Convergent evolution of lizard toe fringes

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Lizard toe fringes are composed of laterally projecting elongated scales and have arisen independently at least 26 times in seven families of lizards. Four different fringe types are identified: triangular, projectional, conical and rectangular. To determine if variation in fringe morphology can be attributed to environmental differences, each independent evolution of a fringe type is identified; correlation of substrate types with evolutionarily independent fringe morphologies are then studied. Variation in fringe morphology shows a strong association with substrate type: triangular, projectional and conical fringes with windblown sand; and rectangular fringes with water. Some aspects of fringe morphology may result from differences in functional requirements, and others may have no adaptive significance. This example of convergent evolution points out difficulties inherent to comparative studies of adaptation and underscores the value of broad comparative surveys which provide an alternative to *ad hoc* adaptive explanations of similarity.

KEY WORDS:—adaptation – comparative method – convergence – lizard toe morphology – locomotion.

CONTENTS

INTRODUCTION

Examples of convergent evolution are often used to suggest adaptive hypotheses of form (Beecher, 1951; Packard, 1972; Cody & Mooney, 1978; Nevo, 1979, Olson & Feduccia, 1980). One way to test these hypotheses is to study association of form with abiotic or biotic features of the environment (Lack, 1966; Harcourt, Harvey, Larson & Short, 1981). If the distribution of a trait can be predicted from these features then the observed variation is considered to be adaptive (Clutton-Brock & Harvey, 1979). Adaptive explanations may be further supported by comparing closely related species that occupy different habitats; differences in morphology or ecology are interpreted

as adaptation to different environments (Crook, 1964; Lack, 1966; Clutton-Brock & Harvey, 1977; Orians & Paine, 1983; Wanntorp, 1983).

Non-adaptive differences in form may also be suggested by comparative analysis (Lauder, 1981). If study fails to reveal patterns of form–environment association or constraints to the evolution of form, then random processes should be considered. The purposes of this paper are to identify an example of convergent evolution, to determine the degree of morphological similarity, and to assess the adaptive significance of morphological variation by associating form and environment.

Toe fringes are laterally projecting elongated scales. They are sometimes cited as an excellent example of convergent evolution (e.g. Bellairs, 1969) since many distantly related lizard taxa apparently have evolved fringes independently. Toe fringes are often cited as an adaptation to locomotion on shifting sand. In the genus *Uma*, the N American fringe-toed lizards, fringes are used both in locomotion across dune surfaces and in 'swimming' through sand (Stebbins, 1944). Other fringed species run across water (Laerm, 1973, 1974), dig (Brain, 1962; Arnold, 1983) and possibly glide (Schiotz & Volsoe, 1959). In some lizards, fringes have been shown to increase the efficiency of locomotion across water and sand (Laerm, 1973, 1974, for *Basiliscus*; Carothers, unpubl. obs., for *Uma*).

Fringes are almost ideal for studies of convergent evolution. Firstly, they are morphologically simple, easily described structures. Like all scales, they are localized elevations and thickenings of the epidermal and dermal tissue (Maderson, 1964) and are often simple elaborations of a medial keel. Second, because fringes have evolved repeatedly and have a high degree of repetition, they allow more rigorous testing of correlations between form and environment. Third, in some studies, environmental elements relevant to the evolution of form may be difficult to identify or measure. Since fringes are located on the feet of lizards, the substrate is a likely candidate with which to explore possible form–environment associations. Luckily, substrate information is available in the literature. Fourth, fringe presence or absence in closely related species does not appear to be correlated with the morphology of other structures. This suggests that they may function independently rather than working as a part of a larger functional system. Independence weakens the hypothesis that fringe presence or shape is due to selection pressure on correlated characters (Emerson, 1982; Lande & Arnold, 1983), although pleiotropic effects may still be present (e.g. Gans, 1974).

METHODS AND MATERIALS

Specimens were studied in the Museum of Vertebrate Zoology, University of California, Berkeley; Los Angeles County Museum of Natural History; Field Museum of Natural History; and California Academy of Science. Literature descriptions of fringes were used where specimens were unavailable (Appendix). To determine the extent of morphological variation, fringes on the fourth toe were studied because they are more highly developed than fringes on other digits, and because previous literature emphasized fourth toe descriptions. Line drawings of fringes were made with a Wild camera lucida and dissecting scope. Whenever possible, several specimens of each species (2–25) were examined to estimate intraspecific variation in fringe shape and length. Based on these

observations, fringes were assigned to four types, and cross-sections were drawn of the fringes of the following species, randomly chosen to represent each fringe type: *Uma scoparia*—triangular fringe; *Scincus scincus*—projectional fringe; *Teratoscincus scincus*—conical fringe; *Basiliscus plumifrons, B. vittatus, Kentropyx altamazonica* and *Hydrosaurus amboinensis*—rectangular fringe.

To omit the possibility that fringe type changes ontogenetically, post-hatching ontogenetic series for species of each fringe type were studied. Availability of specimens partly determined the choice of species to represent each fringe type. For each series 25 or more individuals were studied, and fringe length and variation in shape were qualitatively described. The following species were used to represent the indicated fringe type: *Aporosaura anchietae*—triangular; *Scincus scincus*—projectional; *Teratoscincus scincus* and *Ptenopus garrulus*—conical; *Basiliscus basiliscus*—rectangular.

