

Molecular Evolution and Adaptive Radiation

Edited by

Thomas J. Givnish and Kenneth J. Sytsma
University of Wisconsin – Madison



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I. Givnish, Thomas J. II. Sytsma, Kenneth Jay.

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19 PHYLOGENETIC STUDIES OF CONVERGENT ADAPTIVE RADIATIONS IN CARIBBEAN *ANOLIS* LIZARDS

Todd Jackman, Jonathan B. Losos, Allan Larson,
and Kevin de Queiroz

A clade may be called an adaptive radiation if its constituent lineages have diversified to utilize a number of different aspects of the environment (Simpson 1953). Contrary to some recent discussions of adaptive radiation, the relevant criterion is not the number of species, but the adaptive disparity among these species; even clades with relatively few species can constitute an adaptive radiation if the species demonstrate considerable ecological and morphological disparity (see Chapters 1 and 8). Of course, many of the classic cases of adaptive radiation (e.g., Australian marsupials [Chapter 4], African rift lake cichlids [Chapter 12]) are clades that exhibit extensive amounts of both adaptive diversification and speciation.

Caribbean anoline lizards present a particularly interesting example of adaptive radiation. They entail not one, but four separate instances of radiation, having diversified largely independently on each island of the Greater Antilles. Multiple independent radiations within a clade associated with different geographic regions are not uncommon (e.g., cichlids in each of the African Rift Lakes, or marsupials in Australia and South America); what is striking about the Caribbean anoles is that these independent evolutionary theaters have produced extraordinarily similar radiations, both in terms of the current diversity of adaptive forms and the apparent evolutionary pathway to those forms.

Molecular systematics has contributed greatly to our understanding of the anole radiations. Subsequent to Etheridge's (1960) osteological study (the first modern treatment of anoles), almost every newly developed technique has been applied to this group, including methods based on karyotypes (Gorman and Atkins 1969; Gorman and Stamm 1975; Williams 1989), allozymes (Yang et al. 1974; Gorman and Kim 1976; Gorman et al. 1980a, 1983; Burnell and Hedges 1990), immunological distance (Gorman et al. 1980b; Wyles and Gorman 1980a,b; Shochat and Dessauer 1981; Gorman et al. 1984; Hass et al. 1993), and DNA sequences (Hass et al. 1993). In spite of these studies, a robust phylogenetic hypothesis for the entire group has proven elusive. Indeed, higher-level anoline relationships were left largely unresolved by osteological, karyotypic, and immunological work conducted through 1989 (Figure 19.1; see Cannatella and de Queiroz 1989 and Williams 1989). However, new phylogenetic methods and new data – especially DNA sequences – have recently begun to clarify some of the problematical aspects of anoline phylogeny.

This chapter will attempt to illustrate the utility of molecular systematics as part of an integrative research program aimed at unraveling the patterns and processes

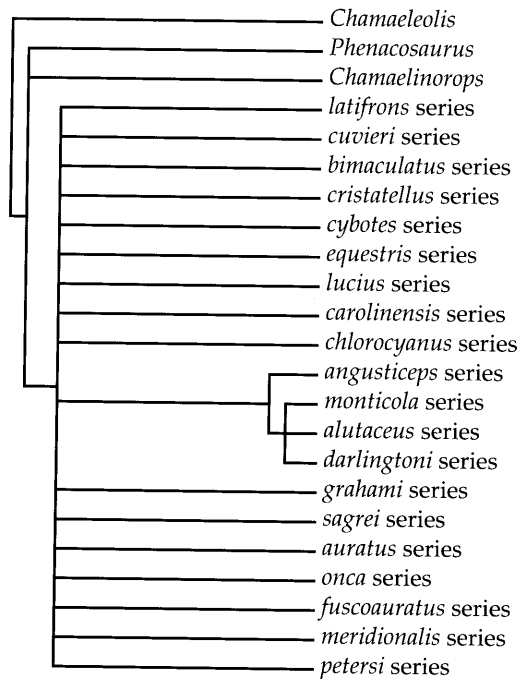


Figure 19.1. Consensus tree based on taxonomic congruence of studies of anoline relationships based on osteological, immunological, and karyotypic data (Cannatella and de Queiroz 1989). Non-capitalized names represent *Anolis* species series. Assignment of West Indian *Anolis* to species groups is not controversial; the relationships among these groups are disputed.

operating in the anoline radiation. In particular, we hope to demonstrate how molecular techniques can provide the historical phylogenetic framework upon which all studies of adaptation must be based (see Lauder 1981; Greene 1986; Coddington 1988; Baum and Larson 1991; Arnold 1994; Larson and Losos 1996). We first discuss recent inferences regarding anole phylogeny based on new DNA data. Then we address three issues in anoline evolution into which molecular systematics provides powerful insights: patterns of adaptive evolution, the significance of key innovations, and patterns of community evolution.

Natural history of Caribbean anoles

In terms of species diversity and sheer biomass, *Anolis* is one of the two dominant vertebrate groups in the Caribbean (the other is the frog genus *Eleutherodactylus*). Currently, 139 species of Caribbean anoles are recognized (Powell et al. 1996) and new species are being discovered every year (e.g., Estrada and Hedges 1995; Diaz et al. 1996). The vast majority (111) of these species occur on the islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico; Figure 19.2). On each of these islands, lineages have adaptively diversified, resulting in species occupy-

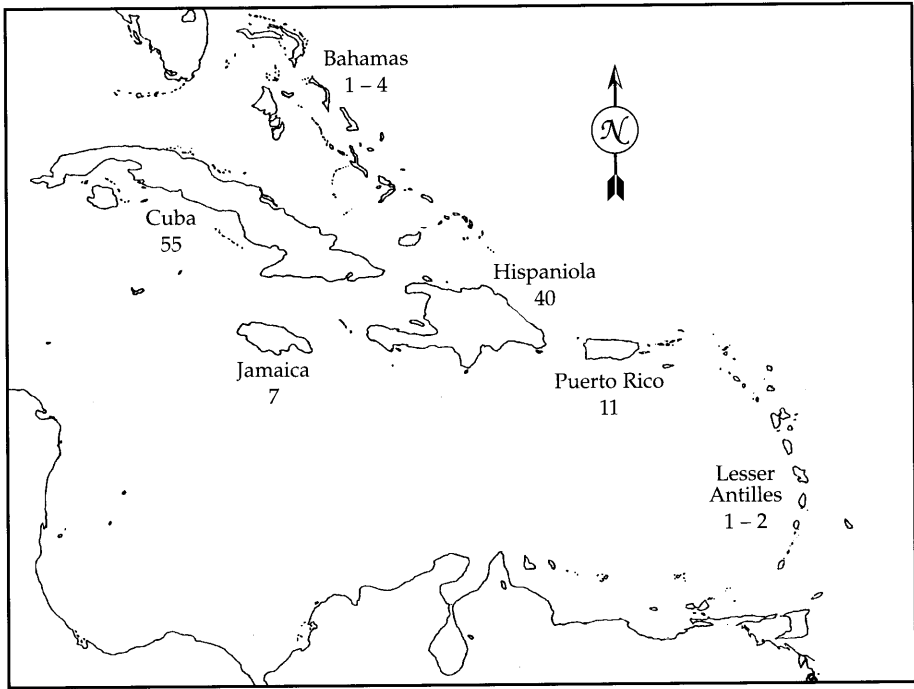


Figure 19.2. Number of anole species (including *Chamaeleolis* and *Chamaelinorops*) per island in the Caribbean.

ing a wide variety of ecological niches and as many as twelve species occurring sympatrically.

