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Convergence and Morphological Constraint in Frogs: Variation in Postcranial Morphology

Sharon B. Emerson

A Contribution in Celebration
of the Distinguished Scholarship of Robert F. Inger
on the Occasion of His Sixty-Fifth Birthday

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- MURRA, J. 1946. The historic tribes of Ecuador, pp. 785-821. In Steward, J. H., ed., *Handbook of South American Indians*. Vol. 2, *The Andean Civilizations*. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.
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Convergence and Morphological Constraint in Frogs: Variation in Postcranial Morphology

Abstract

Morphological variation within the order Anura is often thought to be less than that in other vertebrate orders. Two explanations have been suggested for this repetitive occurrence of similar morphotypes among distantly related species: convergence and morphological constraint. Principal component analysis of postcranial features confirms that morphological variation correlates with locomotor mode. This form-function correlation is taken as evidence of convergence. Furthermore, comparisons of patterns of morphological variation among and within families show that the same features account for similar levels of variation within families and across the order. Similarity of coefficients of variation at different taxonomic levels is taken as evidence that morphological variation is constrained within frogs.

Introduction

Similar postcranial morphological features have appeared repeatedly and independently within and across the major families of frogs (Noble, 1931; Parker, 1932; Emerson, 1976, 1979). Some writers have suggested that the high incidence of convergence is related to the reduced number of skeletal elements of frogs (Parker, 1932; Inger, 1967). This idea follows from the assumption that a smaller number of bones allows a lesser number of possible skeletal variants. Although morphological variation within the order is thought to be slight (Inger, 1967), there have been few studies specifically examining patterns of morphological variation in frogs, other than studies focusing on systematics. Another explanation for the convergence is that similar selective pressures have produced

common morphologies (Lewontin, 1978) among unrelated taxa. But, while the functional significance of the postcranial morphology of frogs is well known (Emerson, 1976, 1978, 1979, 1982; Emerson & Diehl, 1980; Emerson & DeJongh, 1980), few studies (Emerson, 1976; Emerson & Diehl, 1980) have explicitly tested the hypothesis of morphological convergence in the context of adaptation.

The two foregoing ideas are not mutually exclusive. Both similar selective pressures and limited skeletal variation could be involved in the pattern of repetitive morphotypes seen in frogs. The object of this paper is to consider both explanations. Form-function correlations will be used to test the explanation of convergence through adaptation. Functional locomotor groupings will be mapped on patterns of variation in postcranial morphology. The presence of a form-function correlation will be taken as evidence for adaptation. Second, patterns of variation in postcranial morphology will be compared across different systematic levels. The same features accounting for similar levels of variation within families and across the order will be taken as evidence for constraint in skeletal variation.

Historical Background

The postcranial morphology of frogs has provided a fertile field of research for both functional morphologists and systematists. In general, we know that differences in both pelvic morphology and hind limb proportions are correlated with differences in locomotor mode, and that these morphological features are useful as characters in the analysis of systematic relationships among frogs at diverse taxonomic levels. For systematics stud-

ies, differences in relative hind limb length are used to characterize closely related species. Functionally, the length of the hind limb is the distance through which the force acts during jump takeoff and is strongly correlated with jump performance (Dobrowolska, 1973; Zug, 1972; Emerson, 1978). The tibiofibula is the out-lever of the lower leg extensor muscle, and frogs which are specialized for burrowing have a relatively short tibiofibula (Emerson, 1976). There are three patterns of articulation between the vertebral column and pelvis in frogs. Types of articulation tend to be family specific (Emerson, 1979), but there are some interesting exceptions. The three types of iliosacral articulation are correlated with differences in the lengths of the pelvic girdle and presacral transverse processes (Emerson, 1982). Functionally, the type of articulation mediates degree of movement at the joint (Emerson, 1979). The direction and degree of movement are correlated with different locomotor patterns (Emerson, 1979).

Materials and Methods

Forty-one species representing 36 genera from 15 families were selected for the interfamilial study (see Appendix 1 for a list of species). Representatives from all the frog families and locomotor types were included. These particular species were chosen because their articulation type could be confirmed by dissection of museum specimens and because they represent the broadest possible range of frog postcranial morphology and locomotor behavior. For intrafamilial comparisons, 28 species of Hylidae, 26 species of Leptodactylidae, and 32 species of Ranidae were examined (see Appendix 2). The object of these samples was to include as many genera within each family as possible, even if articulation type and locomotor mode could not be determined.

One specimen of each species was measured (see Radinsky, 1981, and Emerson, 1982, for a justification of using single specimens in studies which focus on familial level differences). Measurements on dried skeletons were taken to the nearest one-tenth of a millimeter with dial calipers. The following measurements were taken: length of snout-vent, femur, tibiofibula, tarsus, foot, humerus, radioulna, hand, girdle, urostyle, and ilium; width of ilium; entire length of the last presacral transverse processes; and maximum height of the dorsal

crest of the ilium. (See Zug [1972] and Trueb [1977] for definitions and illustrations of these measurements.)

The original measurements were transformed to correct for the potentially confounding effects of allometry and size-related variation. First, the measurements were converted to logarithms (base 10), and for each group being studied, each measurement was plotted against ilium length, girdle length, or snout-vent length. Reduced major axis equations were calculated of the form: $\log Y = \log a + b \log X$. The reduced major axis equations then became the master equations for the transformation (Appendices 3–6). Subsequently, each measurement for each species was changed to a dimensionless variable by inserting the ilium, girdle, or snout-vent length of that species into the master equation for that measurement to derive an “expected” Y value. The actual Y value was then divided by the expected Y value obtained from measurement. The result is the antilog of the residual from the log-transformed equation (see Emerson & Radinsky, 1980; Radinsky, 1981; Emerson, 1982, for details on this technique).

The families Ranidae, Leptodactylidae, and Hylidae as defined for the principal component analysis in this study include genera which are often placed in separate families of their own. The genera were lumped into these three families rather than split into a larger number of smaller families in order to have a large enough sample size for comparison. I consider this procedure to be justified because the same range of locomotor types and morphological variation exists in the smaller family units as found in the pooled families used in this study. For calculation of dimensionless variables for the study of variation in the family Leptodactylidae, the master equation was derived after first excluding the myobatrachids. This was done because the small number of myobatrachids in the sample did not make it feasible to calculate separate equations. In the case of the Ranidae, master equations were initially generated separately for all three groups, ranids, hyperolids, and rhacophrids. The slopes were so similar among the three groups, however, that the master equations from the ranid subsample were chosen to represent master equations for all three groups (Appendix 6).

The choice of different standard variables against which to regress the other measurements was based on wanting both an independent estimator of size (snout-vent length) and a functionally significant

TABLE 1. Loadings of transformed variables on first four rotated axes, interfamilial data set.

Character*	Factor 1	Factor 2	Factor 3	Factor 4
FEMSV	0.90957	0.20876	-0.10023	-0.07565
TIBFIBSV	0.93605	0.03970	-0.12554	-0.01711
TARSV	0.89434	0.15630	-0.12270	0.06849
FOOTSV	0.51843	0.08004	0.11787	-0.04532
HUMSV	0.21834	0.84078	-0.02710	0.11254
RADULSV	0.12791	0.93404	-0.03407	0.08708
HANDSV	0.54186	0.28134	-0.15793	-0.02196
GIRDLSV	-0.16848	-0.05212	0.95158	-0.19761
ILSV	-0.11894	-0.03626	0.92089	-0.00546
UROSTSV	0.22529	-0.20653	0.28543	-0.32563
TVWGIRDL	0.20981	0.54554	-0.30109	0.08874
TVWSV	0.18781	0.60788	-0.04010	0.02387
ILWIDIL	-0.18430	0.32488	-0.14984	0.3636
HTCRSTIL	0.12169	0.03928	-0.28639	-0.05492
VCLGIRDL	0.06819	0.08004	-0.62331	0.75945
VCLSV	-0.04723	0.11780	-0.03614	0.98043
% Variance	23.0%	17.6%	17.2%	11.8%

* Acronyms are defined in Appendix 3.

standard (girdle and ilium lengths). Previous work (Emerson, 1979, 1982) has shown that locomotor mode was better correlated with girdle and ilium lengths than with snout-vent length.