To determine whether fringe types are dependent on species size, data were collected on maximum adult weights of both live and preserved specimens. Data from both museum specimens and the literature were subjected to a Kruskal–Wallis test (Zar, 1984). If species had a certain fringe type because of common ancestry, their average snout–vent length was used to insure statistical independence. *Acanthodactylus, Eremias*, and *Angolosaurus* were placed in their own group for this analysis, since species in these genera were unique in having triangular fringes on the posterior and projectional fringes on the anterior side of each toe.

To determine if the observed morphological differences among fringe types are adaptive with respect to the substrate, associations were studied among each independent evolution of a fringe from a non-fringed scale and different substrates. Substrate descriptions for each species were taken from the literature (Appendix). General habitat descriptions, such as desert or tropical forest and ways in which fringes are used (e.g. water running, digging, sand swimming), were also noted.

In several cases fringes are primitive in polytypic genera whose species occupy different habitats (*Acanthodactylus, Phrynocephalus* and *Stenodactylus*). In these cases where the ancestral habitat type is difficult to determine, it was assumed that the environment inhabited by the greatest number of congeneric species is most similar to the ancestral habitat type. If most of the species in the fringed genus occupy similar habitats to that of the first fringed ancestor, this technique is valid. Although this may not be the case, alternative methods such as out-group and in-group analyses were rejected for two reasons. Firstly, if fringes are adaptive, the out-group, a non-fringed species, would necessarily occupy a different substrate than the fringed group. Second, cladistic hypotheses necessary for in-group analysis or generality hypotheses are lacking for many fringe-toed lizards. For this study it was further assumed that fringes conveyed the same advantage to the ancestral species as they do to fringed descendants.

RESULTS

Descriptive and taxonomic survey

Fringes are present on the toes of 150 species representing 26 out of 354 genera and seven of 14 families of lizards with legs (for list of recognized taxa see Duellman, 1979; Table 1).

Table 1. Kruskal–Wallis test: maximum snout–vent length vs. fringe type

	Maximum snout–vent length		Sample size	
Fringe type	Mean	Range	Independent evolutions	No. of species
Rectangular	131.9	34.0–194.8	5/6	13/19
Conical	69.0	56.0–95.0	3/3	7/20
Triangular	66.5	50.0–95.0	7/13	23/70
Projectional	106.5	—	1/1	4/5
Projectional & triangular	95.3	63.0–152.0	3/3	17/36

The number in the independent evolutions column is the ratio of the number of independent evolutions for which maximum snout–vent measurements were obtained to the number of times the fringe type has evolved. The numbers in the species column is the number of species for which maximum snout–vent lengths were found, divided by the total number of species with the indicated fringe type.

Fringes were divided into four types (described below) based on shape: triangular, projectional, conical and rectangular. In a few species, two fringe types were found on each toe. Usually, the anterior and posterior sides of the digits have the same type of fringe, but in *Acanthodactylus*, *Angolosaurus* and *Eremias*, anterior fringes were projectional and posterior fringes were triangular. Even more rarely, scales of different fringe types appear side by side on the digit. These special cases will be discussed.

Both intra- and interspecific variation in length was observed for all fringe types. For triangular, projectional and conical fringes, intraspecific variation in length is from less than one-half to greater than the total width of the toe. Intraspecific variation in rectangular fringes is less. This variation did not appear to be correlated to size since lizards of similar snout vent length had fringes that varied significantly in length. Interspecific variation in fringe length is similar for all fringe types.

None of the species studied in post-embryonic ontogenetic series showed changes in fringe type with respect to size. Maximum snout vent length of species also could not account for fringe type differences ($0.25 < P < 0.50$; see Table 1).

Fringe types

When all scales on the toe are keeled, the identification of a weak fringe is difficult. Because the term 'fringe' implies some differentiation of the lateral scale, a fringe was considered present if the keel of the lateral toe scales was slightly longer than the keel of dorsal toe scales. It is not known whether such slight differences are functionally significant.

