MORPHOLOGICAL DIVERSIFICATION AND ADAPTIVE RADIATION: A COMPARISON OF TWO DIVERSE LIZARD CLADES

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Abstract.—We compared the morphological diversity (i.e., the amount of morphological space occupied) of two similar clades, the lizard genera Anolis and Sceloporus. These species-rich monophyletic clades are similar in body size, age of origin, and many aspects of their natural history. We examined a number of morphological traits whose variation is likely to represent adaptation to different aspects of the environment, including body size, limb proportions, head dimensions, and tail length. Examination of the position of species in multidimensional space, based on a principal components analysis, indicates that the morphological diversity of Anolis, which we refer to as disparity, is significantly greater than that of Sceloporus. One potential explanation for this pattern is that morphological diversification in Anolis was facilitated by the evolution of subdigital toe-pads, which allow anoles to use the environment in ways not available to Sceloporus. The geographic location of diversification (tropical and subtropical for Anolis, arid for Sceloporus) may also have been important.

Key words.—Adaptive radiation, Anolis, disparity, diversity, lizard, PCA, Sceloporus.

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The hallmark of an adaptive radiation is the occupation of a great number and wide variety of ecological niches (Simpson 1953). Classic examples include the African Rift Lake cichlids, Hawaiian honeycreepers, and Australian marsupials (Grant 1986; Givnish and Systma 1997). Given that the ecological diversity of clades such as these is extraordinarily great, researchers have investigated why these clades have radiated to such an extent in comparison to other lineages that have not experienced such diversification. Hypotheses include colonization of an area with few competitors, extinction of a previously dominant group, and the acquisition of a key innovation (Simpson 1953; Givnish and Systma 1997).

Before addressing such hypotheses, however, one must ascertain that the extent of evolutionary diversification of a lineage is, indeed, unusually great; otherwise, there is no phenomenon requiring explanation. One possible means of accomplishing this is by comparison of sister groups (Brooks and McLennan 1993). Such comparisons have the advantage that both taxa originated at the same time from the same initial conditions. However, a major drawback to this approach is that the pool of potential comparisons is limited. Thus, if the sister taxon is extremely depauperate in diversity, an unconditional clade may appear extremely diverse by comparison. For example, in the case discussed here, the sister group to anoline lizards is the lizard genus Polychrus (Frost and Etheridge 1989), which contains only five morphologically and ecologically similar species. Consequently, a demonstration that anoles have diversified to a greater extent than Polychrus would not be a strong argument that anoles have radiated to an exceptionally great degree.

An alternative approach is to compare a clade with other clades of similar age and ecology. In this way, one can determine whether a particular clade has diversified to a greater extent than have comparable clades experiencing similar environments for a similar period of time. A particularly conservative test would be to choose another clade of similar age and ecology that has also diversified widely, demonstrating that the focal clade had experienced greater diversification would strongly suggest that the clade was unusually diverse.

We use this approach to test the hypothesis that Caribbean Anolis lizards have experienced an evolutionary radiation, an hypothesis that is suggested by a large and diverse literature (reviewed in Williams 1983; Losos 1994; Jackman et al. 1997). In comparison, we examine lizards of the genus Sceloporus, which overlap with anoles in size (35–180 mm snout–vent length, 0.5–100 grams), are similar in diet (insectivorous) and habitat use (most members of both genera are often found off the ground), and appear to have originated at roughly the same time.

Although many studies of evolutionary radiation focus on the number of species in different clades (e.g., Brooks and McLennan 1993; Heard and Hauser 1995), species number may not correlate strongly with the range of ecological diversity exhibited by a clade (Foote 1991a, 1992); indeed, many species-rich clades contain species that differ little ecologically (e.g., Gittenberger 1991). Consequently, to quantify the extent of adaptive diversification, we measured a variety of morphological characteristics, assuming that variation in these characteristics translates into variation in ecology (e.g., Losos 1990; Sinervo and Losos 1991; see Discussion). We then used these morphometric characters to test the hypothesis that the amount of morphological space occupied by Caribbean Anolis is greater than that occupied by Sceloporus.

Background on the Genera

Anolis is the most species-rich lizard genus with approximately 400 described species, many of which occur on Ca-
ribbean islands (Powell et al. 1996). Anoles have experienced parallel adaptive radiations on each island of the Greater Antilles, producing on each island a constellation of morphologically distinct species adapted to use different parts of the environment (see Williams 1983; Losos et al. 1998). Sceloporus, which is found in North and Central America, is one of the most species-rich genera of lizards, with more than 70 described species and many more yet to be described (Sites et al. 1992). Fossil evidence suggests a similar time of origin for the two genera: the oldest fossil anole dates to the Middle Miocene–Upper Oligocene, whereas the oldest Sceloporus dates to the Lower Miocene (Estes 1983). Immunological data suggests a slightly older date for Anolis (Hedges 1996), but comparable data are not available for Sceloporus.

