

ECOLOGICAL MORPHOLOGY OF CARIBBEAN ANOLES

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ABSTRACT: Anoles have evolved independently on each island in the Greater Antilles, producing a suite of morphologically-distinct species that utilize different microhabitats. Comparisons among islands indicate that the same set of "ecomorphs"—distantly related species that are similar in morphology, ecology, and behavior—has evolved on each island. Despite considerable work on anoles over the past three decades, much remains to be learned about evolution of the ecomorphs. In particular, previous studies have focused on external measurements of gross limb proportions, tail length, mass, and number of lamellae. Using a variety of techniques, we examined these characters in greater detail and investigated a wide variety of other characters. We found that the ecomorph classes represent distinct entities in morphological space when morphological characters are examined in greater detail (e.g., each limb element was treated separately). In addition, we found that the ecomorphs differ in a variety of characters not previously examined, including toe pad area, pectoral and pelvic girdle dimensions, head dimensions, and tail shape. These differences were apparent regardless of how we defined body size, although comparisons of particular characters were affected by which body size variable was used. This finding indicates that convergence in ecomorph evolution extends beyond traits directly linked to habitat use and locomotion. We also examined a number of other taxa that have not traditionally been considered to be members of any ecomorph class. We found that many descendants of ecomorphs living on small islands near the Greater Antilles no longer belong to the ecomorph class of their ancestor. Many Lesser Antillean anoles appear to be trunk-crown anoles, whereas others do not belong to any ecomorph class. Montane anoles of the Greater Antilles and *Chamaelinorops* also do not belong to any ecomorph class, but *Chamaeleolis*, and possibly *Phenacosaurus*, are twig anoles.

Key words: Adaptive radiation; *Anolis*; Convergence; Ecomorphology

EVEN THOUGH THE TERM was not widely used until the early 1970's (Karr and James, 1975; Williams, 1972), ecomorphology—the study of the relationship between morphology and ecology (otherwise known as ecological morphology)—has a long and rich history (Wainwright and Reilly, 1994). Recent years, however, have seen an explosion of interest in the field, sparked by advances both in the ability to measure important aspects of morphology and ecology and in the ability to analyze these features in an explicitly historical context. As a result, contemporary studies go beyond the traditional cataloguing of correlations between morphological and ecological features by using functional morphological studies to investigate the consequences of differences in morphology among species and by employing phylogenetic studies to examine the evolution of putative ecomorphological adaptations

(Losos and Miles, 1994; Motta et al., 1995; Westneat, 1995).

The evolutionary radiation of anoline lizards in the Caribbean is suitable for the study of ecological morphology for several reasons. First, considerable ecological and morphological heterogeneity exists among the 138 recognized species of Caribbean anoles (Powell et al., 1996). Second, anoles are a ubiquitous element of the Caribbean fauna, occurring at high densities in many habitats. Further, most localities contain a number of ecologically and morphologically distinctive species; as many as 11 may coexist at one locality. Third, ecological, behavioral, physiological, and functional morphological data are easy to collect for many species of anoles. Fourth, although understanding of anole phylogeny is far from complete, enough is known to draw conclusions about anole evolution.

For these reasons, the breadth of understanding about anole ecological morphology is surpassed by few other groups. From a large body of literature on the ecology, behavior, and functional mor-

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phology of Caribbean anoles (reviewed in Losos, 1994), the following conclusions can be drawn:

1. Anole assemblages are composed of species that differ in their habitat use (Moermond, 1979*a,b*; Rand, 1964, 1967; Schoener, 1968; Schoener and Schoener, 1971*a,b*). A primary means of habitat partitioning is use of different structural habitats; sympatric species that use the same structural habitat almost invariably differ in body size or use different thermal microhabitats.

2. Species that differ in use of structural habitat also generally differ morphologically and behaviorally. Conversely, species that use similar structural habitats tend to be similar in morphology and behavior (Estrada and Silva Rodríguez, 1984; Irschick and Losos, 1996; Losos, 1990*a,b*; Moermond, 1979*a,b*).

3. Differences in morphology translate into differences in functional capabilities. For example, among species, sprinting and jumping capability is correlated with relative hindlimb length and clinging ability correlates with relative toe pad size (Glossip and Losos, 1997; Irschick et al., 1996; Losos, 1990*a,b*; Losos and Irschick, 1996).

4. Differences in functional capabilities are related to differences in behavior and habitat use among species. For example, relatively long-legged species live in open habitats in which they use their great sprinting and jumping abilities to elude predators and capture prey. By contrast, short-legged species move slowly in both foraging and escaping predators, but use their great agility to move on narrow surfaces (Irschick and Losos, 1998; Losos, 1990*b*; Losos and Irschick, 1996). In the same vein, species with better-developed toe pads are found more frequently on leaves (Schoener, 1968).

5. On each of the major islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico), species have diversified to use a variety of different structural habitat niches (Losos et al., 1998; Williams, 1983). When comparing the evolutionary radiations on each of these islands, one observes that the same set of habitat specialists has evolved on each island (with

several exceptions). For example, each of these islands has one or more species that perch on tree trunks near the ground, jump frequently, and are stocky with extremely long hindlimbs, long tails and few subdigital lamellae. Similarly, each island also has elongate species with short limbs and tails which use extremely narrow surfaces and move very slowly. In all, six such "ecomorph" (sensu Williams, 1972) classes exist. These classes, which contain sets of species similar in morphology, ecology, and behavior, are named for the structural habitat their constituent species normally use. Four of these—the trunk-ground, trunk-crown, twig, and crown-giant ecomorphs—are found on all four Greater Antillean islands. A fifth, the grass-bush ecomorph, is found on all islands but Jamaica, whereas the trunk ecomorph is found only on Hispaniola and Cuba. Phylogenetic analysis indicates that members of the same ecomorph class on different islands are, almost invariably, not closely related (Losos et al., 1998).

Despite extensive research on the anole ecomorphs, much remains to be learned. Previous studies have been limited to examining relatively few external morphometric variables, focusing primarily on the length of the forelimbs, hindlimbs, and tail, number of subdigital lamellae, and body mass. Further, some species on all of the Greater Antillean islands except Puerto Rico may not conform to any of the ecomorph types (e.g., Williams, 1983), but no quantitative analysis has examined this proposition.

This paper will remedy these shortcomings by examining morphometric variation in great detail within and between the ecomorph classes. By using radiographs, we are able to examine each of the major elements in the limb, rather than a single external measurement of limb length. Further, we measure a variety of variables (e.g., girdle, head, and tail dimensions) not previously considered to be related to evolution of the ecomorphs. In addition, we examine a number of species not considered to belong to any of the ecomorph classes.

In particular, we address the following questions:

1. Are additional differences among the ecomorphs apparent that have not previously been investigated (e.g., differences in the length of particular limb elements)?

2. Does the manner in which body size is defined affect conclusions concerning the differences among ecomorphs? How to define size and remove its effect on morphometric variation is extremely controversial (see, e.g., Jungers et al., 1995, and references therein). In this paper, we examine the two most commonly used methods to define size for data sets consisting of linear, non-fixed measurements.

3. Do ecomorph classes differ in morphological traits not previously examined, such as head dimensions?

4. How morphometrically similar to the ecomorphs are species that are not generally considered to belong to one of the ecomorph classes (e.g., some species in the Greater and Lesser Antilles, plus anoles in the genera *Chamaeleolis*, *Chamaelinorops*, and *Phenacosaurus*)?

MATERIALS AND METHODS

We examined 507 specimens of 64 species of anoles, including the genera *Chamaeleolis*, *Chamaelinorops*, and *Phenacosaurus*, which appear to have arisen from within *Anolis* (Hass et al., 1993; Jackman et al., 1997, 1999; see Appendix 1 for a list of the species included in this study). We focused on three sets of characters: external dimensions of the head, body, and tail; detailed measurements of toe structure; and measurements from radiographs of the limbs, girdles, and head.

Morphological Measurements

The first set of measurements were made using a ruler and calipers: Snout-vent length (SVL)—to the nearest 0.5 mm from the tip of the snout to the anterior end of the cloaca; Tail length—from the anterior end of the cloaca to the tip of the tail, except on those individuals with broken or regenerated tails; Head depth—from the highest portion of the head to the bottom of the lower jaw; Tail height and width—at the base of the tail, immediately

posterior to the cloaca. Measurements of tail height and width were discarded if a specimen was judged to be dehydrated or excessively thin because such unhealthy individuals would lead to abnormal measures of tail width; Tail ratio—an index of tail shape, calculated as tail height divided by tail width. Tail crest height—from the top of the crest at its highest point to the body of the tail.

Toe and toepad measurements were made using MorphoSys (Meacham and Duncan, 1990), a computer-driven imaging system. Specimens were placed on their backs on a light table. Because delineation of the precise point at which a toe pad begins is difficult, the area under the entire toe was used as our measure of pad area. Contours of the fore- and hindfeet were magnified with a telephoto lens and captured with a personal computer. From these outlines, we measured length and area of the second and third toes of the forefoot (FF2, FF3) and of the third and fourth toes of the hindfoot (HF3, HF4).

MorphoSys also was used to measure skeletal elements from radiographs: Jaw length—from the tip to the posterior end of the lower jaw; Jaw width—distance between the posterior ends on the interior side of the lower jaw; Pectoral girdle width—the maximal distance between interior points on the clavicle; Pelvic girdle length—measured from the most anterior point on the side of the pubis to the most posterior point on the ilium on the same side of the pelvis; Pelvic width—measured as the widest point of the pelvis; Pelvic angle—the angle formed by the pubic symphysis and the most anterior point on each side of the pubis. Humerus, ulna, femur, tibia, and tarsal lengths were recorded. In addition, the metacarpals on the third toe of a forefoot and the metatarsals of the fourth toe of a hindfoot were also measured and summed. All measurements were taken from the right side of the specimens whenever possible. If measurements could not be taken because the element was broken or did not lie flat on the radiograph plate, then measurements were taken from the left side. Because some specimens were poorly preserved and thus

would not lie flat on a surface, accurate measurements of a number of variables often could not be made from radiographs. The variables most often affected by this problem were the pelvic girdle measurements and jaw width. In addition, on some specimens, other variables could not be measured for a variety of reasons.

All variables were ln-transformed for statistical analyses. Some of the characters (crest height and toe areas) had a value of zero for some species. For these characters, a value of one (in mm or mm²) was added to all measurements prior to ln-transformation.

Mass data were not available for all specimens; further, because some specimens had been eviscerated, mass could not be measured on them. However, mass data were taken from many of the specimens prior to preservation. Data on numbers of lamellae for these specimens are taken from Glossip and Losos (1997).

Evaluation of Ecomorph Status

We took several approaches to determining whether the ecomorph classes occupy different positions in multivariate morphological space. First, we conducted a discriminant function analysis (DFA) to determine whether ecomorph classes defined a priori can be distinguished based on morphometric data. Then, we used two approaches to ask whether the ecomorph classes form discrete clusters in morphological space. First, we conducted a principal components analysis (PCA) using a correlation matrix to reduce the dimensionality of the data; to be conservative (because the first axis, perhaps representing size, accounts for the lion's share of the variation), we included all axes in which at least one variable was marginally correlated ($P < 0.10$) with scores on that axis. Then, using these PC scores, we visualized the relative position of the species using the unweighted paired-group method using arithmetic averages (UPGMA). Because UPGMA phenograms are constrained to depict relationships as simple nested hierarchies, they can distort the relative position of species in morphometric space (de Queiroz and Good, 1997). Thus, as an alternative

way of investigating the relative position of species, we calculated the euclidean distance of every species to every other species using the same PC scores. We also calculated the centroid for each ecomorph class and measured the distance of each species to the centroids. Both the DFA and PCA only used variables previously implicated in ecomorph evolution (e.g., limb and tail length, number of lamellae, mass). Because mass data were unavailable for many specimens, we used species mean values in these analyses.