Triangular fringes are composed of lateral scales that are triangular in dorsal view (Fig. 1). Shape varies from an almost perfect isosceles triangle with the apex projecting perpendicularly from the toe (*Uma*, Fig. 1B) to an obtuse triangle with the apex projecting distally at a 30 degree angle (*Angolosaurus*). The angle of projection is roughly constant within species. Sharply pointed or bulging triangles are found within species and among fringes on an individual digit. Adjacent fringes do not contact or overlap except in *Angolosaurus skoogi* and some individuals of *Aporosaura anchietae*.
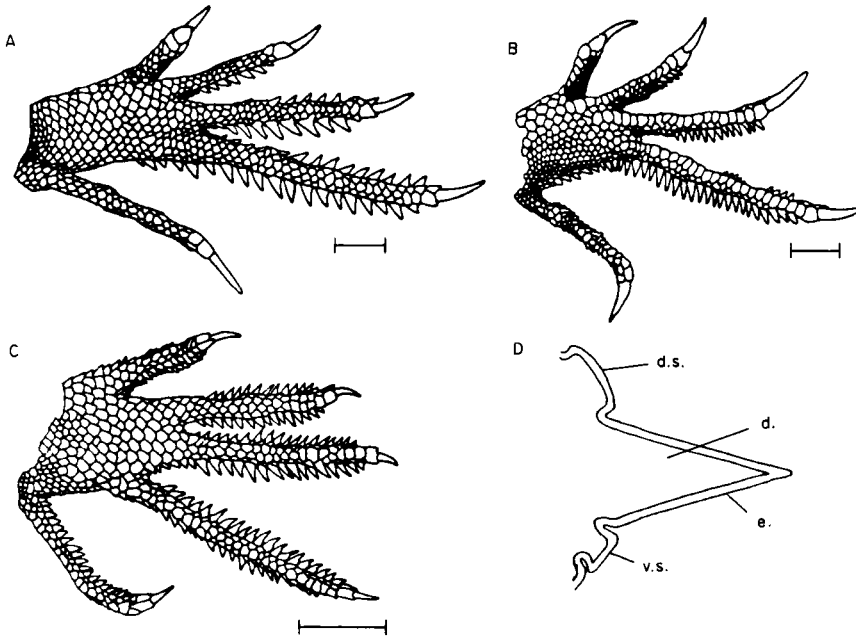
Figure 1. Triangular fringes. A, *Phrynocephalus mystaceus*. B, *Uma notata*. C, *Crossobamon eversmanni*. D, Cross-section of *Uma scoparia* fringe. d.s.—dorsal scale, d.—dermis, e.—epidermis, v.s.—ventral scale. Bars represent 1 cm.

There is considerable variation in the area of scale attachment to the toe. The area may be broad, as in *Uma exsul*, *Acanthodactylus grandis* and *Phrynocephalus scutellatus*, or narrow, as in *U. scoparia*, *Eremias acutirostris* and *Phrynocephalus mystaceus* (Fig. 1A). In general, fringe scales with narrow bases tend to be longer than those with broad bases. Also, very rarely, fringes with narrow bases may be found on the same toe adjacent to fringes with broad bases. These observations suggest that triangular fringe development possibly proceeds as an elongation of the keel and reduction of the scale base. In *E. acutirostris* (Fig. 2A), *E. grammica*, and *E. scripta*, triangular fringe scales with reduced bases have also been found adjacent to projectional fringes. The implications of this will be discussed below. Lizards with triangular fringes range in maximum weight from 1.7 g (*Phrynocephalus rosikowi*) to 75.3 g (*Angolosaurus skoogi*).

Projectional fringes are composed of dorsal or ventral scales that project laterally over the edge of the toe (Fig. 2). The portion of the fringe that extends past the edge of the toe is similar in shape to a triangular fringe with the apex projecting distally at a 45 degree angle to the long axis of the toe. Shape varies among individuals from rounded to pointed to jagged and perhaps results from scale wear. Adjacent fringes do not overlap.

Additional variation is found in the projectional fringe on the anterior side of the toe. The projection is either a simple extension of the scale over the edge of the toe (as in *Acanthodactylus* and in many of the fringed *Eremias*) or it is doubled back on itself and attached dorsally to the opposite side of the toe (as in *Scincus* (Fig. 2B) and *Angolosaurus skoogi*).

Both anterior and posterior projectional fringes are found in all *Scincus* species and in *Eremias acutirostris*, *E. grammica* and *E. scripta*. Additionally, anterior but
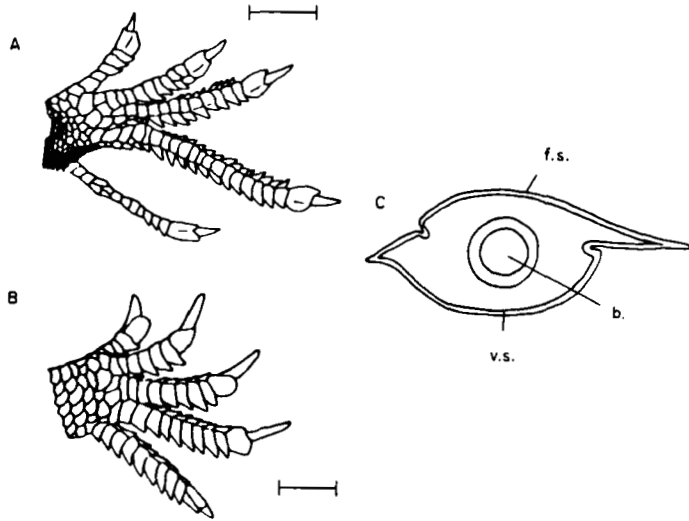
Figure 2. Projectional fringes. A, *Eremias acutirostis*. B, *Scincus scincus*. C, Cross-section of *Scincus scincus* toe. b.— bone, f.s.—fringe scale, v.s.—ventral scale. Bars represent 1 cm.

not posterior projectional fringes are found in most species of the fringed *Eremias*, *Acanthodactylus*, and in *Angolosaurus skoogi*. Lizards with projectional fringes range in maximum weight from 2.7 g (*Eremias scripta*) to 36.7 g (*Scincus scincus*).

