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An Island Radiation: Allozyme Evolution in Jamaican Frogs of the Genus *Eleutherodactylus* (Leptodactylidae)

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ABSTRACT. – **The relationships of the 17 native species of Jamaican frogs of the genus *Eleutherodactylus* (subgenus *Euhyas)* and 10 additional species were examined by sequential electrophoresis at 29 loci. Whereas previous morphological studies have suggested multiple origins, the allozyme data support the monophyly of the Jamaican species. Together with immunological and chromosomal data (presented elsewhere), five species groups of Jamaican *Eleutherodactylus* were defined: *luteolus (grabhami, luteolus,* and *sisyphodemus), gossei (fuscus, gossei, junori, pantoni,* and *pentasyringos), cundalli (cavernicola, cundalli,* and *glaucoreius), jamaicensis (jamaicensis),* and *nubicola (alticola, andrewsi, griphus, nubicola,* and *orcutti).* These relationships, distributional data, and geological data suggest an evolutionary history that began with an initial colonization (probably from Cuba) not long after Jamaica emerged 25 Mya. The structural geology of the island and the uplift of the Blue Mountains in eastern Jamaica (5-10 Mya) appear to have played a large part in subsequent speciation through intra-island vicariance. In some cases, morphological evolution has been extensive and there is no known morphological trait unique to the Jamaican clade. Comparison with other Antillean island radiations of *Eleutherodactylus* confirms widespread morphological convergence through adaptation to similar environments. However, most (10) of the Jamaican species are terrestrial in habits and have retained the primitive morphological features associated with that lifestyle. Two lineage-associated traits of the subgenus *Euhyas,* liver with long and pointed left lobe and absence of vocal sac, are constant in the Jamaican radiation.**

INTRODUCTION

> "... some of the most remarkable and interesting facts in the distribution and affinities of organic forms are presented by islands" (Wallace, 1880:10)

Islands provide an ideal setting for evolutionary radiations. They have well-defined geographic boundaries, and dispersal from other areas often is restricted. The colonist that enters such a contained system may encounter a diverse environment with many unoccupied habitats. Given a sufficiently long period of time and multiple speciation events, the descendant species of that single colonizing lineage may become adapted to and occupy many of those different habitats, the result being an adaptive radiation. However, even more interesting from an evolutionary standpoint are cases where multiple island radiations have occurred, such as in the West Indian lizards of the genus *Anolis* (Williams, 1969, 1983) and frogs of the genus *Eleutherodactylus* (Hedges, 1989). It is in these cases that the concept of adaptive radiation can be more fully explored, because convergence in both morphology and ecology of species on different islands provides strong evidence that they have adapted in similar ways to similar environments.

This study and two companion studies combine allozyme, immunological, and chromosome data to explore one lineage of the multiple island radiations of *Eleutherodactylus,* the Jamaican species. The allozyme data presented herein provide a phylogenetic framework for Jamaican *Eleutherodactylus.* Albumin immunological data (Hass and Hedges, MS) elucidate higher-level relationships and allow a temporal calibration of divergence events. Finally, the rapid rate of chromosome evolution in this group (Bogart and Hedges, 1990) provides important information on close relationships and speciation events. Together, they are part of a much larger

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study attempting to outline the evolutionary history and zoogeography of Antillean *Eleutherodactylus* using molecular techniques.

JAMAICAN *ELEUTHERODACTYLUS*

Eleutherodactylus is the largest vertebrate genus (>450 spp.) and contains neotropical frogs that lay eggs on land which undergo direct development (one species is ovoviviparous). About 130 species are known from the West Indies with 100% endemism in the Greater Antilles: no single species naturally occurs on more than one of the four islands and usually a species is restricted to a relatively small area within an island (Schwartz and Henderson, 1988).

The 17 native Jamaican *Eleutherodactylus* (two additional species have been introduced) are believed to form a monophyletic group (the *luteolus* series) based on an analysis of slow-evolving allozyme loci (Hedges, 1989). However, all previous classifications based on morphology have indicated that the Jamaican *Eleutherodactylus* are not monophyletic and instead represent two or more independent colonizations (Dunn, 1926; Goin, 1954; Schwartz and Fowler, 1973; Crombie, 1977; Schwartz, 1985). Also, two recent cladistic analyses of internal and external morphological characters (G. Flores, pers. comm.; Joglar, 1986) do not support the monophyly of Jamaican *Eleutherodactylus*. Therefore, ten non-Jamaican *Eleutherodactylus* species were included in this study to test the hypothesis of monophyly. These species were selected to represent the morphological and geographical diversity of *Eleutherodactylus* in the Caribbean region.

MATERIALS AND METHODS

The 27 species and collecting localities are given in Appendix I. Sample size was five per species except *richmondi* (n = 4) and *junori* (n = 2). Methods of sample preparation are presented elsewhere (Hedges, 1986, 1989).

Sequential electrophoresis (Coyne, 1982) was used so that convergence of allelomorphs (hereafter referred to as alleles) would be minimized. The primary variable chosen was buffer type, because it has been shown to have substantial effects on mobility (Coyne, 1982). Typically, a locus was storable on gels of only two or three buffer systems. Thus, for most loci, two buffer conditions were used, except for *Aat-2*, *Glud*, and *Ldh-2*, where three conditions were used. In some cases, a higher voltage and/or longer running time was substituted for a different buffer system as an additional condition. Sequential electrophoresis was performed on 26 of the 29 loci (no resolution was obtained with *Adh*, *Icd-1*, and *Icd-2* using additional conditions).

Horizontal starch gel electrophoresis was employed using Sigma starch (S4501) at a concentration of 12.5%, except for Poulik and lithium hydroxide buffer systems, where Electrostarch was used at a concentration of 15%. Buffers were prepared following the methods of Selander et al. (1971). The loci examined and electrophoretic conditions are listed in Table 1. Assays for most of the proteins are given in Hedges (1986), with the following exceptions: *Acon-1* and *Acon-2*, 45 ml 0.2 M tris (pH 8.0), 5 ml 0.086 M *cis*-aconitic acid, 1.5 ml 0.1 M $MgCl_2$, 20 mg isocitrate dehydrogenase, 5 mg NADP, 5 mg MTT, 1 mg PMS (10 mg NADP added to gel before degassing); *Ak*, scored on gels assayed for pyruvate kinase and creatine kinase; *Aat-1* and *Aat-2*, *25* ml tris (pH 8.0), 25 ml Aat stock solution (500 ml dH_2O, 0.365 g alpha-ketoglutaric acid, 1.331 g L-aspartic acid, 2.50 g PVP-40, 0.50 g Na_2EDTA, 14.20 g Na_2HPO_4), 0.1 g fast blue BB. Sucrose was added to all gels at a concentration of 7.5% to improve band resolution (this was necessary for *Acon-1* and *Acon-2*, and especially effective for *Fh* and *Glud)*.

Differences and similarities in electrophoretic mobility were confirmed in comparison runs. To ensure detection of very small differences, samples representing the same presumed allele were alternated on the same gel (see Coyne [1982:Fig.1] for a similar example). This procedure was repeated for all pairs of samples representing the same presumed allele. Initial experi-

TABLE 1. Protein loci and electrophoretic conditions.

Protein[a]	Locus	Enzyme commission number[a]	Electrophoretic conditions		
			First	Second	Third
1. Acid phosphatase	*Acp*	3.1.3.2	10	11	
2. Aconitate hydratase	*Acon-2*	4.2.1.3	1	4	
3. Aconitate hydratase	*Acon-1*	4.2.1.3	1	4	
4. Adenylate kinase	*Ak*	2.7.4.3	1	4	
5. Alcohol dehydrogenase	*Adh*	1.1.1.1	10		
6. Aminopeptidase	*Apep*	3.4.11.11	8	3	
7. Aspartate aminotransferase	*Aat-2*	2.6.1.1	1	4	11
8. Aspartate aminotransferase	*Aat-1*	2.6.1.1	8	4	
9. Creatine kinase	*Ck*	2.7.3.2	12	4	
10. Cytochrome b_5 reductase	*Cr*	1.6.2.2	1	11	
11, Dipeptidase	*Dpep*	3.4.13.11	8	3	
12. Fumarate hydratase	*Fh*	4.2.1.2	6	4	
13. Glucose-6-phosphate isomerase	*Gpi*	5.3.1.9	10	9	
14. Glutamate dehydrogenase	*Glud*	1.4.1.3	1	2	11
15. Glutathione reductase	*Gsr-2*	1.6.4.2	12	14	
16. Glycerol-3-phosphate dehydrogenase	*Gpd*	1.1.1.8	10	13	
17. Isocitrate dehydrogenase	*Icd-2*	1.1.1.42	1[c]		
18. Isocitrate dehydrogenase	*Icd-1*	1.1.1.42	1[c]		
19. L-lactate dehydrogenase	*Ldh-2*	1.1.1.27	5	4	11
20. L-lactate dehydrogenase	*Ldh-1*	1.1.1.27	6	4	
21. Lactoylglutathione lyase	*Lgl*	4.4.1.5	12	9	
22. Malate dehydrogenase	*Mdh-2*	1.1.1.37	5	4	
23. Malate dehydrogenase	*Mdh-1*	1.1.1.37	6	11	
24. Mannose-6-phosphate isomerase	*Mpi*	5.3.1.8	10	9	
25. Phosphoglucomutase	*Pgm*	5.4.2.2	5	4	
26. Protein 2	*Pt-2*	—	8	7	
27. Protein 3	*Pt-3*	—	6	9	
28. Pyruvate kinase	*Pk*	2.7.1.40	1	11	
29. Xanthine dehydrogenase	*Xdh-1*	1.1.1.204	12	4	

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

[b](1) Tris-citrate pH 8.0, 130 v, 5 h; (2) Tris-citrate pH 8.0, 130 v, 6 h; (3) Tris-citrate pH 8.0, 140 v, 6 h; (4) Tris-citrate pH 8.0, 150 v, 6 h; (5) Tris-citrate pH 6.7, 140 v, 5 h; (6) Poulik, 240 v, ca. 6 h; (7) Poulik, 400 v, ca. 7 h; (8) Lithium hydroxide, 325 v, ca. 7 h; (9) Lithium hydroxide, 400 v, ca. 8 h; (10) Tris-versene-borate, 200 v, 5 h; (11) Tris-versene-borate, 250 v, 6 h; (12) Tris-HCl, 200 v, 3 h; (13) Tris-HCl, 250 v, 4 h; (14) Tris-HCl, 250 V, 4,5 h.

[c]Not resolvable on additional conditions.

mentation confirmed that more differences could be detected using this "alternating" method of comparison over one involving single samples run side-by-side. In order to reduce the additional workload, only alleles shared between two or more taxa were compared at an additional condition. Thus hidden variation within a species already determined to have a unique allele (or alleles) at one condition was not examined further because any additional alleles found would be autapomorphic (unique to that species) and therefore not useful in resolving relationships among species. In a few cases, samples were depleted during the sequential runs and therefore the final sample size for those species was smaller than the initial sample size.

