Testing the Hypothesis That a Clade Has Adaptively Radiated: Iguanid Lizard Clades as a Case Study

Jonathan B. Losos[1,*] and Donald B. Miles[2,†]

1. Department of Biology, Campus Box 1137, Washington University, St. Louis, Missouri 63130;
2. Department of Biological Sciences, Ohio University, Athens, Ohio 45701

abstract: The study of adaptive radiations has played a fundamental role in understanding mechanisms of evolution. A recent resurgence in the study of adaptive radiations highlights a gap in our knowledge about determining whether a clade constitutes adaptive diversification. Specifically, no objective criteria exist to judge whether a clade constitutes an adaptive radiation. Most clades, given enough time, will diversify adaptively to some extent; therefore, we argue that the term "adaptive radiation" should be reserved for those clades that are exceptionally diverse in terms of the range of habitats occupied and attendant morphological adaptations. Making such a definition operational, however, requires a comparative analysis of many clades. Only by comparing clades can one distinguish those that are exceptionally diverse (or nondiverse) from those exhibiting a normal degree of adaptive disparity. We propose such a test, focusing on disparity in the ecological morphology of monophyletic groups within the lizard family Iguanidae. We find that two clades, the Polychrotinae and Phrynosomatinae, are exceptionally diverse and that two others, the Crotaphytinae and Oplurinae, are exceptionally nondiverse. Potential explanations for differences in diversity are discussed, as are caveats and future extensions of our approach.

Keywords: adaptive radiation, disparity, iguanid, lizard.

The concept of adaptive radiation—defined in a leading evolution textbook (Futuyma 1998) as "evolutionary divergence of members of a single phylogenetic lineage into a variety of different adaptive forms"—has a long and distinguished history (Givnish 1997; Gillespie et al. 2001). Recent years have seen an upsurge of interest in both the causes and consequences of adaptive radiation, as evi-

* E-mail: losos@biology.wustl.edu.

† E-mail: milesd@oak.cats.ohiou.edu.

denced by many recent reviews, monographs, and symposia (e.g., Givnish and Sytsma 1997; Schluter 2000; *American Naturalist* supplement to volume 156, October 2000; Gillespie et al. 2001).

Nonetheless, we see a major problem impeding progress in the study of adaptive radiation: no quantitative criteria exist to recognize which clades constitute adaptive radiations and which do not. Most clades, given enough time, will diversify, and some, perhaps much, of this diversification will be adaptively driven; hence, by this token, most clades could qualify as adaptive radiations. As a result, the concept of adaptive radiation becomes useless; if any clade that has diversified adaptively qualifies as an adaptive radiation, then the term has no special meaning and simply refers to the routine outcome of normal evolutionary diversification.

To our minds, however, that is not what the originators of the concept had in mind (e.g., Simpson 1949), and it is not why most people today are interested in adaptive radiation. Rather than referring to the usual outcome of the evolutionary process, the term "adaptive radiation" usually refers to the exceptional cases in which a clade has experienced a remarkably great extent of adaptive diversification. Nowhere is this more evident than in evolution textbooks in which the concept is usually illustrated with examples such as Darwin's finches, Hawaiian honeycreepers and silverswords, and marsupials (e.g., Futuyma 1998; Strickberger 2000; Freeman and Herron 2001); similar examples are found in classic works in evolutionary biology (e.g., Grant 1963; Mayr 1963).

The issue of whether a clade constitutes an adaptive radiation might seem like mere semantics, but it is not. A primary objective in studies of adaptive radiations entails identification of the events that serve to trigger an adaptive radiation or the factors that predispose a clade to radiate (e.g., Liem 1973; Vermeij 1974; Lovette et al. 2002). Examples include the focus on the roles of key innovations, mass extinctions, and the colonization of ecologically depauperate areas such as islands and mountaintops (e.g., Givnish and Sytsma 1997). However, before one can meaningfully investigate the factors that promote adaptive ra-

diation, one must first be able to identify the clades on which to focus. That is, before invoking a scenario for the remarkable diversity of a clade, one needs an objective criterion to test the hypothesis that the diversity is truly remarkable.

Consequently, we propose that the term "adaptive radiation" should be restricted to *those clades that exhibit unusually great divergence into a variety of adaptive forms*. In turn, acceptance of this definition requires formulation of a methodology by which workers can test the hypothesis that a clade constitutes an adaptive radiation, as contrasted to the null hypothesis that the extent of divergence is no greater than that expected by chance from a clade undergoing routine evolutionary diversification.

Criteria for Judging Whether a Clade Has Adaptively Radiated

Two aspects of our definition of adaptive radiation are important. First, the clade must have diversified adaptively; that is, species must have evolved adaptations to interact with the environment in different ways, either by using the same habitat or resource in different ways or by adapting to use different habitats or resources. In the last 15 years, a large literature has developed concerning how to study and identify adaptive evolution (Rose and Lauder 1996; Orzack and Sober 2001 and references therein). We will not enter into this discussion here; for our purposes, we will assume that it is possible to investigate whether differences among species are adaptively based.

In contrast to this emphasis on adaptive diversity, many recent studies have compared the extent to which clades, usually sister taxa, differ in the number of species they contain (e.g., Brooks and McLennan 1993). This is a different phenomenon, one that is not necessarily linked to adaptive radiation. Many of the clades commonly considered adaptive radiations (e.g., African Rift Lake cichlids, Caribbean *Anolis* lizards) are both species-rich and adaptively diverse. Nonetheless, the two attributes need not necessarily be linked (Erwin 1992). On the one hand, a species-rich clade may contain little adaptive diversity (e.g., *Albinaria* snails [Gittenberger 1991], salamanders of the *Plethodon glutinosus* group [Highton et al. 1989]); the term "nonadaptive radiation" has been coined for this phenomenon (Gittenberger 1991). Alternatively, some clades with few species may exhibit substantial adaptive diversity. Indeed, a classic example of adaptive radiation, the Geospizidae (Darwin's finches), contains only 15 species! A similar example is provided by the ecologically and morphologically diverse but species-poor lizard family Pygopodidae (Webb and Shine 1994).

