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Evolution of Forelimb Movement Patterns for Prey Manipulation in Anurans

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ABSTRACT Unlike other amphibians, frogs often use their forelimbs to capture and transport prey. In the present study, high-speed videography was used to observe forelimb use during feeding in a diverse group of anurans in order to determine the evolution of forelimb movement patterns among anuran taxa. Data were gathered from 488 individuals representing 104 species, 55 genera, and 16 families. Five distinct behavior patterns were identified: scooping entails using the back of the hand to push prey into the mouth; wiping involves the use of the palm of the hand to push prey, protruding laterally from the mouth, toward the midline; during prey stretching, one end of the prey is held in a stationary position by the hands while the other end is pulled upward by the jaws; in grasping, the palms face the midline or the substrate as the fingers are wrapped around the prey; grasping with wrist rotation is similar to grasping, but the wrists rotate inward as the hands grasp the prey so that the palms face the mouth. The distribution of these behavior patterns was mapped onto the most recent phylogenetic hypothesis for anurans. Maximum parsimony analyses suggest that scooping and wiping are primitive and have been retained by many frog lineages. Wiping was not observed in the pipids, which are the only anurans that lack tongues and use hydraulic transport. Prey stretching appears to have evolved several times in unrelated taxa. Grasping and grasping with wrist rotation appear to have evolved only in arboreal groups, suggesting that the ability to climb is a preadaptation for the ability to grasp prey. Several species were observed using grasping motions in place of the tongue to capture prey. *J. Exp. Zool. 277:417–424, 1997.* © 1997 Wiley-Liss, Inc.

Previous studies on anuran feeding behavior have focused on movements of the head, jaws, and tongue during prey capture. Primitively, frogs use a short tongue and the jaws to apprehend prey (Nishikawa and Cannatella, '91; Nishikawa and Roth, '91; Deban and Nishikawa, '92; Nishikawa et al., '92). However, the use of longer tongues and a diminished role of the jaws in prey capture has evolved multiple times (Nishikawa et al., '92; Anderson, '93; Gray and Nishikawa, '95).

For frogs feeding on large prey, the forelimbs play a significant role in prey manipulation (Anderson, '96; Valdez and Nishikawa, '97). The jaws are used to capture large prey, and the forelimbs are used to transport it into the oral cavity. In contrast, when feeding on small prey, frogs use tongue prehension and transfer the prey to the esophagus without the involvement of the forelimbs.

In contrast to recent advances in our knowledge of the role of tongue and jaw movements, little is known about how anurans use their forelimbs during feeding. Published reports of forelimb movements in frogs are based mainly on unaided visual observations. Forelimb movements described as "scooping" have been observed in *Xenopus laevis* (Avila and Frye, '77, '78) and *Rana pipiens* (Comer and Grobstein, '81). In addition, movements described as "wiping" have been observed during prey transport in *X. laevis, R. pipiens,* and *Hymenochirus boettgeri* (Sokol, '69; Avila and Frye, '78; Comer and Grobstein, '81). However, to our knowledge, there are no published accounts that clearly define forelimb movement patterns or analyze their evolution.

While filming frogs for other studies, we observed that scooping occurred during prey transport as well as prey capture and that some of the movements classified by previous researchers as "wiping" were the same as those referred to as "scooping" by others. These initial observations also revealed that several undescribed forelimb movement patterns are used by anurans. In addition, there appeared to be considerable interspecific variation in the types of movement pattern exhibited among the different species for which sequences were available.

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The goals of this study were (1) to define the forelimb movement patterns used by frogs during feeding and (2) to make preliminary analyses of the evolutionary patterns of forelimb movements among taxa.

METHODS

Videotaping and data collection

Preexisting videos from other studies were used to collect data for 488 individual frogs representing 104 species, 55 genera, and 16 families (Appendix 1). Videos were made with a high-speed video camera (60–180 fps). All videos were made with the frogs in lateral view on a damp paper towel or in shallow water, while feeding on at least one of the following prey types: crickets (*Acheta domesticus*), termites (*Heterotermes* sp. and *Reticulitermes* sp.), flour beetles and mealworms (adult and larval *Tenebrio molitor*), fruit flies (*Drosophila melanogaster*), wax moths and waxworms (adult and larval *Galleria melonella*), sawflies (*Nematus* sp.), *Tubifex* worms, earthworms (*Lumbricus* sp.), goldfish (*Carassius auratus*), frogs (*Pseudacris triseriata*), and mice (*Mus musculus*).