Alleles and multiple loci were ordered from cathode to anode. Alleles detected during the first electrophoretic run were assigned numbers. If additional alleles were detected during the second and third runs,

they were assigned capital letters and small letters, respectively. This was done in a "nested" fashion so that subdivided alleles retain their initial designation, but are uniquely defined by their second and/or third additional designations (see Appendix II). In the case of multilocus systems, protein homology was assessed by the methods described in Hedges (1986).

The electrophoretic data were analyzed by three different methods. Two involve the use of genetic distances and the third is a recently developed method using parsimony.

Genetic Distance Analyses. — A UPGMA phenogram was produced using a modified Cavalli-Sforza distance (Nei et al., 1983). A distance Wagner tree using Swofford's (1981) multiple addition criterion (maxtree = 5) was generated with the Cavalli-Sforza and Edward's (1967) chord distance and rooted with *E. bransfordii* as the outgroup (a species not believed to be close to the Jamaican or other West Indian species; Lynch, 1986). The distance methods of Cavalli-Sforza and Edwards (1967) were chosen over others because they have optimal properties for phylogenetic reconstruction (Wright, 1978; Felsenstein, 1985; Rogers, 1986). A fuller discussion of the general use of these distances and methods is presented elsewhere (Hedges, 1986). Nei's (1978) distances also were generated for use in calibrating divergence events (Hass and Hedges, MS). The genetic distance data and trees were produced with BIOSYS-1 (Swofford and Selander, 1981), modified to incorporate the Cavalli-Sforza distance used by Nei et al. (1983).

Parsimony Analysis. — In this analysis, loci were treated as characters and alleles (or allelic combinations) as character states. Trees were generated using FREQPARS (Swofford and Berlocher, 1987) a parsimony program that utilizes allele frequency data and generates a minimum-length tree using linear programming. Because of the large amount of computer time needed in linear programming, global branch swapping could not be used. Instead, an initial parsimony tree was generated and its distribution of character states was examined for possible alterations in topology that might be more parsimonious. An "adjusted" topology was then input and a new tree length obtained. If that length was shorter, then the procedure was repeated on the new topology. The most-parsimonious tree was one in which no alterations in topology (among a limited number tried) could further reduce its length.

Confidence Limits. — I obtained confidence estimates for the clusters defined in the UPGMA and distance Wagner trees using the bootstrap method (Felsenstein, 1985). In each case, 29 loci were sampled randomly with replacement, and a tree was generated (BIOSYS-1 was modified for this purpose). Confidence estimates for clusters in the original UPGMA and distance Wagner trees were then determined by the frequency of those clusters in 50 bootstrapped trees. Bootstrapping was not used in the parsimony analysis due to the large amount of computer time required with FREQPARS.

RESULTS

Using standard electrophoresis, 472 alleles were detected at 29 presumed genetic loci. An additional 144 alleles were detected using sequential electrophoresis, bringing the total to 616 alleles (Appendix II). No locus was monomorphic. The number of alleles per locus varied from six *(Acp)* to 46 *(Mdh-1),* with a mean of 21.2. Genetic distances and heterozygosities for Jamaican *Eleutherodactylus* are given in Table 2. Distances between Jamaican and non-Jamaican species approached the upper limit (1.0 for Cavalli-Sforza distances and infinity for Nei's distances) and therefore are not shown. Mean heterozygosity (direct count) across all species and all loci was 6.40 (SE = 0.61), but this value probably would be higher if sequential electrophoresis was performed within each species (see Methods). Of the 641 gels used in this study, 611 (95%) involved comparisons (520 gels) or sequential runs (91 gels).

Genetic Distance Analyses

All 17 native Jamaican *Eleutherodactylus* form a monophyletic group in the phenogram (Fig. 1) and the distance Wagner tree (Fig. 2). Among those species, the two

TABLE 2. Modified Cavalli-Sforza distances (Nei et al., 1983) above diagonal and Nei's (1978) distances below diagonal. Mean heterozygosity (direct count) of each species is shown along center diagonal (with asterisk).

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1. *alticola*	0.08*	0.67	0.64	0.68	0.80	0.63	0.76	0.76	0.68	0.68	0.72	0.78	0.57	0.67	0.76	0.76	0.80
2. *andrewsi*	1.04	0.04*	0.73	0.75	0.75	0.71	0.74	0.69	0.53	0.68	0.73	0.72	0.53	0.69	0.76	0.73	0.73
3. *cavernicola*	0.95	1.27	0.06*	0.20	0.81	0.19	0.77	0.76	0.70	0.73	0.71	0.73	0.76	0.74	0.80	0.78	0.80
4. *cundalli*	1.05	1.38	0.18	0.13*	0.82	0.28	0.78	0.78	0.72	0.75	0.72	0.74	0.77	0.74	0.82	0.81	0.81
5. *fuscus*	1.50	1.36	1.69	1.82	0.05*	0.80	0.39	0.81	0.63	0.76	0.64	0.85	0.85	0.69	0.50	0.41	0.81
6. *glaucoreius*	0.91	1.20	0.19	0.29	1.74	0.10*	0.72	0.75	0.68	0.75	0.67	0.73	0.74	0.69	0.76	0.77	0.80
7. *gossei*	1.34	1.33	1.45	1.48	0.47	1.33	0.02*	0.73	0.59	0.72	0.51	0.81	0.78	0.62	0.51	0.49	0.81
8. *grabhami*	1.31	1.13	1.35	1.46	1.67	1.34	1.32	0.05*	0.70	0.79	0.66	0.56	0.73	0.72	0.80	0.75	0.70
9. *griphus*	1.09	0.71	1.19	1.20	0.98	1.17	0.85	1.16	0.05*	0.72	0.64	0.80	0.68	0.64	0.69	0.63	0.77
10. *jamaicensis*	1.05	1.11	1.26	1.30	1.38	1.34	1.23	1.51	1.24	0.06*	0.75	0.83	0.70	0.59	0.76	0.69	0.77
11. *junori*	1.18	1.30	1.20	1.23	0.98	1.10	0.72	1.06	1.05	1.37	0.12*	0.72	0.75	0.62	0.67	0.62	0.79
12. *luteolus*	1.46	1.27	1.31	1.33	1.93	1.26	1.67	0.80	1.63	1.79	1.26	0.00*	0.76	0.79	0.83	0.83	0.61
13. *nubicola*	0.83	0.70	1.34	1.40	1.90	1.29	1.51	1.24	1.10	1.19	1.36	1.39	0.07*	0.69	0.79	0.80	0.80
14. *orcutti*	1.03	1.13	1.30	1.30	1.14	1.17	0.94	1.24	1.01	0.85	0.99	1.55	1.11	0.05*	0.72	0.66	0.73
15. *pantoni*	1.32	1.36	1.51	1.71	0.70	1.50	0.71	1.53	1.16	1.35	1.12	1.72	1.50	1.23	0.05*	0.40	0.87
16. *pentasyringos*	1.31	1.25	1.49	1.55	0.49	1.52	0.61	1.37	0.94	1.08	0.96	1.74	1.55	0.99	0.46	0.11*	0.80
17. *sisyphodemus*	1.48	1.24	1.52	1.60	1.61	1.50	1.61	1.18	1.41	1.36	1.50	0.90	1.53	1.24	1.96	1.48	0.11*

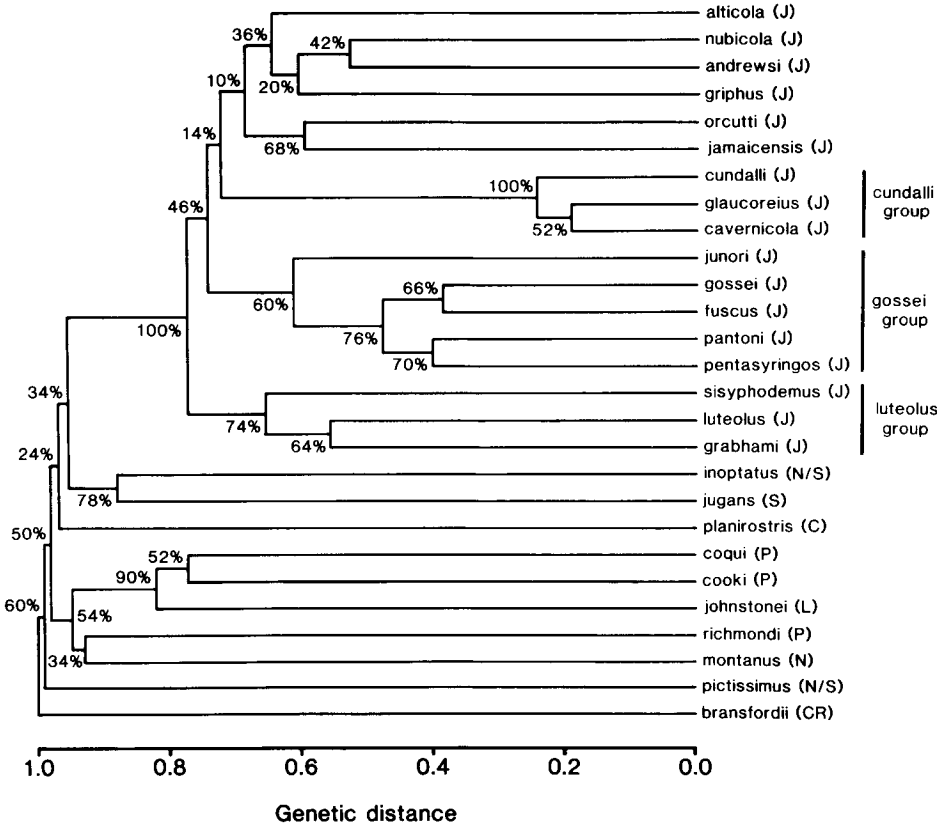

FIG. 1. Phylogenetic tree of modified Cavalli-Sforza distances constructed by the UPGMA method (Sneath and Sokal, 1973). Prager and Wilson's (1976) *F* value = 2.63. Numbers on tree are confidence estimates (percentage of 50 bootstrapped trees defining a group). Geographic areas are indicated in parentheses: C = Cuba, CR = Costa Rica, J = Jamaica, L = Lesser Antilles, N = North Island (Hispaniola), P = Puerto Rico, and S = South Island (Hispaniola).

trees differ in details of the relationships. However, some groups appear in both trees: (1) *cavernicola, cundalli,* and *glaucoreius,* (2) *grabhami, luteolus,* and *sisyphodemus,* (3) *orcutti* and *jamaicensis,* and (4) *fuscus, gossei, junori, pantoni,* and *pentasyringos* (with the latter two as sister species). Three of the remaining four species *(andrewsi, griphus,* and *nubicola)* form a group in the phenogram (Fig. 1) but the four species form two distantly related pairs *(alticola* and *nubicola; andrewsi* and *griphus)* in the other tree (Fig. 2). Relationships among the groups of species in the two trees do not agree.

Confidence estimates obtained by bootstrapping are indicated on the two trees. The 17 native Jamaican species formed a group in all 50 (100%) bootstrapped UPGMA trees and 47 of 50 (94%) bootstrapped distance Wagner trees. Three Jamaican species *(cundalli, cavernicola,* and *glaucoreius)* appeared as a group in all bootstrapped trees. Other groupings were defined in a smaller percentage of bootstrapped trees.

