding *Tylototriton* was not capable of aquatic suction feeding; 4) the ancestor of salamandrids excluding *Tylototriton* was terrestrial; and 5) the adult ancestor of Plethodontidae was terrestrial.

In scenario C (Fig. 8), the adults of the common ancestor were aquatic and capable of suction feeding. Aquatic feeding in adults evolved four times independently in Caudata, *Ambystoma tigrinum*, *A. talpoideum*, and *A. gracile*. Suction feeding evolved subsequently to all four of these transitions and evolved eight times in total. This scenario requires three assumptions in addition to the tree topology: 1) the adult ancestor of *Desmognathus* and *Phaeognathus* was aquatic; 2) the adult common ancestor of *Dicamptodon* and *Ambystoma* was aquatic; and 3) the adult common ancestor of *Dicamptodon* and *Ambystoma* was capable of aquatic suction feeding.

Three radically different arrangements of basal anurans have been proposed in the past ten years (Ford and Cannatella, 1993; Hay et al., 1995; and Maglia et al., 2001). As in salamanders, our analysis of adult character states in the context of all three of these hypotheses resulted in some equivocal internal branches. However, fewer additional assumptions were required to resolve all equivocal branches such that the number of scenarios that could be generated was lower than that seen in salamanders. Despite the very different arrangements of basal clades proposed by Ford and Cannatella (1993), Hay et al. (1995) and Maglia et al. (2001), the different assumptions used to resolve the ancestral character states, and the equivocal internal branches, only three basic scenarios are produced. Figures 9-11 show these three scenarios using only the hypothesis of Ford and Cannatella to arrange the basal branches of the tree.

If we assume that the common ancestor of Anura was terrestrial as an adult (Fig. 9), aquatic feeding evolved independently in *Ascaphus*, *Leiopelma hochstetteri*, *Bombina*, *Discoglossus*, Pipids, *Lepidobatrachus*, *Caudiverbera* and *Rana*, for a total of eight transitions to aquatic feeding. Only one of these transitions to aquatic feeding in adults was associated with the subsequent evolution of suction feeding (in *Hymenochirus*). In addition to the topology of the tree, this scenario assumes that the ancestor of Anura was terrestrial as an adult.

If the common ancestor of Anura was aquatic but did not utilize suction feeding and the common ancestor of *Mesobatrachia* and *Neobatrachia* was terrestrial (Fig. 10), aquatic feeding evolved five times (Anura, *Lepidobatrachus*, *Caudiverbera*, *Rana* and Pipidae). Among frogs, only the transition to aquatic feeding in pipids is associated with the subsequent appearance of suction feeding. Scenario B requires two assumptions in addition to the topology of the tree: 1) the adult phase of the common ancestor of *Discoglossus* and *Alytes* foraged in water; and 2) the adult of the common ancestor of *Mesobatrachia* and *Neobatrachia* was terrestrial. If we modify scenario B and assume that the ancestor of *Mesobatrachia* was aquatic (Fig. 11), then aquatic feeding evolved only twice among the sampled taxa (Anura, and *Lepidobatrachus*), with only *Hymenochirus* evolving suction feeding subsequent to the

ancestral anuran becoming aquatic. The scenario in Figure 11 assumes that the common ancestor of Mesobatrachia foraged in water.

For all of these scenarios, the coding of transitions for the binomial test was unambiguous for all taxa except *Hypogeophis*, *Lepidobatrachus* and pipid frogs. In the scenario in Figure 5, it is unclear whether *Hypogeophis* became an aquatic forager as an adult before or after it lost a suction feeding larval stage. The genus *Grandisonia* is paraphyletic with respect to *Hypogeophis* (Hedges et al. 1993; Hass et al. 1993) and contains some species with direct development (Taylor, 1968). We assume that *Hypogeophis* descended from a *Grandisonia* that had direct development, and we code *Hypogeophis* as having evolved aquatic foraging in the adult stage in the absence of a free-living suction feeding larva. In the case of *Lepidobatrachus*, it does not matter if suction feeding evolved before or after the emergence of aquatic foraging in adults. In either case, we would score the transition to aquatic feeding in adults conservatively relative to the constraint hypothesis (i.e., suction feeding larvae present, suction feeding adult absent). *Hymenochirus* represents the only clade in which transitions to both larval and adult suction feeding were concurrent. This introduces the issue of which stage, the larva or the adult, evolved suction feeding first. If suction feeding evolved in the larva first, then *Hymenochirus* could be given its own transition separate from other pipids which could be coded as a suction feeding adult evolving in a clade with a suction feeding larva. However, Sokol (1977) suggests that suction feeding evolved in the adult stage and is "precociously" present in the larvae. We chose the most conservative path with respect to our constraint hypothesis, giving pipids a single transition to aquatic feeding and coding this transition as suction feeding subsequently evolving in the adult stage without a suction feeding larval life stage being present.

Statistical Analyses

Depending on our assumptions (with respect to ancestral character states and the resolution of equivocal branches), our analysis indicates that suction feeding in adults has evolved anywhere from 9 to 16 times in association with suction-feeding larvae. Suction feeding in adults has failed to emerge beyond transitions to aquatic foraging in two groups with larvae that suction feed (*Lepidobatrachus* and some plethodontids). Suction feeding also failed to emerge anywhere from three to nine times in clades with larvae that do not use suction, depending on the scenarios in Figures 6-11.