Analyses

Patterns of forelimb movement were defined after a frame by frame examination of a subsample of video sequences using a Panasonic AG-6300 VCR (Secaucus, New Jersey). All available sequences were then observed, and the presence or absence of each movement pattern was noted.

The distribution of each forelimb movement pattern across taxa was mapped onto a phylogeny of anurans. We used Ford and Cannatella's ('93) phylogeny of frog families, with two modifications. The family Leptodactylidae is a paraphyletic group (Ford and Cannatella, '93). In the present study, we assumed, based on Frost ('85), that the subfamilies within Leptodactylidae are monophyletic. For the subfamily Ceratophyrinae, the relationships of the genera were resolved based on Maxson and Ruibal ('88). Subfamilies within the family Hylidae were assumed to be monophyletic, based on Frost ('85), and the relationships among the subfamilies were based on Bagnara and Ferris ('75). For every genus, each behavior pattern was coded as present or not observed, and PAUP™ for the Macintosh was used to construct the most parsimonious hypotheses of character-state changes.

In order to provide conservative estimates of the number of character-stage changes, data for a genus were included in an analysis only if the given movement pattern was observed, or if we could make a reasonable determination that the behavior was absent in that genus. If a given movement pattern was not observed, the data were included only if the sample size for large prey (larger than approximately one jaw length) was sufficient (ten sequences or more). This rationale is based on the observation that frogs rarely use forelimbs when feeding on small prey (Anderson, '96; Valdez and Nishikawa, '97). Therefore, unless a sufficient number of feeding sequences involving large prey was observed, it would be inappropriate to conclude that the behavior was absent in that genus.

RESULTS

Patterns of forelimb movement

Five patterns of forelimb movement were identified (Fig. 1): (1) scooping, where the forelimbs extend anteriorly with the fingers splayed, and the back of the hand is then used to shove the prey item posteriorly toward the mouth; (2) wiping, where the palm of the hand is used to push prey, protruding laterally from the mouth, forward toward the midline (the palms may be oriented anteriorly or toward the midline as the forelimb moves away from the mouth); (3) prey stretching, where the mouth grips the prey and pulls it upward while the hands hold the protruding end in a stationary position by grasping it or pinning it to the substrate; (4) grasping, where the fingers wrap around the prey as the forelimbs transport it toward the mouth, the palms facing the midline or the substrate; and (5) grasping with wrist rotation, a grasping motion in which the wrists rotate so that the palms are oriented toward the mouth.

Wiping and prey stretching were observed only during prey transport, whereas the other behavior patterns were observed during prey capture and prey transport. The entire hand is often stuffed into the mouth when scooping, grasping, and grasping with wrist rotation are used for prey transport. One or both forelimbs may be involved in each of the five types of behavior.

Evolutionary changes in behavior patterns

The PAUP analysis indicates that scooping is a primitive behavior pattern in frogs (Fig. 2). All archaeobatrachian and mesobatrachian genera and most neobatrachian genera exhibited this behavior. It occurs at high frequencies in aquatic feeding sequences for members of the families Pipidae (*H. boettgeri* and *X. laevis*), Leptodactylidae (*Caudi-*