After investigating the distinctiveness of the ecomorph classes, we then asked whether other species, not previously considered to be ecomorph species, should be classified within one of these classes. To do so, we calculated the distance of each of these species to members of the ecomorph classes and to the centroids for these classes. We examined four groups of species (Appendix 1):

1. Greater Antillean derivatives: Species that occur on small oceanic islands (e.g., Grand Cayman, Mona) near the Greater Antilles and are clearly derived from a Greater Antillean ecomorph species. Although we include *Anolis acutus* from St. Croix in this category (Roughgarden and Pacala, 1989), further phylogenetic studies are needed to clarify its position within the Puerto Rican *crisatellus* group (see Gorman et al., 1983).

2. Other Greater Antillean species: Species on Cuba, Hispaniola, and Jamaica, usually occurring in montane areas, that are thought to be morphologically and ecologically dissimilar to the ecomorphs (Williams, 1983).

3. Lesser Antillean species: Traditionally considered to be generalized forms distinct from the ecomorphs (Lazell, 1972; Williams, 1972), although recent study indicates that many of them should be considered trunk-crown anoles (Losos and de Queiroz, 1997).

4. Other anoline genera: *Chamaeleolis* (Cuba), *Chamaelinorops* (Hispaniola), and *Phenacosaurus* (South America), genera traditionally considered to be the nearest relatives of *Anolis*, although recent studies have suggested that all arose from within

Anolis (Burnell and Hedges, 1990; Hass et al., 1993; Jackman et al., 1997, 1999; Wyles and Gorman, 1980; but see Case and Williams, 1987). Hass et al. (1993) suggest that *Chamaeleolis* is a giant twig anole; ecological data suggest that *Phenacosaurus* may be one as well (Miyata, 1983). *Chamaelinorops* is a unique anole in both morphology (Forsgaard, 1983) and ecology (Flores et al., 1994).

Examination of Whether Ecomorphs Differ in Morphological Variables

We also investigated whether ecomorphs differ in morphological characters other than those traditionally used to define the ecomorphs. We removed the effect of body size on all variables in two ways. First, we calculated the residual value of each variable regressed against SVL (all variables ln-transformed). Second, we conducted a PCA, as described above, except that mass was not included because data were missing for too many individuals. The first axis of this analysis loaded strongly and positively for all variables (see below). Residual values were calculated, as above, using scores on this axis as a proxy for body size. In both of these analyses, individual values were used. Then, for each character, we used species means of the residuals and conducted Analyses of Variance (ANOVA). Analyses in which residuals were calculated from species means produced similar results.

Because our sample included closely-related species that are morphologically similar, statistical comparisons of them may be inaccurate (Felsenstein, 1985). To circumvent this problem, a phylogenetic analysis of variance was necessary (Garland et al., 1993). The phylogenetic studies of Jackman et al. (1997, 1999) contained 21 of the ecomorph species included in this study. To conduct the phylogenetic ANOVA, we first performed a non-phylogenetic ANOVA on each character using only the subset of species included in the phylogenetic analyses (results of ANOVA's incorporating all species were qualitatively identical to analyses using only these 21 species). We then simulated character evolution along the phylogenetic tree derived from Jack-

man et al. (1997, 1999), thus assigning values to each terminal taxon. We then calculated the *F*-statistic for this simulated data set and repeated the analysis 1000 times. We considered the results significant if fewer than 5% of the simulation trials yielded an *F*-statistic greater than that observed in the real data set. This analysis was conducted twice, using two models of evolution. In the speciation evolution model, we assigned change in the character for a branch of the tree by drawing once from a normal distribution with mean of zero. For the gradual model, the number of draws for a branch was proportional to the length of that branch (we used the branch lengths calculated assuming a molecular clock in Jackman et al., 1999). In simulations using both models, the variance of the normal distribution was calibrated so as to produce a variance among the terminal "species" approximately the same as that observed in the real data set for that character (following Garland et al., 1993). This procedure was repeated for each character.

Due to missing data, we could not include some species in the analysis of ecomorph status above. However, we examined the data that were available for these specimens and qualitatively evaluated their ecomorph status based on differences among ecomorph classes in morphological variables.

RESULTS

Evaluation of Ecomorph Status

Ecomorph species.—The discriminant function analysis was highly significant (Wilks' $\lambda = 0.000$, $F_{90,48} = 6.29$, $P < 0.001$) and classified all ecomorph species to their correct ecomorph class with a probability of 1.0. The first four axes of a principal components analysis accounted for 98.4% of the variation (Table 1). A UPGMA analysis based on the PC scores for each species for these four axes indicates perfect clustering of species by ecomorph type (Fig. 1). Examination of the euclidean distances separating species reveals that, with one exception, the nearest ecomorph neighbor for each species was a member

TABLE 1.—Principal Components Analysis based on morphological measurements.

Variable	I	II	III	IV
SVL	0.965	-0.068	0.045	-0.217
HUMERUS	0.983	0.055	0.149	-0.053
ULNA	0.965	0.129	0.198	0.016
FEMUR	0.965	0.209	0.054	-0.065
TIBIA	0.949	0.276	0.027	0.066
TARSAL	0.931	0.328	-0.081	0.082
METATARSAL	0.967	0.203	-0.081	0.083
METACARPAL	0.977	0.102	0.128	0.075
FF2 LENGTH	0.981	0.083	0.104	0.008
FF3 LENGTH	0.982	0.117	0.062	0.047
HF3 LENGTH	0.982	0.075	-0.094	0.043
HF4 LENGTH	0.968	0.175	-0.129	0.085
FF2 LAMELLAE	0.776	-0.611	0.089	0.048
FF3 LAMELLAE	0.809	-0.572	0.054	-0.008
HF3 LAMELLAE	0.820	-0.540	-0.094	0.019
HF4 LAMELLAE	0.814	-0.510	-0.217	0.059
TAIL	0.875	0.208	-0.392	-0.145
MASS	0.974	-0.006	0.111	-0.135
% Variance	86.4	9.2	2.1	0.7
Eigenvalue	15.5	1.7	0.4	0.1

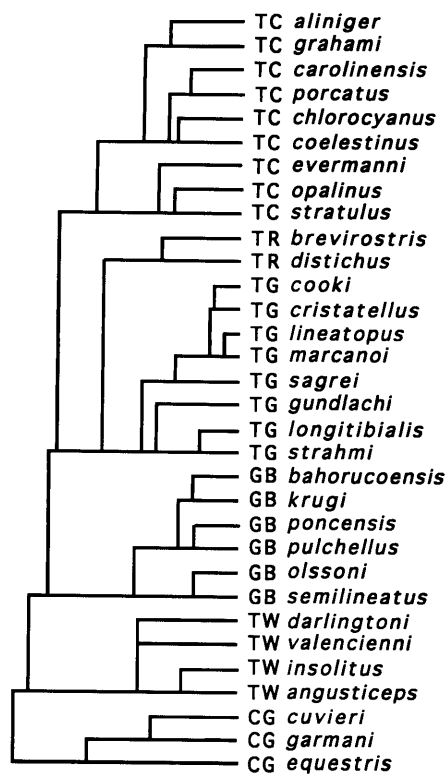


FIG. 1.—UPGMA phenogram of ecomorph species based on the first four principal component axes.

of the same ecomorph class (Appendix 2). The one exception was the twig anole, *Anolis darlingtoni*, whose nearest neighbor (distance [d] = 0.78) is the trunk-crown anole *A. aliniger* (the nearest twig anole to *A. darlingtoni* was *A. insolitus*, with a d of 0.81). Moreover, all ecomorph species were closer to their ecomorph centroid than to the centroid for any of the other ecomorphs (Appendix 2). Nonetheless, very few species were closer to all members of their own ecomorph class than they were to any member of any other class. All trunk-crown and crown-giant anoles were closer to at least one member of another ecomorph class than they were to some member(s) of their own class. By contrast, some grass-bush ($\frac{3}{6}$), trunk-ground ($\frac{1}{8}$), and twig anoles ($\frac{3}{4}$) were closer to all members of their own class than they were to any member of another class, and both trunk anoles were closer to each other than they were to any other species.

Greater Antillean Derivatives.—*Anolis longiceps* lies near its close relative, the trunk-crown *A. porcatus* ($d = 0.15$) and is much closer to the trunk-crown centroid than to any of the other ecomorph centroids. *Anolis acutus*, *A. monensis*, and *A. conspersus* lie near each other ($d < 0.47$) and intermediate between trunk-ground

and trunk-crown anoles (distance to nearest trunk ground anoles: *A. acutus*, $d = 0.54$; *A. conspersus*, 0.42 ; *A. monensis*, 0.58 ; distance to nearest trunk-crown anoles: *A. acutus*, $d = 0.51$; *A. conspersus*, $d = 0.56$; *A. monensis*, $d = 0.47$). Further, the distance of these species to the trunk-crown and trunk-ground centroids is not greatly different (Appendix 2).

Other Greater Antillean Species.—None of these species is closely allied with any of the ecomorph classes. *Anolis christoph-ei* is distant from all ecomorph species, but nearest to two trunk-ground anoles ($d = 0.73$ and 0.81). However, trunk ($d = 0.83$) and trunk-crown anoles are not much further away. Its distance to the trunk and trunk-ground centroids is approximately the same. *Anolis fowleri* is extremely distant from all other ecomorph species ($d > 0.91$) and centroids. *Anolis reconditus* is closer ($d = 0.63$ – 0.98) to trunk ground anoles than it is to any other species.

Lesser Antillean Species.—Many Lesser Antillean species lie closest to the trunk crown anoles and centroid, although some (*Anolis marmoratus*, $d = 0.08$; *A. lividus*, $d = 0.18$; *A. extremus*, $d = 0.25$; *A. luciae*, $d = 0.35$; *A. roquet*, $d = 0.35$; *A. trinitatis*, $d = 0.40$) lie closer to trunk-crown anoles than others (*A. leachi*, $d = 0.51$; *A. bimaculatus*, $d = 0.64$; *A. ferreus*, $d = 0.74$). Several of the larger species are close to crown giants (*A. griseus*, $d = 0.50$; *A. richardi*, $d = 0.63$). *Anolis gingivinus* lies very near to a number of trunk-ground anoles ($d = 0.18$ – 0.29) and to the trunk-ground centroid. *Anolis pogus* is generally closest to grass-bush anoles ($d = 0.39$) and their centroid, but is also close to one trunk-ground anole, *A. sagrei* ($d = 0.54$).

By contrast, the ecomorph affinities of other species are not clear-cut. *Anolis aeneus* is distant from all ecomorph species ($d > 0.70$) and centroids and approximately equally close ($d < 0.83$) to members of the trunk-ground, trunk-crown, twig, and crown-giant classes. *Anolis schwartzi* lies near one trunk crown anole, *A. opalinus* ($d = 0.55$), but is otherwise closest to grass-bush anoles. It is distant from all centroids, but closest to the trunk-crown centroid. Its relative *A. watti* is in-

TABLE 2.—Relationship of characters with svl. All variables except ratios ln-transformed. Note that degrees of freedom are inflated because individuals, rather than species, are used as data points.

Character	r^2	df	F	P
Humerus	0.90	1,475	4092.5	<0.001
Ulna	0.77	1,485	1606.3	<0.001
Metacarpals	0.80	1,485	1985.5	<0.001
Femur	0.83	1,490	2469.7	<0.001
Tibia	0.74	1,491	1364.5	<0.001
Tarsal	0.68	1,492	1064.4	<0.001
Metatarsals	0.76	1,486	1546.0	<0.001
Tail Length	0.67	1,302	611.0	<0.001
Tail Height	0.84	1,415	2229.1	<0.001
Tail Width	0.86	1,413	2484.6	<0.001
Tail Ratio	0.00	1,410	0.2	<0.70
Crest Height	0.16	1,502	95.3	<0.001
FF2 Lamellae	0.47	1,483	435.8	<0.001
FF3 Lamellae	0.54	1,484	579.8	<0.001
HF3 Lamellae	0.54	1,470	560.1	<0.001
HF4 Lamellae	0.52	1,479	510.1	<0.001
FF2 Area	0.93	1,493	6130.3	<0.001
FF3 Area	0.77	1,493	1633.2	<0.001
HF3 Area	0.92	1,494	6054.3	<0.001
HF4 Area	0.91	1,494	5024.0	<0.001
Head Depth	0.90	1,500	4525.0	<0.001
Jaw Width	0.88	1,217	1639.1	<0.001
Jaw Angle	0.17	1,217	46.7	<0.001
Pectoral Width	0.90	1,281	2399.6	<0.001
Pelvis Width	0.82	1,210	980.7	<0.001
Pelvis Length	0.82	1,210	948.9	<0.001
Pelvis Angle	0.02	1,210	6.0	<0.02

intermediate between trunk-ground ($d = 0.66$), trunk-crown ($d = 0.69$) and grass-bush anoles ($d = 0.70$) and is also distant from all centroids, though closest to the trunk-ground centroid.