Regardless of the scenario one subscribes to, both statistical tests reject the null hypothesis of no association between suction feeding in the larval and adult life history stages of amphibians. In all of the scenarios, the concentrated changes test finds a significant association between suction feeding in the larval and adult life stages ($p < 0.01$). The effect of our condensing large terrestrial clades into single taxa only made the test more conservative, as it could only have biased the test towards making a Type II error (i.e., rejecting the constraint hypothesis when it is really true). In contrast, the power of the binomial test is sensitive to the number of independent transitions to aquatic feeding in both frogs and salamanders. If it is assumed that the ancestor of salamanders fed in water and used suction feeding to catch prey (Fig. 8) and that most frogs that foraged in water inherited this behavior from a common ancestor (Fig. 11), the binomial test rejects the hypothesis of constraint (Fig. 11). However, the small number of transitions in these scenarios renders this statistical approach suspect because the smaller sample size is associated with a higher probability of a Type II error.

Discussion

To explore the processes that have led to the current distribution of aquatic feeding behavior and morphology in amphibians, we first infer the ancestral condition of feeding behavior and morphology and identify transitions that have taken place during amphibian phylogenesis. The evolution of larval and adult feeding behavior and morphology will be discussed separately, because they appear to have evolved at least somewhat independently (Elinson, 1990).

The evolution of larval feeding systems

Caecilians

The phylogenetic distribution of life history traits suggests that the most recent common ancestor of caecilians had a larval stage that used suction feeding (Fig. 5). Larvae of the basal caecilian *Epicrionops* are capable of suction feeding and the head morphology of other caecilian larvae (e.g., *Ichthyophis*) indicates that they are also likely to be suction feeders (O'Reilly, 1995, 2000).

Larval suction feeding behavior has been modified or lost several times during caecilian evolution. The life history of viviparous species (e.g., *Dermophis* and *Typhlonectes*) includes a fetus that feeds in the oviduct for many months (Parker, 1936, 1956; M. Wake, 1977, 1982, 1993). Fetal caecilians have a specialized dentition that may be used to scrape epithelial secretions from the walls of the oviduct (Parker and Dunn, 1964; M. Wake, 1977, 1978; Wilkinson, 1991). The mechanism of ingestion has not been observed in fetal caecilians, but their unique oral morphology suggests that the evolution of viviparity in caecilians is associated with the evolution of novel fetal feeding behavior, and hence with the loss of larval suction feeding behavior. The evolution of direct development, as in *Hypogeophis*, is also likely to be associated with the loss of suction feeding behavior and of associated morphological characteristics.

Salamanders

The phylogenetic analysis of larval feeding behavior patterns among living salamanders suggests that, like caecilians, the most recent common ancestor of Caudata had a suction feeding larval stage (Figs. 6-8). Suction feeding is found among all larval salamanders for which there are data, including the basal *Cryptobranchus* (Reilly and Lauder, 1988, 1992; Deban and Marks, 2002; Deban and O'Reilly, 1997). The morphology of larvae representing the Sirenidae and Hynobiidae, which are two of the most basal clades of salamanders (Larson and Dummick, 1993), indicates that they use suction as well. This phylogenetic distribution of suction feeding indicates that suction feeding is the ancestral character state for larval urodeles.

Larval feeding behavior has been lost several times during salamander evolution (Figs. 6-8). The fetuses of viviparous salamandrids perform suction feeding if they are born before metamorphosis (Reilly, 1995), and feed on unfertilized eggs and smaller fetuses while living in the oviduct, but again, the feeding behavior is undescribed (Alcobendas et al., 1996). The larvae of the viviparous *Salamandra atra* feed on both ova and oviductal secretions during their lengthy gestation (M. Wake, 1982, 1993), but the mechanism of ingestion is not known. In direct-developing plethodontids, as in direct-developing caecilians, larval suction feeding behavior and morphology have been lost.

Frogs

The phylogenetic analysis indicates that suspension feeding (*sensu* Lauder, 1985) was the ancestral method of prey capture for larval anurans (Figs. 9-11). Suspension feeding in larval anurans involves the use of a relatively slow buccal-pumping mechanism to filter numerous small food particles simultaneously from a generally targeted part of the water column or substrate. In contrast,

the taxa coded here as suction feeders use single, explosive buccal expansion to capture relatively large prey that are targeted individually. The term "suction feeding" has been used in the context of suspension feeding in many vertebrates, including tadpoles (Sanderson and Wassersug, 1990, 1993; Sanderson and Kupferberg, 1999). However, we do not think it is appropriate to categorize tadpoles as suction feeders because the relatively slow, rhythmic movements used for filter feeding are most likely homologous to the gill irrigation movements other aquatic vertebrates. Gill irrigation movements and suction feeding were apparently distinct behaviors in a common ancestor of living gnathostomes (see Brainerd, 1994 and citations therein). Suspension feeding is found in many basal anurans (Wassersug and Hoff, 1979; Altig and Johnston, 1989; Sanderson and Wassersug, 1993) and thus appears to be the primitive mode of feeding for all anuran larvae.

In many anuran clades, larvae have evolved alternatives to suspension feeding including what may be suction feeding in some groups. Macrophagy (i.e., targeting single large food items for capture) is a prerequisite for suction feeding and is a relatively uncommon mode of feeding in tadpoles, having been reported only in hymenochirine pipids, *Lepidobatrachus*, and a few members of the families Ranidae, Hylidae and Hyperoliidae (Sokol, 1977; Wassersug and Hoff, 1979; Cannatella and Trueb, 1988a; Ruibal and Thomas, 1988; Altig and Johnston, 1989). Unaided observations of the feeding behavior of larval *Hymenochirus* and *Lepidobatrachus* indicate that they use suction when capturing prey (Sokol, 1977; Ruibal and Thomas, 1988). However, the feeding behavior of these and other macrophagous larvae needs further study with high-speed video or cinematography before we can be certain how to categorize their feeding behavior. If any of these tadpoles use suction feeding, then this mode of prey capture may have evolved through precocious development of adult feeding behavior and morphology (Sokol, 1977; Ruibal and Thomas, 1988). Life histories including a non-feeding larval stage, direct development, or viviparity have evolved numerous times (Altig and Johnston, 1989) and are likely to be associated with the complete loss of larval feeding behavior and morphology.