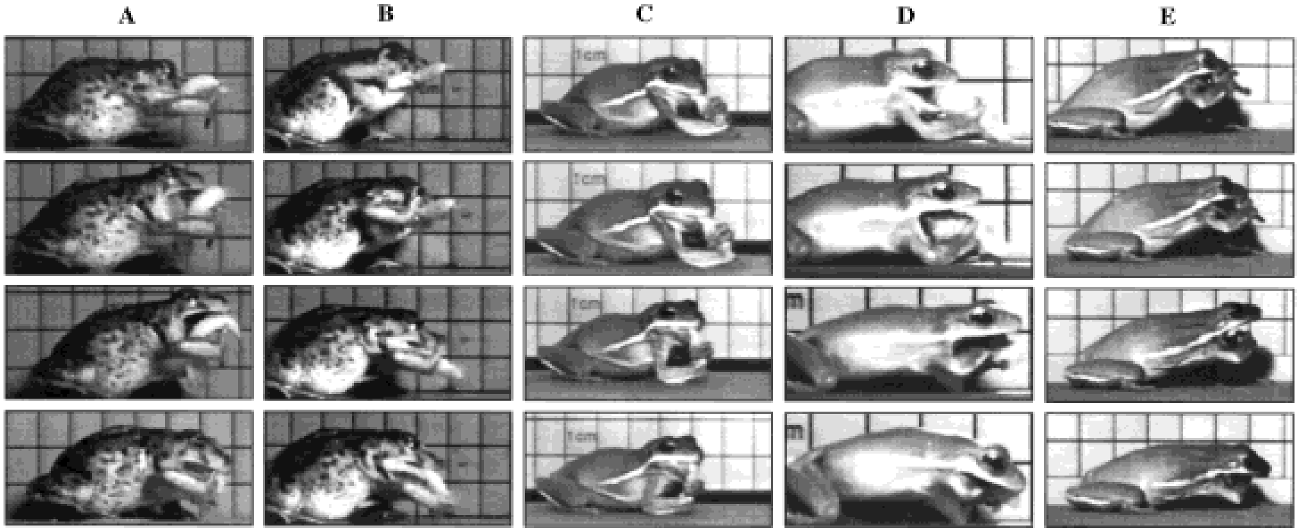

Fig. 1. Forelimb movement patterns for prey acquisition in anurans. **(A)** Scooping (*Scaphiopus hurterii*), **(B)** wiping (*S. hurterii*), **(C)** prey stretching (*Hyla cinerea*), **(D)** grasping (*H. cinerea*), and **(E)** grasping with wrist rotation (*H. cinerea*).

verbera caudiverbera and *Lepidobatrachus llanensis*), and Ranidae (*Occidozyga laevis* and *Pyxicephalus adspersus*). Scooping is used for prey transport in *H. boettgeri* and for both capture and transport in *C. caudiverbera, L. llanensis, O. laevis, P. adspersus,* and *X. laevis.* In sequences in which scooping is used for prey capture, the lunge and scooping movements may occur simultaneously. Often, however, prey acquisition begins with scooping, and then as the prey is brought toward the mouth, the frog lunges forward and engulfs it. More scooping movements may then occur to push the prey further into the mouth. For terrestrial frogs, scooping is used primarily for prey transport and was used for prey capture in only one terrestrial feeding sequence for a semiaquatic ranid, *Phrynobatrachus.* The frog repeatedly responded to the presence of termites on the back of the hand by lifting the hand to the mouth. It then used the tongue to capture the termite from the back of the hand.

Scooping apparently has been lost in two arboreal groups (*Hyalinobrachium* and the hylines), and the phyllomedusine and hemiphractine hylids used it infrequently (1% in *Pachymedusa dacnicolor* to 8% in *Litoria* sp.). Species of *Bufo* scooped infrequently (*B. alvarius, B. asper, B. cognatus, B. rubropunctatus,* and *B. woodhousii*) or not at all (*B. americanus, B. boreas, B. guttatus, B. marinus, B. melanostictus, B. microscaphus, B. punctatus, B. quercicus, B. regularis, B. terrestris,* and three unidentified species of *Bufo*). Also, an unidentified species of *Probreviceps* (family Microhylidae) did not exhibit the behavior, although the other two microhylids that were videotaped feeding on large prey (*Dyscophus guineti* and *Scaphiophryne pustulosa*) displayed scooping at relatively high frequencies (40% and 29%, respectively). The following 15 genera were not observed to use scooping but were not included in the analysis because insufficient sample sizes (n < 10) were obtained for large prey: *Physalaemus, Eleutherodactylus, Melanophryniscus, Schismaderma, Phrynobatrachus, Cacosternum, Mantella, Hemisus, Hyperolius, Breviceps, Callulina, Gastrophryne, Kaloula, Microhyla,* and *Phrynomantis.*

Wiping is also a primitive movement pattern and was observed in more species than any other forelimb movement (Fig. 3). However, it occurred only at low frequencies (<1%) in some bufonids (*B. alvarius, B. americanus, B. cognatus, B. melanostictus, B. rubropunctatus, B. woodhousii,* and *Schismaderma carens*) and not at all in others (*Melanophryniscus stelzneri, B. asper, B. guttatus, B. marinus, B. quercicus,* and *B. terrestris*). The only other frogs that fed on large prey but did not exhibit wiping were the pipids (*Hymenochirus* and *Xenopus*). Twelve genera (*Physalaemus, Eleutherodactylus, Melanophryniscus, Dendrobates, Epipedobates, Cacosternum, Mantella, Hemisus, Breviceps, Gastrophryne, Microhyla,* and *Phrynomantis*) were not included in the analysis because they did not display wiping, and fewer than ten sequences for large prey were observed.