The second important aspect of our restricted definition of adaptive radiation concerns the manner by which one determines that the amount of adaptive diversity exhibited by a clade is unusually great. By its nature, such a determination is comparative, but the question is, What is the appropriate comparison? In recent years, sister taxon comparisons have become the method of choice for comparative biologists (e.g., Brooks and McLennan 1993). The logic behind such comparisons is unassailable. Sister clades have been evolving for the same amount of time since diverging from a common ancestor. Thus, if one wants to investigate the consequences of the evolution of a particular trait, then the appropriate comparison is between a clade characterized by the evolution of that trait and its sister clade without the trait. Examination of a great number of such pairs of taxa can lead to a powerful test of whether the evolutionary presence of the trait is associated with other features, such as high species diversity (e.g., Farrell et al. 1991; Hoglund and Sillen-Tullberg 1994).

Nonetheless, sister taxon comparisons are not appropriate for all questions in comparative biology. In the case of the study of adaptive radiation, sister taxon comparisons are inadequate and, in some cases, positively misleading. The main problem in this case is that sister taxon comparisons limit the comparisons to one, that between a clade and its sister. In principle, determination of whether a clade is unusually diverse requires comparison to a large sample; a single comparison is an insufficient basis for judgment (Sanderson and Donoghue 1996; Magallón and Sanderson 2001).

By the same token, sister taxon comparisons can be misleading if the sister taxon is exceptionally diverse or nondiverse. For example, marsupial and placental mammals are generally considered to be sister taxa. Both clades exhibit substantial adaptive diversity, and each might reasonably be considered an adaptive radiation. Nonetheless, if, as is probably the case, the adaptive diversity of placentals is greater than that of marsupials (Springer et al. 1997), then the latter could not be judged an adaptive radiation by this method. Alternatively, if neither clade is particularly diverse, the more diverse of the two might be considered an adaptive radiation by comparison.

Delineating an appropriate pool of clades to form the basis for comparisons is a necessary first step. Two criteria are important in choosing this pool. First, each clade must be monophyletic. If one is interested in the evolutionary diversity of a group, one must consider all of the descendants of their most recent common ancestor or diversity likely will be underestimated, perhaps substantially.

Second, the clades must be comparable in several respects. Of foremost importance, the clades must be comparable in basic aspects of their biology. As Findley (1979) noted, comparing the extent of diversity of organisms as disparate as humans and frogs is extremely difficult because so many aspects of their biology (e.g., morphology,

ecology, behavior) are radically different, thus rendering meaningful comparison nearly impossible. Only by comparing groups having comparable phenotypic attributes and interacting with the environment in similar ways can one reasonably quantify and compare extent of differentiation.

Even among such clades, however, other factors must be considered. One obvious candidate is the age of the clade. Fossil data document that the morphological diversity of a clade changes through time (e.g., Foote 1991*a*, 1991*b*, 1992, 1999; Wagner 1997). If a general relationship exists between age of a clade and extent of diversity, then comparisons among clades of different ages will be confounded (Magallón and Sanderson 2001). One solution would be to limit comparisons to clades of approximately the same age; an alternative would be to remove the effect of clade age statistically. Depending on the goals of a particular study, other clade attributes (e.g., geographic setting, diet, age of occurrence [if examining fossil clades]) might also need to be considered.

Once an appropriate pool of clades has been selected, identification of adaptive radiations is, at least conceptually, straightforward. Adaptive radiations may be recognized based on the degree of diversification in ecologically relevant morphological traits (Foote 1997, 1999; of course, a comparable approach could be taken with any other phenotypic aspect [e.g., physiology] as long as interspecific phenotypic variation corresponds with adaptation to different aspects of the environment). Thus, a clade that exhibits remarkable radiation in form, regardless of species richness, in comparison to other clades would be considered an adaptive radiation. Following Foote (1999 and references therein), we suggest that disparity—the measure of character distance between species—is a suitable metric to assess differences in morphological variation. Clades that exhibit a large amount of morphological differentiation will be characterized by an unusually large disparity. Of course, where one draws the line for unusual will always be arbitrary. One criterion might be those clades that fall outside 95% confidence limits, although this is a rather conservative standard.

A Case Study: Evolutionary Diversification and Adaptive Radiation in the Lizard Family Iguanidae

Iguanid lizards are an ideal group with which to explore these ideas. The iguanid clade is comprised of eight putatively monophyletic clades (we follow recent treatments in considering these clades as subfamilies within the Iguanidae [e.g., Macey et al. 1997; Schulte et al. 1998; Pough et al. 2001; Zug et al. 2001]; fig. 1). More importantly, though, these clades, with one exception, are comparable in a number of respects. First, they are similar in many
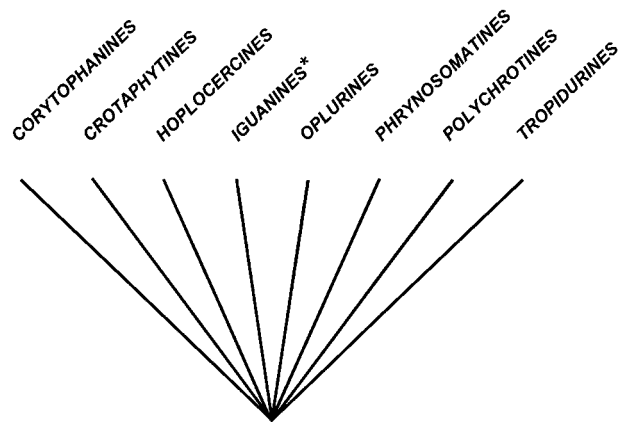

Figure 1: Phylogeny of the Iguanidae (based on Macey et al. [1997] and Schulte et al. [1998]). The Iguanines are excluded from this analysis because they differ fundamentally from other iguanid clades in many aspects of their natural history.

features of morphology, ecology, and behavior. All iguanids are robust, four-legged lizards that live above the ground; most species are territorial, sit-and-wait predators that rely on vision as their primary sensory mode. The exception to these generalizations are the iguanas (Iguaninae). Unlike most other iguanids, iguanas are large, herbivorous lizards that rely more on chemoreception (Schwenk 1993; Cooper 1995, 1996) and exhibit differences in mating and social systems (Trillmich 1984; Phillips 1995; Wikelski et al. 1996; Knapp 2000).