Lissamphibia

Although the relationship among frogs, salamanders and caecilians is still a matter of some debate (e.g., Hedges and Maxson, 1993; Zardoya and Meyer, 2001), the distribution of suction feeding among vertebrates suggests that it is the ancestral method of prey capture for larval amphibians. Although suspension feeding is the ancestral condition for larval anurans, suction feeding is the ancestral state for larval salamanders and larval caecilians. Furthermore, the suction feeding behavior of amphibians appears to be homologous to that of lepidosirenid lungfishes and actinopterygian fishes (Lauder, 1985; Bemis and Lauder, 1986; Wainwright et al., 1989). Thus, regardless of the relationships of the three major clades of living amphibians, it is likely that the most recent common ancestor of Lissamphibia possessed a suction feeding larval stage and that there was a transition from suction feeding to suspension feeding in the larval stage of a common ancestor of anurans.

The evolution of adult feeding systems

Caecilians

With the exception of some typhlonectids and *Hypogeophis*, all known caecilians including members of the most basal clades are terrestrial as adults and capture prey using jaw prehension (Taylor, 1968; Bemis et al., 1983; O'Reilly, 1995, 2000). Thus, terrestrial habits and the use of jaw prehension are most likely ancestral characteristics of adult caecilians (Fig. 5).

Aquatic foraging has evolved independently at least twice, in typhlonectids and in *Hypogeophis* (Fig. 5) and both clades have co-opted the plesiomorphic terrestrial feeding behavior of caecilians for

aquatic feeding. The family Typhlonectidae includes a series of progressively more aquatic genera, derived from terrestrial caeciliids and culminating in the completely aquatic genera *Typhlonectes*, *Potomotyphlus* and *Atretochoana* (Moodie, 1978; Nussbaum, 1986; Wilkinson, 1989; Nussbaum and Wilkinson, 1989; Wilkinson and Nussbaum, 1997, 1999). *Typhlonectes* move more rapidly than terrestrial species during feeding and have incorporated substantial buccopharyngeal expansion into their feeding behavior. However, their feeding behavior is otherwise similar to that of terrestrial adult caecilians (O'Reilly, 1995, 2000). Combined with their phylogenetic position, this suggests that *Typhlonectes* uses the ancestral terrestrial feeding behavior pattern in water with only minor adjustments. *Hypogeophis* is the only amphibious member of the clade of caecilians endemic to the Seychelles Archipelago which also includes *Praslinia* and *Grandisonia* (Nussbaum and Ducey, 1988; Hass et al., 1993; Hedges et al., 1993). *Hypogeophis* has been observed foraging in streams at night (Nussbaum, 1992) and, like typhlonectids, adult *Hypogeophis* also possess cutaneous electroreceptors (Fritsch and Wake, 1986). These facts suggest that *Hypogeophis* regularly forages in water and, like *Typhlonectes*, has co-opted the ancestral terrestrial feeding behavior of caecilians for use in water.

Salamanders

Three general scenarios for the evolution of aquatic feeding in adult salamanders are presented in Figures 6-8. In scenario A, an ancestor of living salamanders did not feed in water and did not suction feed. In scenario B, a common ancestor of salamanders did forage in water, but was not capable of suction feeding. In scenario C, a common ancestor of salamanders foraged in water and was capable of suction feeding, these characteristics being retained by many extant salamanders. There are at least two ways in which scenario C could be true. The first would be that the ancestor of living salamanders had a single life history stage resembling the larvae of extant species. If this were true, then it follows that a terrestrial feeding life stage would have evolved independently four times (Hynobiidae, Plethodontidae, *Rhyacotriton* and the ancestor of Salamandridae + Dicamptodontidae + Ambystomatidae). A second way would be that the ancestor of all salamanders was newt-like. The life history of the theoretical ancestor would include a larva and a distinct semi-aquatic adult phase that was capable of both suction feeding and terrestrial lingual prehension (like *Pleurodeles*). In this case, suction feeding would have been lost at least six times independently, including three times in groups that were apparently still foraging in water (*Rhyacotriton*, the ancestor of Plethodontidae and the ancestor of Hynobiidae exclusive of *Batrachuperus*).

Given the data currently at hand, we find neither of the above scenarios compelling. The first requires that the biphasic life history (with a distinct larval and adult life stage) seen among salamanders to have evolved multiple times. Yet, the terrestrial adult stages in all salamanders share a suite of characteristics that seem unlikely to be the result of convergence (e.g., metamorphosis always mediated by thyroid endocrine axis and use of the hyobranchial apparatus to protract the tongue during prey capture). The second requires that the aquatic feeding adaptations found in newts were lost three times in aquatic lineages. Although such losses are possible, it is difficult to conceive of a selective regime in which suction feeding behavior would be disadvantageous in an aquatic salamander.

