

The Role of Phylogenetics in Evolutionary Ecology

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Systematics has undergone a number of tumultuous upheavals during the past several decades. Before mid-century, organisms were classified subjectively by experts who were allowed to weight characters and character states as they saw fit. Classifications were not even required to reflect true evolutionary relationships.

A new approach developed in the 1960's became known as numerical taxonomy or "phenetics" (Sokal & Sneath 1963). This school exploited cluster analysis and dendrograms to depict classifications. Pheneticists argued that taxonomists should use as many character states as possible and that all should be given equal weight (differential weighting was absolutely forbidden). Similarity was the sole criterion for classification under this phenetics scheme. Eventually, after being challenged (below), numerical taxonomists argued that cluster analysis would often yield good estimates of evolutionary relationships. The issue split into two: (1) how to name organisms and (2) how to reconstruct phylogeny (the former being less interesting and of less practical importance in terms of analyzing evolution).

The pheneticist view was challenged by Hennig (1966), who argued that all classifications should reflect phylogeny. Hennig's school has prevailed, and has come to be known as phylogenetic systematics or "cladistics." Named groups must be monophyletic and must contain all descendents of a common ancestor (artificial groups such as "reptiles" that do not contain all descendents are said to be "paraphyletic"). To construct such classifications that accurately reflect phylogeny, states of numerous characters are determined and carefully analyzed for all species that are members of a given monophyletic group. Ancestral states do not provide any phylogenetic signal, but shared derived, or synapomorphic, character states do contain information that allows phylogenetic inference. Character states that arise independently (convergences) are misleading because they suggest relatedness where there is none. The challenge for phylogenetic systematists is to identify shared derived character states and to exclude convergent ones. Comparison with appropriate related "outgroups" allows systematists to identify ancestral traits and to "polarize" character state changes of probable shared derived characteristics. Parameter space is then searched for the most probable phylogenetic trees using various criteria, including distance (as was originally used by numerical taxonomists), parsimony, and maximum likelihood. A subsampling method (bootstrapping) allows estimation of confidence in various branching patterns (Hillis and Bull 1993). With an adequate data set of characters and character states, a phylogeny can be resolved and a most robust tree identified for use in further analyses.

Using a closely related “outgroup,” such a tree can be “rooted” to produce a “cladogram” that shows probable genealogical relationships among members of the group concerned. Modern molecular techniques, particularly DNA amplification and sequencing, now allow systematists to assemble large character data sets which are used to reconstruct probable phylogenies of diverse monophyletic groups of organisms (Hillis *et al.* 1996). Any phylogeny is no more than a hypothesis, but the advent of molecular approaches combined with increasingly rigorous statistical procedures has greatly increased our confidence in particular “resolved” phylogenetic trees.

Armed with such a phylogeny showing the probable relationships among members of a monophyletic lineage, one can overlay various character states such as behavioral and ecological traits to examine the probable course of evolution (Schluter *et al.* 1997, Pagel 1998, Garland *et al.* 1999). Past history can be recovered, at least to some extent, from current character states. Powerful inferences can then be made about the sequence of changes that probably occurred during the evolution and adaptive radiation of that group. Exploitation of these techniques to their fullest potential obviously requires examination of as many related taxa as possible - extinctions of existing species truly become “lost pages” in the unread book of life. Modern comparative methods have also been developed that allow scientists to reconstruct probable ancestral states from those of surviving descendants. Obviously, we have made substantial progress in beginning to be able to decipher the vanishing book of life!

Vicariance Biogeography

As a consequence of the emerging awareness of continental drift, a vigorous new branch of biogeography has arisen. Prior attempts at explaining current geographic distributions of organisms relied heavily on improbable movements and episodes of dispersal. But the recognition that landmasses themselves actually break apart and move (aquatic systems behave analogously) has enabled distributions to be understood in terms of such geographic or “vicariant” events as well as in terms of dispersal.

Such patterns can be related to features of the geographic history of the area concerned in an “area cladogram” (Figure 1). Indeed, vicariance biogeographers have actually suggested that certain physical geographic events must have occurred (for many years prior to the accumulation of extensive geological evidence, biogeographic distributions were the strongest evidence for continental drift!). Concordances among cladograms for different plant and animal groups in the same general region strongly suggest that common vicariant events underlie their phylogenies (Figure 2).

Phylogeny and the Modern Comparative Method

Evolution of phenotypes (or species) in a range of different environments is analogous to the response of individuals in a nested sequence of experimental treatments (Harvey

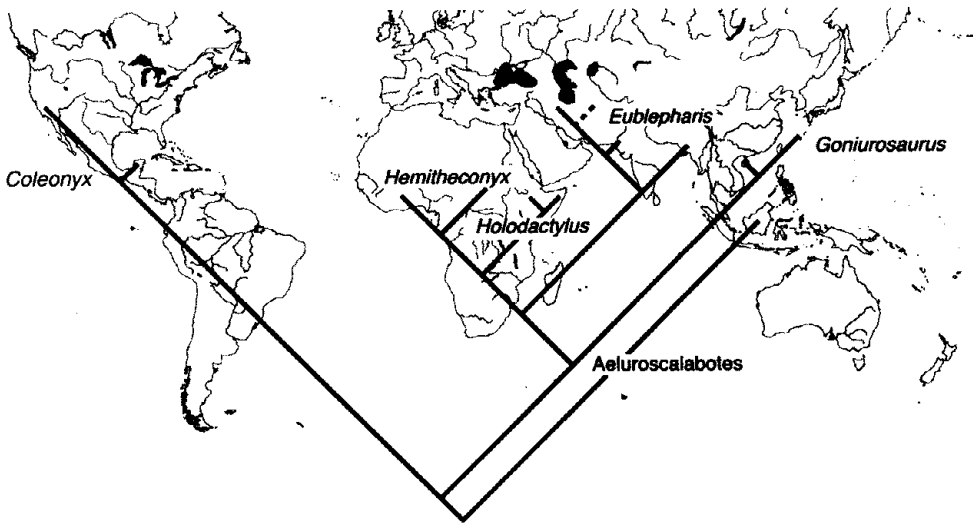


Figure 1. Area cladogram for Eublepharid geckos [From Grismer (1988)].