Molecular data are unable to resolve relationships among these taxa (Macey et al. 1997; Schulte et al. 1998), which suggests the possibility that the clades diverged within a short period of time and thus are approximately the same age (cf. Jackman et al. 1999). Molecular data suggest that this divergence occurred at least 65 million years ago (Macey et al. 1997), a date that is not inconsistent with the fossil record (Estes 1983; Gao and Norell 2000).

Consequently, we ask the question: are any of the iguanid clades unusually diverse relative to the extent of adaptive diversity exhibited by other iguanid clades? Addressing this question is a two-step process: first, we must quantify the extent of adaptive diversity, and then we must evaluate whether any clade's diversity is unusually large.

One advantage of focusing on the Iguanidae is that a considerable amount of research has been conducted on the adaptive significance of morphological variation within this clade. A variety of field and laboratory studies, combining observational and experimental approaches and often conducted within a phylogenetic framework, has established that much of the morphological variation within iguanid clades represents adaptation to differences in habitat use (e.g., Losos 1990; Miles 1994; Irschick et al. 1997;

Vitt et al. 1997; Zani 2000; Kohlsdorf et al. 2001). We focus here on variation in traits for which the adaptive significance of intraclade variation has been particularly well established. An underlying assumption is that the adaptive significance of trait variation is similar among clades; that is, if two taxa differ in some characteristic by a given amount in two clades, then this difference corresponds to a similar amount of divergence in the way the species interact with the environment. For this reason, we exclude the Iguaninae from this analysis. Because of the many fundamental differences in biology between iguanas and other iguanids, the relationship between morphology and ecology is likely to be different between the two groups. For example, most iguanids capture prey by a rapid burst of speed, and variation among species in habitat use is reflected in differences in sprint performance. By contrast, for iguanas, which do not need to move rapidly to acquire their food, the relationship between limb morphology, which is mechanistically linked to sprint performance, and habitat use might be quite different.

Methods

Taxa Included

The Iguanidae contains >900 species (Pough et al. 2001). We measured 101 specimens, choosing species from each clade to maximize the ecological and morphological diversity represented and to represent the morphological diversity present within the major subclades of each clade. Decisions on which species to include were based on literature descriptions, advice of colleagues, previous taxonomic arrangements (on the assumption that evolutionary classifications represented significant aspects of diversity), and availability in museum collections.

Traits Examined

Using calipers, we measured 17 external morphological variables on each specimen: snout-vent length (SVL) from the tip of the snout to the anterior side of the cloaca; tail length from the posterior portion of the cloaca to the tip of the tail; jaw length from the anterior portion of the ear opening to the tip of the snout; jaw width (width of the head at the insertion of the jaw); head depth (depth of the head measured at the ear openings); eye length (length of the external eye opening); ear height (height of the ear opening; depth of the body at the pectoral girdle; body width (maximum width of the body); humerus length (distance from the shoulder to the apex of the elbow); antebrachium length (distance from the elbow to the center of the wrist); manus length (distance from the center of the wrist to the end of the hand); length of the longest digit (IV), measured from the manus to the tip of the claw; shank length (distance from the insertion of the hindleg at the pelvis to the apex of the knee); crus length (distance from the apex of the knee to the center of the ankle); foot length (distance from the center of the ankle to the end of the fourth tarsal); and length of the fourth toe, measured from the posterior end of the fourth tarsal to the tip of the claw on digit IV. All variables were log transformed prior to analysis. In the case of one character (ear height), we used a $\log(x + 1)$ transformation because two species lack external ear openings.

Calculation of Morphological Disparity

Estimating the volume occupied by the various clades, and hence disparity, entails two steps. First, the appropriate metric should be chosen. Following Foote (1995), we used the mean-squared Euclidean distance between species i and j, where $D = \Sigma_{k=1}^{r}(x_{ik} - x_{jk})^2$ and r equals the number of variables, because it is relatively insensitive to sample size.

Second, the type of analysis should match the variables included in the sample. One possible approach would be to calculate the squared Euclidean distance using all 17 morphological traits. However, this assumes that all characters are independent and uncorrelated (Willis et al. 1994). Covariation among variables will affect the estimate of disparity; the greater the covariation, the lower the morphological disparity (Tabachnick and Fidell 2000). We used principal components analysis (PCA) to estimate the patterns of variation and covariation among the morphological characters in the data set. We then retained the species' scores from the PCA axes to calculate the mean-squared Euclidean distance for each species. The use of PCA in estimating disparity in the morphospace has several advantages. First, the measures of disparity are less likely to be affected by taxa that have extremely similar values for several morphological traits. Second, there may be significant redundancy in the characters included in the data set. Hence, one may arbitrarily increase the morphological volume by increasing the number of characters. PCA extracts the major trends of variation in a set of fewer, uncorrelated axes without a major loss of information. We calculated the PCA using the covariance matrix of all 17 characters. Furthermore, each component axis was scaled to be equal to its eigenvalue. This ensures that the interspecific differences in the PCA space are identical to the distances in the original space. Third, by explicitly incorporating the covariances among characters in the analysis, the PCA scores provide a more accurate estimate of the disparity between any two taxa (Willis et al. 1994).