Conical fringes are composed of lateral scales that are circular in cross-section and taper toward the tip (Fig. 3). They give the impression of being thin, delicate and flexible. Minor variation in shape includes a slight flattening of the dorsal surface of the scale. Adjacent fringe scales do not overlap. Lizards with conical fringes range in maximum weight from 4.1 g (*Ptenopus carpi*) to 38.8 g (*Teratoscincus scincus*, Fig. 3A).
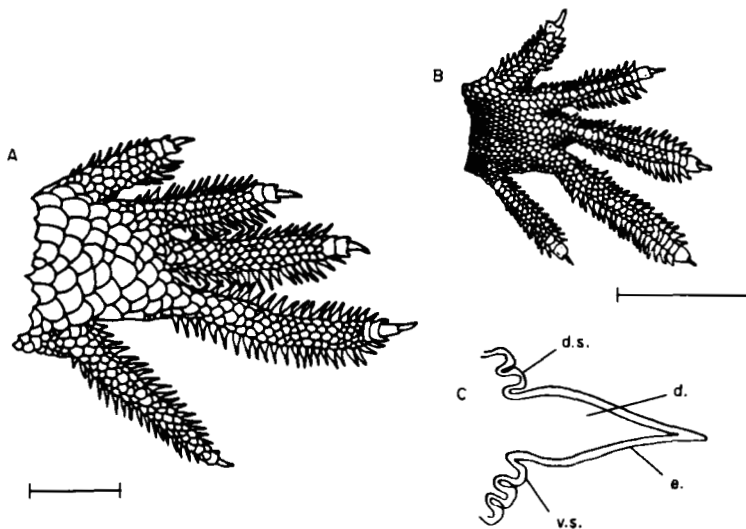

Figure 3. Conical fringes. A, *Teratoscincus scincus*. B, *Ptenopus garrulus*. C, Cross-section of *Teratoscincus scincus* fringe. d.—dermis, d.s.—dorsal scale, e.—epidermis, v.s.—ventral scale. Bars represent 1 cm.
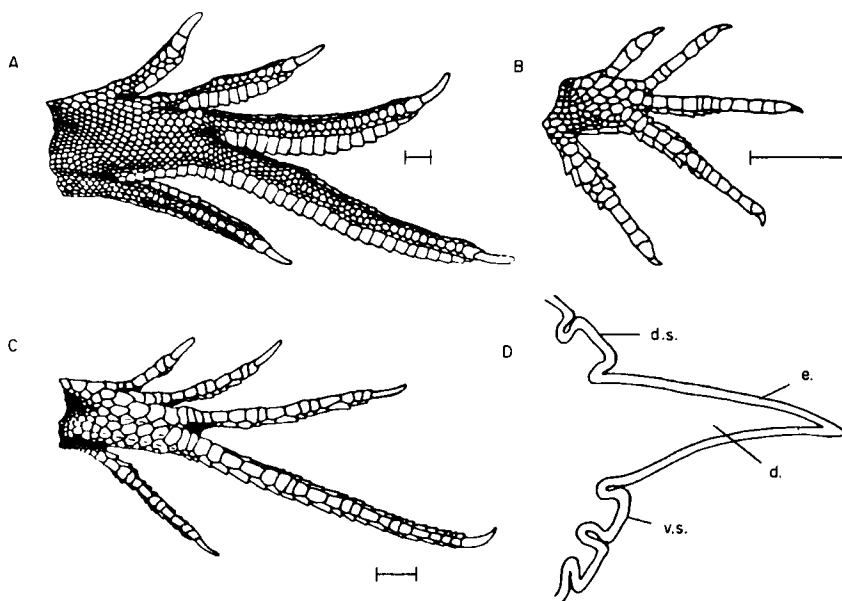
Figure 4. Rectangular fringes. A, *Hydrosaurus pustulosus*. B, *Holaspis guentheri*. C, *Kentropyx calcaratus*. D, Cross-section of *Hydrosaurus amboinensis* fringe. d.– dermis, d.s. dorsal scale, e. epidermis, v.s. ventral scale. Bars represent 1 cm.

Rectangular fringes are composed of lateral scales that are rectangular in shape in dorsal view (Fig. 4). Shape varies from narrow to wide rectangles. Short rectangular fringes have broadly based scales and long fringes have narrowly based scales.

A distinctive characteristic of rectangular fringes is the connection between adjacent scales. The connection is tongue-in-groove with the proximal end of a distal scale fitting into the groove provided by the distal fold of a proximal scale. Dermal tissue is continuous between adjacent fringe scales. This connection is most conspicuous in strongly developed fringes (*Basiliscus* and *Hydrosaurus*, Fig. 4A), and is absent in weakly developed fringes (*Holaspis guentheri*, Fig. 4B; and some species of *Kentropyx*, Fig. 4C).

Rectangular fringes are usually present on the posterior and anterior sides of the toe and on both hands and feet. In all species of *Basiliscus*, however, they are found only on the posterior side of the toes. The *Basiliscus* fringe is also unique among all species except *B. vittatus* in that it folds ventrally to lie flat against the toe when not in use (Laerm, 1973). Species with rectangular fringes vary in maximum weight from 2.4 g (*Holaspis guentheri*) to 296.8 g (*Basiliscus plumifrons*).