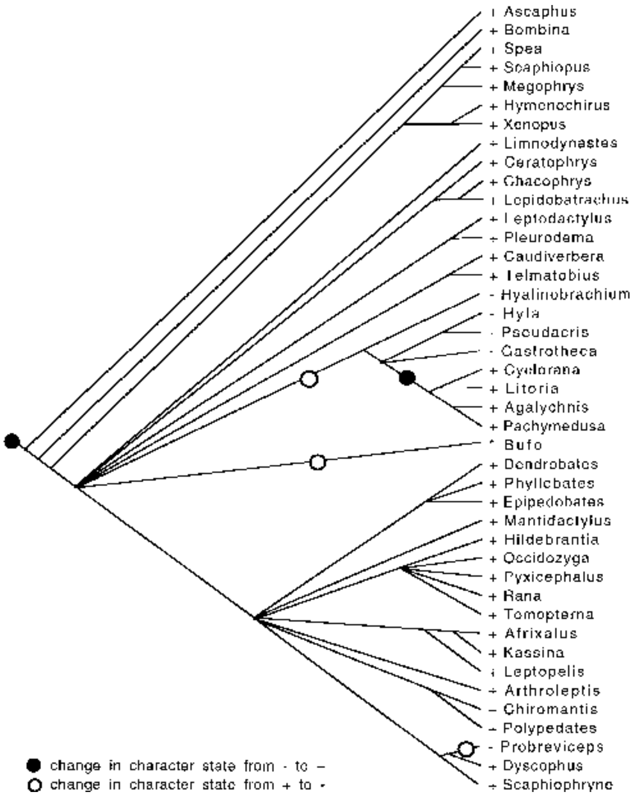

Fig. 2. Changes in character state for scooping: + indicates that scooping was observed, – indicates that scooping was not observed, and * indicates that the behavior was observed in at least one species but not in all species, with sufficient sample sizes, within the genus. For sample sizes, see Appendix 1. The scoop is a primitive character and is widespread among anuran taxa. It apparently has been lost in several small-prey specialists. It also was not observed in *Hyalinobrachium* or in the hylines and occurred at low frequencies in other hylids. Of the three microhylid genera that were fed large prey (*Probreviceps, Dyscophus,* and *Scaphiophryne*), only *Probreviceps* did not exhibit scooping.

Prey stretching is a distinct behavior pattern that was found in six unrelated genera (*Bombina, Telmatobius, Hyla, Gastrotheca, Occidozyga,* and *Kassina*; Fig. 4). This behavior occurred only during feeding on waxworms and mealworms. Twenty-three genera were not included in the analysis because they did not display prey stretching, but too few sequences with large prey were obtained to conclude that the behavior was absent. These were *Physalaemus, Eleutherodactylus, Melanophryniscus, Schismaderma, Dendrobates, Phyllobates, Epipedobates, Phrynobatrachus, Cacosternum, Mantella, Mantidactylus, Hemisus, Afrixalus, Hyperolius, Arthroleptis, Polypedates, Breviceps, Callulina, Gastrophryne, Kaloula, Microhyla, Phrynomantis,* and *Scaphiophryne.*

