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Relationships of West Indian *Anolis* (Sauria: Iguanidae): An Approach Using Slow-Evolving Protein Loci

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ABSTRACT. – Protein variation in 49 West Indian species of the iguanid lizard genus *Anolis* was examined by sequential electrophoresis at 12 slow-evolving loci. The use of this technique nearly doubled the total number of alleles detected (121 before, 233 after). Genetic distance and parsimony analyses identified intra-island radiations on Cuba, Jamaica, Hispaniola, and Puerto Rico, and found little evidence of close inter-island relationships. In most cases, these island radiations (series) defined by protein data were supported by other data (morphology, immunology, chromosomes). No support was obtained for previously defined higher-level groupings (sections and subsections) within the genus. A revised classification is proposed that recognizes 21 series of West Indian *Anolis* (131 spp.) with distributions centering on the following islands or island groups: Cuba *(alutaceus, argillaceous, carolinensis, equestris, lucius,* and *sagrei),* Jamaica *(grahami),* Hispaniola *(chlorocyanus, christophei, cuvieri, cybotes, darlingtoni, distichus, hendersoni, monticola, semilineatus,* and *sheplani),* the Puerto Rican Bank *(cristatellus, occultus),* the northern Lesser Antilles *(bimaculatus),* and the southern Lesser Antilles *(roquet).* No categories above the level of series are recognized due to conflicting evidence for higher-level relationships. Although the existence of *Anolis* on the North Island (Hispaniola) in the Eocene or Oligocene indicates an early arrival of the genus in the West Indies, molecular dating suggests that mid-Tertiary dispersal and not early-Tertiary vicariance best explains the present distribution of the group. Extensive intra-island radiation occurred during the late-Tertiary (Miocene-Present) with relatively little inter-island dispersal among the Greater Antilles.

The iguanid lizard genus *Anolis* (sensu Williams, 1976a, b) comprises over 300 described species. In addition to being the largest amniote genus, it has figured prominently in the ecological, ethnological, and systematic literature. However, the phylogeny of this group has been a continuous challenge to systematists since the initial work done by Etheridge (1960). Williams (1976a, b) published the first comprehensive taxonomy of these animals. His classification relied primarily on osteology and divided the genus into two sections, alpha and beta. These sections originally were established by Etheridge (1960) and are defined osteologically by the absence (alpha) or presence (beta) of transverse processes on posterior caudal vertebrae. Williams further divided the alpha section into two subsections, also osteologically defined. The subsections are based on the shape of the interclavicle, which is arrow-shaped *(punctatus* subsection) or T-shaped *(carolinensis* subsection). Subsections contain series that are defined, again, by osteological characters as well as by karyological and scale characters. Series are further broken into subseries, species groups and subgroups. Most of the systematic work on *Anolis* has involved West Indian taxa (131 spp.).

Albumin immunological data presented by Wyles and Gorman (1980a) and Shochat and Dessauer (1981) did not support the alpha-beta dichotomy. They found that members of the *grahami* series (beta section) and *cristatellus* series (alpha section) clustered more closely with each other than either did with any other series within their own sections. Shochat and Dessauer erected the "Central Caribbean series complex" to include series of alpha and beta anoles that appeared to form a monophyletic group.

Guyer and Savage (1986) proposed a revised classification of *Anolis* after reana-

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lyzing several studies. These studies included karyological, immunological and osteological data, but the final phylogeny was based primarily on osteology. Williams (1989) provides a detailed critique of Guyer and Savage in which many serious errors are discussed. Additional problems with the data and methods of analysis are discussed by Cannatella and de Queiroz (1989). Both critiques recommended rejection of the phylogenetic conclusions and classification proposed by Guyer and Savage. Because no new data were presented in Guyer and Savage, and given the serious problems associated with their paper, their revised classification will not be used here, and their study will not be discussed further.

Previous molecular studies of West Indian *Anolis* have focused primarily on relatively small groups of species from Puerto Rico and the Lesser Antilles (Gorman and Dessauer, 1965, 1966; Gorman and Atkins, 1969; Yang et al., 1974; Gorman and Kim, 1975, 1976; Gorman et al., 1980a, b, 1983; Wyles and Gorman, 1980a). Those studies have been useful in clarifying the relationships of eastern Caribbean *Anolis*. However, two-thirds of West Indian *Anolis* occur on Cuba and Hispaniola (42 and 39 species, respectively; Schwartz and Henderson, 1988). Aside from population studies of one or a few species (Webster and Burns, 1973; Webster, 1975; Perez-Beato and Berovides, 1982; Case and Williams, 1984) and the immunological distance data for *cybotes* (Wyles and Gorman, 1980b), no molecular studies have been published concerning the phylogenetic relationships of species on these two major islands. The only comprehensive molecular study of West Indian *Anolis* relationships (Shochat and Dessauer, 1981) examined two Cuban and two Hispaniolan species, none of which was represented by antisera. As stated by Gorman et al. (1984), the definition of the finer divisions within *Anolis* (series, species groups) remains an unfinished taxonomic task.

Electrophoretic studies rarely involve more than 25 species (Avise and Aquadro, 1982) because of the technical aspect of comparing a large number of alleles at a locus. However, it was shown recently in a study of West Indian frogs of the genus *Eleutherodactylus* (Hedges, 1989) that this constraint can be avoided by simply using only slow-evolving loci. In that case, 84 species were examined in a single study. The specific loci to be used are chosen by first running all species at a suite of loci and then choosing those that have the fewest alleles, up to a number that can be resolved accurately on a gel. Sequential electrophoresis also can be used to reduce allelic convergence by detecting "hidden" variation (Coyne, 1982). It involves using a succession of electrophoretic conditions (usually different gel and electrode buffers) on the same samples. As much as 85–100% of the actual amino acid sequence variation can be detected using this method (Lewontin, 1985).

This study examines the phylogenetic relationships of West Indian *Anolis* using sequential electrophoresis of slow-evolving loci. Forty-nine species from all four Greater Antillean islands, Guadeloupe in the Lesser Antilles, and North America were compared. These new molecular data provide further insight into the relationships of this large genus.

Materials and Methods

Forty-nine species of West Indian *Anolis* were collected (Appendix 1): all seven Jamaican species, 26 of the 38 Hispaniolan species, 9 of 13 from the Puerto Rican Bank, 1 of 20 from the Lesser Antilles, and the single North American species. Cuban *Anolis* were attainable only through Guantanamo Bay Naval Station, thus only 5 of the 42 Cuban species were collected. *Chamaelinorops barbouri* from Hispaniola was included to provide a root for the parsimony trees (see below). Because electrophoretic differences between species and species groups usually are complete with no shared alleles (Avise, 1975; Gorman and Renzi, 1979), only one individual per species was used. Errors that might result from this sampling strategy (e.g., missing some shared alleles) would most likely affect close relationships and not the composition of species groups or larger clusters.

TABLE 1. Protein loci and electrophoretic conditions

Protein	Locus	Enzyme Commission Number[a]	Electrophoretic conditions 1 2 3 4	Stain[c]
Alcohol dehydrogenase	*Adh*	1.1.1.1	5	3
Aspartate aminotransferase	*Aat*	2.6.1.1	5	2
Carboxylesterase-D	*Esd*	3.1.1.1	5	1
Glucose-6-phosphate isomerase	*Gpi*	5.3.1.9	5 4 7	2
Lactate dehydrogenase	*Ldh-1*	1.1.1.27	3 1	3
Lactate dehydrogenase	*Ldh-2*	1.1.1.27	3 1 2 7	3
Lactoyl-glutathione lyase	*Lgl*	4.4.1.5	3 6	1
Phosphoglucomutase	*Pgm*	5.4.2.2	1 2 3 5	2
Protein 1	*Pt-1*	—	4 3 2	3
Protein 2	*Pt-2*	—	4 2 1	3
Protein 3	*Pt-3*	—	4 6	3
Pyruvate kinase	*Pk*	2.7.1.40	5 1	1

[a] Nomenclature Committee of the International Union of Biochemistry (1984).

[b] (1) Tris-citrate pH 8.0, 130 v, 6 h; (2) Tris-citrate pH 6.7, 150 v, 6 h; (3) Poulik, 300 v, ca. 5.5 h; (4) Lithium hydroxide, 350 v, ca. 7 h; (5) Tris-versene-borate, 250 v, 6 h; (6) Tris-HCl, 250 v, 4 h; (7) Tris-citrate EDTA, 300 v, 6 h.

[c] (1) Harris and Hopkinson (1976); (2) Selander et al. (1971); (3) Hedges (1986).

Lizards were transported live to the laboratory for processing or were processed in the field. Blood was collected and tissue samples (heart, liver, kidney, and leg muscle) were returned to the laboratory in liquid nitrogen. Samples were prepared for electrophoresis following the methods of Hedges (1986, 1989). Preserved voucher specimens (Appendix 1) were deposited in the United States National Museum of Natural History (USNM) and the Museum of Comparative Zoology (MCZ).

The 50 species of West Indian anoles were examined using sequential starch gel electrophoresis of 12 slow-evolving loci. Horizontal starch gel electrophoresis was employed using Connaught starch and sucrose at concentrations of 12.5% and 7.5%, respectively. Buffers were prepared following the methods of Selander et al. (1971). The primary variable chosen for sequential electrophoresis was buffer type, because it has substantial effects on mobility (Coyne, 1982). However, not all loci were resolvable on all buffer systems or in all taxa. Therefore, no more than four conditions (usually fewer) were used with each locus. The loci examined, electrophoretic conditions, and stain recipes used are listed in Table 1.

Differences and similarities in electrophoretic mobility were confirmed in comparison runs. By alternating samples that presumably represented the same allele on the same gel, very small differences in mobility were detected. This procedure was repeated for all pairs of samples representing the same presumed allele.

Alleles and multiple loci were ordered from cathode to anode. Alleles detected during the first electrophoretic run were assigned lower-case letters. Additional alleles detected during the second, third and fourth runs were assigned numbers, upper-case letters and lower-case letters, respectively. Thus, subdivided alleles retain their initial designation, but are further defined by additional designations (Appendix 2).