The four sets of transformed variables, those of the families Ranidae, Hylidae, and Leptodactylidae and the interfamilial data set, were first examined by principal component analysis of the correlation matrix followed by varimax rotation. Varimax rotation was chosen so that each factor would have only a few important variables, thus facilitating comparisons among groups. With varimax rotation the axes are orthogonal and therefore uncorrelated (SAS Institute, Inc., 1982). Variation on one axis is not correlated with variation on the others. Subsequently, morphological separation of the major locomotor types of frogs was studied with discriminant function analysis. This was done by classifying the interfamilial data set into nine locomotor types (Appendix 1) and running a canonical discriminant analysis. Acronyms are defined in Appendix 3. Computer analysis was done with an SAS program (SAS Institute, Inc., 1982).

Morphological variation within and across families was compared by use of multivariate coefficients of variation (Van Valen, 1978). For this analysis, the Ranidae were subdivided into three separate family units, the Ranidae, Rhacophoridae, and Hyperolidae (Appendix 2). The myobatrachids were removed from the Leptodactylidae and not included in the analysis (Appendix 2). This regrouping was done to increase the likelihood that

measurements of variation were done on monophyletic families.

The raw data were log transformed and the multivariate coefficient of variation

$$CV = 100 \sqrt{\frac{\sum \text{variance}}{\sum (\text{mean})^2}}$$

was calculated for the 14 measured variables (Appendix 1). The resulting coefficients of variation were compared between the interfamilial data set and each of the following family data sets: the Leptodactylidae, Ranidae, Rhacophoridae, Hyperolidae, and Hylidae.

Locomotor sequences were filmed at 25, 32, and 64 frames/second with a Beaulieux 16-mm camera. Films were analyzed on a Lafayette stop-frame projector. For purposes of comparison, hopping is defined as locomotion in which the animal's jump is less than ten times its body length in a single bound. All quadrupedal locomotion is considered walking.

Results

Multivariate Interfamilial Study

The results of the varimax rotation of the principal components are summarized in Table 1 and Figures 1-6. The loadings of the 16 variables on the first four rotated axes are given in Table 1. The first four axes account for about 69.6% of the total variation. The first axis is determined pri-

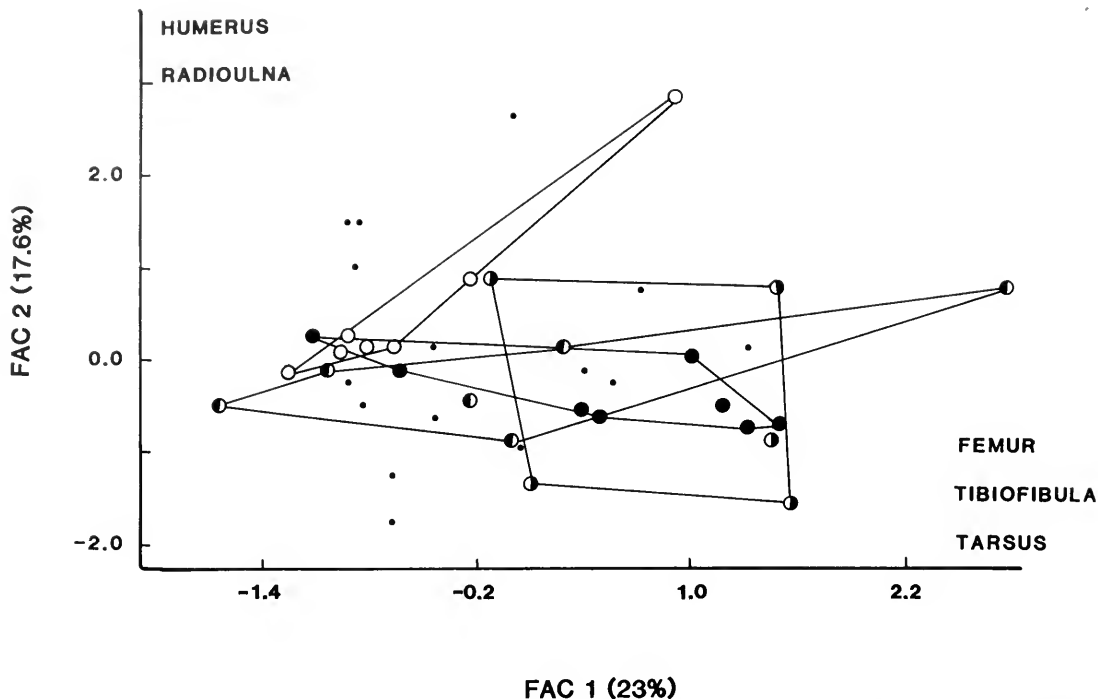


FIG. 1. Factor scores of 41 species for the first two rotated axes of the principal component analysis. Polygons enclose all species of a given family: ○ = bufonids; ● = ranids; ◐ = hylids; ◑ = leptodactylids; ● = scores of species in other families. High loading variables for each factor are indicated on the graph.

marily by femur, tibiofibula, and tarsus length, the second by humerus and radioulna length, the third by ilium and girdle length, and the fourth by vertebral column length.

Figure 1 shows the factor scores for the 41 species for the first two rotated axes. In this figure, minimum convex polygons have been drawn around each of the major families represented in the study, the Bufonidae, Leptodactylidae, Ranidae, and Hylidae. Notice that the polygon is distorted for each family by the presence of at least one outlier species.

The outlier genera are *Atelopus* (Bufonidae), *Eleutherodactylus* (Leptodactylidae), *Kassina* (Ranidae), *Pachymedusa* (Hylidae), and *Agalychnis* (Hylidae). *Atelopus*, *Pachymedusa*, and *Agalychnis* are characterized by having longer forelimbs than other members of their families. These genera use walking locomotion. The locomotor mode of *Eleutherodactylus* was not filmed. *Agalychnis*, *Atelopus*, and *Eleutherodactylus* appear to have relatively long legs in relation to other members of their respective families, while *Kassina* has short legs relative to other family members. *Kassina* also uses a walking locomotion.

Figure 1 also shows that, while members of the

Bufonidae have a unique combination of hind limb and forelimb morphology, the other families are characterized by factor loadings which are quite similar. Variation in hind limb and forelimb length does not sort out by family.

Figure 2 shows the distribution of locomotor types across the factor scores. The first two axes sort out the 41 species into two locomotor types. Minimum convex polygons have been drawn around swimmer-jumpers and walker-hopper-burrowers. Jumpers travel about 10 times their body length in a single bound; hoppers do not. Hoppers and jumpers also have different landing patterns. During hop landing the hind limbs are folded against the body, and the body swings through the forelimbs into the next hop. In jumping, the hind limbs are splayed posterolaterally and the entire body is used to absorb the force of landing.

The frog with the shortest hind limbs is *Pseudophryne occidentalis*. *Pseudophryne* is characterized by walking locomotion. The jumper-swimmers with the shortest hind limbs are *Pipa* and *Xenopus*, two totally aquatic genera. The walker-hopper-burrowers with the longest hind limbs are

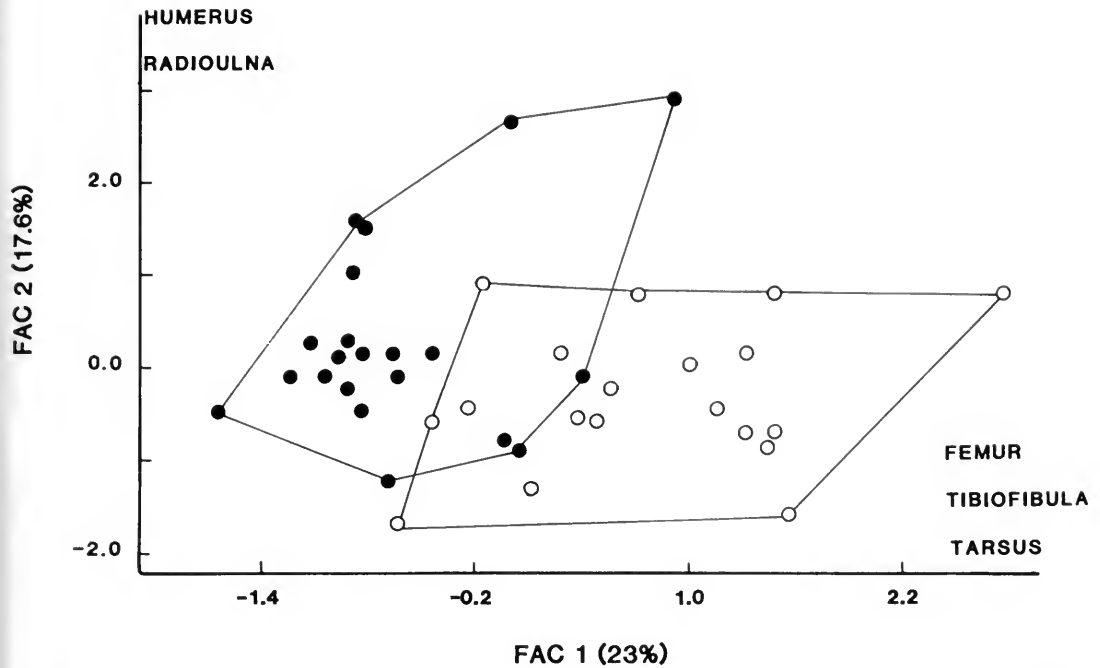


FIG. 2. Factor scores of 41 species for the first two rotated axes of the principal component analysis. Polygons enclose all species of a given locomotor mode: ○ = jumper-swimmers; ● = walker-hopper-burrowers.