Other Anoline Genera.—*Chamaelinorops* is far from all species; its three nearest neighbors are a trunk-crown anole ($d = 0.73$), a twig anole ($d = 0.89$), and a grass-bush anole ($d = 0.92$). *Phenacosaurus* lies closest to the twig anoles, particularly *A. valencienni* ($d = 0.45$). Both are closest to the twig centroid, although *Phenacosaurus* is considerably closer than *Chamaelinorops*.

Examination of Morphological Variables

Analyses using SVL to define size.—All characters increase significantly with SVL except tail ratio (Table 2; because all individuals, rather than species, are used as data points for this analysis, degrees of freedom are overstated in the statistical

TABLE 3.—Analyses of variance for each character among ecomorphs. Variables size-adjusted using SVL.

Character*	df	F	P	Phylogenetic simulations
SVL	5,29	19.44	<0.001	0/1000
Femur	5,29	16.72	<0.001	1/1000
Tibia	5,29	24.11	<0.001	0/1000
Metatarsal	5,29	25.88	<0.001	0/1000
Tarsus	5,29	23.65	<0.001	0/1000
Humerus	5,29	17.50	<0.001	0/1000
Ulna	5,29	19.37	<0.001	0/1000
Metacarpal	5,28	14.73	<0.001	0/1000
FF2 Lamellae	5,29	22.43	<0.001	0/1000
FF3 Lamellae	5,29	14.35	<0.001	6/1000
HF3 Lamellae	5,29	11.60	<0.001	34/1000
HF4 Lamellae	5,29	12.55	<0.001	10/1000
FF2 Area	5,29	14.29	<0.001	2/1000
FF3 Area	5,29	26.02	<0.001	0/1000
HF3 Area	5,29	25.00	<0.001	0/1000
HF4 Area	5,29	41.18	<0.001	0/1000
Mass	5,28	14.43	<0.001	0/1000
Tail Length	5,28	38.09	<0.001	0/1000
Tail Ratio	5,28	11.80	<0.001	2/1000
Crest Height	5,29	1.03	<0.42	697/1000
Lower Jaw Length	5,28	1.34	<0.28	471/1000
Jaw Width	5,24	9.76	<0.001	3/1000
Pectoral Girdle Length	5,26	7.54	<0.001	4/1000
Jaw Angle	5,24	11.68	<0.001	0/1000
Pelvic Girdle Length	5,24	14.84	<0.001	0/1000
Pelvic Width	5,24	15.79	<0.001	0/1000
Pelvic Angle	5,24	11.94	<0.001	0/1000
Head Depth	5,29	9.79	<0.001	21/1000

* All variables represent mean values for each species of residuals against SVL, except SVL and tail ratio. All variables ln-transformed.

analysis; hence, the significance of tail crest height, jaw angle, and pelvis angle are dubious). With the effect of SVL removed, all characters differ among ecomorphs except crest height and lower jaw length (Table 3).

Examination of functionally related characters reveals several interesting trends (Fig. 2; measurements of toe lengths are not included because they are similar to measurements of metacarpal and metatarsal length). With regard to the forelimb, the ecomorphs display consistent trends for each of the limb elements: trunk anoles have the longest humeri, ulnae, and carpals; trunk-ground species are the next longest for all three; and twig ecomorphs have the shortest of each. Among the other three ecomorphs, which are similar in the length of each element, the ordering is constant for each element: trunk-crown, crown-giant, grass-bush. By contrast, the relative lengths of the hindlimb elements are not as consistent among ecomorphs.

Trunk-ground anoles have relatively long hindlimb elements and twig anoles relatively short ones, but the ordering of the other ecomorphs is more variable. In particular, grass-bush anoles have the longest or second-longest tarsals and metatarsals, but trunk anoles have slightly longer femurs and tibias.

A similar situation exists for number of lamellae. The pattern for number of lamellae on the forefeet is nearly identical on FF2 and FF3: trunk-crown anoles have the highest number, followed by trunk anoles. Trunk-ground anoles have the fewest lamellae, and the other three ecomorphs are intermediate. The pattern shifts somewhat for number of lamellae on the hindfeet. Again, trunk-crown anoles have the most lamellae and trunk-ground anoles the fewest. However, trunk anoles have the second (HF3) or third (HF4) fewest lamellae. Also, for HF4, twig anoles have fewer lamellae than crown-giant or grass-bush ecomorphs.

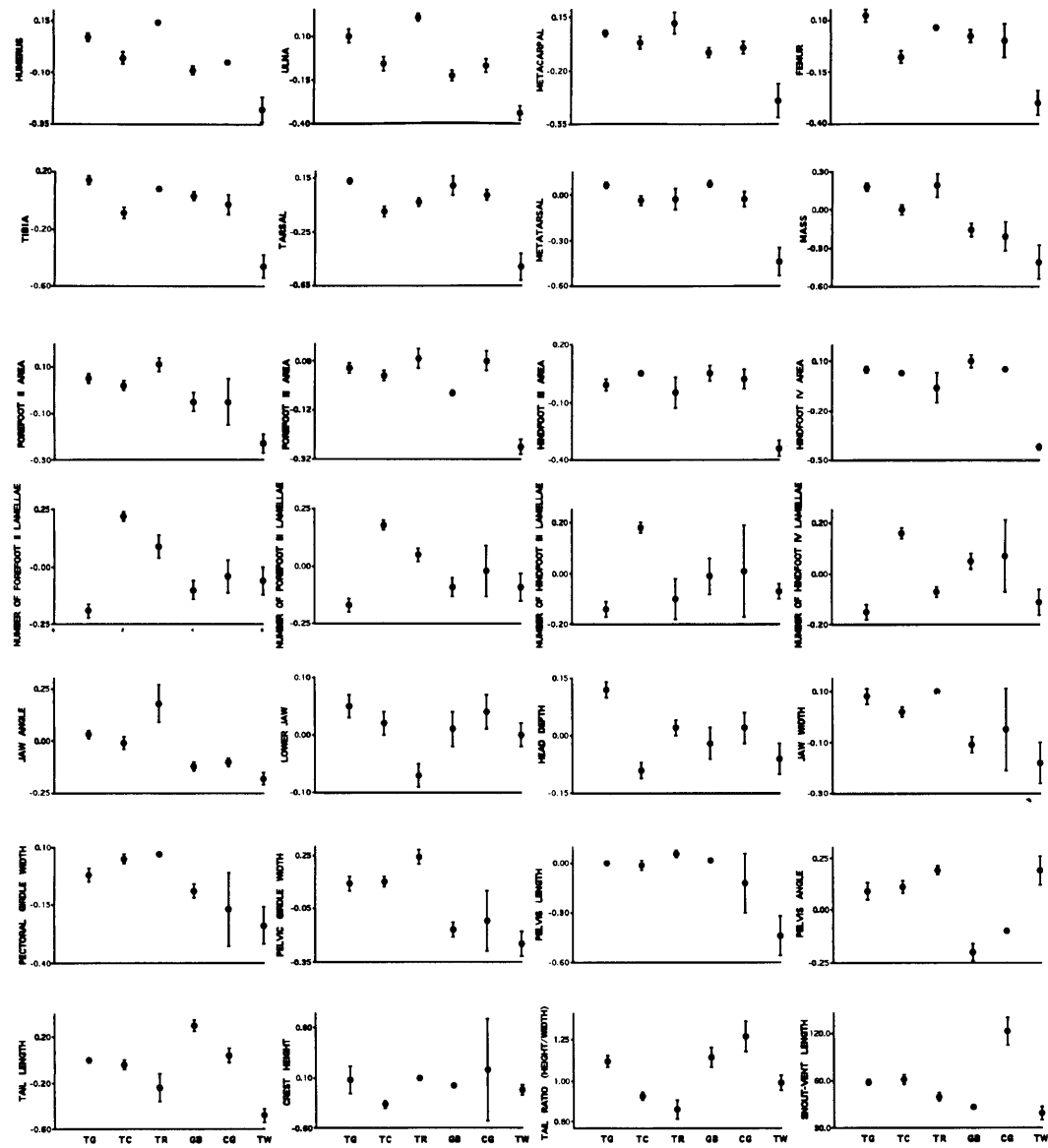


FIG. 2.—Differences among the ecomorph classes in morphological characters. All variables are the mean and first standard error of SVL-residuals except tail ratio and snout-vent length, which are ln-transformed values of non-size-adjusted data.

Abbreviations: TG = Trunk-ground; TC = Trunk-crown; TR = Trunk; GB = Grass-bush; CG = Crown-giant; TW = twig.

For pad area, twig anoles have a considerably smaller area than any of the other ecomorphs. Trunk anoles have the largest area for the forefeet, but not for the hindfeet. No other consistent trends exist.

For tail length, grass-bush anoles have considerably longer and twig anoles con-

siderably shorter tails than other ecomorphs. The tails of trunk anoles are shorter than the other three ecomorphs. Considerable variation exists in the shape of the tail (this analysis is based on non-size-adjusted values because tail ratio is not related to SVL). The vertically flattest

tails (i.e., greatest height-to-width ratio) belong to crown-giants, followed by grass-bush and trunk-ground anoles. The horizontally flattest tails are those of trunk anoles, which are slightly flatter than those of trunk-crown anoles.

The relatively heaviest ecomorphs are the trunk-ground and trunk anoles, followed by the trunk-crown species. The lightest species are the twig anoles, with the grass-bush and crown-giant ecomorphs being approximately the same. In terms of size (as represented by SVL), crown-giants are large, trunk-ground and trunk-crown anoles are intermediate, and the other three classes are small.

Variation also exists in head shape. Trunk-ground anoles have the deepest heads and trunk-crown anoles the shallowest. Twig anoles also have relatively shallow heads, whereas the other three ecomorphs are approximately the same. Trunk anoles have the broadest heads (as measured by jaw angle and width), followed by trunk-ground and trunk-crown anoles. The most slender heads are those of twig anoles.

Differences also exist in the shape of the girdles. Twig anoles have the shortest and narrowest pelvic girdles. The pelvic girdles of grass-bush and crown giants anoles are also narrow, but this narrowness is achieved by a small pelvic angle, rather than by a short pelvis, as in twig anoles. Trunk anoles have the widest pelvises due to their possession of the largest pelvic angle. Trunk anoles also have the widest pectoral girdle, followed by trunk-crown and trunk-ground anoles. Twig and crown-giant ecomorphs have the narrowest pectoral girdles.

Species for Which Data are Incomplete.—For species for which data are incomplete, we compared a species' mean values for each variable to the plots in Fig. 2:

Anolis cybotes.—The measurements support this species' a priori classification as a trunk-ground anole. All measurements correspond to those of trunk-ground anoles except that the metacarpals are longer than those of any other trunk-ground anole.

Anolis occultus, A. sheplani.—Considered twig anoles a priori, both of these

species are similar to the other twig anoles, but more extreme in several respects. Both species are smaller, thinner, and have shorter limb elements than any of the other twig anoles. *Anolis sheplani* has low numbers of lamellae on FF3 and HF4 and *A. occultus* has a much shorter tail than other twig anoles.