The current distribution of adult salamander feeding behavior suggests that tongue prehension is plesiomorphic. All of the terrestrial salamanders for which there are data use tongue prehension to capture prey (Regal, 1966; Larsen and Guthrie, 1975; Thexton et al., 1977; Reilly and Lauder, 1989, 1991; Larsen and Beneski, 1988; Larsen et al., 1989; Findeis and Bemis, 1990; Miller and Larsen, 1990; Lauder and Reilly, 1994). Thus, it seems likely that the ancestral life history of salamanders included an adult stage that used tongue prehension (Bramble and Wake, 1985).

Regardless of whether or not the ancestor of living salamanders foraged in water, it did not utilize suction feeding.

The feeding behavior of many adult aquatic salamanders appears to be homologous to that of larval salamanders. Several species of salamanders no longer have a completely metamorphosed phase in their life history. By becoming sexually mature while at least partially foregoing metamorphosis, these adults retain the suction feeding behavior and morphology of larvae (Erdman and Cundall, 1984; Shaffer and Lauder, 1985; Reilly and Lauder, 1992). However, salamanders of the family Salamandridae have evolved the ability to perform suction feeding after metamorphosis (Matthes, 1934; Özeti and Wake, 1969; Miller and Larsen, 1989). Some components of the feeding morphology of adult aquatic salamanders, such as the labial lobes that occlude the lateral gape, are similar to but not homologous with their larval morphology (Matthes, 1934). The feeding behavior of metamorphosed *Pleurodeles* and *Pachytriton* may be homologous to larval feeding behavior, despite the introduction of some novel adult morphological features that are similar to larval features. *Ambystoma tigrinum* retains suction feeding behavior across metamorphosis despite the loss of some morphological characteristics associated with effective suction feeding (Lauder and Shaffer, 1988). Some plethodontid salamanders also forage in water after metamorphosis. In contrast to the suction feeding salamanders, metamorphosed plethodontids use tongue prehension or jaw prehension to capture prey in water (Schwenk and Wake, 1988, 1993; Deban and Marks, 2002). Given that tongue prehension is most likely the ancestral terrestrial feeding mode for salamanders, it appears that this terrestrial feeding behavior has been co-opted for aquatic feeding. Jaw prehension is also utilized by some hynobiids (e.g., *Salamandrella*) that forage in water but lack any of the morphological characteristics that are always associated with suction feeding.

Frogs

Three general scenarios for the evolution of aquatic feeding in adult frogs are presented in Figures 9-11. In scenario A, an ancestor of living frogs and the ancestor of *Neobatrachia* did not feed in water and did not suction feed. In scenarios B and C, a common ancestor of frogs did forage in water but was not capable of suction feeding. In scenario B, (1) all archeobatrachian frogs that forage in water inherited this behavior from a common ancestor, and (2) the ancestor of *Neobatrachia* and *Mesobatrachia* did not feed in water and did not suction feed. In scenario C, aquatic foraging (without the ability to suction feed) was retained by all aquatic foraging frogs with the exception of *Hymenochirus* (which evolved suction feeding) and *Lepidobatrachus* (which is secondarily aquatic).

Terrestrial, aquatic and amphibious origins have been proposed for Anura (e.g., Gans and Parsons, 1966) and our current knowledge of the systematics and aquatic feeding behavior of frogs makes any of the three scenarios in Figures 9-11 plausible. Based on the distribution of aquatic feeding behavior alone, it is plausible that aquatic foraging is a shared primitive character among many archeobatrachian and mesobatrachian frogs (Fig. 10). Similarly, among neobatrachians, there are numerous aquatic and semi-aquatic taxa but, with the exception of *Lepidobatrachus*, there are no aquatic or semi-aquatic species clearly nested within terrestrial clades. Recent phylogenetic hypotheses for various neobatrachians tend to place aquatic and semi-aquatic species near the base of the group under study. For example, *Taudactylus* is the most basal myobatrachine myobatrachid (Read et al., 2001), while *Occidozyga* (Emerson et al., 2000; Marmayou et al., 2000) and *Trichobatrachus* (Vences et al., 2000) appear to reside near the base of Ranoidea. Even the most basal dendrobatiid, *Aromobates nocturnus* is aquatic (Myers et al., 1991). Improving the resolution of anuran relationships by itself will not resolve the question of how many times aquatic foraging has evolved among frogs. A more detailed analysis of the distribution of aquatic feeding behavior among anurans will be required to test the hypotheses of single *versus* multiple origins of aquatic foraging.

The terrestrial feeding behavior of basal frogs is well documented and includes lunging, limited tongue protrusion, jaw bending and head flexion (Nishikawa and Cannatella, 1991; Nishikawa and Roth, 1991; Nishikawa et al., 1992). The prevalence of these behavioral characteristics in all of the basal taxa observed thus far implies that they represent the ancestral condition for terrestrial feeding in anurans. It is unclear to what degree the aquatic feeding behavior of *Bombina* is representative of other basal anurans. However, the morphology of other amphibious basal frogs such as *Ascaphus* and *Discoglossus* (Arnold and Burton, 1978; Nussbaum et al., 1983) suggests that they are also not capable of suction feeding; they lack a robust hyobranchial apparatus and a means of occluding the lateral gape that adult *Hymenochirus* and other suction feeders possess.

Forearm scooping was observed in several aquatic frogs and it appears to be an ancestral behavior used for prey transport that has been co-opted for prey capture in some clades (Gray et al., 1997). Six of the seven adult frogs in this study (*Bombina*, *Lepidobatrachus*, *Caudiverbera*, *Rana*, *Pipa* and *Xenopus*) scoop prey into their mouths with their forearms (Fig. 3) and at least some anurans use forearm scooping during terrestrial feeding (Comer and Grobstein, 1981; Gray et al., 1997). These data suggest that forearm scooping to capture prey in water has been retained from a common ancestor.