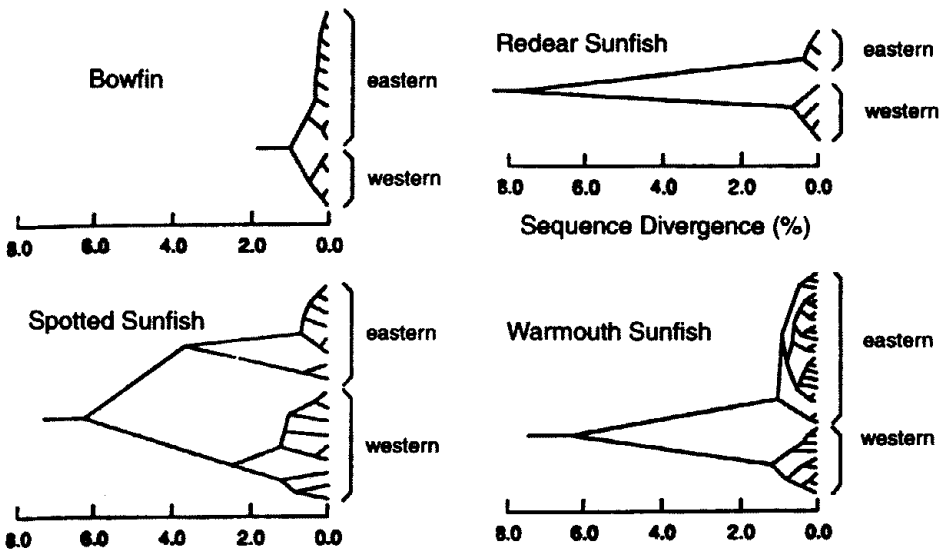


Figure 2. Cladograms depicting sequence divergence among various populations in four different species of fish in the southeastern USA. In all cases, eastern fish are more closely related to other eastern fish than they are to fish from western drainages, whereas western fishes are more closely related to other western fishes. [Adapted from Bermingham & Avise (1986).]

& Pagel 1991). The analogue to an experiment begins by subjecting a population of individuals to the same treatment at the base of a monophyletic tree (Figure 3). Subpopulations are divided and re-divided sequentially after varying intervals of time. Between divisions, each subpopulation is subjected to a particular environmental

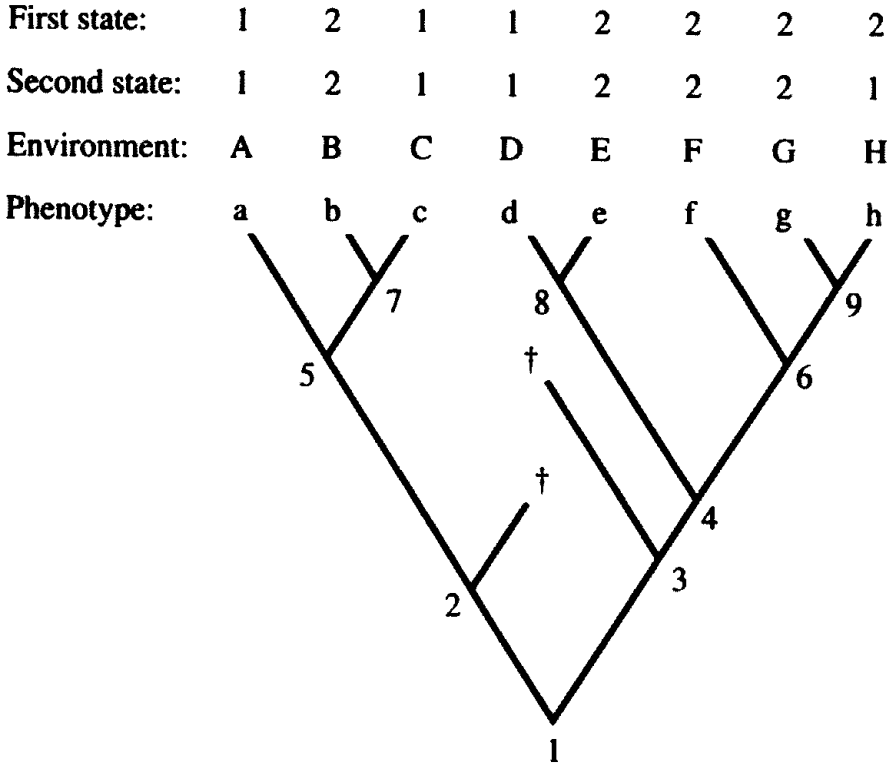


Figure 3. A phylogenetic tree can be viewed as an analogue to a nested experiment. Lineages from nodes 2 and 3 terminating in crosses represent extinct fossils. At the basal node 1, a population is subdivided into two subpopulations, which are subjected to different environmental “treatments.” At each subsequent node, subpopulations are redivided and subjected to new varying “treatments.” Probable states at ancestral nodes can be estimated from states of existing extant species at the tips of the phylogenetic branches. [Adapted from Harvey & Pagel (1991).]

“treatment” that differs from that experienced by other subpopulations. Under this analogy, however, no record is kept of “treatments” administered to various subpopulations. An estimate of the probable historical record of “treatments” and “responses” can be reconstructed, however, from appropriate information on extant lineages, using parsimony, as follows. Past environments for a given lineage are assumed to be similar to present environments (“treatments”). Organisms tend to occupy habitats similar to those occupied by their ancestors.

Extant populations contain information about their evolutionary history because the structure of the phylogenetic tree is known (Figure 3). For example, parsimony (minimal evolution) suggests that the ancestral subpopulation at node 4 is likely to have had condition 2 at both states because a majority of descendant subpopulations exhibit that condition. However, node 5 would be more likely to have exhibited condition 1 as

judged from the prevalent condition among its descendents. The ancestral condition at the base of the phylogeny, node 1, could have been either condition 1 or condition 2 at both states. Note also that the states of extant subpopulations tend to covary across environments (“treatments”), making the condition of either state a good predictor of the condition of the other state. Phenotypes a and d have probably undergone convergent evolution, and phenotype b has probably converged on phenotypes e, f, g, all of which would appear to have retained the probable ancestral state 2, 2.

Probable ancestral states can be inferred from existing states of descendents using simple averages or in more complex ways involving maximum likelihood that minimize squared changes along all links of a phylogenetic tree (Huey & Bennett 1987; Garland *et al.* 1991; Schluter *et al.* 1997; Pagel 1998; Garland *et al.* 1999). If branch lengths are known, such averages can be inversely weighted by the estimated distance between taxa. Although this approach is somewhat circular, it allows one to trace probable past evolutionary scenarios. An example for evolution of body temperatures among Australian scincid lizards is shown in (Figure 4); this analysis suggests that the skink genus *Ctenotus* has evolved a higher active body temperature and that some of its scincid relatives have evolved lower active body temperatures.