Character Analysis

Due to the virtual absence of similarity between the ingroup and the outgroup *(bransfordii),* the latter could not be used to root the tree in the character analysis. Among the remaining 26 species, the genetic distance analyses strongly supported the group containing all Jamaican species, and therefore it was considered the ingroup and the remaining nine West Indian

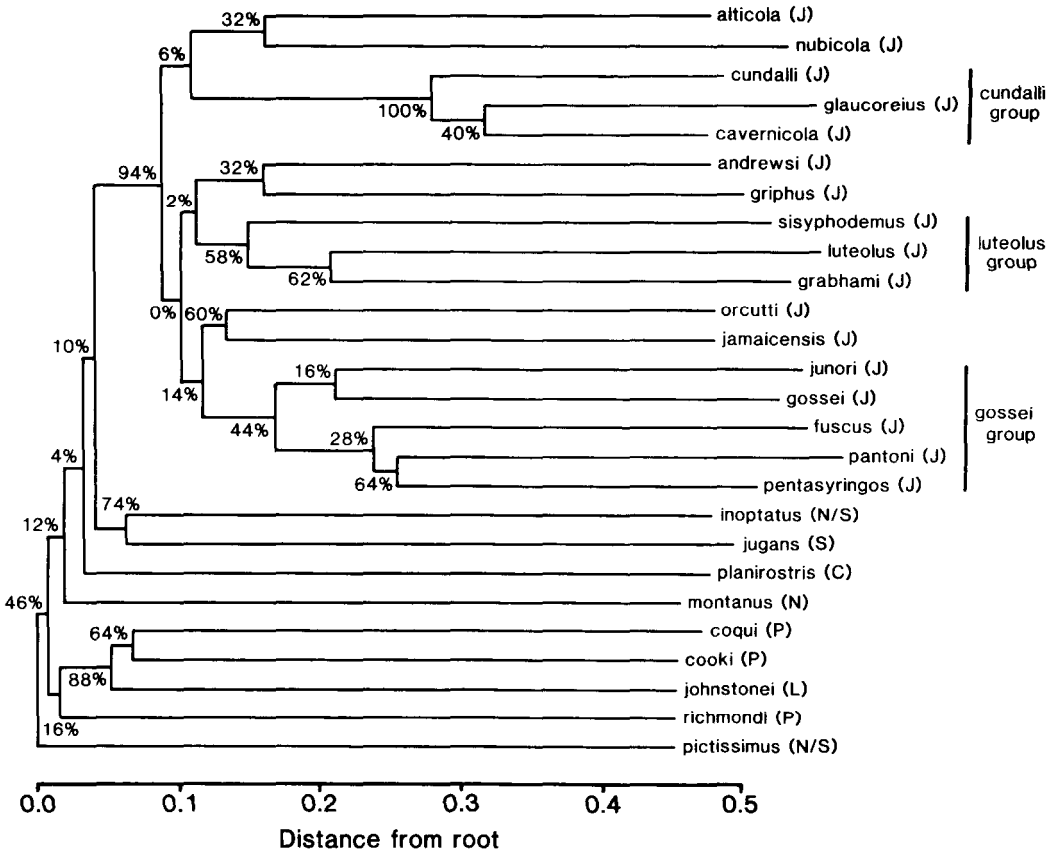

FIG. 2. Phylogenetic tree of Cavalli-Sforza chord distances (unoptimized branch lengths) constructed by distance Wagner method using multiple addition criterion (Swofford, 1981) and rooted with *Eleutherodactylus bransfordii* (not shown). Prager and Wilson's (1976) *F* value = 1.45 (after optimization). Abbreviations as in Fig. 1

species were treated as an outgroup. Studies of slow-evolving allozyme loci (Hedges, 1989) and albumin immunological distances (Hass and Hedges, MS) also support the monophyly of the Jamaican species.

Three most-parsimonious trees of equal length (466.3) were obtained which were shorter than the UPGMA (478.8), distance Wagner (476.2), and initial Wagner Parsimony (not shown: 475.1) topologies of the Jamaican species (lengths for those latter three trees were obtained by using FREQPARS with coded topologies). The three most-parsimonious trees differ only in the branching order of three major groups of Jamaican *Eleutherodactylus:* (A) *grabhami, luteolus,* and *sisyphodemus;* (B) *fuscus, gossei, griphus, junori, pantoni,* and *pentasyringos;* and (C) *alticola, andrewsi, cavernicola, cundalli, glaucoreius, jamaicensis, nubicola,* and *orcutti.* These three groups are similar to those obtained in the UPGMA distance analysis (except for the placement of *griphus),* although the branching order of species within the groups differs. A cladogram (Fig. 3) showing character-state changes (listed in Appendix III) in Jamaican *Eleutherodactylus* is a strict consensus tree of those three most-parsimonious trees of the Jamaican species.

DISCUSSION

Phylogeny: Allozymes

The genetic distance data strongly support the monophyly of native Jamaican

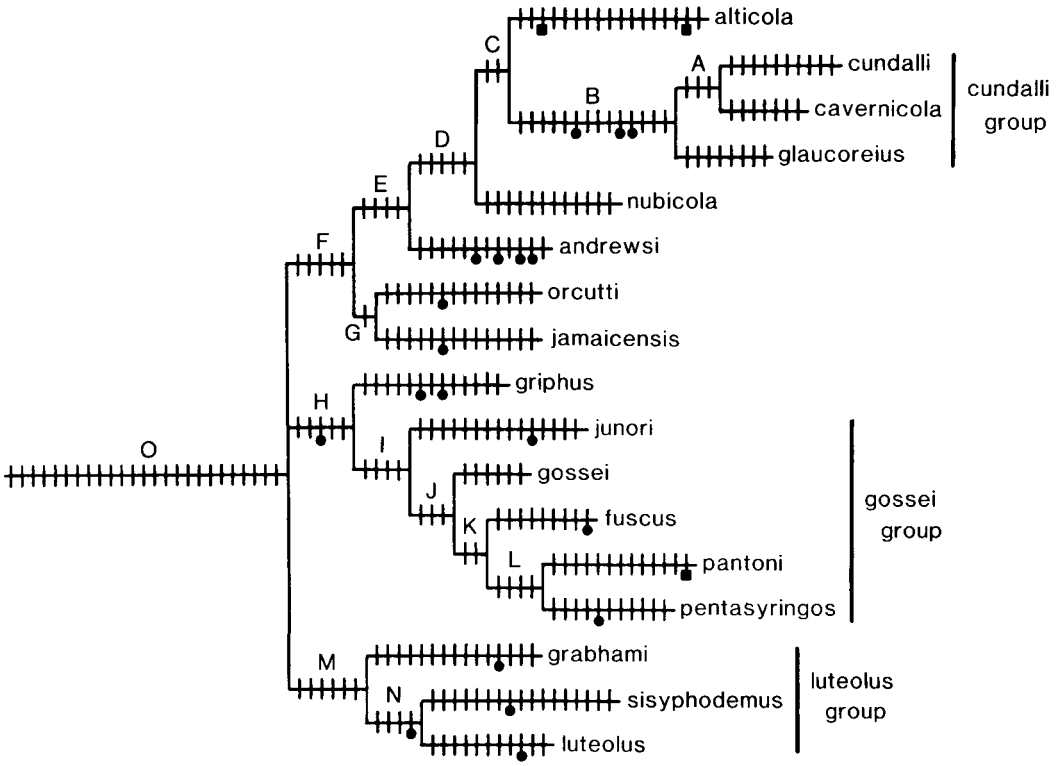

FIG. 3. Most-parsimonious cladogram of Jamaican *Eleutherodactylus* (strict consensus of three most-parsimonious trees) using FREQPARS (Swofford and Berlocher, 1987) and rooted with 9 non-Jamaican species. Changes in character states (alleles or allelic combinations) are indicated by cross bars and are listed in Appendix III. Closed circles (convergence) and closed squares (reversals) are indicated. Total length of each of the three most-parsimonious trees is 466.3

Eleutherodactylus. At three loci, 16 of the 17 Jamaican species share the same allele not found in the other species: Adh^{3} (all except *jamaicensis),* Cr^{8B} (all except *gossei),* and $Xdh\text{-}1^{4C}$ (all except *pantoni).* In each case, the exceptional species had a unique allele (autapomorphy). An additional allele, $Icd\text{-}1^{9}$, is present in all Jamaican species (except *fuscus), inoptatus* (Hispaniola), and *richmondi* (Puerto Rico). However, in another study using an additional buffer system at that locus (Hedges, 1989), the two latter species and *nubicola* each were found to have different alleles, and thus $Icd\text{-}1^{9}$ appears to be another defining allele for the Jamaican species. Besides allelic similarities, other characteristics of the allozyme data not normally used in systematic studies provide further support for the monophyly of the Jamaican species. For example, there is a *quantitative* difference involving band intensity at allele Adh^{3}: it is considerably lighter than alleles of non-Jamaican species at that locus. A similar intensity difference exists at *Icd-1* (Hedges, 1989:Fig. 5).

Another unifying characteristic of the Jamaican species involves the relative nobilities of alleles on the gel. At some loci (e.g., *Aat-2, Ck, Glud, Gpd, Pgm, Pt-2, Pt-3,* and *Pk),* the alleles of Jamaican species form a group apart from other taxa (see Appendix II). This is especially evident at *Ck,* where the Jamaican species have 8 very close alleles (8A–8H) which were indistinguishable on the initial buffer system and are all faster than alleles of the other taxa. Richardson and Smouse (1976) found a similar relationship between phylogenetic affinity and relative mobility in *Drosophila.*

However, this is only a general correlation, with many exceptions, and therefore a poor criterion for ordering allelic states in transformation series as suggested by Mickevich and Mitter (1983), especially because different buffer systems often result in different orderings of alleles.

Among the Jamaican species, the relationships defined by the two genetic distance analyses and character analysis agree in some cases and disagree in others. The groups defined in all three analyses are (1) *orcutti* and *jamaicensis,* (2) *cavernicola, cundalli,* and *glaucoreius,* (3) *fuscus, gossei, junori, pantoni,* and *pentasyringos* (with the last two as sister species), and (4) *grabhami, luteolus,* and *sisyphodemus.* A major area of disagreement involves the relationships of *alticola, andrewsi, griphus,* and *nubicola.* Together with *orcutti,* those species form a karyotypically well-defined group (Bogart and Hedges, 1990). However, these species cluster with *jamaicensis* only in the UPGMA phenogram (Fig. 1). The placement of *jamaicensis* with *orcutti* is not supported by chromosome data and therefore the single allele *($Dpep^{20}$)* shared exclusively by those species probably is convergent. The pairing of *alticola* and *nubicola,* and of *andrewsi* and *griphus* is supported by chromosome data yet those two pairs do not cluster in the distance Wagner tree (Fig. 2). In the cladogram (Fig. 3), the trio of rock- and cave-dwelling species, *cavernicola, cundalli,* and *glaucoreius,* clusters with *alticola,* a high elevation species whose affinities by all other indications (see below) are with *nubicola.* Thus alleles $Apep^{9B}$ and Cr^{10} likely are convergent (or symplesiomorphic). Also, *griphus* appears as an early offshoot of the group containing *junori, gossei, fuscus, pantoni,* and *pentasyringos* in Fig. 3 but is placed with the Blue Mountain species *(alticola, andrewsi, nubicola,* and *orcutti)* by all other findings (see below) including the genetic distance analyses. Thus, among the three analyses of the same allozyme data set, the phenetic analysis shows slightly better agreement with other data sets (immunology, chromosomes, and morphology). Studies using artificially generated phylogenies have found that the abilities of different methods of phylogenetic reconstruction depend on the topology of the original tree, rate of change (constant/variable; fast/slow), number of characters, and type of data analyzed (Tateno et al., 1982; Nei et al., 1983; Sokal, 1983; Fiala and Sokal, 1985; Sourdis and Krimbas, 1987; Kim and Burgman, 1988; Rohlf and Wooten, 1988; Sourdis and Nei, 1988). No single method was superior in all situations. However, under a stochastic model (constant rate of change), such as that proposed for allozyme evolution (Kimura, 1968, 1983; Nei, 1987), a UPGMA phenogram will estimate the true phylogeny better than other methods (maximum parsimony, maximum likelihood) with an average number of characters (<50; Sokal, 1983; Rohlf and Wooten, 1988). Also, parsimony methods are not expected to perform well with high rates of change (e.g., large numbers of alleles) such as encountered here (Felsenstein, 1983a, b). This may explain the apparently better results obtained with the UPGMA phenogram in this study.