We chose to focus on morphological variation in shape independent of body size (which varies substantially

Table 1: Results from a principal component analysis of 17 morphological characters

	PC axis 1	PC axis 2	PC axis 3	PC axis 4	PC axis 5	PC axis 6
Snout-vent length (SVL)	−.47	−.39	.02	−.39	.10	.14
Body width	.75	−.40	−.46	.04	−.02	.03
Pectoral depth	−.21	−.39	.26	.67	−.41	−.11
Pectoral width	.68	−.36	−.46	−.13	.06	.16
Brachium	−.51	.09	−.09	−.04	.47	−.47
Antebrachium	−.36	.02	−.19	−.14	.33	−.58
Hand	.07	.37	−.18	−.48	−.30	−.41
Finger length	−.19	.36	−.09	−.54	−.48	−.35
Shank	−.28	.46	−.06	.34	.59	.01
Crus	−.15	.56	−.34	.40	.43	.26
Foot	−.20	.82	−.23	.19	−.16	.22
Long toe	−.19	.78	−.21	−.04	−.37	.19
Jaw length	−.66	−.44	.23	−.01	.13	.07
Head width	.23	−.71	.16	−.06	−.12	−.03
Head height	−.38	−.62	.34	.36	−.30	−.08
Eye length	−.51	−.29	.41	−.36	.06	.43
Ear height	.81	.24	.52	−.01	.06	−.02
Eigenvalue	.030	.018	.012	.006	.005	.004
Percent variance explained	33	20	14	7	7	5

Note: The analysis was based on the size-adjusted traits. Values are the loadings for each of the first four PC axes.

among species included in this study). This decision is conservative, because the groups we find to be most and least disparate in shape are also those that exhibit the greatest and least amounts of variation in overall size. To remove the effects of size from the data, we used Mosimann's (1970) geometric-mean method, which removes the influence of size without distorting group structure (Butler and Losos 2002). We defined a size variable to equal the geometric mean of all 17 variables. Because we log-transformed the variables, the index of size becomes the arithmetic average of all 17 variables. We then obtained a size-free measurement of each trait by taking the difference between each variable and our index of size. In the PCA using these 17 size-free variables, we retained the number of axes that cumulatively account for 85% of the variation in the original data set.

We used the bootstrap to determine whether the disparity of a clade was unusually large or small. For each clade, we randomly drew with replacement the same number of species from a pool containing all species from all clades. Because the clades differ in their position in morphological space, PCA scores for each species in the bootstrap pool were adjusted so that the centroids for each clade were identical. The disparity of a clade was considered unusually large or small if the value was in one of the 2.5% tails of the distribution based on 1,000 bootstraps.

In these analyses, the expected value in the bootstraps was independent of the number of species in the sample. However, the greater the sample size, the narrower the

distribution around this mean. As a result, the 2.5% cutoff values changed as a function of number of species in the clade. Consequently, a disparity value that would be judged significant for one sample size might not be so judged for a smaller sample size, even though the dispersion of the species would be identical. For heuristic purposes, we indicate the cutoff values determined for the clade with the most species represented. However, based on their own sample sizes, the oplurines and phrynosomatines would have been nonsignificant.

Results

The first six axes explained 85% of the total variation in the morphological data set (table 1). The results from the PCA indicate a substantial amount of morphological variation exists among families. Furthermore, the morphological volume describes variation in morphological traits related to trophic differentiation (head characters) and locomotor performance (limb characters).

Although species-rich clades generally have more disparity, this relationship is far from perfect (fig. 2). Indeed, the second most speciose clade, the tropidurines, has lower disparity than several substantially smaller clades. The polychrotines have the highest mean-squared distance and are well above the two-tailed, 5% confidence limit. Phrynosomatines are also slightly above this threshold. At the other extreme, oplurines and crotaphytines exhibit significantly little morphological disparity.
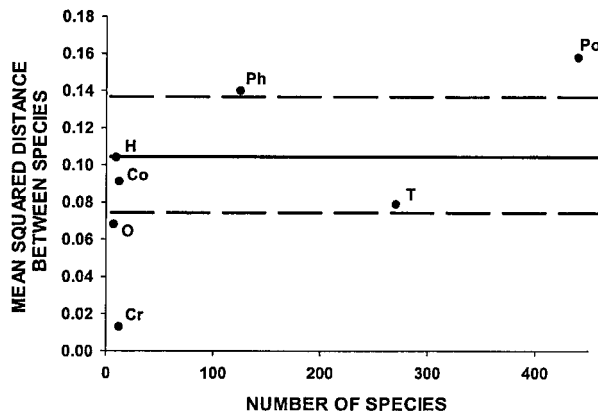
Figure 2: Morphological disparity of iguanid clades. In the bootstrap analyses, the expected value (solid line) was independent of sample size, but the distribution around the mean narrowed with increasing sample size. For heuristic purposes, dashed lines represent the 2.5% cutoff values in the bootstrap for the clade with the largest number of specimens examined. The *X*-axis is the number of currently recognized species in each clade.

Discussion

To have any utility, the concept of adaptive radiation must be comparative: some clades represent adaptive radiations and others do not. Moreover, the assessment of whether a clade represents an adaptive radiation must be relative to other, similar clades. If the concept were not relative to similar clades, then few clades would seem to be remarkably diverse in comparison to, for example, mammals or angiosperms. Thus, the assessment of whether a clade represents an adaptive radiation should be in relation to other clades similar in age and biological attributes.

The lizard family Iguanidae is a remarkably diverse clade that includes species exhibiting morphological adaptations for an incredible array of life styles. Our examination of seven of the eight subfamilies comprising the Iguanidae reveals that most of these clades also contain substantial diversity. The tropidurine subfamily, for example, contains species adapted for living in or on sand, ground, rocks, grass, trees, and crevices. What our analysis highlights, however, is that for clades of robust, four-legged, territorial iguanid lizards that use a sit-and-wait foraging mode and that have been diversifying for approximately 65 million years, a substantial extent of ecological and morphological diversity is the norm. Only polychrotine and phrynosomatine lizards are exceptional at the 95% level. Hence, if one were interested in what factors trigger particularly diverse radiations, at least in nonherbivorous iguanid lizards, then one should focus on these two clades; the remaining subfamilies, not being unusually diverse, would

not merit investigation for these purposes. At the other end of the extreme, of course, one might also be interested in the exceptionally low levels of disparity exhibited by oplurines and crotaphytines.

Factors Leading to Exceptional Divergence

To investigate the factors promoting exceptional levels of disparity, one might be tempted to look at attributes characterizing an entire exceptionally disparate clade. However, an alternative possibility is that a subclade within the clade evolved some attribute, causing that subclade and the entire clade to which it belongs to evolve exceptional disparity. Were this the case, then it would be attributes of the subclade, rather than of the entire clade, that triggered the radiation.

