Caribbean Journal of Science, Vol. 26, No. 1-2, 31-44, 1990

University of Puerto Rico, Mayagüez

The Jamaican Radiation of *Anolis* (Sauria: Iguanidae): An Analysis of Relationships and Biogeography Using Sequential Electrophoresis

S. BLAIR HEDGES AND KRISTI L. BURNELL

Department of Zoology, University of Maryland, College Park, Maryland 20742[1]

ABSTRACT. – The relationships of the six native species of Jamaican Anolis and five additional West Indian species were examined by sequential starch gel electrophoresis at 28 loci. The protein data are in agreement with published albumin immunological data supporting the monophyly of the native Jamaican species. These six species and one from the Cayman Islands *(conspersus)* form the *grahami* series. Our protein data support the recognition of three species groups within this series: the *grahami* group *(garmani, grahami,* and *opalinus),* the *lineatopus* group *(lineatopus* and *reconditus),* and the *valencienni* group *(valencienni).* Although not examined here, *conspersus* is included in the *grahami* group based on morphology.

The biogeographic history of Jamaican *Anolis* is placed in a geological time frame with the use of the molecular clock. Colonization of Jamaica probably occurred in the mid Miocene (14 mya). Most speciation within the radiation apparently occurred during the Pliocene and may have been associated with sea level fluctuations. Although the Jamaican species have converged with species on other islands, there is little evidence of morphological and ecological convergence within the radiation.

Lizards of the genus *Anolis* are widely distributed in the West Indies, numbering over 130 species (Schwartz and Henderson, 1988). Recently, their relationships and classification have been the topic of debate. Guyer and Savage (1986) divided the genus into multiple genera based on a reanalysis of some published data sets. However, serious errors and confusions in this reanalysis led Cannatella and de Queiroz (1989) and Williams (1989) to reject that revised classification. Our recent electrophoretic study of 49 West Indian *Anolis* using slow-evolving loci (Burnell and Hedges, 1990) partially supported Williams' (1976) classification at lower levels (species groups and series) but not at higher levels (sections and subsections). We revised that classification and recognized 21 series of West Indian *Anolis.* One of those is the *grahami* series, which includes all native Jamaican species and one in the Cayman Islands.

Jamaican Anolis: An Island Radiation?

There are six native and one introduced species of *Anolis* on Jamaica. The latter, *sagrei,* is a Cuban species that likely was introduced by man based upon its rapid range expansion in Jamaica (Underwood and Williams, 1959; Williams, 1969; pers. ohs.). Five of the native species are islandwide in distribution whereas the sixth, *reconditus,* is restricted to the Blue Mountains in eastern Jamaica.

The ecology and behavior of Jamaican *Anolis* have been well-studied (Rand, 1967a, b; Schoener and Schoener, 1971; Hicks, 1973; Trivers, 1976; Jenssen, 1977; Hicks and Trivers, 1983). However, little attention has been given to the relationships and biogeography of this anole fauna. The first discussion of relationships was by Underwood and Williams (1959), who continued the recognition of *valencienni* as a separate genus *(Xiphocercus)* that included *darlingtoni* of Hispaniola. Both are relatively large, cryptic species with some similarities in pattern, scalation, and behavior. Of the remaining five species, *grahami* and *opalinus* were placed in the *grahami* group, *lineatopus* and *reconditus* in the *lineatopus* group, and *garmani* in the *garmani* group.

[1]Current address: Department of Biology, 208 Mueller Lab, Penn State University, University Park, Pennsylvania 16802 (SBH); and Department of Biological Sciences, University of California, Santa Barbara, California 93106 (KLB).

Several geographic variants of *grahami* and *lineatopus* were recognized as subspecies, and they suggested that each of the three groups on Jamaica was part of a more widely distributed group of *Anolis.*

Williams' (1976) formal classification of West Indian anoles, based largely on the osteological study of Etheridge (1960), did not recognize the genus *Xiphocercus* and instead placed *valencienni* with *sagrei* (and other Cuban species) in the *sagrei* series of *Anolis.* The five remaining Jamaican species and *conspersus* from the Cayman Islands were placed in a single series *(grahami)* and species group *(grahami).*

Shochat and Dessauer (1981) presented albumin immunological distances for the Jamaican species. Despite the limited scope of their comparative data set (only two Cuban and two Hispaniolan species were examined), low distances (8-15) among Jamaican species and higher distances (19-67) to species from other islands suggested that all six native Jamaican *Anolis* form a monophyletic group. However, because only one Jamaican species *(valencienni)* was represented by an antiserum, the relationships among those six species could not be resolved.

Chromosome data now are available for over 80 species of *Anolis* (German, 1973; Peccinini-Scale, 1981; Hedges and Hass, unpubl.) and species in the *grahami* series stand out in sharing an uncommon number, $2N = 30$ (although previously unreported, the diploid number of *reconditus* is 30; Hass and Hedges, unpubl. data). However, the situation is complex, with at least *grahami* (and apparently *opalinus)* having considerable intraspecific variation in chromosome number (30-37; Blake, 1986). Also, *conspersus,* and possibly *opalinus,* are sexually heteromorphic (German and Atkins, 1966, 1968; German, 1973). Presently, the karyotypic data provide insufficient information on the relationships of the Jamaican species.