Atelopus, *Gastrophryne*, and *Bombina*. *Gastrophryne* travels about eight and one-half times its body length in a single bound (Zug, 1978). It is not surprising, therefore, that it has one of the highest relative hind limb lengths of any of the hoppers. Interestingly, *Bombina* is a modest hopper (Wermel, 1934) despite its relatively long hind limbs; it travels about four times its body length in a single bound (Dobrowolska, 1973). The tarsus of *Bombina* is long for a walker-hopper-burrower (Dobrowolska, 1973), and that limb segment is, in theory, an important contributor to jump performance. Why, then, is *Bombina* such a poor jumper? *Bombina* has a very low takeoff angle during hopping (Emerson, pers. obs.) and often places its feet lateral to the body during takeoff, rather than close to the side of the body.

While a longer arm increases potential stride length during walking, *Dendrobates* and *Atelopus* are unusual among walker-hopper-burrowers in the extreme length of their forelimbs. *Atelopus* has an unusual walking mode. Unlike most walkers, *Atelopus* does not flex the vertebral column when the forelimb is protracted (see Barclay, 1946, and Emerson, 1979, for descriptions of the common quadrupedal locomotion pattern of frogs); instead, the back is held straight. Second, the long legs and

arms are not folded as tightly at the joints during protraction and retraction, and the body is held higher off the ground than with the more typical walking locomotion. The hopping locomotion of *Dendrobates* is not unusual, but the animals do often hold the anterior part of the body off the substrate, and the males have intraspecific combat involving use of the forelimbs. It is possible that the length of the forelimbs is related to the aggressive intraspecific behavior of the males. *Agalychnis* and *Pachymedusa*, two hylid genera with long forelimbs, appear to use slow walking locomotion similar to that of *Atelopus*; they do not appear to flex the vertebral column, the arms and legs are less protracted than those of walkers with lateral undulation, and the walk speed is much slower (Emerson, 1979).

Among walkers, *Melanophryniscus*, *Oreophrynella*, and *Atelopus* show an interesting morphological and behavioral cline. *Melanophryniscus* has the shortest hind limbs of the three genera and typical walking locomotion with vertebral flexure. *Oreophrynella* has a shortened presacral vertebral column and longer hind limbs. Behaviorally, it lacks vertebral flexure, shows a more lateral positioning of the limbs, and also has a more elevated body. *Oreophrynella* has a relatively shorter stride

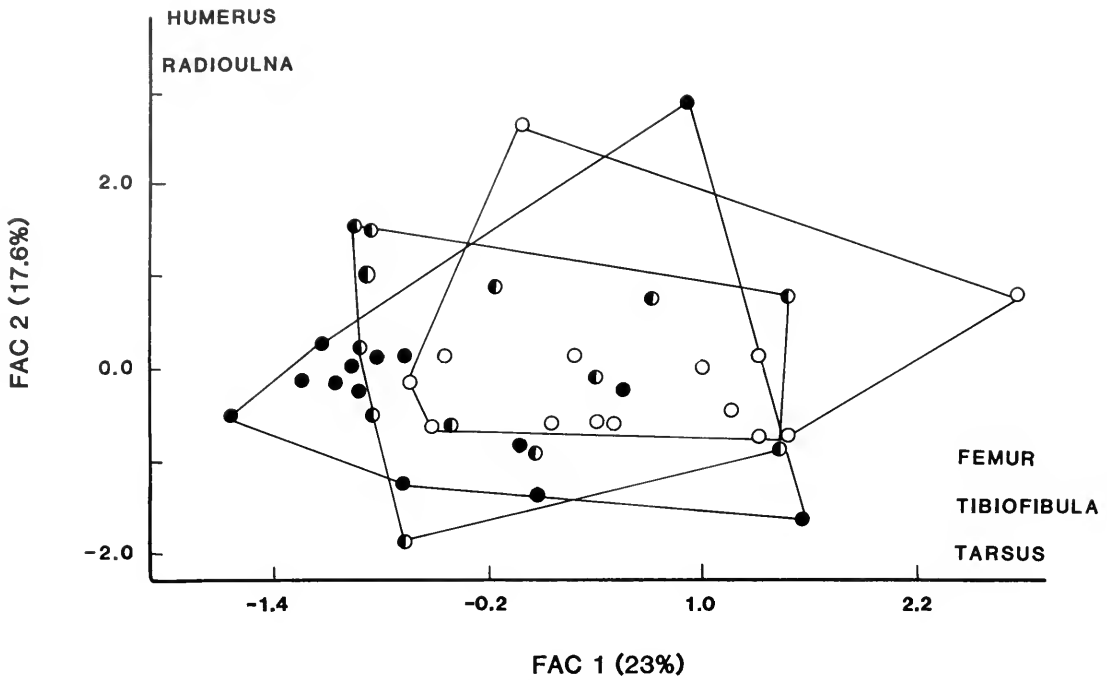


FIG. 3. Factor scores of 41 species for the first two rotated axes of the principal component analysis. Polygons enclose all species of a given articulation type: ○ = type I; ● = type IIA; ○ = type IIB.

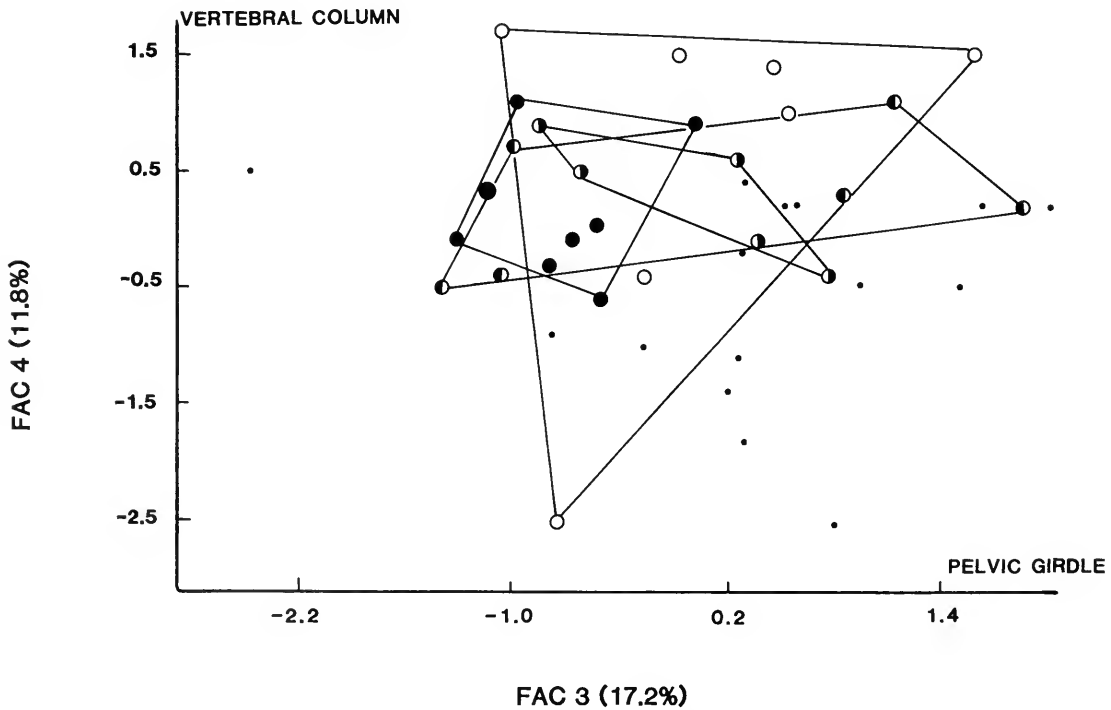


FIG. 4. Factor scores of 41 species for the third and fourth rotated axes of the principal component analysis. Polygons enclose all species of a given family: ○ = bufonids; ● = ranids; ○ = hylids; ○ = leptodactylids; ● = scores of species in other families. High loading variables for each factor are indicated on the graph.