To examine this possibility, we measured the disparity of clades within the Polychrotinae (fig. 3). The analysis indicates that one of the subclades, the para-anoles + the leiosaurs, is not particularly disparate, but that the other, the anoles + *Polychrus*, would be judged exceptional. Moreover, within that subclade, the clade composed of only the anoles exhibits exceptionally high disparity (sampling was not sufficient to examine disparity within anole clades). Hence, this analysis suggests that it is traits that characterize the anoles that should be examined to study what factors trigger exceptional diversification in this clade. Although it is not the purpose of this article to explore such topics, two related factors that may be relevant are the evolution of subdigital toe pads, which permit movement on narrow and smooth surfaces, and the evo-
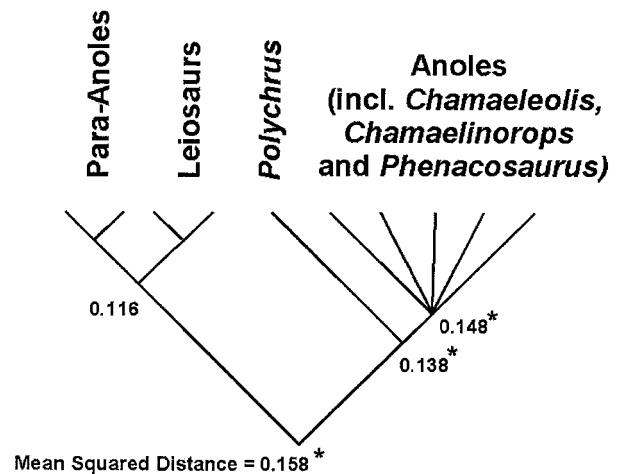

Figure 3: Morphological disparity for subclades within the Polychrotinae (phylogeny based on one of three equally parsimonious phylogenies in Frost and Etheridge [1989]). Asterisks indicate clades that would be judged to have significantly great disparity.

lution of arboreality, which adds a third habitat dimension in which to specialize. Perhaps surprisingly, despite all of their diversity, most other iguanid clades have not extensively explored the arboreal habitat. Thus, the diversity of anoles may have resulted from finding a way to occupy and diversify within this habitat dimension.

A similar analysis (not shown) of the Phrynsomatinae indicates that it is the sand lizard clade (*Phrynosoma*, *Callisaurus*, *Uma*, *Holbrookia*, and *Cophosaurus*) that exhibits exceptional disparity, whereas its sister clade (comprising *Sceloporus*, *Petrosaurus*, *Sator*, *Uta*, and *Urosaurus*) contains relatively little disparity. Hence, for this clade, investigation should focus on the factors that have made the sand lizards so disparate.

The Relationship between Species Richness and Adaptive Disparity

One might expect that, all else equal, a relationship would exist between the number of species in a clade and the amount of adaptive disparity of that clade. However, as we noted in the introduction, this relationship does not necessarily hold; some clades are species-rich but display little adaptive diversity, whereas other clades contain few species but much adaptive diversity. Our results reinforce this conclusion. Most notably, the corytophanines and hoplocercines, despite containing a handful of species each, both exhibit greater adaptive disparity than the Tropidurinae, a clade containing approximately 20-fold greater species richness but lacking in ecomorphological diversity (Kohlsdorf et al. 2001; Schulte 2001). Thus, although some clades are quite diverse in both species diversity and adaptive disparity (e.g., cichlids), we conclude that the factors regulating species proliferation and adaptive diversification are only weakly linked.

Comparisons beyond the Iguanidae

Of course, one might counter our arguments by suggesting that iguanid clades are predisposed to exhibit adaptive radiation, perhaps as a result of some of their shared attributes. Thus, it could be argued, by limiting our consideration only to iguanid clades, it becomes difficult to detect the exceptional diversity of many clades within the Iguanidae. This is the same argument we leveled against sister taxon comparisons, only at a greater scale: if many clades in a comparison are exceptionally diverse, then few will seem exceptional in comparison to each other.

Our data cannot address the hypotheses that multiple clades within the Iguanidae represent adaptive radiations and that iguanid clades are more likely to radiate than are noniguanid clades. These are testable hypotheses that constitute a logical next step. What is needed is additional data on noniguanid clades that are comparable in as many respects as possible to iguanid clades. A good starting point would be examination of clades within the Acrodonta (composed of agamids and chamaeleons), the sister taxon to the Iguanidae, which share similar biological attributes to the clades we examined. In turn, the Iguania (Acrodonta + Iguanidae) is generally considered to be the sister taxon to all other extant lizards (but see Harris et al. 2001). Hence, the next logical expansion would be to select other lizard clades as similar as possible to iguanians.

A problem with this approach is that more distantly related clades are likely to show divergence in key biological attributes, which diminishes any meaningful comparison. For example, although snakes probably evolved from some type of lizard (Greene 1997; Tchernov et al. 2000), comparison of iguanian lizards and snakes would be problematic given the many differences in morphology, behavior, and ecology between these clades. Although this example is extreme, it is true that among lizards, distantly related clades differ in many respects. For example, noniguanian lizards tend to differ from iguanians in geographic distribution, body form, foraging mode, social behavior, and other attributes (though not all clades differ in all respects). As a result, the relationship between morphology and ecology is likely to differ between clades because of greatly divergent patterns of natural selection; indeed, variation in a trait (or trait complex) may reflect adaptive differentiation in one clade and be the result of nonadaptive processes in another (McPeek 1997; McPeek and Brown 2000).

Caveats

Four caveats to our approach must be mentioned. First, we have not included fossil data. In the case of iguanid lizards, we had no choice, as the fossil record of iguanians is sparse (though recent findings are promising [e.g., Gao and Hou 1995; Gao and Norell 2000]). Consequently, our general approach represents a snapshot in time, based only on currently extant members of a clade. Given that the disparity of a clade may wax and wane through time (Foote 1991*a*, 1991*b*, 1992, 1996; Wagner 1997; Lupia 1999), our approach may fail to identify as an adaptive radiation a clade that diversified greatly in the past but for which much of the diversity has been lost (e.g., crocodilians [Buffetaut 1989; Brochu 2001], hyraxes [Rasmussen 1989], rhyncophelians [Evans et al. 2001]). Methods have been developed to study the morphologic disparity of a clade through time (Foote 1991*a*, 1992, 1999), although assessing the adaptive basis of diversification can be difficult for extinct taxa with no living counterparts (Radinksy 1987; Lauder 1995). Consequently, integrating these methods for fossil data with phylogenetic information and data on extant

taxa would be desirable. Recent incorporation of phylogenetic data into the examination of morphological disparity in fossil taxa is an important step in this direction (Wagner 1997; Eble 2000).