Genetic Distance Analyses.— UPGMA phenogram (Sneath and Sokal, 1973) was generated using modified Cavalli-Sforza distances (Nei et al., 1983) and a distance Wagner tree was produced from Cavalli-Sforza and Edwards (1967) chord distances. A discussion of the preferential use of these distances and methods is detailed in Hedges (1986). In particular, the distances of Cavalli-Sforza and Edwards (1967) have optimal properties for systematic, com-

pared with other measures such as Rogers (1972) and Nei's (1972) distances (Rogers, 1984; Felsenstein, 1985b). BIOSYS-1 (Swofford and Selander, 1981), modified to incorporate the Cavalli-Sforza distance of Nei et al. (1983), was used to produce trees from genetic distance data.

Character Analyses.— Character analyses were performed on the allelic data using PAUP (Phylogenetic Analysis Using Parsimony; version 3.0) computer software. Each locus was treated as a character and alleles as unordered character states. Where heterozygotes were encountered in which one allele was shared with other species and the other allele was unique (2.0% of data set), the unique allele was not used in the analysis because it did not provide information relevant to tree topology. In cases where both alleles of a heterozygote were shared with two or more species, the allele was chosen that would result in the least amount of homoplasy. Because this special coding of alleles was only rarely done (3 out of 600 pairs of alleles scored), PAUP was considered to be more appropriate for data analysis than the computationally-intensive frequency parsimony program FREQPARS (Swofford and Berlocher, 1987). The global branch swapping option of PAUP was used to find the most-parsimonious tree (MPT) or trees.

Confidence Limits.— A bootstrapping method (Felsenstein, 1985a) was used to obtain confidence estimates on groupings in the two distance trees and the character analysis. In each case, the loci were treated as characters and sampled randomly with replacement to obtain individual bootstrapped trees. For the distance analyses, this was accomplished with a modified version of BIOSYS-1, and the percentage of bootstrapped trees supporting each cluster were placed directly on the genetic distance tree (thus preserving branch length information). In PAUP, the bootstrap option generated a majority-rule consensus tree (Margush and McMorris, 1981) of 50 bootstrapped trees.

As Felsenstein (1985a) pointed out, a relatively large number of characters is needed to obtain 95% significance for a phylogeny. The data set used in his example and most in the literature (i. e., typical data sets in systematic) fall short of the needed characters for statistical significance. This study is no exception, but we believe that bootstrapping is a useful method to apply in all situations, if only to show relative levels of support for the different clusters on a tree.

RESULTS

There were 233 alleles detected at the 12 presumptive loci. The number of alleles per locus ranged from six to 33 with an average of 19.4. There were 121 alleles detected before sequential electrophoresis, thus the use of additional buffer systems nearly doubled the total number of alleles detected. In one species *(ricordii)* at one locus *(Pt-1),* no resolution was obtained beyond the first buffer system; those initial alleles *($Pt\text{-}1^{b,i}$)* were treated as unique in the analyses. Only 14 heterozygotes were observed, accounting for 2.3% of the total data set.

Genetic Distance Analyses.— The tree of modified Cavalli-Sforza distances (Fig. 1) has a cophenetic correlation coefficient of 0.81 and Prager and Wilson's (1976) F-value of 7.26. In general, species form intra-island groups that are concordant with morphology (taxonomy based on Williams [1976a] and Gorman et al. [1980b, 1983], or defined herein [see below]). Examples are representatives of the *chlorocyanus, cristatellus, cuvieri, cybotes, distichus, grahami, hendersoni,* and *semlineatus* series. Some previously defined morphological groups are unsupported or split into separate units. These include the *monticola* series (here the *christophei* and *monticola* series), the *occultus* series (here the *occultus* and *sheplani* series), and the *sagrei* species group (here the *sagrei* series). The Hispaniolan aquatic anole *eugenegrahami,* previously of uncertain affinities, clusters with a group from the same island, the *distichus* series. Two species in the *carolinensis* species group (here the *carolinensis* series), *carolinensis* and *porcatus,* do not cluster.

Higher-level relationships in Fig. 1 are less concordant with morphological data and more concordant with geography and previous molecular data (Gorman et al.,

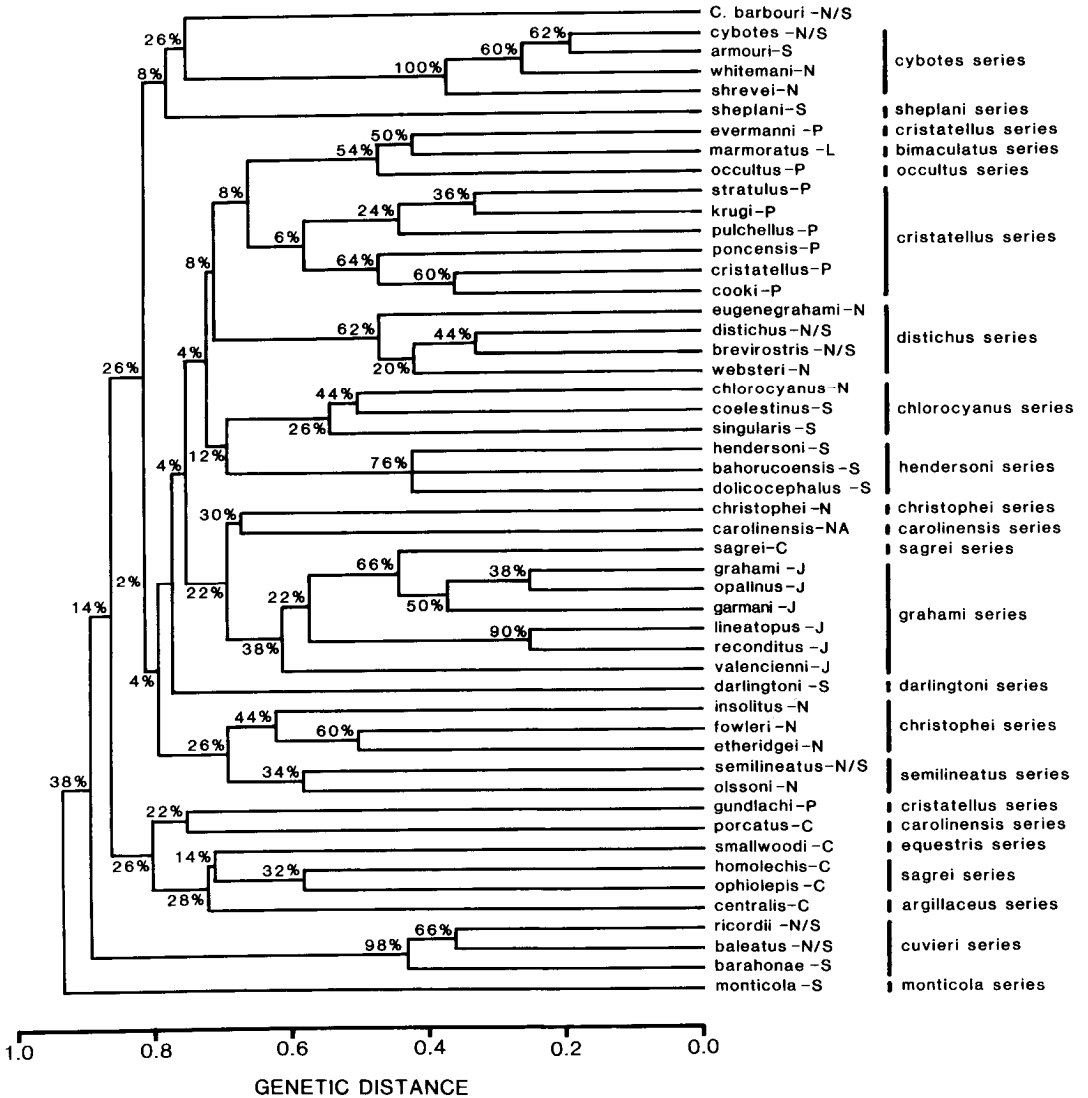


FIG. 1. Phylogenetic tree of 49 species of *Anolis* and *Chamaelinorops barbouri* constructed by UPGMA clustering of modified Cavalli-Sforza distances. Geographic abbreviations are: C, Cuba; N, Hispaniola—North Island; S, Hispaniola—South Island; J, Jamaica; L, Lesser Antilles; P, Puerto Rico; U, United States. Numbers on tree are the proportion of bootstrapped trees defining each group.

1980a, b, 1983; Shochat and Dessauer, 1981). For example, *Chamaelinorops barbouri* of Hispaniola clusters with the *cybotes* series, also from Hispaniola. The beta section anoles (*grahami* and *sagrei* series) do not form a monophyletic group, and the remaining anoles (alpha section) are not partitioned into the *carolinensis* and *punctatus* subsections (Williams, 1976a). Except for *sagrei*, the Cuban species representing several diverse morphological groupings cluster together.

The distance Wagner tree (Fig. 2) has a cophenetic correlation coefficient of 0.88 and Prager and Wilson's (1976) F-value of 3.07 (after branch-length optimization; Swofford, 1981). In general, the groupings are similar to those in the phenogram, although part of the *cristatellus* series clusters with the *hendersoni* series.