The large number of autapomorphic alleles in this study primarily was the result of including ten distantly related non-Jamaican species. Although it was necessary to include those species due to the disagreement between morphological and molecular data in this group, the additional alleles caused an increase in homoplasy (allelic convergence). Electrophoresis becomes less efficient as the number of alleles increases due to the higher probability of convergence in mobility. Allelic convergence can be reduced with sequential electrophoresis but it is difficult to avoid when there are a large number of alleles at a locus. Differences between the genetic distance and parsimony analyses may be partially a result of this apparent homoplasy. The approach using slow-evolving loci (Hedges, 1989) was developed primarily to overcome this constraint in electrophoretic analysis, so that a large number of species can be compared without the proportionately large number of alleles.

Phylogeny: Allozymes, immunology, and Chromosomes

The allozyme data presented herein and elsewhere (Hedges, 1989) establish the

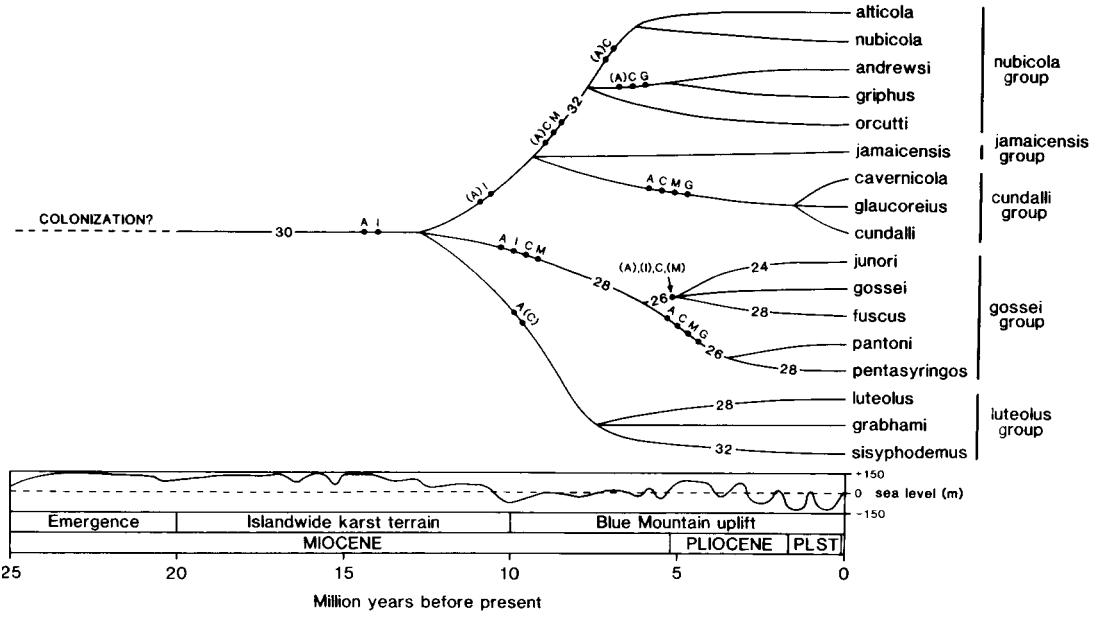

FIG. 4. Best estimate of the relationships of Jamaican *Eleutherodactylus* showing congruence of allozymes (A: this study), immunology (I: Hass and Hedges, MS), chromosomes (C: Bogart and Hedges, 1990), morphology (M: Schwartz and Fowler, 1973; this study), and geography (G: allopatric or parapatric distribution). Parentheses indicate partial support. Numbers on tree are diploid chromosome number changes (Bogart and Hedges, 1990). Times of divergence are based on genetic distances (Nei, 1978) calibrated with the immunological clock (Hass and Hedges, MS). Sea level changes and geologic time scale are from Haq et al. (1987). Events in the geologic history of Jamaica are based on Robinson et al. (1970), Horsfield (1973), Comer (1974), Arden (1975), and Buskirk (1985).

monophyly of Jamaican *Eleutherodactylus* and provide a framework for the relationships of the species. Albumin immunological distances (Hass and Hedges, MS) further support the monophyly of the Jamaican species and allow estimates of times of divergence. Chromosome analysis (Bogart and Hedges, 1990) contribute information on relationships within species groups and identification of sister species. Together, the information from these three data sets can be combined into a single estimate of the relationships of Jamaican *Eleutherodactylus* (Fig. 4). The allopatric or parapatric distribution of some closely-related species lends geographic support to those relationships.

Species Groups. — There are five species groups of Jamaican *Eleutherodactylus* (Hedges, 1989) supported by combinations of allozymes, immunology, chromosomes, and morphology (Fig. 4). The *luteolus* group contains *grabhami, luteolus,* and *sisyphodemus.* It is supported primarily by the allozyme data (alleles $Acon\text{-}2^{7A}$ and $Pt\text{-}3^{5}$ are found only in those three species, and alleles at six other loci are present in two of the three), but a relationship between two of the species *(grabhami* and *sisyphodemus)* is suggested by chromosome analyses (Bogart and Hedges, 1990:Fig. 6). All three species are restricted to western Jamaica.

The *gossei* group contains *fuscus, gossei, junori, pantoni,* and *pentasyringos.* Those species form a well-defined group by allozyme (alleles Gpd^{17} and $Pt\text{-}3^{10B}$), immunological, and chromosome data. In addition, they are morphologically similar, with reduced digital tips, a stocky habitus, tan or brown dorsal coloration, and a red or orange groin (flash marks). However, all of those morphological traits may be primitive. Two closely related species, *pantoni* (2n = 26) and *pentasyringos* (2n = 28), differ in chromosome number (Bogart and Hedges, 1990) and advertisement call but

are parapatric and morphologically similar (Schwartz and Fowler, 1973). Allozyme (alleles *Acon-1*[15], *Ak*[3B], *Gpd*[13], and *Pk*[3E]) and chromosome data support their close relationship. Two other species, *fuscus* (2n = 28) and *junori* (2n = 24), have restricted ranges in western and central Jamaica and appear to be derivatives of *gossei* (2n = 26) through fission and fusion (respectively) of different chromosomes (Bogart and Hedges, 1990). The lowest immunological distance from the *gossei* antiserum (6) is to *junori*. The allozyme data are unclear on the relationships of *fuscus, gossei,* and *junori.* Allele *Dpep*[16B] is found only in *gossei* and *fuscus,* and allele *Gpi*[14] occurs only in *gossei* and *junori.* In external morphology, *junori* is virtually indistinguishable from *gossei* (Schwartz and Fowler, 1973). Although *fuscus* and *pentasyringos* clustered in a study of slow-evolving loci (Hedges, 1989), that was due to allele *Acp*[2c], which appears to be convergent when chromosome data and these additional allozyme data are considered.

The *cundalli* group contains three closely related allopatric species *(cavernicola, cundalli,* and *glaucoreius)* that have uniquely shared alleles at nine loci *(Acon-1*[2], *Acon-2*[8], *Aat-2*[13], *Ck*[8D], *Dpep*[14], *Glud*[17B], *Ldh-2*[8], *Lgl*[10], and *Pgm*[5D]*).* They also form a well-defined group based on chromosomes and morphology. They have relatively long limbs, large eyes, a tuberculate dorsum, and large digital tips. The *jamaicensis* group includes only a single bromeliad-dwelling species. Crombie (1977) originally placed *jamaicensis* in its own group to recognize its morphological distinctiveness among West Indian species. However, allozyme and immunological data place it within the Jamaican radiation and close to the *cundalli* and *nubicola* groups. Because its relationship to those two groups remains unresolved, it is left in a separate monotypic group.

The *nubicola* group contains the remaining five species: *alticola, andrewsi, griphus, nubicola,* and *orcutti.* All but one are restricted to the mountains of eastern Jamaica. The exception, *griphus,* occurs in west-central Jamaica (Crombie, 1986). The strongest evidence in support of the *nubicola* group is its derived 2n = 32 karyotype (Bogart and Hedges, 1990), although one allozyme analysis (Fig. 1) also defined this group (with the inclusion of *jamaicensis).* Allele *Gpd*[15B] is found only in *alticola, griphus, nubicola,* and *orcutti.* Two chromosomal characters support the close relationship of *alticola* and *nubicola,* a grouping which also is defined by five shared alleles *(Aat-1*[7A], *Aat-2*[12], *Ck*[8B], *Glud*[16], and *Icd-2*[3]*).* Among the remaining three species, *andrewsi* and *griphus* have similar karyotypes (Bogart and Hedges, 1990:Fig. 10) and appear to be sister species, a finding supported by one of the allozyme trees (Fig. 2) and shared alleles *Dpep*[16C], *Glud*[21B], and *Icd-2*[15]. Both species also are similar in body size (small) and allopatric in distribution. The western species *(griphus)* is found in leaf litter of limestone forest. Although *andrewsi* previously was known only from high-elevation montane forest in the Blue Mountains, it was found recently in limestone forest leaf litter in the John Crow Mountains of eastern Jamaica (Hedges and Thomas, 1989). Thus, these two species occur in similar ecological situations. The fifth species, *orcutti,* inhabits streams in the Blue Mountains and has interdigital foot webbing.

The relationships of these five species groups (Fig. 4) largely are unresolved. One of the allozyme analyses (Fig. 1) suggests that the *luteolus* group was the earliest offshoot of the Jamaican radiation. Immunological data are somewhat equivocal: *luteolus* group species are the most distant from the *gossei* antiserum, but are not the most distant from the *nubicola* antiserum. Although *luteolus* karyotypically is the most different Jamaican species, chromosome evolution is too rapid to reconstruct relationships of the groups (Bogart and Hedges, 1990). However, the association of the *cundalli, jamaicensis,* and *nubicola* groups is supported by allozymes and immunology.