Studies of anoline assemblages have played an important role in the development of theories of community ecology (e.g., Schoener 1968, 1974; Roughgarden 1974). A wealth of data suggests that interspecific competition among anoles plays an important role in structuring anoline assemblages (see review by Losos 1994). In particular, co-occurring species almost invariably differ in either *body size* (correlated with prey size [Roughgarden 1974; Schoener 1968; Schoener and Gorman 1968]), *structural habitat* (e.g. perch height and diameter), or *microclimate* (shade vs. open sun) (Rand 1964, 1967; Schoener and Schoener 1971a,b; Moermond 1979a,b). For example, eight species of anoles occur at the Luquillo Experimental Forest in Puerto Rico. Three species occur high in the trees, of which one is small-bodied, one intermediate, and one large. Two other species perch on tree trunks and forage on the ground; one occurs in open, sunlit habitats, the other in closed forest. Of the two species that use grassy habitats and shrubs, one is found usually in the open and the other in shaded microhabitats. The last species is very small and is found primarily on twigs, probably at all heights.

Both experimental and unintentional manipulations, as well as observations of natural systems, indicate that species alter their behavior and habitat use depending on whether another species is present. In Jamaica, for example, *Anolis opalinus* perches higher when *A. lineatopus* is present than when it is absent (Jenssen 1973). Similarly,

Table 19.1. Morphological characteristics of anole ecomorph classes. Data from Losos (1990a, 1992, unpubl.); all lengths are in mm. Morphological differences are discussed in Glossip and Losos (1997) and Beuttell and Losos (unpubl.). Lamellae tabulated are those underlying the third and fourth phalanges of pedal digit IV.

Ecomorph	Snout-vent length	Shape	Hindlimb length	Forelimb/hindlimb length ratio	Tail length	Color	Number of lamellae
Crown-giant	> 120	intermed.	intermed.	intermed.	intermed.	green or brown	28-42
Grass-bush	35-50	slender	long	low	very long	brown with yellow stripe	13-21
Trunk	40-60	intermed.	mod. long	mod. high	short	gray	17-18
Trunk-crown	45-80	intermed.	intermed.	intermed.	intermed.	green	19-30
Trunk-ground	50-75	stocky	long	low	long	brown or gray	15-21
Twig	35-85	very thin	very short	high	short	white	15-28

Schoener (1975) showed that the four most geographically widespread anoles in the Caribbean – *A. carolinensis*, *A. distichus*, *A. grahami*, and *A. sagrei* – all adjust their perch height depending on the other species with which they co-occur at a given locality.

The evolutionary effects of such habitat shifts become apparent when populations differing in habitat use are compared. Habitat differences among populations of *A. carolinensis* and *A. sagrei* are correlated with differences in the number of subdigital lamellae on the toepad (Lister 1976) and hindlimb length (Losos et al. 1994). Larger differences of the same kind are associated with habitat differences among sympatric species in the Greater Antilles (see below).

When comparing the anoles found on the Greater Antilles, the most striking observation is that the same set of ecological types – termed “ecomorphs” (Rand and Williams 1969; Williams 1972) – occur on each of these islands. Six ecomorph classes have been identified (Table 19.1). Each is composed of a set of morphologically and behaviorally similar species that utilize a similar micro-environment. The ecomorphs are named for the part of the arboreal or terrestrial environment they most frequently use: trunk-ground, trunk, trunk-crown, crown-giant, twig, and grass-bush (Plate 4). Morphometric analyses indicate that members of the same ecomorph class cluster in morphological space (Figure 19.3; Losos 1992; Losos and de Queiroz 1997). Several studies show that members of a given ecomorph class are similar also in ecology and behavior (Losos 1990 a,b; Irschick and Losos 1996).

Williams (1972) proposed that the ecomorphs evolved as a result of competition-driven resource partitioning. This study, two decades ahead of its time, used a phylogeny for Puerto Rican anoles based on osteological and karyotypic data to infer patterns of morphological and ecological evolution. Williams suggested that the original colonizing species on Puerto Rico was morphologically unspecialized. As new

species were added to the island by speciation, competition led to resource partitioning, which in turn led to the evolution of the different ecomorphs. A re-analysis of this hypothesis conducted 20 years later (Losos 1992) and discussed below, confirmed most of Williams' phylogenetic interpretations.

Three other important aspects of the Caribbean anoline radiation must be mentioned. First, not all ecomorphs are represented on each island. Cuba and Hispaniola have all six ecomorph classes, Puerto Rico has all but the trunk anoles, and Jamaica has all but the grass-bush and trunk anoles. Thus, sets of ecomorphs on the different islands are nested, with the smaller islands having subsets of the ecomorphs found on the larger ones. In addition, not all Greater Antillean species belong to one of the six ecomorph classes. However, ecomorph species are numerically dominant in

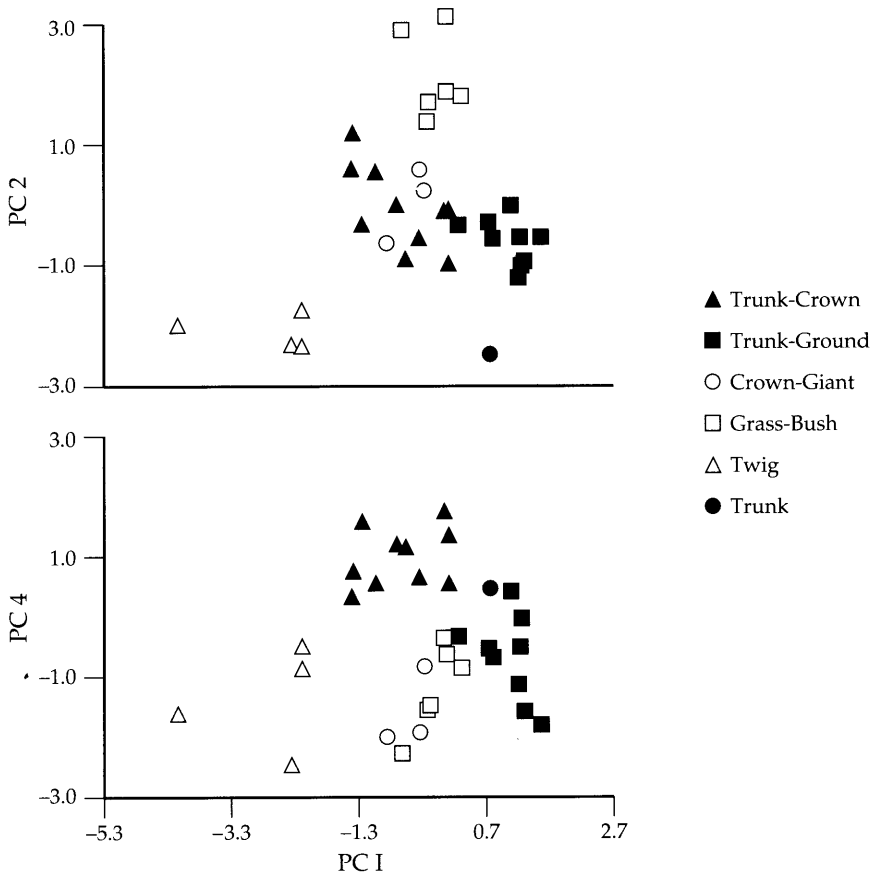


Figure 19.3. The position of the Greater Antillean ecomorphs in a morphological space defined by a principal components analysis (PCA). Variables in the analysis were body mass, hind- and forelimb length, tail length, and number of lamellae underlying the third and fourth phalanges of pedal digit IV. The effect of size was removed from each of these variables by using residuals from regressions against snout-vent length (SVL); these regressions used species means. In addition, SVL was also included in the PCA. PC 3 loads only for SVL and is not shown; only crown-giants are clearly distinguished from other ecomorphs on the basis of this axis. Figure from Losos and de Queiroz (1997).

almost all sites within the Greater Antilles; in fact, at many localities, particularly in the lowlands (and in all of Puerto Rico), only species categorized as ecomorphs can be found. Relatively few Greater Antillean species (21 of 111, including species in Cuban *Chamaeleolis* and Hispaniolan *Chamaelinorops*) cannot be placed into one of the standard ecomorph classes. These non-ecomorph species occupy distinctive ecological niches (e.g., streams) and are morphologically distinct, and do not have parallels on other islands (Williams 1983).