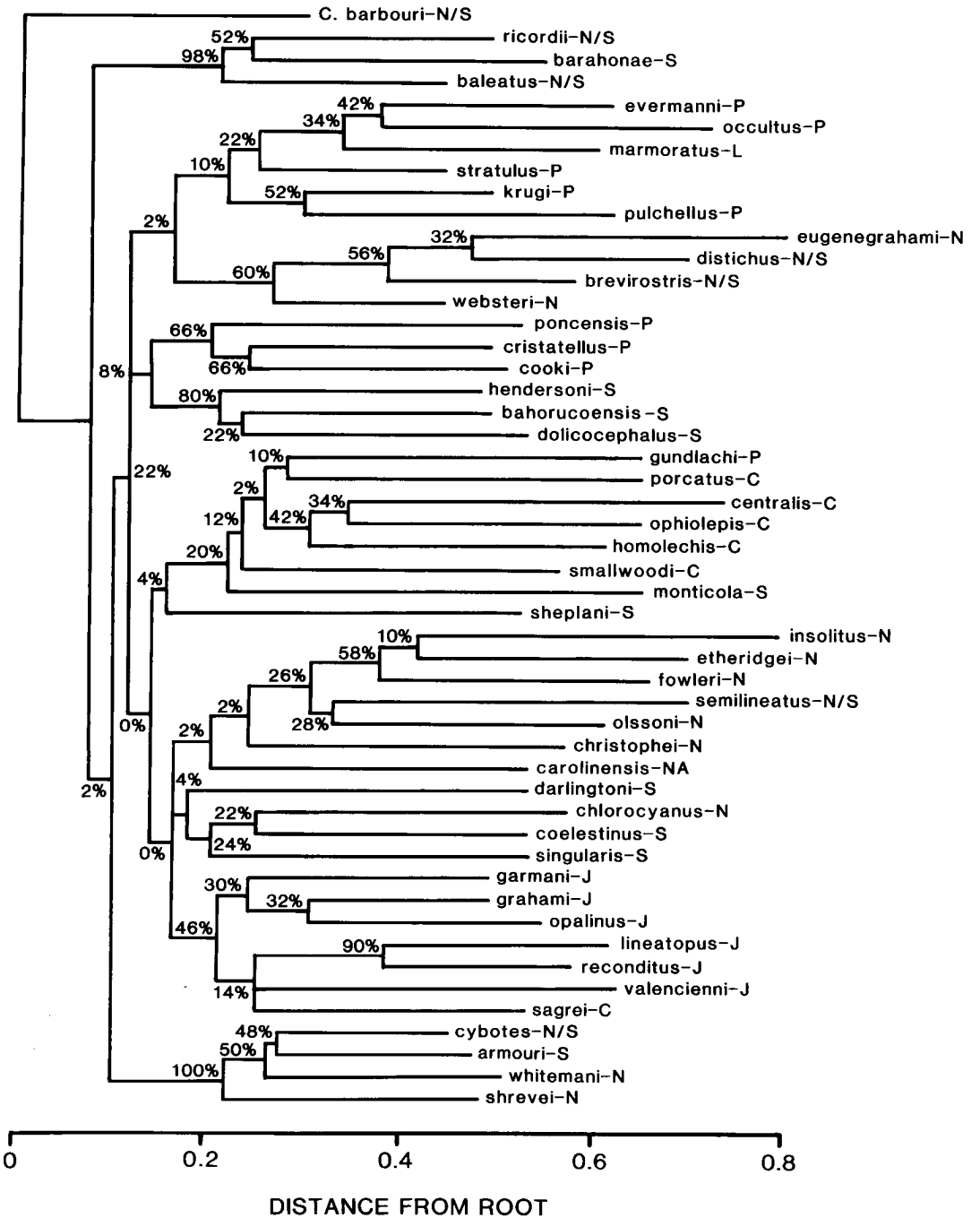


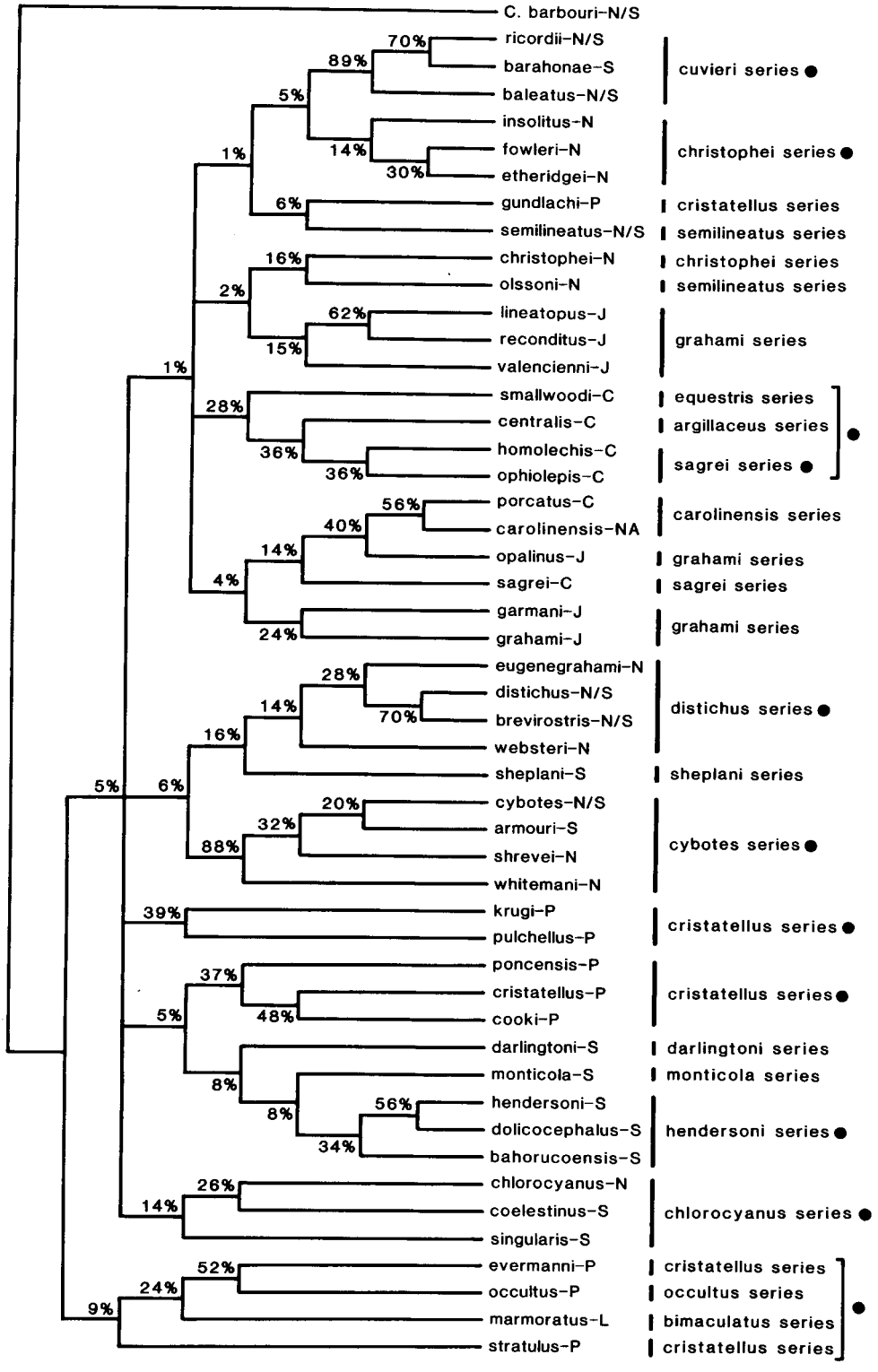
FIG. 2. Phylogenetic tree of 49 species of *Anolis* and *Chamaelinorops barbouri* constructed by the distance Wagner method using Cavalli-Sforza and Edwards (1967) chord distance and rooted with *Chamaelinorops*. Numbers on tree are the proportion of bootstrapped trees defining each group.

Character Analyses.— Only three heterozygotes (0.5% of data set) were found where both alleles were shared with other species ($Esd^{n/t}$ in *pulchellus* and *cooki* and $Pk^{c1/d}$ in *occultus).* In these cases, the allele used in the analysis was chosen to minimize homoplasy (Esd^{n} and Pk^{c1}, respectively). A character analysis was performed on the data set containing all 50 species and a large number (> 2000) of MPT's was found. Each MPT had a length of 257 and a consistency index (CI) of 0.80. Although this large number of MPT's was expected due to the small number of characters, large number of unordered character states, and large number of species, it presents a problem in that the topology of those MPT's is biased by the initial order of species. This was confirmed by comparing consensus trees generated from different orderings of species. The bootstrap tree of the PAUP analysis (Fig. 3) provides a more unbiased representation of the groupings defined in the parsimony analysis. The groups defined in this tree also show considerable agreement with morphology and geography and are identical to most of the groups defined in the distance analyses. However, two large island radiations defined in the distance analyses and previous studies, the *cristatellus* series (Puerto Rico), and the *grahami* series (Jamaica), each are broken into smaller clusters in the character parsimony analysis. Thus, the distance analyses, and specifically the UPGMA tree (Fig. 1), show slightly better agreement with morphology, geography, and previous molecular and chromosomal studies on West Indian *Anolis*.

Working with an artificially generated "known" phylogeny, Sokal (1983) also found that a phenetic analysis resulted in a better estimate of phylogeny than a cladistic analysis when a relatively small number of characters was used. Specifically, when the number of characters divided by two times the number of taxa (minus three) results in a value less than one (e.g., 0.12 in this study), then a phenogram will provide a better estimate of the true phylogeny than a cladogram (Sokal, 1985). Recent computer simulation studies using a stochastic model of evolution found similar results (Rohlf and Wooten, 1988; Sourdis and Nei, 1988). However, it is evident from these studies and others (Tateno et al., 1982; Nei et al., 1983; Fiala and Sokal, 1985; Sourdis and Krimbas, 1987; Kim and Burgman, 1988) that no single method is superior to all others in all situations.

Outgroup Rooting.— The use of *Chamaelinorops* as a root in Figs. 2 and 3 is open to debate. It has been recognized as a separate genus since its description (Schmidt, 1919), and was considered by Etheridge (1960) and Williams (1976a) to be phylogenetically outside of *Anolis.* However, albumin immunological distances (AID's) to some Hispaniolan species of *Anolis* suggested a close relationship (Wyles and Gorman, 1980b). More recently, Case and Williams (1987) have reinterpreted the immunological data of Wyles and Gorman, based on their own electrophoretic data, as evidence that albumin is "slowly evolving in one or several of these species." Evaluation of the morphological evidence pertaining to *Chamaelinorops* led Case and Williams to conclude that there was no evidence for a close relationship with "any specific group of *Anolis."* Finally, two recent cladistic analyses of morphological characters (Etheridge and de Queiroz, 1988; Cannatella and de Queiroz, 1989) came to different conclusions regarding the phylogenetic position of *Chamaelinorops.* Considering all of the above, the relationship of *Chamaelinorops* to the major anole lineages remains an unsettled question.