The three pipids (*Pipa*, *Xenopus* and *Hymenochirus*) that were included in this study displayed different feeding behavior patterns. Contrary to previous reports (Sokol, 1969; Avila and Frye, 1977, 1978), *Xenopus* and *Pipa* do not appear to be suction feeders, at least in the sense of Lauder and Liem (1981). *Xenopus* overtake prey by lunging (i.e., ram feeding) and often use their forelimbs to scoop larger prey into their mouths (Avila and Frye, 1978), while *Pipa* seem to use forearm scooping exclusively to ingest even the smallest prey items. In contrast, *Hymenochirus* have not been observed to use forearm scooping. Instead, they use suction to accelerate prey into their mouths (Sokol, 1969; Fig. 4). The phylogenetic position of *Hymenochirus* (Cannatella, 1985; Cannatella and Trueb, 1988a, 1988b), combined with the hypothesis that suction feeding evolved in adult *Hymenochirus* before appearing in larvae (Sokol, 1977), implies that their feeding behavior has evolved from aquatic feeding behavior similar to that seen in *Pipa* and *Xenopus*. Regardless of the sequence of appearance of suction feeding in *Hymenochirus*, the results of the phylogenetic analysis indicate that suction feeding evolved in an ancestor of *Hymenochirus* after a shift from terrestrial to aquatic foraging in an ancestor of the Pipidae (Fig. 9). The feeding behavior of adult *Hymenochirus* has diverged from other pipids and converged with that of lungfish, aquatic salamanders and larval caecilians (O'Reilly, 1995).

Lissamphibia

The adult stage of the most recent common ancestor of all amphibians was most likely terrestrial or amphibious in its foraging habits but the distribution of feeding behavior in living taxa offers no clues with respect to what type of prey capture behavior was used by this ancestor. The extant terrestrial members of the three major groups display fundamentally different ingestion mechanisms. Caecilians use only jaw prehension to capture prey, whereas frogs use tongue prehension to capture small prey and jaw prehension to capture large prey (Anderson and Nishikawa, 1996; Valdez and Nishikawa, 1997). Although terrestrial frogs and salamanders both use tongue prehension to capture prey, the mechanism of tongue protraction is different. Salamanders use the hyobranchial skeleton, which is incorporated into the tongue, to achieve tongue movement, whereas frogs use only extrinsic tongue muscles (Roth et al., 1990; Lauder and Reilly, 1994). Such fundamental differences in biomechanics suggest that tongue prehension probably evolved independently in Anura and Caudata.

Suction feeding is the most common mode of aquatic prey capture in amphibians, yet our analysis indicates that it has evolved secondarily among extant amphibians twice at most: in adults and

larvae of *Hymenochirus* and in larvae of *Lepidobatrachus*. It is unclear whether suction feeding appeared first in the larval or adult stage in *Hymenochirus*. In either case, it is highly unlikely that *Hymenochirus* has retained suction feeding from the common ancestor of all amphibians, given its phylogenetic position. If further analysis of *Lepidobatrachus* larvae and other macrophagous tadpoles reveals that they do not suction feed, we would conclude that suction feeding has evolved only once among living amphibians, having been retained from fishes in all groups other than *Hymenochirus*.

Conclusions

Overall, the results of these analyses are consistent with the hypothesis that the appearance of derived life history patterns decreases the probability that suction feeding will evolve in secondarily aquatic adult amphibians. The results of the concentrated changes test are consistent with the constraint hypothesis in all of the proposed scenarios. The results of the binomial test also supports the hypothesis in all but the most extreme scenario that we have proposed (6C and 7C combined). So, if the current distribution of aquatic feeding behavior in adult amphibians evolved in the context of numerous secondary invasions of aquatic habitats, then there is an unambiguous phylogenetic association of suction feeding in larvae and adults that offers strong support for the constraint hypothesis.

If, on the other hand, there have been relatively few transitions to aquatic feeding in adult amphibians (scenarios 6C and 7C combined), then the phylogenetic pattern would be unable to provide strong evidence for or against the constraint hypothesis. A small number of transitions would limit the sample size available for any test of association and decrease the statistical power of that test (increasing the probability of a Type II error). In other words, if there are only a few transitions to sample, then the hypothesis cannot be tested statistically and the approach of testing for non-random associations among characters would be inappropriate.

An additional problem with interpreting the results of the binomial test is the strong phylogenetic bias in the distribution of transitions to aquatic foraging with different outcomes. When estimating the confidence of the results of the binomial test, the degree of statistical independence of the transitions to aquatic feeding must be taken into account. By limiting the statistical analysis to only transitions rather than considering each taxon independently, we have greatly dampened potential phylogenetic biases in the analysis (Ridley, 1983, 1986). However, the transitions themselves are not statistically independent events, each varying in its phylogenetic affinities with the others. This would not be of much concern if the four different types of transitions were distributed more evenly across all of the groups examined, but in this study certain types of transitions are heavily biased towards either frogs, salamanders or caecilians. For example, most of the transitions to aquatic suction feeding are among salamanders, while most of the non-suction feeding aquatic adults are either frogs or caecilians. This lack of phylogenetic homogeneity among the transitions weakens the conclusions we can draw from the results of the binomial test by increasing the chance of a Type I error (accepting the constraint hypothesis when we should reject it). In other words, the uneven distribution of transitions with each outcome suggests that salamanders may possess some as yet undetermined characteristics (other than having suction feeding larvae) that incline them toward evolving suction feeding, and that frogs and caecilians in turn lack these characteristics.