Evolutionary History

There are two major centers of *Eleutherodactylus* species density in Jamaica (Fig. 5): the west-central karst region and the Blue Mountains in the east. In each region, as many as eight species are sympatric, or

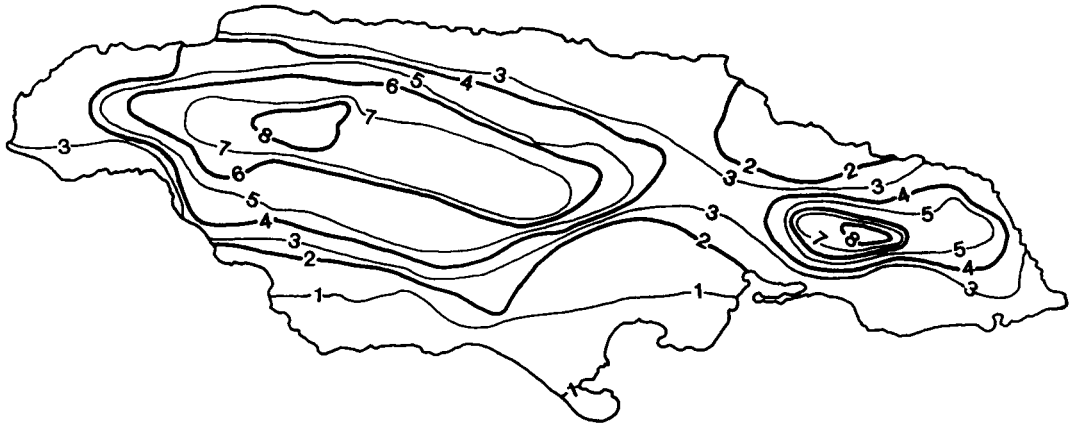

FIG. 5. Map showing species density of Jamaican *Eleutherodactylus* (number of sympatric or nearly sympatric species). Distributional data from Schwartz and Fowler (1973), Crombie (1977, 1986), and Hedges and Thomas (1989).

nearly so. In the west, those species are *cundalli, gossei, grabhami, griphus, jamaicensis, luteolus, pantoni,* and *sisyphodemus*. In the east, they are *alticola, andrewsi, glaucoreius, gossei, jamaicensis, nubicola, orcutti,* and *pantoni* (or *pentasyringos).* Only three species *(gossei, jamaicensis,* and *pantoni)* are common to both regions. When the distributions of Jamaican *Eleutherodactylus* (Fig. 6) are compared with their relationships (Fig. 4), it can be seen that this regional endemism is a result of both within-group speciation *(luteolus* group in the west, *nubicola* group in the east) and a superimposed pattern of

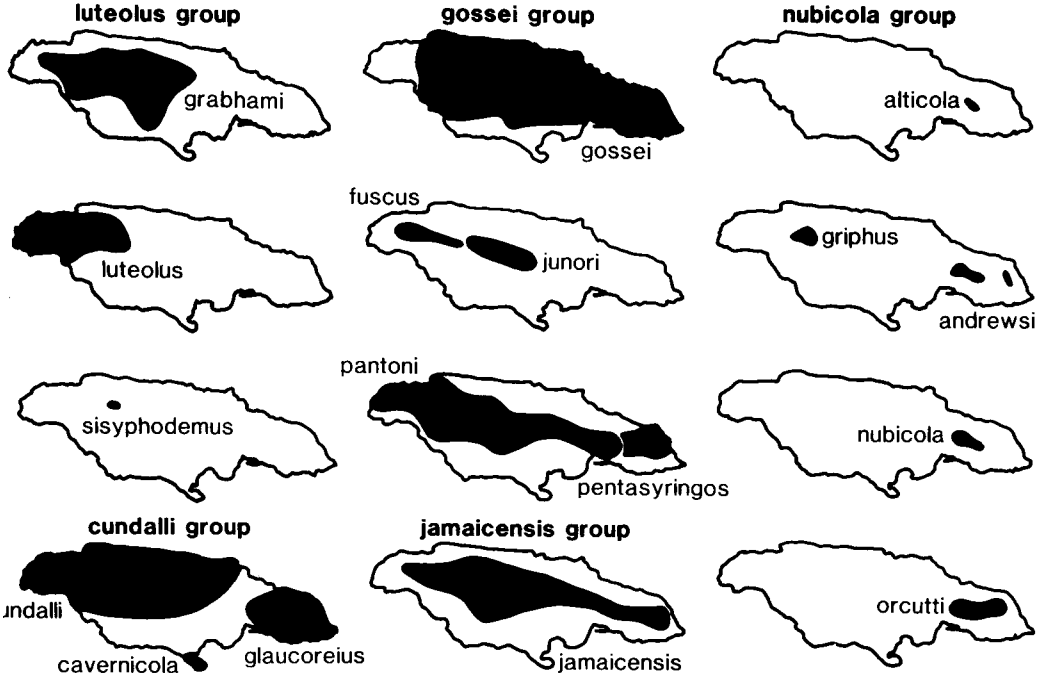

FIG. 6. Distributions of Jamaican *Eleutherodactylus* (data sources as in Fig. 5).

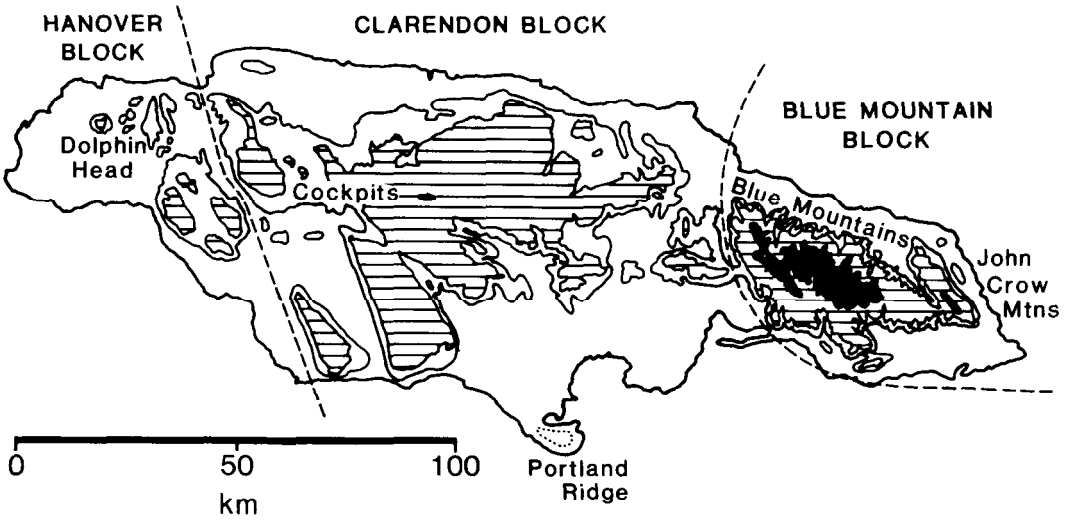

FIG. 7. Topographic and geologic map of Jamaica showing areas of endemism for *Eleutherodactylus* (see text). Unpatterned = 300-500 m; horizontal lines = 500-1000 m; black = >1000 m; Dolphin Head = small mountain (540 m) in west; Cockpits = west-central karst region; Portland Ridge = limestone hill (150 m) on southern peninsula; Blue Mountains = major range in east, highest peak = 2256 m; John Crow Mountains = limestone ridge in extreme east (> 1000 m). Dashed lines indicate boundaries of structural blocks (Horsfield and Roobol, 1974; Jackson and Smith, 1979).

allopatric sister species *(pantoni/pentasyringos, cavernicola/cundalli/glaucoreius, andrewsi/griphus).* The species distributions are most noticeably correlated with the major topographic feature on the island, the Blue Mountains (>2300 m) in the east (Fig. 7), as pointed out by Schwartz and Fowler (1973). Species distributed in western and central Jamaica, where the karst terrain and vegetation are more homogeneous, do not show such a common pattern. The elevated species density in the west-central region known as the Cockpits (Fig. 7) may be artificial, the result of inadequate collecting in other suitable areas, or recent extinction of adjacent populations due to habitat destruction. However, rainfall in this region is relatively high compared with surrounding areas (Asprey and Robbins, 1953; Vickers, 1979).

By integrating the phylogenetic and distributional data with the geological history of Jamaica, it is possible to shed light on the evolutionary history of this island radiation. Albumin immunological data (Hass and Hedges, MS) and Nei's (1978) genetic distances (Table 2) were used to calibrate divergence events. This was done by obtaining average genetic distances for divergence points using the slope of the albumin immunological distance/Nei's D correlation (12.9) thus resulting in a calibration of 1 Nei's D = 7.7 million years. This slope is very low when compared with slopes of other groups (Wyles and German, 1980), a result of the higher allelic resolution with sequential electrophoresis. Comparison of genetic distance/time calibrations among groups (Avise and Aquadro, 1982) should take into account such methodological differences. The diversity in calibrations observed maybe due in large part to those differences rather than entirely a result of variance in rates of protein evolution.

Initial Colonization. — A major constraint on biogeographic hypotheses involving Jamaica's terrestrial biota is the submergence of the island from the mid-Eocene (40 Mya) to the late Oligocene or early Miocene (25 Mya). This is well documented by the thick limestone sequences of the period lacking terrestrial sediments (Robinson et al., 1970; Horsfield, 1973; Comer, 1974; Horsfield and Roobol, 1974; Steineck, 1974; Arden, 1975; Kashfi, 1983; Wadge and

Dixon, 1984; Buskirk, 1985). This "White Limestone Group" covers most of Jamaica except for the Blue Mountain region in the east (Robinson et al., 1970), where presumably it has been eroded away. Because limestone strata immediately adjacent to the Blue Mountains are as pure as elsewhere (Horsfield and Roobol, 1974), it is doubtful that any land was emergent there, either. The submergence of Jamaica primarily was due to large-scale subsidence of 1-2 km or more (Steineck, 1974; Wadge and Dixon, 1974) in addition to normal processes of erosion. Thus it is unlikely that any part of Jamaica was above water during most of the Oligocene, aside from occasional low-lying cays (Arden, 1975) which probably would not have supported a continuous lineage of *Eleutherodactylus.*

In the late Oligocene or early Miocene (25 Mya) when uplift began, Jamaica became emergent and was situated about 700 km west of its present position, relative to North America (Pindell and Dewey, 1982; Sykes et al., 1982). Jamaica has not been attached to any other island or continent since its emergence and therefore the entire terrestrial biota of the island most likely had its origin by dispersal within the last 25 million years.

The first emergent land areas in Jamaica were in the north central region, exposing thick sequences of Oligocene limestone (Comer, 1974; Horsfield, 1973; Robinson et al., 1970; Wadge and Dixon, 1984). Because Jamaican *Eleutherodactylus* form a monophyletic group, only one colonization event is needed to explain their presence on the island. The affinities of Jamaican *Eleutherodactylus* are with species in the subgenus *Euhyas* inhabiting Cuba and the southern portion (South Island) of Hispaniola (Hedges, 1989). However, the source for the Jamaican species cannot be distinguished by available evidence on relationships.

At the time of emergence, Jamaica was closest to the South Island of Hispaniola (200 km to the east), a separate tectonic block from the North Island. Early colonization from the Hispaniolan South Island is unlikely, however, because it probably also was submerged (Buskirk, 1985) or recently emergent. A more likely source for Jamaican *Eleutherodactylus* was Cuba, an island or complex of islands (at that time) which may have been continuously emergent during the Tertiary (Pardo, 1975; Mattson, 1984) and the only other source for frogs of the subgenus *Euhyas*.