However, among the many alternative placements of the root within Figs. 2 and 3 (e.g., midpoint, or using any combination of series as the outgroup), none would change the major conclusions of this study: the definitions of the series. This is because the parsimony algorithm results in a single network (undirected tree) which is unaffected by placement of the root. The topology of the resulting tree maintains the branching pattern of the network except for the immediate vicinity of the root. As long as the root is not placed within a terminal series, all series in Figs. 2 and 3 will remain defined regardless of the placement of the root. Thus, although the different roots possible for Figs. 2 and 3 may


C. barbouri–N/S
ricordii–N/S
barahonae–S
baleatus–N/S
insolitus–N
fowleri–N
etheridgei–N
gundlachi–P
semilineatus–N/S
christophei–N
olssoni–N
lineatopus–J
reconditus–J
valencienni–J
smallwoodi–C
centralis–C
homolechis–C
ophiolepis–C
porcatus–C
carolinensis–NA
opalinus–J
sagrei–C
garmani–J
grahami–J
eugenegrahami–N
distichus–N/S
brevirostris–N/S
websteri–N
sheplani–S
cybotes–N/S
armouri–S
shrevei–N
whitemani–N
krugi–P
pulchellus–P
poncensis–P
cristatellus–P
cooki–P
darlingtoni–S
monticola–S
hendersoni–S
dolicocephalus–S
bahorucoensis–S
chlorocyanus–N
coelestinus–S
singularis–S
evermanni–P
occultus–P
marmoratus–L
stratulus–P
70%
89%
5%
14%
30%
1%
6%
16%
2%
62%
15%
1%
28%
36%
36%
56%
40%
14%
4%
24%
28%
14%
70%
16%
5%
6%
20%
32%
88%
39%
37%
48%
5%
8%
8%
56%
34%
26%
14%
52%
24%
9%
cuvieri series
christophei series
cristatellus series
semilineatus series
christophei series
semilineatus series
grahami series
equestris series
argillaceus series
sagrei series
carolinensis series
grahami series
sagrei series
grahami series
distichus series
sheplani series
cybotes series
cristatellus series
cristatellus series
darlingtoni series
monticola series
hendersoni series
chlorocyanus series
cristatellus series
occultus series
bimaculatus series
cristatellus series

affect some higher-level relationships, they would have essentially no effect on the series defined in this study.

DISCUSSION

The most controversial aspect of the systematic of *Anolis* has been the higher-level relationships within the genus. One of the major conflicts concerns the monophyly of the beta section, which includes approximately 120 species from Jamaica, Cuba, and the mainland (Middle and South America). Williams (1976a, 1989), considered it to be monophyletic based on a single osteological character (transverse processes on posterior caudal vertebrae; Etheridge, 1960). Albumin immunological data, however, suggest that the Jamaican beta anoles *(grahami* series) are most closely related to alpha anoles *(bimaculatus* and *cristatellus* series) in the eastern Caribbean (Gorman et al., 1980b, 1984; Shochat and Dessauer, 1981).

The results of this study provide additional molecular evidence that the beta section is not monophyletic. The *grahami* series (beta section) clusters with alpha section anoles from Hispaniola and the eastern Caribbean more closely than with most of the Cuban alpha and beta anoles examined (Fig. 1). This lends support to Shochat and Dessauer's (1981) "Central Caribbean series complex," but with the inclusion of several series of Hispaniolan alpha anoles that were not examined by those authors. With those Hispaniolan species, the complex now forms a more geographically continuous group. However, there are no defining alleles for this complex and thus its recognition as a monophyletic group remains to be established.

The new protein data also address another controversy in the systematic of *Anolis:* the affinities of the *cybotes* series. These Hispaniolan species are similar in morphology (arrow-shaped interclavicle) to Puerto Rican species in the *cristatellus* series. On the basis of osteology (Etheridge, 1960), those two series have been grouped together in the *punctatus* subsection (Williams, 1976a). Immunological (Wyles and Gorman, 1980b; Shochat and Dessauer, 1981) and previous allozyme data (Gorman et al., 1983) indicated that the *cybotes* series is not close to the *cristatellus* series. These electrophoretic data (Fig. 1) support that finding.

Many of the higher-level relationships defined in this study are associated with relatively low bootstrapped confidence limits and therefore should be treated with caution. However, some of the patterns are concordant with other data and worthy of mention. Perhaps the most interesting is the clustering of the Cuban series. The species that form this group are morphologically diverse, belonging to the *argillaceus, equestris,* and *sagrei* series (Figs. 1 and 3). This "Cuban group" is defined by $Pt\text{-}2^{b1}$, which is shared by all four species and not found elsewhere. Additionally, $Ldh\text{-}2^{e3Ab}$ clusters *centralis, homolechis,* and *ophiolepis,* and Pk^{a} further defines the subgroup of *homolechis* and *ophiolepis.*

Another higher-level pattern involves the cohort of series from the eastern Caribbean *(bimaculatus, cristatellus,* and *occultus).* These three series form a cluster that in turn joins with the *distichus* series of Hispaniola in Fig. 1 (although not in Fig. 3). Allele Esd^{n} occurs in nearly all of the species of the *cristatellus* and *distichus* series and nowhere else. The single species in the *occultus* series shares Aat^{e} with *marmoratus (bimaculatus* series) and *evermanni (cristatellus* series). Besides the obvious geographic concordance, a close relationship between the *bimaculatus* and *cristatellus* series derives support from both osteology (Etheridge, 1960) and chromosomes (Gorman et al., 1968, 1983; Gorman and Atkins, 1969). Although the albumin immunological distances between species in these two series are relatively low, the *cristatellus* series is closer to the Jamaican *grahami* series based on those data (Shochat and Dessauer,

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FIG. 3. Phylogenetic tree of 49 species of *Anolis* and *Chamaelinorops barbouri* constructed by PAUP (parsimony analysis) and rooted with *Chamaelinorops.* Numbers on tree are the proportion of bootstrapped trees defining each group. Dots indicate clusters also defined in Figs. 1 or 2.

1981). Immunological distances are not available for nearly all of the Cuban and Hispaniolan species and therefore such relationships are difficult to assess. The weight of the evidence (osteology, chromosomes, and electrophoresis) argues for an eastern Caribbean clade that includes the *bimaculatus, cristatellus,* and *distichus* series. Whether or not the *occultus* series is part of that clade (as suggested here) will have to be addressed by additional data.

A Revised Classification

The classification of West Indian *Anolis* has enjoyed considerable attention since the initial osteological study of Etheridge (1960). Williams (1976a) proposed a detailed classification, based largely on Etheridge's work. The finer divisions of Williams' classification (series and levels below) for the most part have not been challenged. This is unfortunate, because most of the recent phylogenetic studies of West Indian *Anolis* have used series as the unit of analysis, assuming them to be monophyletic. In this study, nine of the 13 series recognized by Williams (1976a) were represented by more than one species and seven were found not to be monophyletic.

The higher-level categories of Williams' classification (sections and subsections), osteologically defined, and the relationships of his series have been contested primarily by immunological data (Gorman et al., 1980a, b, 1983, 1984; Shochat and Dessauer, 1981) and partially by karyological data (Gorman, 1973; Peccinini-Scale, 1981; Gorman et al., 1983). The lack of agreement among these data sets is exemplified by the almost completely unresolved consensus tree of osteological, karyological, and immunological data (Cannatella and de Queiroz, 1989:Fig. 5). However, consensus methods may not be appropriate in this case because the lack of agreement penetrates even some of the terminal OTU's (series). Also, the comparison is confounded further by confusions over the composition of series used by Cannatella and de Queiroz, many of which do not correspond to the series of Williams (1976a) and none of which were defined (see Williams, 1989).

The results of this study are in better accord (but not complete agreement) with the immunological data. In particular, both molecular data sets indicate that the sections (alpha and beta) and subsections *(carolinensis* and *punctatus)* are not monophyletic. For that reason, we propose that these higher-level categories be abandoned.

Although little support was found for the monophyly of Williams' (1976a) series, the intra-island radiations defined in this study largely correspond to his species groups. We propose that all of these generally well-supported clades of West Indian *Anolis* be recognized as series. Although the actual category used is somewhat arbitrary (but see Williams, 1976a:5-6), it is necessary that all of the clades be recognized at the same taxonomic level. This is because their relationships presently are unresolved, or at best, poorly resolved and should not be reflected in the classification (i.e., *sedis mutabilis).* Some of the clades are large enough that the category of series is more appropriate than species group, allowing additional categories to be used for finer divisions within the clade.

In this revised classification of West Indian *Anolis* (Table 2), series are listed alphabetically by island or island group (for convenience) and species described since Williams' classification are included (no changes are proposed for the mainland series; Etheridge, 1960; Williams, 1976b). Taxonomic and distributional data for each of the species are listed in Schwartz and Henderson (1988) and distributions of the series are shown in Fig. 4. Clearly-defined clades within series are treated as species groups and subgroups (the category of superspecies is not used). The following discussion will not present morphological definitions of the series and species groups, but instead will focus on the new allelic data presented in this study. In fact, it is possible that some series defined by molecular data never will be uniquely defined on morphological grounds.

Cuba

The Alutaceus Series (10 spp.).—This is one of three series that were unrepresented here. Garrido (1980) revised this series of