**Materials and Methods**

We assessed differences in the range of morphological diversity (termed disparity; see review in Foote 1997) between Anolis and Sceloporus by quantifying various aspects of body shape and size. We applied principal component analyses (PCA) on the variance-covariance matrices defined by the morphological measurements. We accounted for variation due to size and shape in a series of PCA analyses. The procedures we used allowed us to characterize the patterns of variation for individual characters (traits or measurements) as well as to examine the covariation among traits. We used the variance associated with each of these size and shape variables as our measure of disparity because it is a measure of dispersion about the mean and quantifying the variance provides an overall assessment of the individual distances from that mean (Sokal and Rohlff 1995). For a given sample size, greater distances from the mean (i.e., greater variance) equals greater morphological disparity (i.e., occupation of a greater hypervolume of morphospace; for discussion of approaches to quantifying disparity, see Wills et al. 1994 and Foote 1997).

Finally, we compared Anolis and Sceloporus using separate and pooled variance-covariance matrices. The separate analyses permitted us to examine each group independently, unaffected by the variance and covariance structure of the other group. We used these analyses to examine total variance and body size (defined as the first principal component axis; see Bookstein 1989) within each group. To directly compare various aspects of shape between Anolis and Sceloporus, which requires a common size variable, we used a series of pooled PCAs.

**Taxa Included**

We examined one specimen from 48 species, 24 of Anolis and 24 of Sceloporus (the Appendix lists the species; museum numbers are available upon request). However, taxa were deliberately and nonrandomly chosen to maximize morphological and ecological differences. We included the three anoline genera Chamaeleonorops, Chamaeleolis, and Phenacosaurus because recent phylogenetic studies indicate that they all arose from within Anolis (Jackman et al. 1999 and references therein). Similarly, we included Sator because some studies suggest that it arose from within Sceloporus, although other studies indicate that Sceloporus is monophyletic (reviewed in Sites et al. 1992; Reeder and Wiens 1996; Wiens and Reeder 1997; Schulte et al. 1998).

**Measurements**

We measured 15 variables on each specimen. (Note that we name some of the measurements according to their underlying bones, but the measurements were taken externally and thus may not exactly correspond.) The variables were: (1) snout-vent length (svl), from the end of the snout to the beginning of the opening of the vent; (2) tail length, from the end of the opening of the vent to the end of the tail (all specimens had unregenerated tails); (3) jaw length, from the beginning of the ear opening to the end of the snout; (4) head width, the distance across the head measured at the anterior end of the ear; (5) body depth at pectoral girdle; (6) body width at pectoral girdle; (7) antebrachium length, from the apex of the elbow to the center of the wrist; (8) manus length, from the center of the wrist to the end of the hand; (9) metacarpal length, from the posterior tip of the claw on manus IV to the manus; (10) shank length, from the point at which the limb enters the body wall to the apex of the knee; (11) crus length, from the apex of the knee to the center of the ankle; (12) foot length, from the center of the ankle to the end of the foot; (13) metatarsal length, from the posterior tip of the claw on pedal digit IV to the foot; (14) scale number, number of scales circling the widest point on the abdomen; and (15) scale length, the longest axis on a typical scale along the flank of the lizard.

Body measurements were taken using a ruler to measure svl and tail length and calipers to measure all other variables. Initially, the body measurements were taken repeatedly on a set of 10 lizards until reproducible results were attained. If consecutive measurements differed by less than 5%, the measurement was considered reproducible. Because of the position in which specimens were preserved, we were not able to take consistent measurements on the upper forelimb (which was often not preserved in a flattened position in the same plane as the rest of the specimen). Thus, this variable was excluded. Because of the variability for the other forelimb elements, each of these was measured twice and the average of the two measurements was used in the analysis. Both fore- and hind-limb measurements were taken on the left side of the lizard, unless that side was preserved in a distorted position. All body measurements were ln-transformed.

Scale measurements were made using a dissecting light microscope. The microscope was used to count the number of scales encircling the widest portion of the abdomen on each lizard. A representative scale was chosen halfway between the fore- and hind limb on the flank of the lizard. The longest axis of this scale was measured under the microscope.

**Statistical Analyses Using Separate Sceloporus and Anolis Datasets**

We compared various aspects of disparity among species within Anolis and Sceloporus using variance-covariance matrices and principal component analyses. We conducted separate PCAs for each of these clades and defined total variance within each dataset as the sum of all the eigenvalues. This sum is also equal to the sum of the diagonal elements within
each variance-covariance matrix (i.e., the sum of the variances for all measurements).