In our recent electrophoretic study of West Indian *Anolis* (Burnell and Hedges, 1990), all six native Jamaican species *(grahami* series) and *sagrei* formed a group. However, examination of the data revealed that *sagrei* likely was misplaced on the tree due to allelic convergence with members of the *grahami* series. In that study, 12 slow-evolving loci and sequential electrophoresis were used to elucidate clusters of species (species groups and series). In this study, we focus on the relationships of the Jamaican species using an expanded data set (28 slow- and fast-evolving loci) in an effort to resolve their relationships and test the hypothesis that they form a single island radiation. The technique of sequential electrophoresis (Coyne, 1982) again is used in order to uncover hidden alleles and obtain a more robust estimate of phylogeny. For comparison, we also present an estimate of relationships based on an analysis of published morphological data.

Materials and Methods

Protein variation in 11 species of West Indian *Anolis* was examined at 28 genetic loci. Lizards were collected in the field from 1983 to 1987 (localities and sample sizes are given in Appendix 1). All six native Jamaican species and a Jamaican population of *sagrei* were obtained. Four additional species *(carolinensis, cristatellus, cybotes,* and *darlingtoni)* were included for comparison and to provide rooting for the parsimony tree. In the case of one Jamaican species, *valencienni,* two populations were examined: one from the interior of the island (Cockpit Country) and the other from the isolated Portland Ridge peninsula. The latter population, which exhibits some morphological differences, was included to assess its taxonomic status. Preserved voucher specimens are deposited in the United States National Museum of Natural History (USNM) and Museum of Comparative Zoology (MCZ).

Tissue samples (heart, liver, kidney and leg muscle) were prepared for electrophoresis following the methods of Hedges (1986, 1989a). 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 and no more than four conditions were used with each locus (see

TABLE 1. Protein loci and electrophoretic conditions.

Protein	Locus	Enzyme Commission Number[a]	Electrophoretic conditions	Stain[c]
			1 2 3 4	
Acid phosphatase	*Acp*	3.1.3.2	5	5
Aconitate hydratase	*Acon-l*	4.2.1.3	1 2	2
Aconitate hydratase	*Acon-2*	4.2.1.3	1 2	2
Adenylate kinase	*Ak*	2.7.4.3	1 2	1
Aspartate aminotransferase	*Aat*	2.6.1.1	5	3
Creatine kinase	*Ck-2*	2.7.3.2	6	2
Cytochrome b_5 reductase	*Cr*	1.6.2.2	1	2
Dipeptidase (dl-leucyl-dl-alanine)	*Dpep*	3.4.13.11	1 5	5
Fumarate hydratase	*Fh*	4.2.1.2	3	2
Glucose-6-phosphate isomerase	*Gpi*	5.3.1.9	5 4 7	3
Glycerol-3-phosphate dehydrogenase	*Gpd*	1.1.1.8	5	3
Lactate dehydrogenase	*Ldh-1*	1.1.1.27	3 1	5
Lactate dehydrogenase	*Ldh-2*	1.1.1.27	3 1 2 7	5
Lactoyl-glutathione lyase	*Lgl*	4.4.1.5	6 3	2
Malate dehydrogenase	*Mdh*	1.1.1.37	1	5
Malate dehydrogenase (NADP)	*Me*	1.1.1.40	4 5	4
Mannosephosphate isomerase	*Mpi-1*	5.3.1.8	4 5	4
Mannosephosphate isomerase	*Mpi-2*	5.3.1.8	4 5	4
Phosphoglucomutase	*Pgm-1*	2.7.5.1	1 2	3
Phosphoglucomutase	*Pgm-2*	2.7.5.1	1 2	3
Phosphoglucomutase	*Pgm-3*	2.7.5.1	1 2 3 5	3
Phosphogluconate dehydrogenase	*Pgd*	1.1.1.44	5 1	3
Protein 1	*Pt-1*	—	4 3 2	5
Protein 2	*Pt-2*	—	4 1 2	5
Protein 3	*Pt-3*	—	4 6	5
Pyruvate kinase	*Pk*	2.7.1.40	5 1	1
Tripeptidase (leu-gly-gly)	*Tpep*	3.4.13.11	1 5	5
Xanthine dehydrogenase	*Xdh*	1.2.1.37	5 6 3	5

[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) Buth and Murphy (1980); (2) Harris and Hopkinson (1976); (3) Selander et al. (1971); (4) Siciliano and Shaw (1976); (5) Hedges (1986).

Hedges, 1989a, b). For some populations, the final sample size was lower because some samples were exhausted during sequential electrophoresis. The loci examined, electrophoretic conditions, and stain recipes used are listed in Table 1.

Alleles and multiple loci were coded 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.

Genetic Distance Analysis

The electrophoretic data were analyzed using genetic distances. A UPGMA phenogram was generated using a modified Cavalli-Sforza chord distance (Nei et al., 1983). Nei's (1978) distances also were calculated for the purpose of estimating times of divergence (see below). A distance Wagner tree was produced with the Cavalli-Sforza and Edwards (1967) chord distance using the multiple addition criterion (Swofford, 1981) and was rooted with *cybotes* as the outgroup (see additional comments be-

TABLE 2. Nei's (1978) genetic distances above diagonal and modified Cavalli-Sforza distances below diagonal for 12 populations of *Anolis*. Estimates of mean heterozygosity are given on the diagonal.