Second, the anoline adaptive radiation entails diversification not only in structural habitat, but in thermal microclimate as well. Some species have adapted to cool montane climates, whereas others occur in hot and arid habitats (e.g., Ruibal 1961; Huey and Webster 1976; Hertz 1980, 1981). Divergence in microclimate has occurred independently of adaptation to structural habitats, but is more common in species of certain ecomorph classes (e.g., trunk-ground anoles, grass-bush anoles) than others (Losos 1994 and references therein). Adaptation to different microclimates apparently permits members of the same ecomorph class to occur sympatrically through a partitioning of different thermal conditions (Schoener and Schoener 1971a,b; Huey and Webster 1976); indeed, this thermal partitioning is so well defined that individuals from two species may occupy the same tree at different times of the day, depending upon whether the tree is in the shade or in the sun (Schoener 1970; Huey and Webster 1976).

Third, in addition to *Anolis*, three other genera of anoles are commonly recognized, though only two of them occur in the West Indies. *Phenacosaurus* contains a small number of South American species that are similar to Greater Antillean twig anoles (Miyata 1983). Members of the Cuban genus *Chamaeleolis* (4 recognized spp.) are also superficially similar to twig anoles, but much larger (Hass et al. 1993). By contrast, *Chamaelinorops* (1 sp.) from Hispaniola is distinct from all other anoles in morphology, ecology, and behavior (Forsgaard 1983; Jenssen and Feely 1991; Flores et al. 1994). Etheridge (1960) concluded that all three of these genera are part of *Anolis*, but recent workers have placed some or all of them outside of *Anolis* (e.g., Guyer and Savage 1986, 1992; Williams 1989). Recent molecular studies have cast doubt on the latter hypothesis, suggesting that *Chamaeleolis* and *Chamaelinorops* fall within *Anolis* (Wyles and Gorman 1980a; Burnell and Hedges 1990; Hass et al. 1993; but see Case and Williams 1987).

Analysis of the anole radiation

Molecular systematics

We investigated anoline phylogeny by examining 1,455 base pairs of DNA encoding the mitochondrial *ND2* gene and five mitochondrial transfer RNAs (Figure 19.4; Jackman et al. [unpubl.] provide details of the sequencing protocol). We included 53 anoles as well as 2 outgroups, including all recognized anoline genera; although we do not follow Guyer and Savage (1986, 1992) in splitting *Anolis* into four genera, we have included representatives of all of their taxa. Although we included only 31 of 90 ecomorph species in this analysis, the phylogenetic affinities of the remaining ecomorph species not included in this study are clear. For example, the *A. alutaceus* series

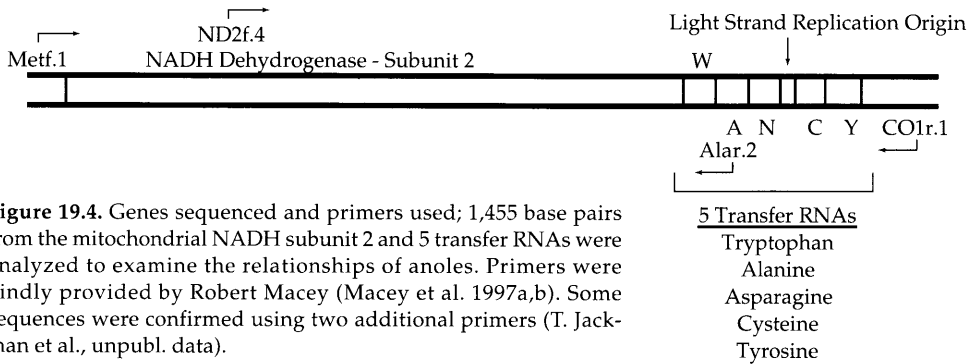


Figure 19.4. Genes sequenced and primers used; 1,455 base pairs from the mitochondrial NADH subunit 2 and 5 transfer RNAs were analyzed to examine the relationships of anoles. Primers were kindly provided by Robert Macey (Macey et al. 1997a,b). Some sequences were confirmed using two additional primers (T. Jackman et al., unpubl. data).

of Cuba contains 15 very similar species, all of which are grass anoles; two members of this series, *A. alutaceus* and *A. vanidicus*, are included in our study. Similarly, the *A. cybotes* series of Hispaniola contains eight trunk-ground anoles that are morphologically very similar; two of these (*A. marcanoi*, *A. strahmi*) are included in our analysis. Although these groups were initially defined on the basis of morphological evidence, immunological and electrophoretic studies generally support the close relationships of member species (Wyles and Gorman 1980a,b; Hass et al. 1993). Only one ecomorph series (the Hispaniolan *A. sheplani* lineage of twig anoles) is not included in our sample; all other ecomorph species are represented by a closely related species belonging to the same ecomorph class. Hence, our analysis of patterns of ecomorph evolution is unlikely to be compromised by partial sampling of species.

To evaluate specific phylogenetic hypotheses in a statistical framework, we used the Wilcoxon signed-ranks test (Templeton 1983). This test asks whether an alternative phylogenetic hypothesis is significantly less parsimonious than the most parsimonious topologies. The trees are compared character-by-character to investigate whether differences in the number of steps required for each character differs between the alternative trees. The differences in the numbers of steps between alternative phylogenetic hypotheses are then ranked and these rankings are used as the basis for the test (see Larson 1994 for a detailed description). For example, to test the hypothesis that *Anolis* is monophyletic, we compared the most parsimonious tree recovered from our data to the shortest tree produced from our data in which *Anolis* was monophyletic.

Figure 19.5 presents the most parsimonious tree derived from our DNA sequence data, using an unweighted analysis. Both *a priori* and *a posteriori* tests for saturation of substitutions (multiple substitutions occurring at the same site between lineages being compared) were employed (T. Jackman et al., unpubl. data). *A priori* tests consisted of comparisons of transition-to-transversion ratios at different site categories (Holmquist 1983), as well as examination of maximum likelihood distances plotted against the number of differences (Moritz et al. 1992). *A priori* tests suggested that only silent transitional changes may be saturated with mutations. An *a posteriori* test for differences in homoplasy (de Queiroz 1989; Larson 1994) showed a significant