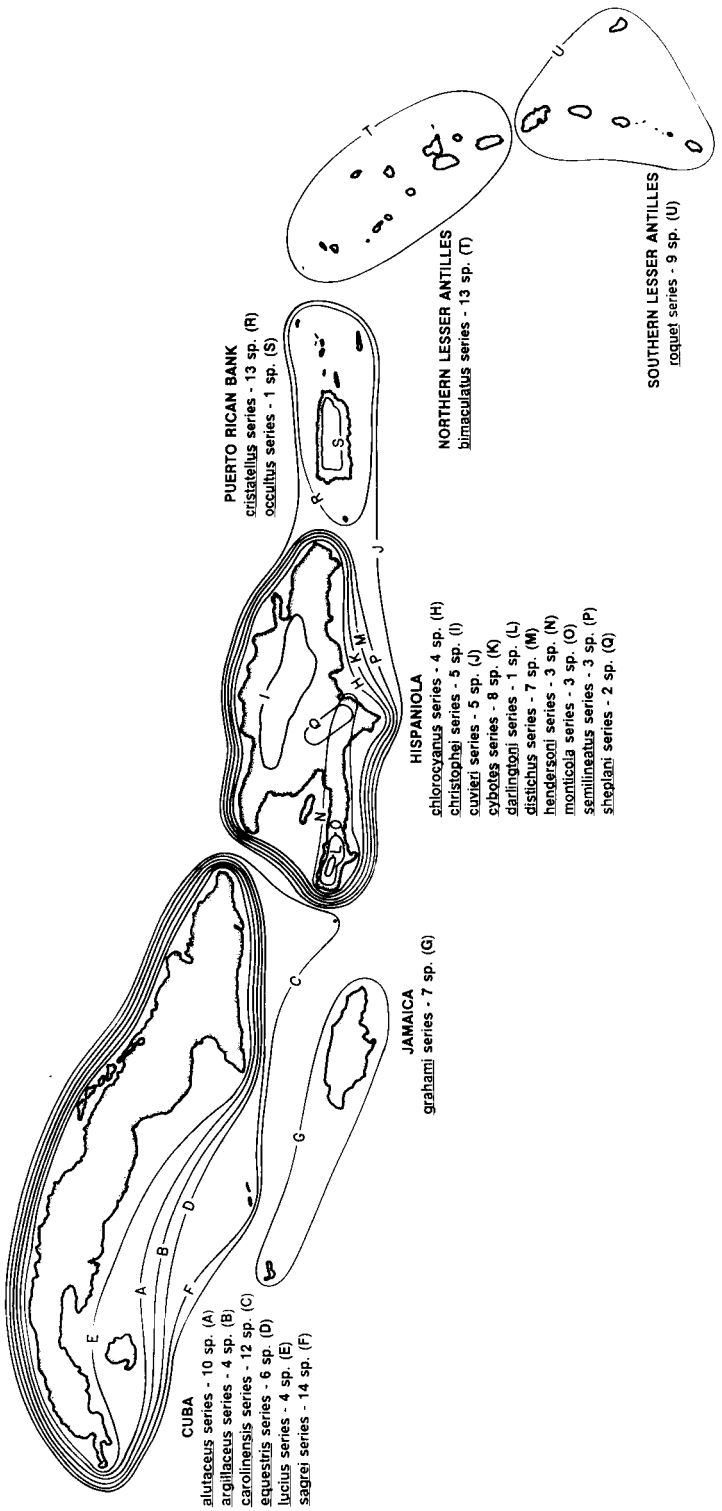

FIG. 4. Distributions of the series of West Indian *Anolis*. Ranges extending outside of the Greater and Lesser Antilles are not shown.

TABLE 2. Revised classification of West Indian *Anolis*.[1]

Cuba

alutaceus series (C)
- *alutaceus* group (C)
  - *alutaceus* (C)
  - *anfiloquioi* (C)
- *clivicola* group (C)
  - *clivicola* (C)
- *cyanopleurus* group (C)
  - *cupeyalensis* (C)
  - *cyanopleurus* (C)
  - *fugitivus* (C)
  - *juangundlachi* (C)
  - *mimus* (C)
- *spectrum* group (C)
  - *spectrum* (C)
  - *vanidicus* (C)

argillaceus series (C)
- *argillaceus* (C)
- *centralis** (C)
- *loysiana* (C)
- *pumilus* (C)

carolinensis series (B, C, CI, NI, NA)
- *carolinensis* group (B, C, CI, NI, NA)
  - *allisoni* subgroup (B, C)
    - *allisoni* (B, C)
  - *carolinensis* subgroup (B, C, CI, NI, NA)
    - *brunneus* (B)
    - [*carolinensis** (NA)]
    - *fairchildi* (B)
    - *longiceps* (NI)
    - *maynardi* (CI)
    - *porcatus** (C)
    - *smaragdinus* (B)
  - *isolepis* subgroup (C)
    - *isolepis* (C)
  - *angusticeps* group (B, C)
    - *angusticeps* (B, C)
    - *guazuma* (C)
    - *paternus* (C)

equestris series (C)
- *equestris* group (C)
  - *baracoae* (C)
  - *equestris* (C)
  - *luteogularis* (C)
  - *noblei* (C)
  - *smallwoodi** (C)
- *pigmaequestris* group (C)
  - *pigmaequestris* (C)

lucius series (C)
- *lucius* group (C)
  - *lucius* (C)
  - *argenteolus* (C)
  - *vermiculatus* group (C)
    - *bartschi* (C)
    - *vermiculatus* (C)

sagrei series (B, C, CA, CI, J, NA)
- *allogus* group (C)
  - *ahli* (C)
  - *allogus* (C)
- *homolechis* group (C)
  - *homolechis* (C)
  - *jubar** (C)
  - *quadriocellifer* (C)
- *imias* group (C)
  - *imias* (C)
- *mestrei* group (C)
  - *mestrei* (C)
- *ophiolepis* group (C)
  - *ophiolepis** (C)
- *rubribarbus* group (C)
  - *rubribarbus* (C)
- *sagrei* group (B, C, CA, CI, J, NA)
  - *bremeri* (C)
  - *delafuenti* (C)
  - *luteosignifer* (CI)
  - *nelsoni* (SI)
  - *sagrei** (B, C, CA, CI, J, NA)

Hispaniola

chlorocyanus series (N, S)
- *aliniger* group (N, S)
  - *aliniger* (N, S)
  - *singulars** (S)
- *chlorocyanus* group (N, S)
  - *chlorocyanus** (N)
  - *coelestinus** (S)

christophei series (N)
- *christophei** (N)
- *etheridgei** (N)
- *fowleri** (N)
- *insolitus** (N)
- *rimarum* (N)

cuvieri series (N, P, S)
- *cuvieri* group (P)
  - *cuvieri* (P)
- *ricordii* group (N, S)
  - *baleatus** (N)
  - *barahonae** (S)
  - *ricordii** (N, S)
- *roosevelti* group (P)
  - *roosevelti* (P)

cybotes series (N, S)
- *armouri** (S)
- *cybotes** (N, S)
- *haetianus* (S)
- *longitibialis* (S)
- *marcanoi* (N)
- *shrevei** (N)
- *strahmi* (S)
- *whitemani** (N, S)

darlingtoni series (S)
- *darlingtoni** (S)

distichus series (B, N, S)
- *altavelensis* group (S)
  - *altavelensis* (S)
- *brevirostris* group (N, S)
  - *brevirostris** (N, S)
  - *caudalis* (N, S)
  - *marron* (S)
  - *websteri** (N)
- *distichus* group (B, N, S)
  - *distichus** (B, N, S)
- *eugenegrahami* group (N)
  - *eugenegrahami** (N)

hendersoni series (S)
- *bahorucoensis** (S)
- *dolichocephalus** (S)
- *hendersoni** (S)

monticola series (S)
- *koopmani* (S)
- *monticola** (S)
- *rupinae* (S)

semilineatus series (N, S)
- *alumina* (S)
- *olssoni** (N, S)
- *semilineatus** (N, S)

sheplani series
- *placidus* (N)
- *sheplani** (S)

TABLE 2. Continued.

	Jamaica	
grahami series (J)	*grahami** (J)	*reconditus** (J)
conspersus (CI)	*lineatopus** (J)	*valencienni** (J)
*garmoni** (J)	*opalinus** (J)	
	Puerto Rican Bank	
cristatellus series (B, P, MI)	*pulchellus* group (P)	*occultus* series (P)
cristatellus group (B, P, MI)	*gundlachi** (P)	*occultus** (P)
*Cooki** (P)	*krugi** (P)	
*cristatellus** (P)	*poncensis** *(P)*	
desechensis (P)	*pulchellus** (P)	
ernestwilliamsi (P)	*stratulus* group (P, SC)	
monensis (MI)	*acutus (SC)*	
scriptus (B)	*evermanni** (P)	
	*stratulus** (P)	
	Lesser Antilles	
bimaculatus series (L)	*marmoratus** (L)	*roquet* group (L, SA)
bimaculatus group (L)	*occulatus* (L)	*griseus* subgroup (L)
bimaculatus subgroup (L)	*wattsi* group (L)	*griseus* (L)
bimaculatus (L)	*forresti* (L)	*richardi* subgroup (L, SA)
gingivinus subgroup (L)	*pogus* (L)	*richardi* (L, SA)
gingivinus (L)	*schwartzi* (L)	*roquet* subgroup (L)
nubilus (L)	*wattsi* (L)	*aeneus* (L)
sabanus (L)	*roquet* series (L, SA)	*extremus* (L)
leachi subgroup (L)	*luciae* group (L, SA)	*roquet* (L)
leachi (L)	*[blanquillanus* (SA)]	*trinitatus* subgroup (L)
marmoratus subgroup (L)	*[bonairensis* (SA)]	*trinitatus* (L)
ferreus (L)	*luciae* (L)	
lividus (L)		

[1] Series are grouped by island or island group in which most of the species occur (no relationships among the series are implied). Natural distributions are indicated by the following abbreviations: B = Bahamas, C = Cuba, CA = Central America, CI = Cayman Islands, J = Jamaica, L = Lesser Antilles, MI = Mona Island, N = North Island (Hispaniola), NA = North America, NI = Navassa Island, P = Puerto Rican Bank, S = South Island (Hispaniola), SA = South America and associated islands, SC = St. Croix, and SI = Swan Island. Species used in this study are indicated with an asterisk and brackets denote extralimital species.

grass anoles, which he considered a subgenus, and defined four species groups. Unlike Williams (1961, 1976a), he did not include the three Hispaniolan grass anoles *(alumina, olssoni,* and *semilineatus)* here placed in the *semilineatus* series.

The Argillaceus Series (4 spp.).—Williams (1976a) treated this series as a species group within his *carolinensis* series. Only one of the four species *(centralis)* was examined, and it was found to cluster with other Cuban species *(equestris* and *sagrei* series) in all three trees (Figs. 1-3).

The Carolinensis Series (12 spp.).—As defined here, this series of "green anoles" is equal to Williams' (1976a) *carolinensis* species groups, and his two subgroups *(angusticeps* and *carolinensis)* are raised to species group level. Only *carolinensis* and *porcatus* were examined here. Two alleles shared by these two species, Aat^{d} (also found in *opalinus*, but presumably convergent) and $Ldh\text{-}1^{j}$ likely are synapomorphies, but three symplesiomorphies (Lgl^{g1}, Pgm^{b3b}, and Adh^{f}) force a clustering of *gundlachi* and *porcatus* in the distance trees (Figs. 1, 2). The character-parsimony tree (Fig. 3) correctly groups *carolinensis* and *porcatus*, which are closely related species (Williams, 1976a). The relatively low AID (31) between *angusticeps* and *carolinensis* (Wyles and Gorman, 1980a) compared with other

distances from *carolinensis* supports their placement in the same series.