Population	1	2	3	4	5	6	7	8	9	10	11	12
1 *cybotes*	(0.08)	1.854	1.645	1.512	1.994	1.644	1.858	1.887	2.184	2.171	1.573	2.182
2 *darlingtoni*	0.846	(0.05)	1.478	1.327	1.758	1.661	1.650	1.878	1.911	1.898	1.604	1.687
3 *garmani*	0.821	0.786	(0.07)	0.339	0.618	0.486	0.440	1.051	0.866	0.922	1.275	1.076
4 *grahami*	0.792	0.752	0.293	(0.09)	0.645	0.395	0.520	1.058	0.882	0.930	1.121	1.066
5 *lineatopus*	0.868	0.832	0.486	0.489	(0.09)	0.551	0.427	0.909	0.710	0.743	1.316	1.161
6 *opalinus*	0.817	0.821	0.397	0.353	0.439	(0.07)	0.525	0.918	0.856	0.858	1.023	0.969
7 *reconditus*	0.857	0.821	0.401	0.446	0.372	0.444	(0.09)	0.861	0.813	0.866	1.274	1.078
8 *sagrei*	0.857	0.846	0.653	0.667	0.606	0.606	0.596	(0.04)	1.245	1.309	1.328	1.358
9 *valencienni* (1)	0.893	0.857	0.587	0.596	0.519	0.577	0.576	0.708	(0.02)	0.076	1.634	1.265
10 *valencienni* (2)	0.893	0.857	0.606	0.604	0.535	0.580	0.596	0.724	0.081	(0.04)	1.622	1.354
11 *cristatellus*	0.799	0.805	0.731	0.690	0.732	0.657	0.734	0.754	0.807	0.807	(0.13)	1.633
12 *carolinensis*	0.893	0.821	0.667	0.667	0.693	0.627	0.679	0.741	0.719	0.739	0.807	(0.02)

low). Of the non-Jamaican species examined here, *cybotes* was the most distant in our study using slow-evolving loci (Burnell and Hedges, 1990). 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.

A bootstrapping method (Felsenstein, 1985) was used to obtain confidence estimates on groupings in the trees. The loci were treated as characters and sampled randomly with replacement to obtain individual bootstrapped trees (BIOSYS-1 was modified for this purpose). The confidence limits obtained from 100 bootstrapped trees (i.e., the number of trees defining each cluster) then were placed directly on the original trees (UPGMA and distance Wagner) of 28 different loci. This differed slightly from Felsenstein's (1985) procedure but allowed the original distance trees to be used rather than consensus trees.

Morphological Analysis

We coded the morphological data presented in Underwood and Williams (1959) for analysis with PAUP (Phylogenetic Analysis Using Parsimony; Swofford, 1989). Only phylogenetically-informative characters (characters with at least two states, each occurring in more than one taxon) were used. Two characters (scales separating supraorbital semicircles and scales between interparietal and supraorbital semicircles) were omitted because of overlapping character states. The characters and character states used are listed in Appendix 2. In the case of character "q" (pericardial pigmentation), no data were given for *garmani, sagrei,* and *valencienni* by Underwood and Williams (1959). Thus, we examined specimens of those species in the USNM for that character. All character states were treated as unordered and the trees were rooted with *sagrei.*

RESULTS

There were 161 alleles detected before sequential electrophoresis and 213 detected after, resulting in an increase of 52 alleles (32%). Only one locus was monomorphic *(Pt-2).* Allelic variation in the 27

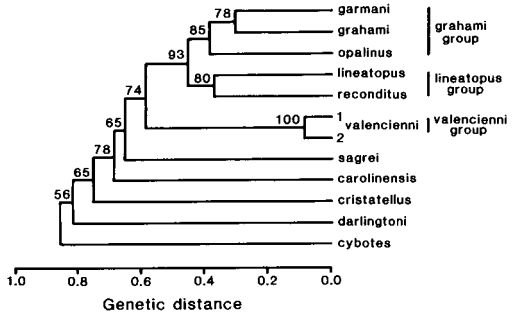

FIG. 1. Phylogenetic tree of the six native Jamaican species of *Anolis* and five non-Jamaican species constructed by UPGMA clustering (Sokal and Rohlf, 1962) of modified Cavalli-Sforza distances. Numbers on tree are bootstrapped confidence limits.

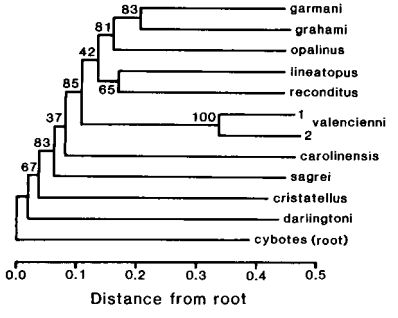

FIG. 2. Phylogenetic tree of the six native Jamaican species of *Anolis* and five non-Jamaican species constructed by the distance Wagner method using Cavalli-Sforza and Edwards (1967) chord distance and rooted with *A. cybotes.* Numbers on tree are bootstrapped confidence limits.

variable loci is given in Appendix 3. Genetic distances and heterozygosities are presented in Table 2.