A related problem is that timing of diversification may differ among clades; some clades may diversify immediately after origination, whereas diversification in other clades may not begin until long after the clade originated. Accounting for such differences will be difficult without fossil data (cf. Magallón and Sanderson 2001).

Second, our analysis was based on the approximately equal age of all seven iguanid clades, thus making unnecessary the need to account statistically for effects of clade age on extent of diversification. However, to examine clades of different ages as in our subclade analysis above, we will need to expand our methodology to account for age effects. For example, by comparing the disparity of polychrotine and phrynosomatine subclades to that expected for older clades, our test is biased against finding an exceptional amount of disparity in the subclades. The para-anole + leiosaur clade, for example, might have been judged exceptionally disparate if compared with clades of comparable age. Further work is needed in this area.

Third, clades may diversify in many different ways. Thus, for example, some clades may diversify with respect to the habitats they use, whereas others may diversify in the types of food they eat. As a result, any assessment of adaptive radiation will be limited to the specific types of adaptations and resources examined. In this study, for example, we have focused on morphological adaptations to using different types of habitats. However, a number of iguanid clades (e.g., polychrotines, tropidurines) exhibit substantial physiological variation that represents adaptation to different thermal regimes (Huey 1982).

Moreover, one can always quibble with the traits examined. For example, one tropidurine clade has an enlarged keel on its jaw possibly used for burial in sand (Etheridge 2000). Because we have only included quantitative traits present in all taxa, such traits have not been included. For the most part, such traits are present in few species within a clade; thus, the exclusion of such traits probably only slightly underestimates a clade's adaptive diversity. One exception may be the enlarged toepads of anoles, which are found in most polychrotines and which show substantial adaptive diversity among those species (Peterson 1983; Glossip and Losos 1997; Beuttell and Losos 1999; Macrini et al., in press). As a result of not including measurements of toe pads, the extent of adaptive diversity within polychrotines may be substantially underestimated relative to other iguanid clades, none of which possesses enlarged toepads.

More generally, though, we emphasize that organisms interact with their environments in countless different ways, and thus adaptive radiation can occur in correspondingly many different ways. It is thus possible that a clade may constitute an adaptive radiation with regard to one set of characteristics and not with regard to another. Thus, any comparative examination of extent of adaptive diversification will be limited in scope to a particular subset of adaptive characteristics.

Moreover, we emphasize that phenotypic variation cannot be assumed to be adaptive. For iguanids, we have good reason to believe that variation in the traits we have examined represents adaptive differentiation, but for other groups, the evidence for such a link may be less compelling.

Finally, fourth, as with any phylogenetic comparative method, our results are contingent on the accuracy of our underlying phylogenetic information. Indeed, while we were preparing this manuscript, several new phylogenetic hypotheses for iguanid relationships were published (Frost et al. 2001; Harris et al. 2001; Schulte 2001). One suggestion, in particular, is intriguing: Frost et al. (2001) argue that corytophanids are nested within polychrotines. If, in fact, this is correct, then the disparity of the combined clade of polychrotines and corytophanines would be even greater than the already exceptional disparity estimated from polychrotines alone. In most respects, however, these studies do not strongly support conclusions at variance with the studies on which we have relied (Frost and Etheridge 1989; Macey et al. 1997; Schulte et al. 1998), and Schulte (2001) strengthens the case that the iguanid clades are of approximately the same age. Moreover, some of the results of these recent studies are contradictory. The bottom line is that iguanid phylogeny is still unsettled, and further systematic study is needed to understand the timing and pattern of iguanid diversification.

Conclusions

To be of utility in guiding evolutionary inquiry, study of adaptive radiation should be limited to those clades that exhibit exceptionally great adaptive diversity. Among seven biologically similar clades within the Iguanidae, our analysis highlights only two that are exceptionally diverse in comparison to the amount of variation normally produced by nonherbivorous iguanid lizards evolving over a period of approximately 65 million years. Future studies interested in examining the factors that promote evolutionary diversity thus should focus on attributes of the particularly diverse subclades within the Polychrotinae and Phrynosomatinae. More generally, we have provided a quantitative approach for comparing the adaptive disparity of clades. This approach will be of value in evolutionary studies addressing many questions other than the identification of adaptive radiations.

Acknowledgments

Literature Cited

Beuttell, K., and J. B. Losos. 1999. Ecological morphology of Caribbean anoles. Herpetological Monographs 13:1–28.

Brochu, C. A. 2001. Crocodylian snouts in space and time: phylogenetic approaches toward adaptive radiation. American Zoologist 41:564–585.

Brooks, D. R., and D. A. McLennan. 1993. Comparative studies of adaptive radiation with an example from parasitic flatworms (Platyhelminthes: Cercomeria). American Naturalist 142:755–778.

Buffetaut, E. 1989. Evolution. Pages 26–41 *in* C. A. Ross, ed. Crocodiles and alligators. Facts on File, New York.

Butler, M. A., and J. B. Losos. 2002. Multivariate sexual dimorphism, sexual selection and adaptation. Ecological Monographs (in press).

Cooper, W. E., Jr. 1995. Foraging mode, prey chemical discrimination, and phylogeny in lizards. Animal Behaviour 50:973–985.

———. 1996. Preliminary reconstructions of nasal chemosensory evolution in Squamata. Amphibia-Reptilia 17:395–415.

Eble, G. J. 2000. Contrasting evolutionary flexibility in sister groups: disparity and diversity in Mesozoic atelostomate echinoids. Paleobiology 26:56–79.

Erwin, D. H. 1992. A preliminary classification of evolutionary radiations. Historical Biology 6:133–147.