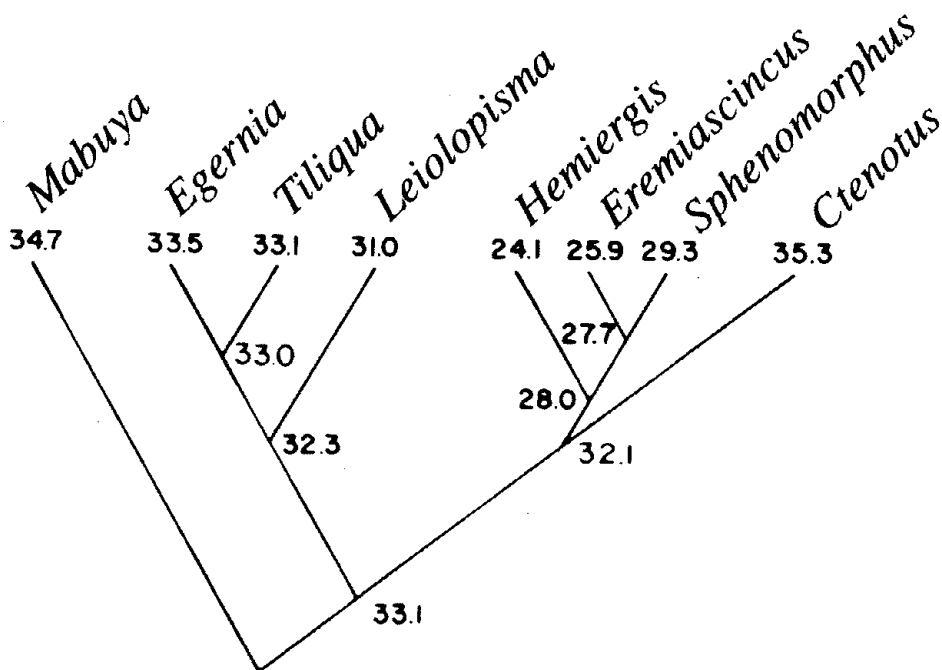


Figure 4. Active body temperatures among seven genera of Australian skinks, with inferred ancestral body temperatures at various nodes. Note the high body temperature of *Ctenotus* and the lower body temperatures of its relatives *Hemiergis*, *Eremiascincus*, and *Sphenomorphus*. [Adapted from Huey & Bennett (1987).]

Huey & Bennett (1987) and Garland *et al.* (1991) examined the influence of phylogeny on coadaptation of thermal physiology in some Australian skinks, including several species of *Ctenotus*. Their work, plus Greer's (1980) comments, suggest that most, but not all, *Ctenotus* display appreciably higher body temperatures than related skinks. Apparently, acquisition of this "key innovation" (Simpson 1953, Futuyma 1986; Nitecki 1990) may have been a factor that allowed *Ctenotus* to become active diurnal lizards and to radiate to fill many new niches. An alternative, but not necessarily mutually exclusive, hypothesis is that aridification itself has allowed these lizards to diversify.

Huey & Slatkin (1976) analyzed costs and benefits of lizard thermoregulatory tactics, and identified the slope of the regression of body temperature against ambient environmental temperature as a useful inverse measure of the degree of passivity in regulation of body temperature. On such a plot of active body temperature versus ambient temperature, a slope of one indicates true poikilothermy or totally passive thermoconformity (air temperature and body temperature are perfectly correlated), whereas a slope of zero reflects the other extreme of perfect thermoregulation. Lizards span this entire thermoregulation spectrum (Pianka 1986).

Among active diurnal heliothermic species, regressions of body temperature on air temperature are fairly flat (for several species, including some quite small ones, slopes do not differ significantly from zero). Both thermoregulators and some thermoconformers maintain higher body temperatures than do species intermediate between them along this thermoregulatory spectrum. These thermoconformers, *C. ariadnae*, *quatuordecimlineatus* and *piankai*, maintain relatively high body temperatures by being active during the heat of mid-day inside spinifex tussocks. At least two evolutionary pathways for increasing body temperature are suggested. The hypothesis that elevated body temperatures are derived can be tested by comparative methods, as well as the hypothesis that each thermoregulatory strategy has evolved only once within *Ctenotus*. I plan to undertake a comprehensive study of evolution of thermoregulation within *Ctenotus* using modern comparative methods. Body temperatures at ancestral nodes will be estimated. The notion that elevation of body temperature has been important in the adaptive radiation of *Ctenotus* suggests two testable hypotheses: (1) Higher body temperature is a derived condition within *Ctenotus*, and has arisen multiple times, and (2) Lineages that have evolved higher body temperatures are more species rich than those which are not (Barraclough *et al.* 1998; Goudet 1999).

Such a comparative phylogenetic study should lead to a much more sophisticated understanding of *Ctenotus* ecology. Some *Ctenotus* species, such as *leae* and *leonhardii*, are active thermoregulators whereas other species, such as *piankai*, are, comparatively speaking, thermoconformers. The position of any particular species along this thermoregulation spectrum reflects a great deal about its complex activities in space and time (Pianka 1993).

Phylogenetically Independent Contrasts

Until recently, ecologists have seldom considered how phylogenetic relatedness might affect observed patterns of covariation among phenotypic traits. Plotting various traits against one another, species-by-species, is flawed because data points are not strictly speaking independent (e.g., Felsenstein 1985, Harvey & Pagel 1991, Garland *et al.* 1999). For example, if species exhibiting high values for both traits are closely related and those with lower values represent a distantly related clade of species that are themselves closely related, then any observed correlation is really based on a sample size closer to two, rather than the total number of species. The effect is similar to over-estimating degrees of freedom. A method of analysis that corrects for phylogenetic relatedness, known as “independent contrasts,” was suggested by Felsenstein (1985, 1988). This method compares differences between related taxa, which are independent. Independent contrasts transform the data to make them independent and identically distributed. Ancestral states can also be estimated and used in independent contrasts. Confidence intervals can be estimated as well (Garland *et al.* 1999).