To place confidence limits around each eigenvalue and eigenvector, we performed PCAs on bootstrapped datasets composed of randomly selected specimens (for methods, see Diaconis and Efron 1983; Marcus 1990). We repeated the bootstrap procedure 500 times for each genus and defined the 95% confidence limits for each eigenvalue or eigenvector coefficient as the mean ± (1.96 × standard deviation). For each principal component axis, any range extending past zero indicated that either the variance accounted for by that axis (eigenvalue) or the correlation between a measurement and the axis (eigenvector loading) was not significantly different from zero. In addition, we recalculated total variance, as defined above, using only significant eigenvalues, which were those eigenvalues that were significantly greater than zero and whose eigenvector had at least one coefficient significantly greater than zero. Finally, we summed all eigenvalues for each bootstrap run and calculated a mean total variance for Anolis and Sceloporus and tested for a difference between these means using Welch’s approximate t-test (Sokal and Rohlf 1995). For these analyses, we hypothesized that the total variance (defined three different ways, as described above) will be greater in Anolis than Sceloporus, indicating that Anolis shows greater disparity among taxa than Sceloporus.

Because we wanted to maintain the variance structure when calculating principal components, measurements were not standardized (i.e., PCAs were performed on variance-covariance matrices of ln-transformed data and not correlation matrices). As a result, the scale number and scale length measurements were omitted from all PCAs because they were not measured in the same units as the other variables. We conducted F-tests for these two variables to test for differences in scale variability between Anolis and Sceloporus.

Statistical Analyses Using a Pooled Sceloporus and Anolis Dataset

We conducted a PCA using a dataset that combined Sceloporus and Anolis and employed a method developed by Burnaby (1966) to correct for size (for complete description of the method, see Rohlf and Bookstein 1987). We defined size as the first principal component derived from a pooled within-group covariance matrix, using each genus as a group (i.e., the error mean square matrix from MANOVA; see Rohlf and Bookstein 1987). We then mathematically removed this size vector (henceforth referred to as “Burnaby size”) from the original ln-transformed data using the methods described by Burnaby (1966) and conducted a second PCA using the total covariance matrix from the “size-free” data. This set of procedures produces not only a single size vector, defined from pooled Anolis and Sceloporus data, and size-free principal components, but also size-free “raw” variables from which additional analyses can be conducted. We demonstrate that in this allometric size vector, the correlations between each of the original variables and size are strong and positive, but not equal. As with the separate Anolis and Sceloporus datasets, we conducted a bootstrap PCA and Burnaby analysis to place 95% confidence limits on both the eigenvalues and eigenvectors. Bootstrapped datasets were composed of 24 species from each clade. Species were randomly selected, with replacement, from the original datasets. In this way, the original within-group samples sizes were preserved. We repeated this procedure 500 times and generated a mean and standard deviation for each eigenvalue and eigenvector coefficient. We used the same criteria here as we used in the Anolis and Sceloporus bootstrap procedures to identify significant eigenvalue or eigenvector coefficients.

Pooling of covariances matrices, as described above, assumes that the variance-covariance matrices from Anolis and Sceloporus are homogeneous. We tested this assumption using Bartlett’s modification of the likelihood-ratio test (SAS Institute 1989; see also Morrison 1990). As with the PCAs conducted on the separate Anolis and Sceloporus datasets, we omitted scale number and scale length measurements from the pooled-matrix and Burnaby analyses.

Allometry

We calculated multivariate interspecific allometric coefficients from each of the PCAs by first deriving a theoretical isometric vector. This vector is calculated as (p^0.5, p^-0.5, . . ., p^-0.5), with p equal to the number of variables in the analysis (Jolicoeur 1963; Morrison 1990). We then divided each of the first eigenvector coefficients by its corresponding isometric coefficient, with the resulting quotient equal to the allometric coefficient for each variable (see Marcus 1990). In other words, the first eigenvector coefficient for each variable was divided by 1/13^0.5 or 0.2774.

Results

Anolis and Sceloporus Datasets Held Separate

Total variance, calculated as the sum of all eigenvalues, was nearly three times greater in Anolis than Sceloporus (Table 1). In both the Anolis and Sceloporus analyses, size (i.e., principal component axis 1) accounted for nearly all within-genus variation (96% in Anolis and 93% in Sceloporus). However, four and three additional axes exhibited significant variation in Anolis and Sceloporus, respectively (Table 1). As with total variance, significant total variance, calculated using only those significant eigenvalues, was also three times greater in Anolis than Sceloporus (Table 1). Much of the difference in total variance between Anolis and Sceloporus can be attributed to the fact that Anolis is significantly more variable in size than Sceloporus (F = 3.062; df = 23; P < 0.01; Fig 1). Nevertheless, even if the eigenvalue from axis 1 is not included in the calculation of significant total variance, Anolis is nearly twice as variable as Sceloporus, which indicates that Anolis exhibits greater variation in both the size and shape variables. Finally, mean total variance, based on 500 bootstrap runs for both the Anolis and Sceloporus data, was significantly greater in Anolis than in Sceloporus (t' = 62.65; df = 499; P < 0.0001; Table 1).