Estes, R. 1983. Encyclopedia of paleoherpetology. Fischer, Stuttgart.

Etheridge, R. 2000. A review of lizards of the *Liolaemus wiegmannii* group (Squamata, Iguania, Tropiduridae), and a history of morphological change in the sand-dwelling species. Herpetological Monographs 14:293–352.

Evans, S. E., G. V. R. Prasad, and B. K. Manhas. 2001. Rhynchocephalians (Diapsida: Lepidosauria) from the Jurassic Kota Formation of India. Zoological Journal of the Linnean Society 133:309–334.

Farrell, B. D., D. E. Dussourd, and C. Mitter. 1991. Escalation of plant defense: do latex and resin canals spur plant diversification? American Naturalist 138:881–900.

Findley, J. S. 1979. Comparisons of frogs, humans, and chimpanzees. Science 204:434–435.

Foote, M. 1991*a*. Morphological and taxonomic diversity in a clade's history: the blastoid record and stochastic simulations. Contributions from the Museum of Paleontology, University of Michigan 28:101–140.

———. 1991*b*. Morphological patterns of diversification: examples from trilobites. Palaeontology 34:461–485.

———. 1992. Paleozoic record of morphological diversity in blastozoan echinoderms. Proceedings of the National Academy of Sciences of the USA 89:7325–7329.

———. 1995. Morphological diversification of Paleozoic crinoids. Paleobiology 21:273–299.

———. 1996. Models of morphological diversification. Pages 62–86 *in* D. Jablonski, D. H. Erwin, and J. H. Lipps, eds. Evolutionary paleobiology. University of Chicago Press, Chicago.

———. 1997. The evolution of morphological disparity. Annual Review of Ecology and Systematics 28:129–158.

———. 1999. Morphological diversity in the evolutionary radiation of Paleozoic and post-Paleozoic crinoids. Paleobiology 25(suppl.):1–199.

Freeman, S., and J. C. Herron. 2001. Evolutionary analysis. 2d ed. Prentice Hall, Upper Saddle River, N.J.

Frost, D. R., and R. Etheridge. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). University of Kansas Museum of Natural History Miscellaneous Publications 81:1–65.

Frost, D. R., R. Etheridge, D. Janies, and T. A. Titus. 2001. Total evidence, sequence alignment, evolution of polychrotid lizards, and a reclassification of the iguania (Squamata: Iguania). American Museum Novitates 3343:1–38.

Futuyma, D. J. 1998. Evolutionary biology. 3d ed. Sinauer, Sunderland, Mass.

Gao, K., and L. Hou. 1995. Iguanians from the Upper Cretaceous Djadokhta Formation, Gobi Desert, China. Journal of Vertebrate Paleontology 15:57–78.

Gao, K., and M. A. Norell. 2000. Taxonomic composition and systematics of the late Cretaceous lizard assemblages from Ukhaa Tolgod and adjacent localities, Mongolian Gobi Desert. Bulletin of the American Museum of Natural History 249:1–118.

Gillespie, R. G., F. G. Howarth, and G. K. Roderick. 2001. Adaptive radiation. Pages 25–44 *in* S. Levin, ed. Encyclopedia of biodiversity. Vol. 1. Academic Press, San Diego, Calif.

Gittenberger, E. 1991. What about non-adaptive radiation? Biological Journal of the Linnean Society 43:263–272.

Givnish, T. J. 1997. Adaptive radiation and molecular systematics: issues and approaches. Pages 1–54 *in* T. J. Giv-

nish and K. J. Sytsma, eds. Molecular evolution and adaptive radiation. Cambridge University Press, Cambridge.

Givnish, T. J., and K. J. Sytsma, eds. 1997. Molecular evolution and adaptive radiation. Cambridge University Press, Cambridge.

Glossip, D., and J. B. Losos. 1997. Ecological correlates of number of subdigital lamellae in anoles. Herpetologica 53:192–199.

Grant, V. 1963. The origin of adaptations. Columbia University Press, New York.

Greene, H. W. 1997. Snakes: the evolution of mystery in nature. University of California Press, Berkeley.

Harris, D. J., J. C. Marshall, and K. A. Crandall. 2001. Squamate relationships based on C-mos nuclear DNA sequences: increased taxon sampling improves bootstrap support. Amphibia-Reptilia 22:235–242.

Highton, R., G. C. Maha, and L. R. Maxson. 1989. Biochemical evolution in the slimy salamanders of the *Plethodon glutinosus* complex in the eastern United States. Illinois Biological Monographs 57:1–153.

Hoglund, J., and B. Sillen-Tullberg. 1994. Does lekking promote the evolution of male-biased size dimorphism in birds? on the use of comparative approaches. American Naturalist 144:881–889.

Huey, R. B. 1982. Temperature, physiology, and the ecology of reptiles. Pages 25–91 *in* C. Gans and F. H. Pough, eds. Biology of the reptilia. Vol. 12. Physiology (C). Academic Press, London.

Irschick, D. J., L. J. Vitt, P. Zani, and J. B. Losos. 1997. A comparison of evolutionary radiations in mainland and West Indian *Anolis* lizards. Ecology 78:2191–2203.

Jackman, T. R., A. Larson, K. de Queiroz, and J. B. Losos. 1999. Phylogenetic relationships and tempo of early diversification in *Anolis* lizards. Systematic Biology 48:254–285.

Knapp, C. R. 2000. Home range and intraspecific interactions of a translocated iguana population (*Cyclura cychlura inornata* Barbour and Noble). Caribbean Journal of Science 36:250–257.

Kohlsdorf, T., T. Garland, Jr., and C. A. Navas. 2001. Limb and tail lengths in relation to substrate usage in *Tropidurus* lizards. Journal of Morphology 248:151–164.

Lauder, G. V. 1995. On the inference of function from structure. Pages 1–18 *in* J. Thomason, ed. Functional morphology in vertebrate paleontology. Cambridge University Press, New York.

Liem, K. F. 1973. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. Systematic Zoology 22:425–441.

Losos, J. B. 1990. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. Ecological Monographs 60:369–388.

Lovette, I. J., E. Bermingham, and R. E. Ricklefs. 2002.