If a correlation between traits remains significant after applying these techniques to remove phylogenetic effects of relatedness, then confidence that traits concerned covary as suspected is strengthened considerably.

Appropriate phylogenetically based statistical procedures to factor out the effects of phylogenetic relatedness were first worked out by Ridley (1983) and Felsenstein (1985, 1988), and later extended by Grafen (1989), Maddison (1990), Harvey and Pagel (1991), Martins & Garland (1991), Garland (1992), Garland *et al.* (1992, 1993), Hansen and Martins (1996), Martins (1996), Martins & Hansen (1997), Schluter *et al.* (1997), Pagel (1998), Garland *et al.* (1999), among others.

A Variety of Other Examples

Calls of birds and frogs are often schematicized using sonograms, plotting frequency versus time, as in Figure 5 (Ryan & Rand 1995). Probable ancestral calls were estimated from those of living descendents.

Body size has evolved rapidly in varanid lizards, also known as monitors. The fossil record and present geographic distribution suggests that varanids arose in Laurasia and subsequently dispersed to Africa and Australia. Two major lineages have undergone extensive adaptive radiations in Australia: one evolved small body size (subgenus *Odatria* = pygmy monitors), whereas the other lineage (subgenus *Varanus*) remained large and several members evolved gigantism. Small body size also evolved in an arboreal lineage of two species in an Asian clade. Two members of this Asian clade appear

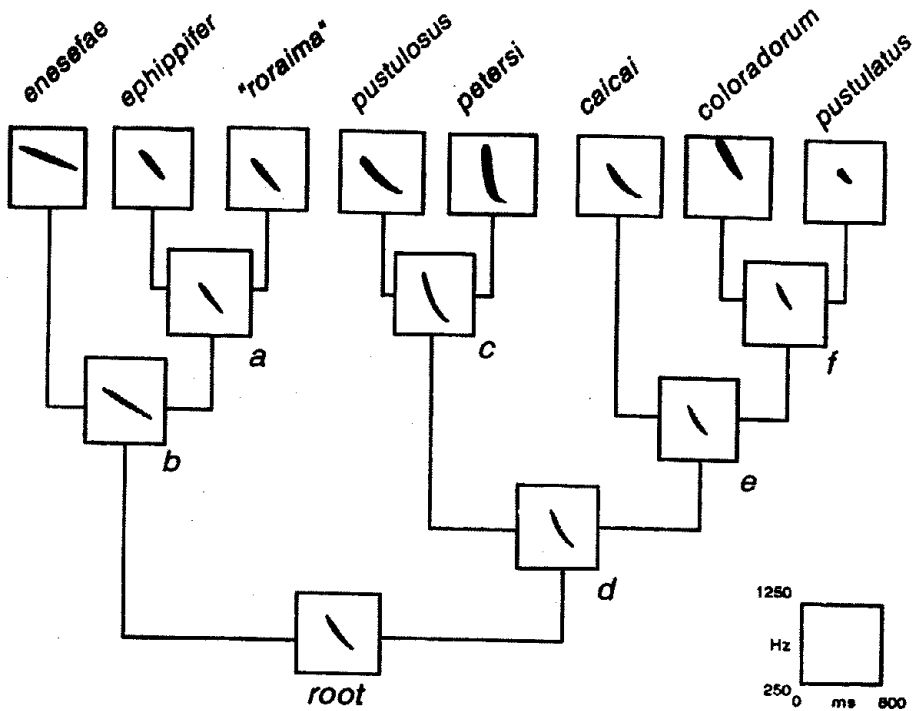


Figure 5. Sonographs of calls of various species of *Physalaemus* frogs, and those reconstructed for various ancestors [From Ryan & Rand (1995).]

to have dispersed to northern Australia in the recent past. An island monitor has evolved gigantism (*Varanus komodoensis*). An extinct Pleistocene fossil varanid from Australia (*Megalania prisca*), originally placed in the genus *Varanus*, was the largest lizard known, reaching a total length of 7 m (600 kg). In Figure 6, body sizes of extant species are plotted on a phylogeny along with presumed body sizes at ancestral nodes, as inferred using the modern comparative method (Pianka 1995). Phylogenetically independent contrasts coupled with branch lengths identify several instances of very rapid evolution of body size, both between and within clades (Pianka 1995, see also Garland *et al.* [1993] and Garland & Adolph [1994] on identifying rapid evolutionary events with independent contrasts).

In a similar analysis, McGuire (1998) demonstrated that large body size has evolved repeatedly among various lineages of southeast Asian gliding agamid lizards (genus *Draco*).

Losos (1992) reconstructed probable sequences of evolution of various *Anolis* ecotypes for Jamaica and Puerto Rico (Figures 7 and 8). During the buildup of these lizard assemblages, estimated intermediate sequences of stages are strikingly similar. Except for the presence of the grass-bush ecotype on Puerto Rico, extant communities are also