Speciation. — The early evolution of Jamaican *Eleutherodactylus* may have been influenced by the island's three structural blocks (Fig. 7; Horsfield and Roobol, 1974; Arden, 1975; Jackson and Smith, 1979). Although north-central Jamaica (Clarendon block) was the first to emerge (Robinson et al., 1970), the eastern Blue Mountain block soon followed, but probably as an island, separated from the Clarendon block by an older structural feature, the Wagwater Trough (Steineck, 1974:Fig. 7; Jackson and Smith, 1979:Fig. 6b). Extreme western Jamaica (Hanover block) initially may have been a third island separated from the Clarendon block by the Montpelier-Newmarket graben. As uplift continued during the Miocene, these islands coalesced but the mid-Tertiary limestone platform was not breached until the late Miocene (8 Mya; Comer, 1974). Thus, Jamaica was exclusively a land of karst terrain during the first 10– 15 million years after emergence, and this landform presently occupies two-thirds of the island.

The *luteolus* group contains three species inhabiting primarily karst areas in west-central Jamaica (Fig. 6). At least two of those species *(grabhami* and *luteolus)* occur on the extreme western Hanover block, and it is possible that this geological feature may have influenced the early evolution of the group. One species, *sisyphodemus,* is a small cryptic leaf-litter inhabitant of the Cockpits known only from two localities (Crombie, 1977) whereas the other two species are more widespread. All three are sympatric and their distributions do not suggest a vicariant event that may have been involved in their evolution.

Two of the five *gossei* group species, *gossei* and *pantoni,* are nearly islandwide in distribution. Another species, *fuscus,* occurs in extreme western Jamaica where *gossei* is absent, but the ranges of those two species overlap by about 10-30 km (Fig. 6). In east-

ern Jamaica, *pentasyringos* is narrowly sympatric with *pantoni* in the central Blue Mountains (Hedges and Thomas, 1989) and they do not show signs of intergradation or hybridization (Schwartz and Fowler, 1973). Although *fuscus* and *pentasyringos* have 28 chromosomes, apparently they were derived from 26 chromosome ancestors *(gossei* and *pantoni,* respectively) by Robertsonian fission (Bogart and Hedges, 1990). The fifth species, *junori* (2n = 24), appears to have been derived from *gossei* by fusion. Although the two presently are sympatric, the allozyme data suggest that they diverged in the late Miocene or early Pliocene possibly when dryer climates prevailed resulting in contracted ranges and refugia (similar to those in the Pleistocene). Sea level has fluctuated considerably during the last 10 million years (Fig. 4; Haq et al., 1987) and these changes also may have been responsible for disrupting distributions, leading to speciation. An hypothesized scenario of speciation in the *gossei* group involving refugia and allopatric speciation is presented in Bogart and Hedges (1990:Fig. 15).

The *cundalli* group is represented by three allopatric and closely related species: *cavernicola, cundalli,* and *glaucoreius.* Although each is morphologically and genetically distinct, the differences are not great as evidenced by the fact that *glaucoreius* previously was considered a subspecies of *cundalli* (Schwartz and Fowler, 1973). Their allopatric distributions (Fig. 6) and probable Pleistocene divergence suggest that a climate-related vicariant event was responsible. During Pleistocene glaciation, dry climates prevailed in the West Indies (Pregill and Olson, 1981) and the ranges of the mesic forest-associated animals contracted. The physiography of Jamaica and distribution of its vegetation (Asprey and Robbins, 1953) indicate that there were possibly refugia in west-central Jamaica and the eastern mountains, two areas presently with high rainfall (Vickers, 1979) and well-developed forest (see also Bogart and Hedges, 1990:Fig. 15). These likely were refugia for *cundalli* and *glaucoreius,* respectively.

Portland Ridge is a low limestone hill on a peninsula in southern Jamaica, and harbors the third *cundalli* group species, *cavernicola.* Several other amphibian and reptile species inhabiting Portland Ridge also are morphologically differentiated from their nearest relatives on Jamaica (Lynn, 1940; Schwartz and Fowler, 1973). The limestone ridge and associated forest habitat of Portland Ridge is not continuous with that of mainland Jamaica and therefore presently it is an ecological island for many species. In addition, the low elevation of the connecting land indicates that Portland Ridge was an island during interglacial periods of the Pleistocene when sea level was slightly higher. Both forms of isolation probably are responsible for the differentiation of *cavernicola.* The bromeliad-dwelling *jamaicensis* has a wide distribution (Fig. 6), and it is unclear what factors led to its divergence from the *cundalli* and *nubicola* groups.

The evolution of *nubicola* group clearly was associated with the uplift of the Blue Mountains during the last 10 million years. Two sister species, *andrewsi* and *griphus,* are allopatric (Fig. 6) and apparently of vicariant origin. However, the remaining three species *(alticola, nubicola,* and *orcutti)* are sympatric in the upper elevations of the Blue Mountains and thus it is unclear what led to their initial divergence.

In summary, of the seven sister-species groupings of Jamaican *Eleutherodactylus,* four appear to be the result of allopatric speciation based on their present distributions *(andrewsi/griphus, cavernicola/cundalli/glaucoreius, gossei/fuscus,* and *pantoni/pentasyringos).* Each of the remaining three species pairs *(alticola/nubicola, gossei/junori,* and *grabhami/luteolus)* have sympatric distributions.

Morphological Evolution

Adaptive Radiation. — An adaptive radiation is the diversification of a single lineage through speciation, usually referring to the rapid filling of vacant ecological niches (Osborn, 1902; Romer, 1966). In contrast, situations where speciation in a group (often of geographical isolates) is not accompanied by significant morphological or ecological change could be referred to

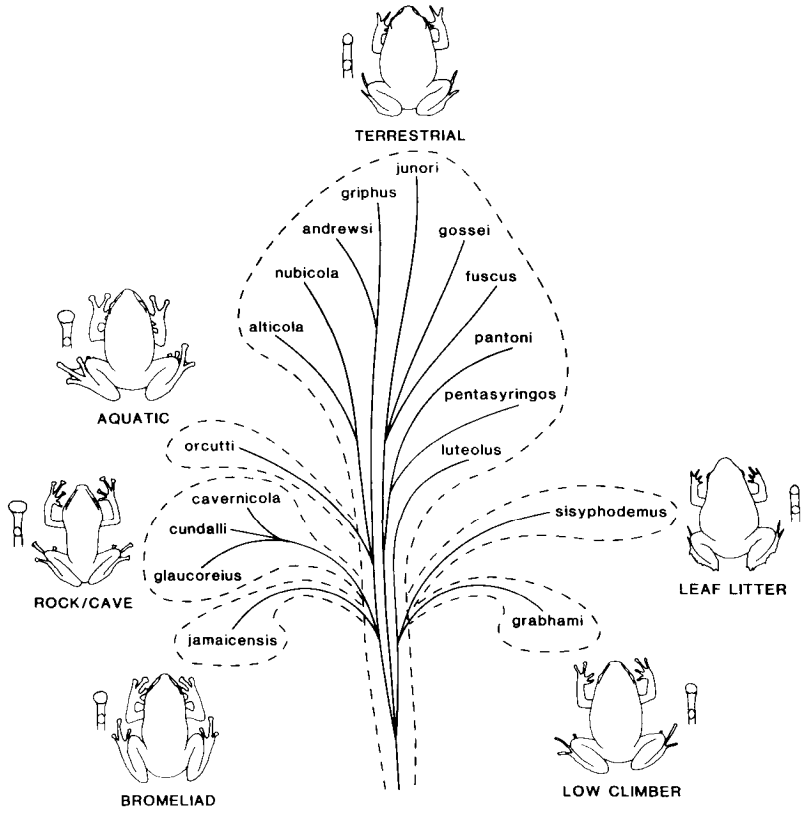

FIG. 8. The adaptive radiation of Jamaican *Eleutherodactylus* illustrating morphological evolution and ecomorphs. Shown are body outlines and third finger (ventral view) illustrating shape but not size differences. Ecomorph characteristics are: bromeliad—dorsoventrally flattened body, large rounded digital pads; rock/cave—long limbs, large oblong or triangular digital pads; aquatic—streamlined habitus, interdigital foot webbing, large rounded digital pads; terrestrial—stocky habitus, small digital pads; leaf litter—flat dorsum, leg fringe, small digital pads; low climber—slightly enlarged digital pads. Drawings based on the following United States National Museum specimens: 244498 *(jamaicensis),* 250740 *(cundalli),* 244518 *(orcutti),* 250929 *(gossei),* 244542 *(sisyphodemus),* and 249987 *(grabhami).*

as non-adaptive radiations (Hedges, 1989). West Indian frogs of the genus *Eleutherodactylus* have undergone one or both types of radiations on each of the four Greater Antilles and on Guadaloupe in the Lesser Antilles (Hedges, 1989). The island of Hispaniola is a composite of two tectonic blocks that have only recently collided, and each has its own radiation (or radiations) of *Eleutherodactylus.* A similar pattern involving island radiations is seen in lizards of the genus *Anolis* (Williams, 1969; Burnell and Hedges, MS) and has led to the concept of ecomorph: categories of convergence in ecology and morphology of species on different islands (Williams, 1972, 1983).

During the 20 million years since the *Eleutherodactylus* colonist arrived on Jamaica, there has been considerable morphological evolution (Fig. 8). It is not surprising that all previous workers on Jamaican *Eleutherodactylus* have hypothesized multiple colonization to explain such morphological diversity. However, with the relationships established by allozyme, immunological, and chromosome data, morphological changes can be placed in a phylogenetic perspective resulting in a better understanding of rates of morphological evolution.

Eleven of the 17 Jamaican *Eleutherodactylus* are ground-dwelling species, and all

but one *(sisyphodemus)* of those species are similar in body form (Fig. 8). Therefore, the adaptive radiation on Jamaica has been largely an exploitation of the terrestrial environment, in contrast with radiations of arboreal species (subgenus *Eleutherodactylus)* on the North Island of Hispaniola and Puerto Rico (Hedges, 1989). Other members of the group which includes the Jamaican taxa, the subgenus *Euhyas,* are found on Cuba and Hispaniola and primarily are terrestrial (ground-dwelling) species. This habitat preference and associated morphological features (stocky habitus, small digital tips, smooth ventral skin) appear to be primitive traits in the group. Thus the initial colonist to Jamaica apparently was a ground-dwelling species not unlike current members of the *gossei* group in appearance. Other primitive features in the subgenus *Euhyas* that presumably were possessed by the initial colonist include a large liver (with pointed left lobe), three glandular areas, white testes, and the absence of a vocal sac (Hedges, 1989).

One small ground-dwelling species, *sisyphodemus,* is specialized in both ecology and morphology, occupying pockets of leaf litter in undisturbed limestone forest (Crombie, 1977). In conjunction, it has evolved an extremely cryptic leaf-like morphology, with extensions of skin on the hind legs (tarsal fringe) and a flat dorsum. These features are unique among West Indian *Eleutherodactylus* and may represent a long period of adaptation to a limestone forest leaf litter environment.