In addition to the degree to which size accounted for total variation in Anolis and Sceloporus, size also differed qualitatively between these two genera. Table 2 shows the allometric coefficients for both genera. Although some measurements exhibit high correspondence (e.g., tail length, jaw
Table 1. Eigenvalues from the principal component analyses (PCAs) computed from separate Anolis and Sceloporus datasets. Total variance equals sum of eigenvalues; significant total variance equals sum of significant eigenvalue coefficients (bold); mean total variance is the mean of the total variances from the 500 bootstrap runs (see text).

<table>
<thead>
<tr>
<th>PCA axis</th>
<th>Anolis</th>
<th>Sceloporus</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4.1583</td>
<td>1.3581</td>
</tr>
<tr>
<td>2</td>
<td>0.0834</td>
<td>0.0426</td>
</tr>
<tr>
<td>3</td>
<td>0.0300</td>
<td>0.0204</td>
</tr>
<tr>
<td>4</td>
<td>0.0181</td>
<td>0.0102</td>
</tr>
<tr>
<td>5</td>
<td>0.0154</td>
<td>0.0060</td>
</tr>
<tr>
<td>6</td>
<td>0.0114</td>
<td>0.0052</td>
</tr>
<tr>
<td>7</td>
<td>0.0044</td>
<td>0.0036</td>
</tr>
<tr>
<td>8</td>
<td>0.0026</td>
<td>0.0029</td>
</tr>
<tr>
<td>9</td>
<td>0.0017</td>
<td>0.0019</td>
</tr>
<tr>
<td>10</td>
<td>0.0012</td>
<td>0.0012</td>
</tr>
<tr>
<td>11</td>
<td>0.0009</td>
<td>0.0005</td>
</tr>
<tr>
<td>12</td>
<td>0.0006</td>
<td>0.0004</td>
</tr>
<tr>
<td>13</td>
<td>0.0002</td>
<td>0.0001</td>
</tr>
<tr>
<td>Total variance</td>
<td>4.3283</td>
<td>1.4532</td>
</tr>
<tr>
<td>Significant total variance</td>
<td>4.2942</td>
<td>1.4314</td>
</tr>
<tr>
<td>Mean total variance</td>
<td>3.8437</td>
<td>1.3406</td>
</tr>
</tbody>
</table>

length), the genera differ dramatically in other measurements, especially metacarpal and metatarsal lengths, foot length, and body width (Table 2). One point of interest is the fact that in Anolis the allometries for the elements within both the fore- and hindlimbs were roughly equal, whereas those for Sceloporus were quite variable. In other words, fore- and hindlimb shape, as a function of size, was constant within Anolis, but variable in Sceloporus (e.g., the relative lengths of the crus and foot in Anolis is the same between a small and large individual or species, but in Sceloporus a large individual or species would have a relatively longer crus and shorter foot than a smaller individual or species). This pattern is reversed in body height and width, with Sceloporus being the more constant taxon.

Variability in scale number (F = 0.962; df = 23, 23; P > 0.90) or scale length (F = 1.549; df = 23, 23; P > 0.30) did not differ between Anolis and Sceloporus. However, scale number was significantly larger (t = 11.71; df = 46; P < 0.0001) and scale size was significantly smaller (t = -6.301; df = 46; P < 0.0001) in Anolis than in Sceloporus.

Anolis and Sceloporus Datasets Pooled

The results from the PCA of the size-adjusted data are consistent with the results from the previous set of analyses (Table 3). Based on the bootstrap analysis, only axes 1, 2, 4, and 5 showed significant variance (i.e., eigenvalues) and had at least one significant eigenvector coefficient. However, Anolis and Sceloporus showed significantly different variation only in axes 2 and 5 (F-value, Table 3; Fig. 2). Figure 2 shows the significantly greater variation in morphospace for Anolis than for Sceloporus; this greater variation is related to the variables with significant correlation with these size-adjusted axes: snout-vent length, tail length, jaw length and width, and foot and metatarsal lengths (see Table 3). Furthermore, the means for Anolis and Sceloporus differed significantly for axis 2, but not for axis 5 (t-values, Table 3), which indicates that, relative to overall size, Anolis is sig-

Fig. 1. Frequency histogram for size (principal component 1) based on separate analyses for Anolis and Sceloporus. A normal curve is placed over each of the histogram plots to better illustrate the greater variance in Anolis than Sceloporus.