It has been argued that, under many circumstances, suction feeding is the optimal method of aquatic prey capture (e.g. Muller and Osse, 1984; Lauder, 1985). The persistence of taxa with suction-feeding larvae but aquatic adults that do not suction feed is not a challenge to the constraint hypothesis per se, but it does imply that, in some cases, suction feeding may not be the optimal mode of prey capture. The constraint hypothesis does not require that all aquatic taxa with suction

feeding larvae evolve suction feeding in the adult stage. However, it clearly implies that most aquatic lineages, if given the opportunity, would gain a selective advantage by acquiring the ability to suction feed. Therefore, it is curious that several species included in this study have suction feeding larvae, yet do not suction feed as adults. Some of these species feed on relatively large prey (e.g., *Gyrinophilus* and *Lepidobatrachus*) and suction may be of little use in capturing massive prey in water. Several plethodontid salamanders feed on moderate-sized prey in water as adults (Martof and Scott, 1957) but do not suction feed (Deban and Marks, 2002). Plethodontid salamanders possess derived tongue-protraction mechanisms that appear to be in direct mechanical conflict with the requirements of suction feeding (Wake, 1982; Deban, 1997). Therefore, these animals may not have evolved suction feeding because it would undermine tongue protraction performance (Deban and Marks, 2002).

Schwenk (1995) concludes that phylogenetic patterns by themselves are not strong evidence for the presence of constraints, and points out that a cogent argument requires a plausible proximal mechanism that generates the phylogenetic pattern. One could envision that the loss of larval morphological characteristics or motor patterns needed for suction feeding might impede the subsequent evolution of suction feeding in adults. However, the available data suggest that it is only the loss of morphological characteristics, not motor patterns, that drives the phylogenetic association of adult and larval suction feeding. Motor patterns associated with suction feeding sometimes occur in clades that are not capable of suction feeding. Buccal expansion via hyobranchial depression has evolved at least three times independently from the ancestor of bony fishes, among typhlonectid caecilians, pipid frogs, and turtles (Lauder and Prendergast, 1992; Lemell and Weisgram, 1997; Van Damme and Aerts, 1997; Summers et al., 1998), yet some of these taxa cannot suction feed. Lauder and Shaffer (1988) found that *Ambystoma tigrinum* retains the muscle activity pattern used by larvae for suction feeding after metamorphosis, yet they cannot suction feed effectively because they lack certain morphological characteristics, such as labial lobes (Lauder and Shaffer, 1986; Lauder and Reilly, 1988; Shaffer and Lauder, 1988). Furthermore, morphological characteristics needed for suction feeding (e.g., lobes to occlude the lateral gape and a heavily ossified hyobranchial apparatus) are never present in amphibians that do not use suction feeding.

The quantitative analysis of phylogenetic patterns is a powerful approach for exploring the role of constraints during the emergence and evolution of complex systems. This is especially true in groups, such as Lissamphibia, in which convergent and parallel evolution is rampant, allowing multiple putatively "constrained" and "unconstrained" lineages to be compared (Schwenk and Wagner, 2003). However, phylogenetic patterns are only one source of information about potential constraints. We do not believe that statistically significant phylogenetic patterns are a requirement for valid arguments regarding the presence of constraints. Such arguments need only be consistent with the developmental, functional and phylogenetic patterns available for study.

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Appendix 1

Preserved specimens examined. Catalog numbers are from specimens in the collections of the Museum of Vertebrate Zoology, University of California Berkeley (MVZ) and the University of Michigan Museum of Zoology (UMMZ).

Gymnophiona

Ichthyophis bannanicus (UMMZ 190479-81), *Praslinia cooperi* (UMMZ 182990, 180851, 177460, 183006, 175294).

Caudata

Ambystoma gracile (MVZ 98232, 98241, 98267, 98298, 98314), *A. talpoideum* (MVZ 144950, 144952-953), *A. texanum* (MVZ 12654-55, 24972, 170892, 170887-888), *A. macrodactylum* (MVZ 69750 [10 specimens], 80047-48), *A. maculatum* (MVZ 188012, 188016, 90744), *Amphiuma means* (MVZ 198745, 198751, 198755), *Batrachuperus karlschmidti* (MVZ 203637-641), *B. longdongensis* (MVZ 208609-611, 208613), *B. tibetanus* (MVZ 216661-665, 216669-671), *B. yenyuanensis* (MVZ 204303-304), *Eurycea junaluska* (MVZ 186701-703), *E. nana* (MVZ 68383 [12 specimens], 121020-024), *E. neotenes* (MVZ 121197, 121218, 121298, 121371, 121376), *E. tynerensis* (MVZ 74879-81), *Gyrinophilus palleucus* (MVZ 92118), *G. porphyriticus* (MVZ 92206, 92210), *Hynobius leechi* (MVZ 205654-661), *Necturus maculosus* (MVZ 25535-35, 152658), *N. alabamensis* (MVZ 197712-718), *Onychodactylus fischeri* (MVZ 200603-605), *Onychodactylus japonicus* (MVZ 129397-401), *Pseudotriton montanus* (MVZ 143976-977, 146224, UMMZ 141946), *Rhyacotriton cascadae* (MVZ 158344-349), *R. kezzeri* (MVZ 197348, 197352, 197355, 197359, 197361), *R. olympicus* (MVZ 173450-451, 173458, 185907), *Salamandrella keyserlingii* (MVZ 200581, 200584, 200596), *Taricha torosa* (MVZ 199221, 199234, 199249, 199258, 199271), *Triturus alpestris* (MVZ 74543-545), *Typhlomolge rathbuni* (MVZ 52902), *Typhlotriton spelaeus* (MVZ 74882, 52900).