Comparative analysis

Relationships among fringe-toed lizards

In most cases, studies of relationships among fringe-toed lizards are detailed enough to identify independent evolution among and within fringe types (Appendix). Fringes that are derived at the specific or subspecific level are easily identified because all closely related taxa are fringeless. Fringes are considered derived at the generic level if all species of the genus are fringed (e.g.

Acanthodactylus, Basiliscus, Phrynocephalus, Scincus, Teratoscincus). Fringes have most likely evolved six times in agamids, once in cordylids, four times in gekkonids, nine times in iguanids, four times in lacertids, once in scincids, and once in teiids. In only a few cases (*Amphibolurus, Eremias, Liolaemus* and *Stenodactylus*) were detailed systematic analyses necessary to determine the number of times fringes had evolved within the genus. Storr (1965, 1966) and Cei (1979) worked out the relationships among *Amphibolurus* and *Liolaemus*, respectively. The fringed species of *Eremias* in SE Europe and Asia are believed to be closely related (Boulenger, 1921). Only *Stenodactylus* (Gekkonidae) presents a problem. Alternative phylogenetic hypotheses have claimed that fringes are either primitive for the genus (Kluge, 1967) or have evolved repeatedly within the genus (Arnold, 1980). I assume that fringes in *Stenodactylus* are homologous and have evolved only once. This systematic difficulty is represented by a question mark in Table 3.

Environments of fringe-toed lizards

Table 2 shows the substrate types and geographic distribution of lizards known to have fringed toes. A majority of fringe-toed lizards are found on either a sand or hardpan substrate. Some are riparian: they are known to be both arboreal and to swim or run over the surface of the water. One lizard, *Holaspis guentheri*, is completely arboreal.

If the independent evolutions of each fringe type are identified and the environment determined as explained in the previous section, the substrate data may be tabulated as shown in Table 3. Fringe-toed lizards are divided conveniently into two general habitat types: tropical forest and desert. Fringes appear to have evolved at least 19 out of 26 times in a desert environment on windblown sand, and only six times in a tropical forest.

DISCUSSION

Fringes are a good example of convergent evolution with which to test adaptive explanations of form. Since they have arisen independently at least 26 times, they provide sufficient data points for correlative studies.

Four fringe types which appear to be discrete have been defined: these types do not change during the life of an individual. Because fringe type is also independent of body size, differences in fringe shape may be adaptive with respect to different environmental selection pressures. That is, these differences in shape are not simply due to different responses because of size to a similar selection pressure.

To determine the adaptive significance of difference types of fringes it is necessary to correlate fringe form with some environmental variable. Sometimes correlation studies simply answer the question "How often is a given character found in a given environment?" To study adaptational questions, however, simple character–environment correlations may be misleading. For example, in one genus, a single population of a single species may have fringes while in another the entire genus may be fringed. To determine if fringes are evolutionarily associated with a particular type of environment, each independent evolution of fringes (in one case identified at a population level, the other at a generic level) should be given equal weighting (Ridley, 1983). This is not simply a matter of statistical independence (Clutton-Brock & Harvey, 1977; Krebs & Davies, 1978; Harvey, Clutton-Brock & Mace, 1980; Harcourt *et al.*,

Table 2. Phylogenetic, geographic and habitat distribution of genera with fringe-toed species of lizards

	No. SP	FT	N Am.	S Am.	S Af.	N Af.	N Eu.	As.	Au–As.
Iguanidae									
Callisaurus	1/1	T	s						
Phrynosoma	1/1	T	s						
Uma	5/5	T	s						
Ctenoblepharis	1/1	T		s					
Liolaemus	2/2	T		s					
Tropidurus	1/1	T		s					
Basiliscus	5/5	R		r					
Uranoscodon	1/1	R		r					
Chalarodon	1/1	T		s					
Teiidae									
Kentropyx	8/8	R		r					
Cordylidae									
Angolosaurus	1/1	TP			s				
Lacertidae									
Aporosaura	1/1	T			s				
Meroles	8/8	T			sh				
Holaspis	1/1	R				a			
Acanthodactylus	17/25	TP				sh	sh		
Eremias	5/10	TP					s		
Scincidae									
Scincus	5/5	P				s	s		
Gekkonidae									
Ptenopus	2/3	C			sh				
Teratoscincus	2/4	C				s	s		
Crossobamon	1/1	T					s		
Stenodactylus	8/13	C					sh	sh	
Agamidae									
Uromastyx	1/1	T					?		
Phrynocephalus	10/42	T					sh	sh	
Amphibolurus	4/5	T							sh
Hydrosaursus	3/3	R							r
Physignathus	1/1	R							r

Code: a = arboreal, h = hardpan, r = riparian, s = sand, FT = fringe type, C = conical, P = projectional, R = rectangular, No. SP = ratio of the number of species observed to the number of known species with fringes, T = triangular. The question mark indicates that the habitat for *Uromastyx aegyptius* is unknown. A single specimen from the Persian Gulf is fringed and substrate information was not available for this individual. N Am. = N America, S Am. = S America, S Af. = S Africa, N Af. = N Africa, N Eu. = N Europe, As. = Asia, Au.–As. = Australasia.