Anolis etheridgei.—This species is most similar to the trunk-ground anoles. It has extremely long hindlimb elements comparable in length only to the trunk-ground anoles; the tarsals are even longer than those of any trunk-ground anoles. The forelimb elements are less consistent. The humerus and the ulna are in the range of several ecomorphs; the ulna is shorter than that of all trunk-ground anoles; however, the metacarpals are longer than those of any trunk-ground anole species. Numbers of lamellae are comparable to those of trunk-ground anoles, but this species is smaller than any trunk-ground anole.

Chamaeleolis barbatus.—These lizards are similar to twig anoles in many respects, only much larger. They exhibit extremely short hindlimb elements, all consistent with twig anoles. Forelimb elements are also short, but not quite as short as those of twig anoles. Numbers of lamellae are low and consistent with twig anoles, as is tail length. Mass data are unavailable, but this species appears slender for its length and thus appears comparable to twig anoles in this respect as well.

Analyses Using Principal Components to Define Size.—In the principal components analysis using data from all individuals, the first axis accounts for 83% of the variation (Table 4). All variables load strongly and positively on this axis, with limb elements and SVL loading higher than numbers of lamellae and tail length. In subsequent analyses, scores on this axis are used as a proxy for size.

With the effect of size removed, all characters differ among ecomorphs except pelvic girdle length, crest height, HF3 area, HF4 area, and pectoral girdle length [the last two variables being marginally non-significant (Table 5)]. In the phylogenetic simulations, all of these variables

TABLE 4.—Principal Components analysis using data from all individuals.

Variable*	I
SVL	0.961
Tail Length	0.855
Humerus	0.978
Ulna	0.963
Femur	0.960
Tibia	0.947
Metatarsal	0.929
Metacarpal	0.973
Tarsus	0.960
FF2 Lamellae	0.805
FF3 Lamellae	0.834
HF3 Lamellae	0.823
HF4 Lamellae	0.819
% Variance	82.9
Eigenvalue	10.8

* All variables ln-transformed.

are non-significant, as well as FF2 area which is marginally non-significant.

Examination of functionally related characters reveals that, even though the

differences in body size among the ecomorph classes are very similar regardless of how size is defined (compare Figs. 2, 3), trends for some characters differ between the analyses (e.g., pad area, head depth). Nonetheless, trends for other characters are broadly similar (e.g., limb elements, number of lamellae, tail length).

With regard to the forelimb, the ecomorphs display consistent trends for each of the limb elements in the PCA-size analysis: trunk anoles have the longest humeri, ulnae, and metacarpals and trunk-ground species are the next longest for all three. No consistent pattern exists for the other four ecomorphs. As with the previous analysis, the relative lengths of the hindlimb elements are not consistent among ecomorphs. Trunk-ground anoles are the longest or nearly the longest for each element, whereas twig and trunk-crown anoles generally have short elements, except that the trunk-crown anoles have long

TABLE 5.—Analyses of variance for each character among ecomorphs. Variables size-adjusted using the first principal components axis.

Character*	df	F	P	Phylogenetic simulations
Size	5,27	16.60	<0.001	0/1000
SVL	5,29	21.24	<0.001	0/1000
Femur	5,29	11.88	<0.001	28/1000
Tibia	5,29	15.40	<0.001	2/1000
Tarsal	5,29	21.18	<0.001	0/1000
Metatarsal	5,29	12.27	<0.001	1/1000
Humerus	5,29	15.98	<0.001	0/1000
Ulna	5,29	10.10	<0.001	5/1000
Metacarpal	5,28	7.50	<0.001	0/1000
FF2 Lamellae	5,29	29.14	<0.001	0/1000
FF3 Lamellae	5,29	16.86	<0.001	0/1000
HF3 Lamellae	5,29	7.60	<0.001	31/1000
HF4 Lamellae	5,29	9.85	<0.001	13/1000
FF2 Area	5,29	5.25	<0.002	71/1000
FF3 Area	5,29	6.43	<0.001	10/1000
HF3 Area	5,29	1.44	<0.25	145/1000
HF4 Area	5,29	2.49	<0.06	105/1000
Mass	5,26	8.00	<0.001	16/1000
Tail Length	5,28	12.81	<0.001	3/1000
Crest Height	5,29	1.36	<0.30	618/1000
Lower Jaw Length	5,28	7.15	<0.001	2/1000
Jaw Width	5,22	2.77	<0.05	17/1000
Pectoral Girdle Length	5,22	2.16	<0.10	109/1000
Jaw Angle	5,22	3.67	<0.02	0/1000
Pelvic Girdle Length	5,20	1.96	<0.15	773/1000
Pelvic Width	5,20	5.28	<0.005	37/1000
Pelvic Angle	5,20	10.46	<0.001	8/1000
Head Depth	5,29	19.57	<0.001	0/1000

* All variables represent mean values for each species of residuals against PCA 1 except size, which is the score on the first axis of a PC analysis (Table 4).

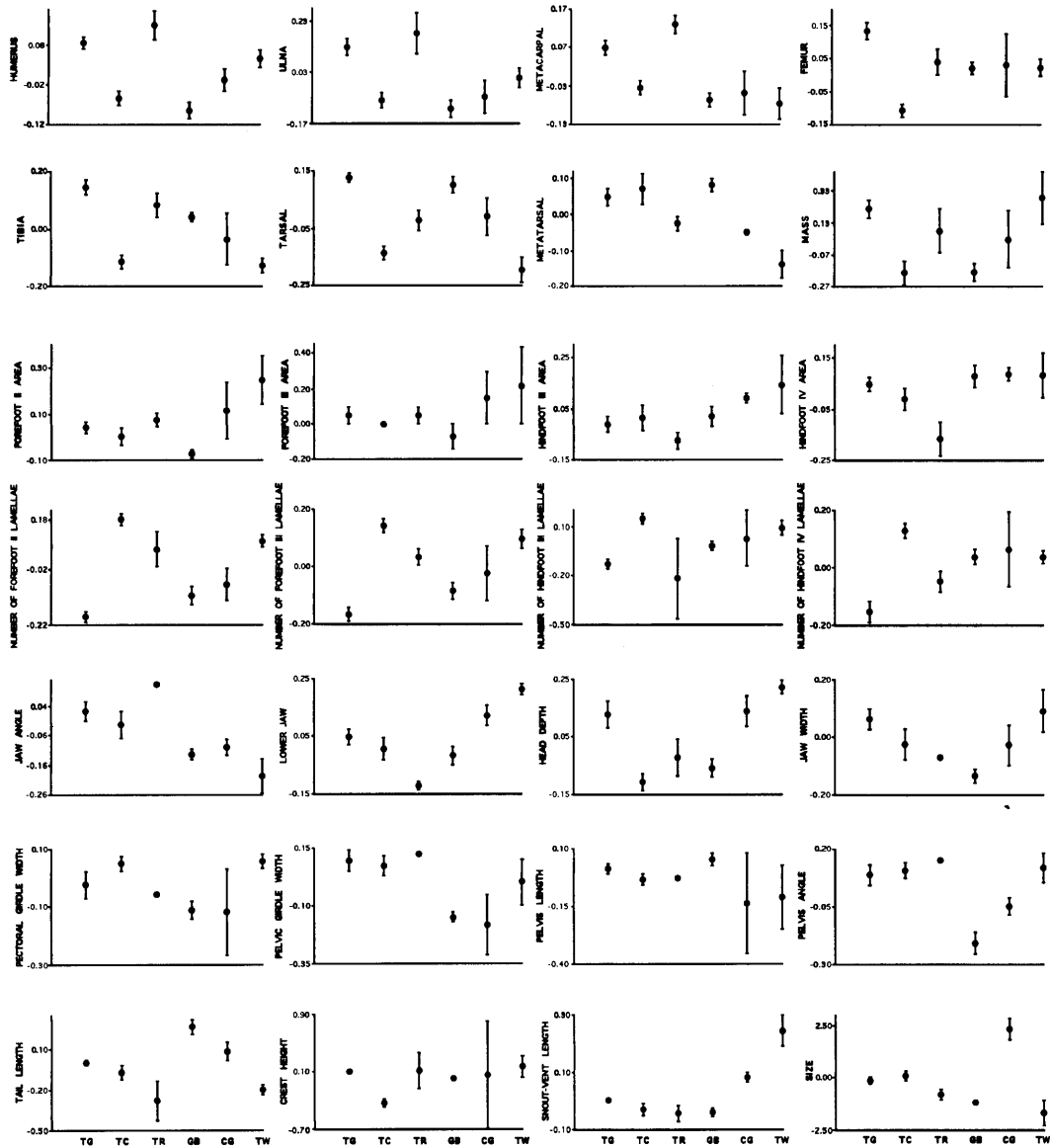


FIG. 3.—Differences among the ecomorphs in morphological characters. All variables are the mean and first standard error of PCA-size-residuals except size, which is the score on the first axis of a principal components analysis on non-size-adjusted data.

metatarsals and twig anoles have moderately long femurs. Grass-bush anoles are also notable in being intermediate in femur and tibia length, but having long tarsals and metatarsals.

The two forefeet toes are almost identical to each other in patterns of number of lamellae, as are the patterns on the two hindfoot toes. Overall, trunk-crown anoles

have the most lamellae on all toes and trunk-ground anoles the fewest. However, the ordering among the other four ecomorphs differs between the fore- and hindfeet.

For pad area, twig and crown-giant anoles generally have the largest areas. Grass-bush anoles have the smallest area on the forefeet, but greater areas on the hindfeet.

For HF4, by far the largest of toes, all ecomorphs have pads of approximately the same area except those of the trunk anoles, which are considerably smaller.

For tail length, grass-bush anoles have the longest tails and twig and trunk anoles the shortest. Unlike all of the other variables, tail ratio is not related to PCA I ($r^2 = 0.00$, $F_{1,224} = 0.4$, $P < 0.55$), so the results reported in Fig. 2, which were based on non-sized adjusted values, are relevant to this analysis.

The relatively heaviest ecomorphs are the trunk-ground and twig anoles, followed by the trunk and crown-giant species. The slightest species are the grass-bush and trunk-crown anoles.

Twig anoles have the deepest heads, followed by trunk-ground and crown-giant anoles. The heads of the other three ecomorphs are all considerably shallower. The widest heads, as determined by jaw width, belong to trunk-ground and twig anoles, with grass-bush anoles the narrowest. However, the largest jaw angle belongs to the trunk anoles, whereas grass-bush, crown-giant, and twig anoles have the narrowest angle. This discrepancy between jaw width and angle is a result of differences in head length (as measured by jaw length); trunk anoles have the shortest heads and twig anoles the longest, which explains how trunk anoles can have the greatest jaw angle and still have a small jaw width (and vice-versa for twig anoles).

Differences also exist in the shape of the girdles. Grass-bush and crown-giant anoles have narrow girdles as determined both by width and by pelvic angle. Both trunk and trunk-ground anoles have broad pelvic girdles, but only moderately long pectoral girdles, whereas the reverse is true of twig anoles. In the case of the twig anoles, however, even though width of their pelvic girdles is not as great as some of the other ecomorphs, the angle of their pelvises is comparable.

Species for which the data are incomplete.—Due to missing data, these taxa could not be included in the principal components analysis; consequently, no value for PCA I is available and, thus, residual values could not be calculated.

DISCUSSION

Reality of the Ecomorph Classes

To test whether the ecomorph classes represent discrete morphological clusters, we used three methods, each of which has its advantages and disadvantages. Discriminant function analysis investigates whether groups, defined a priori, are distinguishable on the basis of morphology. The ecomorph classes were defined originally using morphological, as well as ecological and behavioral, data. Our analyses confirm that the ecomorphs are, indeed, distinguishable on the basis of these characters.

This analysis, however, does not address the question of whether a worker who had not previously classified the species would recognize that the classes cluster discretely in morphological space. That is, although the DFA indicates that the ecomorphs can be distinguished by some combination of morphological characters, would one recognize the same groupings if all characters were examined and none were weighted? To address this question, we first visualized the relative position of species using UPGMA phenograms. This is a means of representing the relative positions of species in a multi-dimensional space in an easily interpretable manner. Interpretation of the UPGMA phenogram is clear-cut: each of the ecomorphs clusters perfectly, suggesting that all members of each ecomorph class are morphologically more similar to all of the other members of their class than they are to any species in another ecomorph class.