Clade-specific morphological diversification and adaptive radiation in Hawaiian songbirds. Proceedings of the Royal Society of London B, Biological Sciences 269:37–42.

Lupia, R. 1999. Discordant morphological disparity and taxonomic diversity during the Cretaceous angiosperm radiation: North American pollen record. Paleobiology 25:1–28.

Macey, J. R., A. Larson, N. B. Ananjeva, and T. J. Papenfuss. 1997. Evolutionary shifts in three major structural features of the mitochondrial genome among iguanian lizards. Journal of Molecular Evolution 44:660–674.

Macrini, T. E., D. J. Irschick, and J. B. Losos. In press. Ecomorphological difference in toepad characteristics between mainland and island anoles. Journal of Herpetology.

Magallón, S., and M. J. Sanderson. 2001. Absolute diversification rates in angiosperm clades. Evolution 55:1762–1780.

Mayr, E. 1963. Animal species and evolution. Belknap, Cambridge, Mass.

McPeek, M. A. 1997. Measuring phenotypic selection on an adaptation: lamellae of damselflies experiencing dragonfly predation. Evolution 51:459–466.

McPeek, M. A., and J. M. Brown. 2000. Building a regional species pool: diversification of the *Enallagma* damselflies in eastern North America. Ecology 81:904–920.

Miles, D. B. 1994. Covariation between morphology and locomotory performance in sceloporine lizards. Pages 207–235 *in* L. J. Vitt and E. R. Pianka, eds. Lizard ecology: historical and experimental perspectives. Princeton University Press, Princeton, N.J.

Mosimann, J. 1970. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. Journal of the American Statistical Association 65:930–945.

Orzack, S. H., and E. R. Sober. 2001. Adapationism and optimality. Cambridge University Press, Cambridge.

Peterson, J. A. 1983. The evolution of the subdigital pad in *Anolis*. I. Comparisons among the anoline genera. Pages 245–283 *in* A. G. J. Rhodin and K. Miyata, eds. Advances in herpetology and evolutionary biology. Museum of Comparative Zoology, Harvard University, Cambridge, Mass.

Phillips, J. A. 1995. Does cadence of *Iguana iguana* displays facilitate individual recognition? Behavioral Ecology and Sociobiology 37:337–342.

Pough, F. H., R. M. Andrews, J. E. Cadle, M. L. Crump, A. H. Savitzky, and K. D. Wells. 2001. Herpetology. 2d ed. Prentice Hall, Upper Saddle River, N.J.

Radinsky, L. B. 1987. The evolution of vertebrate design. University of Chicago Press, Chicago.

Rasmussen, D. T. 1989. The evolution of the Hyracoidea:

a review of the fossil evidence. Pages 57–78 *in* D. R. Prothero and R. M. Schoch, eds. The evolution of perissodactyls. Oxford University Press, New York.

Rose, M. R., and G. V. Lauder. 1996. Adaptation. Academic Press, San Diego, Calif.

Sanderson, M. J., and M. J. Donoghue. 1996. Reconstructing shifts in diversification rates on phylogenetic trees. Trends in Ecology & Evolution 11:15–20.

Schluter, D. 2000. The ecology of adaptive radiation. Oxford University Press, Oxford.

Schulte, J. A., II. 2001. A phylogenetic and ecological analysis of iguanian lizard evolution. Ph.D. diss. Washington University, St. Louis.

Schulte, J. A., II, J. R. Macey, A. Larson, and T. J. Papenfuss. 1998. Molecular tests of phylogenetic taxonomies: a general procedure and example using four subfamilies of the lizard family Iguanidae. Molecular Phylogenetics and Evolution 10:367–376.

Schwenk, K. 1993. The evolution of chemoreception in squamate reptiles: a phylogenetic approach. Brain Behavior and Evolution 41:124–137.

Simpson, G. G. 1949. The meaning of evolution. Yale University Press, New Haven, Conn.

Springer, M. S., J. A. W. Kirsch, and J. A. Chase. 1997. The chronicle of marsupial evolution. Pages 129–161 *in* T. J. Givnish and K. J. Sytsma, eds. Molecular evolution and adaptive radiation. Cambridge University Press, Cambridge.

Strickberger, M. W. 2000. Evolution. 3d ed. Jones & Bartlett, Boston.

Tabachnick, B. G., and L. S. Fidell. 2000. Using multivariate statistics. 4th ed. Harper Collins, New York.

Tchernov, E., O. Rieppel, H. Zaher, M. J. Polcyn, and L. L. Jacobs. 2000. A fossil snake with limbs. Science 287: 2010–2012.

Trillmich, K. G. K. 1984. The mating system of the marine iguana *Amblyrhynchus cristatus*. Zeitschrift für Tierpsychologie 63:141–172.

Vermeij, G. 1974. Adaptation, versatility, and evolution. Systematic Zoology 22:466–477.

Vitt, L. J., J. P. Caldwell, P. A. Zani, and T. A. Titus. 1997. The role of habitat shift in the evolution of lizard morphology: evidence from tropical *Tropidurus*. Proceedings of the National Academy of Sciences of the USA 94: 3828–3832.

Wagner, P. J. 1997. Patterns of morphologic diversification among the Rostroconchia. Paleobiology 23:115–150.

Webb, J. K., and R. Shine. 1994. Feeding habits and reproductive biology of Australian pygopodid lizards of the genus *Aprasia*. Copeia 1994:390–398.

Wikelski, M., C. Carbone, and F. Trillmich. 1996. Lekking in marine iguanas: female grouping and male reproductive strategies. Animal Behaviour 52:581–593.

Willis, M. A., D. E. G. Briggs, and R. A. Fortey. 1994. Disparity as an evolutionary index: a comparison of Cambrian and recent arthropods. Paleobiology 20:93–130.

Zani, P. A. 2000. The comparative evolution of lizard claw and toe morphology and clinging performance. Journal of Evolutionary Biology 13:316–325.

Zug, G. R., L. J. Vitt, and J. P. Caldwell. 2001. Herpetology: an introductory biology of amphibians and reptiles. 2d ed. Academic Press, San Diego, Calif.

Associate Editor: Mark A. McPeek