The Equestris Series (6 spp.).—Considered the *equestris* species group by Williams (1976a), this series contains the crown-giant anoles of Cuba. Only *smallwoodi* was examined here, and it was found to cluster with species in other Cuban series of anoles.

The Lucius Series (4 spp.).—As proposed by Williams, this series of long-limbed Cuban anoles contains two species groups *(lucius* and *vermiculatus).* None of the species was examined here.

The Sagrei Series (5 spp.).—This series corresponds to Williams (1976a) *sagrei* species group. Of the three species examined here, *homolechis* and *ophiolepis* form a group with other Cuban species, and *sagrei* clusters with Jamaican species in the *grahami* series. However, immunological data (Shochat and Dessauer, 1981) and additional electrophoretic data (Hedges and Burnell, 1990) indicate that the *grahami* series is monophyletic and does not include *sagrei.* Also, *sagrei* shares Gpi^{bC} with *ophiolepis* suggesting that it is misplaced on the tree.

Hispaniola

The Chlorocyanus Series (4 spp.).—This morphologically well-defined series of Hispaniolan green anoles consists of four species (Williams, 1965, 1976a) of which three were examined in this study: *chlorocyanus, coelestinus,* and *singulars.* The protein data (allele Esd^{l}; *coelestinus* has autapomorphic allele Esd^{m}) also support the monophyly of this group. In addition, the *chlorocyanus* group (considered a superspecies by Williams, 1976a) of *coelestinus* (South Island) and *chlorocyanus* (North Island) is supported both by protein data ($Pt\text{-}3^{hl}$ [although shared convergently with *christophei]* and $Ldh\text{-}2^{bA}$) and morphology (Williams, 1965).

The Christophei Series (5 spp.).—This complex of North Island anoles is morphologically diverse. Schwartz's (1973) original description of *fowleri* suggested a relationship with *etheridgei* based on blue eyes and crossbanding. Morphologically, *insolitus* is a twig anole which does not resemble either of the other species, however, it shares with *fowleri* a diploid chromosome number (2N = 44) not found in any other species of *Anolis* examined (Webster et al., 1972; Gorman, 1973; Peccinini-Seale, 1981; Williams, 1989). Williams (1976a) placed *etheridgei* and *fowleri* in the *monticola* series and *insolitus* in the *darlingtoni* series, but later (Williams, 1983:353), he associated *fowleri* with *darlingtoni.* However, South Island *monticola* is very different electrophoretically from either *etheridgei* or *fowleri.* Likewise, South Island *darlingtoni* is electrophoretically distinct from *insolitus.* Although morphologically divergent, the species in this series all occur on the North Island of Hispaniola and at least three *(etheridgei, fowleri,* and *insolitus)* share alleles Esd^{O} (also found in *sheplani* but considered here to be convergent) and Lgl^{b}. The clustering of *carolinensis* and *christophei* (Fig. 1) is due to the sharing of a single, presumably convergent, allele (Esd^{g}). Otherwise, *christophei* belongs in the series of North Island species to which it is morphologically and geographically associated *(christophei* also shares allele $Ldh\text{-}1^{b}$ with *fowleri).* Although not examined, the North Island species *rimarum,* placed in the *etheridgei* subgroup by Williams (1976a), is assumed to be a member of this series.

The Cuvieri Series (5 spp.).—This series of crown-giant anoles consists of five species from Hispaniola and the Puerto Rican Bank. Only the three Hispaniolan species *(baleatus, barahonae,* and *ricordii),* morphologically a well-defined group (Williams, 1962), were examined here. They share alleles Adh^{h} (also shared by *etheridgei), Gpi^{i2B}* (except *ricordii), $Ldh\text{-}2^{i2}$* (except *barahonae)* and $Pt\text{-}2^{d}$ (except *baleatus).* In addition, alleles Esd^{c} and Lgl^{a} are found only in these species.

Although Williams (1976a) placed one of the two Puerto Rican Bank species *(cuvieri)* in its own group and the other *(roosevelti)* with the three Hispaniolan species in the *ricordii* group, no corroborative data were presented. That arrangement likely is based on differences in the inscriptional rib formulae noted by Etheridge (1960). However, some features of scalation (scales across snout, lamellae under 4th toe) listed by Williams (1962:Table 2) would appear to unite the two Puerto Rican Bank species in a more geographically plausible group. Here, we take a conservative position and

place *roosevelti* in its own group without reflecting relationships of the three species groups until more data become available.

The *Cybotes Series* (8 spp.).—This complex of eight largely allopatric Hispaniolan species of the trunk/ground ecomorph was placed in the *cybotes* subseries of the *bimaculutus* series by Williams (1976a), but was raised to full series by Gorman et al. (1980b) based on albumin immunological data (Shochat and Dessauer, 1981; Wyles and Gorman, 1980a, b). The four species examined in this study *(armouri, cybotes, shrevei,* and *whitemani)* form a group in all three trees (Figs. 1-3). This series does not show affinities with any of the species of the old *bimaculatus* series in Figs. 1 and 2, although it clusters with *sheplani* and the *distichus* series in Fig. 3. Alleles Pgm^{d3} and Esd^{d} were found only in these four species of the *cybotes* series.

The Darlingtoni Series (1 sp.).—As proposed by Williams, this series included two twig anoles, *darlingtoni* and *insolitus.* The electrophoretic data indicate that the two species are morphologically convergent, and that the North Island *insolitus* is related to other North Island species *(christophei* series). The South Island *darlingtoni* is not close to any other species and therefore is placed in its own series.

The Distichus Series (7 spp.).—This complex of Hispaniolan species, except for *eugenegrahami,* initially was placed in the *acutus* series by Gorman and Atkins (1969). Williams (1976a) later placed the complex, along with two Puerto Rican species *(evermanni* and *stratulus),* in the *stratulus* subseries of the *bimaculatus* series. Based on an electrophoretic study, Gorman et al. (1980a, 1983) placed the distichoids in the *cristatellus* subseries of the *cristatellus* series. The only other molecular data for this group (Shochat and Dessauer, 1981) showed it to be equally close to both the *bimaculatus* and *grahami* series. The electrophoretic data now warrant the recognition of the *distichus* complex as a separate series of Hispaniolan species with possible affinities to the *bimaculatus* and *cristatellus* series (Fig. 1).

An important addition to this series is the species *eugenegrahami.* This species is one of two aquatic West Indian anoles (the other is the Cuban *vermiculatus).* Because of its unique lifestyle and morphology, the affinity of *eugenegrahami* has remained a question since its discovery (Schwartz, 1978). Based on osteology, Williams (in Schwartz, 1978) considered it to be in its own subseries and species group within the *bimaculatus* series of the alpha section. Upon reanalysis of the osteological data, Williams (1989) recently revised his assessment of *eugenegrahami* and placed it in the *carolinensis* subsection. The protein data (allele Adh^{i} is unique to the four species examined), however, associate it most closely with the distichoids. This arrangement is supported by the similar habitus of those species: long limbs and a relatively short snout.

The Hendersoni Series (3 spp.).—This complex of three long-snouted South Island bush anoles is well-defined morphologically (Williams, 1963; Schwartz, 1978) and electrophoretically *(*$Ldh\text{-}2^{e2}$*).* Additionally, the cluster of *dolicocephalus* and *hendersoni* is defined by allele Adh^{j} *(bahorucoensis* has the primitive allele Adh^{f}*).*

The Monticola Series (3 spp.).—As proposed by Williams, this series included four North Island species *(christophei, etheridgei, fowleri,* and *rimarum)* here placed in the *christophei* series. As defined here, the *monticola* series includes only the three South Island species that formed Williams' *monticola* subgroup. Although only one of the three species *(monticola)* was examined in this study, the three form a morphologically and chromosomally well-defined clade (Webster et al., 1972; Williams and Webster, 1974). Phonetically (Fig. 1), *monticola* is the most divergent species of *Anolis* examined. However, the parsimony trees place it with either the Puerto Rican species (Fig. 2) or the South Island species of the *hendersoni* series (Fig. 3). In the latter case, this is the result of sharing Aat^{j} with *dolicocephalus* and Esd^{r} with *dolicocephalus, bahorucoensis,* and *darlingtoni.* This suggests a possible relationship with these two South Island series *(hendersoni* and *darlingtoni).*

The Semilineatus Series (3 spp.).—This series of Hispaniolan grass anoles consists of three species (Williams, 1976a) of which two were examined in this study: *olssoni* and *semilineatus.* Both species cluster in Figs. 1 and 2 because they have a low genetic

distance, but do not cluster in Fig. 3 because they have no derived alleles in common. According to Williams (1961, 1976a), they are related to a large group of Cuban grass anoles, here considered the *alutaceus* series, of which there were no other representatives in this study.

The Sheplani Series (2 spp.).—A closely-related North Island/South Island pair of twig anoles are placed in this series. Although only *sheplani* was examined here, it was compared with *placidus* in another study using 38 protein loci and found to have a low genetic distance typical of closely related species (Hedges and Thomas, 1989). Williams (1976a) originally placed *sheplani* with *occultus* in the *occultus* series, but recently (Williams, 1989) considered them to be quite dissimilar. In this study, *sheplani* also was not found to be close to *occultus* or to any other species of *Anolis.* For that reason, it is placed in its own series with *placidus.*

Jamaica

The Grahami Series (7 spp.).—This series is clearly-defined chromosomally (Gorman, 1973), immunologically (Shochat and Dessauer, 1981) and geographically (all species occur on Jamaica and the Cayman Islands). The Cuban species *sagrei (sagrei* series) occurs on Jamaica but presumably it was introduced based on recent range expansion in Jamaica (Underwood and Williams, 1959; Williams, 1969). It was found to be outside of the Jamaican radiation in a more detailed electrophoretic study of the Jamaican species using additional loci and individuals (Hedges and Burnell, 1990). The inclusion of *valencienni* in the *grahami* series is in agreement with chromosomal (Gorman, 1973) and immunological (Shochat and Dessauer, 1981) data and indicates that it is morphologically convergent with other West Indian twig anoles (Williams, 1983; Hedges and Thomas, 1989). Three alleles define this series: Esd^{1} is shared by all members except *lineatopus* and *reconditus, Gpi*^{bA} is common to all members except *lineatopus* and *valencienni* (which both share allele Gpi^{bB}), and $Ldh\text{-}2^{e4b}$ is shared by all members except *grahami.*

The Puerto Rican Bank

The Cristatellus Series (13 spp.).—Most of the Puerto Rican Bank *Anolis* and one species each from Mona Island and the Bahamas are believed to form a single radiation (Williams, 1972) and have been placed in the *cristatellus* subseries of the *cristatellus* series (Williams, 1976a). Chromosomal (Gorman et al., 1968; Gorman and Atkins, 1969; Gorman et al., 1983), immunological (Wyles and Gorman, 1980a; Shochat and Dessauer, 1981), and electrophoretic (Gorman et al., 1983) data have added support for this clade, here treated as a series. In this study, six of the eight species from the *cristatellus* series formed a group (Fig. 1): *cooki, cristatellus, krugi, poncensis, pulchellus,* and *stratulus.* Although Esd^{n} occurs only in these species, *evermanni,* and three species of the *distichus* series, there are no defining alleles for the *cristatellus* series. The species groups recognized here are based largely on the results of Gorman et al.'s (1983) study using karyotypic and electrophoretic data.