The disadvantage of the UPGMA approach is that, by representing relationships as nested hierarchies, it can distort the relative position of species in multivariate space (de Queiroz and Good, 1997). In particular, this method cannot illustrate the situation in which one point lies intermediate between two other points. Rather, the intermediate point will be paired with the nearer of the other two points and members of this pair, in turn, will be portrayed as equally distant to the third species. This distortion can be avoided by directly examining the euclidean distances between all pairs of species. The

TABLE 6.—Pairwise morphological distance between members of the different ecomorph classes on each island. Species used for these comparisons are the most widespread representative of each ecomorph class on each island (see text). Representatives of some of the ecomorph classes for some of the islands were not included in the study.

Comparison	Cuba	Hispaniola	Jamaica	Puerto Rico
Crown-giant vs. Twig	2.644	—	1.434	—
Crown-giant vs. Trunk-crown	1.139	—	1.094	2.282
Crown-giant vs. Trunk-ground	2.156	—	1.177	1.409
Trunk-crown vs. Trunk-ground	1.509	1.579	0.944	1.535
Trunk-crown vs. Twig	1.752	1.951	1.430	—
Trunk-ground vs. Twig	1.651	1.715	1.641	—

disadvantage of the euclidean distance approach is that no definitive criteria exist by which one can decide whether ecomorph clusters are discrete.

Examination of the euclidean distances indicates that the situation is not as clear-cut as the UPGMA phenogram suggests. Although the ecomorph classes form discrete clusters in morphological space, the gaps between these clusters are not immense. As a result, members of one ecomorph class are often closer to members of another class than they are to some members of their own class. In particular, the trunk-crown and crown-giant classes are widely dispersed in morphological space such that all species are closer to some species in other classes than they are to members of their own class.

Nonetheless, the nearest ecomorph neighbor of each species is a member of the same ecomorph class (with one exception) and all species lie closer to the centroid for their own ecomorph class than to the centroid of any of the other classes. Consequently, we conclude that the ecomorph classes are discrete and real entities, with the exception of one anomalous species pair, the twig anole *A. darlingtoni* and the trunk-crown anole *A. aliniger*, which are nearest neighbors in morphological space. Ecologically, *A. aliniger* is a trunk-crown anole (Losos, unpublished data; Rand and Williams, 1969). Almost nothing is known about the habitat use of *A. darlingtoni*; hence, we cannot refute the hypothesis that this species has been misclassified (i.e., that it is not really a twig anole). Nonetheless, based on superficial examination, *A. darlingtoni* appears similar to other twig anoles (Thomas and Hedges,

1991; we should caution, in addition, that we only had one specimen of *A. darlingtoni*; examination of additional specimens would be valuable).

Williams (1983) suggested that the Jamaican species are less differentiated than members of the ecomorph classes on the other Greater Antillean islands. To test this hypothesis, we examined the distance between members of each ecomorph class on each island [however, we did not include the ecomorph classes that do not occur on Jamaica (grass bush and trunk)]. To make our calculations, we chose one member of each ecomorph class on each island; if more than one member of a class occurred on an island, we chose the species that is most common and widely distributed. The species we chose were: Cuba—*Anolis angusticeps*, *A. equestris*, *A. porcatus*, *A. sagrei*; Hispaniola (no crown-giant in our sample)—*A. chlorocyanus*, *A. marcanoi*, *A. insolitus*; Jamaica—*A. garmani*, *A. grahami*, *A. lineatopus*, *A. valencienni*; Puerto Rico (no twig anole)—*A. cuvieri*, *A. cristatellus*, *A. evermanni*. Of the six pairwise comparisons of members of two ecomorph classes, the pair from Jamaica always had a smaller distance than the distance separating pairs on any of the other islands (Table 6). Thus, we conclude that the Jamaican ecomorphs are, indeed, less differentiated than ecomorph species on other islands. Among the remaining three islands, none consistently had distances greater or less than the others.

Why this should be so is not clear. Jamaica appears to have been underwater in the Miocene; consequently, anoles have been present on Jamaica for a shorter period than on other islands (see Crother

and Guyer, 1996; Hedges et al., 1992; Hedges, 1996). Hence, one possibility is that not enough time has transpired for the evolution of all six ecomorph types. Because two of the ecomorph classes are absent from Jamaica, the remaining species may not have had the need to specialize to such a great extent to maximize structural habitat partitioning. However, Puerto Rico is also missing trunk anoles, yet the ecomorphs on that island are not less differentiated than on Cuba and Hispaniola, which have all six ecomorphs. Clearly, more work is needed to shed light on this question.

Of all of the trunk-crown anoles, *A. stratulus* and *A. opalinus* are the species most morphologically similar to the trunk anoles. Superficially, they appear to have a flattened body habitus reminiscent of the Hispaniolan trunk anoles *A. distichus* and *A. brevirostris*. In terms of habitat use, *A. opalinus* occupies much the same habitat as the trunk anoles (Jenssen, 1973; Losos, 1990a; Rand, 1967; Schoener and Schoener, 1971b), but *A. stratulus* is most abundant in the branches high in the canopy (Reagan, 1992). Behaviorally, however, neither species shows the locomotor pattern of the *A. distichus* species group, which is unique in its pattern of repeated short sprints (Moermond, 1979a,b); rather, the movement patterns of *A. opalinus* and *A. stratulus* are typical of trunk-crown anoles (Losos, 1990a,b). Hence, we conclude that these two species, though similar to trunk anoles in some respects, belong in the trunk-crown class.

The Importance of the Manner in Which Size is Removed

Before one can investigate differences in shape between species, one first must remove the confounding effect of differences in body size. How to go about doing so, however, is widely debated (see Jungers et al., 1995, and references therein). In this study, we used two commonly used measures of size, snout-vent length and the first axis of a principal components analysis, to investigate to what extent results depended on which measure of size was chosen.

Both of these methods have their advantages and disadvantages. Snout-vent length is commonly used by herpetologists as an index of size because it accords with their perceptions: longer animals seem bigger. For example, the Jamaican anoles *A. grahami* (trunk-crown), *A. lineatopus* (trunk-ground), and *A. valencienni* (twig) are approximately similar in SVL and, therefore, seem to be about the same size, even though they differ substantially in length of the limbs, tail, mass, and number of lamellae. Further, among both species and individuals, SVL is highly correlated with all other variables (Table 1). Finally, using a single variable as a proxy for size simplifies the biological interpretation of analyses. In such analyses, when the effect of size is removed using residuals, the residuals can easily be interpreted as the measurement of a given variable with the effect of SVL removed.

Three objections can be raised to using SVL as a proxy for size. First, one might argue that, in terms of the biomechanics of locomotion, mass might be a more relevant index of size than SVL. Mass, however, has its own problems: it can fluctuate greatly depending on a variety of intrinsic and environmental conditions and measurements are often not possible on museum specimens, which often are not preserved intact. In any case, mass and SVL are highly correlated in anoles (Losos et al., 1994; Stamps et al., 1994).

Second, size and body length may be related, but they need not be synonymous. By equating the two, one removes the possibility of detecting species that are the same size, but differ in length. For example, in analyses using SVL as the proxy for size, we found that twig anoles generally had short limbs and tails and low mass for their size; the opposite result was found for trunk-ground anoles. However, an alternative interpretation might be that both ecomorph classes have equal limb, tail, and mass proportions, but the twig anoles are extremely long-bodied and the trunk-ground anoles extremely short-bodied. If this were true, then using SVL as the measure of size would lead to mistaken con-

clusions about the differences in size and shape between these species.

Third, using a single variable as the index of size leads to the risk of correlated error. If SVL for a specimen is measured with error, and then all variables are regressed against this erroneous measure, all residuals will be greater (lesser) than they should be if the measured SVL value is smaller (larger) than the correct value. As a result, a correlation among variables might erroneously be created. One way of determining how serious a risk this is would be to randomly add or subtract one mm (the maximum likely error in SVL measurement) to some individuals and re-run the analysis to see to what extent the relationships among residuals change. Our unpublished analyses indicate that the extent of error introduced in this fashion is probably minimal.

The advantages and disadvantages of using scores on the first axis of a principal components analysis are the reverse of those for equating SVL with size. The main advantage of using PCA I scores is that the best estimate of size arguably may be achieved by allowing all variables to contribute, rather than just one. If the magnitude and direction of loadings on PCA I are comparable for all variables, then this axis may be said to reflect the contribution of all variables to a general size index. In this way, the measure of size is not confounded with a single aspect of morphology and the risk of measurement error is greatly reduced because the size measure is a compound of all the variable measurements.

On the other hand, the use of PCA I is not without problems. First, although all variables often do load with approximately similar magnitude on the first axis, the loadings are never the same. Thus, some variables invariably have a greater effect in determining size than do other variables. In our analysis, for example, the limb elements exhibit loadings substantially higher than the lamella number loadings (Table 1). Is PCA I really an index of size, or is it an index of limb length and, to a somewhat lesser extent, number of lamellae? Some workers simply use the subse-

quent axes as measures of shape, but the biological interpretation of such variables becomes even more problematic because usually each axis exhibits a range of loadings from the different variables. In particular, variables that load less strongly on PCA I are usually those that load most strongly on subsequent axes. Is this just an indication that these variables exhibit more size-independent variation or, alternatively, could this simply result because PCA I is not an index of size and simply explains more of the variation in some variables than in others, thus leaving the variation in the other variables to be explained on subsequent axes?

In addition, one might ask whether an index of size really should incorporate information from all variables. For example, based on body length and mass, grass anoles are small. However, they also have extraordinarily long tails. Are these small anoles with very long tails or moderate-sized anoles that are short-bodied and light? More generally, this method tends to work against recognizing species with extreme features because those extreme features will be incorporated into the estimation of size, thus making the feature, relative to size, seem not so extreme. Using a single variable, such as SVL, as an index of size avoids this problem, as long as the variable used is not the one that evolves to extremes in some species (examination of Figs. 2 and 3 indicates that this may not be a problem because the relative size of the ecomorph classes, whether determined by SVL or PCA I, differs little in the two analyses).

Morphological Variation Among the Ecomorphs

The ecomorph classes traditionally have been differentiated on the basis of limb and tail proportions and toepad characteristics. Regardless of whether size is defined using SVL or PCA I, variation exists among the ecomorph classes in these variables. These findings confirm previous quantitative studies (Glossip and Losos, 1997; Losos, 1990a, 1992).

In addition to these variables, we decided to investigate whether the ecomorphs

differ in variables potentially unrelated to locomotion and habitat use. The ecomorph classes differ in the shape of the head, tail, and limb girdles, again regardless of which index of size is used. The functional significance of these variables has never been investigated, but we can suggest hypotheses: differences in head proportions could relate to mode of locomotion by shifting the center of balance of a lizard, to differences in the size or type of prey, or to differences in social structure—ecomorphs in which male-male combat is more severe might require greater biting capability; differences in girdle structure perhaps affect the mobility of the limb, which might be particularly important for species moving in cluttered arboreal environments (Peterson, 1972, 1984); and differences in tail shape might be related to display behavior—at least some species with vertically-flattened tails (i.e., a large tail ratio) lift their tails, which sometimes sport high crests, in aggressive encounters (e.g., Gorman, 1968; Ortiz and Janssen, 1982).

Another possibility is that species which routinely use narrow diameter surfaces must have a stream-lined body habitus both for efficient locomotion and crypsis. This would lead to the prediction that twig, trunk-crown, and grass-bush anoles should have lower jaw and pelvis angles and short jaw and girdle widths. Inspection of Figs. 2 and 3 provides moderate support for this hypothesis. Grass-bush anoles, in particular, seem to follow the predictions, as do twig anoles when SVL-residuals are examined.