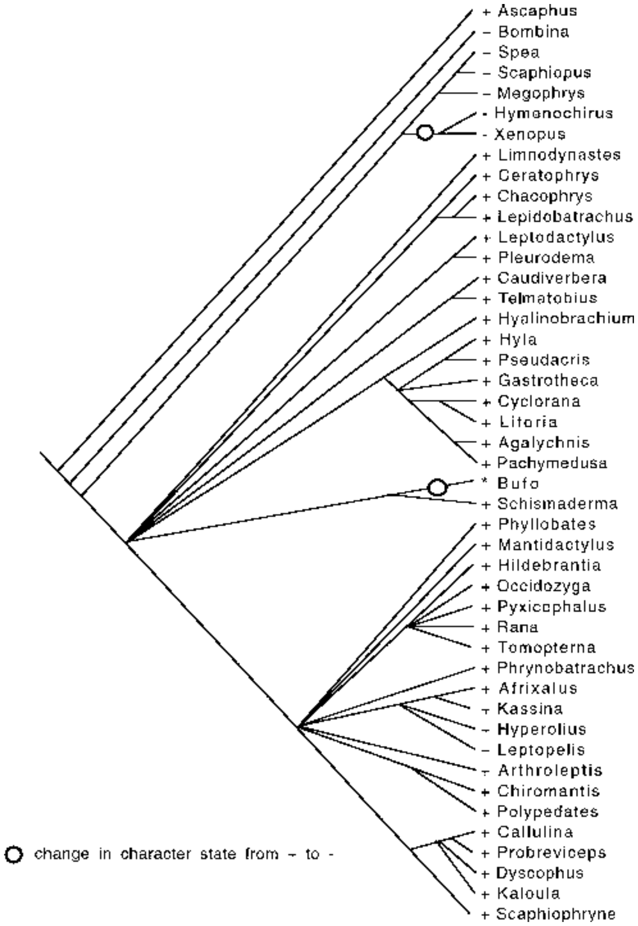

Fig. 3. Changes in character state for wiping. Symbols as for Figure 2. The wipe is a primitive character and is widespread among taxa. It is apparently absent in small-prey specialists and some *Bufo* species. The only other frogs that did not exhibit the behavior were the pipids (*Hymenochirus* and *Xenopus*).

Grasping is a derived behavior that appears to have evolved at least three times in four arboreal families (once in Hylidae and Centrolenidae, once in Hyperoliidae, and once in Rhacophoridae; Fig. 5). All genera examined in each of these families exhibited the behavior. Grasping with wrist rotation was observed only in hylids (Fig. 5). All hylids exhibited the behavior except for *Cyclorana,* which was the only nonarboreal hylid examined. The following genera were not included in the phylogenetic analyses because they did not display the behavior, and fewer than ten feeding sequences for large prey were obtained: *Physalaemus, Eleutherodactylus, Melanophryniscus, Schismaderma, Dendrobates, Phyllobates, Epipedobates, Phrynobatrachus, Cacosternum, Mantella, Mantidactylus, Afrixalus,*

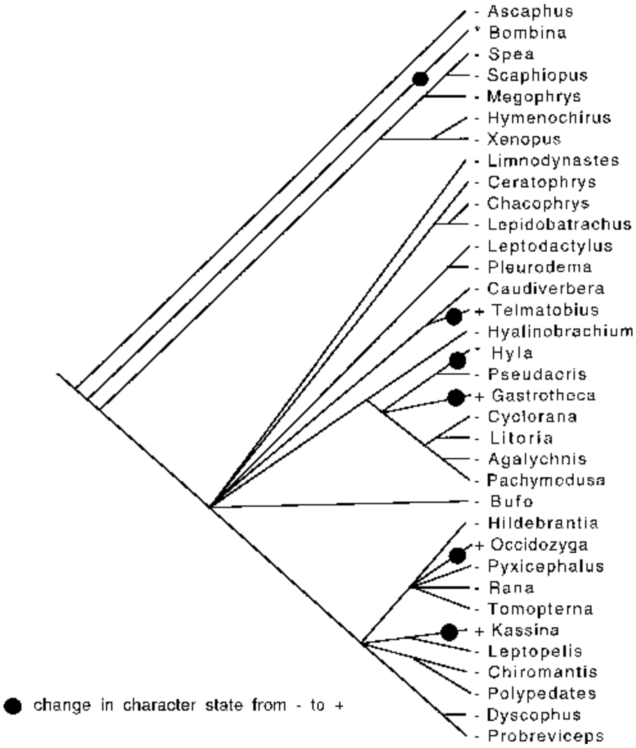

Fig. 4. Changes in character state for prey stretching. Symbols as for Figure 2. This movement pattern appears to have evolved at least six times in unrelated taxa.