1981; see Felsenstein, 1985, for discussion of the approaches used by these authors), for as Wanntorp (1983: 158) noted, "the adaptive value of traits should be studied on the level where they appear as apomorphies" (derived characters). This approach requires the investigator to determine the cladistic relationships of the taxa of interest and the polarity of character states within the clades being studied.

Adaptive differences in morphology

Evidence from the study of convergence

The association of fringe type with substrate type indicates that fringes have evolved in response to selection pressures during locomotion on two substrates:

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Table 3. Habitat distribution and sample size of fringe types

	Tropical forest		Desert	Sample size	
	Riparian	Not riparian	Windblown sand	Independent evolutions	Species
Rectangular	5	1		6/6	19/19
Triangular			12	12/13	35/70
Projectional			1	1/1	5/5
Conical			3	3/3?	12/20
Triangular & Projectional			3	3/3	23/36

Numbers in the habitat columns designate the number of times that the fringe type is believed to have evolved in the indicated habitat. The number in the species column is the number of species with habitat references divided by the total number of species with the indicated fringe type. The number in the independent evolutions column is the number of independent evolutions for which I was able to estimate a habitat divided by the total number of times that the indicated fringe type has evolved. The question mark indicates that alternative phylogenetic hypotheses have been proposed (see text). *Acanthodactylus, Angolosaurus* and *Eremias* were placed in their own group since individuals of each species have both triangular and projectional fringes (see text).

water and sand. (I assume here that water is the important substrate for rectangular fringed lizards which are also arboreal.) The one exception may be the gliding lacertid, *Holaspis guentheri*. The animal's ability to flatten its body laterally is thought to account for its aerodynamic qualities (Schiotz & Volsoe, 1959). It is unknown whether its fringes play a significant role in gliding efficiency or manoeuvrability. If they do, this may be a case in which different selection pressures have produced similar morphologies.

Preliminary functional evidence

Studies have already shown that fringes allow lizards to run more efficiently on sand and water (Carothers, unpubl. obs.; Laerm, 1973, 1974 respectively). These studies, however, have not explored functional differences with respect to fringe morphology. The purpose of the following section is to speculate on functional reasons for the differences in fringe morphology; more rigorous testing of these ideas is necessary.

The water-runners and sand-runners differ markedly in one aspect of fringe morphology. Scales of fringe types found on sand are denticulate, projecting independently from the toe. Adjacent scales of water-running fringes contact each other. A functional analysis may support an adaptive explanation for these differences.

Preliminary work I have done with fringe models in flow tanks suggests that rectangular fringes provide more drag than denticulate fringes of the same surface area. This discrepancy in drag production may be caused by differences in flow patterns around the fringes: for denticulate fringes, water flows between adjacent scales; for rectangular fringes, contacting adjacent scales prevent such flow.

Manipulation of fringe models through sand suggests that sand does not flow between adjacent scales of denticulate fringes. Since they project further out from the toe than rectangular fringes of the same surface area, denticulate

fringes could provide a greater effective surface area during locomotion on sand. Thus, denticulate and rectangular fringes could be more effective on sand and water substrates, respectively.

Evidence from the study of divergence

Comparison of closely related taxa occupying different habitats also supports an adaptive hypothesis for fringes. Most populations of *Callisaurus draconoides* lack fringes and live on hard pan or sandy washes. However, *C. d. crinitis* is found in windblown sandy areas of northern Baja California (R. L. Seib, pers. comm.; Smith, 1946) and is weakly fringed. Arnold (1983) proposed that in *Acanthodactylus* covariation of fringe length with habitat is so strong that "it seems reasonable to use degree of pectination to predict substrate type in cases where it is unknown." If the distribution of a trait can be predicted based on ecological criteria then it seems reasonable to assume that the observed variation is adaptive (Clutton-Brock & Harvey, 1979). Although variation in scale length occurs in species of all fringe types, locality descriptions of habitat from museum specimens are not sufficiently detailed to pursue intraspecific correlation studies between fringe length and substrate type.

Non-adaptive differences in morphology

Differences in fringe morphology cannot be explained solely by differences in substrate type; triangular, projectional and conical fringes are all found on windblown sand. Further, these fringe types appear to be used in similar ways: running, digging and burying in sand. This implies either that descriptions of fringe use are not detailed enough to detect functional differences, or that differences in fringe type may be non-adaptive. Unfortunately, more detailed information on fringe use is not available.

Two lines of evidence indicate that morphological differences among sand fringe types may not always be adaptive. Firstly, in *Angolosaurus skoogi*, species of the fringed *Eremias*, and some species of *Acanthodactylus*, projectional and triangular fringes are found on opposite sides of the same toe. In *Eremias acutirostris*, *E. grammica* and *E. scripta*, they are found side by side on a single toe. These observations suggest that differences in function may be absent. Second, projectional fringes are found only on the toes of lizards which possess three or fewer series of scale rows encircling the toe. The small number of rows may necessitate the use of dorsal or ventral scales to form lateral projections. If so, a small number of scale rows may structurally restrict fringe development to a projectional morphology.