Significant differences in most of these variables among the ecomorphs existed regardless of whether SVL or PCA I was used as a proxy for body size. However, the interpretation of specific variables was affected greatly by choice of size. In particular, when SVL-residuals were used, twig anoles had relatively low values for almost all variables. No comparable generality can be made about the PCA-residual analyses, although grass-bush anoles often exhibited low values. The explanation for the different interpretation of twig anole morphology in the two analyses is obvious; twig

anoles have long bodies and relatively short limb and tail dimensions. Hence, compared to body length, all other variables are relatively small, but when all variables are considered in determining size, a given twig anole species appears to be much smaller and, hence, residual variable values appear much greater (which explains, for example, why twig anoles are relatively heavy-bodied in the PCA-residual analyses).

The Ecomorph Status of Other Greater Antillean Species

Among species occurring on small islands near the Greater Antilles, the results are mixed. *Anolis longiceps* is clearly a trunk-crown anole, but neither *A. conspersus*, which is descended from the trunk-crown *A. grahami* (Hedges and Burnell, 1990; Underwood and Williams, 1959), nor *A. monensis*, which is related to the trunk-ground *A. cristatellus* (Gorman et al., 1983), lies very near its ancestral ecomorph class; by contrast, a previous analysis based on external measurements found them to lie near their ancestral ecomorph class (Losos and de Queiroz, 1997). In addition, *A. acutus*, whose phylogenetic affinities are uncertain, is also morphologically intermediate.

In agreement with Williams' (1983) statement, a number of montane Greater Antillean species do not exhibit clear-cut affinities to any of the ecomorphs. Of these species, only *A. etheridgei* is morphologically similar to one of the ecomorphs, the trunk-ground anoles. Little is known about the ecology of this Hispaniolan species, except that it appears to occur in the shade of bushes (Rand and Williams, 1969). The other Greater Antillean species were morphologically distant from all ecomorphs.

Previous workers have suggested that *Chameleolis* is a giant twig anole (Hass et al., 1993), although little is known about its habitat use or behavior. Our analysis confirms this suggestion, at least in terms of morphology. Thus, one might argue that the twig anole ecomorph class spans the entire size range of anoles, from the smallest to among the largest. Alternatively, one

could create an additional ecomorph category, the "twig giants." Indeed, Williams (1983) did present a more refined analysis recognizing nine ecomorph classes. However, the hallmark of the ecomorphs is convergent evolution on multiple islands; hence, creating a new ecomorph category for a form found only on one island is not in the spirit in which the ecomorph concept was originally proposed (Williams, 1972).

In addition to *Chamaeleolis*, the South American *Phenacosaurus* also exhibits many morphological similarities to twig anoles. This genus is also not well-known ecologically, but it appears similar to twig anoles in habitat use (Miyata, 1983).

The Ecomorph Status of Lesser Antillean Species

All species from one-species islands are similar to trunk-crown anoles, although *A. ferreus* is much less similar than the others due to its large size. In addition, among species from two-species islands, *A. trinitatis* is similar to trunk-crown anoles, *A. gingivinus* to trunk-ground anoles, and *A. griseus* and *A. richardi* to crown-giants; the ecomorph affinities of other species are not obvious. These results are in agreement with a previous analysis (Losos and de Queiroz, 1997). This similarity to Greater Antillean ecomorphs is not a result of recent common ancestry; neither the northern or southern Lesser Antillean anoles, each of which forms a monophyletic clade, is particularly closely related to any ecomorph species (Creer et al., submitted; Schneider, 1993). To the extent that the Lesser Antilles provide a snapshot of the early stages of anole adaptive radiation, then these findings suggest that the trunk-crown anoles may represent the initial stage in ecomorph evolution (see discussion in Losos and de Queiroz, 1997).

CONCLUSIONS

These analyses indicate that the *Anolis* ecomorph concept is robust. Regardless of how size is defined, and how precisely the variables are measured (e.g., measuring total limb length versus each element separately, number of lamellae on one toe ver-

sus on many toes [compare this study vs. Losos (1990a, 1992)], the same results emerge: the ecomorph classes are morphologically distinct. Anoles thus represent the best-documented case of convergent evolution of entire faunas, a phenomenon that is widely-cited, but for which few detailed studies exist; those cases that have been examined quantitatively usually fail to find strong evidence of convergence (e.g., Blondel et al., 1984; Mares, 1980; Pianka, 1986), except in properties of the community as a whole, such as niche-packing (e.g., Fox, 1987; Mares, 1980; Ricklefs and Travis, 1980).

Explanations for the remarkable convergence of anoles should probably consider factors specific to anoles as well as those concerning the environment in which they occur. Given that such convergence does not appear to have occurred among mainland anoles [although much more work needs to be done on them (Irschick et al., 1997)], further work probably should focus on the insular environment and how it differs from mainland environments. If, as Hedges et al. (1992) maintain, Caribbean islands were devastated by the end-Cretaceous meteor impact (but see Crother and Guyer, 1996; Hedges, 1996), then the ability of anoles to colonize extraordinarily depauperate environments may also have been important. The present distribution of anoles suggests that trunk-ground and trunk-crown anoles are better dispersers than other ecomorphs (Schoener, 1975; Williams, 1969). What role this may have played in the repeated patterns of ecomorph evolution remains to be determined (as does the broader question of the relative importance of vicariance versus dispersal in determining Caribbean anole distributions).

Perhaps the most interesting finding from this research is that convergence among ecomorphs extends to characters seemingly unrelated to locomotion. Given that the ecomorphs differ in their use of structural habitat, differences in limb lengths and toe-pad characteristics are unsurprising. Some of the characters for which we document convergence, such as toe-pad area and girdle dimensions, are

plausibly related to locomotion. However, other characters, such as head dimensions and tail shape, are not so obviously related to locomotion [nor is sexual dimorphism in body size, which also varies among ecomorphs (Butler et al., submitted)]. Hence, the convergent evolution of ecomorphs represents more than adaptation to move effectively through different structural habitats. Future work should focus on how differences in habitat use are related to other aspects of anole biology, such as territoriality, food acquisition, and predator-avoidance, and how these factors, in turn, may select for suites of different characters.

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APPENDIX I

Species Included in This Study

Species	Island*
Crown-Giant	
<i>A. cuvieri</i>	Puerto Rico
<i>A. equestris</i>	Cuba
<i>A. garmani</i>	Jamaica
Grass-Bush	
<i>A. bahorucoensis</i>	Hispaniola
<i>A. krugi</i>	Puerto Rico
<i>A. olssoni</i>	Hispaniola
<i>A. poncensis</i>	Puerto Rico
<i>A. pulchellus</i>	Puerto Rico
<i>A. semilineatus</i>	Hispaniola
Trunk	
<i>A. brevirostris</i>	Hispaniola
<i>A. distichus</i>	Hispaniola
Trunk-Crown	
<i>A. aliniger</i>	Hispaniola
<i>A. carolinensis</i>	Bahamas, Florida†
<i>A. chlorocyanus</i>	Hispaniola
<i>A. coelestinus</i>	Hispaniola
<i>A. evermanni</i>	Puerto Rico
<i>A. grahami</i>	Jamaica
<i>A. opalinus</i>	Jamaica
<i>A. porcatus</i>	Cuba
<i>A. stratulus</i>	Puerto Rico
Trunk-Ground	
<i>A. cooki</i>	Puerto Rico
<i>A. cristatellus</i>	Puerto Rico

APPENDIX I—Continued.

Species	Island*
<i>A. cybotes</i>	Hispaniola
<i>A. gundlachi</i>	Puerto Rico
<i>A. lineatopus</i>	Jamaica
<i>A. longitibialis</i>	Hispaniola
<i>A. marcanoii</i>	Hispaniola
<i>A. sagrei</i>	Cuba, Jamaica††
<i>A. strahmi</i>	Hispaniola
Twig	
<i>A. angusticeps</i>	Bahamas, Cuba
<i>A. darlingtoni</i>	Hispaniola
<i>A. insolitus</i>	Hispaniola
<i>A. occultus</i>	Puerto Rico
<i>A. sheplani</i>	Hispaniola
<i>A. valencienni</i>	Jamaica
Greater Antillean Derivatives	
<i>A. acutus</i>	St. Croix
<i>A. conspersus</i>	Grand Cayman
<i>A. longiceps</i>	Navassa
<i>A. maynardi</i>	Little Cayman
<i>A. monensis</i>	Mona
Other Greater Antillean Species	
<i>A. christophei</i>	Hispaniola
<i>A. etheridgei</i>	Hispaniola
<i>A. fowleri</i>	Hispaniola
<i>A. reconditus</i>	Jamaica
Lesser Antillean Species	
<i>A. aeneus</i>	Lesser Antilles-2
<i>A. bimaculatus</i>	Lesser Antilles-2
<i>A. extremus</i>	Lesser Antilles-1
<i>A. ferreus</i>	Lesser Antilles-1
<i>A. gingivinus</i>	Lesser Antilles-2
<i>A. griseus</i>	Lesser Antilles-2
<i>A. leachi</i>	Lesser Antilles-2
<i>A. lividus</i>	Lesser Antilles-1
<i>A. luciae</i>	Lesser Antilles-1
<i>A. marmoratus</i>	Lesser Antilles-1
<i>A. pogus</i>	Lesser Antilles-2
<i>A. richardi</i>	Lesser Antilles-2
<i>A. roquet</i>	Lesser Antilles-1
<i>A. sabanus</i>	Lesser Antilles-1
<i>A. schwartzi</i>	Lesser Antilles-2
<i>A. trinitatis</i>	Lesser Antilles-2
<i>A. wattsi</i>	Lesser Antilles-2
Other Genera	
<i>Chamaeleolis chamaeleonides</i>	Cuba
<i>Chamaelinorops barbouri</i>	Hispaniola
<i>Phenacosaurus heterodermus</i>	South America

* Numbers after Lesser Antillean species indicate whether the species occurs on a one-species or two-species island.

† And a number of other islands as well.

†† Recent colonist of Jamaica, possibly human-assisted (Williams, 1969); also occurs on other islands.

APPENDIX II

Euclidean Distances Between All Species Based on Position on the First Four Axes of a Principal Components Analysis. Values at the Bottom are the Distance of Each Species to the Centroids for Each of the Ecomorph Classes.