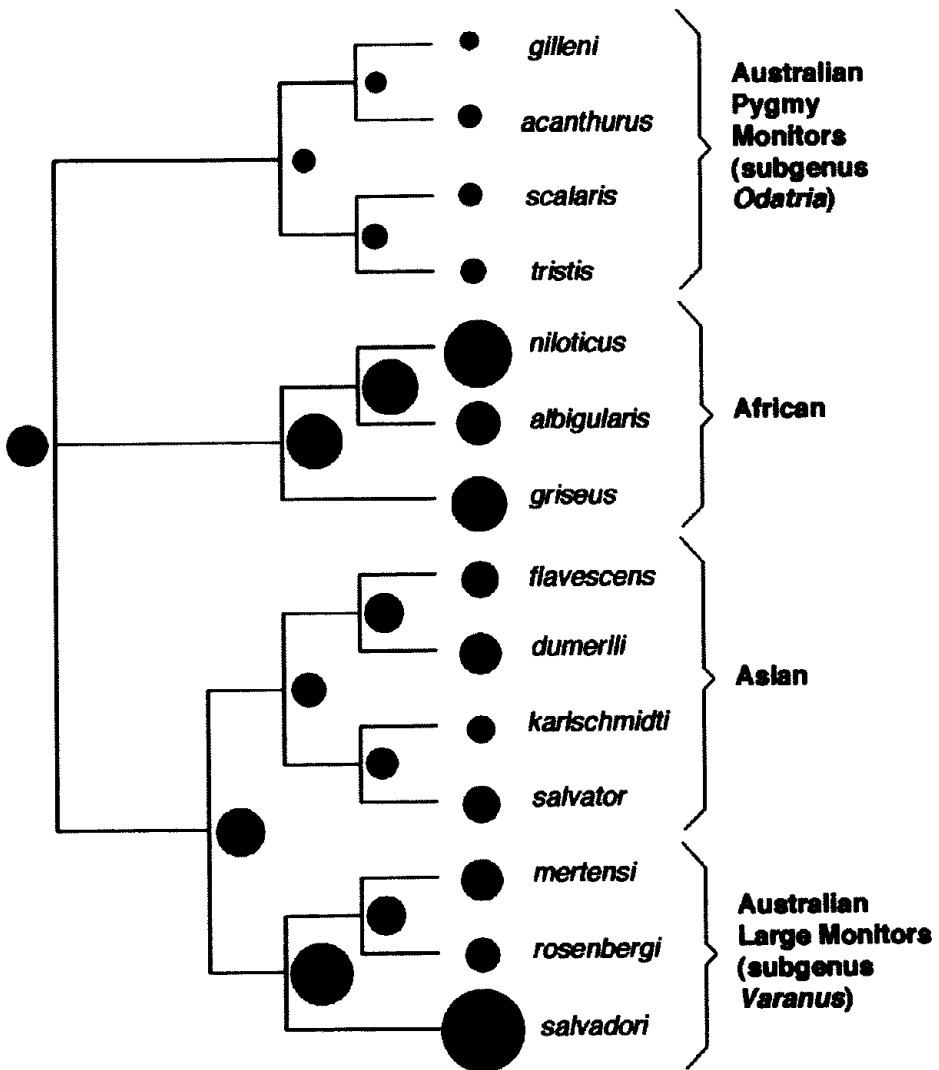


Figure 6. Probable course of evolution of body size among varanid lizards [From Pianka 1995.]

very similar.

My graduate student, Wendy Hodges (pers. comm.) has plotted parity on a phylogeny for horned lizards (genus *Phrynosoma*) showing that live-bearing has probably arisen only once (Figure 9) within the genus. She is currently gathering further DNA sequence data to better resolve this phylogeny and she plans to look at the evolution of various other features including body size, body temperature, diet, spinosity, and antipredator blood squirting.

Another of my graduate students, Bryan Jennings, is studying the so-called “legless” flap-footed lizards of Australia. Pygopodids evolved from Diplodactyline geckos

(Kluge 1974, 1976). Eight genera and about 35 species are recognized. *Paradelma* (monotypic) and *Pygopus* (3 species) are heavy bodied terrestrial species that feed on large arthropods. One genus, *Lialis* (2 species), is very snake-like (Patchell & Shine 1986b) and feeds largely on other lizards, especially skinks. Two genera, *Aprasia* (8

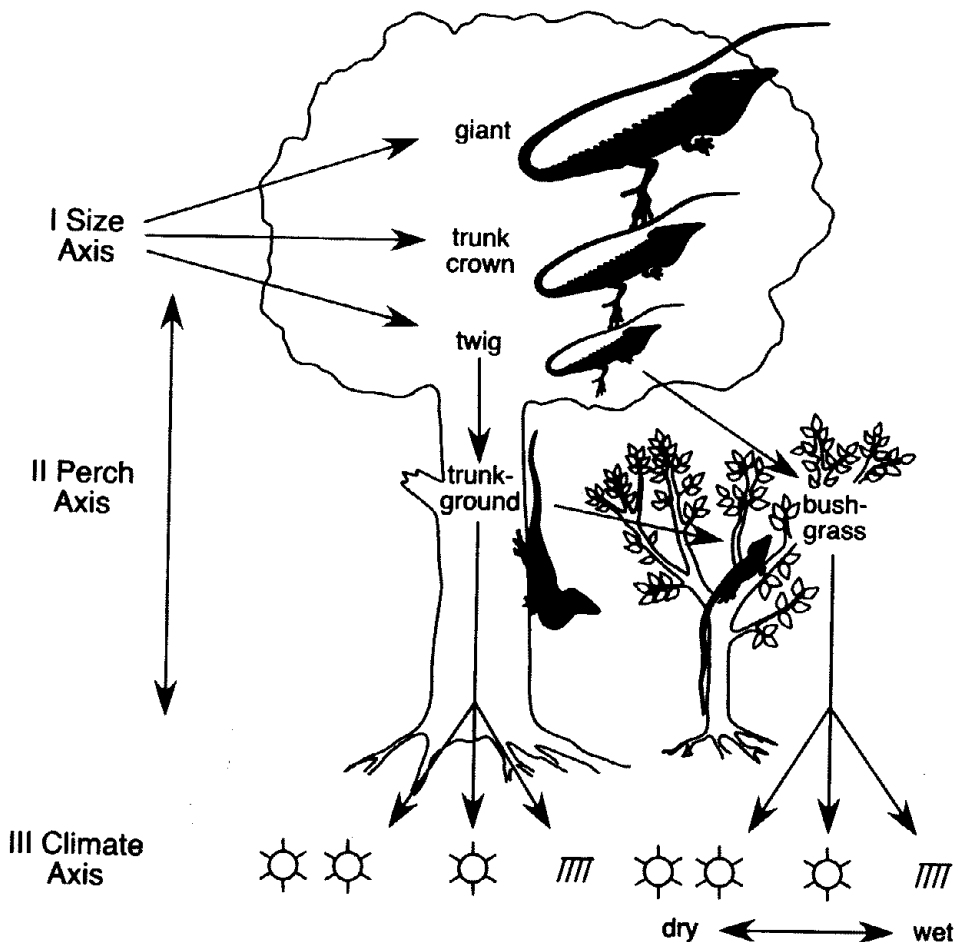


Figure 7. Ecological axes of importance in the evolution of *Anolis* lizards leading to ecotypes of Williams (1983).

species) and *Ophidiocephalus* (monotypic), are fossorial. The genus *Delma* (18 species) includes both terrestrial and arboreal forms, all of which are active diurnal lizards. *Aclys* (monotypic) is a very highly elongate arboreal relative of *Delma*, commonly known as "Javelin lizards." The eighth very distinctive and different genus, *Pletholax*, also monotypic, is a small slender, keeled, diurnal arboreal lizard.