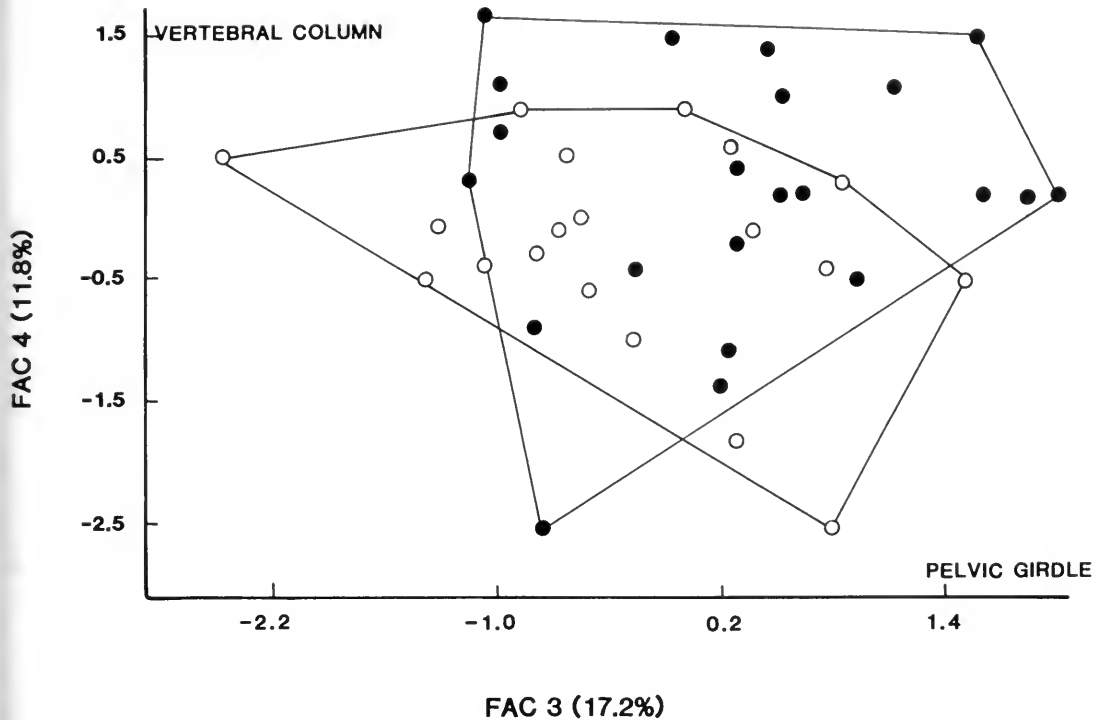


FIG. 5. Factor scores of 41 species for the third and fourth rotated axes of the principal component analysis. Polygons enclose all species of a given locomotor mode: ○ = jumper-swimmers; ● = walker-hopper-burrowers.

length than *Melanophryniscus* because it does not protract the limbs as far during locomotion, and consequently is a slower walker. *Atelopus* has the longest hind limbs and forelimbs of the three genera. It also lacks vertebral flexion. *Atelopus* is characterized by having a slow walking locomotion with relatively laterally placed limbs and by having the body elevated off the ground.

Figure 3 shows the distribution of the three major articulation types (Emerson, 1979) along the first two axes. The articulation types are not distinguished by differences in forelimb and hind limb.

In Figure 4, minimum convex polygons have been drawn around factor scores of individuals from the four major families. Clearly, differences in vertebral column length and pelvic girdle length do not distinguish the different family groups. On the average, ranids have shorter pelvic girdles than bufonids. The leptodactylid and hylid species in this study show overlapping pelvic girdle lengths.

Figure 5 shows the distribution of the two major locomotor types along the third and fourth axes. The locomotor groups designated in this study are not distinguished by differences in vertebral column and pelvic girdle length.

Figure 6 shows the distribution of the three ma-

lor articulation types among the factor scores. While there is a great deal of overlap among articulation types, individuals of types I and IIA tend to have longer girdles than type IIB.

Intrafamilial Comparisons

Table 2 summarizes the results of the principal component analysis on three anuran families, the Leptodactylidae, Hylidae, and Ranidae. The amount of variance explained on each of the first four axes and the factors with the highest loadings on each axis are included. The same variables load most heavily on each axis for the Hylidae and Leptodactylidae. A similar amount of variance is explained by each axis. In the Ranidae the highest loadings on the fourth axis are humerus and radioulna rather than vertebral column.

All three families show the same variables contributing most heavily to the first three axes: length of the femur, tibiofibula, tarsus, pelvic girdle, and transverse process. A similar amount of variance is accounted for by each of the four major axes within each of the families and among all frogs in the interfamilial sample. The interfamilial sample

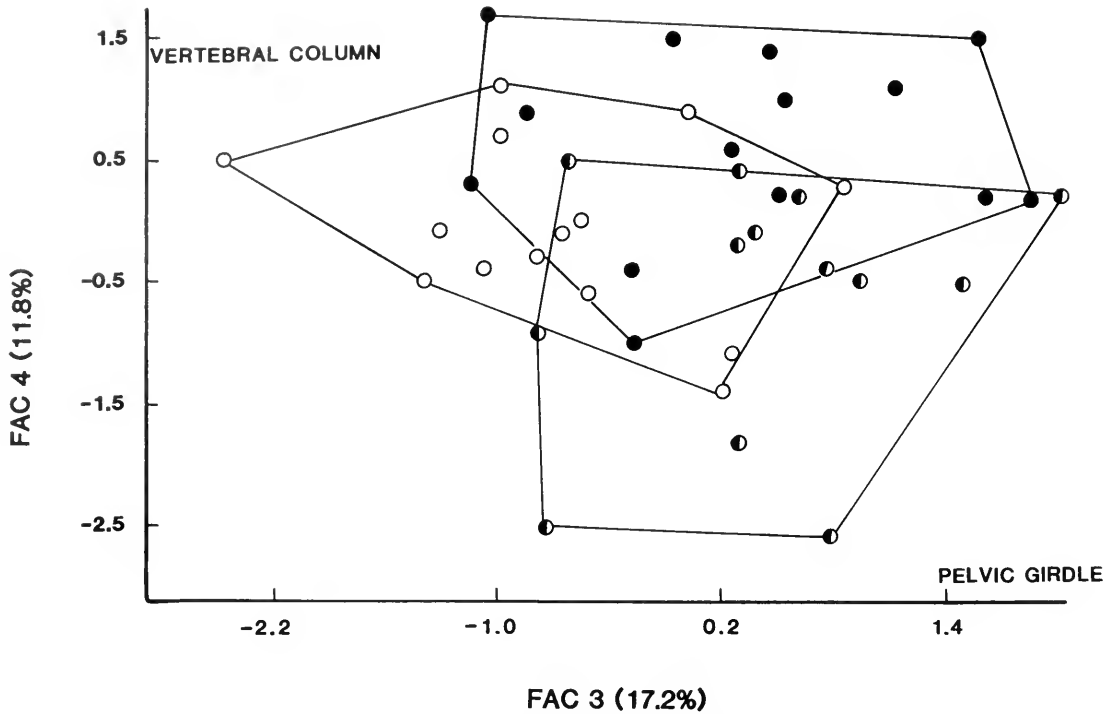


FIG. 6. Factor scores of 41 species for the third and fourth rotated axes of the principal component analysis. Polygons enclose all species of a given articulation type: ● = type I; ● = type IIA; ○ = type IIB.

differs in that forelimb length is more variable than within families.

Many of the morphological features listed above appear as variable at the intrafamilial level as at the interfamilial level. In the interfamilial sample, however, only a few representative genera were chosen for each family. It is important, therefore, to examine whether these genera encompass the entire range of variation found within the family

when a larger sample is analyzed. For the Bufonidae and Leptodactylidae, the entire range of variation in hind limb length is included in the interfamilial subsample. For the Hylidae and Ranidae it is more complicated.

The range of variation represented by the 41 species interfamilial subsample is a good reflection of the total range of variation in hind limb length across frogs, but the mean factor scores for the

TABLE 2. Variables loading on first four factors and the variance explained by each factor.