Table 2. Multivariate interspecific allometric coefficients derived from the first principal component from separate Anolis and Sceloporus datasets and a pooled within-group covariance matrix (Burnaby size). An allometric coefficient equal to one indicates isometry.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Anolis size</th>
<th>Sceloporus size</th>
<th>Burnaby size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snout-vent length</td>
<td>0.89</td>
<td>0.98</td>
<td>0.92</td>
</tr>
<tr>
<td>Tail length</td>
<td>0.95</td>
<td>0.93</td>
<td>0.95</td>
</tr>
<tr>
<td>Jaw length</td>
<td>0.92</td>
<td>0.94</td>
<td>0.93</td>
</tr>
<tr>
<td>Jaw width</td>
<td>1.02</td>
<td>1.13</td>
<td>1.05</td>
</tr>
<tr>
<td>Body height</td>
<td>1.22</td>
<td>1.17</td>
<td>1.21</td>
</tr>
<tr>
<td>Body width</td>
<td>0.96</td>
<td>1.22</td>
<td>1.03</td>
</tr>
<tr>
<td>Antebrachium length</td>
<td>1.04</td>
<td>1.11</td>
<td>1.06</td>
</tr>
<tr>
<td>Manus length</td>
<td>1.05</td>
<td>0.94</td>
<td>1.03</td>
</tr>
<tr>
<td>Metacarpal length</td>
<td>1.06</td>
<td>0.89</td>
<td>1.02</td>
</tr>
<tr>
<td>Shank length</td>
<td>0.94</td>
<td>1.06</td>
<td>0.97</td>
</tr>
<tr>
<td>Cr sust length</td>
<td>0.96</td>
<td>1.04</td>
<td>0.98</td>
</tr>
<tr>
<td>Foot length</td>
<td>0.97</td>
<td>0.78</td>
<td>0.92</td>
</tr>
<tr>
<td>Metatarsal length</td>
<td>0.97</td>
<td>0.66</td>
<td>0.88</td>
</tr>
</tbody>
</table>
### Table 3. Principal component axes derived from the total covariance matrix of size-adjusted variables (Anolis and Sceloporus data pooled). Bold indicates those variables that are significantly correlated with the respective axis. $F$- and $t$-values correspond to tests to determine differences between Anolis and Sceloporus (see Fig. 2).

<table>
<thead>
<tr>
<th>Size-adjusted variables</th>
<th>Axis 1</th>
<th>Axis 2</th>
<th>Axis 4</th>
<th>Axis 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snout-vent length</td>
<td>0.18</td>
<td>-0.79</td>
<td>0.15</td>
<td>0.39</td>
</tr>
<tr>
<td>Tail length</td>
<td>0.87</td>
<td>0.28</td>
<td>-0.29</td>
<td>0.22</td>
</tr>
<tr>
<td>Jaw length</td>
<td>0.63</td>
<td>-0.73</td>
<td>0.21</td>
<td>0.08</td>
</tr>
<tr>
<td>Jaw width</td>
<td>-0.70</td>
<td>-0.53</td>
<td>-0.07</td>
<td>0.06</td>
</tr>
<tr>
<td>Body height</td>
<td>-0.45</td>
<td>-0.28</td>
<td>-0.24</td>
<td>-0.24</td>
</tr>
<tr>
<td>Body width</td>
<td>-0.82</td>
<td>0.02</td>
<td>0.42</td>
<td>0.16</td>
</tr>
<tr>
<td>Antebrachium length</td>
<td>0.03</td>
<td>0.23</td>
<td>0.25</td>
<td>-0.40</td>
</tr>
<tr>
<td>Manus length</td>
<td>-0.72</td>
<td>0.45</td>
<td>0.27</td>
<td>0.26</td>
</tr>
<tr>
<td>Metacarpal length</td>
<td>-0.66</td>
<td>0.39</td>
<td>0.48</td>
<td>0.15</td>
</tr>
<tr>
<td>Shank length</td>
<td>0.67</td>
<td>0.06</td>
<td>-0.24</td>
<td>-0.38</td>
</tr>
<tr>
<td>Crus length</td>
<td>0.63</td>
<td>0.34</td>
<td>-0.10</td>
<td>-0.48</td>
</tr>
<tr>
<td>Foot length</td>
<td>0.21</td>
<td>0.81</td>
<td>0.37</td>
<td>-0.19</td>
</tr>
<tr>
<td>Metatarsal length</td>
<td>-0.01</td>
<td>0.83</td>
<td>0.37</td>
<td>0.19</td>
</tr>
<tr>
<td>Eigenvalue</td>
<td>0.08659</td>
<td>0.04732</td>
<td>0.01689</td>
<td>0.01147</td>
</tr>
<tr>
<td>% Variance</td>
<td>43.3</td>
<td>23.6</td>
<td>8.4</td>
<td>5.7</td>
</tr>
<tr>
<td>$F$-value</td>
<td>1.533</td>
<td>2.703*</td>
<td>1.136</td>
<td>3.615**</td>
</tr>
<tr>
<td>$t$-value</td>
<td>7.809***</td>
<td>-3.512**</td>
<td>1.223</td>
<td>0.416</td>
</tr>
</tbody>
</table>

* $P < 0.05$; ** $P < 0.005$; *** $P < 0.0001$.