The remaining ten ground-dwelling species *(alticola, andrewsi, fuscus, gossei, griphus, junori, luteolus, nubicola, pantoni,* and *pentasyringos)* are placed in the terrestrial ecomorph and probably have changed little in habits and habitus since the initial colonization. However, there is significant diversity in body size among these species, probably a way of reducing interspecific competition. This especially is apparent when body size of sympatric ground-dwelling species is compared at different localities across Jamaica (Fig. 9). One interesting exception to this pattern of body size stratification involves *griphus* and *sisyphodemus:* both species are syntopic, nearly

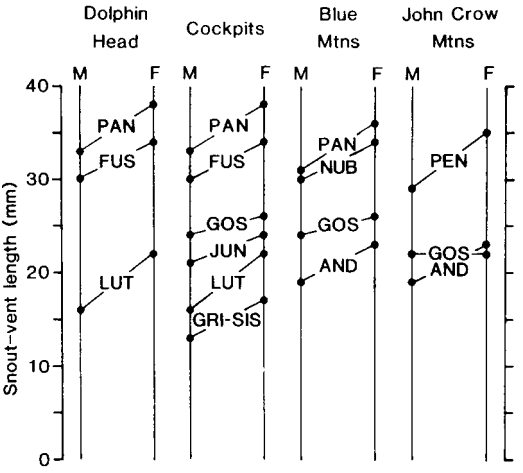

FIG. 9. Body size (average snout-vent length in mm) of sympatric species of ground-dwelling (terrestrial and leaf litter ecomorphs) *Eleutherodactylus* at four localities accross Jamaica (data from Schwartz and Fowler, 1973; Crombie, 1977, 1986; and Hedges, unpubl. data). M = male, F = female.

identical in body size, and occupy pockets of leaf litter in limestone forest. Of the two, *sisyphodemus* has a more specialized morphology (Fig. 8). The affinities of *griphus* with the *nubicola* group may explain this difference. If *griphus* is a relatively recent invader from the Blue Mountains (where limestone forest is uncommon), then probably it had a shorter period of time to evolve the specialized leaf litter morphology. Most of the ground-dwelling species occasionally are found on rocks and low vegetation, and one species *(junori)* even prefers such sites for vocalizing (Dunn, 1926; Schwartz and Fowler, 1973; pers. obs.).

The evolution of long limbs and large digital tips has allowed one lineage of Jamaican *Eleutherodactylus,* the *cundalli* group, to exploit extensive areas of limestone rock and caves on this predominantly karst island. These morphological features, along with relatively large eyes and a rough dorsum characterize the rock/cave ecomorph, which has convergent representatives on the other three Greater Antillean islands (Hedges, 1989). One member of the *luteolus* group, *grabhami,* also is a climbing species but usually is found low to the ground on rocks and vegetation.

Bromeliads are abundant in Jamaica, es-

pecially in limestone forest, and *jamaicensis* occupies this habitat exclusively. Morphological features associated with this lifestyle include a dorsoventrally flattened body and large rounded digital tips. The flattened body, also seen in two bromeliad-dwelling hylid frogs in Jamaica *(Hyla marianae* and *H. wilderi),* probably is advantageous for slipping down between bromeliad leaves. Rounded digital tips are associated with arboreality in West Indian *Eleutherodactylus* whereas truncated or notched digital tips are associated with rock-dwelling habits (Hedges, 1989) suggesting that these shape differences have selective advantages on particular substrates.

Finally, one species in the *nubicola* group, *orcutti,* has invaded the aquatic adaptive zone and occupies streams and waterfalls in the Blue Mountains. A streamlined habitus and webbed toes are the major morphological adaptations associated with this lifestyle. Because surface drainage has been a feature of Jamaican physiography only since the Blue Mountain uplift breached the limestone platform (8 Mya; Comer, 1974), the aquatic adaptations of *orcutti* apparently have evolved in less than eight million years.

Of the six ecomorphs that can be recognized for Jamaican *Eleutherodactylus* (Fig. 8), four *(aquatic, bromeliad, rock/cave,* and *terrestrial)* have convergent representatives on the other Antillean islands (Hedges, 1989) and appear to represent adaptation to similar environments. The ecology of most West Indian *Eleutherodactylus* is poorly known. When more data become available, the presently defined ecomorphs should be examined more rigorously.

Lineage-Associated Traits. — Morphological stasis is considered to be evidence of either stabilizing selection (Schmalhausen, 1949; Charlesworth et al., 1982; Kirkpatrick, 1982; Williamson, 1987) or developmental constraints (Alberch, 1982, 1988; Wake et al., 1983; Smith et al., 1985; Wake and Larson, 1987). Developmental constraints are defined as "biases on the production of variant phenotypes or limitations on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system" (Smith et al., 1985). A third possible explanation is that the trait in question is selectively neutral, and that most of the variants are not seen because they are deleterious and eliminated by purifying selection. This is the currently favored model for allozyme evolution (Kimura, 1968, 1983; Nei, 1987) but it is only rarely mentioned in the context of morphological evolution, primarily because many morphological traits appear to be adaptive.

The idea that at least some morphological traits are nonadaptive is not new (Darwin, 1859; Huxley, 1932) and has been given recent attention (Gould and Lewontin, 1979; Levinton, 1983; Nei, 1987; Zuckerkandl, 1987). Morphological stasis in a selectively neutral trait may be the result of strong purifying selection eliminating nearly all of the variants except for one (or a few). Stabilizing selection is compatible with a model of neutral variation (Kimura, 1983) but in the neutral model, negative (purifying) selection is stressed rather than positive (canalizing) selection. The predictions of the two models also differ: stabilizing selection results in stasis whereas purifying selection will leave one (stasis) or many variants depending on the intensity of selection. The existence of nonadaptive morphological variation has been experimentally determined (Robertson, 1967) and is a possible explanation for many useful taxonomic characters, such as variation in reptile and insect genitalia and some skeletal features of vertebrates (although alternative explanations have been proposed). Other examples are given in Gould and Lewontin (1979).

Stabilizing selection is known to be an important mechanism of morphological evolution in natural populations (Haldane, 1954; Mayr, 1963). However, the importance of developmental constraints in evolution is unclear. Most examples document cases of limited phenotypic variability (Alberch, 1980, 1982, 1988; Smith et al., 1985) but have alternative (selective) explanations. One proposed method of distinguishing developmental constraints from selection involves comparing two different taxa whose members have been exposed to

a similar range of ecological conditions (Smith et al., 1985). Morphological convergence is better explained by selection, whereas a lineage-associated trait may be evidence of a developmental constraint or nonadaptive character. Distinguishing between the latter two possibilities ultimately may be difficult. In the absence of a detailed developmental and genetic analysis, the hypothesis of developmental constraint might be favored (for lineage-associated traits) if it can be shown that variation in the character affects fitness. Otherwise, it may be a nonadaptive trait.

The multiple island radiations of West Indian *Anolis* and *Eleutherodactylus* provide a rare opportunity to examine these competing theories of morphological evolution. The widespread morphological convergence discussed in the previous section suggests that selection and not developmental constraint is the major mechanism involved in morphological evolution in these groups. Although it is possible that the traits considered to be convergent are similar because they were constrained by the same developmental pathways and evolved in parallel (Smith et al., 1985; Levinton, 1986), the strong correlation between structural and environmental diversity argues in favor of selection. Detailed studies of character transformation in the island radiations of *Eleutherodactylus* will be necessary to distinguish between convergence and parallel evolution.

Nonetheless, there are some lineage-associated morphological traits in these frogs. There are no known morphological traits that define the Jamaican radiation, but those species do possess some primitive traits that have been conserved in the western Caribbean clade (subgenus *Euhyas),* which includes radiations on Cuba, Jamaica, and the South Island of Hispaniola (Hedges, 1989). Specifically, all Jamaican species (and most in the subgenus) have a liver with a long and pointed left lobe, and lack a vocal sac. Species of the eastern Caribbean clade (subgenus *Eleutherodactylus),* which includes radiations on the North Island of Hispaniola, Puerto Rico, and Guadeloupe, have smaller livers with rounded left lobes, and possess an external vocal sac. There is variation in both of these traits, with some species possessing livers of intermediate shape and at least two species are polymorphic (present/absent) for a vocal sac, although this variation does not appear to be present in the Jamaican species.

All species of Jamaican *Eleutherodactylus* exhibit dorsal pattern polymorphism. As many as 10 pattern variants can occur in a single species, and each of the variants is shared among some or all of the species (Goin, 1954, 1960; Lynch, 1966; Schwartz and Fowler, 1973; Crombie, 1977). Although some of these pattern variants, such as middorsal stripe and dorsolateral stripes, are found in other species of *Eleutherodactylus* (e.g., Hedges et al., 1987:Fig. 2), close inspection reveals that the patterns shared by the Jamaican species have subtle similarities which tend to unite them as a group. Also, one pattern type common to the Jamaican species, "picket," has been found in only one non-Jamaican species (Goin, 1960). Thus, pattern polymorphism would appear to be another lineage-associated trait in Jamaican *Eleutherodactylus.*

Liver shape may bean example of a nonadaptive morphological trait. It is not obvious what selective advantage would be conferred with different liver shapes. If differences in mass underlie the shape differences (presently unknown), an adaptive argument could be made regarding energy reserves. The presence or absence of a vocal sac, on the other hand, is a potential candidate for a developmental constraint. The anuran vocal sac is believed to be important in resonating and radiating sound (McAlister, 1959; Bogert, 1960; Watkins et al., 1970; Martin, 1972; Littlejohn, 1977). Many species of anurans that lack a vocal sac are voiceless. However, all but one species of Jamaican *Eleutherodactylus* have an advertisement call yet lack a vocal sac (the call is unknown in *griphus).* In some species *(pantoni* and *pentasyringos),* the call is quite loud. If the absence of a vocal sac is a developmental constraint in Jamaican *Eleutherodactylus* (and other species in the subgenus *Euhyas),* its effect is not obvious. Because most anurans have the laryngeal apparatus that produces sound (Watkins et

al., 1970; Littlejohn, 1977), it is not remarkable that those species can produce sound, but it is surprising that they can produce an apparently "normal" call without a vocal sac (Hedges, 1987). *Eleutherodactylus* from the North Island of Hispaniola, Puerto Rico, and the Lesser Antilles (subgenus *Eleutherodactylus)* have an external vocal sac and their calls generally are more "whistle-like" in quality and may be louder. The only species of that subgenus on Jamaica *(johnstonei),* introduced in the 19th century, gives the impression of being vocally overpowering when calling with native Jamaican species, but that may be due to population size differences. If an analysis of call characteristics of species with and without vocal sacs revealed differences predicted by knowledge of vocal sac function, then a stronger argument could be made for the absence of a vocal sac being a developmental constraint.

Previous discussions of developmental constraints have focused largely on plethodontid salamanders, morphologically a highly conservative group (Alberch, 1980, 1981, 1982, 1983; Wake et al., 1983; Larson, 1984; Wake and Larson, 1987). Although frogs also are considered to be morphologically conservative (Wilson et al., 1977; Cherry et al., 1978), preliminary evidence from the island radiations of *Eleutherodactylus* suggests that developmental constraints may not be an important evolutionary mechanism in this group. However, considerably more work needs to be done on morphological evolution and phylogeny in this group and others before generalities can be made. Groups such as West Indian *Anolis* and *Eleutherodactylus* which have undergone multiple adaptive radiations on different islands provide an ideal system for studying morphological evolution because convergent and lineage-associated traits can be distinguished.