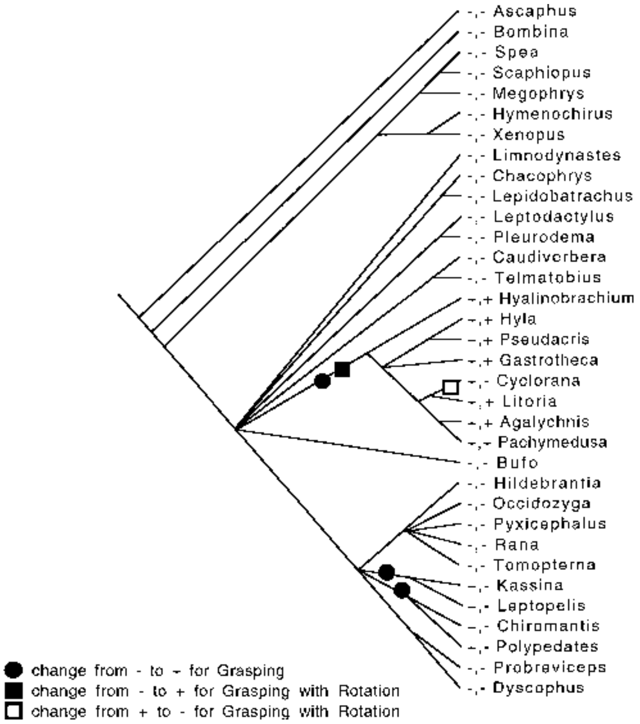

Fig. 5. Changes in character state for grasping and grasping with wrist rotation. Symbols as for Figure 2. Grasping appears to have evolved three times in arboreal groups. Grasping with wrist rotation appears to have evolved once in the hylids and was subsequently lost in *Cyclorana* (the only terrestrial hylid examined).

Hyperolius, Arthroleptis, Breviceps, Callulina, Gastrophryne, Kaloula, Microhyla, Phrynomantis, and *Scaphiophryne.*

In several sequences, grasping and grasping with wrist rotation were used to capture prey. For each of five arboreal species (*Hyla arenicolor, Gastrotheca* sp., *Agalychnis callidryas, P. dacnicolor,* and *Leptopelis* sp.), one sequence was observed in which the normal lunge and tongue movements were absent and prey was captured with forelimb grasping movements. In each of these sequences, the frog was recovering from missing or dropping the prey.

DISCUSSION

Evolution of forelimb movement patterns

In the present study, we identified five distinct forelimb movement patterns used for prey manipulation in frogs. Two of the patterns (scooping and wiping) appear to be primitive and are widespread among anuran taxa, and three patterns (prey stretching, grasping, and grasping with wrist rotation) are derived and exhibited by only a few taxa.

Scooping is particularly well developed in aquatic frogs. In *H. boettgeri,* scooping is used only for prey transport, but in five species (*X. laevis, L. llanensis, C. caudiverbera, P. adspersus,* and *O. laevis*) it is used for both capture and transport. These results are in agreement with previous descriptions of the feeding behavior of *X. laevis* (Avila and Frye, '77, '78) but are in disagreement with the description of the feeding behavior of *H. boettgeri* (Sokol, '69), in which scooping was not observed. Sokol ('69) concluded that *H. boettgeri* uses only "wiping movements" during prey transport. However, we found that the movements used by *H. boettgeri* for prey transport are identical to those used by *X. laevis* for prey capture and very different from the "wiping" motions for transport in *R. pipiens* (Comer and Grobstein, '81).

Although scooping is widespread among anuran taxa, it occurs less frequently in terrestrial neobatrachians. The hylids and centrolenids that were examined seldom scooped. This may be due to the fact that hylids and centrolenids have evolved other (perhaps more efficient) mechanisms of forelimb use, such as grasping (discussed below). The low frequency of scooping in bufonids is likely due to the high percentage of small prey they consumed. Three microhylid species (*Dyscophus guineti, Scaphiophryne pustulosa,* and *Probreviceps* sp.) were filmed feeding on large prey, and two of these species (*D. guineti* and *S. pustulosa*) exhibited scooping at relatively high frequencies. On the other hand, *Probreviceps* sp. did not exhibit the behavior even when feeding on earthworms. (*Probreviceps* exhibits wiping motions but at about half the frequency of the other two microhylids.) We hypothesize that, because most brevicipitines are small-prey specialists, *Probreviceps* has evolved the ability to capture large prey secondarily but has not regained the ability to use scooping motions for prey acquisition. *Probreviceps* has evolved an extremely large, highly protrusible tongue (Nishikawa et al., '92), which may compensate for the reduction in forelimb movements during prey acquisition.