The Occultus Series (1 sp.).—Immunological data (Shochat and Dessauer, 1981) suggested that the Puerto Rican twig anole *occultus* is not close to any particular lineage of West Indian *Anolis,* although the lowest distance reported (36; Wyles and Gorman, 1980a) is to a Puerto Rican species, *cuvieri (cuvieri* series). Also, its primitive karyotype would appear to exclude it from the chromosomally well-defined Puerto Rican Bank radiation, the *cristatellus* series (Gorman and Atkins, 1969). Morphologically, it resembles the Hispaniolan twig anole *sheplani* in some respects, leading Williams (1976a) to place the two together in the *occultus* series. However, his position recently has been revised in favor of convergence for those similarities (Williams, 1989).

In this study, *occultus* was found to cluster with species in the *bimaculatus* series *(marmoratus)* and *cristatellus* series *(evermanni)* due to a single shared allele (Aat^{e}). This suggests a possible affinity with those two geographically proximal series in Puerto Rico and the northern Lesser Antilles.

The Northern Lesser Antilles

The Bimaculatus Series (13 spp.).—The immunological data of Shochat and Dessauer (1981) provide strong evidence for the monophyly of this series, which occupies the islands north of Martinique. The species groups and subgroups listed in Table 2 correspond to the results of an electrophoretic analysis of this series (Gorman and Kim, 1976:Fig. 2). The single species examined here, *marmoratus*, showed affinities with *cristatellus* and *occultus* series of the adjacent Puerto Rican Bank.

The Southern Lesser Antilles

The Roquet Series (7 spp.).—This series of anoles appears to be distantly related to other West Indian species and has affinities with South American taxa (Williams, 1976b; Gorman et al., 1980a, b, 1983; Shochat and Dessauer, 1981). The species groups and subgroups listed here are based on the results of electrophoretic (Yang et al., 1974: Fig. 3) and immunological (Shochat and Dessauer, 1981) data. No species from this series was examined here.

BIOGEOGRAPHY

The complex geologic history of the Caribbean region undoubtedly has influenced different Antillean groups in different ways. Current models support considerable plate tectonic movement of the islands, with a proto-Antilles situated in the position of present-day Middle America in the late Cretaceus (Pindell and Dewey, 1982; Sykes et al., 1982; Mann and Burke, 1984; Ross and Scotese, 1988; Perfit and Williams, 1989). The vicariance model suggests that the proto-Antillean biota, continuous with that of North and South America, fragmented along with the islands during the Tertiary (Rosen, 1976, 1978, 1985). Before the wide acceptance of plate tectonics, dispersal was the primary model of West Indian biogeography (Arlington, 1938, 1957; Simpson, 1956; Williams, 1969), and this view has been held by some recent authors (Pregill, 1981; Briggs, 1984). Others have combined dispersal and vicariance scenarios (MacFadden, 1980, 1981; Hedges, 1982, 1989; Buskirk, 1985; Williams, 1989). However, anything more than conjecture is difficult because the geologic history still is incompletely known, the West Indian Tertiary vertebrate fossil record is poor, and we know very little about the phylogenetic relationships of most groups (Hedges, 1989; Perfit and Williams, 1989; Williams, 1989).

The biogeographic history of *Anolis* is as controversial as its relationships. Previous discussions based on morphology have stressed inter-island dispersal while at the same time have acknowledged intra-island radiation and convergence (Williams, 1969, 1972, 1983). The results of this study (Fig. 1) support previous molecular studies of *Anolis* (Gorman et al., 1980a, b, 1983, 1984; Shochat and Dessauer, 1981) in identifying a general pattern of agreement between phylogeny and geography. A similar pattern was found in an equally diverse West Indian group, frogs of the genus *Eleutherodactylus* (Hedges, 1989). This pattern suggests that inter-island dispersal was less frequent in the past than was previously believed.

An important aspect of any biogeographic analysis is the establishment of a time frame. The only pre-Quarternary West Indian *Anolis* fossils are from Eocene or Oligocene amber deposits on the North Island of Hispaniola (Rieppel, 1980; new dating in Lambert et al., 1985). Unfortunately, they do not provide the crucial information on times of divergence. For that, we must turn to the only other source available for dating: albumin immunological distances (Wyles and Gorman, 1980a; Shochat and Dessauer, 1981; Gorman et al., 1984). Using the immunological clock (1 AID = 0.60 million years) calibrated for diverse groups such as iguanid lizards (Gorman et al., 1971), frogs (Maxson et al., 1975), and mammals (Wilson et al., 1977), these data allow us to make some biogeographic inferences.

The break-up of the proto-Antilles occurred about 60–65 mya (Pindell and Dewey, 1982; Duncan and Hargraves, 1984), which corresponds to an immunological distance of about 100. The highest AID's reported within *Anolis* (81–82) are between Middle American species (Gorman et al.,

1984). Among Antillean species, and between Antillean and Middle American species, AID's range from 0-67 with many inter-island distances less than 30 (Wyles and Gorman, 1980a; Shochat and Dessauer, 1981; Gorman et al., 1984). Unless the rate of albumin evolution in *Anolis* is greatly reduced relative to other vertebrate groups studied (Wilson et al., 1977; Wyles and Gorman, 1980a), this indicates that dispersal, and not vicariance, best explains the biogeographic history of West Indian *Anolis*. The immunological data suggest a scenario involving inter-island dispersal in the mid-Tertiary followed by late-Miocene to Present intra-island speciation.

Jamaica apparently was completely submerged during the Oligocene, and has been above water only for about the last 20 million years (references in Buskirk [1985] and Hedges [1989]). Thus, the immunological dating of the Jamaican radiation (<10 my; Shochat and Dessauer, 1981:Table 1) is in agreement with that geological constraint.

Hispaniolan *Anolis* do not exhibit the major North Island/South Island dichotomy found in *Eleutherodactylus* (Hedges, 1989). Although the *christophei* series (North Island) and the *hendersoni* and *monticola* series (South Island) follow that pattern, the remaining five series contain species from both regions. This is not unexpected, however, because most presumably are recent radiations post-dating the joining of the North and South Islands and contain closely related species. This especially is evident in the allopatric distributions and high degree of morphological similarity seen in species of the *cuvieri, cybotes, distichus, hendersoni,* and *sheplani* series. The North Island/South Island sister species of the *chlorocyanus* series (Williams, 1965) and *sheplani* series (Hedges and Thomas, 1989) provide a further example of post-collisional dispersal and divergence probably associated with sea level and climatic fluctuations in the late Pliocene and Pleistocene (Pregill and Olson, 1981). The considerable morphological differences and sympatry of species in the *christophei* series, most restricted to montane areas in the Cordillera Central of the North Island, suggest that it is an older radiation.

The radiations of *Anolis* on the Puerto Rican Bank *(cristatellus* series) and the northern Lesser Antilles *(bimaculatus* series) are relatively recent (<10 my; Shochat and Dessauer, 1981:Table 1). Lesser Antillean *Anolis* on islands south of Dominica *(roquet* series) have affinities with groups in South America (Gorman et al., 1980b). Thus, it appears that the *Anolis* of the northern Lesser Antilles originated by dispersal from Puerto Rico or Hispaniola and not from South America or the southern Lesser Antilles. Also, the affinities of the *distichus* series (Hispaniola) with the *bimaculatus* and *cristatellus* series suggests Miocene dispersal from Hispaniola to Puerto Rico. The North Island and Puerto Rico have been closely associated throughout the Tertiary (Pindell and Dewey, 1982; Mann and Burke, 1984; Pindell and Barrett, 1989), which probably explains these concordant patterns of inter-island relationships.

The Bahamas are relatively flat limestone islands that have changed greatly in size with fluctuating sea levels of the Pliocene and Pleistocene. There are only four endemic Bahamian *Anolis:* three in the *carolinensis* series and one in the *cristatellus* series. There is little doubt that dispersal from Cuba (in the former case) and dispersal from Puerto Rico (in the latter case) led to the origin of these species. Thus, it would appear that the large Bahamas Platform, affixed to the North American plate since its origin in the Mesozoic (Dietz et al., 1970), has played only a minor role in the biogeographic history of West Indian *Anolis.*

Any comprehensive synthesis of Caribbean biogeography (e.g., Rosen, 1976, 1985; Buskirk, 1985) is only as strong as the data or phylogenies used. Few West Indian groups have been as well studied as *Anolis* and *Eleutherodactylus* yet many aspects of the relationships of those two groups still are unclear. The reanalysis or synthesis of previously published data sets may glean new insights, but major advances in our understanding of biogeography in this complex region likely will come from the accumulation of new data.

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APPENDIX 1

Localities and Voucher Specimens

CUBA—*centralis*—Guantanamo Bay Naval Station, John Paul Jones Hill, at peak, 151 m (USNM 286816); *homolechis*—Guantanamo Bay Naval Station, golf course, 25 m (USNM 286817); *ophiolepis* mo Bay Naval Station, golf course, 25 m (USNM 286818); *porcatus* Bay Naval Station, golf course, 25 m (USNM 286819); *smallwoodi*—Guantanamo Bay Naval Station, horse corral, 20 m (USNM 286820).

GUADELOUPE—*marmoratus* loupe, Basse Terre, Pointe de la Grande Anse, near Trois Rivieres, 0 m (USNM 286911).