Factors	Interfamilial sample		Intrafamilial samples					
	Variables	% Variance	Hylidae		Leptodactylidae		Ranidae	
			Variables	% Variance	Variables	% Variance	Variables	% Variance
I	Femur Tibiofibula Tarsus	23.0%	Tibiofibula Femur Tarsus	21.0%	Femur Tibiofibula Tarsus	26.9%	Femur Tibiofibula Tarsus	26.9%
II	Humerus Radioulna	17.6%	Pelvic girdle Ilium	17.0%	Pelvic girdle Ilium	17.8%	Pelvic girdle Ilium	17.2%
III	Pelvic girdle Ilium	17.2%	Transverse process	15.7%	Transverse process	16.2%	Transverse process	16.4%
IV	Vertebral column	11.8%	Vertebral column	15.0%	Vertebral column	13.0%	Humerus radioulna	13.4%

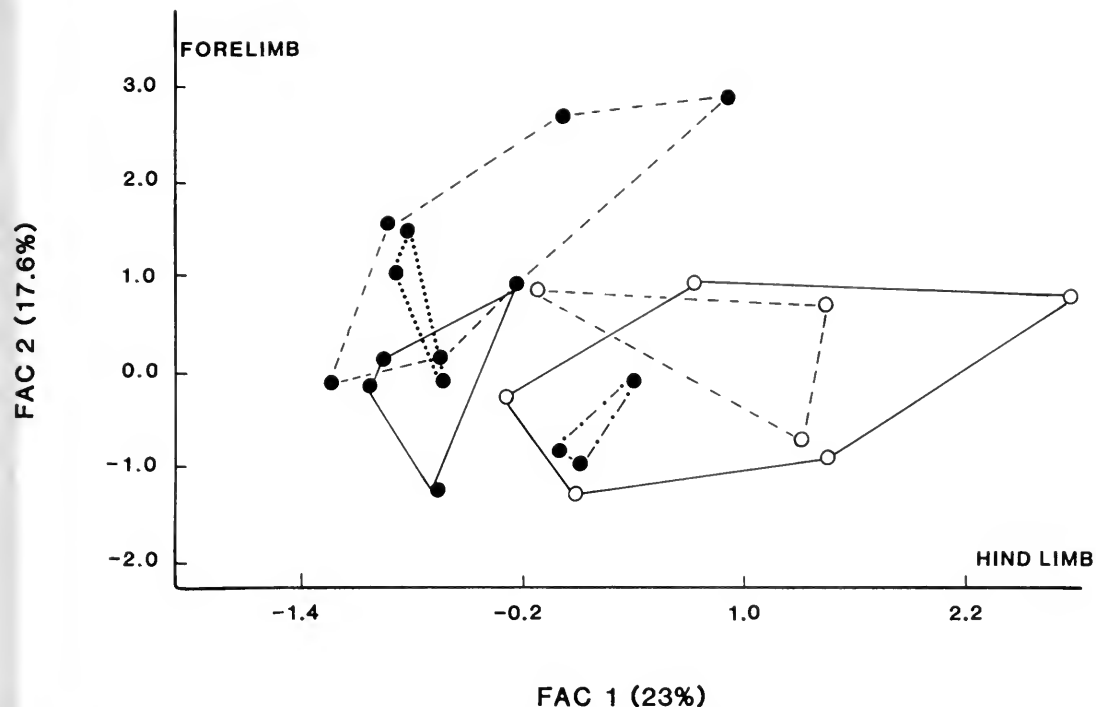


FIG. 7. Factor scores of 41 species for the first two rotated axes of the principal component analysis. Polygons enclose all species of a given locomotor mode: ● --- = walker-hoppers; ● = hopper-burrowers; ● — = walker-hopper-burrowers; ● - - - = hoppers; ○ — = jumpers; ○ - - - = jumper-walkers; ● = all species classified as walker-hopper-burrowers in Figure 2; ○ = all species called jumper-swimmers in Figure 2.

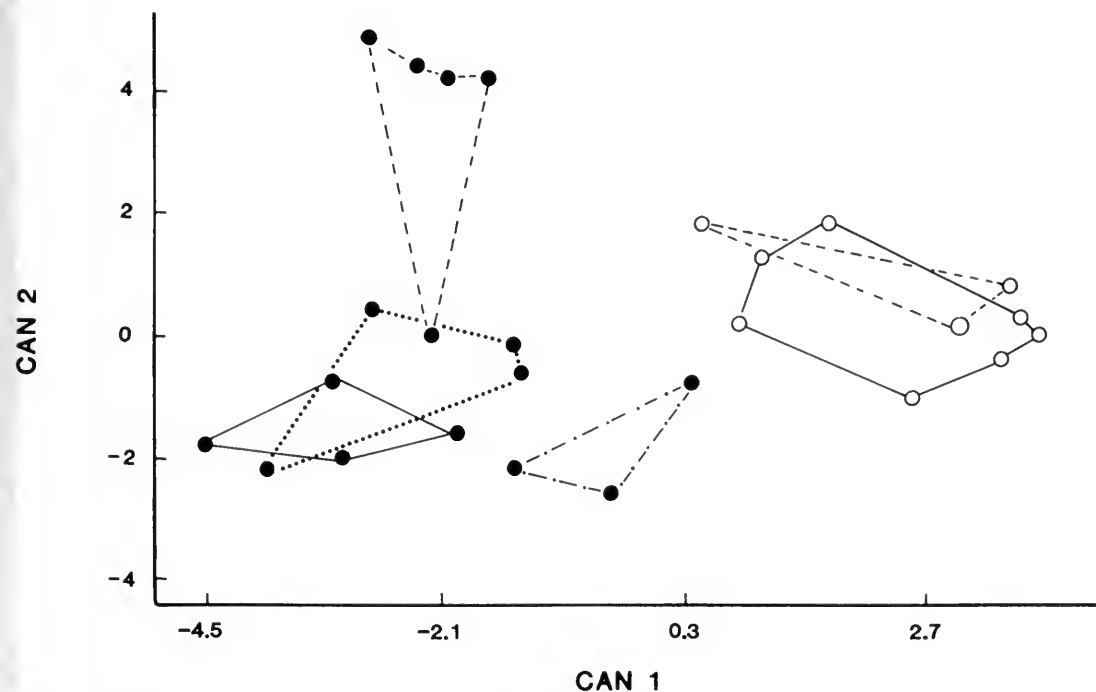


FIG. 8. Separation of locomotor modes along the first two canonical variates of the canonical discrimination analysis. Polygons enclose all species of a given locomotor mode. Symbols are the same as in Figure 7.

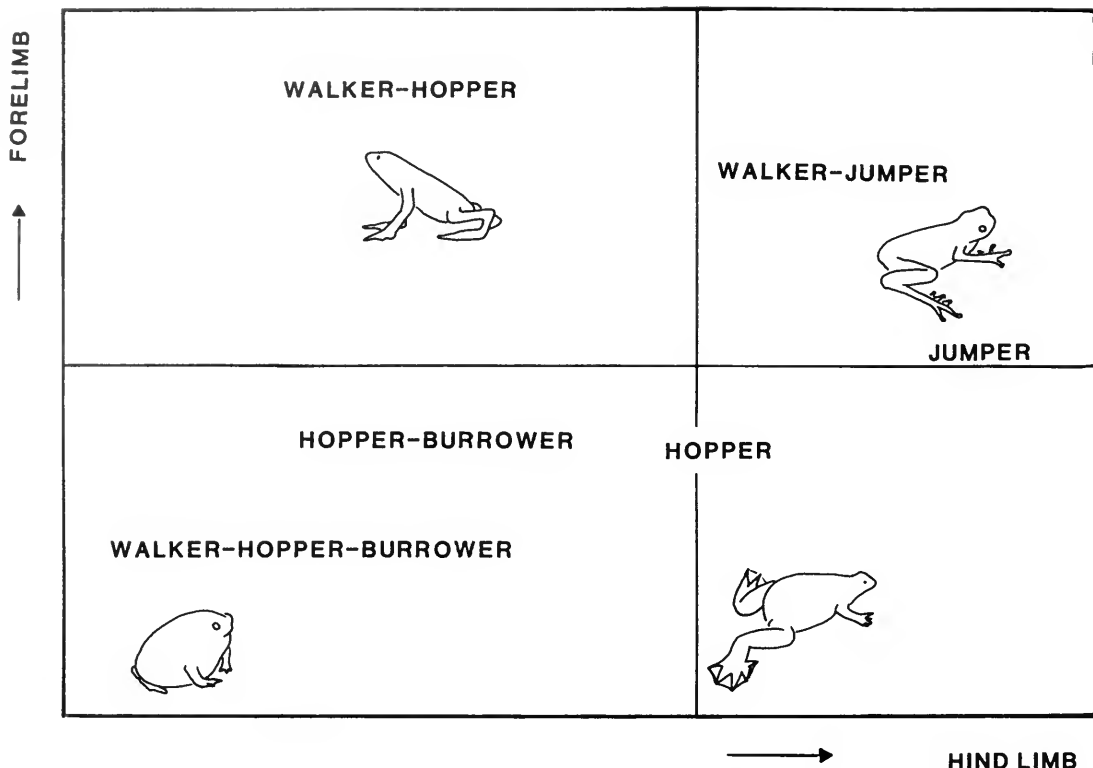


FIG. 9. Diagrammatic representation of frog limb morphospace. Locomotor modes are mapped according to results from principal component analysis.