Anolis and Sceloporus do not differ significantly in size, Anolis is more variable in size than Sceloporus (Table 4). In addition, Anolis is significantly more variable than Sceloporus in size-adjusted snout-vent, jaw, shank, and crus lengths (Table 4, Fig. 3).

The within-group covariance matrices for Anolis and Sceloporus are not homogeneous (Bartlett’s modification of the likelihood-ratio test: $\chi^2 = 154.397; df = 91; P < 0.001$), thereby introducing a bias into our pooled PCAs. In an effort to estimate the effects of this bias, we regressed Burnaby size against Anolis and Sceloporus size (axis 1 from the separate analyses) and found that Burnaby size corresponded exactly to the size variables calculated from the independent datasets (Fig. 4; $r^2 = 1.00$ for both regressions). However, because the allometric coefficients for Anolis and Sceloporus are not the same, Burnaby size is not equal to either Anolis or Sceloporus size (Table 2). In fact, the allometric coefficients resulting from the pooled dataset are between those of the independent datasets and in some cases approximately equal to their midpoint. Because Burnaby size is not equal to Anolis or Sceloporus size, the size variable that was removed from the original ln-transformed data was neither Anolis nor Sceloporus size. This means that in all probability some residual within-group (i.e., Anolis or Sceloporus) allometric size remained in the size-adjusted data. Although this may have altered slightly the composition of the size-adjusted axes, residual size in these axes should not have biased the comparison between Anolis and Sceloporus given the extremely high correlation between Burnaby, Anolis, and Sceloporus size measures.

### Discussion

**Has Anolis Adaptively Radiated to a Greater Extent than Sceloporus?**

Anolis is significantly more variable than Sceloporus in size and body, jaw, and hind-limb shape. In contrast, we found no single variable or dimension in which Sceloporus was more variable than Anolis. Taken together, these data indicate that the within-taxon disparity in Anolis is significantly greater than that in Sceloporus. Nevertheless, to establish that greater morphological disparity in Anolis equates to an adaptive radiation requires that the characters exhibiting this greater disparity are products of adaptive evolution.

The adaptive significance of the morphological characters used in this study is well established. For example, different structural habitats select for different aspects of locomotor performance. Broad, flat surfaces favor the evolution of increased sprinting capabilities, whereas narrow surfaces tend to select for careful sure-footed movement. Comparative and functional studies indicate that Anolis and Sceloporus have adapted to these different structural habitats by evolving changes in limb length (Losos 1990; Sinervo and Losos 1991; Miles 1994; Irschick and Losos 1998; for an example in another clade of lizards, see also Pianka 1986). Similarly, variation in jaw size in these lizards is associated with dif-
Table 4. Comparison between *Anolis* and *Sceloporus* means and standard deviations (in parentheses) for Burnaby size and size-adjusted variables (see Fig. 3). *t*-value equals results from Welch’s approximate *t*-test for samples with unequal variances (Sokal and Rohlf 1995).

<table>
<thead>
<tr>
<th>Variable</th>
<th><em>Anolis</em></th>
<th><em>Sceloporus</em></th>
<th><em>F</em>-value</th>
<th><em>t</em>-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Burnaby size</td>
<td>9.566 (2.038)</td>
<td>10.006 (1.158)</td>
<td>3.096**</td>
<td>-0.920</td>
</tr>
<tr>
<td>Snout-vent length</td>
<td>1.7019 (0.110)</td>
<td>1.639 (0.052)</td>
<td>4.423***</td>
<td>2.533*</td>
</tr>
<tr>
<td>Jaw length</td>
<td>0.462 (0.119)</td>
<td>0.162 (0.052)</td>
<td>5.209***</td>
<td>4.405***</td>
</tr>
<tr>
<td>Shank length</td>
<td>-0.007 (0.099)</td>
<td>-0.113 (0.064)</td>
<td>2.360*</td>
<td>2.463*</td>
</tr>
<tr>
<td>Crus length</td>
<td>-0.046 (0.114)</td>
<td>-0.113 (0.069)</td>
<td>2.697*</td>
<td>2.463*</td>
</tr>
</tbody>
</table>

* *P < 0.05; ** *P < 0.01; *** *P < 0.0005.