	cooki	crstatellus	gundlachi	lineatopus	longitibialis	marcanoi	sagrei
cooki	0.000						
crstatellus	0.197	0.000					
gundlachi	0.745	0.724	0.000				
lineatopus	0.180	0.267	0.573	0.000			
longitibialis	0.872	0.776	0.570	0.778	0.000		
marcanoi	0.222	0.314	0.578	0.131	0.726	0.000	
sagrei	0.451	0.646	1.016	0.515	1.211	0.505	0.000
strahmi	0.783	0.635	0.710	0.740	0.304	0.712	1.182
aliniger	1.102	1.120	1.797	1.260	1.866	1.321	1.126
carolinensis	1.117	1.174	1.784	1.258	1.800	1.288	1.032
chlorocyanus	1.377	1.408	1.991	1.500	2.117	1.579	1.352
coelestinus	1.209	1.253	1.739	1.299	1.854	1.368	1.172
evermanni	1.509	1.535	1.842	1.541	2.166	1.662	1.541
grahami	0.847	0.840	1.386	0.944	1.556	1.048	0.987
opalinus	1.034	1.093	1.522	1.106	1.827	1.208	1.032
porcatus	1.551	1.575	2.214	1.699	2.179	1.733	1.509
stratulus	1.527	1.570	1.851	1.558	2.233	1.673	1.538
brevirostris	0.803	0.742	1.068	0.832	1.242	0.896	1.095
distichus	1.261	1.194	1.295	1.236	1.598	1.338	1.538
bahorucoensis	1.134	1.324	1.579	1.172	1.853	1.176	0.703
krugi	1.025	1.195	1.571	1.098	1.805	1.122	0.651
olssoni	1.675	1.844	2.114	1.733	2.191	1.676	1.278
poncensis	1.011	1.195	1.562	1.092	1.729	1.065	0.579
pulchellus	1.221	1.389	1.820	1.321	1.958	1.307	0.823
semilineatus	1.734	1.915	2.174	1.787	2.334	1.753	1.306
cuvieri	1.495	1.409	1.592	1.504	1.262	1.490	1.727
equestris	2.079	2.047	2.483	2.159	2.390	2.203	2.156
garmani	1.106	1.054	1.496	1.177	1.344	1.198	1.277
angusticeps	1.580	1.563	2.177	1.735	1.982	1.698	1.651
darlingtoni	1.023	0.972	1.619	1.170	1.601	1.204	1.217
insolitus	1.589	1.570	2.156	1.733	2.039	1.715	1.678
valencienni	1.481	1.403	2.085	1.641	1.853	1.641	1.666
conspersus	0.428	0.424	0.925	0.487	1.055	0.578	0.675
longiceps	1.427	1.459	2.088	1.572	2.058	1.602	1.371
monensis	0.577	0.647	1.057	0.624	1.350	0.737	0.659
acutus	0.543	0.635	1.118	0.625	1.319	0.707	0.550
christophei	0.810	0.873	0.831	0.725	1.315	0.823	0.908
fowleri	1.073	1.088	1.414	1.130	1.132	1.051	1.119
reconditus	0.976	0.930	0.649	0.859	0.630	0.856	1.226
aeneus	0.778	0.723	1.408	0.934	1.239	0.932	0.975
bimaculatus	1.398	1.387	1.665	1.416	1.889	1.528	1.509
extremus	0.952	0.975	1.492	1.044	1.671	1.142	1.009
ferreus	1.239	1.191	1.462	1.249	1.641	1.360	1.434
gingivinus	0.183	0.274	0.726	0.208	0.894	0.292	0.482
griseus	1.188	1.176	1.392	1.195	1.322	1.212	1.297
leachi	1.258	1.254	1.656	1.313	1.828	1.415	1.347
lividus	0.727	0.712	1.320	0.845	1.440	0.938	0.894
luciae	0.837	0.852	1.365	0.925	1.503	1.015	0.927
marmoratus	0.839	0.844	1.404	0.943	1.577	1.045	0.955
pogus	0.951	1.147	1.271	0.944	1.576	0.930	0.543
richardi	0.905	0.877	1.027	0.885	0.901	0.878	1.088
roquet	0.793	0.802	1.398	0.912	1.485	0.989	0.890
sabanus	0.928	0.973	1.466	1.014	1.684	1.114	0.944
schwartzi	1.067	1.196	1.439	1.085	1.842	1.172	0.897
trinitatis	0.818	0.832	1.492	0.969	1.485	1.009	0.879
wattsi	0.664	0.813	1.052	0.665	1.425	0.744	0.518
Chamaelinorops	1.194	1.286	1.909	1.353	1.991	1.365	1.032

APPENDIX II—Continued.

	cooki	crstatellus	gundlachi	lineatopus	longitibialis	marcanoi	sagrei
Phenacosaurus	1.605	1.511	2.179	1.757	2.012	1.784	1.827
tg	0.291	0.270	0.504	0.192	0.593	0.164	0.658
tc	1.073	1.112	1.670	1.185	1.843	1.275	1.071
tr	1.004	0.937	1.140	1.000	1.392	1.089	1.294
gb	1.257	1.439	1.767	1.325	1.940	1.303	0.826
cg	1.476	1.419	1.797	1.534	1.619	1.556	1.635
tw	1.347	1.305	1.959	1.506	1.808	1.497	1.483
	strahmi	aliniger	carolinensis	chlorocyanus	coelestinus	evermanni	grahami
strahmi	0.000						
aliniger	1.654	0.000					
carolinensis	1.633	0.684	0.000				
chlorocyanus	1.923	0.567	0.663	0.000			
coelestinus	1.701	0.878	0.532	0.539	0.000		
evermanni	2.030	1.208	1.414	0.930	1.032	0.000	
grahami	1.367	0.600	0.872	0.682	0.746	0.816	0.000
opalinus	1.693	0.815	1.221	0.955	1.140	0.803	0.590
porcatus	1.976	0.838	0.485	0.705	0.756	1.603	1.152
stratulus	2.115	1.290	1.703	1.276	1.495	0.691	1.009
brevirostris	1.106	1.241	1.631	1.628	1.689	1.562	1.007
distichus	1.484	1.563	1.988	1.792	1.876	1.384	1.167
bahorucoensis	1.855	1.394	1.176	1.435	1.255	1.605	1.341
krugi	1.757	1.101	0.867	1.111	0.946	1.384	1.076
olssoni	2.218	1.912	1.481	1.988	1.751	2.429	2.029
poncensis	1.709	1.268	1.078	1.455	1.327	1.795	1.341
pulchellus	1.909	1.218	0.923	1.319	1.202	1.782	1.374
semilineatus	2.356	1.887	1.484	1.890	1.674	2.257	1.977
cuvieri	1.158	1.940	1.578	1.965	1.578	2.282	1.726
equestris	2.206	1.743	1.331	1.421	1.162	1.935	1.696
garmani	1.166	1.255	0.880	1.239	0.881	1.676	1.094
angusticeps	1.794	1.398	1.637	1.931	2.083	2.533	1.779
darlingtoni	1.375	0.783	1.286	1.323	1.527	1.680	0.968
insolitus	1.854	1.387	1.779	1.951	2.166	2.435	1.734
valencienni	1.589	1.092	1.319	1.535	1.684	2.187	1.430
conspersus	0.914	0.959	0.918	1.087	0.863	1.208	0.564
longiceps	1.867	0.804	0.343	0.701	0.676	1.571	1.086
monensis	1.240	0.890	1.051	1.029	0.962	0.957	0.468
acutus	1.205	0.830	0.771	0.913	0.718	1.073	0.506
christophei	1.310	1.461	1.634	1.609	1.513	1.249	1.023
fowleri	1.085	1.618	1.214	1.805	1.478	2.274	1.590
reconditus	0.731	1.889	1.685	1.968	1.588	1.926	1.475
aeneus	1.010	0.850	0.820	1.203	1.129	1.740	0.938
bimaculatus	1.748	1.284	1.260	0.960	0.782	0.636	0.808
extremus	1.499	0.634	0.743	0.523	0.520	0.743	0.248
ferreus	1.485	1.263	1.265	1.058	0.863	0.822	0.738
gingivinus	0.812	1.112	1.071	1.312	1.093	1.403	0.784
griseus	1.244	1.579	1.131	1.480	0.996	1.730	1.299
leachi	1.662	1.008	0.962	0.679	0.509	0.693	0.612
lividus	1.242	0.550	0.793	0.739	0.764	0.994	0.181
luciae	1.335	0.729	0.676	0.657	0.465	0.913	0.348
marmoratus	1.392	0.548	0.848	0.663	0.755	0.834	0.075
pogus	1.625	1.521	1.357	1.639	1.428	1.707	1.378
richardi	0.854	1.571	1.229	1.612	1.193	1.811	1.271
roquet	1.298	0.583	0.568	0.632	0.524	1.044	0.352
sabanus	1.530	0.661	0.787	0.575	0.581	0.706	0.286
schwartzi	1.790	1.180	1.325	1.198	1.195	0.933	0.910
trinitatus	1.290	0.561	0.396	0.743	0.648	1.343	0.625
wattsi	1.391	1.139	1.194	1.254	1.133	1.143	0.825
Chamaelinorops	1.843	0.728	1.007	1.160	1.369	1.700	1.144
Phenacosaurus	1.732	1.085	1.505	1.529	1.780	2.078	1.394

APPENDIX II—Continued.

	strahmi	alniger	carolinensis	chlorocyanus	coelestinus	evermanni	grahami
tg	0.558	1.366	1.344	1.621	1.403	1.688	1.062
tc	1.665	0.489	0.692	0.358	0.558	0.780	0.370
tr	1.266	1.372	1.788	1.679	1.754	1.438	1.038
gb	1.931	1.431	1.108	1.500	1.314	1.857	1.499
cg	1.451	1.541	1.124	1.434	1.060	1.872	1.391
tw	1.587	1.081	1.434	1.630	1.816	2.176	1.427
	opalinus	porcatus	stratulus	brevirostris	distichus	bahorucoensis	krugi
opalinus	0.000						
porcatus	1.525	0.000					
stratulus	0.572	1.946	0.000				
brevirostris	0.960	1.967	1.307	0.000			
distichus	1.047	2.289	1.086	0.662	0.000		
bahorucoensis	1.233	1.613	1.627	1.677	2.006	0.000	
krugi	1.047	1.299	1.480	1.570	1.894	0.331	0.000
olssoni	2.058	1.819	2.517	2.334	2.797	0.934	1.059
poncensis	1.281	1.511	1.769	1.555	2.009	0.431	0.490
pulchellus	1.362	1.302	1.837	1.777	2.205	0.518	0.453
semilineatus	1.944	1.820	2.346	2.357	2.755	0.772	0.925
cuvieri	2.251	1.751	2.666	2.066	2.355	2.180	2.012
equestris	2.220	1.139	2.519	2.564	2.727	2.305	2.021
garmani	1.638	1.070	2.072	1.686	1.984	1.672	1.433
angusticeps	1.892	1.752	2.405	1.584	2.189	2.092	1.947
darlingtoni	1.061	1.488	1.527	0.786	1.288	2.732	1.536
insolitus	1.742	1.922	2.202	1.390	1.959	2.123	1.990
valencienni	1.748	1.314	2.233	1.536	2.025	2.152	1.916
conspersus	0.947	1.318	1.399	0.981	1.272	1.201	1.005
longiceps	1.461	0.154	1.905	1.885	2.224	1.481	1.172
monensis	0.529	1.451	0.983	0.841	1.052	1.056	0.881
acutus	0.766	1.208	1.246	1.077	1.362	0.931	0.706
christophei	0.863	2.055	1.080	0.832	0.864	1.274	1.248
fowleri	1.956	1.527	2.483	1.781	2.279	1.545	1.446
reconditus	1.802	2.065	2.150	1.521	1.725	1.721	1.661
aeneus	1.337	1.077	1.872	1.186	1.686	1.521	1.299
bimaculatus	1.155	1.439	1.254	1.655	1.557	1.680	1.435
extremus	0.679	1.023	1.064	1.233	1.377	1.251	0.962
ferreus	1.169	1.470	1.332	1.480	1.403	1.731	1.493
gingivinus	1.019	1.510	1.488	0.902	1.276	1.106	0.982
griseus	1.777	1.398	2.164	1.863	2.101	1.602	1.425
leachi	1.039	1.134	1.257	1.563	1.580	1.530	1.251
lividus	0.682	1.098	1.155	0.952	1.208	1.315	1.051
luciae	0.845	1.000	1.255	1.243	1.435	1.232	0.952
marmoratus	0.543	1.136	0.992	0.996	1.179	1.299	1.032
pogus	1.272	1.830	1.672	1.501	1.848	0.393	0.612
richardi	1.702	1.573	2.124	1.594	1.892	1.538	1.406
roquet	0.856	0.897	1.320	1.194	1.460	1.239	0.949
sabanus	0.576	1.099	0.975	1.203	1.344	1.151	0.874
schwartzi	0.550	1.712	0.789	1.237	1.322	0.864	0.787
trinitatis	1.059	0.744	1.571	1.285	1.664	1.250	0.963
wattsi	0.693	1.640	1.091	1.024	1.252	0.769	0.703
Chamaelinorops	1.052	1.250	1.561	1.343	1.822	1.189	1.016
Phenacosaurus	1.659	1.478	2.067	1.452	1.844	2.313	2.065
tg	1.272	1.769	1.721	0.882	1.302	1.327	1.255
tc	0.645	0.928	1.042	1.308	1.478	1.240	0.935
tr	0.948	2.108	1.155	0.332	0.331	1.819	1.708
gb	1.469	1.511	1.914	1.856	2.263	0.376	0.474
cg	1.952	1.192	2.345	2.036	2.285	1.967	1.726
tw	1.564	1.557	2.058	1.266	1.830	1.969	1.787