Possible non-adaptive reasons for differences between conical fringes and the other two sand fringe types are not as clear. Since conical fringes are found only in the Gekkonidae it is possible that some factor common to gekkos restricts fringe development to a conical form. This hypothesis loses some credibility, however, since one gekko, *Crossobamon eversmanni*, has triangular fringes. Alternatively, a factor common to gekkos may permit a conical morphology unattainable by other lizard families. Comparative functional and embryological studies are necessary to identify further adaptive and non-adaptive differences.

CONCLUSIONS

This analysis of lizard toe fringes emphasizes some difficulties inherent to comparative studies of adaptation. Firstly, phylogenetic hypotheses are necessary to identify evolutionary convergence and divergence. Phylogenies of sufficient detail are not always available. Second, identifying the component of the environment that is relevant to some morphological feature may be difficult. In cases where interaction is readily apparent, such as fringes, this may not be a problem. Third, identification of environmental factors present during the evolution of a character is rarely possible, and these factors must be estimated. Fourth, care should be taken to use separate evolutionary transitions as data points; species are not necessarily statistically independent points because their similarities may be the result of common ancestry.

Comparative study suggests that certain morphological differences between types of lizard toe fringes may be adaptive. The evidence for these adaptive differences are based on environmental correlation studies, using examples of both convergent and divergent evolution. Those morphological differences which do not vary with environmental factors are possibly non-adaptive.

This study underscores the value of broad comparative surveys. Historical questions concerning adaptation can be addressed. If systematic study reveals that similar features are indeed convergent, then repeated association of morphology with environmental factors suggests the adaptive significance of form. This approach thereby provides an alternative to *ad hoc* adaptive explanations of similarity.

ACKNOWLEDGEMENTS

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APPENDIX

The following is a list of the taxa used in this study. Species not examined but reported to have fringes are marked with an asterisk. References for fringe identification and habitat are given in parentheses. References for systematic analysis are marked by two asterisks.

AGAMIDAE: *Amphibolurus* (Storr, 1966**), *A. clayi** (Storr, 1966), *A. femoralis* (Storr, 1965), *A. fordi* (Storr, 1965), *A. isolepis* (Storr, 1965; Pianka, 1971), *A. maculatus** (Storr, 1965), *Hydrosaurus amboinensis*, *H. pustulosus, H. weberi* (Ditmars, 1933; Taylor, 1922, for all species), *Phrynocephalus affinis, P. arabicus* (Haas & Battersby, 1959; Arnold, 1980), *P. axillaris, P. caudivolvulus** (Boulenger, 1887), *P. clarkorum** (Anderson & Leviton, 1967; Clark, Clark, Anderson & Leviton, 1969), *P. frontalis** (Boulenger, 1887), *P. guttatus, P. helioscopus* (Clark & Clark, 1973), *P. interscapularis* (Boettger, 1887), *P. luteoguttatus* (Minton, 1966; Clark *et al.*, 1969), *P. maculatus* (Minton, 1966; Arnold, 1977), *P. mystaceus* (Minton, 1966), *P. nejdensis** (Haas, 1957; Steyn, 1962), *P. olivieri, P. ornatus* (Minton, 1966; Clark *et al.*, 1969), *P. przewalskii** (Boulenger, 1887), *P. reticulatus, P. rossikowi, P. scutellatus* (Minton, 1966; Clark *et al.*, 1969), *P. theobaldi, P. versicolor, P. vlangalii, Physignathus lesueuri* (Cogger, 1975; Moody, 1980), *P. maculilabris** (De Rooij, 1915), *P. temporalis** (De Rooij, 1915), *Uromastyx aegyptius.*
    CORDYLIDAE: *Angolosaurus skoogi* (Steyn, 1962; Papenfuss, pers. comm.)
    GEKKONIDAE: *Crossobamon eversmanni* (Boettger, 1887), *Ptenopus carpi* (Brain, 1962; Papenfuss, pers. comm.), *P. garrulus* (Brain, 1962; Papenfuss, pers. comm.), *Stenodactylus* (Kluge, 1967**; Arnold, 1980**), *S. affinis** (Arnold, 1980), *S. arabicus* (Arnold, 1975, 1977, 1980), *S. doriae** (Werner & Broza, 1969; Arnold, 1975, 1977, 1980), *S. leptocosymbotes** (Leviton & Anderson, 1967; Arnold, 1975, 1977, 1980), *S. major* (Leviton & Anderson, 1967), *S. maynardi** (Smith, 1935), *S. orientalis** (Minton, 1966), *S. petrii** (Werner & Broza, 1969; Arnold, 1980; Papenfuss, pers. comm.), *S. pulcher** (Arnold, 1977, 1980), *S. slevini** (Haas & Battersby, 1959; Arnold, 1980), *S. yemensis** (Arnold, 1980), *Teratoscincus bedriagai, T. microlepis* (Minton, 1966), *T. przewalskii** (Pope, 1935), *T. scincus* (Minton, 1966; Arnold, 1975).
    IGUANIDAE: *Basiliscus barbouri* (Maturana, 1962), *B. basiliscus* (Barden, 1943; Maturana, 1962; Rand & Marx, 1967; Fitch, 1973; Laerm, 1973), *B. galeritus* (Maturana, 1962), *B. plumifrons* (Barden, 1943; Snyder, 1949; Maturana, 1962; Hirth, 1963; Fitch, 1973; Laerm, 1974), *B. vittatus* (Ruthven, 1912; Maturana, 1962; Hirth, 1963; Fitch, 1973; Laerm, 1973, 1974), *Callisaurus draconoides* (Smith, 1946; Seib, pers. comm.), *Chalarodon madagascariensis* (Blanc & Carpenter, 1969; Blanc, 1971), *Ctenoblepharis adspersus* (Cei, 1979), *Liolaemus* (Cei, 1979**), *L. multimaculatus** (Cei, 1979), *L. rabinoi** (Cei, 1979), Phrynosoma m'calli (Mosauer, 1932; Smith, 1946; Kaufman, pers. comm.; Papenfuss, pers. comm.), *Tropidurus thoracicus* (Dixon & Wright, 1975), *Uma exsul* (Schmidt & Bogert, 1947; Norris, 1958), *U. inornata* (Stebbins, 1944; Smith, 1946; Norris, 1958), *U. notata* (Smith, 1946; Hesse, Allee & Schmidt, 1951; Norris, 1958), *U. paraphygas** (Pough, Morafka & Hillman, 1978; Zalusky, Gaudin & Swanson, 1980), *U. scoparia* (Buxton, 1946; Smith, 1946), *Uranoscodon superciliosa* (Beebe, 1944; Hoogmoed, 1973).
    LACERTIDAE: *Aporosaura anchietae* (Louw & Holm, 1972; Werner, 1977; Robinson & Cunningham, 1978), *Acanthodactylus boskianus* (Werner, 1968), *A. boueti** (Boulenger, 1921), *A. cantoris* (Smith, 1935), *A. erythrurus* (Busack, pers. comm.), *A. felicis** (Arnold, 1977), *A. fraseri* (Boulenger, 1921), *A. grongrorhynchatus** (Leviton & Anderson, 1967; Arnold, 1977), *A. grandis* (Boulenger, 1921), *A. haasi* (Leviton & Anderson, 1967), *A. masirae** (Arnold, 1977), *A. micropholis** (Minton, 1966), *A. opheodurus** (Arnold, 1977), *A. pardalis* (Minton, 1962), *A. robustus, A. savignyi** (Boulenger, 1921), *A. schmidti** (Arnold, 1977), *A. schreiberi* (Werner, 1968), *A. scutellatus* (Werner, 1968), *A. tristrami* (Boulenger, 1921), *A. vulgaris** (Boulenger, 1921), *Eremias* (Boulenger,