Anura

Agalychnis callidryas (UMMZ 118864 [10 specimens]), *Ascaphus trueii* (UMMZ 54303 [12 specimens]), *Bombina orientalis* (UMMZ 15482 [3 specimens]), *Ceratophrys ornata* (UMMZ 98834 [4 specimens]), *Hemisus guttatum* (UMMZ 151611 [15 specimens]), *Megophrys* sp. (UMMZ 186015 [7 specimens]), *Phyllomedusa vaillanti* (UMMZ 154854 [12 specimens]), *Rhinophryne dorsalis* (UMMZ 129641[50+ specimens]), *Spea multiplicata* (UMMZ 118891 [10 specimens]).

Appendix 2.

Coding of prey-capture behavior in terminal taxa. For larvae, 0 = aquatic suction feeding, 1 = no suction feeding. For adults, 2 = no aquatic feeding, 3 = aquatic feeding, 4 = no suction feeding, 5 = suction feeding. Taxa that are coded based on the presence or absence of suction feeding morphology (e.g., labial lobes or ossified hyobranchia) are marked as "morphology" in the source column. Coding of evidence is as follows: M = morphology, AO = aided observations (e.g., videography), UO = unaided observations, NL = no larvae (direct development or viviparity), T = terrestrial habit.

Taxon	Larval mode	Evidence	Source	Adult foraging		Adult mode	Evidence	Source
Caecilians								
<i>Epicrionops</i>	0	AO	O'Reilly 1995, this study	2	4	UO	O'Reilly 1995	
<i>Ichthyophis</i>	0	M	O'Reilly 1995, this study	2	4	AO	O'Reilly 1995, this study	
<i>Scolecomorphus</i>	1	NL	M. Wake 1977	2	4	AO	O'Reilly 1995	
<i>Typhlonectes</i>	1	NL	M. Wake 1977	3	4	AO	O'Reilly 1995, this study	
<i>Caecilia</i>	1	NL	M. Wake 1977	2	4	UO	O'Reilly 1995	
<i>Siphonops</i>	1	NL	M. Wilkinson pers. comm. 1995	2	4	AO	O'Reilly 1995	
<i>Dermophis</i>	1	NL	M. Wake 1977	2	4	UO	O'Reilly 1995	
<i>Schistometopum</i>	1	NL	M. Wake 1977	2	4	UO	O'Reilly 1995	
<i>Praslinia</i>	0	M	Nussbaum 1992, this study	2	4	M	this study	
<i>Grandisonia</i>	0/1	NL, M	R. A. Nussbaum pers. comm. 1996	2	4	UO	O'Reilly 1995	
<i>Hypogeophis</i>	1	NL	Nussbaum 1992	3	4	AO	this study	
Salamanders								
<i>Siren</i>	0	M	this study	3	5	AO	this study, Reilly and Lauder 1992	
<i>Cryptobranchus</i>	0	AO	Deban unpublished	3	5	AO	Cundall, et al. 1987, Reilly and Lauder 1992	
<i>Hynobius-n</i>	0	M	this study	3	5	M	Sasaki 1924	
<i>Hynobius</i>	0	M	this study	3	4	M	Larsen, et al. 1989	
<i>Salamandrella</i>	0	M	this study	3	4	AO	this study	
<i>Onychodactylus</i>	0	M	this study	3	4	M	this study	
<i>Batrachuperus</i>	0	M	this study	3	5	M	this study	
<i>Amphiuma</i>	0	M	this study	3	5	AO	Erdman and Cundall 1984, Reilly and Lauder 1992	

<i>Rhyacotriton</i>	0	M	this study	3	4	AO	Larsen, pers. comm. 1995
<i>Necturus</i>	0	M	this study	3	5	AO	Reilly and Lauder 1992
<i>Tylototriton</i>	0	M	this study	2	4	UO	Miller and Larsen 1989
<i>Pleurodeles</i>	0	AO	this study	3	5	AO	Miller and Larsen 1989, this study
<i>Salamandra atra</i>	1	NL	M. Wake 1982	2	4	T	Arnold and Burton 1978
<i>S. salamandra</i>	0	AO	Reilly, 1995	2	4	UO	Miller and Larsen 1989
<i>Salamandrina</i>	0	M	this study	2	4	T	Miller and Larsen 1990
Other Salamandridae							
<i>Notophthalmus</i>	0	UO	Reilly and Lauder 1988	3	5	AO	Reilly and Lauder 1988
<i>Notophthalmus-n</i>	0	UO	Reilly and Lauder 1988	3	5	AO	Reilly and Lauder 1988
<i>Taricha</i>	0	M	this study	3	5	AO	Miller and Larsen 1989
<i>Triturus</i>	0	M	Matthes 1934, this study	3	5	AO	Matthes 1934
<i>Triturus-n</i>	0	M	this study	3	5	M	this study
<i>Paramesotriton</i>	0	M	this study	3	5	AO	Miller and Larsen 1989
<i>Cynops</i>	0	M	this study	3	5	AO	Miller and Larsen 1989
<i>Pachytriton</i>	0	M	Thiesmeier and Hornberg 1997	3	5	AO	Miller and Larsen 1989, this study
<i>Dicamptodon copei</i>	0	M	Nussbaum et al. 1983, this study	3	5	M	Nussbaum et al. 1983, this study
other <i>Dicamptodon</i>	0	AO	Reilly and Lauder 1992	2	4	T, M	Nussbaum et al. 1983, this study
<i>Ambystoma gracile</i>	0	M	this study	2	4	T, M	Nussbaum et al. 1983, this study
<i>A. gracile-n</i>	0	M	this study	3	5	M	this study
<i>A. talpoideum</i>	0	M	this study	2	4	T, M	Petraska 1998, this study
<i>A. talpoideum-n</i>	0	M	this study	3	5	M	this study
<i>A. maculatum</i>	0	M	Hoff et al. 1984	2	4	T	Petraska 1998, this study
<i>Linguadlapsus</i>	0	M	this study	2	4	T	Petraska 1998, this study
<i>A. tigrinum</i>	0	AO	Reilly and Lauder 1992	2	4	T	Larsen and Guthrie 1975
<i>A. tigrinum-n</i>	0	AO	Shaffer and Lauder 1985	3	5	AO	Shaffer and Lauder 1985
other <i>Ambystoma</i>	0	M	this study	2	4	T, M	Petraska 1998, this study