Wiping, another primitive behavior, was absent only in the pipids (*H. boettgeri* and *X. laevis*). Pipids lack tongues and use hydraulic flow for prey transport (Avila and Frye, '78; Sokol, '69). Thus, wiping may function to orient prey for lingual transport and may have been lost secondarily in the tongueless pipids.

Prey stretching appears to be a derived behavior and was observed in only a few unrelated taxa. The function of this behavior is unclear, and its occurrence in so few, diverse taxa is difficult to explain. Comparisons of ecology and prey-capture performance between closely related species in which one species exhibits the behavior (e.g., *Bombina bombina*) and the other does not (e.g., *B. variegata*) may elucidate any possible roles of prey stretching. It may function to kill the prey. Anurans that exhibit prey stretching may feed on noxious prey, which need to be killed before they are swallowed in order to prevent damage to the oral cavity.

Grasping appears to have evolved only in arboreal groups (defined here as frogs possessing expanded toepads). Because grasping movements for prey transport are similar to those for climbing, we hypothesize that the ability to climb is a preadaptation for the use of forelimbs to grasp prey.

Grasping with wrist rotation apparently has evolved only once in a common ancestor of the Hylidae. Interestingly, wrist rotation during grasping was not observed in *Cyclorana novaehollandiae,* the only nonarboreal hylid that was examined. Because *C. novaehollandiae* has retained the ability to grasp prey but apparently has lost the ability to rotate the wrist, we hypothesize that terrestrial frogs may experience selection for reduced wrist rotation. Comparative studies of the forelimb morphology of frogs are currently under way and should elucidate the underlying biomechanical differences that allow some frogs to perform grasping with wrist rotation.

Use of forelimbs to capture prey

In most frogs, forelimb movements are used for prey transport, but the use of scooping to assist with prey capture is common for frogs feeding in water and has been observed also in terrestrial feeding sequences for *R. pipiens* (Comer and Grobstein, '81). Tactile stimulation from prey on the back of the hand triggers *R. pipiens* to lift the hand to the mouth. The tongue is then used to retrieve the prey from the hand (Comer and Grobstein, '81). In the present study, we observed a similar behavior in *Phrynobatrachus* in response to termites climbing on the back of the hand. No other species were observed to use forelimbs in this manner, but this is likely because prey were generally placed on the substrate directly in front of the frogs and were usually captured before they touched the frogs.

The only other forelimb movement pattern used for prey capture was grasping. Four hylids and one hyperoliid were observed using grasping movements to recapture prey after it had been missed or dropped. In each case, the frog grabbed the escaped prey with its hand and stuffed it into its mouth. This behavior was never observed unless the frog had just completed an unsuccessful prey-capture attempt, suggesting that prey-acquisition behaviors initiate forelimb grasping movements, which may then be used for prey capture in the event that the prey escapes. As far as we know, this is the first time that the use of grasping to capture prey has been documented for a lower vertebrate.

In conclusion, the diversity of feeding behavior in frogs seems to be an ideal system in which to study the evolution of movement patterns. Although previous studies have focused on the role of the jaws and tongue in anuran prey capture, the results of this study indicate that the forelimbs also play an important role in both prey capture and transport. We identified five distinct movement patterns used by anurans to capture and transport large prey. All of these movements were used for the manipulation of large prey. Two of these movements (scooping and wiping) are basal and widespread and three (prey stretching, grasping, and grasping with wrist rotation) are derived. Grasping movements evolved at least three times in arboreal species, suggesting that the ability to climb is a preadaptation for the ability to grasp prey during feeding. In addition, grasping movements are occasionally used in place of the tongue to recapture prey that were missed or dropped. The physiological bases and ecological consequences of the evolution of movement patterns would provide interesting studies for future research.