1921**), *E. acutirostris* (Minton, 1966), *E. aporosceles** (Boulenger, 1921; Smith, 1935), *E. arguta* (Boulenger, 1921), *E. fasciata* (Boulenger, 1921), *E. grammica* (Boettger, 1887), *E. intermedia** (Boettger, 1887), *E. lineolata* (Boulenger, 1921; Leviton & Anderson, 1970), *E. persica* (Boettger, 1887; Boulenger, 1921), *E. scripta* (Boettger, 1887; Boulenger, 1921; Smith, 1935), *E. vermiculata** (Boulenger, 1921), *Holaspis guentheri* (Boulenger, 1921; Schiotz & Volsoe, 1959), *Meroles ctenodactyla** (Boulenger, 1921; FitzSimons, 1943; Haacke, 1965), *M. cuneirostris* (Boulenger, 1921; FitzSimons, 1943; Louw & Holm, 1972; Werner, 1977; Robinson & Cunningham, 1978), *M. knoxi* (FitzSimons, 1943; Haacke, 1965), *M micropholidota** (FitzSimons, 1943), *M. reticulata** (Boulenger, 1921; FitzSimons, 1943), *M. suborbitalis* (Boulenger, 1921; Haacke, 1965; Papenfuss, pers. comm.), *M. transaspica** (Boulenger, 1921; FitzSimons, 1943).

SCINCIDAE: *Scincus arenarius* (Minton, 1962), *S. hemprichii*, *S. officinalis** (Mosauer, 1932), *S. philbyi*, *S. mitranus* (Smith, 1935, Haas & Battersby, 1959), *S. scincus* (Mosauer, 1932).

TEIIDAE: *Kentropyx altamozonica* (Cadle, pers. comm.), *K. borkianus* (Hoogmoed, 1973), *K. calcaratus* (Fitch, 1968; Boos & Quesnel, 1971; Vanzolini, 1972; Hoogmoed, 1973; Dixon & Soini, 1975; Magnusson & Lima, 1984), *K. paulensis** (Gallagher & Dixon, 1980), *K. pelviceps* (Duellman, 1978), *K. striatus* (Boos & Quesnel, 1971; Vanzolini, 1972; Hoogmoed, 1973), *K. vanzoi** (Gallagher & Dixon, 1980), *K. viridistriga* (Gallagher & Dixon, 1980).