Genetic Distance Analysis

The UPGMA phenogram (Fig. 1) using the modified Cavalli-Sforza distance has a cophenetic correlation coefficient of 0.98 and Prager and Wilson's (1976) F-value of 4.26. The distance Wagner tree (Fig. 2) has a cophenetic correlation coefficient of 0.99 and a Prager and Wilson's F-value of 1.51.

The phenogram (Fig. 1) and the distance Wagner tree (Fig. 2) both support the monophyly of the Jamaican species *(sagrei* is treated as a Cuban species in this study). Also, the relationships of the Jamaican species are identical in both trees. Each places *valencienni* by itself *(valencienni* group) as the most distant species and divides the remaining five species into two groups: (1) *garmani, grahami,* and *opalinus (grahami* group), and (2) *lineatopus* and *reconditus (lineatopus* group). Within the *grahami* group, *garmani* and *grahami* cluster as sister species. Confidence limits for the clusters in the two trees differ but tend to be higher in the UPGMA tree. They show relatively strong support for most clusters within the Jamaican radiation.

Of the non-Jamaican species, *sagrei* is the closest species to the Jamaican radiation in the UPGMA tree, followed by *carolinensis, cristatellus, darlingtoni,* and *cybotes.* The branching order in the distance Wagner tree is the same, except that *carolinensis* and *sagrei* are reversed. The study using slow-evolving loci (Burnell and Hedges, 1990) also found *cybotes* to be the most distant species in the UPGMA tree (Fig. 1). Rooting by the midpoint of the longest path (instead of outgroup rooting with *cybotes)* in the distance Wagner analysis produced a tree identical to Fig. 2. Also, rooting the tree with any of the non-Jamaican species (including *sagrei)* or any combination of those species does not affect the monophyly or relationships of the Jamaican species.

Morphological Analysis

All 945 possible trees of the seven species (rooted with *sagrei)* using the 17 informative morphological characters (Table 3) were generated with the ALLTREES option of PAUP. The single most-parsimonious tree (Fig. 3) has a length of 28 and a consistency index of 0.75 (excluding uninformative characters). It clusters *lineato-*

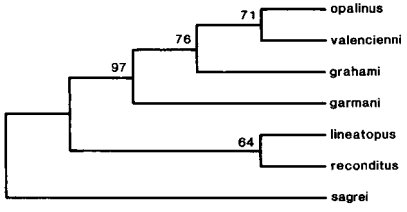

FIG. 3. The single most-parsimonious phylogenetic tree of the six native Jamaican species of *Anolis* constructed by PAUP using 17 morphological characters (Table 3) and rooted with *A. sagrei.* Numbers on tree are bootstrapped confidence limits.

TABLE 3. Morphological variation in Jamaican *Anolis*

Species	Characters[1]																
	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q
garmani	1	1	1	2	2	1	2	2	2	2	1	2	1	1	2	2	2
grahami	2	1	1	2	2	1	3	1	2	2	2	2	2	1	1	2	1
lineatopus	1	2	1	1	2	2	2	2	4	1	1	1	2	2	2	1	2
opalinus	2	1	2	2	1	1	2	3	1	2	2	2	1	2	1	1	1
reconditus	1	2	1	1	2	2	2	2	4	1	1	2	2	2	2	1	2
valencienni	2	1	2	2	1	1	1	1	1	2	2	2	1	2	2	2	2
sagrei[2]	1	2	1	2	2	1	3	2	3	1	1	1	2	2	2	1	2

[1] See Appendix 2 for descriptions of characters and character-states.
[2] Outgroup.

pus and *reconditus* in one group, and the remaining four species in another. In the latter group, *garmani* is the most distant species, with *grahami* next, and then *opalinus* and *valencienni* as sister species. Using the morphological data with the topology of the protein trees (Figs. 1 and 2), there were 9 extra steps resulting in a consistency index of 0.57.

DISCUSSION

Relationships

The electrophoretic data presented here support the monophyly of the Jamaican species. This agrees with the finding of Shochat and Dessauer (1981) based on immunological distance data and leaves little doubt that these species are the result of a single island radiation.

There is less agreement concerning the relationships of the species in the *grahami* series. Williams (1976) placed *conspersus* with *grahami* in the *grahami* superspecies, suggesting that they were sister species. We have no electrophoretic data bearing on the position of *conspersus.* Of the three species groups defined here, the *lineatopus* group is in complete agreement with morphology (Fig. 4). The two members of that group *(lineatopus* and *reconditus)* are very similar in appearance. Compared with other species in the *grahami* series, they have long snouts with well-defined frontal ridges bearing a central depression. The dewlaps usually are not uniformly pigmented; most have a central orange area with a wide pale margin. Further support for the close relationship of these two species is evident in their allopatric distribution: *reconditus* replaces *lineatopus* in the upper elevations of the Blue Mountains. Within *lineatopus,* there is considerable geographic variation in dewlap and body coloration, and four subspecies have been recognized (Underwood and Williams, 1959). Although this study focuses on species relationships, a detailed examination of variation in *lineatopus* is worthy of future investigation.