Ranidae and the Hylidae in the interfamilial sample are lower than those for the families when a larger number of species is analyzed. The hylid genera sampled in the interfamilial study have shorter hind limbs than many members of the family. The low endpoint is accurate, but not the high. Ranids are similar; there are ranids with longer hind limbs than those in the interfamilial sample, but the shortest hind limb genera have been included. The range of forelimb, pelvic girdle, vertebral column, and transverse process variation within the large sample of each family is similar to that in the interfamilial sample, with the exception of a couple of extreme outliers.

Hemiphractus has unusually long transverse processes among hylids, while *Ooedozyga* has unusually long transverse processes and a short pelvic girdle among ranids.

Locomotor Groups of Frogs

While Figure 2 shows that differences in hind limb and forelimb are correlated with locomotor

mode, only two general categories were recognized: swimmer-jumpers and walker-hopper-burrowers. In fact, there are nine locomotor modes among the 41 species in the interfamilial sample (Appendix 1). When locomotor type is divided more finely, hind limb and forelimb differences—the characters explaining the most variation in the principal component analysis—do not map directly on locomotor mode (fig. 7). For example, jumpers and hoppers have overlapping hind limb lengths and walker-hoppers and walker-hopper-burrowers show some overlap in forelimb and hind limb lengths. Nonetheless, there are some striking examples of convergence (fig. 7). The three hoppers belong to three separate families but have converged toward a common hind limb length. The walker-hopper-burrowers from four different families have similar limb proportions. The jumpers include species from four families.

In the canonical discriminant analysis, separation of the locomotor groups is along somewhat different morphological axes than in the principal component analysis (fig. 8). Femur, tarsus, humerus, girdle, and transverse process lengths have

TABLE 3. Standardized canonical coefficients for the first two canonical variates.

Character	Canonical I	Canonical II
FEMSV	0.8523	2.0953
TIBFIBSV	0.1657	2.3443
TARSV	1.4295	0.0175
FOOTSV	-0.3364	-0.5710
HUMSV	-1.0080	-0.4069
RADULSV	-0.0023	0.8558
HANDSV	-0.2300	0.1450
GIRDLSV	-0.7834	0.1603
UROSTSV	0.3538	-0.5506
TVWGIRDL	-0.6759	1.7144
ILWIDIL	0.2815	0.0632
HTCRSTIL	0.3093	-0.4832
VCLSV	-0.7438	-0.3354

the highest standardized canonical coefficients for the first canonical variable (table 3). Femur, tibiofibula, and transverse process lengths have the highest coefficients for the second canonical variable. When the variance within groups is minimized, the first canonical variable separates jumpers and hoppers, and the second canonical variable separates the walker-hoppers from the walker-burrowers from the walker-hopper-burrowers. Diagrammatically, the relationship between limb length and locomotor mode is summarized in Figure 9. Outlines of taxa representing the major locomotor modes have been drawn to aid in the visualization.

Coefficients of Variation

Table 4 summarizes the multivariate coefficients of variation for five frog families and the interfamilial data set. Two of the families have coefficients of variation that are slightly higher than that of the interfamilial sample. The other families have coefficients of variation that are slightly lower than that of the interfamilial sample.

TABLE 4. Coefficients of variation.

	Interfamilial sample	Intrafamilial sample				
		Hylidae	Leptodactylidae	Ranidae	Rhacophoridae	Hyperolidae
No. species	41	28	19	15	10	7
No. variables	14	14	14	14	14	14
Multivariate CV	20.83%	14.62%	21.9%	21.2%	15.2%	12.0%

Discussion

Convergence

Hind limb and forelimb lengths are clearly the most important aspects of postcranial morphology in distinguishing among the locomotor modes of frogs, and also account for the largest amount of variation in postcranial morphology across families. Figure 7 shows that there has been convergence in limb proportions among unrelated frogs with the same locomotor mode, but within any single locomotor mode there is still a fair amount of variation. This variation does not necessarily weaken the case for convergence; rather, it affirms, I think, the complexity of the biological world.

All jumpers, by our definition, travel more than 10 times their body length in a single bound. That does not mean, however, that all jumpers must have the same hind limb length and jump capability. Within a locomotor mode there are differences in performance. Secondly, a locomotor mode may require a threshold morphological configuration but not be limited by a morphology that extends past that minimum. For example, to burrow it may be necessary to have a certain minimum hind limb length (see Emerson, 1976, for the functional explanation), but when the hind limb length shortens beyond that threshold it does not restrict the animal from digging. There may be differences in digging performance, but they may not be significant in the natural history of the animal.

I would suggest that much of the variation in pertinent morphology within a locomotor mode is related to the peculiar phylogenetic history of the unrelated animals. And, consequently, that convergence needs to be thought of as a relative phenomenon. The diagrammatic representation of locomotor types on limb morphospace suggests that walkers have longer forelimbs, yet the jumping-walking locomotor mode cannot be separated morphologically from the jumpers in the interfa-

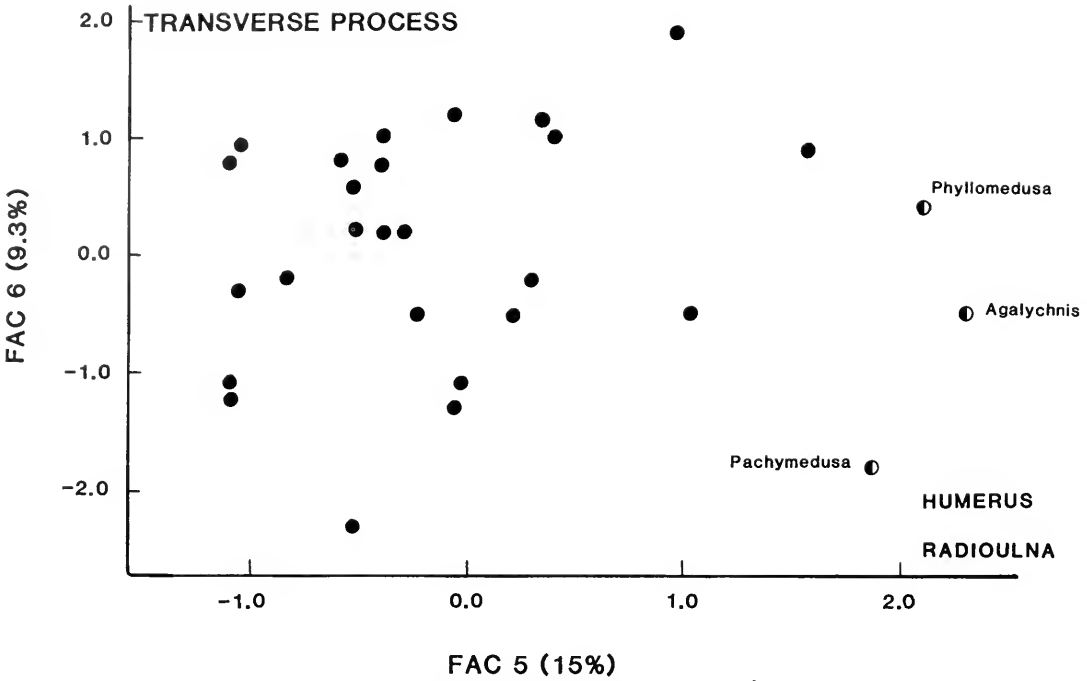


FIG. 10. Factor scores of hylid species for the fifth and sixth rotated axes of the principal component analysis. Jumper-walker genera are identified by name; ● = other species of the family.