Jennings has assembled an extensive mtDNA data set for almost all the members of this group. When he resolves their phylogenetic relationships, he will use the resulting

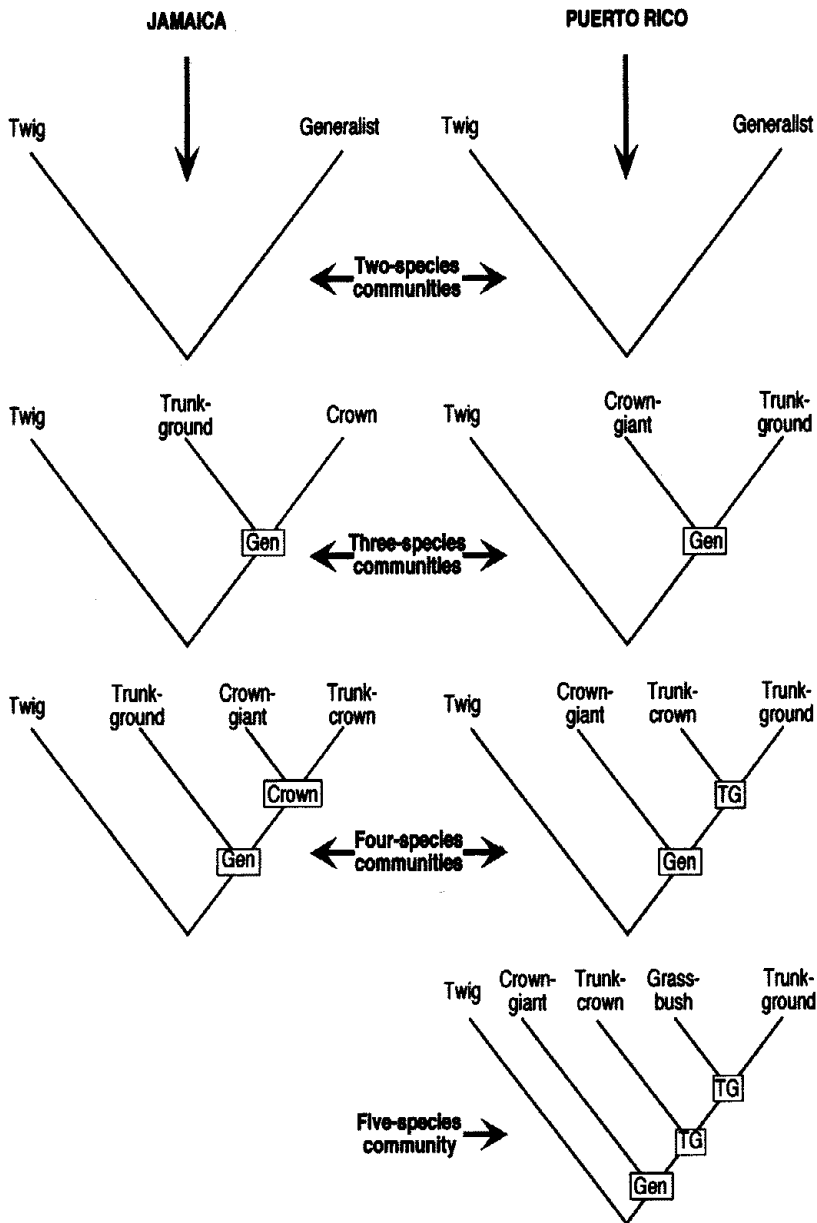


Figure 8. Reconstruction of the probable course of evolution of community structure among *Anolis* lizards on Jamaica (left) and Puerto Rico (right). Except for the absence of the grass-bush ecotype on Jamaica, anole communities on the two islands are very similar today, despite their independent evolutionary histories. [Adapted from Losos (1992).]

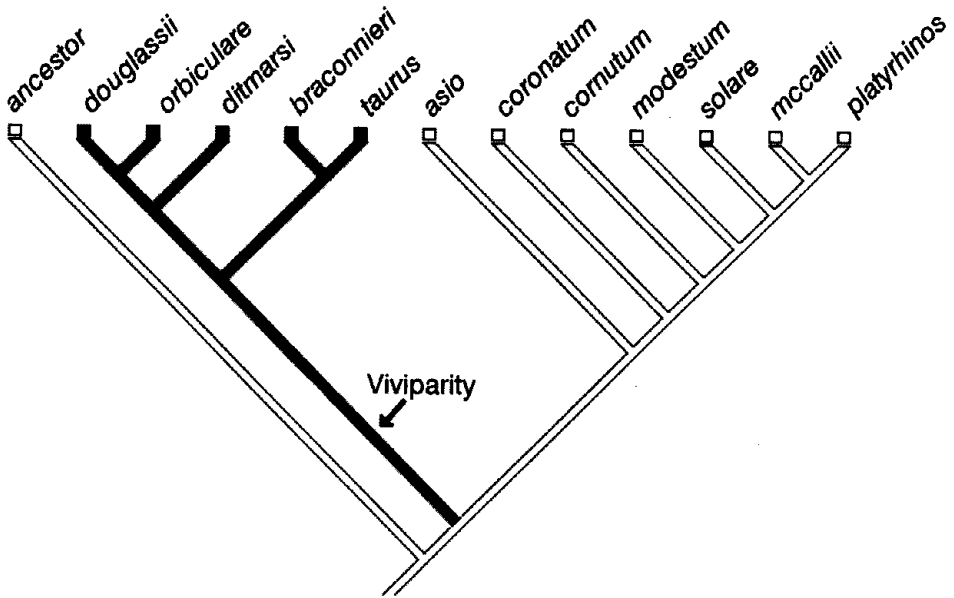


Figure 9. Phylogenetic relationships among 13 species of horned lizards, genus *Phrynosoma*. Viviparity appears to have arisen only once.

tree to examine the evolution of ecology and morphology to understand the adaptive radiation and biogeography of Pygopodids.