The relationships of the remaining four species *(garmani, grahami, opalinus,* and *valencienni)* not only differ between the electrophoretic (Figs. 1 and 2) and morphological (Fig. 3) analyses presented here, but also from the hypothesis of relationships (Fig. 4) proposed by Underwood and Williams (1959). The primary difference between the two trees based on morphology (Figs. 3 vs. 4) is the position of *valencienni.* Underwood and Williams considered *valencienni* to be the most distant Jamaican species, while the parsimony analysis of their data joins *opalinus* and *valencienni* as sister species. In the latter case, two features of head scalation (unkeeled frontal scales and a weakly defined canthal ridge)

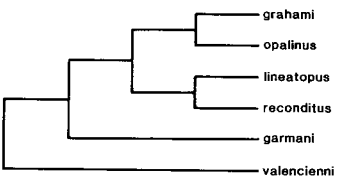

FIG. 4. Phylogenetic tree of the six native Jamaican species of *Anolis* based on the hypothesis of relationships proposed by Underwood and Williams (1959).

and the shape of the ear opening (round) are the characters primarily responsible for this pattern of relationship. The resemblance, however, is only superficial because these two species have other significant scale and pattern differences.

The groupings proposed by Underwood and Williams (1959) were based on a few selected characters deemed to be more important than others. They believed that several striking pattern similarities of *grahami* and *opalinus* (mottling in intermediate color phases, blue around the base of tail) indicated a close relationship. Also, they noted that the pericardium is deeply pigmented in these two species compared with other Jamaican taxa, and that both have a voice (apparently an antipredatory response). Two of those characters (mottling and voice) were not included in our analysis because they were not consistently scored in all species by Underwood and Williams. An additional character not mentioned by them is dewlap size: *grahami* and *opalinus* have distinctly smaller dewlaps than other Jamaican species. This difference is well-illustrated in Jenssen (1977: Fig. 2).

The grouping of *garmani* and *grahami* by our electrophoretic data also draws support from morphology. They are the only two Jamaican species with a relatively uniform green body coloration, and both can change rapidly to dark brown or black (features which also are present in *conspersus).* Dewlap color provides some support for our *grahami* group, which contains (on Jamaica) *garmani, grahami,* and *opalinus.* All three have bright yellow and/or orange dewlaps, although the non-Jamaican member of that group *(conspersus)* has a blue dewlap. The dewlap colors of *lineatopus* and *reconditus* are orange and yellow but the colors never are as intense as in the species of the *grahami* group. The dewlap color of *valencienni* varies from gray/brown to red and purple, but never is bright yellow or orange.

Our analysis of unweighed morphological data from Underwood and Williams (1959) was presented to provide a morphological "baseline" for comparison with the protein analysis. However, it is evident from the clustering of *opalinus* and *valencienni* in that tree that homoplasy is present. Although Underwood and Williams selected only a few characters that showed support for their groups, their results are in better agreement with the protein data. Because of the strong morphological evidence for a *grahami/opalinus* cluster, we feel that the relationships of the Jamaican species in the *grahami* group are best left unresolved (a trichotomy representing *garmani/grahami* and *opalinus/grahami,* but not *opalinus/garmani).* The Cayman Island species *conspersus* is here placed in the *grahami* group, probably closest to *grahami* (Williams, 1976).

Biogeography

From the viewpoint of Jamaica's biota, the most important event in the geologic history of that island was its mid-Tertiary submergence. The blanket of Oligocene limestone that covers most of the island, largely free of terrestrial sediments, strongly suggests that Jamaica was underwater for 10–15 million years (Robinson et al., 1970; Horsfield, 1973; Comer, 1974; Horsfield and Roobol, 1974; Arden, 1975; Kashfi, 1983). If submergence was complete, as the evidence suggests, then the entire flora and fauna of Jamaica must have arrived by dispersal. The first opportunity for colonization was in the late Oligocene or early Miocene (25 mya).

Because the *grahami* series is monophyletic, only one colonization of Jamaica by *Anolis* is required. Morphologically, the Jamaican species resemble some *Anolis* from Cuba and the mainland in possessing transverse processes (beta condition) on posterior caudal vertebrae (Etheridge, 1960; Williams, 1976). Immunologically (Wyles and German, 1980; Shochat and Dessauer, 1981; German et al., 1984), species from Puerto Rico *(cristatellus* series), Mexico *(gadovi),* Cuba *(equestris),* and Curaçao *(lineatus)* are the closest to the *grahami* series. The slow-evolving protein data (Burnell and Hedges, 1990) were unable to resolve the sister group of the *grahami* series and thus the origin of the Jamaican radiation remains a question to be addressed by future studies.

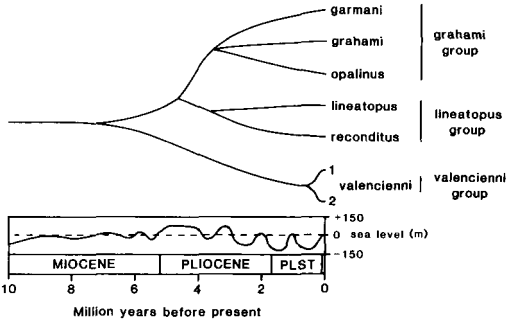

FIG. 5. Proposed phylogenetic tree of the Jamaican radiation of *Anolis (grahami* series) showing estimated times of divergence based on molecular clock calibrations. Sea level changes are from Haq et al. (1987).