miliar study (fig. 8). If, however, forelimb morphology of *Pachymedusa* and *Agalychnis*, two jumper-walkers, is compared with that of other members of the same family, a different picture emerges. Figure 10 plots the results of part of the

principal component analysis run on the postcranial morphology of the family Hylidae (see Appendix 2 for species). Forelimb variables load most heavily on the fifth axis. Notice that while *Agalychnis* and *Pachymedusa* do not have unusually

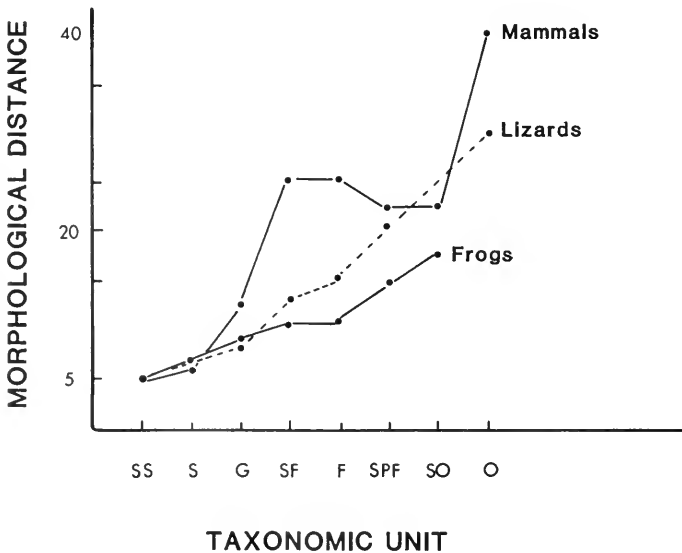


FIG. 11. Morphological distance plotted as a function of taxonomic level for three groups of vertebrates (data from Cherry et al., 1982). SS = subspecies; S = species; G = genus; SF = subfamily; F = family; SPF = superfamily; SO = suborder; O = order.

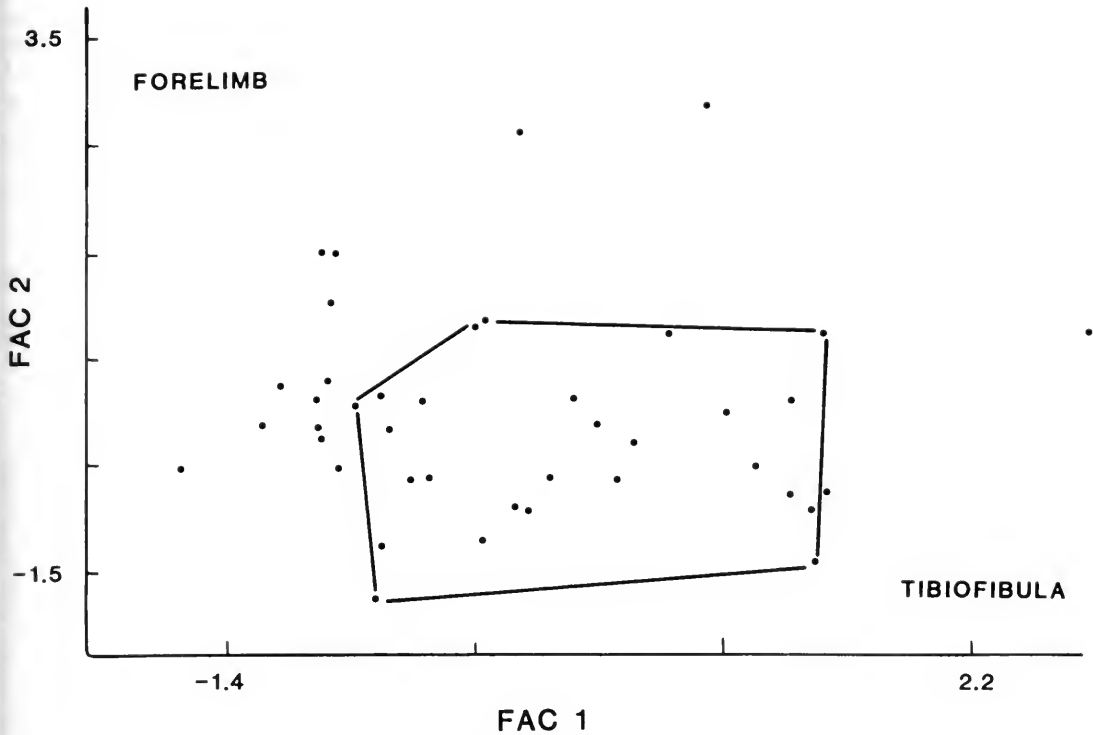


FIG. 12. Factor scores of 41 species for the first two rotated axes of the principal component analysis. Lines enclose species sampled by Cherry et al., 1982; each dot represents a separate species.

long forelimbs compared to other jumpers across different families, they do have long forelimbs relative to other hylids.

Variation

An interesting outcome of this study is that similar aspects of postcranial morphology are the most variable within and between families, and these features account for about the same amount of variation on each axis. The most striking difference is that in the interfamilial sample forelimb variation is much more important.

Recently, an attempt has been made to compare morphological variation among vertebrate classes using a standardized set of measurements to calculate a "morphological distance" (Cherry et al., 1978; Cherry et al., 1982; Wilson et al., 1984). When such morphological distances are plotted for three vertebrate groups as a function of taxonomic level, two patterns emerge (fig. 11; data from Cherry et al., 1982). First, there is increasing morphological distance at higher taxonomic categories within each vertebrate group. Secondly, frogs show

less morphological distance at higher taxonomic levels than either lizards or mammals. This finding lends support to the notion that frogs are less diverse morphologically than other vertebrate groups, but there have been a number of criticisms of the morphological distance measurement. Critics have pointed out both conceptual and statistical problems (Findley, 1979; Atchley, 1980; Hafner et al., 1984). The data from this study highlight yet another problem. While over 1,200 frogs were measured for the 1982 study (Cherry et al., 1982), the results of the present work indicate that the authors seriously undersampled morphological diversity. Two components of the morphological distance measurement are forelimb length and tibiofibula length. These variables have high loadings on the first two axes of the principal component analysis from this study. Figure 12 shows the diversity sampled in the 1982 study compared to the range of morphology represented by the 41 species in this study. That underestimation, if unique to the frog sample, could account for the differences in morphological distance between frogs and lizards and mammals.

A much more serious problem with the mor-

phological distance studies is the fact that taxonomic categories above the species level have no objective biological definition. There is no reason, a priori, for a family of mammals to be based on the same criteria as a family of frogs. Higher categories are defined by the systematists who do the work on the group. The categories do not have any intrinsic biological properties. For this reason, it seems unlikely that we can gain insight into the relative variability of frogs compared to other vertebrates by making comparisons across classes.

We can, however, look at the question another way. Empirical data from bats show that the variances of shape characters increase about an order to magnitude between the generic and familial levels (Lemen & Freeman, 1984). Increasing morphological variability with taxonomic level is consistent with how higher taxonomic levels are generally defined. We can ask whether frogs conform to this pattern. Do frogs show the expected relationship of increased variability with higher taxonomic levels? When the relative variability of the interfamilial data set is compared with that of the several frog family data sets, there is little difference in the levels of variation. Within- and between-family data sets show similar multivariate coefficients of variation (table 4). If increasing variation with taxonomic level is the common pattern among vertebrates, then frogs do appear to be an exception: Ordinal level variation is less than expected.

The seemingly low level of morphological variation within frogs has been ascribed to their high degree of morphological specialization (Inger, 1967). The striking similarity in patterns of postcranial variation within and between families suggests that there is some set of constraints shaping the variation. The nature of those constraints, however, remains unknown.