Plethodontid Salamanders

<i>Desmognathus</i> I							
<i>D. aeneus</i>	1	NL	Marks 1995	2	4	T	Marks 1995
<i>D. wrighti</i>	1	NL	Bruce 1991	2	4	T	Bruce 1991
<i>Desmognathus</i> II				4			
<i>D. quadramaculatus</i>	0	AO	Deban and Marks 2002;	3	4	AO	Deban and Marks 2002; Deban 1997

<i>D. marmoratus</i>	0	AO	Deban and Marks 2002; Deban 1997	3	4	AO	Schwenk and Wake 1993; Deban 1997
<i>D. monticola</i>	0	M	this study	3	4	M, AO	Larsen and Beneski 1988
<i>Pbaeognathus</i>	1	NL	Bruce 1991	2	4	T	Bruce 1991
<i>Hemidactylum</i>	0	M	Rose 1995b; Richmond 1999	2	4	T	Bishop 1941; Neill 1963
<i>Typhlotriton</i>	0	M	this study	3	4	M	Brandon 1971; Hilton 1909
<i>Typhlotriton-n</i>	0	M	this study	3	5	M	this study
<i>Eurycea I</i>							
<i>Eurycea junaluska</i>	0	M	this study	2	4	T	Petraska 1998
<i>E. quadrigitata</i>	0	M	this study	2	4	T	Carr, 1940; Lee, 1971; Petraska 1998
<i>Eurycea II</i>							
<i>E. longicauda</i>	0	M	Rose 1995a	3	4	M	Rose 1995a
<i>E. wilderi</i>	0	M	Rose 1995a,b; Wilder 1925	3	4	M	Wilder 1925; Bishop 1941
<i>Paedomolge</i>							
<i>E. nana</i>	0	M	this study	3	5	M	this study
<i>E. neotenes</i>	0	M	this study	3	5	M	this study
<i>E. tynerensis</i>	0	M	this study	3	5	M	this study
<i>E. rathbuni</i>	0	M	this study, Rose 1995a	3	5	M	this study
<i>Gyrinophylus</i>	0	AO	Deban and Marks 2002; Deban 1997	3	4	AO	Deban and Marks 2002; Deban 1997
<i>Gyrinophylus-n</i>	0	M	this study	3	5	M	this study
<i>Stereochilus</i>	0	AO	Deban, unpublished data	3	4	M	Deban 1997
<i>Pseudotriton ruber</i>	0	AO	Deban and Marks, 2002; Deban 1997	3	4	AO	Deban and Marks 2002; Deban 1997
<i>P. montanus</i>	0	M	this study	3	4	M	this study
Bolitoglossini	1	NL	Wake 1966	2	4	T	Wake 1966
Plethodontini	1	NL	Wake 1966	2	4	T	Wake 1966

Frogs

<i>Pipa pipa</i>	1	NL	Sokol 1977	3	4	AO	this study
<i>Hymenochirrus</i>	0	M	Sokol 1977, Wassersug and Hoff 1979	3	5	AO	this study
<i>Ceratophrys</i>	1	M	this study; Duellman and Trueb 1986	2	4	T, M	Duellman and Lizana 1994
<i>Chacabryss</i>	1	M	Faivovich and Carrizo 1992	2	4	T, AO	this study

<i>Lepidobatrachus</i>	0	UO	Ruibal and Thomas 1988	3	4	AO	this study
<i>Caudiverbera</i>	1	M	this study	3	4	AO	this study
<i>Bufo</i>	1	M	Wassersug and Hoff 1979	2	4	T, M	Blair 1972; Gans and Gorniak 1982; Duellman and Trueb 1986
Hylinae	1	M	Wassersug and Hoff 1979	2	4	T, M	Deban and Nishikawa 1992; Duellman and Trueb 1986
<i>Cyclorana</i>	1	M	this study	2	4	T, M	Valdez and Nishikawa 1997; Cogger 1992
Phyllomedusinae	1	M	this study	2	4	T, M	Gray and Nishikawa 1995; Duellman and Trueb 1986
<i>Phrynomantis</i>	1	M	Passmore and Carruthers 1979	2	4	T, M	Passmore and Carruthers 1979; Nishikawa et al., 1992
<i>Hemisus</i>	1	M	this study	2	4	T, M	Passmore and Carruthers 1979; Ritter and Nishikawa 1995
<i>Rana</i>	1	M	Wassersug and Hoff 1979	3	4	AO	Anderson 1993; this study