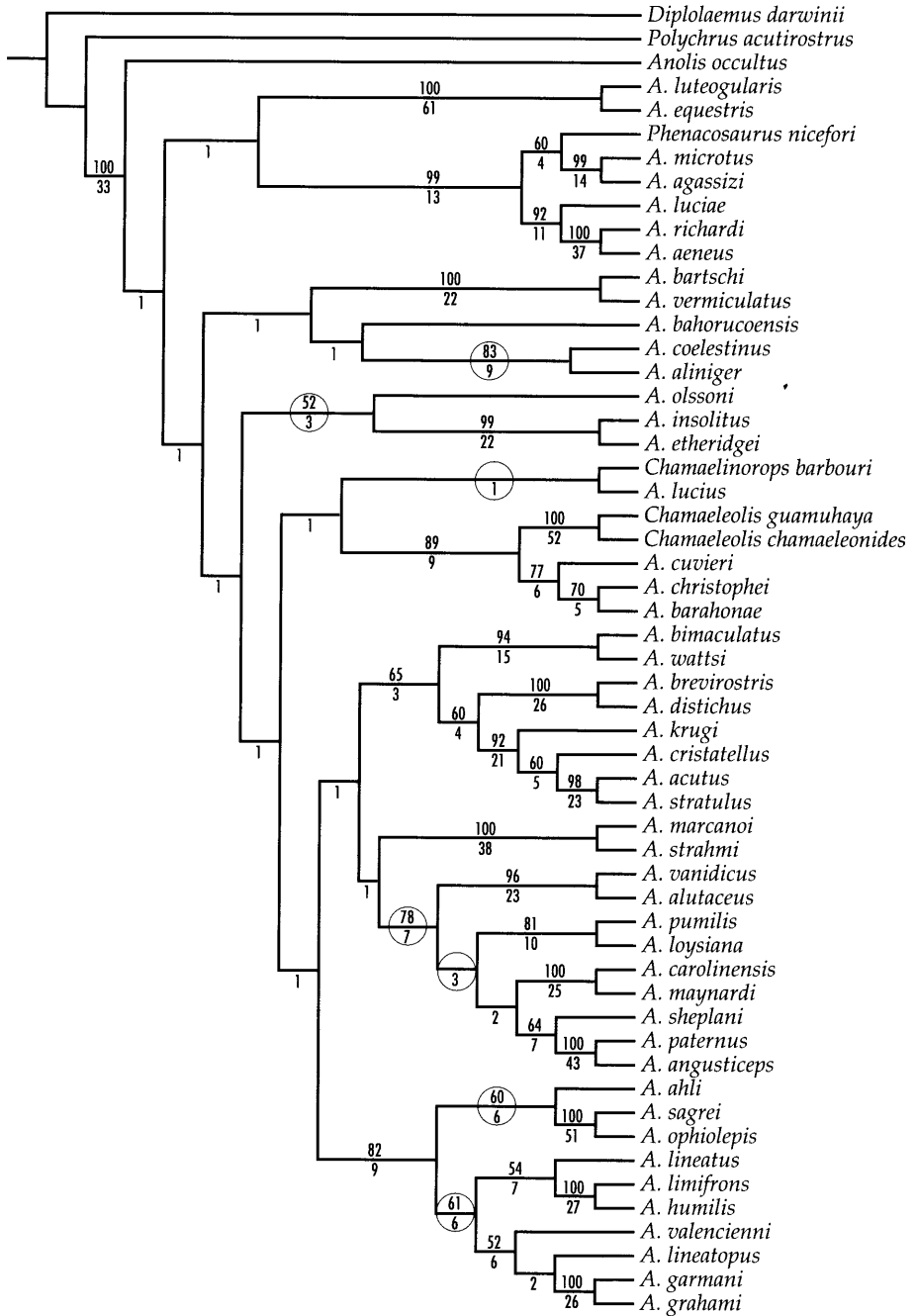


Figure 19.5. The most parsimonious tree based on an unweighted maximum parsimony analysis of DNA sequences (T. Jackman et al., unpubl. data). Bootstrap values (Felsenstein 1985a) greater than 50% are above and to the left of the nodes; decay index values (Bremer 1988) are below and to the left of the nodes. The length of the tree is 8,889 steps, based on 866 informative characters. The consistency index is 0.38. Circles indicate nodes for which support increases ($\geq 5\%$ for bootstrap analyses, ≥ 2 steps for decay analysis) when silent transitions are omitted.

increase in the number of inferred homoplasies for silent transitions. The removal of silent transitions significantly affected the tree only by improving support for the nodes circled in Figure 19.5. Consequently, we concluded that the signal-to-noise ratio in this data set is fairly high, and that the high levels of noise in silent transitions do not have a major effect on tree topology.

Several significant conclusions follow from the most parsimonious tree (Figure 19.5). First, *Anolis* is paraphyletic with respect to the other three anole genera, and we are able to reject the hypothesis that *Anolis* is monophyletic (Table 19.2). We were also able to reject the hypotheses that *Anolis* is monophyletic with respect to the other two Caribbean genera alone (Table 19.2).

Second, considerable inter-island movement has occurred during the evolution of *Anolis*. If we use parsimony to reconstruct the distribution of ancestral forms using MacClade (Maddison and Maddison 1992), Hispaniola appears as the ancestral location for many of the deepest nodes in the phylogeny (Figure 19.6). Thirteen lineages have engaged in inter-island dispersal: six to Cuba, three to Puerto Rico, one to Jamaica (not including a recent colonization of Jamaica by the Cuban *A. sagrei* species group [Williams 1969]), two to Hispaniola (one ancient and one relatively recent), and one to Central America. Contrary to previous discussions (e.g., Williams 1969; Guyer and Savage 1986), our analysis indicates that Central America was reinvaded by a lineage of Caribbean anoles.

Table 19.2. Tests of phylogenetic hypotheses using the Wilcoxon signed-rank test.

Hypothesis	T_s^1	n^2	z^3	Probability
<i>Anolis</i> is monophyletic ⁴	10,545	234	3.78	< 0.001
<i>Anolis</i> is monophyletic relative to <i>Chamaelinorops</i> and <i>Chamaeleolis</i> – alpha and beta subsections monophyletic ⁵	7,398	207	2.04	< 0.05
<i>Phenacosaurus</i> is sister to the other anoline genera	10,210	210	1.53	NS
All ecomorph classes are monophyletic	10,184	375	11.93	< 0.001
Species on each island in the Greater Antilles form a monophyletic radiation ⁶	9,501	233	4.01	< 0.001

¹Wilcoxon signed-ranks statistic.

²Number of characters that differed in numbers of changes on the two trees.

³Normal approximation when $n > 100$ (Zar 1984).

⁴The scenario of Guyer and Savage (1986).

⁵The scenario of Williams (1969); all *Anolis* are traditionally placed in the alpha or beta subsections.

⁶This hypothesis can also be rejected for each island individually except Jamaica.

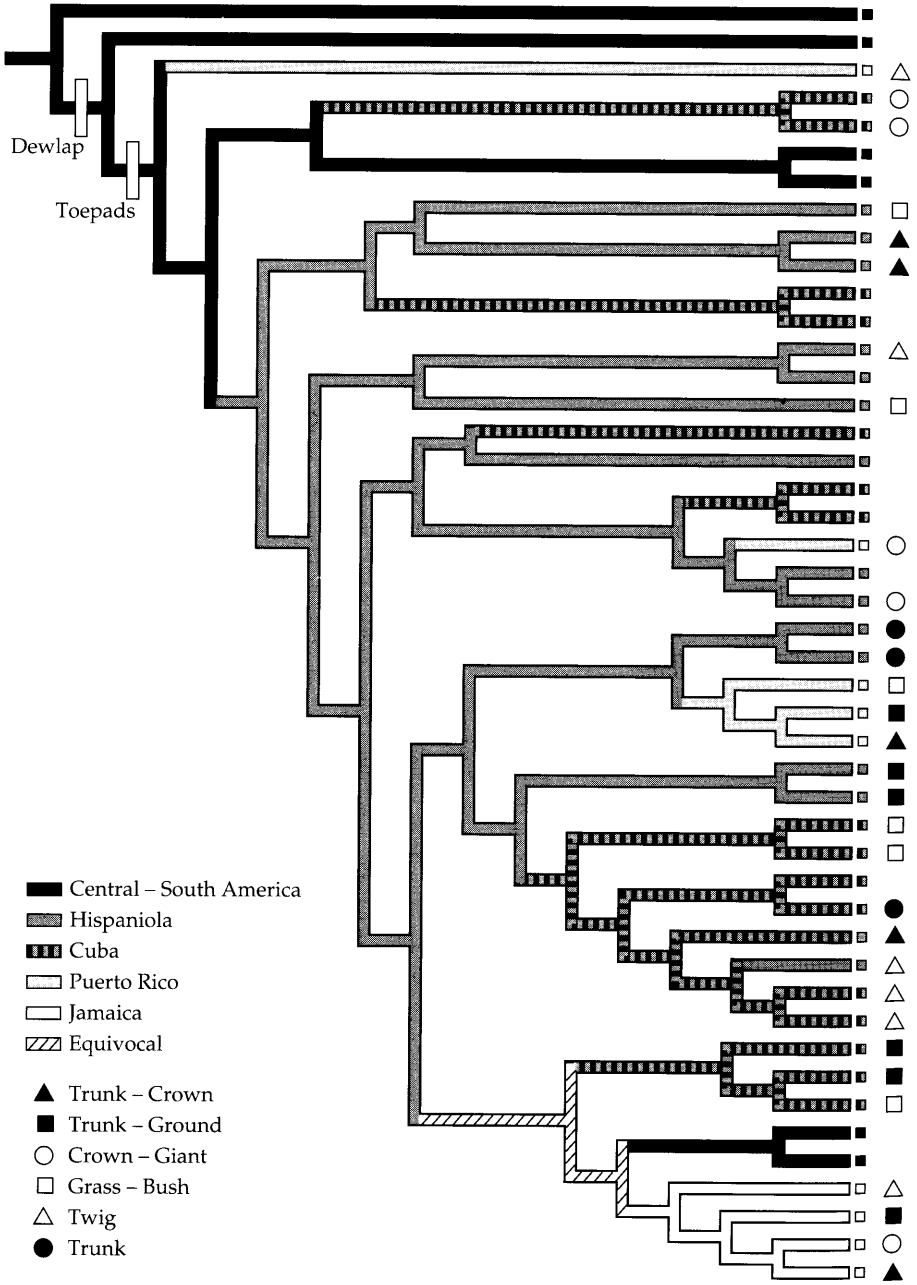


Figure 19.6. Geographic relationships and ecomorph evolution in Caribbean anoles. Phylogeny is the same as in Figure 19.5, but taxa from small islands (e.g., northern and southern Lesser Antilles, St. Croix, Malpelo) are omitted. Species names are replaced by ecomorph symbols. Ancestral states for geographic location were reconstructed using parsimony; character-states (= geographic locations) were considered unordered. Omission of some taxa does not alter the reconstruction because all small islands represent autapomorphic character-states. *Anolis carolinensis* was treated as if it were from Cuba (it actually occurs in Florida, the Bahamas, and elsewhere) because it is closely related to and surely derived from the Cuban species *A. porcatius* (Buth et al. 1980). Evolution of the anole dewlap and expanded subdigital toepads, as inferred by parsimony, is indicated by open bars. Both features have been secondarily lost in several taxa (not shown).

Given the apparent evolutionary lability of geographic distribution, perhaps one should not give too much credence to the particular reconstruction based on our present molecular tree. Alternative geographic scenarios account for current species distributions nearly as well. For example, a reconstruction in which Cuba is the ancestral location for all Caribbean anoles and has never been re-invaded requires only three additional steps. Nevertheless, our molecular phylogeny can rule out one extreme hypothesis, that each island represents a monophyletic radiation (Table 19.2). Furthermore, although the geologic history of the Caribbean is still controversial (Hedges 1996; Crother and Guyer 1996), it is difficult to see how a simple vicariance scenario could explain the distribution of lineages among islands. Explaining patterns such as this will require complex scenarios that may incorporate elements of dispersal, extinction, and restricted ancestral geographic ranges. The extent to which these scenarios will also include a vicariance component remains to be determined (see Hedges 1996; Crother and Guyer 1996).

Third, the tree reveals a number of poorly supported nodes at the deepest levels of the phylogeny. Lack of resolution could result from substitutional saturation that obscures phylogenetic signal, or from a rapid successive branching of lineages. Many evolutionary biologists have suggested that species colonizing depauperate regions may diversify rapidly (e.g., Simpson 1953; Rensch 1959); in this situation, branching of numerous lineages would occur nearly simultaneously on an evolutionary time scale.

For several reasons, we believe the anoline situation most likely reflects rapid, successive branching of lineages (T. Jackman et al., unpubl. data). Within the anoles, 866 informative characters exist (772 with silent transitions removed). As noted above, saturation of substitutions can be shown only for silent transitions. Moreover, short reconstructed branches characterize the deep nodes in the tree regardless of the methods used to reconstruct the branches or whether silent sites are included or excluded. Furthermore, branch lengths from trees constructed using only amino acid and tRNA transversion characters (the most conservative sets of characters) were similarly short. Tests involving subsampling of taxa also demonstrate that a rapid radiation occurred between the major anoline lineages.

Other data sets that have been used to examine anoline relationships suffer from a similar lack of resolution deep in the tree (Cannatella and de Queiroz 1989; Burnell and Hedges 1990; Hass et al. 1993). A combined analysis of species in common between our data set, 16S DNA data (Hass et al. 1993), allozyme data (Burnell and Hedges 1990), and morphological data produced a phylogenetic hypothesis almost entirely congruent with the trees presented here (T. Jackman et al., unpubl.). An immunological data set (Hass et al. 1993) could not be included in the combined analysis because the data are in the form of distances rather than discrete characters. Nonetheless, the phylogeny produced in the analysis by Hass et al. (1993), involving eight taxa, agreed with our DNA study in the close relationships of several taxa (e.g., *Chamaeleolis* and *A. cuvieri*, and members of the *A. cristatellus* series), as well as in indicating many short internal branches. The immunological analysis also suggested some discrepant relationships among the shorter branches of the tree, but these relationships were not robust when the immunological data were analyzed using different methods (Hass et al. 1993).

Adaptation

Integral to the study of adaptive radiation is the study of adaptation itself; a clade constitutes an adaptive radiation only if lineages within the clade have adapted to different ecological roles. Here we follow Gould and Vrba (1982, p. 5) in defining an adaptation as a feature that was "built by natural selection for the function it now performs."

Investigating the adaptive status of a feature thus requires information on its evolutionary history, which necessitates a phylogenetic perspective. The hypothesis of adaptation implies that (1) a trait currently provides an advantage at some task (such as locomotion or feeding) that itself promotes survival or fecundity; and that (2) this trait and its associated advantage in performance arose in a lineage experiencing a selective regime that would also have favored evolution of the trait. If such a trait instead arose in a lineage whose descendants only later entered a selective regime favoring that trait, then the trait would constitute an "exaptation" (Greéne 1986; Codrington 1988; Baum and Larson 1991; Arnold 1994; Larson and Losos 1996).

Studies on anoline adaptation have focused on two traits: subdigital toepads (Figure 19.7) and the length of the hindlimbs. Because toepads are widely distributed in anoles and are absent in *Polychrus* and all more distant outgroups, we may conclude that toepads evolved in the ancestral anole (Figure 19.6), although they have been secondarily reduced or lost in some taxa (Peterson and Williams 1981). Because *Polychrus*, like *Anolis*, is arboreal, we may conclude also that toepads initially evolved in an arboreal species. Laboratory studies indicate that toepads provide clinging ability on smooth surfaces, similar to those of leaves and the bark of some trees, and that species with larger pads have greater clinging ability (Irschick et al. 1996). Hence, the conclusion that toepads evolved as an adaptation to enhance arboreal capabilities seems reasonable. This proposition is further bolstered by the observation that similar pads have evolved convergently in two other clades of arboreal lizards, geckos, and praesinohaemid skinks (discussed in Larson and Losos 1996).

Toepad characteristics vary among anoles, especially in the size of the pad and the number of transversely expanded scales (termed lamellae) that form the pad. Based on the functional studies cited above (Irschick et al. 1996), larger pads probably confer greater clinging ability. It seems likely that species with more lamellae may have greater ability to mold the toepad to narrow or irregular surfaces, but this hypothesis requires additional functional data.

Comparisons among ecomorph classes indicate that they differ systematically in pad size and number of lamellae, even after the effect of body size is removed (Table 19.3). Because members of the same ecomorph class are not necessarily closely related (see below), these results indicate that similar morphological features have evolved independently in species occupying similar habitats. Such parallel evolution has been considered strong evidence of adaptation; this conclusion is bolstered when the functional consequences of the trait are understood as well.

Variation among species in hindlimb length relative to body size also appears adaptive. Species in different ecomorphs differ systematically in relative hindlimb length (Table 19.3). The functional consequences of differences in limb length are well understood: species with longer limbs have greater running capabilities on broad

surfaces (Losos 1990b). On narrow surfaces, long-legged species run no faster than short-legged species but stumble more frequently (Losos and Sinervo 1989; Losos and Irschick 1996).

Hence, one might hypothesize that long legs are an adaptation for moving rapidly on broad surfaces, whereas short legs are adaptive for moving without difficulty on narrow surfaces. In support of this hypothesis, behavioral studies indicate that longer-legged species run more frequently (Table 19.4) and run faster in nature than shorter-legged species (D. Irschick and J. Losos, unpubl. data). Comparisons among species indicate a relationship between relative hindlimb length and both mean perch diameter and mean perch height (Table 19.4); the relationship is negative in the height-hindlimb regression. In a multiple regression involving both perch diameter and height, more of the variance in relative hindlimb length is explained and both variables are individually more significant (Table 19.4).

We interpret this comparative finding as demonstrating that species that use broader surfaces tend to have longer legs, as predicted from the functional studies. Terrestrial species tend to have longer legs than more arboreal species, presumably because they frequently use the broadest surface of all, the ground. This difference in relative

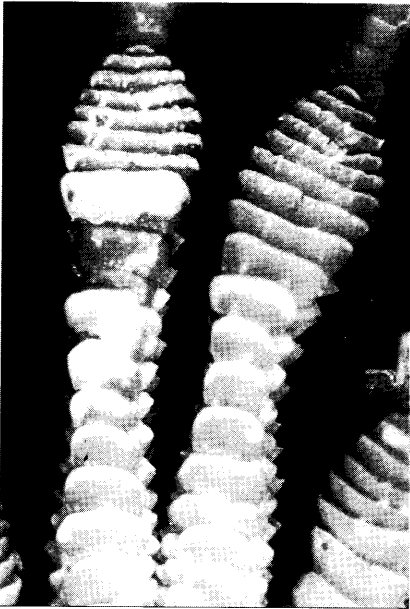


Figure 19.7. Toepads of *A. sagrei* from Cuba. Each toepad consists of a number of transverse scales, termed lamellae. Each lamella is covered with millions of microscopic hairs, termed setae. Adhesion is thought to occur as a result of the intermolecular forces generated between electrons on the setae and on the surface (Cartmill 1985; Irschick et al. 1996 and references therein).

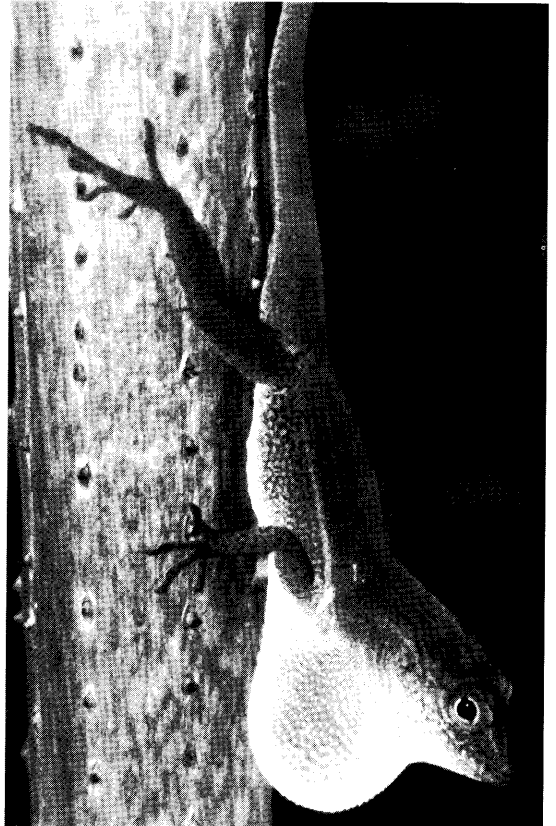


Figure 19.8. Male of *A. lineatopus* extending dewlap.

hindlimb length is perhaps most vivid between twig anoles and grass-bush anoles (see Table 19.1), which utilize similar mean perch diameters ($d_{tw} = 2.0$ cm vs. $d_{gb} = 2.4$ cm) but differ strikingly in their use of broad surfaces. Twig anoles usually perch at 2 m or more in height and rarely come to the ground; grass-bush anoles do much of their foraging and interacting on the ground and run considerably more frequently (31% of movements vs. 9% in twig anoles; see Losos 1990a, 1992, unpubl. data). Hence, we conclude that limb length has evolved adaptively with respect to habitat use in anoles. The probable functional explanation underlying this adaptive evolution relates to the differing demands for movement on surfaces of different breadths.

Key innovations

A key innovation can be viewed as a character that permits members of a clade to interact with the environment in a manner unavailable to members of its sister taxon that lacks that key character (Larson et al. 1981). If the key innovation provides evolutionary access to many adaptive zones, then it may lead to an adaptive radiation, but the two are not necessarily linked: adaptive radiation can occur in the absence of the evolution of a key innovation, as when a species colonizes an environment with many unutilized resources; conversely, a key innovation can occur

Table 19.3. Phylogenetically structured analyses of variance for toepad area, number of lamellae, and hindlimb length across ecomorphs.¹ The effect of body size has been removed by analyzing the residuals after regressing each variable against snout-vent length, using mean values for each species. Data are drawn from Losos (1990a, 1992, unpubl. data), Glossip and Losos (in press), and K. Beuttell and J. Losos (unpubl. data). Degrees of freedom (d.f.) differ because data for toepad area are available for fewer species.

Variable	F	d.f.	Non-phylogenetic P^2	No. of simulations producing F values greater than observed	
				Speciational model	Gradual model
Pad area	38.79	5,16	< 0.001	0/1000	0/1000
# lamellae	3.07	5,23	0.029	53/1000	65/1000
Hindlimb length	12.65	5,23	< 0.001	0/1000	0/1000

¹Because closely related species may be phenotypically similar, statistical analyses such as these should be conducted within a phylogenetic context. Garland et al. (1993) provided a means of conducting phylogenetically structured analyses of variance by simulating character evolution on the phylogeny to establish a null distribution of F-statistics, with which to compare observed ANOVA values. Using this method, we find that an F-statistic as great as that seen in the real data is rarely achieved in the simulations for any of the variables; we thus conclude that statistical differences exist among the ecomorphs for these variables. We assumed two modes of character evolution: (1) the **speciational model** (*sensu* Garland et al. 1993) assumes that the amount of character change along each branch is drawn from the same distribution; (2) the **gradual model** assumes that the expected amount of change along on a branch is proportional to the length of that branch in time. To calculate branch lengths, we fitted the DNA data to a molecular clock model (T. Jackman et al., unpubl. data).

²Probabilities from ordinary, phylogenetically unstructured ANOVA.

Table 19.4. Analyses of covariation in run frequency and hindlimb length with perch height and diameter, using the method of independent contrasts (Felsenstein 1985b; Garland et al. 1992). Phylogenies for each analysis were generated from Figure 19.5 by deleting taxa for which data were unavailable. Each analysis was performed twice, using speciation and gradual models of evolutionary change (see Table 19.3). Contrast standardization was investigated using the method of Garland et al. (1993); all contrasts were found to be appropriately standardized. All regressions were conducted through the origin (Garland et al. 1992).

Dependent variable	Independent variable(s)	r ²	F	d.f. ¹	P
Gradual model:					
Run frequency	Hindlimb length	0.48	12.80	1,14	0.003
Hindlimb length	Perch diameter	0.12	4.16	1,30	0.050
Hindlimb length	Perch height	0.13	4.41	1,30	0.044
Hindlimb length ²	Perch diameter, height	0.27	6.03	2,29	0.006
Speciation model:					
Run frequency	Hindlimb length	0.52	15.13	1,14	0.002
Hindlimb length	Perch diameter	0.14	4.81	1,30	0.036
Hindlimb length	Perch height	0.19	7.09	1,30	0.012
Hindlimb length ²	Perch diameter, height	0.34	8.20	2,29	0.002

¹Degrees of freedom differ because ecological data are available for more species than are locomotor behavior data. In the ecological analyses, data for *A. porcatius* were substituted for those from *A. carolinensis* and data for *A. guazuma* were substituted for *A. paternus*. In the locomotor behavior analyses, substitutions were *A. cybotes* for *A. marcanoi* and *A. chlorocyanus* for *A. coelestinus*. Because these species pairs are closely related and belong to the same ecomorph class, substitution of these species in the phylogenies used in the statistical analyses is appropriate. Data from Losos (1990a, 1992, unpubl. data) and Irschick and Losos (1996).

²In the multiple regressions, the significance values for the independent variables in the gradual and speciation analyses, respectively, are: 0.013 and 0.003 for perch height, and 0.014 and 0.009 for perch diameter.

without leading to adaptive radiation, as when members of a lineage interact with the environment in a new manner, but the lineage does not diversify. In the case of anoles, toepads may constitute a key innovation linked to adaptive radiation. The toepads of anoles allow them to use a variety of arboreal niches in a manner not possible in ancestral arboreal lizards lacking pads.

A concept often confounded with key innovation is the idea that some characters may promote speciation or retard extinction and thus be responsible for the species richness (or poverty) of a clade (see discussion in Heard and Hauser [1994] and references therein). With more than 300 described species, the anoline clade is large relative to its sister taxon *Polychrus* and to most other recognized lizard clades. Exceptions include a number of clades (e.g., Gekkonidae, Scincidae) that appear to be considerably older; this latter statement must be evaluated cautiously at present, however, because we lack phylogenetic and temporal information on many of the most relevant clades, particularly within the Iguania. One might ask whether the evolution of any particular character is responsible for the striking species richness of anoles.

The dewlap, an extensible fold of skin located on the throat, also characterizes the clade containing anoles plus *Polychrus* (see Plate 4, Figure 19.8). Male anoles (and

females of some species) display their dewlaps in many contexts, including aggression, courtship, and predator deterrence (Leal and Rodríguez-Robles 1997). Species differ in the size, color, and patterning of their dewlaps (see Williams and Rand 1977). Observations (Rand and Williams 1970; Echelle et al. 1971; Williams and Rand 1977) and experiments (Losos 1985) suggest that attributes of the dewlap are important in species recognition. Consequently, factors that promote evolutionary change in dewlap appearance could have the incidental effect of causing populations to speciate (cf. Endler 1992; Marchetti 1993). One such possibility is that, when anoline populations occupy new habitats, they may experience different light environments (Fleishman 1992). Because some colors are seen more effectively than others in particular situations (e.g., open sun, deep shade [Endler 1993]), selection might favor evolutionary change in dewlap color in the new habitat; this change, in turn, might lead to reproductive isolation from the parental species. In this way, the evolution of the dewlap may have led to increased rates of speciation and thus be responsible, at least in part, for the great species richness of this clade.

We conclude that ecological differentiation and accelerated rates of speciation in anoles are likely to have their causal bases in different characters. Expanded toepads – while permitting evolution of arboreality – seem unlikely to accelerate rates of speciation, unless partitioning of arboreal habitats per se explains the high rates of anoline speciation (Rice and Hostert [1993] summarize experimental evidence that habitat differentiation can lead to higher rates of speciation). Likewise, dewlaps appear causally associated with speciation but are not required for the invasion of arboreal habitats – unless they provide a system of communication essential in arboreal environments. Further investigations may reveal that evolutionary interactions between toepads and dewlap underlie both the ecological disparity and taxonomic diversity of anoles.

Evolution of community structure

The presence of four of the six ecomorph classes on all four of the Greater Antilles could be explained in many ways: (1) they might each have arisen once and then dispersed to the other islands; (2) they might each have arisen independently on each island; or (3) they might have had a complex history, involving different numbers of independent origins and subsequent dispersal events in each case.

In agreement with previous studies, our DNA data clearly contradict the first hypothesis. Rather, each ecomorph class has evolved independently on each island (Figure 19.7). Indeed, with the exception of the crown-giants of Hispaniola (*A. barahonae*) and Puerto Rico (*A. cuvieri*), and the twig anoles of Cuba and Hispaniola, no members of the same ecomorph on different islands are even closely related. The Templeton test indicates that the most parsimonious tree (Figure 19.5) is significantly shorter than the shortest tree in which each of the ecomorph classes is monophyletic (Table 19.2). Although it is possible that one ecomorph may be the ancestral type from which the others evolved multiple times, anoline radiations clearly occurred independently on each island of the Greater Antilles.

Given that the ecomorphs have evolved mostly independently on each island, one might then ask whether the sequence of ecomorph evolution has been the same on all four islands. Previous phylogenies for the anoles of Jamaica and Puerto Rico have been used to reconstruct the evolution of ecomorphs based on parsimony reconstructions of morphological evolution (Losos 1992). Use of parsimony assumes that rates of evolution have not been so high that parallelism or reversal for ecomorphological characteristics would occur extensively within individual islands (Larson and Losos 1996).

The historical trajectory of ecomorphological evolution appears to have been remarkably similar on Jamaica and Puerto Rico (Figure 19.9). On both islands, the two-ecomorph stage contained a twig anole and a generalist (a morphological intermediate not corresponding to any of the extant ecomorphological classes). At the three-ecomorph stage, both islands had a crown-giant and a twig anole; in addition, Puerto Rico had a trunk-crown anole, whereas Jamaica had a species living in the crown, but not clearly identifiable as either a crown-giant or a trunk-crown anole. At the four-ecomorph stage, the islands were again identical. Finally, the fifth ecomorph to evolve on Puerto Rico was the grass-bush anole, the one that is absent from Jamaica.

Three shortcomings with this earlier study must be noted. First, the Jamaican phylogeny (Hedges and Burnell 1990) was constructed using methods whose assumptions may be violated by the data (Irschick et al., unpubl. data). Second, the Puerto Rican phylogeny was an amalgamation of several studies that used osteological, karyotypic, allozymic, and immunological data (Losos 1990a). Because different taxa were included and data were of different types (discrete characters, distances), the various data could not be combined explicitly to produce the phylogeny. Although several of the relationships in Figure 19.5 do not agree with the phylogenetic hypotheses previously used to reconstruct ecomorph evolution, these relationships should be considered tentative until more species are added.