References in prey size (Schoener 1968; Schoener and Gorman 1968; Roughgarden 1974; DeMarco 1985), differences in scale size are related to adaptation to different hydric environments (reviewed in Malhotra and Thorpe 1997), and variation in body size, as well as dimensions of limb girdles, have important functional and ecological implications (Petterson 1972; Miles 1994). Consequently, we conclude that the morphological variation documented here likely has an adaptive basis and, further, that the extent of adaptive radiation is greater among *Anolis* than *Sceloporus*.

A morphological character not included in our study was that of toe-pad structure. *Anolis* toe-pads vary extensively among species in both size and the number of scales that compose the pad (Glossip and Losos 1997; Beuttel and Losos 1999). *Sceloporus*, however, does not have toe-pads, so measurements of this character were not used in this study. Inclusion of toe-pads would have further reinforced the conclusion that morphological disparity is greater among *Anolis* than among *Sceloporus*.

Although we have shown that *Anolis* exhibits greater morphological disparity than *Sceloporus*, one could argue that our choice of taxa to compare with *Anolis* was arbitrary. Why not compare *Anolis* to all sceloporine lizards, the clade to which *Sceloporus* and nine other genera belong? We think our comparison to only *Sceloporus* is appropriate because of the many similarities between the two clades: both contain many species, most of which are relatively small (maximum adult svs 35–180 mm), insectivorous, and to some degree arboreal. In contrast, other (i.e., non-*Sceloporus*) sceloporine lizards occupy a wide variety of different habitats and exploit the environment in ways unlike those of *Anolis* and *Sceloporus*. For example, some species are mainly terrestrial and inhabit open, arid-scrub or sand dune environments (e.g., the “sand lizards”; Etheridge and de Queiroz 1988), whereas others are specialized, rock-dwelling species (e.g., *Petrosaurus*). By choosing two similar clades, we avoid potential problems that might be caused if some habitats or life-history traits were inherently more or less favorable to morphological

Fig. 3. Bivariate plots showing the ordination of four size-adjusted variables with Burnaby size. Each variable was size-adjusted using the method of Burnaby (1966). Because Burnaby size has been removed from each of these four variables, no correlation exists between these variables and Burnaby size for both *Anolis* and *Sceloporus*. The purpose of these plots is to visualize the relative amount of morphospace occupied by *Anolis* and *Sceloporus*. 

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(Lizard Adaptive Radiation 1231)
diversification. This rationale also provides a nonarbitrary means for delimiting which part of the nested hierarchy of a phylogeny is appropriate for comparative study.

The greater morphological disparity exhibited by anoles is paralleled by greater ecological disparity. Anole assemblages are generally larger than those of Sceloporus; the maximum number of sympatric anoles is 11 (Soroa, Cuba; L. Rodríguez Schettino, pers. comm.), whereas the maximum number of sympatric Sceloporus of which we are aware is seven (southern Sierra Madre Occidental [Wilson and McCranie 1979]; however, these seven species may not actually occur together at any one site). This greater sympatric diversity of Anolis is partially a result of the greater diversity of habitats exploited, including streams, caves, and rock walls, as well as extensive subdivision of the arboreal habitat. In contrast, Sceloporus habitat use is less varied, usually consisting of the occupation of broad surfaces, including tree trunks, rocks, and the ground (references in Sites et al. 1992). Given the greater breadth of habitat use displayed by anoles, their greater morphological disparity is not surprising.

Why Is Anolis More Disparate than Sceloporus?

Given that Anolis displays greater morphological and ecological disparity than Sceloporus, one might inquire as to why this is the case. Below we discuss several possible hypotheses.

Island versus Continental Radiation

Islands are well known for their adaptive radiations. The presumed mechanism is that a colonizing species enters a depauperate habitat and then radiates to use the ecological niches that are usually occupied by other lineages on the mainland (Mayr 1963; Carlquist 1970; Williamson 1981; Grant 1986). A priori, our comparison between Caribbean Anolis and mainland Sceloporus would appear to be another example of this phenomenon. However, Anolis also has radiated extensively in Central and South America; island and mainland Anolis lizards seem to display comparable levels of morphological disparity (Irschick et al. 1997). Thus, this explanation does not seem to account for our findings.

Temperate versus Tropical Radiation

Diversity of many types of organisms, including lizards (Arnold 1972), is greatest in the tropics and decreases with distance from the tropics. Thus, the differences we report may be simply a reflection of the different distributions, both present and historical, of the two clades. Whereas Anolis radiated in tropical and subtropical environments, Sceloporus diversified in northern locals; current scenarios place the ancestral Sceloporus stock in the arid habitats of western Mexico (Sites et al. 1992). One could thus argue that differences in ecological factors between temperate, subtropical, and tropical environments lead to greater opportunities for habitat specialization and diversification in tropical and subtropical environments relative to those available in arid environments (Orians 1969).