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Appendix 1. Numbers of species, individuals, and sequences for each genus

Family	Genus	Number of Species	Number of Individuals	Number of Sequences	Prey1
Ascaphidae	*Ascaphus*	1	10	44	ww(44)
Bombinatoridae	*Bombina*	3	34	301	c(6), ew(17), t(107), ww(171)
Megophryidae	*Megophrys*	2	16	131	ew(131)
Pelobatidae	*Scaphiopus*	2	7	106	ff(25), ww(81)
	Spea	1	18	103	ff(9), ww(94)
"Leptodactylidae"	*Caudiverbera*	1	7	35	c(23), gf(2), ww(10)
	Ceratophrys	2	10	77	c(5), fg(6), ms(21), ww(45)
	Chacophrys	1	2	54	ms(2), ww(52)
	Eleutherodactylus	2	6	36	c(4), t(32)
	Lepidobatrachus	1	5	41	c(10), ew(18), gf(8), ms(5)
	Leptodactylus	2	2	14	c(8), ww(6)
	Physalaemus	1	3	73	ff(48), t(25)
	Pleurodema	1	8	156	ew(4), t(101), ww(51)
	Telmatobius	1	6	18	ew(4), ww(14)
"Myobatrachidae"	*Limnodynastes*	1	5	64	ff(45), ww(19)
Centrolenidae	*Hyalinobrachium*	1	4	47	ff(3), t(44)
Hylidae	*Agalychnis*	1	5	36	c(36)
	Cyclorana	1	6	308	ew(22), ff(44), ms(8), t(156), w&78)
	Gastrotheca	2	3	22	ww(22)
	Hyla	8	53	272	bt(1), (13), ff(15), mw(1), t(46), ww(194)
	Litoria	5	9	49	c(2), ew(1), ww(46)
	Pachymedusa	1	9	120	c(77), ww(20)
	Pseudacris	1	6	65	c(3), ff(25), sf(35), ww(2)
Bufonidae	*Bufo*	18	101	1611	bt(10), c(30), ew(4), ff(197), t(240, ww(1130)
	Melanophryniscus	1	2	75	ff(75)
	Schismaderma	1	3	49	t(49)
Dendrobatidae	*Dendrobates*	2	8	283	ff(283)
	Epipedobates	1	4	53	ff(53)
	Phyllobates	1	4	98	ff(96), ww(2)
"Ranidae"	*Cacosternum*	1	2	35	t(35)
	Hildebrantia	1	1	14	ww(14)
	Mantella	1	5	82	ff(61), t(21)
	Mantidactylus	1	3	68	ff(63), ww(5)
	Occidozyga	1	3	12	ew(11), ww(1)
	Phrynobatrachus	1	4	80	ff(33), t(47)
	Pyxicephalus	1	4	19	ew(19)
	Rana	6	15	120	c(9), ff(13), ew(15), ww(83)
	Tomopterna	1	2	43	c(10), T(17), ww(16)
Hemisotidae	*Hemisus*	1	19	517	t(517)
Hyperoliidae	*Afrixalus*	1	1	2	c(2)
	Hyperolius	2	2	70	c(4), ff(33), t(32), ww(1)
	Kassina	1	2	21	c(10), ww(11)
	Leptopelis	1	3	70	c(2), mt(1), t(9), ww(58)
Arthroleptidae	*Arthroleptis*	1	1	3	t(3)
Rhacophoridae	*Chiromantis*	2	3	27	c(2), mt(13), ww(12)
	Polypedates	1	1	4	c(1), ww(3)
Microhylidae	*Breviceps*	1	3	119	ff(20), t(99)
	Callulina	1	9	333	ff(7), t(326)
	Dyscophus	1	3	71	c(5), ff(43), ww(23)
	Gastrophryne	1	6	154	ff(135), t(19)
	Kaloula	3	12	297	ff(78), t(219)
	Microhyla	3	9	278	ff(168), t(110)
	Phrynomantis	1	7	261	ff(80), t(181)
	Probreviceps	1	5	127	ew(17), t(108), ww(2)
	Scaphiophryne	2	7	262	ff(50), t(205), ww(7)

Sample sizes for each prey type are shown in parentheses. Abbreviations for prey type are bt, beetle; c, cricket; ew, earthworm; ff, fruit fly; gf, goldfish; fg, frog; ms, mouse; mw, mealworm; mt, moth; st, sawfly; t, termite; and ww, waxworm. Quotations indicate metataxa (Sensu Ford and Cannatella, '93).