HISPANIOLA—*Chamaelinorops barbouri*—Dominican Republic, Barahona, Tejunde (13 km SSW of La Guázara), 975 m (USNM 286895); *A. armouri*—Haiti, Sud Est, Gros Cheval, ca. 15 km W via logging roads (NE slope of Pic La Selle), 2020 m (USNM 286896); *bahorucoensis*—Dom. Rep., Barahona, Cabral, 15.3 km S, 6.7 km E, 1340-1370 m (USNM 286871); *baleatus*—Dom. Rep., La Vega, Jayaco, 7 km W on road to Constanza, 760 m (USNM 286872); *barahonae*—Dom. Rep., Barahona, Barahona, 19.5 km SW, 880 m (USNM 286873); *brevirostris* Rep., Pedernales, Oviedo, 5 m (USNM 286874); *chlorocyanus*—Dom. Rep., Elías Piña, Río Rio Limpio, 700 m (USNM 286875); *christophei*—Dom. Rep., La Vega, Jayaco, 7 km W on road to Constanza, 760 m (USNM 286876); *coelestinus* Sud, Camp Perrin, 13.5 km N, 680 m (USNM 286897); *cybotes*—Dom. Rep., Barahona, Barahona, vie. of, 0 m (USNM 286880); *darlingtoni*—Haiti, Grande Anse, Marché Léon, 11.2 km S, 1.9 km E, 1360 m (MCZ 173207); *distichus* Rep., Barahona, Puerto Alejándro, vic. of, 425 m (USNM 286882); *dolicocephalus*—Haiti, Sud, ca. 5-6 km NW Les Platons, ca. 900 m (USNM 286900); *etheridgei*—Dom. Rep., Elías Piña, Loma Nalga de Mace, N slope (3.2 km S, 4.0 km E Río Limpio), 1270 m (USNM 286883); *eugenegrahami*—Haiti, Nord, Plaisance, 9.0 km NE, 130 m (USNM 286901); *fowleri*—Dom. Rep., Peravia, La Horma, 13 km NW, 1770 m (USNM 266303); *hendersoni*—Haiti, Sud Est, Sequin, 15 km SW, 600 m (USNM 286902); *insolitus* Rep., Peravia, La Horma, 10.5 km NW, 1645 m (tissue voucher 102956); *monticola*—Haiti, Sud, Camp Perrin, 13.5 km N, 680 m (USNM 286905); *olssoni*—Haiti, Artibonite, Ça Soleil, 10.4 km NW, 130 m (USNM 286906); *ricordii*—Haiti, Nord Ouest, Balladé, 1 km N (7.8 km S Port-de-Paix) (USNM 286907); *semilineatus*—Dom. Rep., El Seibo, El Valle, 22 km WNW (16 km to Trepada Alta, ca. 6 km by trail to Montebonito), 76 m (USNM 286890); *sheplani*—Dom. Rep., Barahona, Cabral, 20.8 km S, 975 m (tissue voucher 102530); *shrevei*—Dom. Rep., Vega, Constanza, ca. 37 km SE (via new road to San Jose de Ocoa), 2300 m (USNM 286894); *singularis*—Haiti, Sud Est, Gros Cheval, ca. 15 km W via logging roads (NE slope of Pic La Selle), 2020 m (USNM 286908); *websteri*—Haiti, Artibonite, Ça Soleil, 10.4 km NW, 130 m (USNM 286909); *whitemani*—Haiti, Artibonite, Ça Soleil, 10.4 km NW, 130 m (USNM 286910).

JAMAICA—*garmani* Duncans, 0.3 km W at jct. with Silver Sands access road, 80 m (USNM 286836); *grahami*—St. Mary, Port Maria, 2.9 km NW (Dowling House), 5 m (USNM 286841); *lineatopus*—St. Mary, Port Maria, 2.9 km NW (Dowling House), 5 m (USNM 286847); *opalinus* Portland Cave (USNM 286850); *reconditus*—Portland, Section, ca. 1-3 km WNW (USNM 286852); *sagrei*—St. Mary, Port Maria, 2.9 km NW (Dowling House), 5 m (USNM 286858); *valencienni*—Trelawny, Quick Step, vic. of, 395 m (USNM 286860).

PUERTO RICO—*cooki*—Playa de Tamarindo, 5 m (USNM 286821); *cristatellus*—Río Piedras, University of Puerto Rico campus (USNM 286823); *evermanni*—El Yunque, vic. of peak, 1000 m (USNM 286824); *gundlachi*—El Yunque, vic. of peak, 1000 m (USNM 286825); *krugi*—El Yunque, vic. of peak, 1000 m (USNM 286826); *oc-*

cultus — El Yunque, vic. of University of Puerto Rico Biological House (USNM 286829); *poncensis* - Parguera, vic. of, 10 m (USNM 286831); *pulchellus* – Ponce, 11 km W on rt 2, 0 m (USNM 286832); *stratulus*— Río Piedras, University of Puerto Rico campus (USNM 286833).

UNITED STATES — *carolinensis* — South Carolina, Jasper County, near Tillman (USNM 286915).

APPENDIX 2. Protein variation for 50 taxa of anoline lizards at 12 Slow-Evolving Loci.

Taxon	Locus											
	Aat	Adh	Esd	Gpi	Ldh-1	Ldh-2	Lgl	Pgm	Pk	Pt-1	Pt-2	Pt-3
centralis	c	f	s	Clc	i2	e3Ab	i	blAc	f2	b3A	bl	al
homolechis	b	f	j	C1F	c3	e3Ab	g1	b2b	a	h2	bl	f3
ophiolepis	c	f	1	bC	a, c2	e3Ab	g1	d2	a	hl	bl	d
porcatus	d	f	q	h3A	j	j	g1	b2b	f1	a 3	c 2	h4
smallwoodi	f	f	h	clC	cl	c	g1	b2b	C2	g	bl	a2
rnarmoratus	f	f	1	f3	c3	e1a	g1	blAc	c l	b3B	b2	h5
C. barbouri	f	k	k	clC	f	e1a	e	a, b2a	g l	i l	b2	f9
armouri	f	e	b,d	al	g2	e4c	g1	d3	g l	i3B	b2	f8
bahorucoensis	g	f	r	h3D	c2	e2	g1	blAb	g l	d	b2	c 3
baleatus	f	h	c	i2B	b l	i2	a, c	b2b	g l	b3B	b2	i3
barahonae	f	h	c	i2B	c1	d3	a	b2b	g l	blC	d	i2
brevirostris	h	i	n	c1C	c4	e4c	g1	blAb	c l	b3B	b2	f4
chlorocyanus	f	f	f	h3D	c2	bA	g1	b2b	b	b l A	b2	hl
christophei	c	a	i	bB	b2	e5	g1	blAb	f4	b lC	b2	hl
coelestinus	h	f	m	gB	c2	bA	g1	blAb	d	blB	b2	hl
cybotes	f	e	d	d2	g2	e4c	g1	d3	g l	i3B	b2	f4
darlingtoni	f	f	r	i2D	g l	f1	h	blAb	d	—	b2	h2
distichus	h	i	n	c1C	e2	g	g1	blAb	cl	a2	b2	f6
dolicocephalus	j	j	r	h3B	c3	e2	g1	blAb	g l	a lC	b2	f7
etheridgei	c	h	o	c1E	c2	f2A	b	blAb	g l	e	b2	c 3
eugenegrahami	f	i	t	c1C	c2	h	g1	blAb	c1	blC	b2	f6
fowleri	c	g	o	d3	b2	e3B	b	blAb	g l	c	b2	f7
hendersoni	g	j	p	h2	c2	e2	g1	blAb	g l	alB	b2	f2
insolitus	c	f	o	e	c2	d2	b	b2b	g2	i2B	b2	fl
monticola	j	f	r	f3	d	e1a	f	blAa	c2	blC	cl	f10
olssoni	c	f	a	c2	b2	e4b	e	blAb	g l	b2A	b2	c 2
ricordii	f	h	c	i2A	b l	i2	a	b2b	g l	b,i	d	il
semilineatus	c	f	g	c1B	c2, i 1	e4b	d	c	g l	b2B	b2	f2
sheplani	f	c	o	gA	e1	f2Ba	g1	blAe	h	i4	b2	cl
shrevei	f	e	d	a2	h	e4c	d	d3	g l	i3B	b2	fl
singulars	f	f	f	bD	c2	bB	g1	blAc	d	a lA	b2	h6
websteri	f	i	n	c1C	c4	e3Aa	g1	blAb	g l	b3B	b2	f2
whitemani	f	e	d	d2	g3	e4d	g1	d3	g l	i3B	b2	f8
garmani	f	f	1	bA	b3	e4b	g1	blAb	h	b3C	bl	g l
grahami	f	f	1	bA	c3	e4a	g1	blAb	h	b4C	b2	g2
lineatopus	c	e	v	bB	c3	e4b	g1	blAb	i	i3C	b2	c1
opalinus	d	f	1	bA	c3	e4b	g1	blAb	e	b4C	b2	g2
reconditus	c	e	v	bA	c3	e4b	g1	blAb	i	f	b2	c 3
sagrei	c	f	1	bC	c3	e4b	g1	blAb	e	i2A	b2	a3
valencienni	a	d	1	bB	c3	e4b	g2	blAb	f3	i3C	b2	e
cooki	g	f	n, t	i l	d	e4b	g1	blAd	g l	i3A	b2	f5
cristatellus	g	f	n	d1, i2C	d	e4d	g1	blAd	g l	b3B	b2	fl1
evermanni	e	f	e, n	cID	c3	i1	g1	blAc	c l	b3B	b2	h3
gundlachi	e	f	g	cIA	c3	e4d	g1	b2b	h	b4A	a	j
krugi	i	f	n	f2	c3	bB	g1	b2b	g l	b3B	b2	f2
Occultus	e	b, f	u	c1C	c3	e1a	g1	blAc	cl, d	i3A	b2	b
poncensis	k	f	n	i2D	d	f2Bb	g1	blB, dl	g l	b4B	b2	f7
pulchellus	i	f	n, t	f1	c3	a, e1b	g1	b2b	g l	b4B	b2	f6
stratulus	f	f	n	h1	c3	d1	g1	blAc	g l	b3B	b2	f2
carolinensis	d	f	i	h3C	i	k	g1	blAb	e	alA	b2	f12