My ex grad student, Gad Perry, has studied foraging mode among lizards (Perry 1995, 1999). Average numbers of moves per minute are plotted on a phylogeny in Figure 10. This phylogenetic analysis suggests that, among this group of lacertid lizards, the

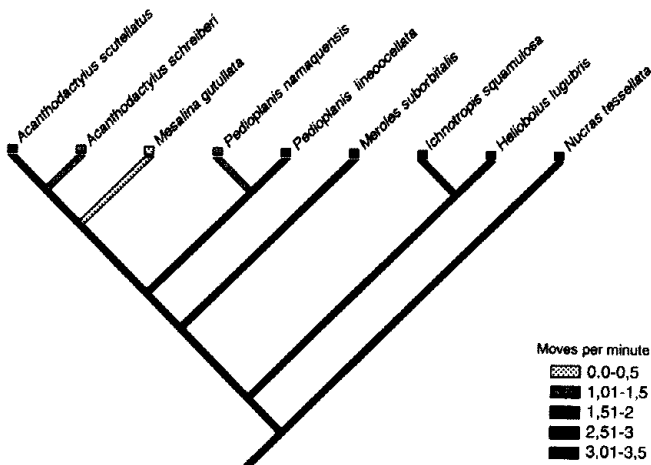


Figure 10. Moves per minute among nine species of lacertid lizards suggest that the ancestral state is widely foraging and that the sit-and-wait ambush foraging mode is derived. [From Perry (1995).]

ancestral state was widely foraging and that sit-and-wait ambush foraging is derived. The situation among all lizards would, however, appear to be reversed, with sit-and-wait being ancestral and widely foraging the derived condition (Cooper 1994). Another interesting trait that varies among Australian *Ctenotus* skinks is the condition of subdigital toe lamellae, the two extremes being keeled and callused (Figure 11). The callused condition is presumed to be ancestral because other outgroup skink gen-



Figure 11. Diagrammatic representation of the condition of toe lamellae among various species of Australian *Ctenotus* skinks.

era display it. *Ctenotus pantherinus* has the largest geographic range of any *Ctenotus*, and appears to be the sister taxon to other *Ctenotus* (Figure 12). Various subspecies of *C. pantherinus* display different toe lamellar states: *acripes*, *ocellifer* and *pantherinus* have sharp keels, but *calyx* has broad calli. Subspecies of *pantherinus* would appear to form a monophyletic group in which sharp keeled toe lamellae have evolved but reverted back to broad calli in *calyx*. Sharp keeled toe lamellae have appear to have arisen independently in another lineage of *Ctenotus* which includes *brooksi*, *calurus*, *colletti*, *leae*, and *schomburgkii* (Figure 12).

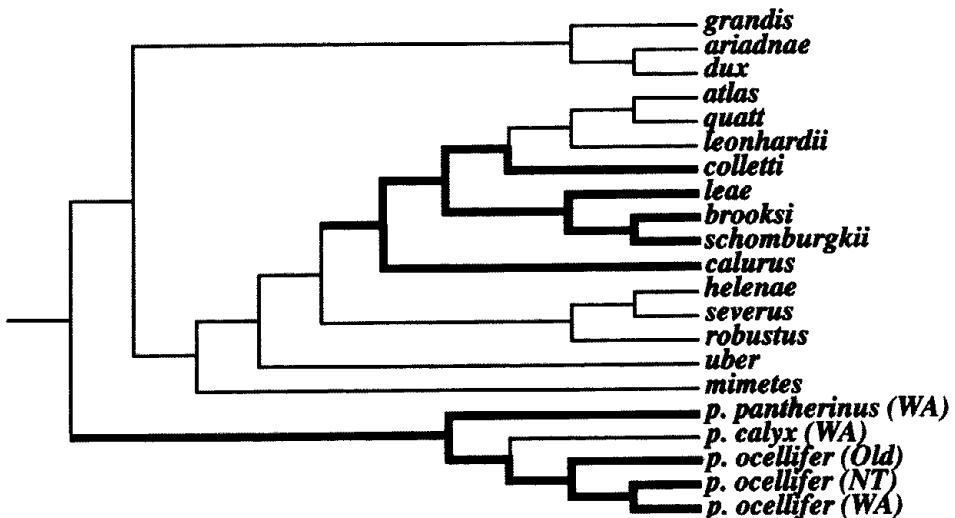


Figure 12. Sharp keeled toe lamellae appear to have arisen at least twice among *Ctenotus* skinks with one reversion back to the callused condition in the subspecies *calyx*.

Evolutionary Ecomorphology

Population biologists have long appreciated that an animal's morphology reflects its ecology. Consider desert lizards. Species that spend a lot of time in the open away from cover tend to have longer hind legs, relative to their snout-vent length, than those that stay closer to safe retreats. Longer legs increase running speed (Bonine & Garland 1999, and references therein), hence facilitating use of open spaces (Pianka 1986).

However, long-legged species move very clumsily through dense vegetation demonstrating that there is actually a premium on shorter legs for species that exploit such closed-in microhabitats. Terrestrial species tend to have longer hind legs than arboreal species. Among sympatric lizards, limb proportions are correlated with their adaptations for climbing, burrowing, and other movements.

Digging species typically possess larger front feet and more powerful forelegs than species that do not do much digging with their front limbs. Fossorial species have reduced appendages or lack them altogether. Numerous other anatomical correlates of the use of space exist. Arboreal lizards are typically slender and long-tailed, with claws or toe lamellae well suited for climbing. Indeed, number of toe lamellae, as well as their surface area, are intimately related to climbing ability.

Among nocturnal geckos, terrestrial species tend to have larger eyes than arboreal species. Head proportions and jaw length are often reasonably accurate indicators of the size of a lizard's prey. Dentition sometimes reflects still more subtle aspects of diet, such as the agility and hardness of prey (Hotton 1955).

Such ecomorphological correlates may ultimately enable ecological predictions based on anatomical data (Karr & James 1975, Ricklefs & Travis 1980, Ricklefs *et al.* 1981, Winemiller 1991). Morphological measures can often be estimated more easily and more objectively than ecological parameters. Morphometrics may represent average long-term responses to selection and hence reflect environmental conditions better than more direct measurements of the immediate ecological milieu. Because anatomical parameters are usually much easier to estimate objectively than ecological ones, a variety of recent studies attempt to exploit such morphological correlates of ecology to make anatomical maps of ecological space and, in turn, to use these to analyze various aspects of community structure; these efforts have dealt with vertebrate taxa as divergent as bats, birds, fish, and lizards (Findley 1973, 1976; Gatz 1979a, 1979b; Karr & James 1975; Ricklefs & Travis 1980; Pianka 1986; Ricklefs *et al.* 1981; Winemiller 1991). In this approach, each species is represented as a point in an n -dimensional hypervolume whose coordinates are the morphological variates. These may be standardized as desired or log transformed. Euclidean distances between species are calculated as measures of dissimilarity. Distances from the centroid of the hypervolume can be exploited to judge the overall size of morphological space. If desired, dimensionality can be reduced and orthogonality achieved by changing coordinate systems, using

a multivariate procedure such as principal components analysis (euclidean distances between species remain unchanged when axes are rotated). Spacing patterns between species, such as nearest neighbor distances, and other aspects of their position in morphological space can then be examined.