However, this argument is not entirely convincing. Many lizard clades exist in the tropics and have not diversified to nearly as great an extent as anoles. Indeed, the range of Sceloporus extends as far south as Panama. If geographic distribution were the only factor responsible for the differences in disparity between these two clades, then we would expect to see a diverse tropical radiation of Sceloporus. However, the southern distribution of Sceloporus consists of only one species group (indeed a single species or species complex). In contrast, the southern range of Sceloporus has a disjunct distribution with most of the species occurring further to the north in Central America. Thus, the tropical species could represent a recent secondary invasion of the tropics that has not had enough time to diversify (Savage 1982; Sites et al. 1992). Further research is needed to clarify this point.

Age of Lineage

Currently available data could be interpreted to suggest that Anolis is as much as 15 million years older than Sceloporus, if one uses the immunological data available for Anolis and the fossil data available for Sceloporus (see Materials and Methods). Thus, one could argue that the more extensive Anolis radiation is simply a result of longer evolutionary history. However, even if Anolis is older than Sceloporus, it is not clear that one would expect a clade that is 35 million years old to be more disparate then a clade that is 20–25 million years old. Indeed, recent work (Foote 1992, 1996) demonstrates that disparity of a lineage does not necessarily increase in a linear fashion over spans of millions of years.

Differences in Rates of Extinction and Speciation

One possible explanation for the greater morphological diversity of Anolis is that this morphological diversity is simply a consequence of the greater number of species (i.e., species richness) of Anolis relative to Sceloporus. Anolis contains approximately five times as many species as Sceloporus. Assuming that the two clades are roughly equal in age and the number of species in Anolis is not a function of overzealous taxonomic splitting, this difference must result from
higher speciation rates and/or lower extinction rates in *Anolis*. If, in fact, morphological differentiation occurred randomly, then the evolution of a clade would resemble a random walk through morphological space. As a result, a more speciose (or species-rich) clade would be expected to diffuse passively through a greater volume of morphological space than a less speciose clade (Foote 1991b).

We consider this hypothesis incomplete for these data for two reasons. First, given that the morphological diversification of both clades involved characters with clear adaptive significance, the random walk model for morphological differentiation does not appear to be applicable. Second, this hypothesis would only serve to redirect investigation toward the question of why *Anolis* has so many more species than *Sceloporus*. Indeed, some of the other hypotheses we have posed concerning morphological diversity could also apply to species richness. However, although interesting, hypotheses about the causes of differences in species richness and the linkage between species richness and morphological diversification are beyond the scope of this paper.

**Key Innovations**

Key innovations are traits that allow a lineage to interact with the environment in a novel way (Simpson 1953; Liem 1973; Larson et al. 1981). In some cases, the evolution of a key innovation may lead to an adaptive radiation, but the two are not necessarily linked (Mayr 1960). The expanded toe-pads of anoles may be considered a key innovation because they give the lizards exceptional clinging ability, which allows them to use arboreal habitats in novel ways not available to lizards without toe-pads (reviewed in Larson and Losos 1996). Indeed, anoles subdivide the arboreal habitat much more finely than other, non-pad-bearing, arboreal lizards. Thus, the possession of toe-pads may have facilitated the anole adaptive radiation by allowing species to use, and then adapt to, a wide variety of different habitats.

This key innovation hypothesis may be tested by examining the two other lizard clades that have convergently evolved similar toe-pads, geckos and praesinohaemid skinks (Williams and Peterson 1982). If the evolution of toe-pads is responsible for the great disparity seen in anoles, then we might expect to see unusually high levels of disparity in these other lineages as well. The family Gekkonidae is one of the most species-rich and diverse lizard families and also one of the oldest (Estes 1983). In contrast, the praesinohaemid skink clade does not contain many species; their ecology is still poorly known and requires further study to examine this hypothesis.

**Conclusion**

Both *Anolis* and *Sceloporus* have diversified greatly. Nonetheless, our findings indicate that the morphological disparity of anoles is considerably greater than that of *Sceloporus*. Given that these two clades are similar in many respects, we might ask what intrinsic or extrinsic factors are responsible for the greater diversity of anoles. We suggest that the evolution of a key innovation, the subdigital toe-pad of anoles, may have played a role in this diversification. The geographic setting in which diversification occurred also may have been significant. These hypotheses deserves further attention. More generally, we have outlined a comparative approach that may be used to test the hypothesis that a clade has experienced an adaptive radiation.

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**Literature Cited**


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APPENDIX

Included Taxa

Anolis clade:

Sceloporus clade: