Evolution, 57(10), 2003, pp. 2383–2397

PHYLOGENETIC ANALYSIS OF ECOLOGICAL AND MORPHOLOGICAL DIVERSIFICATION IN HISPANIOLAN TRUNK-GROUND ANOLES (*ANOLIS CYBOTES* GROUP)

RICHARD E. GLOR,[1,2] JASON J. KOLBE,[1,3] ROBERT POWELL,[4,5] ALLAN LARSON,[1,6] AND JONATHAN B. LOSOS[1,7]
[1]*Department of Biology, Campus Box 1137, Washington University, St. Louis, Missouri 63130-4899*
[2]*E-mail: glor@biology.wustl.edu*
[3]*E-mail: kolbe@biology.wustl.edu*
[4]*Department of Biology, Avila University, 11901 Wornall Road, Kansas City, Missouri 64145-1698*
[5]*E-mail: powellr@mail.avila.edu*
[6]*E-mail: larson@wustlb.wustl.edu*
[7]*E-mail: losos@biology.wustl.edu*

Abstract.—*Anolis* lizards in the Greater Antilles partition the structural microhabitats available at a given site into four to six distinct categories. Most microhabitat specialists, or ecomorphs, have evolved only once on each island, yet closely related species of the same ecomorph occur in different geographic macrohabitats across the island. The extent to which closely related species of the same ecomorph have diverged to adapt to different geographic macrohabitats is largely undocumented. On the island of Hispaniola, members of the *Anolis cybotes* species group belong to the trunk-ground ecomorph category. Despite evolutionary stability of their trunk-ground microhabitat, populations of the *A. cybotes* group have undergone an evolutionary radiation associated with geographically distinct macrohabitats. A combined phylogeographic and morphometric study of this group reveals a strong association between macrohabitat type and morphology independent of phylogeny. This association results from long-term morphological evolutionary stasis in populations associated with mesic-forest environments (*A. c. cybotes* and *A. marcanoi*) and predictable morphometric changes associated with entry into new macrohabitat types (i.e., xeric forests, high-altitude pine forest, rock outcrops). Phylogeographic analysis of 73 new mitochondrial DNA sequences (1921 aligned sites) sampled from 68 geographic populations representing 12 recognized species and subspecies diagnoses 16 allopatric or parapatric groupings of populations differing from each other by 5–18% sequence divergence. At least some of these groupings appear to have attained species-level divergence from others. Evolutionary specialization to different macrohabitat types may be a major factor in the evolutionary diversification of Greater Antillean anoles.

Key words.—Adaptive radiation, *Anolis*, comparative analysis, diversification, morphometrics.

Received June 18, 2002. Accepted May 16, 2003.

Variation in habitat use and morphology may be strongly correlated among populations independent of their phylogenetic relatedness (Harvey and Pagel 1991; Wainwright and Reilly 1994), which suggests an important role for natural selection. Directional selection may produce independent evolution of similar morphological features in lineages that enter similar habitats (i.e., convergence or parallelism), whereas stabilizing selection may produce long-term morphological stability (i.e., stasis) in lineages that maintain a particular habitat type (Schluter 2000; Levinton 2001). For example, independent evolutionary entry into benthic environments has produced similar adaptations in different lineages of stickleback fishes (Schluter and McPhail 1993), whereas Australian rainforest lizards that occupy evolutionarily stable habitats are remarkably similar morphologically despite millions of years of phylogenetic separation (Schneider and Moritz 1999; Schneider et al. 1999; Smith et al. 2001).

The evolutionary radiation of Greater Antillean *Anolis* lizards exhibits a strong evolutionary association between morphology and microhabitat use (Williams 1983; Losos 1990). This relationship results from repeated evolution of anole communities that regularly include four or more species of microhabitat specialists, termed ecomorphs, whose morphological and behavioral differences are functionally related to microhabitat use. For example, microhabitat specialists that use broad surfaces have long legs that permit rapid movement on tree trunks and the ground, whereas species that use narrow surfaces have short legs and move more slowly. Similarly, species that live high in the canopy tend to have large toe pads that provide enhanced clinging ability, whereas species living near the ground have poorly developed pads. Similar sets of microhabitat specialists have evolved independently on each Greater Antillean island (Williams 1983; Mayer 1989; Losos et al. 1998). Molecular phylogenetic studies and fossil anoles preserved in amber suggest that microhabitat specialization is ancient, in most cases having evolved more than 15 million years ago (de Queiroz et al. 1998; Jackman et al. 1999).

A less studied dimension of the Caribbean anole radiation involves more recent speciation and morphological diversification within ecomorph categories. Most anole speciation in the Greater Antilles has occurred within ecomorphs (Losos 1996); on Cuba, for example, a single clade of grass/bush anoles includes 14 recognized species (Burnell and Hedges 1990; Schwartz and Henderson 1991). More generally, 108 species belong to a recognized ecomorph category, but only 17 evolutionary transitions among these categories are needed to explain this diversity (Losos et al. 1998).

Despite stasis in ecomorphological features associated with microhabitat partitioning, closely related species within an ecomorph category often live in distinct macrohabitat types and may be expected to differ in associated phenotypic characters (we use ''microhabitat'' to denote use of different

TABLE 1. Taxonomic status, macrohabitat, and geographic range of taxa in the *Anolis cybotes* group included in this study. Taxonomy follows Schwartz and Henderson (1991). *Anolis whitemani* ssp. represents a population included in the original description of *A. whitemani* that remained subspecifically unassigned due to a lack of material when subspecies were described (Schwartz 1980). Categories of macrohabitat are defined on the basis of previous studies (Williams 1963, 1975; Schwartz 1979, 1980, 1989; Schwartz and Henderson 1982, 1991; Powell and Carr 1990; Lenart et al. 1994). The ecology of *A. haetianus* populations endemic to the Tiburon Peninsula is not well known. *Anolis haetianus* is included only in the phylogeographic analysis, whereas *A. w. lapidosus* is included only in the morphometric analysis due to absence of available samples.

Taxon	Habitat	Geographic range
A. c. cybotes	mesic to semixeric forests	Hispaniola, islandwide
A. c. ravifaux	small offshore islands: semixeric, rock outcrops	Isla Soana and Isla Catalina off the southeastern coast of the Dominican Republic
A. marcanoi	mesic to semixeric forests	south-central Dominican Republic
A. w. whitemani	xeric scrub forests and semideserts	central Hispaniola
A. w. breslini	xeric scrub forests and semideserts	northwestern Haiti
A. w. lapidosus	xeric scrub forests and semideserts	western Haiti
A. w. ssp.	xeric scrub forests and semideserts	northwestern Dominican Republic
A. longitibialis	rock outcrops	southern Barahona Peninsula and Isla Beata
A. strahmi	rock outcrops	northern and southern slopes of the Sierra de Baoruco
A. armouri	upland pine forests	Sierra de Baoruco
A. shrevei	upland pine forests	Cordillera Central
A. haetianus	mesic forests?	extreme western Tiburon Peninsula

structural niches at a given location and ''macrohabitat'' to denote geographic variation in vegetation, topography, and climatic features). For example, a species that uses the trunk-ground microhabitat may inhabit mesic forest, whereas a closely related species may use trunk-ground microhabitats in more xeric areas. Divergence in morphological features related to geographically variable macrohabitats may represent an important and distinct dimension of the Caribbean anole radiation.

Focusing on the *Anolis cybotes* group from Hispaniola, we present the first detailed analysis of morphological diversification within a clade retaining a single ecomorph type. This group includes eight species of trunk-ground anoles occupying five geographically distinct kinds of macrohabitat (Table 1). We present a phylogenetic analysis of mitochondrial DNA (mtDNA) haplotypes within and between species in the *A. cybotes* group to reconstruct the evolutionary history of the group and to identify deeply divergent haplotype clades that may diagnose evolutionary lineages. Multivariate morphometric analyses of ecologically important characters are then used to quantify the morphometric distinctness among and cohesiveness within different lineages and macrohabitat categories. These data together permit a phylogenetic analysis of ecological factors and evolutionary processes important to explaining a largely unexplored dimension of anole diversity.

MATERIALS AND METHODS

Study System

The *A. cybotes* group contains eight species endemic to Hispaniola and several smaller offshore islands (Schwartz 1989; Schwartz and Henderson 1991). Members of this group display five discrete categories of macrohabitat type (Table 1). The nominate form (*A. cybotes*) occupies the widest range of macrohabitats, from mesic to semixeric forests and occurs across Hispaniola (Fig. 1). This widespread species contains three subspecies, one on mainland Hispaniola (*A. c. cybotes*) and two from smaller offshore islands (*A. c. doris* from Île de la Gonâve and *A. c. ravifaux* from Islas Saona and Catalina). One of the island subspecies (*A. c. ravifaux*) is ecologically distinct from mainland populations, occupying semixeric scrub forests, often with exposed rock outcrops (Schwartz and Henderson 1982). This macrohabitat type is similar to that occupied by *A. longitibialis* and *A. strahmi*, but because the ecology of this species is poorly known, we conservatively consider it a distinct macrohabitat type. The seven remaining species are surrounded geographically by *A. c. cybotes* (Table 1, Fig. 1).

Anolis marcanoi is difficult to distinguish morphologically and ecologically from *A. cybotes* and is restricted to a small area in the south-central Dominican Republic; it is considered a genetically distinct sibling species to *A. cybotes* (Webster 1975; Williams 1975; Hertz 1980; Losos 1985; Schwartz 1989). Two species, *A. longitibialis* and *A. strahmi*, occupy macrohabitats consisting primarily of rock-outcrops and cliffs on the Barahona Peninsula. *Anolis armouri* and *A. shrevei* occupy high-altitude pine forests in the Sierra de Baoruco and Cordillera Central, respectively. *Anolis whitemani* comprises four disjunct populations whose distribution coincides almost perfectly with the distribution of xeric scrub forests and semideserts on Hispaniola. *Anolis haetianus* is a poorly known species from the extreme western tip of the Tiburon Peninsula in Haiti.

Phylogenetic Analyses

We extracted and amplified mtDNA as described by Jackman et al. (1999). Initially, we ran reactions with the Promega (Madison, WI) fmol DNA sequencing system as described by Macey et al. (2000). Additional reactions were run with Big-Dye Terminator Ready-Reaction Kits (Perkin-Elmer, Wellesley, MA) on an ABI (tm) 373A (PE Applied Biosystems, Inc., Foster City, CA). We sequenced approximately 1900 bp of mtDNA, including complete sequence for genes encoding ND2, $tRNA^{Met}$, $tRNA^{Ile}$, $tRNA^{Trp}$, $tRNA^{Ala}$,

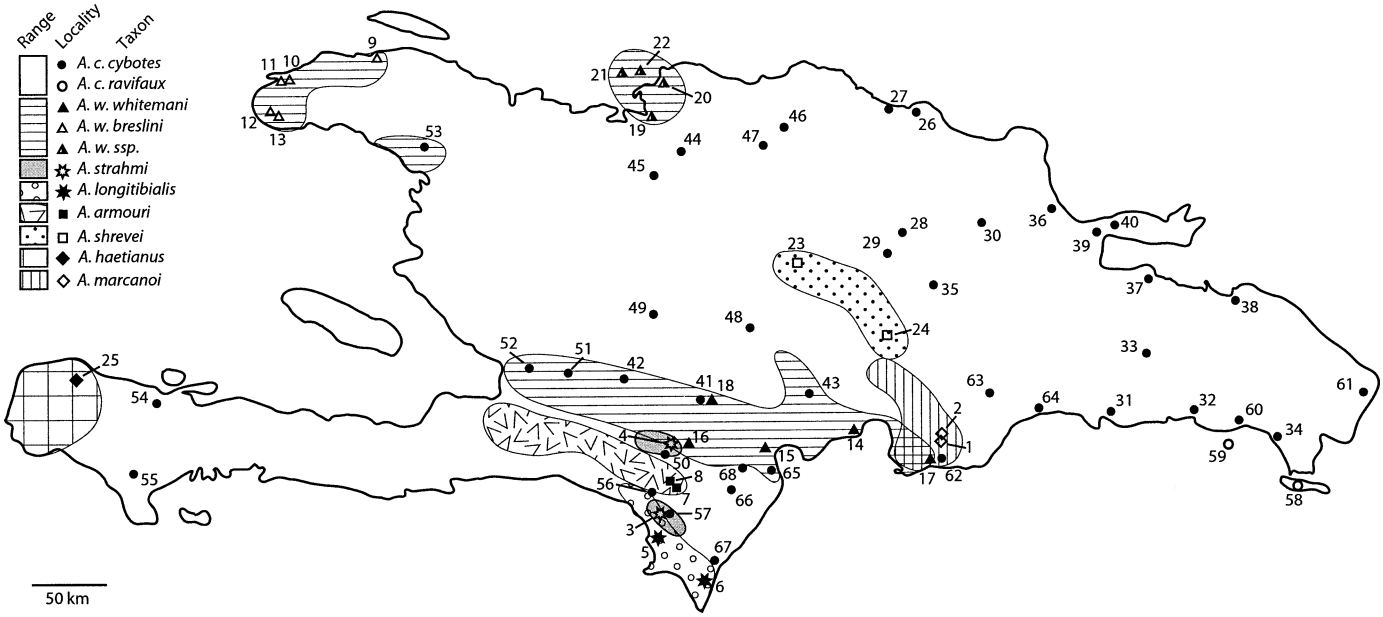

FIG. 1. Geographic ranges of cybotoid anoles based on maps of Schwartz and Henderson (1991) and sampling localities for populations included in our phylogenetic study. *Anolis cybotes cybotes* exists everywhere except high altitudes (above 1650 m) and extremely xeric regions in western Haiti and the southern Barahona Peninsula.

$tRNA^{Asn}$, $tRNA^{Cys}$, $tRNA^{Tyr}$, the origin of light-strand replication, and a portion of ND1 and COI. Sequences were obtained with primers L3878, L4221, L4437, L4882a, L5550, L5556b, H4419, H4980, H5617a, and H5934 (Macey et al. 1997, 1998, 2000). Sequences were aligned manually using structural models for tRNA genes (Kumazawa and Nishida 1993; Macey et al. 1997).

Anolis cristatellus and *A. distichus* were used as outgroups (Jackman et al. 1999). We obtained sequences for all eight species in the *A. cybotes* group and, with the exception of *A. haetianus*, we sampled at least two individuals from each named taxon. Additional haplotypes were sequenced for two widespread species (*A. cybotes* and *A. whitemani*). Within *A. whitemani*, we examined one or two individuals from 13 localities, including five localities for *A. w. whitemani*, four for *A. w. breslini*, and four for a subspecifically unassigned population in the northwestern Dominican Republic (Schwartz 1980; Powell and Carr 1990; Schwartz and Henderson 1991; Burns et al. 1992; Fig. 1). For *A. cybotes*, we sampled 36 individuals of *A. c. cybotes* from 35 localities across Hispaniola and two individuals of *A. c. ravifaux* from Isla Saona and Isla Catalina (Schwartz and Henderson 1982; Fig. 1). Samples from *A. c. doris* were not available. To assess genetic variation within local populations, we sequenced the genes encoding ND2, $tRNA^{Trp}$, and $tRNA^{Ala}$ (~1000 bp) in three or four additional individuals for 16 populations of *A. c. cybotes* (populations 27, 28, 30, 31, 33, 35, 37, 38, 40, 43, 46, 48, 49, 60, 61, and 64) and one population of *A. whitemani* ssp. (population 22), *A. armouri* (population 7), and *A. shrevei* (population 24). See Appendix 1 for a list of specimens included in the molecular study.

Phylogenetic trees were reconstructed using both maximum parsimony and Bayesian criteria. PAUP* 4.0b10 (Swofford 2002) was used to generate phylogenetic trees under maximum parsimony using 100 heuristic searches with random addition of sequences; starting trees for TBR branch swapping were obtained using stepwise addition. Decay indices (branch support of Bremer 1994), and 1000 bootstrapped replicates with 25 random additions per replicate were used to assess support for individual nodes. Decay indices were calculated in PAUP* using constraint trees generated in MacClade 4 (Maddison and Maddison 2000). Trees were generated under Bayesian criteria using MrBayes 2.01 (Huelsenbeck and Ronquist 2001), running four chains for 1×10^6 generations. We used Modeltest 3.0 (Posada and Crandall 1998), which conducts a series of hierarchical likelihood-ratio tests to compare alternative models of evolution, to select maximum-likelihood parameters for Bayesian analysis. Base-change ratios and the gamma shape parameter were estimated with maximum likelihood from a neighbor-joining tree. Posterior-probability values were used as measures of support for the Bayesian topology. Monophyly of each named taxon and habitat-type category was also tested using the Templeton test (Templeton 1983) as implemented by PAUP*; analogous likelihood-based tests were not computationally feasible. Although assumptions of the Templeton test have been questioned (Goldman et al. 2000), it is generally a conservative criterion of branch support (Lee 2000; Melville et al. 2001; Townsend and Larson 2002) and appears more conservative than an alternative test recommended to replace it (Buckley 2002).

Haplotype trees were superimposed on a map of sampled populations to identify contiguous geographic areas within which mitochondrial haplotypes coalesce to form strongly supported clades. Groups of populations identified in this manner were used to diagnose genetically differentiated populations tentatively interpreted as separate evolutionary lineages. Mean distances between major haplotype clades were

TABLE 2. Pairwise haplotype sequence divergences within and between 16 population lineages identified by our phylogeographic analysis (see Figs. 2, 3, 5). Tamura-Nei corrected distances are above the diagonal, and uncorrected fractions of sites differing between aligned sequences are below the diagonal. Values in bold on the diagonal are mean Tamura-Nei corrected distances among haplotypes within inferred population lineages.

	Out-groups	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
Outgroups	**0.24**	0.28	0.26	0.27	0.27	0.27	0.27	0.28	0.29	0.28	0.28	0.27	0.28	0.28	0.28	0.27	0.28
A	0.23	**0.03**	0.22	0.23	0.22	0.21	0.21	0.22	0.22	0.22	0.22	0.22	0.21	0.22	0.22	0.20	0.23
B	0.21	0.18	**0.02**	0.13	0.18	0.17	0.17	0.18	0.18	0.17	0.17	0.17	0.16	0.17	0.17	0.17	0.17
C	0.22	0.19	0.12	**0.00**	0.19	0.17	0.18	0.19	0.19	0.19	0.19	0.18	0.18	0.18	0.19	0.18	0.18
D	0.22	0.19	0.16	0.16	**0.01**	0.10	0.14	0.11	0.11	0.11	0.11	0.13	0.11	0.13	0.13	0.15	0.18
E	0.22	0.18	0.14	0.15	0.09	**0.04**	0.13	0.12	0.12	0.11	0.12	0.12	0.10	0.11	0.13	0.13	0.16
F	0.22	0.18	0.15	0.16	0.12	0.12	**0.03**	0.14	0.14	0.14	0.14	0.12	0.13	0.11	0.13	0.14	0.18
G	0.23	0.19	0.15	0.16	0.10	0.11	0.12	**0.03**	0.05	0.06	0.08	0.13	0.12	0.13	0.14	0.14	0.18
H	0.23	0.18	0.15	0.16	0.10	0.11	0.12	0.05	**0.02**	0.06	0.07	0.13	0.13	0.13	0.14	0.14	0.17
I	0.23	0.19	0.15	0.16	0.10	0.10	0.12	0.06	0.06	**0.04**	0.08	0.12	0.12	0.13	0.13	0.14	0.17
J	0.23	0.19	0.15	0.16	0.10	0.11	0.12	0.07	0.07	0.07	**0.05**	0.13	0.12	0.13	0.14	0.15	0.18
K	0.22	0.19	0.15	0.16	0.12	0.11	0.11	0.12	0.11	0.11	0.12	**0.05**	0.12	0.12	0.14	0.14	0.16
L	0.23	0.18	0.14	0.15	0.10	0.09	0.12	0.11	0.11	0.11	0.11	0.11	**0.01**	0.12	0.13	0.12	0.15
M	0.23	0.19	0.15	0.16	0.12	0.10	0.10	0.11	0.11	0.12	0.12	0.11	0.11	**0.06**	0.13	0.13	0.17
N	0.23	0.19	0.15	0.16	0.11	0.11	0.12	0.12	0.12	0.12	0.12	0.12	0.11	0.12	**0.06**	0.13	0.17
O	0.22	0.17	0.15	0.15	0.13	0.12	0.12	0.13	0.13	0.13	0.13	0.12	0.11	0.12	0.12	**0.02**	0.16
P	0.23	0.20	0.15	0.16	0.15	0.14	0.15	0.15	0.15	0.15	0.15	0.14	0.13	0.15	0.14	0.14	**0.03**

calculated by MEGA 2.0 (Kumar et al. 2001) using both uncorrected distances and distances corrected for superimposed substitutions using the distance measure of Tamura and Nei (1993). Molecular estimates of divergence time were based on an expected evolutionary rate of 0.65% divergence per lineage per million years based on estimates from homologous sequences of other iguanian lizards (Macey et al. 1998) using Tamura-Nei corrected sequence divergences (Tamura and Nei 1993).

Morphometric Analyses

We quantified 12 morphological variables in 13 populations representing seven of the eight species in the *A. cybotes* group (not enough specimens of *A. haetianus* were available) and populations representing four deeply divergent mtDNA haplotype clades in each of the two widespread species (*A. cybotes* and *A. whitemani*; Table 2; Figs. 2, 3). Morphological variables were selected to cover a wide range of features, many of which have been used in earlier studies of anole ecological morphology (e.g., Losos 1990; Beuttell and Losos 1999) and/or have recognized adaptive significance (Losos 1990; Irschick et al. 1996; Irschick and Losos 1998, 1999). External measurements on museum specimens taken using a ruler and calipers included: snout-vent length (SVL) to the nearest 0.5 mm from the tip of the snout to the anterior end of the cloaca, head length from the tip of the snout to the anterior edge of the ear opening, head width at the widest point on the head, and head height just posterior to the eyes. MorphoSys (Meacham and Duncan 1990), a computer-driven imaging system, was used to measure the following skeletal elements from radiographs: humerus, ulna, femur, tibia, first and second phalanges on the fourth toe of the hindfoot, and pelvic width, measured as the widest point across the pelvis. Lamellae on the second and third phalanges of the fourth toe of the hind limb were counted using a monocular lens (Glossip and Losos 1997). All measurements were made twice on each individual and the mean was used for analyses. Limb measurements were taken on the right side of the animal unless bones were broken or abnormal. All variables were ln-transformed prior to statistical analyses. We removed effects of body size on all variables by calculating the residual value of each variable regressed against SVL. These residuals and ln-SVL were entered into a principal components analysis (PCA) using a correlation matrix to reduce the dimensionality of the data; see Beuttell and Losos (1999) for discussion of various approaches to removing effects of size.

Comparative Analyses

Comparative analyses were used to examine the relationships among phylogeny, habitat use, and morphology. In general, comparative analyses must correct for nonindependence of species due to shared phylogenetic history (Felsenstein 1985). However, because phylogenetically corrected analyses may be overly conservative when phylogenetic effects are absent or weak (Abouheif 1999; Losos 1999), we began by testing for significant phylogenetic effects on observed morphometric variation. First, a Mantel test was used to compare matrices of pairwise patristic and morphometric distances. Patristic distances, or phylogenetic path lengths, were calculated from a tree derived by transforming branch lengths on the Bayesian phylogeny with nonparametric rate smoothing, which relaxes the assumption of a strict molecular clock by allowing rates to vary across branches (Sanderson 1997). Morphometric similarity was quantified by calculating Euclidean distances between all pairs of populations based on PC scores (for this and all subsequent analyses, the mean score of each principal component for each population was used to avoid pseudoreplication). The Mantel test was conducted with 1000 replications using PASSAGE 1.0 (available via http://www.public.asu.edu/~mrosenb/Passage/). We then tested whether phylogenetic effects existed for each morphological variable (PC axis) independently by conducting the test for serial independence of Abouheif (1999). This method uses the C-statistic to test for autocorrelation between

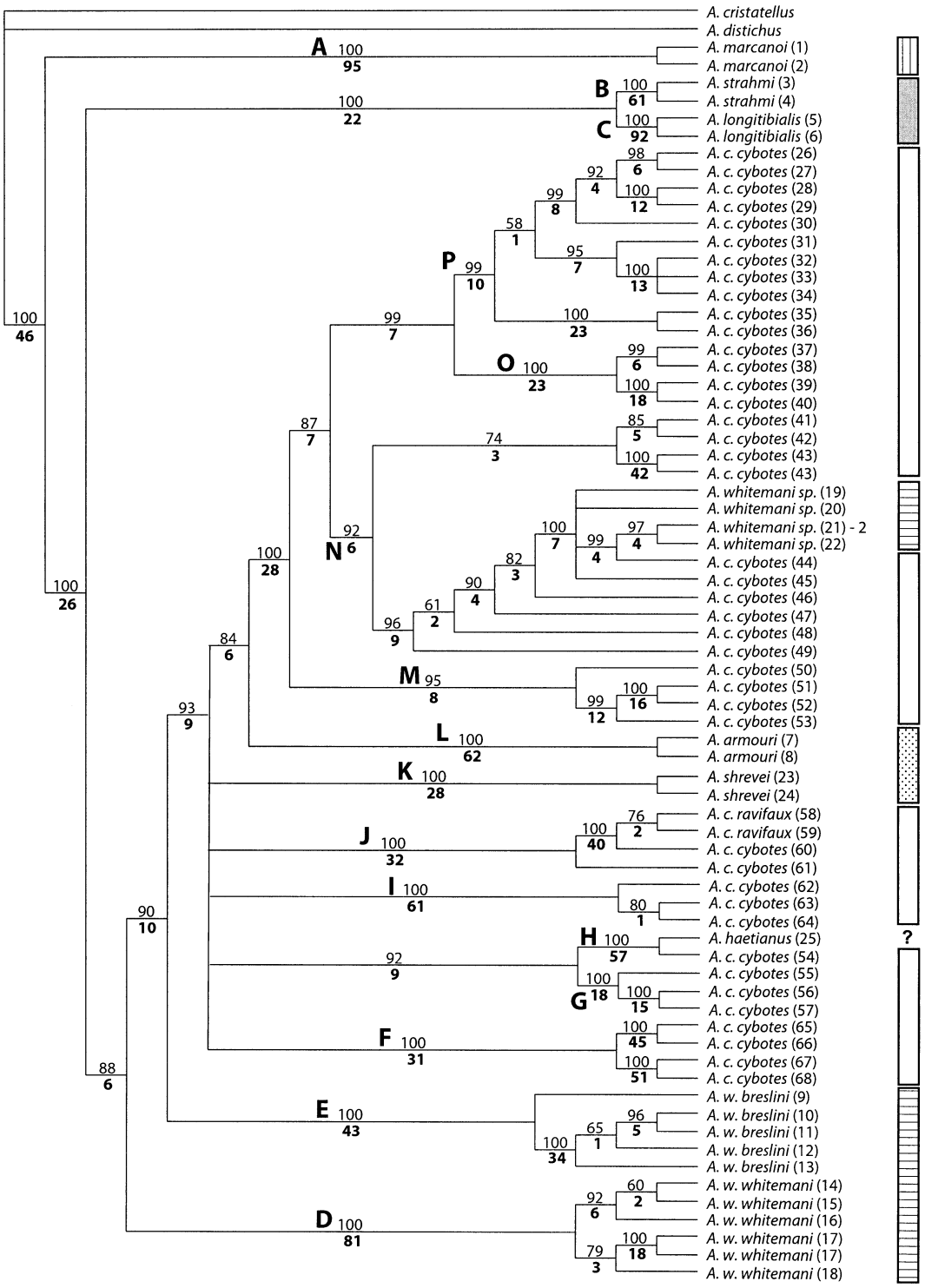

FIG. 2. Strict consensus of 45 equally most parsimonious mitochondrial DNA haplotype trees. Bootstrap values are shown above nodes, and decay indices below. Two haplotypes sampled from *Anolis whitemani* ssp. population 21 were identical. Categories of habitat use are indicated by bars: horizontal lines, xeric forests/semideserts; no fill, mesic/semixeric forest; vertical lines, offshore islands; shading, rock outcrops; stippling, pine forest. Nodes representing diagnosable evolutionary lineages that are concordant with geography are labeled with a letter code: A, *A. marcanoi*; B, *A. strahmi*; C, *A. longitibialis*; D, *A. w. whitemani*; E, *A. w. breslini*; F, Eastern Barahona Peninsula (*A. c. cybotes*); G, southern Tiburon Peninsula and western Barahona Peninsula (*A. c. cybotes*); H, northwestern Tiburon Peninsula (*A. haetianus* and *A. c. cybotes*); I, south-central Dominican Republic (*A. c. cybotes*); J, eastern Dominican Republic and offshore islands (*A. c. cybotes* and *A. c. ravifaux*); K, *A. shrevei*; L, *A. armouri*; M, central Haiti and southwest Dominican Republic (*A. c. cybotes*); N, western Dominican Republic (*A. c. cybotes* and *A. whitemani* sp.); O, central Dominican Republic (*A. c. cybotes*); P, northeastern Dominican Republic (*A. c. cybotes*).

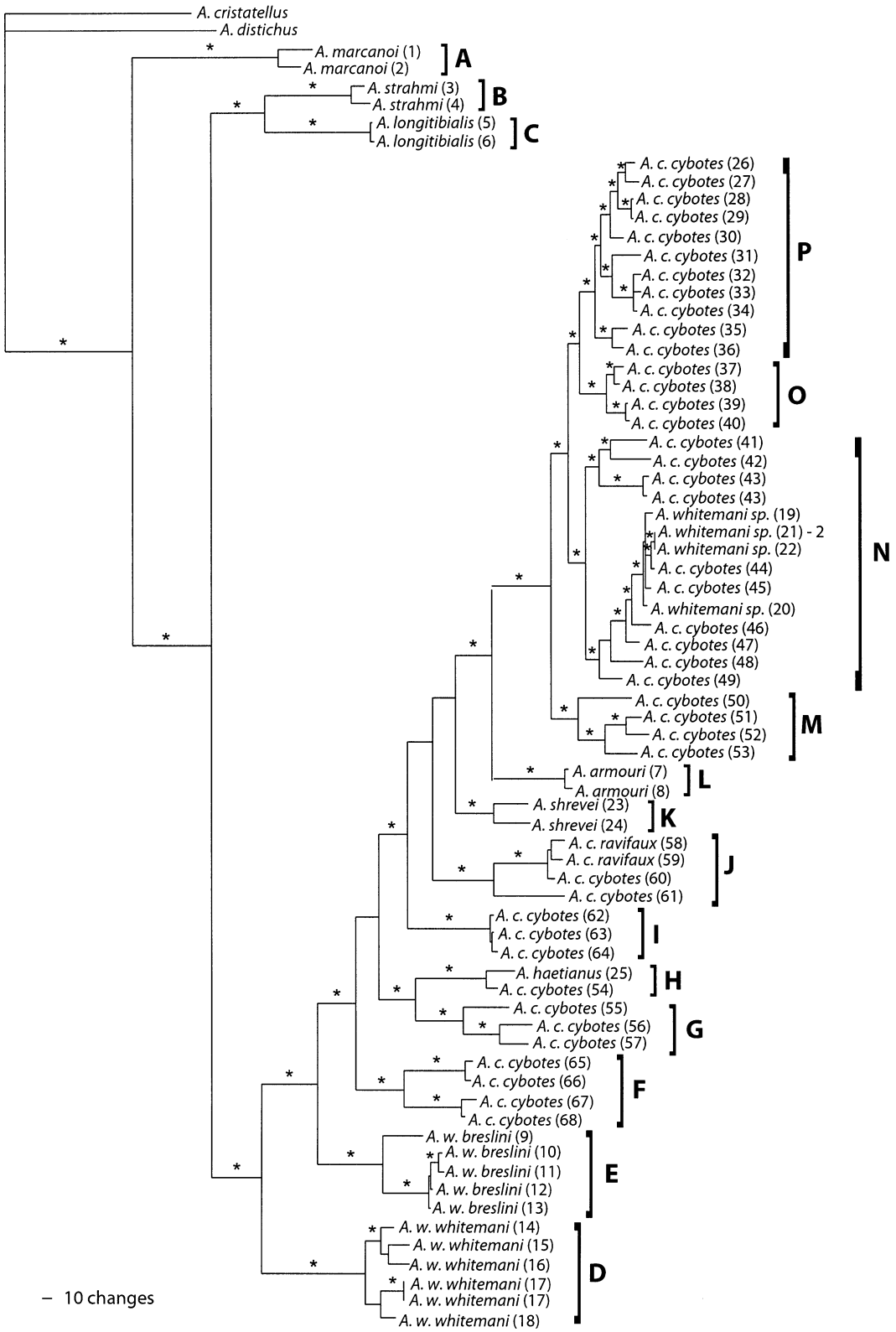

FIG. 3. Bayesian phylogeny of mitochondrial DNA haplotypes. Nodes with an asterisk have posterior probabilities greater than 95%. Branch lengths represent means from 1900 trees sampled (one tree sampled every 500 generations) following the burn-in period of 50,000 generations. Sixteen evolutionary lineages diagnosed by strongly supported and geographically cohesive haplotype clades are denoted A–P (Fig. 2).

adjacent nodes on a fully resolved phylogeny; positive autocorrelation occurs if phylogenetically adjacent observations are similar. Because the order of terminal nodes in any phylogeny is arbitrary (each node can be rotated), randomization analyses were used to reshuffle tip values. The test for serial independence and associated randomization testing were conducted with the program Phylogenetic Independence by J. Reeve and E. Abouheif (available via http://life.bio.sunysb.edu/ee/ehab).

Phylogenetic analyses of variance were used to test the hypothesis that populations in different macrohabitat types differ morphologically (Garland et al. 1993; Losos and Chu 1998). For these analyses, we first simulated morphometric evolution under a Brownian model along the ultrametrically transformed Bayesian phylogeny. The Brownian model is a standard one for evolution of continuous variables and is often robust to violations of its assumptions (Díaz-Uriarte and Garland 1996). Simulations were conducted in the PDSIMUL module of PDAP (Garland et al. 1993), resulting in 1000 sets of simulated tip values for each morphological variable (PC axis). We then grouped populations into five defined categories of habitat use and conducted a multivariate analysis of variance (MANOVA) on each simulated dataset. The resulting *F*-values were compared to the *F*-value calculated from the original dataset. If fewer than 5% of the simulated datasets yielded an *F*-value greater than the original value, we considered the results significant. Given that the MANOVA results were significant, we conducted similar analyses on each morphometric variable independently using univariate analyses of variance (ANOVAs) to identify variables that differed among the habitat categories. We also conducted standard nonphylogenetic MANOVAs and ANOVAs.

Finally, phylogenetic and nonphylogenetic discriminant function analyses (DFA) were used to ask whether the categories of habitat use could be discriminated morphologically. This analysis was conducted using the same simulated data used for ANOVAs, and significance was assessed by comparing the *F*-value derived from the real dataset to *F*-values derived from simulated datasets.

RESULTS

Phylogenetic Analyses

Seventy-three new mitochondrial DNA sequences form a dataset of 1921 aligned sites. Absence of premature stop codons, functional stability of the tRNA genes, and strong bias against guanine in the light strand all suggest that these sequences are authentic mitochondrial DNA (Zhang and Hewitt 1996). A total of 970 characters are variable, of which 811 are parsimony informative. Parsimony analysis produces 45 equally most parsimonious trees of 3817 steps (Fig. 2). ModelTest selects the HKY + I + G model for Bayesian analyses with a transition/transversion ratio of 5.12 and a gamma shape parameter of 0.72. Bayesian analysis produces a well-resolved strict consensus tree with a mean likelihood score of −20444.92 (SD = 9.01), following a burn-in period of 50,000 generations (Fig. 3).

The maximum-parsimony and Bayesian haplotype phylogenies have well-supported topologies and are highly congruent. *Anolis marcanoi* is strongly supported as the sister taxon to a clade containing all other cybotoid anoles (Templeton test: $P < 0.001$). The two rock-dwelling species, *A. longitibialis* and *A. strahmi*, are strongly supported as sister taxa (Templeton test: $P < 0.001$) and together form the sister taxon to a clade containing all other taxa except *A. marcanoi*. Monophyly is strongly rejected for both widespread species, *A. cybotes* and *A. whitemani* (Templeton tests: $P < 0.001$ for both species). Excluding *A. whitemani* haplotypes from the northwestern Dominican Republic, which are deeply nested within *A. cybotes*, the remaining *A. whitemani* haplotypes do not form a monophyletic group, although the hypothesis of monophyly cannot be rejected (Templeton test: $P < 0.20$). Monophyly of *A. c. cybotes* is rejected (Templeton test: $P < 0.001$) based on its phylogenetic position with respect to five other taxa: *A. c. ravifaux*, *A. armouri*, *A. haetianus*, *A. shrevei*, and the northwestern Dominican Republic population of *A. whitemani*. Haplotypes from *A. c. ravifaux*, *A. haetianus*, and *A. whitemani* are each phylogenetically closest to the geographically closest *A. c. cybotes* haplotypes, whereas haplotypes from *A. armouri* group with a clade of haplotypes from *A. cybotes* that occurs across much of northern Hispaniola. The phylogenetic position of *A. shrevei* is not well supported, but its haplotypes appear to form the sister group to the clade containing northern Hispaniolan *A. c. cybotes* + *A. armouri* + northwestern Dominican *A. whitemani* in both maximum-parsimony and Bayesian analyses (Figs. 2, 3). Haplotypes from the two pine-forest species, *A. shrevei* and *A. armouri*, do not form a monophyletic group in either tree, but monophyly of this grouping cannot be rejected (Templeton test: $P < 0.62$).

Phylogeographic analysis of mitochondrial DNA haplotypes identifies 16 well-supported, geographically circumscribed haplotype clades within the *A. cybotes* complex (denoted by letters A–P in Figs. 2, 3, 4). Although additional such clades may be delimited in some cases, our conservative approach focuses on clades that are characterized by a high ratio of within versus between clade genetic divergence: haplotypic divergence among the 16 clades that we have identified averages 0.15, whereas divergence within them is considerably less (mean 0.03). The 16 phylogeographic groupings identified should correspond at least roughly to what might be considered separate species using Cracraft's (1989) phylogenetic species concept and to the lineages diagnosed as the first step of invoking Templeton's (1998) cohesion species concept. However, further sampling and analyses of other independent genetic markers are needed to identify the limits of species-level taxa in this group. For our analyses, haplotype clades A–P are tentatively treated as distinct population-level evolutionary lineages.

Seven lineages correspond to previously diagnosed species or subspecies (A: *A. marcanoi*, B: *A. strahmi*, C: *A. longitibialis*, D: *A. w. whitemani*, E: *A. w. breslini*, K: *A. shrevei*, L: *A. armouri*). Six additional lineages belong to a single subspecies, *A. c. cybotes* (F, G, I, M, O, P). Three lineages (H, J, N) group populations representing more than one previously recognized species or subspecies. Lineage H includes a population attributed to *A. haetianus* and another attributed to *A. c. cybotes*. Lineage J contains two populations attributed to *A. c. cybotes* and two others recognized as *A. c. ravifaux*.

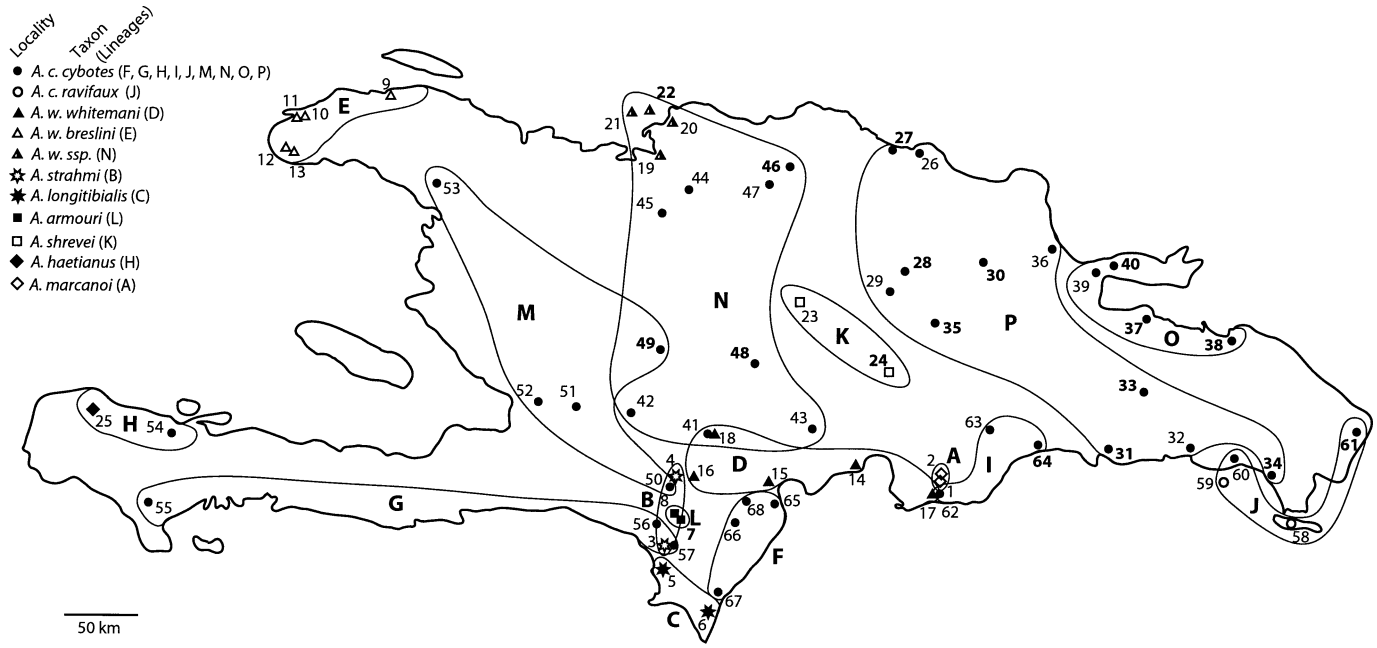

FIG. 4. Geographic distributions of 16 evolutionary lineages (Figs. 2, 3). Additional haplotypes (4–6) were sampled from population numbers in bold. Overlap between lineages M and N, D and I, D and N, and B and G represents sympatric occurrence of two distinct evolutionary lineages.

Lineage N includes nine populations of *A. c. cybotes* and four others considered *A. whitemani* (Figs. 2, 3, 4). Sampling of four to six haplotypes from each of 19 populations confirms coalescence within lineages, with the single exception that population 49 of *A. c. cybotes* contains three haplotypes from lineage N and two haplotypes from lineage M.

Sympatric occurrence is reported for five pairs of lineages: A and D, I and D, D and N, G and B, and M and N (Fig. 4). Morphological and ecological distinctness indicates that gene exchange is unlikely between the first four pairs: *A. c. cybotes* (N and I) and *A. w. whitemani* (D) are genetically, morphologically, and ecologically distinct where sympatric, as are *A. c. cybotes* (G) and *A. strahmi* (B), and *A. c. cybotes* (D) and *A. marcanoi* (A). The fifth pair may represent gene exchange resulting from recent geographic contact between formerly separated lineages (M and N) of *A. c. cybotes*, although reproductive compatibility between these populations has not been studied.

Both *A. cybotes* and *A. whitemani* include several deeply divergent evolutionary lineages that are as distinct from each other genetically as are lineages previously diagnosed as separate species. *Anolis whitemani* comprises two lineages formerly considered separate subspecies (E: *A. w. breslini* and D: *A. w. whitemani*) and part of a third lineage (lineage N), which also includes geographically adjacent populations of *A. c. cybotes*. *Anolis cybotes* comprises nine deeply divergent evolutionary lineages. Corrected distances between lineages identified within *A. cybotes* range from 0.05 to 0.18, whereas corrected distances between previously recognized species and subspecies of the *A. cybotes* complex range from 0.10 to 0.28. Only one of the *A. cybotes* lineages (J) includes populations that have been diagnosed as a separate subspecies, *A. c. ravifaux* from Islas Saona and Catalina. The geographic proximity of *A. c. ravifaux* populations and *A. c. cybotes* populations of lineage J and the high similarity among their haplotypes suggest a very recent geographic separation of *A. c. ravifaux* from its closest Hispaniolan relatives.

Morphometric Analyses

Morphometric data are reported from 13 populations, representing seven of the eight recognized species, four populations of *A. cybotes* and four populations of *A. whitemani* (Table 3). Sampling within *A. cybotes* represents four deeply divergent lineages, three representing *A. c. cybotes* (lineage P, population 26; lineage F, population 65; lineage I, population 64) and one representing *A. c. ravifaux* from Islas Soana and Catalina (lineage J, populations 58 and 59; Fig. 4). Each of the three deeply divergent populations of *A. whitemani* are included (lineages D, E, and N) as well as *A. w. lapidosus* from western Haiti, for which genetic material is not available.

Five principal components account for 80.7% of the observed variation (Table 4, Fig. 5). Based on factor-loading scores, we interpret PC1 as a measure of relative limb length; PC2 as a measure of head shape; PC3 as a trade-off between relative pelvis width and lamella number versus relative head height; PC4 as a measure of overall size, as represented by SVL; and PC5 as a measure of relative lamella number (Table 4). All three populations of *A. c. cybotes* cluster tightly in multivariate morphometric space, whereas *A. c. ravifaux* from the smaller offshore islands is similar to the rock-dwelling *A. longitibialis* along most axes (Fig. 5). The other mesic to semixeric forest species, *A. marcanoi*, is closest to *A. cybotes* in multivariate measurements (Table 5). The four *A. whitemani* populations are similar to each other and to *A. c. cybotes*

TABLE 3. Populations included in morphometric analyses (see Appendix 2 for a list of specimens measured). For *Anolis cybotes*, numbers following locality names refer to specific sampling localities in our phylogenetic analysis (Fig. 1).

Taxon	Population	*N*
A. marcanoi	Peravia Province, Dominican Republic	35
A. armouri	Pedernales Province, Dominican Republic	27
A. shrevei	La Vega Province, Dominican Republic	47
A. longitibialis	Pedernales Province, Dominican Republic	35
A. strahmi	Pedernales Province, Dominican Republic	28
A. c. cybotes	Sosua, Dominican Republic (26)	21
A. c. cybotes	Santo Domingo, Dominican Republic (64)	29
A. c. cybotes	Barahona, Dominican Republic (65)	30
A. c. ravifaux	Isla Saona and Isla Catalina, Dominican Republic (58, 59)	30
A. whitemani whitemani	Southern Dominican Republic	47
A. w. breslini	Nord Ouest Province, Haiti	17
A. w. lapidosus	Artibonite Province, Haiti	11
A. w. ssp.	Monte Cristi Province, Dominican Republic	26

along most axes except for *A. w. breslini*, which is divergent from other *A. whitemani* along many axes. Furthermore, all four *A. whitemani* populations are distinguished from *A. c. cybotes* by their slender pelvises and deep heads (PC3; Fig. 5). The two pine-forest species are similar to each other along each PC axis, sharing short limbs, broad pelvises, small heads, small overall body size, and low lamellar counts (Fig. 5). The two rock-dwelling species share long limbs and large body size, but differ along other axes, particularly with regard to head shape (PC2); *A. strahmi* has a much smaller head than each of the other populations measured (Fig. 5).

Phylogenetic relationships between the populations included in our comparative analysis are shown in Figure 6. Phylogenetic relatedness and morphological similarity are not significantly correlated (Mantel test: $P = 0.097$). This result is confirmed by the test of serial independence, which failed to reveal a significant phylogenetic effect for any of the PC axes (Table 6). This lack of a relationship results because distantly related populations from similar habitats are morphologically similar, and closely related populations in different habitats are morphologically divergent (Table 5). For example, among the populations measured, population 26 of *A. c. cybotes* is phylogenetically closest to the northwestern Dominican population of *A. whitemani* and the pine-forest species, *A. armouri*, but is morphometrically closest to the other two populations of *A. c. cybotes* (Table 5).

TABLE 4. Principal component (PC) analyses. Percent variation and eigenvalue scores indicate relative contributions of the five major PC axes to explaining total variation. Factor loadings for 11 morphometric variables on five PC axes account for 80.7% of the variation (13 populations measured). Factor-loading scores above 0.5 are in bold.

	PC1	PC2	PC3	PC4	PC5
Percent variation	35.46	19.20	9.89	8.34	7.81
Eigenvalue	4.26	2.31	1.19	1.00	0.94
Humerus	**0.80**	0.23	0.18	0.01	−0.16
Ulna	**0.89**	0.04	−0.05	0.01	−0.06
Pelvis	−0.26	0.42	**0.56**	0.03	−0.44
Femur	**0.91**	0.15	−0.06	0.00	0.07
Tibia	**0.93**	0.14	−0.19	0.00	0.08
Hind 1	**0.78**	0.30	0.06	0.00	−0.02
Hind 2	0.21	**0.55**	0.40	−0.02	−0.09
Head width	**−0.52**	**0.72**	0.05	−0.00	0.09
Head length	−0.31	**0.80**	−0.16	0.00	0.11
Head height	−0.13	**0.68**	**−0.51**	−0.00	0.24
Lamellae	0.09	−0.07	**0.59**	−0.07	**0.78**
Snout-vent length	−0.01	−0.01	0.03	**1.00**	0.07

Both phylogenetic and nonphylogenetic multivariate analyses of variance (MANOVAs) strongly support the hypothesis that categories of habitat use differ morphologically (Table 6). Nonphylogenetic and phylogenetic ANOVAs suggest that several variables contribute to these differences; three of five PC axes (PC1, PC3, PC4) differ significantly among habitats in the nonphylogenetic ANOVAs, although one of these (PC3) is nonsignificant in a phylogenetically corrected ANOVA.

The nonphylogenetic discriminant-function analysis is highly significant ($P < 0.001$) and all populations are reclassified to the correct category of habitat use. These results are upheld in the phylogenetic analysis, in which none of the simulated datasets produced *F*-values as high as those observed for the real data.

DISCUSSION

Morphometric features observed in the *A. cybotes* group correspond closely to macrohabitat type independent of phylogenetic affinities. This pattern appears to represent morphological evolutionary stasis in populations associated with mesic/semixeric forest environments (*A. c. cybotes* and *A. marcanoi*) and predictable morphometric changes associated with entry into new macrohabitat types.

Multivariate morphometric analyses find strong differences between species in different macrohabitat types, and univariate analyses (Table 6) show that SVL (PC4), relative limb length (PC1), and relative pelvis width/relative head height (PC3) differ markedly among macrohabitat types. Discriminant-function analysis of morphology distinguishes macrohabitat types more strongly than expected from phylogenetic simulations and classifies each population to its correct macrohabitat type. Numerous lineages show long-term stability of ancestral morphologies and macrohabitat associations, whereas other local populations undergo evolutionary divergence associated with novel macrohabitats. Some macrohabitat associations have evolved multiple times with similar morphological consequences.

The mesic-to-semixeric forest macrohabitat and associated morphometric characteristics of *A. c. cybotes* and *A. marcanoi*

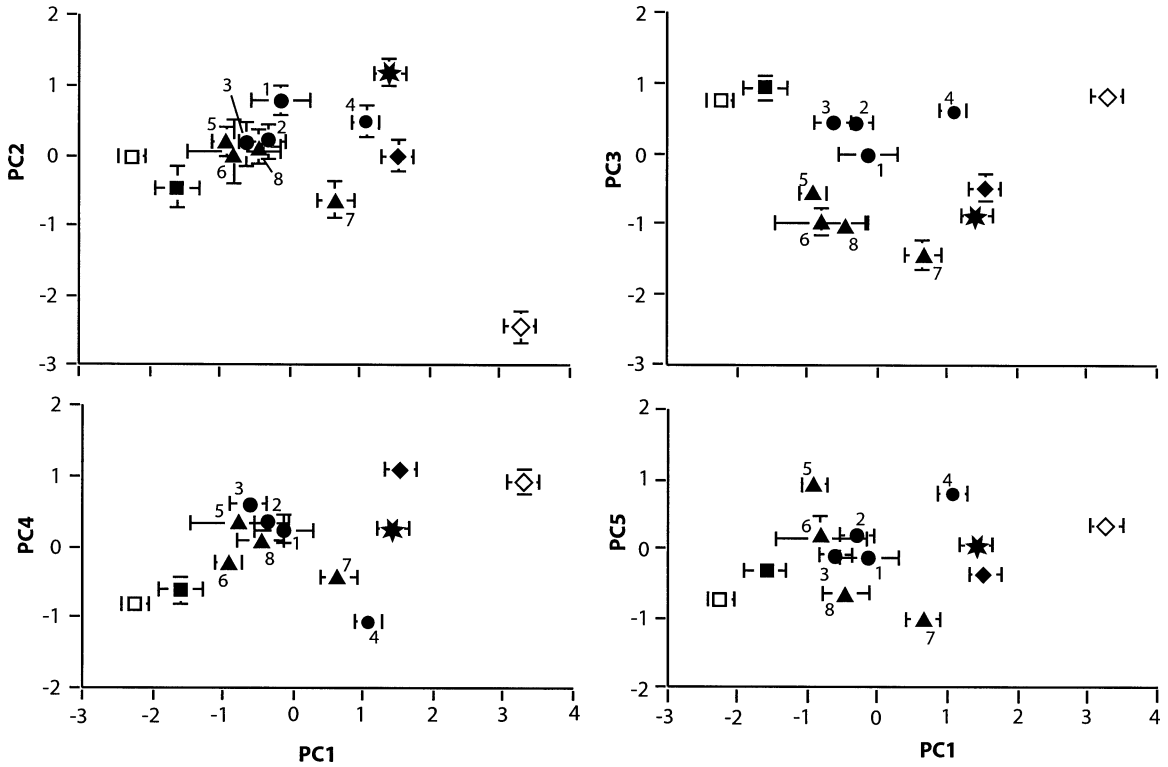

FIG. 5. Principal component analysis. PC axes 2–5 are each plotted against PC1. Whiskers indicate standard errors. Shapes indicate categories of habitat use: circles, mesic/semixeric forests (1, *Anolis cybotes cybotes* [lineage P, population 26]; 2, *A. c. cybotes* [lineage F, population 65]; 3, *A. c. cybotes* [lineage I, population 64]; 4, *A. marcanoi*); triangles, xeric forest/semidesert (5, *A. w. whitemani*; 6, *A. w. lapidosus*; 7, *A. w. breslini*; 8, *A. whitemani* ssp.); squares, upland pine forest (open, *A. shrevei*; filled, *A. armouri*); diamonds, rock outcrops (open, *A. strahmi*; filled, *A. longitibialis*); star, satellite islands (*A. c. ravifaux*).

appear ancestral for the *A. cybotes* complex and show long-term evolutionary stability across populations belonging to four deeply divergent haplotype clades. Although populations in this macrohabitat category are deeply divergent from each other and do not form a monophyletic group, our morphometric analysis finds that populations of *A. c. cybotes* are nearly identical and that *A. marcanoi* is most similar to *A. c. cybotes* (Table 5, Fig. 5). The morphometric similarity of *A. marcanoi* and *A. c. cybotes* supports the observations of Williams (1975), who described them as sibling species that could be reliably distinguished only by dewlap color or protein electrophoresis (Webster 1975). Despite these similarities, our results indicate that *A. marcanoi* and *A. cybotes* are not sister taxa; instead, their divergence spans the deepest phylogenetic split in the *A. cybotes* complex. Sequence divergence among their haplotypes is substantial (~18%, Table 2), exceeding divergences measured among all species in the *A. grahami* series (Jackman et al. 2002) and suggesting evolutionary divergence beginning as long as 13 million years ago (Macey et al. 1998). We attribute the morphological sim-

TABLE 5. Matrix of pairwise patristic and morphometric Euclidean distances. Patristic distances derived from ultrametric Bayesian topology are above the diagonal; Euclidean distances based on mean principal-component scores are below the diagonal. Letters correspond to lineages identified in Figures 2, 3, and 5. E, *Anolis whitemani breslini*; P, *A. cybotes cybotes* (population 27); N, *A. whitemani* ssp.; L, *A. armouri*; K, *A. shrevei*; J, *A. c. ravifaux*; I, *A. c. cybotes* (population 64); F, *A. c. cybotes* (population 65); D, *A. w. whitemani*; B, *A. strahmi*; C, *A. longitibialis*; A, *A. marcanoi*.

	E	P	N	L	K	J	I	F	D	B	C	A
E	—	0.334	0.334	0.334	0.334	0.334	0.334	0.334	0.398	0.509	0.509	0.684
P	2.444	—	0.069	0.151	0.2	0.214	0.224	0.279	0.398	0.509	0.509	0.684
N	1.552	1.351	—	0.151	0.2	0.214	0.224	0.279	0.398	0.509	0.509	0.684
L	3.351	2.319	2.425	—	0.2	0.214	0.224	0.279	0.398	0.509	0.509	0.684
K	3.729	2.7	2.678	0.905	—	0.214	0.224	0.279	0.398	0.509	0.509	0.684
J	2.42	1.837	2.279	4.014	4.422	—	0.224	0.279	0.398	0.509	0.509	0.684
I	2.796	0.989	1.625	1.772	2.292	2.677	—	0.279	0.398	0.509	0.509	0.684
F	2.714	0.852	1.711	1.896	2.501	2.412	0.518	—	0.398	0.509	0.509	0.684
D	2.796	1.614	1.743	2.222	2.612	2.751	1.69	1.52	—	0.509	0.509	0.684
B	4.367	4.841	5.04	5.538	6.373	4.484	4.749	4.494	5.306	—	0.321	0.684
C	2.221	2.112	2.311	3.876	4.448	1.577	2.431	2.279	3.089	3.347	—	0.684
A	3.059	2.106	2.909	3.107	3.706	2.288	2.573	2.084	2.486	4.195	2.776	—

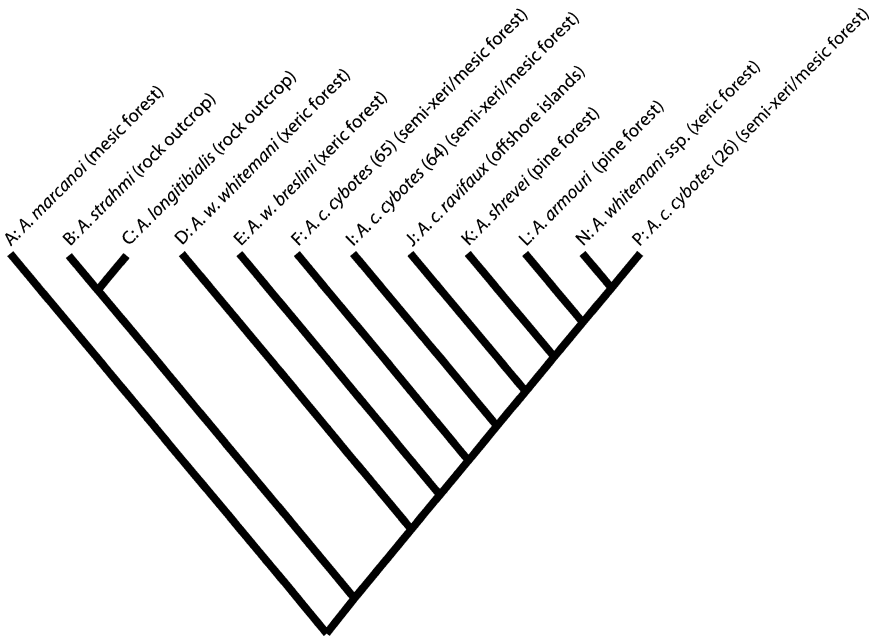

FIG. 6. Phylogenetic relationships between populations included in our morphometric analysis. This topology was used for all phylogenetic comparative analyses.

ilarity of *A. c. cybotes* and *A. marcanoi* to long-term evolutionary stasis associated with stabilizing selection in their mesic-to-semixeric forest macrohabitat.

Morphological evolutionary stasis has occurred in *A. c. cybotes* and *A. marcanoi* over the same time interval that other populations have diverged ecologically and morphologically. The rock-outcrop and pine-forest macrohabitat types both represent morphometrically distinct groupings of populations that presumably arose from an ancestral condition resembling the shared ecological and morphometric characteristics of *A. c. cybotes* and *A. marcanoi*. Three of the five named taxa that render *A. c. cybotes* nonmonophyletic (*A. haetianus*, *A. c. ravifaux*, northwestern Dominican *A. whitemani* ssp.) have haplotypes most closely related to those of geographically proximate *A. c. cybotes* populations, suggesting that these ecologically and geographically restricted forms have recently diverged from an ancestor resembling local populations of *A. c. cybotes*.

TABLE 6. Results of comparative morphometric analyses. The first column presents *P*-values from the test for serial independence, which tested for significant phylogenetic effects. Remaining columns include results from analyses of variance, which tested for morphological differences between categories of habitat use defined a priori. *P*-values represent the probability of obtaining an *F*-value from 1000 simulated datasets greater than the value obtained from the actual data. Significant values are in bold.

	Test for serial independence	Nonphylogenetic analysis of variance	Phylogenetic analysis of variance
PC1	0.163	**0.010**	**0.014**
PC2	0.794	0.142	0.320
PC3	0.583	**0.013**	0.066
PC4	0.081	**0.001**	**0.002**
PC5	0.481	0.712	0.785
MANOVA		**0.001**	**0.001**

Multiple evolutionary origins of some categories of habitat use and associated morphological features suggest that particular habitats predictably elicit similar adaptive evolutionary responses by directional selection. For example, *A. whitemani* is polyphyletic, comprising three phylogenetically distinct lineages (D, E, part of N) that occur in xeric forest/semidesert habitats and share keeled ventral scales and morphometric features (Fig. 5). Populations of *A. whitemani* are morphometrically similar to populations of *A. c. cybotes* along most axes, but are distinguished along PC axis 3 by their slender pelvises and deep heads (Fig. 5). The ecological and morphological features that have been used to diagnose *A. whitemani* have evolved independently at least twice, once in a common ancestor of *A. w. whitemani* and *A. w. breslini* and once in populations from xeric forests in the northwestern Dominican Republic. The hypothesis that *A. whitemani* from the northwest Dominican Republic is evolutionarily distinct from other populations of *A. whitemani* and is more closely related to nearby populations of *A. cybotes* is further supported by the dewlap color observed in this population. Unlike *A. breslini* and *A. w. whitemani*, which have striking white dewlaps, this population has a pale yellow dewlap, indistinguishable from that observed in nearby populations of *A. c. cybotes* (Schwartz 1980; Powell and Carr 1990; Burns et al. 1992; see fig. 4C of Crother 1999).

A similar situation is observed in features associated with a rock-dwelling ecology, which have evolved independently in *A. c ravifaux* and in a common ancestor of *A. longitibialis* and *A. strahmi*. *Anolis longitibialis* and *A. strahmi* live in macrohabitats dominated by rock outcrops and spend most of their time using such surfaces (Schwartz 1979, 1989; Gifford et al. 2002). The macrohabitat of *A. c. ravifaux* is not well studied, but the small offshore islands that it inhabits (Isla Catalina, in particular) have many exposed rock outcrops, which the lizards use (Schwartz and Henderson 1982).

Nonetheless, in the absence of more complete ecological data, we took the conservative course of not assigning this taxon to the rock-outcrop macrohabitat type a priori. However, morphometric analyses place *A. c. ravifaux* with the rock-dwelling species *A. longitibialis*, particularly with respect to limb length, confirming predictions made from their observed use of rock outcrops (Table 5, Fig. 5). Previous studies have found correlations between long limbs and rock-dwelling or saxicolous macrohabitats in lizards (Vitt et al. 1997; Losos et al. 2002). We therefore hypothesize that the morphometric features shared by *A. longitibialis*, *A. strahami*, and *A. c. ravifaux* are adaptations to saxicolous conditions separately derived from an ancestral morphology similar to that of *A. c. cybotes* and *A. marcanoi*.

Morphological adaptations associated with entry into xeric and saxicolous macrohabitats have arisen rapidly relative to the morphological evolutionary stability of populations that remain within a macrohabitat type. The saxicolous *A. c. ravifaux* populations and northwestern Dominican xeric-forest populations of *A. whitemani* probably diverged from ancestral populations resembling mesic-forest populations of *A. c. cybotes* within the past million years, based on expected rates of haplotypic evolution. Haplotypes from the *A. whitemani* population from the northwest Dominican Republic do not form a reciprocally monophyletic group with respect to those from nearby populations of *A. c. cybotes*, and haplotypes of *A. c. ravifaux* differ by only 1% sequence divergence from those of nearby *A. c. cybotes*. These results suggest a pattern of evolutionarily rapid adjustment of mesic/semixeric adapted populations to xeric or saxicolous macrohabitats, followed by evolutionary stability of morphological characters associated with macrohabitat specialization.

Phylogeographic Structure

Extensive geographic structuring of mtDNA haplotypes in the *A. cybotes* group reveals unanticipated genetic differentiation among geographic populations within *A. whitemani* and *A. cybotes*. Both of these widespread species contain geographically circumscribed mtDNA haplotype clades that replace each other geographically and differ by more than 10% sequence divergence (Table 2). Within *A. whitemani*, population-level lineages D (*A. w. whitemani*) and E (*A. w. breslini*) inferred from mtDNA haplotype clades (Fig. 2) are supported by other kinds of evidence; Schwartz (1980, 1989) considered the morphological distinctness of these two subspecies sufficient to suggest species-level divergence. Its morphological distinctness, monophyly of sampled mtDNA haplotypes, deep divergence from all other sampled haplotypes (~10% or more), and geographical isolation collectively support separate species status for *A. breslini*.

Within *A. cybotes*, populations grouped by our mtDNA analysis as lineages F, G, I, M, O, and P in Figure 2 show no obvious morphological differentiation, and lack independent evidence of their genetic distinctness. Similar patterns of geographic genetic differentiation have been found for mtDNA haplotypes within other widespread anole species (Malhotra and Thorpe 1994, 2000; Schneider 1996; Glor et al. 2001), and several widespread species codistributed on Jamaica show congruent regional patterns of geographic genetic differentiation (Jackman et al. 2002). These observations suggest that morphological diagnoses may underestimate the number of distinct evolutionary lineages in anoles, although the patterns suggested by mitochondrial haplotypic variation require further testing, preferably with nuclear genetic markers, for this hypothesis to be confirmed (Irwin 2002; Stenson et al. 2002).

Conclusion

This study complements earlier studies of anoles by identifying a previously overlooked aspect of the anole radiation. Earlier studies have emphasized ecomorphological specialization to different aspects of the structural microhabitat, documenting independent evolution of communities of sympatric microhabitat specialists that partition available resources along axes such as perch height and perch diameter (Rand 1967; Williams 1983; Losos 1990; Losos et al. 1998). For example, trunk-ground specialists have long hind limbs and stout bodies well suited for clinging to low, broad perches and chasing prey on the ground, whereas twig anoles have evolved short limbs and slender bodies ideal for scaling narrow perches high in trees (Williams 1983; Losos 1990; Irschick and Losos 1998). However, most speciation in Greater Antillean anoles has occurred within these well-known categories (Losos 1996), and our study shows that ecomorphological evolution has occurred within the trunk-ground species belonging to the *A. cybotes* group along a different ecological axis associated primarily with differences between allopatrically distributed macrohabitat types (i.e., xeric, mesic, high-altitude, rock outcrops). As a result, morphologically divergent populations of the *A. cybotes* group typically exist allopatrically or parapatrically rather than sympatrically. Moreover, both long-term morphological stasis and independent evolution of similar morphological features in similar environments are important to explaining the observed pattern of morphological diversity.

This pattern of diversification is not likely to be restricted to the *A. cybotes* group and may be tested further by examining other groups of anoles having comparable geographic and climatic variation. For example, of the three trunk-ground anoles on Puerto Rico, one is restricted to xeric-scrub forests (*A. cooki*), one to open mesic forests (*A. cristatellus*), and one to shaded mesic forests (*A. gundlachi*; Hertz et al. 1993). We hypothesize that the Greater Antillean *Anolis* radiation is hierarchically structured with several distinct phases of speciation and adaptation, with each phase resulting from different selective pressures and culminating in specialization along different environmental axes (Schluter 2000; Danley and Kocher 2001).

Acknowledgments

S. B. Hedges generously provided genetic material for this study, including all of our Haitian samples. We also thank J. A. Ottenwalder for facilitating all of our fieldwork in the Dominican Republic. M. Mota and A. Schubert in Areas Protegidas y Biodiversidad and G. Santana in Departamento de Vida Silvestre assisted with permits and provided logistical support in the Dominican Republic. T. Townsend, K. Kozak, C. Schneider, and two anonymous reviewers provided helpful

comments on an earlier draft of this manuscript. R. Sosa and members of Avila College REU programs assisted with specimen collection. We thank J. Simmons and L. Trueb at the University of Kansas Natural History Museum, J. Hanken at the Museum of Comparative Zoology, J. Strasburg, and C. Crooks for assistance in obtaining museum specimens. Financial support was provided by National Science Foundation grant DEB-9982736.

Literature Cited

Abouheif, E. 1999. A method for testing the assumption of phylogenetic independence in comparative data. Evol. Ecol. Res. 1: 895–909.

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

Bremer, K. 1994. Branch support and tree stability. Cladistics 10: 295–304.

Buckley, T. R. 2002. Model misspecification and probabilistic tests of topology: evidence from empirical data sets. Syst. Biol 51: 509–523.

Burnell, K. L., and S. B. Hedges. 1990. Relationships of West Indian *Anolis* (Sauria: Iguanidae): an approach using slow-evolving protein loci. Caribbean J. Sci. 26:7–30.

Burns, J. K., C. A. Cunningham, R. A. Dupuis, M. N. Trask, J. S. Tulloch, R. Powell, J. S. Parmerlee, Jr., K. L. Kopecky, and M. L. Jolley. 1992. Lizards of the Cayos Siete Hermanos, Dominican Republic, Hispaniola. Bull. Chicago Herp. Soc. 27: 225–232.

Cracraft, J. 1989. Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. Pp. 28–59 *in* D. Otte and J. A. Endler, eds. Speciation and its consequences. Sinauer, Sunderland, MA.

Crother, B. I. 1999. Caribbean amphibians and reptiles. Academic Press, San Diego, CA.

Danley, P. D., and T. D. Kocher. 2001. Speciation in rapidly diverging systems: lessons from Lake Malawi. Mol. Ecol. 10: 1075–1086.

de Queiroz, K., L.-R. Chu, and J. B. Losos. 1998. A second *Anolis* lizard in Dominican amber and the systematics and ecological morphology of Dominican amber anoles. Amer. Mus. Novit. 3249:1–22.

Díaz-Uriarte, R., and T. Garland. 1996. Testing hypotheses of correlated evolution using phylogenetically independent contrasts: sensitivity to deviations from Brownian motion. Syst. Biol. 45: 27–47.

Felsenstein, J. 1985. Phylogenies and the comparative method. Am. Nat. 125:1–15.

Garland, T., Jr., A. W. Dickerman, C. M. Janis, and J. A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. Syst. Biol. 42:265–292.

Gifford, M. E., Y. M. Ramos, R. Powell, and J. S. Parmerlee. 2002. Natural history of a saxicolous anole, *Anolis longitibialis* from Hispaniola. Herpetol. Nat. Hist. 9:15–20.

Glor, R. E., L. J. Vitt, and A. Larson. 2001. A molecular phylogenetic analysis of diversification in Amazonian *Anolis* lizards. Mol. Ecol. 10:2661–2668.

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

Goldman, N., J. P. Anderson, and A. G. Rodrigo. 2000. Likelihood-based tests of topologies in phylogenetics. Syst. Biol. 49: 652–670.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford Univ. Press, Oxford, U.K.

Hertz, P. E. 1980. Comparative physiological ecology of the sibling species *Anolis cybotes* and *A. marcanoi*. J. Herpetol. 14:92–95.

Hertz, P. E., R. B. Huey, and R. D. Stevenson. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. Am. Nat. 142:796–818.

Huelsenbeck, J. P., and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17:754–755.

Irschick, D. J., and J. B. Losos. 1998. A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. Evolution 52:219–226.

———. 1999. Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribbean anoles. Am. Nat. 154: 293–305.

Irschick, D. J., C. C. Austin, K. Petren, R. N. Fisher, J. B. Losos, and O. Ellers. 1996. A comparative analysis of clinging ability among pad-bearing lizards. Biol. J. Linnean Soc. 59:21–35.

Irwin, D. E. 2002. Phylogeographic breaks without geographic barriers to gene flow. Evolution. 56:2383–2394.

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

Jackman, T. R., D. J. Irschick, K. de Queiroz, J. B. Losos, and A. Larson. 2002. Molecular phylogenetic perspective on evolution of lizards of the *Anolis grahami* series. J. Exp. Zool. 294:1–16.

Kumar, S., K. Tamura, I. B. Jakobsen, and M. Nei. 2001. MEGA2: molecular evolutionary genetics analysis software. Bioinformatics 17:1244–1245.

Kumazawa, Y., and M. Nishida. 1993. Sequence evolution of mitochondrial transfer-RNA genes and deep-branch animal phylogenetics. J. Mol. Evol. 37:380–398.

Lee, M. S. Y. 2000. Tree robustness and clade significance. Syst. Biol. 49:829–836.

Lenart, L., R. Powell, J. S. Parmerlee, D. D. Smith, and A. Lathrop. 1994. The diet and a gastric parasite of *Anolis armouri*, a cybotoid anole from montane pine forests in southern Hispaniola. Herpetol. Nat. Hist. 2:97–100.

Levinton, J. S. 2001. Genetics, paleontology, and macroevolution. 2d ed. Cambridge Univ. Press, Cambridge, U.K.

Losos, J. B. 1985. An experimental demonstration of the species-recognition role of *Anolis* dewlap color. Copeia 1985:905–910.

———. 1990. Ecomorphology, performance capability, and scaling of West-Indian *Anolis* lizards: an evolutionary analysis. Ecol. Monogr. 60:369–388.

———. 1996. Ecological and evolutionary determinants of the species-area relation in Caribbean anoline lizards. Phil. Trans. Roy. Soc. London B 351:847–854.

———. 1999. Uncertainty in the reconstruction of ancestral character states and limitations on the use of phylogenetic comparative methods. Anim. Behav. 58:1319–1324.

Losos, J. B., and L. R. Chu. 1998. Examination of factors potentially affecting dewlap size in Caribbean anoles. Copeia 1998:430–438.

Losos, J. B., T. R. Jackman, A. Larson, K. de Queiroz, and L. Rodriguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science 279: 2115–2118.

Losos, J. B., P. L. N. Mouton, R. Bickel, I. Cornelius, and L. Ruddock. 2002. The effect of body armature on escape behaviour in cordylid lizards. Anim. Behav. 64:313–321.

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

Macey, J. R., J. A. Schulte, N. B. Ananjeva, A. Larson, N. Rastegar-Pouyani, S. M. Shammakov, and T. J. Papenfuss. 1998. Phylogenetic relationships among agamid lizards of the *Laudakia caucasia* species group: testing hypotheses of biogeographic fragmentation and an area cladogram for the Iranian Plateau. Mol. Phylogenet. Evol. 10:118–131.

Macey, J. R., J. A. Schulte, A. Larson, N. B. Ananjeva, Y. Z. Wang, R. Pethiyagoda, N. Rastegar-Pouyani, and T. J. Papenfuss. 2000. Evaluating trans-tethys migration: an example using acrodont lizard phylogenetics. Syst. Biol. 49:233–256.

Maddison, D. R., and W. P. Maddison. 2000. MacClade 4: analysis of phylogeny and character evolution. Ver. 4.0. Sinauer Associates, Sunderland, MA.

Malhotra, A., and R. S. Thorpe. 1994. Parallels between island

lizards suggests selection on mitochondrial-DNA and morphology. Proc. Roy. Soc. London B 257:37–42.
———. 2000. The dynamics of natural selection and vicariance in the Dominican anole: patterns of within-island molecular and morphological divergence. Evolution 54:245–258.
Mayer, G. C. 1989. Deterministic patterns of community structure in West Indian reptiles and amphibians. Ph.D. diss., Harvard University, Cambridge, MA.
Meacham, C. A., and T. Duncan. 1990. Morphosys. Ver. 1.26. University Herbarium, Univ. of California, Berkeley.
Melville, J., J. A. Schulte II,and A. Larson. 2001. A molecular phylogenetic study of ecological diversification in the Australian lizard genus *Ctenophorus*. J. Exp. Zool. 291:339–353.
Posada, D., and K. A. Crandall. 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14:817–818.
Powell, R., and D. K. Carr. 1990. *Anolis whitemani* Williams. Catalogue of American Amphibians and Reptiles 462:1–2.
Rand, A. S. 1967. The ecological distribution of anoline lizards around Kingston, Jamaica. Breviora 272:1–18.
Sanderson, M. J. 1997. A nonparametric approach to estimating divergence times in the absence of rate constancy. Mol. Biol. Evol. 14:1218–1231.
Schluter, D. 2000. The ecology of adaptive radiation. Oxford Univ. Press, New York.
Schluter, D., and J. D. McPhail. 1993. Character displacement and replicate adaptive radiation. Trends Ecol. Evol. 8:197–200.
Schneider, C. J. 1996. Distinguishing between primary and secondary intergradation among morphologically differentiated populations of *Anolis marmoratus*. Mol. Ecol. 5:239–249.
Schneider, C., and C. Moritz. 1999. Rainforest refugia and evolution in Australia's Wet Tropics. Proc. Royal Soc. London B. 266: 191–196.
Schneider, C. J., T. B. Smith, B. Larison, and C. Moritz. 1999. A test of alternative models of diversification in tropical rainforests: ecological gradients vs. rainforest refugia. Proc. Natl. Acad. Sci. USA 96:13869–13873.
Schwartz, A. 1979. A new species of cybotoid anole (Sauria, Iguanidae) from Hispaniola. Breviora 451:1–27.
———. 1980. Variation in Hispaniolan *Anolis whitemani* Williams. J. Herpetol. 14:399–406.
———. 1989. A review of the cybotoid anoles (Reptilia: Sauria: Iguanidae) from Hispaniola. Milwaukee Public Mus. Contrib. Biol. and Geol. 78:1–32.
Schwartz, A., and R. W. Henderson. 1982. *Anolis cybotes* (Reptilia, Iguanidae): the eastern Hispaniolan populations. Milwaukee Public Mus. Contrib. Biol. and Geol. 49:1–8.
———. 1991. Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history. Univ. of Florida Press, Gainesville.
Smith, T. B., C. J. Schneider, and K. Holder. 2001. Refugial isolation versus ecological gradients. Genetica 112:383–398.
Stenson, A. G., A. Malhotra, and R. S. Thorpe. 2002. Population differentiation and nuclear gene flow in the Dominican anole (*Anolis oculatus*). Mol. Ecol. 11:1679–1688.
Swofford, D. 2002. PAUP*: phylogenetic analysis using parsimony (* and other methods). Sinauer, Sunderland, MA.
Tamura, K., and M. Nei. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial-DNA in humans and chimpanzees. Mol. Biol. Evol. 10:512–526.
Templeton, A. R. 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and apes. Evolution 37:221–244.
———. 1998. The role of molecular genetics in speciation studies. Pp. 131–156 *in* R. DeSalle and B. Schierwater, eds. Molecular approaches to ecology and evolution. Birkhäuser, Boston, MA.
Townsend, T., and A. Larson. 2002. Molecular phylogenetics and mitochondrial genomic evolution in the Chamaeleonidae (Reptilia, Squamata). Mol. Phylogenet. Evol. 23:22–36.
Vitt, L. J., J. P. Caldwell, P. A. Zani, and T. A. Titus. 1997. The role of habitat shift in the evolution of lizard morphology: evidence from tropical *Tropidurus*. Proc. Natl. Acad. Sci. USA 94: 3828–3832.
Wainwright, P. C., and S. M. Reilly. 1994. Ecological morphology. Univ. of Chicago Press, Chicago.
Webster, T. P. 1975. An electrophoretic comparison of the Hispaniolan lizards *Anolis cybotes* and *A. marcanoi*. Breviora 431: 1–8.
Williams, E. E. 1963. *Anolis whitemani*, new species from Hispaniola (Sauria, Iguanidae). Breviora 197:1–8.
———. 1975. *Anolis marcanoi* new species: sibling to *Anolis cybotes*: description and field evidence. Breviora 430:1–9.
———. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. Pp. 326–370 *in* R. B. Huey, E. R. Pianka, and T. W. Schoener, eds. Lizard ecology, studies of a model organism. Harvard Univ. Press, Cambridge, MA.
Zhang, D.-X., and G. M. Hewitt. 1996. Nuclear integrations: challenges for mitochondrial DNA markers. Trends Ecol. Evol. 11: 247–251.

Corresponding Editor: B. Sinervo

Appendix 1

Sampling for Molecular Study

GenBank accession numbers for sequences included in this study are AY263003–AY263114. Localities for tissues used in this study and voucher specimen numbers (in parentheses): BWMC, Bobby Witcher Memorial Collection, Avila University; MCZ, Museum of Comparative Zoology, Harvard University; KU, Museum of Natural History, Kansas University; REG, Richard E. Glor field series; USNM, U.S. National Museum; RT, Richard Thomas field series; JBL, Jonathan B. Losos field series; KdQ, Kevin de Queiroz field series; all localities in Dominican Republic unless noted otherwise. Specimens noted with an asterisk were additional individuals sampled from each population that were not included in phylogenetic analysis. *Anolis cristatellus* (RT 13042): *A. distichus* (REG 648): *A. marcanoi*, 1. 5.6 km N of Highway 2 on road to Recondo (REG 560); 2. Road to Recondo (JBL 275): *A. strahmi*; 3. Road to Los Mercedes (JBL 451); 4. 1.2 km NE of Aguacate, N18 19 586 W71 41 236 (REG 631): *A. longitibialis*; 5. Pedernales (JBL 452); 6. 2.5–3.7 km S Los Tres Charcos (BWMC 6293): *A. armouri*; 7,8. Sierra de Baoruco N18 16 242 W071 43 365 (REG 523, 527, 644–646*): *A. w. breslini*; 9. Haiti, Port de Paix (TO); 10. Haiti, Nord'Ouest, Mole St. Nicolas (USNM 194564); 11. Haiti, Mole St. Nicolas at Rivière Côtes de Fer (USNM 194550); 12. Haiti, Nord'Ouest, about 3.5 miles SW of Bombardopolis (USNM 194602); 13. Haiti, Bombardopolis (USNM 194625): *A. w. whitemani*; 14. 3–5 km ESE Canoa, road to Puerto Alejandro (REG 486); 15. Monte Rio, on the coast S Azua (REG 435); 16. Road between Duverge and Puerto Escondito, near water pumping station, N18 21 521 W071 31 949 (REG 607); 17. 8 km WNW Baní (REG 469, REG 474); 18. 5 km E Neyba (junction of road to Cabral) (BWMC 6240): *A. whitemani* ssp.; 19. Pepillo Salcedo (Manzanillo) (REG 481); 20. Monte Cristi (REG, 457); 21. Cayo Monte Grande (REG 495, REG 498); 22. Isla Cabras (REG 443, 688*, 692*, 693*, 697*): *A. shrevei*; 23. Valle de Bao (USNM 193297); 24. 37.3 km N of San Jose de Ocoa (from town square) on Rt. 41 (REG 1207, REG 1208–1211*): *A. haetianus*; 25. Haiti, Grand' Anse, 0.8 km E of Dame-Marie (USNM 191956): *A. c. cybotes*; 26. Sosua (REG 427); 27. 9.7 km W Sosua, N19 45 854 W070 25 465 (REG 818, 819–821*); 28. 1 km N La Vega, Estation Agricultura Saleciano (BWMC 6561–6563*, 6565); 29. 22.1 km SW La Vega road to Jarabocoa (BWMC 6560); 30. 2.5 km SW of San Francisco de Macoris (REG 713*, 714, 715–717*); 31. Boca Chica (BWMC 6571–6573*, 6574); 32. 26 km W La Romana Highway 2 (BWMC 6576); 33. 4.7 km W of Hato Mayor, N19 16 232 W070 17 638 (REG 784, 785–788*); 34. Bayahibe (BWMC 6578); 35. Bonau (BWMC 6566*, 6567, 6569*, 6570*, REG 1492*); 36. 2 km SE of Nagua, N19 21 093 W069 49 146 (REG 847); 37. Los Haitises (REG 218, 723*, 729–731*, 739*); 38. 1.9 km W Miches, N18 57 760 W069 01 559 (REG 741–742*, REG 743, REG 744–745*); 39. 2.3 km W of Sanchez, N19 14 344 W069 38 239 (REG 836); 40. 2.5 km N of C-5 on road to Las Terenas, N19 14 735 W069 35 707 (REG 843, REG 1309–1312*); 41. 5 km E Neyba (jct road to Cabral) (BWMC 6243); 42. 16 km

N of Cacique Enriquillo (USNM 161505); 43. 1 km N on Highway 2 toward Los Yayas graveyard (BWMC 6249, 6250, 6251*); 44. W of Copey on road to Pepillo Salcedo, N19 26 531 W071 22 213 (REG 681); 45. 10.2 km S of Dajabon on road to Restoracion, N19 28 999 W071 38 143 (REG 679); 46. 2.4 km S of Los Hidalgos, N19 39 170 W071 03 338 (REG 698, 699–702*); 47. 0.9 km N of Highway 1 at Maizel, N19 39 170 W071 03 338 (REG 708); 48. 10.6 km SE of San Juan, N18 44 912 W071 08 205 (REG 658, REG 1366–1369*); 49. Comendador, just east of Elias Pinas, N18 52 423 W071 41 556 (REG 650, 652–655*); 50. 1.0 km NE of Aguacate, N18 19 555 W071 41 366 (REG 632); 51. Haiti, L'Ouest, 18.1 km E of Thomazeau (USNM 191605); 52. Haiti, Centre, 16 km N of Croix de Bouquets (USNM 191709); 53. Haiti, L'Artibonite, 19.5 km N of Ca Soleil (USNM 192416); 54. Haiti, Grand' Anse, 5.8 km S of Pestel (USNM 191752); 55. Haiti, Sud, 2.4 km S of Ducis (USNM 191727); 56. 26.5 km N of Pederales on road to Los Arroyos, N18 11 593 W071 46 049 (REG 615); 57. Just past 16 km marker on Alcoa road about 8 km N of intersection w/ Oviedo to Pedernales highway, N18 02 384 W071 41 427 (REG 625); 58. Isla Saona (BWMC 6040); 59. Isla Catalina (BWMC 6055); 60. 4.9 km W of La Romana, N18 23 861 W069 01 119 (REG 1072*, 1074–1075*, 1076); 61. Punta Cana docks, N18 30 265 W068 22 579 (REG 792–793*, 794, 795–796*); 62. Bani (de Queiroz); 63. Just E of Madrigal, N18 36 134 W070 09 008 (REG 865); 64. Santo Domingo, Hotel Embajador (BWMC 6581, 6582–6585*); 65. Barahona, Hotel Riviera Beach (BWMC 6404); 66. Loma Remigio (BWMC 6323); 67. Lago Oviedo (BWMC 6283); 68. 18.1–18.6 km S Cabral (BWMC 6403)

Appendix 2

Sampling for Morphological Study

Codes as in Appendix 1. *A. armouri*—BWMC 5144–5146, 5201–5203, 5205, 5207, 5441, 5448–5450, 5452; REG 519–523, 526–532, 643, 647: *A. c. cybotes* (locality 26)—REG 402–403, 405, 408, 412–413, 417–418, 421–422, 425–426, 428, 446–447, 449–450, 452–455: *A. c. cybotes* (locality 65)—BWMC 2488, 3143–3144, 3148, 4151, 3545–3549, 4545–4546, 4548, 4550, 4552, 4556–4557, 4559, 5232–5234, 5254–5255, 5257–5258, 5261–5262, 6405, 6407–6408: *A. c. cybotes* (locality 64)—BWMC 3534, 3536–3537, 3541, 3562–3564, 3567, 3569, 3573, 3575–3577, 3579–3582, 5456, 5460, 5462–5463, 5483–5484, 6581–6585: *A c. ravifaux* (Isla Saona and Isla Catalina)—BWMC 6042, 6044–6054, 6057–6059, 6061–6062, 6065, 6069, 6072–6074, 6113–6118, 6122–6123: *A. longitibialis*—BWMC 6294, 6297–6298, 6300, 6302–6303, 6306, 6527–6528, 6530, 6532–6533, 6535, 6537–6539, 6543, 6547–6550; MCZ 151828–151839; REG 563: *A. marcanoi*—MCZ 131824–131825, 131831, 131848, 131850–131851, 143241, 143243–143245, 143248–143249, 150515, 165218, 173211; KU 259861–259865, 259867–259868, 259871, 259873, 259879–259880, 259882–259885, 259888; REG 559–560, 869–870: *A. shrevei*—KU 246975–246980, 246983, 246989–246990, 246992, 246996, 247004–247015, 247017, 247036, 247043, 247051–247053, 247065, 247067–247068, 247072–247076, 247090, 247094, 247099, 247106–247112: *A. strahmi*—REG 622, 624, 626, 627, 631, 636; MCZ 132383, 146828, 146835, 146837, 146842, 146847, 151849, 151850, 151852, 151859–151861, 151879, 151880, 151882–151886, 151894, 151899: *A. whitemani* sp. (Monte Cristi)—REG 437–438, 440–441, 456–459, 462, 464–465, 467, 481–482, 494, 496, 498–499, 501, 505–506, 508–509, 513–514, 517: *A. w. whitemani*—BWMC 4134, 4136–4137, 4228–4230, 4232, 4234, 4384, 4429–4433, 4475, 4478–4479, 4485–4487, 4489, 4491–4493, 5457–5458, 5464, 5479–5481, 6155, 6240, 6241; REG 430–431, 434–435, 437, 473, 476–477, 485–489, 641: *A. w. breslini*—KU 246146–246153, 246155, 246164–246171: *A. w. lapidosus*—KU 246175–246176, 246180, 246184–246186, 246188–246192.