Third, the anoles on Puerto Rico, rather than representing a monophyletic radiation like those on Jamaica (except the recent colonist *A. sagrei*), consist of three clades: *A. cuvieri*, *A. occultus*, and the members of the *A. cristatellus* species group. Due to lack of information on phylogeny of the entire genus, the Puerto Rican anoles were treated as monophyletic, with the proviso that future information might alter our understanding; an alternative possibility is that one of these clades had evolved its particular ecomorph prior to arriving in Puerto Rico. Examination of the DNA phylogeny (Figure 19.5) fails to resolve this question. None of the twig anoles is closely related to *A. occultus*; hence, the *A. occultus* lineage most likely evolved into a twig anole independently. The hypothesis that the twig ecomorph represents the ancestral condition among anoles is non-parsimonious. By contrast, the *A. cuvieri* clade is closely related (but not the sister taxon) to the Hispaniolan crown-giants; consequently, the ancestor of *A. cuvieri*, which may not have occurred on Puerto Rico, may have already become a crown-giant by the time it existed independently on Puerto Rico. Hence, although the two- and three-species stages in the Jamaican and Puerto Rican radiations may have been very similar in ecomorph composition (assuming that the phylogenies used in these analyses withstand further examination), we cannot eliminate the possibility that some of the ecomorphs evolved prior to occurrence on Puerto Rico.

Interpretation of the sequence of ecomorph evolution on Cuba and Hispaniola is hindered because it is difficult to determine which lineages specialized *in situ* and which were already specialized by the time they first occupied their present islands. Nonetheless, inspection of the DNA phylogeny (Figure 19.6) suggests that Cuba and Hispaniola may not have followed the same sequence of ecomorph evolution as that suggested for the other two islands. In particular, the oldest clades (as determined both by topological position of the clade in the phylogenetic tree and by estimated time of divergence based on number of DNA changes on each branch [T. Jackman et al., unpubl.

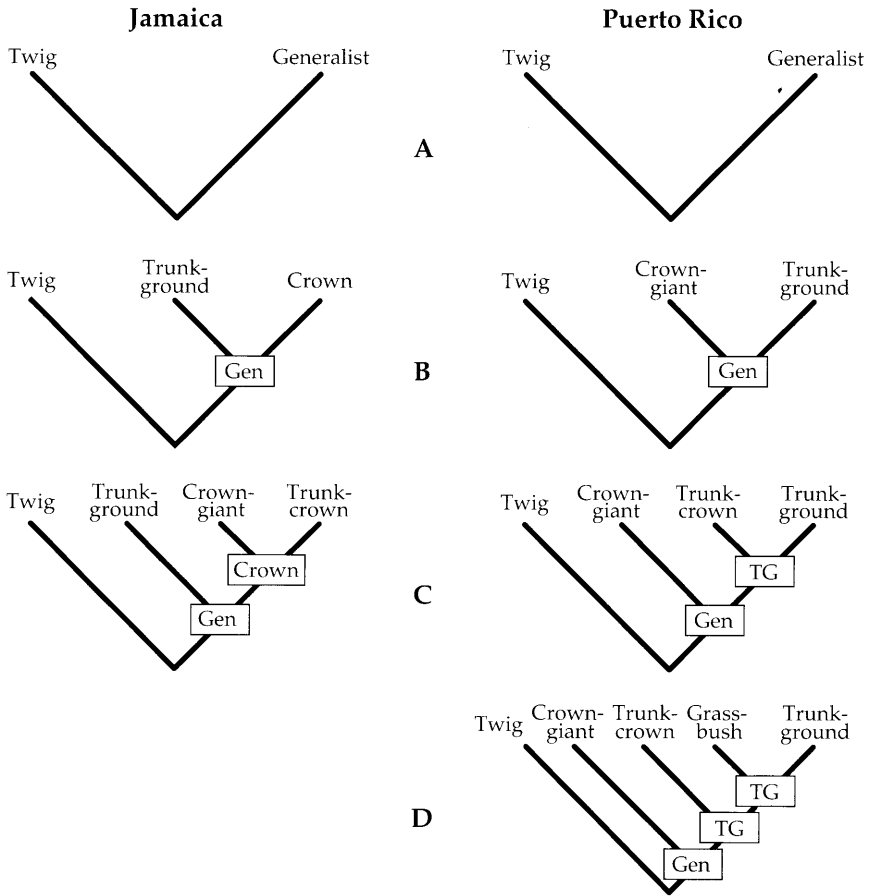


Figure 19.9. Reconstruction of ecomorph evolution on Jamaica and Puerto Rico at the (a) two-, (b) three-, (c) four-, and (d) five-ecomorph stages. Ancestral states were estimated by reconstructing ancestral values for scores on principal components axes (see Figure 19.4). Once the value of PCA axes 1-4 had been estimated, the positions of ancestors in PCA space were plotted. If an ancestor fell within the boundaries defined by extant members of an ecomorph class, then the species was considered to be a member of that ecomorph class. If the ancestor did not fall within the boundaries of any of the ecomorphs and fell in an intermediate position between the ecomorph spaces, then it was considered a generalist. Randomization analyses indicate that parsimony does not necessarily reconstruct generalists at deep nodes within the tree and that the congruence between the two reconstructions is greater than expected by chance (Losos, 1992). Morphology of basal ancestors was not reconstructed because of lack of firm knowledge of the sister taxa to these radiations. (Figure from Losos [1992] with permission.)

data) do not include twig anoles, which were the first ecomorphs inferred to have evolved on Puerto Rico and Jamaica. However, our analysis omitted one clade of twig anoles from Hispaniola. Hence, this conclusion will need to be re-evaluated when this lineage is included. In addition, grass-bush anoles are relatively early diverging lineages and crown-giants may be relatively late diverging lineages in Hispaniola, contrary to the pattern on Jamaica and Puerto Rico. Consequently, we conclude that available evidence rejects the hypothesis that the sequence of ecomorph evolution has been identical on all four islands, even though the evolutionary outcome has been very similar.

Conclusions

Despite more than 30 years of systematic studies of the anoline radiation, much still remains to be resolved. In addition to clarifying phylogenetic relationships within and between the taxa on each of the Greater Antilles, molecular studies will be useful for studying diversification in the little studied continental anolines. Within the Caribbean, more research (both ecological and phylogenetic) needs to be done on the larger islands of Cuba and Hispaniola. Although the relatively modest radiations of Puerto Rico and Jamaica have been well studied, the large number of anoline species and ecological roles on Cuba and Hispaniola require further investigation.

Nonetheless, the combination of systematic, field, and laboratory research makes clear that anoles are a paradigmatic example of adaptive radiation – four times over! Independently on each of the islands of the Greater Antilles, anoles have adaptively diversified to occupy a similar spectrum of disparate ecological roles. Given historical contingencies and ecological differences among islands, one might have expected radiations on the islands to have resulted in striking differences in ecology and morphology of the component species, but this prediction is not realized; rather, the same roles have been filled repeatedly. Further ecological research should investigate why the outcome of anoline radiation is so predictable, in contrast to most other radiations examined. Gould (1989, p. 51) has argued that historical contingency plays such an important role in evolutionary diversification that a “replay of the tape [of evolutionary diversification] would lead evolution down a pathway radically different from the road actually taken.” We suggest that, at least for anoles of the Greater Antilles, the tape has been replayed, four times, and the outcome has been substantially the same each time.

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