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Appendices

Appendix 1: Interfamilial Sample

Species	Articulation type	Locomotor mode
Pipidae		
<i>Xenopus laevis</i>	I	Swimmer
<i>Pipa pipa</i>	I	Swimmer
Ascaphidae		
<i>Ascaphus truei</i>	IIB	Jumper
Discoglossidae		
<i>Bombina orientalis</i>	I	Hopper
<i>Discoglossus pictus</i>	IIA	Jumper
Rhinophrynyidae		
<i>Rhinophrynus dorsalis</i>	IIA	Walker-hopper-burrower
Pelobatidae		
<i>Pelobates fuscus</i>	I	Hopper-burrower
<i>Scaphiopus couchii</i>	I	Hopper-burrower
<i>Megophrys monticola</i>	I	Walker-hopper
Bufonidae		
<i>Bufo boreas</i>	IIA	Walker-hopper-burrower
<i>Bufo blombergii</i>	IIA	Walker-hopper
<i>Bufo americanus</i>	IIA	Walker-hopper
<i>Bufo calamita</i>	IIA	Walker-hopper-burrower
<i>Atelopus varius</i>	IIA	Walker-hopper
<i>Melanophryniscus stelzneri</i>	IIA	Walker-hopper
<i>Oreophrynella quelchii</i>	I	Walker
Rhinodermatidae		
<i>Rhinoderma darwini</i>	I	Jumper
Leptodactylidae		
<i>Notaden bennetti</i>	IIA	Walker-hopper-jumper
<i>Pseudophryne occidentalis</i>	IIA	Walker-burrower
<i>Physalaemus pustulosus</i>	IIA	Hopper
<i>Leptodactylus melanonotus</i>	IIB	Jumper
<i>Eleutherodactylus rhodopis</i>	IIB	Jumper
<i>Telmatobius marmoratus</i>	IIB	Jumper
Hylidae		
<i>Pseudacris triseriata</i>	IIA	Jumper
<i>Hyla cinerea</i>	I	Jumper
<i>Phrynohyas venulosa</i>	IIA	Jumper
<i>Agalychnis callidryas</i>	I	Jumper-walker
<i>Pachymedusa dacnicolor</i>	I	Jumper-walker
Dendrobatidae		
<i>Dendrobates tinctorius</i>	IIB	Walker-hopper
Ranidae		
<i>Rana clamitans</i>	IIB	Jumper
<i>Polypedates leucomystax</i>	IIB	Jumper
<i>Rhacophorus pardalis</i>	IIB	Jumper-walker
<i>Chiromantis rufescens</i>	IIB	Jumper
<i>Hyperolius marmoratus</i>	IIB	Jumper
<i>Leptopelis aubryi</i>	IIB	Jumper
<i>Leptopelis bocagii</i>	IIB	Hopper-burrower
<i>Kassina senegalensis</i>	IIA	Walker
Microhylidae		
<i>Kaloula pulchra</i>	I	Walker-hopper-burrower
<i>Hypopachus muelleri</i>	IIA	Walker-hopper-burrower
<i>Gastrophryne carolinensis</i>	I	Hopper
<i>Phrynomerus bifasciata</i>	I	Walker-burrower

Hylidae

Acris crepitans
Acris gryllus
Pachymedusa dacnicolor
Agalychnis callidryas
Smilisca baudinii
Smilisca phaeota
Hyla arenicolor
Hyla cinerea
Hyla gratiosa
Hyla lichenata
Osteopilus septentrionalis
Osteopilus brunneus
Litoria caerulea
Litoria infrafenata
Litoria lesuerii
Litoria alboguttata
Phrynohyas venulosa
Pseudacris triseriata
Pseudacris ornata
Pternohyla fodiens
Tripurion spatulatus
Hemiphysalus scutatus
Osteocephalus buckleyi
Phyllomedusa iheringii
Gastrotheca marsupiata
Nyctimystes papua
Nyctimystes narinosa
Cyclorana platycephala

Leptodactylidae

Eleutherodactylus bufoniformis
Eleutherodactylus rhodopis
Physalaemus pustulosus
*Neobatrachus pictus**
Leptodactylus labialis
Leptodactylus melanonotus
Leptodactylus ocellatus
Pleurodema bibroni
Pleurodema bufonia
*Notaden bennetti**
Telmatobius culeus
Telmatobius marmoratus
Crossodactylus dispar
Hylodes lateristrigatus
Limnomedusa macroglossa

Leptodactylidae (Continued)

Lithodytes lineatus
Eupsophus monticola
*Heleioporus albopunctatus**
*Limnodynastes dorsalis**
*Limnodynastes ornatus**
*Pseudophryne occidentalis**
Odontophrynus americanus
Batrachophrynus macrostomus
Ceratophryx ornata
Hylorina sylvatica
Caudiverbera caudiverbera

Ranidae

Pyxicephalus adpersa
Philautus bimaculatus†
Amolops jerboa
Afrixalus wittei‡
Chiromantis rufescens†
Cryptothylax greshoffi‡
Hyperolius marmoratus‡
Kassina senegalensis‡
Leptopelis aubryi‡
Leptopelis bocagii‡
Ooiedozyga laevis
Nyctixalus pictus†
Ceratobatrachus guentheri
Rana clamitans
Rana sylvatica
Conraua goliath
Arthroleptides martiensseni
Arthroleptis stenodactylus
Discodeles bufoniformis
Kassina maculata‡
Platymatnis guppyi
Staurois natator
Phrynobatrachus krefftii
Mantidactylus gutturalis†
Rhacophorus appendiculatus†
Rhacophorus dugritei†
Rhacophorus pardalis†
Rhacophorus colletti†
Polypedates leucomystax†
Polypedates dennysi†
Ptychadena mascareniensis
Hemisus marmoratus

* Myobatrachids. † Rhacophorids. ‡ Hyperolids.

Appendix 3: Master Equations for Interfamilial Sample

Variable	Slope (b)	log a	Y	X
FEMSV	1.000	+0.435	Femur	Snout-vent
TIBFIBSV	0.958	+0.352	Tibiofibula	Snout-vent
TARSV	0.887	+0.472	Tarsus	Snout-vent
FOOTSV	1.040	+0.626	Foot	Snout-vent
HUMSV	0.975	+0.539	Humerus	Snout-vent
RADULSV	0.986	+0.695	Radioulna	Snout-vent
HANDSV	1.110	+0.834	Hand	Snout-vent
GIRDLSV	1.060	+0.475	Girdle	Snout-vent
ILSV	1.050	+0.515	Ilium	Snout-vent
UROSTSV	1.050	+0.624	Urostyle	Snout-vent
TVWGIRDL	1.020	+0.526	Transverse process	Pelvic girdle
TVWSV	1.120	+1.090	Transverse process	Snout-vent
ILWIDIL	0.941	+0.212	Ilium width	Ilium
HTCRSTIL	0.834	+0.867	Height of dorsal crest on ilium	Ilium
VCLGIRDL	0.939	+0.008	Vertebral column	Pelvic girdle
VCLSV	1.033	+0.521	Vertebral column	Snout-vent

Appendix 4: Master Equations for Hylidae Intrafamilial Sample

Variable	Slope (b)	log a
FEMSV	0.942	+0.279
TIBFIBSV	0.931	+0.230
TARSV	0.996	+0.588
FOOTSV	0.882	+0.271
HUMSV	1.044	+0.693
RADULSV	0.986	+0.727
HANDSV	1.100	+0.806
GIRDLSV	1.069	+0.508
ILSV	1.093	+0.593
UROSTSV	1.094	+0.691
TVWGIRDL	0.752	+0.175
TVWSV	0.811	+0.569
ILWIDIL	0.017	-0.646
VCLGIRDL	0.963	+0.033
VCLSV	1.046	+0.549

Appendix 5: Master Equations for Leptodactylidae Intrafamilial Sample

Variable	Slope (b)	log a
FEMSV	0.963	+0.342
TIBFIBSV	0.968	+0.324
TARSV	0.960	+0.613
FOOTSV	0.941	+0.354
HUMSV	1.057	+0.667
RADULSV	0.989	+0.689
HANDSV	1.376	+1.368
GIRDLSV	0.993	+0.384
ILSV	0.938	+0.342
UROSTSV	0.966	+0.468
TVWGIRDL	1.081	+0.530
TVWSV	1.102	+0.994
ILWIDIL	0.198	-0.551
VCLGIRDL	0.960	+0.044
VCLSV	0.970	+0.440

Appendix 6: Master Equations for Ranidae Intrafamilial Sample

Variable	Slope (b)	log a
FEMSV	1.031	+0.401
TIBFIBSV	1.037	+0.380
TARSV	1.002	+0.632
FOOTSV	0.985	+0.332
HUMSV	1.030	+0.640
RADULSV	0.978	+0.690
HANDSV	1.032	+0.668
GIRDLSV	1.114	+0.615
ILSV	1.009	+0.454
UROSTSV	0.982	+0.496
TVWGIRDL	0.966	+0.300
TVWSV	1.149	+1.026
ILWIDIL	0.015	-0.667
VCLGIRDL	0.879	-0.090
VCLSV	1.026	+0.535





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