There are no pre-Quaternary fossils of Jamaican *Anolis* and therefore the only means of providing a time frame for the biogeographic history of this group is with the immunological clock (Wilson et al., 1977). Although the clock has been tentatively calibrated in iguanid lizards (German et al., 1971), the calibration (one albumin immunological distance unit = 0.6 million years) is the same as that used in other groups (Maxson et al., 1975; Wilson et al., 1977).

The mean AID (albumin immunological distance) between species in the *grahami* series and those in the *cristatellus* series (sensu Burnell and Hedges, 1990) is 23.7 ± 1.5 (2 SE), which corresponds to about 14 ± 0.9 mya (mid-Miocene) as the estimated time of colonization of the island. As noted above, a variety of species have similarly low immunological distances to the *grahami* series and therefore this calibration does not require acceptance of the *cristatellus* series as its sister group. This estimated date of colonization is in accordance with the geologic history of Jamaica, because the island was fully emergent at that time.

The only portion of the phylogeny of Jamaican *Anolis* that can be dated directly with immunological distance data is the beginning of the radiation (divergence of *valencienni).* This is because *valencienni* was the only Jamaican species used as an antiserum in Shochat and Dessauer (1981). The mean AID to *valencienni* from the other Jamaican species, 11.8 ± 2.32, corresponds to a divergence date of 7 ± 1.4 mya. Estimates of divergence dates for other portions of the phylogenetic history of Jamaican *Anolis* can be obtained with Nei's (1978) genetic distances (Table 2) calibrated with the date of divergence for *valencienni* (11.8 AID = 0.84 D = 7 my). Thus, one Nei's D equals about 8.4 my, a value less than half that reported for other groups (Thorpe, 1982), but a result of the additional allelic differences detected by sequential electrophoresis. Using that calibration, the evolutionary history of the Jamaican radiation can be placed in a framework of geologic time (Fig. 5).

Except for *reconditus,* which is allopatric with *lineatopus,* the remaining Jamaican species are sympatric and thus their distributions do not aid in understanding biogeographic history of the group. Because spatial separation is believed to be the most frequent mechanism of speciation in animals (Futuyma, 1986), it is assumed that each of the sympatric species of Jamaican *Anolis* was once allopatric with its closest relative. Probably one of the most frequent causes of isolation in island populations is the raising of sea level, often creating additional islands. A comparison of sea level changes (Haq et al., 1987) with the phylogeny of the *grahami* series (Fig. 5) reveals that four out of the five possible species divergence events (bifurcations) may have taken place during the early and middle Pliocene when there were sea level highs. The general influence of these Pliocene sea level highs on speciation can be tested by examining the evolutionary history of other groups inhabiting islands and looking for unusually high rates of speciation during that time. The only comparable study is that of the 17 native Jamaican *Eleutherodactylus* (Hedges, 1989a). In that study, the radiation was estimated to begin at about 13 mya and four of the 16 divergence events occurred during the Pliocene sea level highs, not an unusually high number. Given the uncertainties involved in estimating phylogenies and dating times of divergence, it is clear that considerably more comparative data need to be gathered before sea level highs can be confidently tied to increased rates of speciation.

A more recent period of sea level and climatic fluctuation occurred during the Pleistocene (Pregill and Olson, 1981). Although the speciation events responsible for the six Jamaican *Anolis* almost certainly predated this period (Fig. 5), it is quite likely that the intraspecific variation present in *grahami* and *lineatopus* (Underwood and Williams, 1959) as well as *valencienni* (Fig. 5) is the result of those changes in sea level and vegetation.

Morphological Evolution

Although the six Jamaican *Anolis* represent a relatively recent radiation (since the late Miocene), they have diverged significantly in morphology and ecology to be convergent with species on other islands. These convergent types are called ecomorphs (Williams, 1972). On Jamaica, five of the species each are placed in a separate ecomorph while the sixth, *reconditus* (94 mm SVL), is considered to be a montane generalist and therefore outside of the ecomorph categories (Williams, 1983). Of those five remaining species, *valencienni* (80 mm) is the most specialized in being a twig-giant. Species in the twig ecomorphs (twig-giants and twig-dwarfs) commonly have short limbs, long snouts covered with enlarged scales, a relatively short prehensile tail, and cryptic coloration. Along with their cryptic morphology, they have a unique defensive behavior of remaining motionless when disturbed (Williams, 1983; Hedges and Thomas, 1989). These species search slowly for prey, and in the case of *valencienni,* they forage from the ground to high in the canopy of trees (Hicks and Trivers, 1983).

The trunk-ground ecomorph is represented on Jamaica by *lineatopus (65* mm SVL). These species are relatively large (>60 mm SVL), have long legs, and forage on the ground or low on the trunk. Also, they perch on tree trunks with their heads oriented downward and will flee in that direction when disturbed (Rand, 1967b; Williams, 1983).

The three Jamaican species of the *grahami* group *(garmani, grahami,* and *opalinus)* forage primarily in the crown of trees or high on the trunk. The largest is *garmani* (120 mm), a crown-giant. Members of that ecomorph have large heads and a vertebral crest. They are canopy foragers and are aggressive when disturbed. The other two Jamaican crown anoles are *grahami* and *opalinus.* Both are members of the trunk-crown ecomorph, subdivided by Williams (1983) into large *(grahami,* 55 mm) and small *(opalinus,* 47 mm) species. Representatives of this ecomorph are not especially distinctive in morphology. They forage on leaves and branches and will move upwards when disturbed.