The assumption is usually made that the arrangement of species in morphological space accurately reflects their ecological relationships, although this assumption is not easily verifiable and has seldom been directly tested.

In one such study (Pianka 1986), ten morphometric variates were measured for each individual lizard collected: snout-vent and tail length, the length, width, and depth of the head, and the lengths of the jaw, forefoot, forearm, hindfoot, and hindleg. Even though sexual dimorphism occurs in some species, sexes were lumped for simplicity and ease of analysis. These measurements were strongly positively correlated with one another over all 92 species (mean correlation coefficient = 0.75). Average morphometric measures were used to represent each species as a point in a 10-dimensional morphospace. Each measurement was given equal weight by standardizing by subtraction of the mean value for all 92 species and division by the standard deviation across all species: this z transformation standardization procedure results in a mean score of 0.0 and a standard deviation of 1.0 for each variate. Distances from this standardized hypervolume's centroid (representing the overall "average" lizard species) were calculated for each species and averaged for each continental lizard fauna. Euclidean distances between all pairs of species were computed, and nearest neighbor distances identified for each. Various morphometric statistics were computed for each continent separately as well as for all intracontinental plus intercontinental pairs of species.

Anatomically, Kalahari lizard species are appreciably more similar than are North American or Australian lizard species. Both the overall average and nearest neighbor Euclidean distances are smaller and less variable in Kalahari lizards than on the other two continental-desert lizard systems. Euclidean distances between species are most variable in Australia, probably partially due to the larger number of species there.

The overall volume of morphospace occupied by Kalahari lizards, as judged by distances from the centroid, is more compact than that occupied by lizards in North America and Australia. These data were subjected to multivariate analysis (principal components) to reduce dimensionality.

This method changes the coordinate system by identifying new orthogonal axes (principal components) that reduce residual variance most efficiently. When all 92 species are considered together, the first three principal components reduce overall variance by 77.7 percent, 11.6 percent, and 6.7 percent (total 96 percent), respectively. Thus, 96 percent of the information present in the original data remains present in just these three new independent dimensions. Centroids for each continental fauna deviate from the overall centroid of all 91 species. Interestingly enough, even on these very crude morphological dimensions, the Australian agamid ant specialist the thorny devil

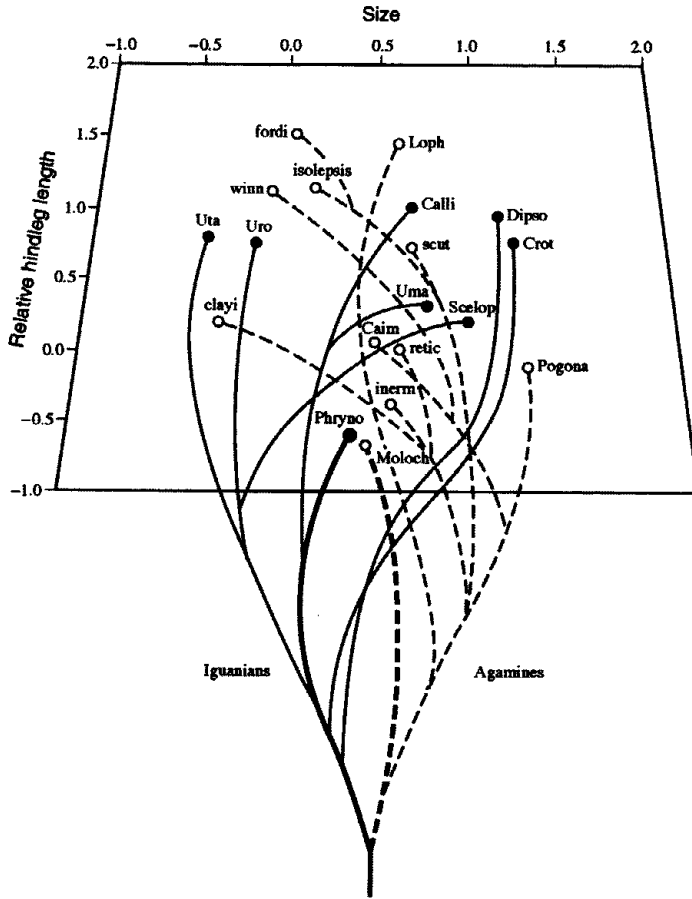


Figure 13. Positions of various lizard species on the first two principal components of a 10-dimensional morphospace corresponding roughly to body size and relative leg length, along with a current hypothesis for phylogenetic relationships among species. Note that the Australian thorny devil *Moloch horridus* and its American "ecological equivalent," the desert horned lizard *Phrynosoma platyrhinos*, are actually closer to one another than either is to another member of its own saurofauna. [Key: Uta = *Uta stansburiana*, Uro = *Urosaurus graciosus*, Calli = *Callisaurus draconoides*, Dipso = *Dipsosaurus dorsalis*, Gamb = *Gambelia wislizeni*, Uma = *Uma scoparia*, Scelop = *Sceloporus magister*, Phryno = *Phrynosoma platyrhinos*, Moloch = *Moloch horridus*, inerm = *Ctenophorus inermis*, retic = *Ctenophorus reticulatus*, Caim = *Caimanops amphiboluroides*, clayi = *Ctenophorus clayi*, winn = *Diporiphora winnecke*, isolepis = *Ctenophorus isolepis*, fordii = *Ctenophorus fordii*, Loph = *Lophognathus longirostris*, scut = *Ctenophorus scutulatus*, Pogona = *Pogona minor*.]

Moloch horridus and its distant relative and American "ecological equivalent," the iguanian desert horned lizard *Phrynosoma platyrhinos*, are actually closer to one another than either is to another member of its own continent's lizard fauna (Figure 13). This analysis constitutes an objective example of convergent evolution and demonstrates the power of using the phylogenetic approach in ecology. However, this analy-

sis has not yet been tested using modern phylogenetically based statistical methods. I am collaborating with Peter Midford and Ted Garland to develop tests that can be applied to data like these. Such new methods should improve future analyses of this sort.

Acknowledgments

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