APPENDIX II—Continued.

	olssoni	poncensis	pulchellus	semilineatus	cuvieri	equestris	garmani
olssoni	0.000						
poncensis	0.823	0.000					
pulchellus	0.741	0.350	0.000				
semilineatus	0.376	0.820	0.686	0.000			
cuvieri	2.294	2.091	2.121	2.446	0.000		
equestris	2.488	2.317	2.148	2.494	1.440	0.000	
garmani	1.924	1.596	1.571	2.009	0.731	1.069	0.000
angusticeps	2.177	1.707	1.776	2.352	2.301	2.644	1.924
darlingtoni	2.212	1.494	1.601	2.269	2.040	2.285	2.539
insolitus	2.356	1.771	1.877	2.484	2.519	2.841	2.105
valencienni	2.344	1.851	1.856	2.483	1.845	2.025	1.434
conspersus	1.791	1.172	1.282	1.805	1.332	1.718	0.830
longiceps	1.688	1.377	1.176	1.696	1.665	1.164	0.978
monensis	1.830	1.092	1.226	1.772	1.793	2.004	1.251
acutus	1.601	0.946	1.026	1.567	1.566	1.751	0.984
christophei	2.093	1.368	1.598	2.026	2.089	2.518	1.703
fowleri	1.460	1.324	1.390	1.694	0.989	1.836	0.916
reconditus	2.110	1.727	1.898	2.194	1.050	2.069	1.136
aeneus	1.797	1.278	1.328	1.920	1.295	1.693	0.811
bimaculatus	2.372	1.841	1.818	2.260	1.750	1.446	1.215
extremus	1.927	1.296	1.279	1.850	1.715	1.548	1.045
ferreus	2.398	1.841	1.856	2.329	1.541	1.457	1.059
gingivinus	1.680	1.044	1.227	1.718	1.418	1.966	1.013
griseus	1.855	1.620	1.616	1.917	0.722	1.220	0.496
leachi	2.173	1.643	1.593	2.080	1.650	1.298	1.026
lividus	1.946	1.263	1.308	1.925	1.618	1.680	0.993
luciae	1.847	1.259	1.254	1.803	1.492	1.441	0.832
marmoratus	1.988	1.290	1.322	1.934	1.767	1.731	1.127
pogus	1.074	0.527	0.788	1.008	2.098	2.457	1.682
richardi	1.813	1.500	1.584	1.916	0.708	1.590	0.625
roquet	1.801	1.202	1.193	1.782	1.483	1.457	0.804
sabanus	1.873	1.218	1.214	1.780	1.801	1.662	1.141
schwartzi	1.785	1.070	1.180	1.616	2.308	2.342	1.740
trinitatis	1.657	1.117	1.084	1.691	1.418	1.444	0.739
wattsi	1.612	0.881	1.069	1.526	1.965	2.227	1.464
Chamaelinorops	1.569	0.919	0.919	1.573	2.301	2.301	1.690
Phenacosaurus	2.642	2.054	2.071	2.736	2.093	2.169	1.646
tg	1.812	1.219	1.448	1.897	1.396	2.175	1.152
tc	1.900	1.267	1.213	1.809	1.879	1.602	1.180
tr	2.555	1.766	1.975	2.543	2.190	2.626	1.811
gb	0.603	0.346	0.269	0.509	2.150	2.259	1.655
cg	2.153	1.919	1.856	2.236	0.673	0.809	0.378
tw	2.217	1.635	1.709	2.346	2.133	2.417	1.700
	angusticeps	darlingtoni	insolitus	valencienni	conspersus	longiceps	monensis
angusticeps	0.000						
darlingtoni	0.962	0.000					
insolitus	0.432	0.810	0.000				
valencienni	0.776	0.849	0.964	0.000			
conspersus	1.772	1.114	1.798	1.490	0.000		
longiceps	1.710	1.441	1.884	1.306	1.204	0.000	
monensis	1.840	1.070	1.773	1.659	0.463	1.350	0.000
acutus	1.787	1.143	1.801	1.568	0.327	1.089	0.341
christophei	2.187	1.424	2.058	2.116	0.887	1.947	0.607
fowleri	1.684	1.663	1.943	1.543	1.146	1.396	1.518
reconditus	2.363	1.875	2.441	2.118	0.947	1.941	1.281
aeneus	1.142	0.830	1.298	0.798	0.767	0.985	1.048
bimaculatus	2.541	1.756	2.532	2.081	0.994	1.395	1.007
extremus	1.902	1.161	1.891	1.543	0.624	0.954	0.557

APPENDIX II—Continued.

	angusticeps	darlingtoni	insolitus	valencienni	conspersus	longiceps	monensis
ferreus	2.407	1.617	2.401	1.928	0.832	1.416	0.935
gingivinus	1.725	1.135	1.743	1.566	0.295	1.384	0.514
griseus	2.299	1.884	2.466	1.894	0.923	1.288	1.326
leachi	2.280	1.544	2.294	1.819	0.850	1.089	0.893
lividus	1.630	0.857	1.609	1.287	0.472	1.021	0.478
luciae	1.879	1.192	1.907	1.503	0.463	0.911	0.569
marmoratus	1.737	0.932	1.688	1.412	0.585	1.069	0.453
pogus	2.073	1.696	2.086	2.170	1.120	1.689	0.998
richardi	2.104	1.704	2.252	1.786	0.766	1.448	1.198
roquet	1.695	1.043	1.736	1.321	0.476	0.806	0.606
sabanus	1.920	1.174	1.892	1.613	0.638	1.023	0.478
schwartzi	2.185	1.474	2.077	2.121	1.025	1.617	0.608
trinitatis	1.464	0.983	1.569	1.106	0.619	0.634	0.816
wattsi	1.974	1.314	1.911	1.916	0.703	1.522	0.387
Chamaelinorops	1.125	0.891	1.097	1.270	1.292	1.183	1.146
Phenacosaurus	0.990	0.759	0.989	0.448	1.583	1.492	1.671
tg	1.728	1.214	1.747	1.622	0.572	1.643	0.792
tc	1.840	1.131	1.821	1.508	0.802	0.874	0.675
tr	1.882	1.014	1.666	1.766	1.087	2.035	0.893
gb	1.972	1.780	2.068	2.068	1.339	1.378	1.284
cg	2.217	1.871	2.422	1.664	1.178	1.131	1.586
tw	0.421	0.569	0.438	0.558	1.486	1.520	1.535
	acutus	christophei	fowleri	reconditus	aeneus	bimaculatus	extremus
acutus	0.000						
christophei	0.875	0.000					
fowleri	1.255	1.832	0.000				
reconditus	1.189	1.283	1.166	0.000			
aeneus	0.877	1.512	0.908	1.386	0.000		
bimaculatus	0.978	1.359	1.945	1.542	1.542	0.000	
extremus	0.485	1.129	1.583	1.512	1.018	0.691	0.000
ferreus	0.915	1.267	1.793	1.326	1.379	0.308	0.698
gingivinus	0.440	0.779	1.079	0.878	0.829	1.249	0.860
griseus	1.056	1.667	0.977	0.908	1.184	1.218	1.212
leachi	0.802	1.365	1.751	1.538	1.297	0.312	0.450
lividus	0.454	1.046	1.436	1.402	0.760	0.932	0.346
luciae	0.392	1.133	1.384	1.319	0.893	0.704	0.230
marmoratus	0.494	1.021	1.590	1.511	0.929	0.865	0.259
pogus	0.926	1.063	1.455	1.493	1.496	1.747	1.343
richardi	0.973	1.451	0.771	0.566	1.033	1.374	1.254
roquet	0.414	1.196	1.304	1.372	0.729	0.877	0.305
sabanus	0.443	1.044	1.617	1.529	1.076	0.741	0.139
schwartzi	0.774	0.743	1.940	1.719	1.562	1.239	0.891
trinitatis	0.576	1.392	1.106	1.443	0.503	1.170	0.601
wattsi	0.508	0.546	1.560	1.336	1.269	1.244	0.845
Chamaelinorops	1.103	1.573	1.660	2.129	1.085	1.869	1.182
Phenacosaurus	1.658	2.101	1.894	2.275	1.045	2.047	1.543
tg	0.771	0.867	1.052	0.756	0.921	1.513	1.170
tc	0.612	1.254	1.676	1.718	1.065	0.852	0.232
tr	1.182	0.781	2.018	1.592	1.420	1.572	1.264
gb	1.092	1.576	1.414	1.844	1.479	1.877	1.400
cg	1.321	2.030	1.146	1.345	1.148	1.339	1.314
tw	1.516	1.905	1.640	2.153	0.909	2.195	1.575
	ferreus	gingivinus	griseus	leachi	lividus	luciae	marmoratus
ferreus	0.000						
gingivinus	1.093	0.000					
griseus	1.093	1.051	0.000				
leachi	0.417	1.124	1.118	0.000			
lividus	0.828	0.683	1.232	0.716	0.000		
luciae	0.650	0.726	0.989	0.462	0.351	0.000	

APPENDIX II—Continued.

	ferreus	gingivinus	griseus	leachi	lividus	luciae	marmoratus
marmoratus	0.808	0.787	1.336	0.661	0.180	0.376	0.000
pogus	1.742	0.972	1.580	1.630	1.334	1.293	1.343
richardi	1.190	0.794	0.429	1.278	1.172	1.028	0.302
roquet	0.805	0.717	1.039	0.614	0.273	0.192	0.358
sabanus	0.769	0.840	1.276	0.534	0.392	0.313	0.273
schwartzi	1.303	1.018	1.736	1.174	0.983	0.990	0.874
trinitatis	1.089	0.788	1.054	0.889	0.489	0.493	0.610
wattsi	1.218	0.616	1.446	1.154	0.828	0.847	0.798
Chamaelinorops	1.854	1.279	1.949	1.612	1.063	1.243	1.073
Phenacosaurus	1.899	1.685	2.105	1.812	1.289	1.554	1.379
tg	1.317	0.332	1.175	1.413	0.949	1.031	1.068
tc	0.901	1.008	1.381	0.596	0.450	0.423	0.339
tr	1.403	1.054	1.958	1.536	1.036	1.301	1.040
gb	1.917	1.250	1.621	1.684	1.441	1.358	1.453
cg	1.207	1.373	0.579	1.185	1.314	1.117	0.431
tw	2.055	1.479	2.092	1.946	1.287	1.568	1.390
	pogus	richardi	roquet	sabanus	schwartzi	trinitatis	wattsi
pogus	0.000						
richardi	1.420	0.000					
roquet	1.303	1.049	0.000				
sabanus	1.245	1.299	0.387	0.000			
schwartzi	0.898	1.664	1.054	0.753	0.000		
trinitatis	1.325	1.045	0.319	0.664	1.247	0.000	
wattsi	0.661	1.299	0.890	0.735	0.436	1.042	0.000
Chamaelinorops	1.311	1.851	1.101	1.137	1.244	0.974	1.188
Phenacosaurus	2.332	2.003	1.390	1.613	2.115	1.262	1.969
tg	1.086	0.818	1.009	1.157	1.275	1.038	0.856
tc	1.382	1.434	0.417	0.242	0.900	0.625	0.922
tr	1.651	1.718	1.292	1.231	1.237	1.449	1.095
gb	0.634	1.575	1.326	1.325	1.191	1.247	1.061
cg	2.002	0.851	1.114	1.422	2.049	1.064	1.800
tw	1.951	1.910	1.388	1.600	1.921	1.203	1.728
	Chamaelinorops	Phenacosaurus	tg	tc	tr	gb	cg
Chamaelinorops	0.000						
Phenacosaurus	1.360	0.000					
tg	1.469	1.757	0.000				
tc	1.044	1.497	1.320	0.000			
tr	1.566	1.626	1.061	1.355	0.000		
gb	1.147	2.288	1.450	1.366	2.043	0.000	
cg	2.016	1.875	1.501	1.442	2.139	1.934	0.000
tw	0.984	0.658	1.512	1.520	1.538	1.911	2.003
	tw						
tw	0.000						