A phylogenetic perspective is essential for understanding the evolution of morphological and behavioral traits that make up the ecomorphs of Greater Antillean *Anolis.* The concept itself implies convergence, yet a knowledge of relationships is necessary before convergence can be demonstrated. Although the relationships of West Indian *Anolis* still are poorly known at many levels, island radiations and morphological convergence appear to be the common theme (Williams, 1969, 1976, 1983; Burnell and Hedges, 1990). A knowledge of relationships within each of these separate radiations is a goal of future research, although significant progress already has been made with the Puerto Rican species (German et al., 1968,1980, 1983). Such fine tuning of relationships will be necessary before we can begin to understand how these complex morphologies and ecologies have evolved and converged. The relationships of the Jamaican species proposed here (Fig. 5), although still not fully resolved, offer an initial framework for analyzing this simple radiation.

The oldest member of the Jamaican radiation is *valencienni,* and this species is the most specialized in morphology and ecology. Although the Blue Mountain endemic species *reconditus* is a generalist, it probably evolved from a ground foraging *lineatopus*-like ancestor that entered habitat with vacancies in *Anolis* niches. The unifying ecological trait of the three *grahami* group species is the occupation of tree crown habitat, which suggests that the common ancestor of the group also was a crown anole.

The Jamaican radiation of *Anolis* is small and does not include several of the ecomorphs found on other islands (e.g., aquatic, grass, bush, twig-dwarf). When future studies begin to unravel the details of phylogeny in the larger Antillean radiations of this genus, it maybe possible to identify common patterns of ecomorph evolution.

Acknowledgments. —The following persons generously provided assistance in the field: M. Coggiano, C. A. Hass, C. Mayer, M. and W. Stephenson, and R. Thomas. Collecting permits and general support were received from P. Fairbairn and A. Haynes (Jamaica), G. Hermatin, E. Magny, P. Paryski, R. Pierre-Louis, and F. Sergile (Haiti), S. and Y. Inchaustegui (Dominican Republic), and E. Cardona (Puerto Rico). H. Dowling provided use of the Dowling House, Jamaica. BIOSYS-1 and PAUP computer programs were made available by D. Swofford. C. A. Hass offered helpful comments on the manuscript. Supported in part by the University of Maryland Computer Science Center and the National Science Foundation (grants BSR 8307115 to Richard Highton and BSR 8906325 to SBH).

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Accepted: 20 March 1990.

APPENDIX 1

Localities, Sample Sizes, and Voucher Specimens

HISPANIOLA — *cybotes* — Dominican Republic, Barahona, vicinity of Barahona, 0 m (*n* = 5; USNM 286877-881); *darlingtoni* — Haiti, Grande Anse, Marché Léon, 11.2 km S, 1.9 km E, 1360 m (*n* = 5; USNM 286898-899, MCZ 173207, and two tissue vouchers).

JAMAICA – *garmani* – Trelawny, 0.3 km W Duncans at jct. with Silver Sands access road, 80 m (*n* = 3; USNM 286834–836); *grahami*— St. Mary, 2.9 km NW Port Maria (Dowling House), 5 m (*n* = 5; USNM 286837-841); *lineatopus* — St. Mary, 2.9 km NW Port Maria (Dowling House), 5 m (*n* = 5; USNM 286844-848); *opalinus* — Clarendon, Portland Cave (*n* = 4; USNM 286843,286849-851); *recortditus* - Portland, ca. 1-3 km WNW Section (*n* = 2; USNM 286852-853); *sagrei* — St. Mary, 2.9 km NW Port Maria (Dowling House), 5 m (*n* = 5; USNM 286854-858); *valencienni* - 1—Trelawny, vicinity of Quick Step, 395 m (*n* = 2; USNM 286859-860); *valencienni* - 2—Clarendon, Portland Cave (*n* = 3; USNM 286861-863).

PUERTO RICO — *cristatellus* — Rio Piedras, University of Puerto Rico campus (*n* = 5; USNM 286822-823 and three tissue vouchers).

UNITED STATES — *carolinensis* — South Carolina, Jasper County, near Tillman (*n* = 5; USNM 286912-916).

APPENDIX 2

Characters and Character-States Used in Morphological Analysis

Character a—supraorbital semicircles (1) sharply keeled or (2) bluntly keeled; b—frontal area (1) flat or (2) with depression; c—frontal scales (1) keeled or (2) unkeeled; d—internarial eminence (1) present or (2) absent; e—canthal ridge (1) weak or (2) sharp; f—scales between suboculars and canthal ridge (1) 0-1 or (2) 2–3; g—interparietal size (1) variable, (2) one half supraorbital disc, or (3) approximately equal to supraorbital disc; h—size of ear opening (1) small, (2) moderate, or (3) large; i—shape of ear opening (1) round, (2) oval, (3) vertical, or (4) vertically oval; j—dewlap scales (1) keeled or (2) unkeeled; k—dorsal scales (1) keeled or (2) unkeeled; l—ventral scales (1) keeled or (2) unkeeled; m—dorsal scales in tail whorls (1) three or (2) four; n—general body color (1) bright green or (2) not bright green; o—blue at base of tail (1) present or (2) absent; p–color change (1) not present or weak or (2) pronounced; pericardium (1) deeply pigmented or (2) little or no pigment present.

APPENDIX 3. Protein variation in 12 taxa of anoline lizards at 27 variable loci.

Locus	Taxon					
	cybotes	*darlingtoni*	*garmani*	*grahami*	*lineatopus*	*opalinus*
Acp	a	c	b	b	b	a
Acon-1	a	e	c	c	c	c
Acon-2	c	g4(0.12) j (0.88)	f1 (0.17) g3(0.33) k2 (0.5)	b (0.1) f1 (0.6) g3(0.1) k2(0.2)	f2 (0.3) g2(0.6) k1(0.1)	i2 (0.88) k2(0.12)
Ak	b2	b1	b2	b2	b2	b2
Aaf	e	e	e	b (0.1) e (0.9)	c	d
Ck-2	c	b	b	b	b	b
Cr	f	h	c	c	c	c
Dpep	a (0.9) d (0.1)	j2	f1 (0.83) h (0.17)	f1 (0.5) i (0.5)	f1 (0.7) i (0.3)	f1
Fh	a	a	a	a	a (0.5) b (0.5)	a
Gpi	b1	c	a1	a1	a2	a1
Gpd	a	h	b (0.83) f (0.17)	b (0.4) c (0.6)	b	b (0.5) f (0.5)
Ldh-1	e	d	a	b	b	b
Ldh-2	b	a1	a2b	a2a	a2b	a2b
Lgl	a	b	a	a	a	a
Mdh	c	c	b	b	b	b
Me	a (0.8) c (0.2)	h2(0.2) j1(0.8)	h1	i1	j2	b (0.12) d (0.88)
Mpi-1	a (0.1) d1(0.1) f (0.8)	k	e1	e1	b (0.1) e2(0.8)	e1
Mpi-2	a1	c	b2	b2	b2	b2
Pgm-1	b3(0.1) c2(0.6) e (0.2) f (0.1)	b3	c1	c1	b2(0.8) d1(0.2)	b2(0.25) c1 (0.63) f (0.12)
Pgm-2	b	a	a	a	a	a
Pgm-3	c	ba	ba	ba	ba	ba
Pgd	g1	k (0.33) l (0.34) m (0.33)	f1 (0.17) g2(0.17) h (0.66)	g2(0.2) h (0.6) i1 (0.2)	g3	i2
Pt-1	d2B	c	b2	b1	d2A	b1
Pt-3	c2(0.9) d3(0.1)	e	f1	f2	b2	f2
Pk	e7	a	e2	e2	f (0.9) g (0.1)	b
Tpep	b	c	d1	c	d2	e2 f1
Xdh	e (0.25) f (0.75)	g	dA	f	c1	c1

APPENDIX 3. Continued.

Locus	Taxon					
	reconditus	*sagrei*	*valencienni-1*	*valencienni-2*	*cristatellus*	*carolinensis*
Acp	b	b	b (0.75) d (0.25)	b (0.17) d (0.83)	a	b
Acon-1	c	c	c	c	c	b
Acon-2	g2(0.75) k1(0.25)	f3 (0.9) i1 (0.1)	k2	k2	d (0.2) e (0.6) g1(0.2)	a
Ak	b2	b2	b2	b2	b2	a
Aat	c	c	a	b	f	d
Ck-2	b	b	a	a	b	b
Cr	c (0.75) e (0.25)	b	a	g	a (0.8) c (0.2)	d
Dpep	f2	c	g	b (0.33) j1 (0.67)	d	e
Fh	a	a	a	a	a	a
Gpi	a1	a3	a2	a2	b2	d
Gpd	b	f	g	g	e	d
Ldh-1	b	b	b	b	c	f
Ldh-2	a2b	a2b	a2b	a2b	a1	c
Lgl	a	a	c	c	a	a
Mdh	b	a	b	b	d	e
Me	i2 (0.25) k (0.75)	e2	g	g	e1(0.1) f1 (0.4) i2 (0.1) j1 (0.4)	f2
Mpi-1	f1	h	e1	c (0.17) e1 (0.83)	d2(0.5) i (0.5)	e1
Mpi-2	b2	b1	b2	b2	a2	b2
Pgm-1	b1(0.75) d1(0.25)	a	b2	b2	b2(0.25) d2(0.25) g (0.5)	b2
Pgm-2	a	a	a	a	a (0.8) b (0.1) c (0.1)	a
Pgm-3	ba	ba(0.1) a (0.9)	ba	ba	bb	ba
Pgd	g4	b1(0.1) c (0.8) d (0.1)	j	j	a2(0.9) e (0.1)	b2(0.1) al (0.8) f2 (0.1)
Pt-1	d3	d1	d2A	d2A	b1	a
Pt-3	a (0.25) b3(0.75)	b1	d1	d1	d2	c1
Pk	f	b	c	c	d	b (0.9) e2(0.1)
Tpep	d1	e1 (0.9) f2 (0.1)	h	h	g	a
Xdh	c2	b1	dB	dB	b2	a