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APPENDIX I

Localities and Voucher Specimens

Sample size was five per species, except for *junori* (2) and *richmondi* (4). Numbers refer to preserved specimens in the United States National Museum of Natural History.

JAMAICA: *alticola* Lynn, St. Thomas, Blue Mountain Peak, 266337-341; *andrewsi* Lynn, St. Andrew, Hardwar Gap, 266347-351; *cavernicola* Lynn, Clarendon, Jackson's Bay Cave, 266353-359; *cundalli* Dunn, Trelawny, ca. 11 km WNW Quick Step, 266360-364; *fuscus* Lynn and Dent, St. James, 3.2 km W Mocho, 266376-380; *glaucoreius* Schwartz and Fowler, St. Andrew, 0.8 km W Hardwar Gap, 266365-369; *gossei* Dunn, St. James, 3.2 km W Mocho, 266383-387; *grabhami* Dunn, Trelawny, ca. 11 km WNW Quick Step, 266391-395; *griphus* Crombie, Trelawny, ca. 11 km WNW Quick Step, 266401-405; *jamaicensis* Barbour, St. Andrew, ca. 2.4 km NW Hardwar Gap, tissue vouchers only; *junori* Dunn, Trelawny, 9.5 km WNW Troy, 269239-240; *luteolus Gosse,* Trelawny, 3.7 km NW Windsor, 269241-245; *nubicola* Dunn, St. Andrew, Hardwar Gap, 266426-430; *orcutti* Dunn, Portland, 4.2 km N Hardwar Gap, 266436-440; *pantoni* Dunn, Trelawny, 10.1 km NW Troy, 266446-450; *pentasyringos* Schwartz and Fowler, Portland, 2.3 km S Fellowship, 266451-455; *sisyphodemus* Crombie, Trelawny, ca. 11 km WNW Quick Step, 266466-467 and 3 tissue vouchers. CUBA: *planirostris* Cope, Jamaica, St. Mary, 2.9 km N Port Maria (introduced), 266461-464 and 1 tissue voucher. HISPANIOLA: *inoptatus* Barbour, Dominican Republic, Pedernales, 0-1.8 km N Los Arroyos, 257754-758; *jugans* Cochran, Haiti, Sud Est, 8.0 km NW Seguin, 266315-317, 269277-278; *montanus*

Schmidt, Dominican Republic, La Vega, 18 km SE Constanza (via old road), 266305-309; *pictissimus* Cochran, Dominican Republic, Barahona, Los Patos, 266310-314. PUERTO RICO: *cooki* Grant, 2.9 km SW Yabucoa, 266318-322; *coqui* Thomas, Pico El Yunque (at radio towers), 266323-327; *richmondi* Stejneger, within a 2.5 km radius of Pico El Yunque, 266328-331. LESSER ANTILLES: *johnstonei* Barbour, Jamaica, Trelawny, 8.0-8.9 km NW Troy (introduced), 266414 and 4 tissue vouchers. COSTA RICA: *bransfordii* (Cope), Heredia, Finca La Selva, 266332-336.

APPENDIX II

Allelic Variation

Allelic variation is presented for all 27 species of *Eleutherodactylus* examined at 29 protein loci. Alleles are listed in the order of loci in Table 1. Each allele is defined by the combination of conditions under which it was detected (Table 1): number (first condition), capital letter (second condition), and small letter (third condition). Allele frequencies are indicated in brackets.

JAMAICA: *alticola*—2A,10,11 14[.75], 3A, 3, 9B, 12, 7A, 8A[.1]/8B[.9], 8B, 1, 5A[.67]/10C[.33], 4, 12[.3]/16[.7], 2D, 6[.5]/15B[.5], 3[.3]/12[.7], 9, 1, 8, 5A, 17, 1[.2]/3[.8], 1[.1]/10[.3]/18[.6],5C[.9]/13[.l],10C,8,9B[.3]/9G[.7],4C; *andrewsi*—2A, 15B[.63]/22[.37],4, 9B, 3, 9C, 9a, 7B, 8F, 8B, 16C, 14A, 6B, 21B, 2D, 19B,15,9,7d,8,5A,9,14[.5]/18[.5],llB,ll,10C, 14B,9B[.9]/10[.1],4C; *cavernicola*—2A,8,2,2, 3, 9B, 13, 9A[.5]/9B[.5], 8D, 8B, 14, 12[.33]/13B[.67], 20, 13a[.25]/17B[.75], 2D[.6]/2E[.4], 14[.9]/16[.1],13,9,8,8,10,5,16A,10,5D,10C,17, 2C, 4C; *cundalli*—2A, 2[.1]/8[.9], 2, 2, 3[.4]/8[.6],9B,9A[.13]/13[.87],9B,8D,8B,14,7[.38]/13A[.62], 10, 13a[.8]/17B[.2], 2D[.1]/2E[.9], 1[.1]/14[.9], 6[.3]/13[.7], 9, 8, 8[.9]/12[.1], 10, 6[.1]/17[.9], 9[.1]/11[.8]/22B[.1], 10, 5B[.6]/5D[.4], 10C, 17, lB[.6]/9F[.4]/4C; *fuscus*—2C, 15C, 11A, 9B, 3, 9D, 14E, 7B, 8F, 8B, 16B, 10A, 6B[.1]/15[.9], 14, 2E, 17, 17, 4, 7b, 9B, 5A, 17, 16A[.6]/28B[.3]/32[.1], 11A[.9]/20[.1], 1[.1]/5C[.9], 10B, 14D, 3F, 4C; *glaucoreius*—2A, 2[.25]/8[.75],2,4,3,9B,13,9B,8D,8B,14,13B,11, 13b[.67]/17B[.33], 2D[.75]/2E[.25], 16, 6[.3]/13[.7], 9, 8, 8, 5A[.25]/10[.75], 2[.17]/17[.83], 13[.5]/16A[.5],3A[.12]/10[.88],5D,10C,17,9C, 4C;
7B,8F,8A,16B,10A,6B[.38]/14[.62],15a,2E,17, 13,9,7b,9B,5A,17,5,11A,5C,10B,14E,3D,4C; *grabhami*—2A, 7A[.9]/15C[.1], 13, 8B, 3, 9A, 7[.1]/11[.3],7B,8E,8B,9,17,6B[.88]/16A[.12], 10, 2G, 19A, 13, 9, 17a, 8, 5A, 7[.9]/18[.1], 23A[.83]/31[.17],6,10,5,13,5C,4C; *griphus*—2A, 11, 4, 8B, 3, 9D, 14B, 7B, 8F, 8B[.5]/9B[.5], 16C,10A,9B,21B,2E,7[.5]/15B[.5],15,9,7a,8, 5A, 5, 7[.75]/16A[.25], 11A[.75]/21[.25], 5C, 10C, 17, 3C, 4C; *jamaicensis*—2A, 13A, 4[.3]/11B[.7],2,5,7,15B,7B,8C,8B,20,10B,19B,17A, 2D, 15A, 8, 9, 7b, 9A, 5A, 17, 8[.75]/16C[.25], 11B[.7]/19[.3], 5C, 10C, 3B, 9A[.6]/9D[.4], 4C; *junori*—21A,17,11
11A[.5],8E,8B,8,8A,6B[.25]/14[.75],15b,2E, 17, 13, 5[.5]/9[.5], 7c, 8, 5A, 17, 2[.25]/7[.5]/17A[.25],4[.5]/11A[.5],5A,10B,12,2B,4C; *luteolus*—2A,7A,1
17,6B,21D,2F,11,13,9,17b,8,5B,7,12,11C,10, 5,15B,5A,4C; *nubicola*—2A,7B,4,5,3,9C,8[.2]/12[.1]/14C[.7], 7A, 8B, 8B, 7, 10B, 6B, 11[.6]/16[.4],2C,15B,3,9,14,8,5A,15,8[.25]/16B[.75], 11B,11,10C,10,9B[.6]/9E[.4],4C; *orcutti*—2A, 15A,3,1[.1]/4[.9],3,7,14D,7B,8C,8B,20,4,19A, 21A,2E,15B,5[.3]/9[.7],9,7b,8,5A,17,4[.33]/17b[.67],11B,5C,4,16B,2D,4C; *pantoni*—2A, 12[.3]/21[.7], llA[.83]/15[.17], 3B, 3, 9D, 14E, 11B, 8F, 8B, 3[.3]/6[.7], 5B, 6B, 18, 2B, 13[.6]/17[.4], 6, 9, 7b, 9B, 5A, 17, 16A[.9]/28A[.1], 3B[.1]/11A[.9], 5C, 10B, 14A, 3E, 4A; *pentasyringos*—2C,3[.2]
15[.17], 3B, 3, 9D, 14E, 7B, 8F, 8B, 5, 8B, 6B[.7]/16B[.3], 10[.25]/20[.75], 2E, 13[.7]/17[.3], 8, 9, 7b,9B,2B[.2]/5A[.8],17,6[.3]/15[.1]/16A[.4]/25[.2], 11A[.9]/22[.1], 5C, 10B, 3A[.12]/16A[.88], 3E, 4C; *sisyphodemus*—2A, 7A[.4]/15C[.6],9B,9B,3,7,16,7B,8H,8B[.67]/9A[.33], 12[.8]/17B[.2], 14B, 6A, 21C, 2F, 10, 8, 9, 2[.4]/4[.2]/6[.4],8,2A[.1]/5B[.9],8,21[.75]/23B[.25], 12[.8]/23[.1]/25[.1],3[.6]/12[.4],5,15A,4[.9]/6[.1],4C. CUBA: *planirostris*—2A,24,5,9A,7, 6, 10b, 3, 4, 5, 10, 6, 9C[.1]/17[.9], 19, 2A[.6]/21[.4],22,18,6,11,7B,9C,12,24,14,4,9,9,3B,3. HISPANIOLA: *inoptatus*—2A,5,8, 5, 8, 12, 6[.8]/11[.2],4B,4,12,6,10A,4,1,18,3,2K,18,1[.5]/4[.5],9[.9]/10[.1],15,10,1,14,27[.25]/36A[.75], 2[.1]/5B[.9],6[.1]/14[.9], 10A, 5A, 1A, 2; *jugans*—2A,25[.9]/28
12[.9],9E,2b,6,6,6[.7]/10B[.2]/13[.l],16A,16, 5,[.17]/9A[.83],8,2H,9,4[.8]/14[.2],7,10, 10[.7]/13[.3],3,16,10,15,9,6,4,8B,1; *montanus*—2A,18,19,7,17,1,1
5[.4],2,3,11,2,2,1,2J,4,10,2,3,5,9B,11,22A, 17[.9]/24[.1], 15[.9]/17[.1], 2, 6, 5D[.8]/7[.2], 4B[.5]/4F[.5]; *pictissimus*—2B, 14, 1, 8C, 4, 4A,

10a,4,5,1,13,18,22,9,2E,12,21,8,16,7A,6,10, 20[.2]/33[.8],5A[.6]/8[.4],8[.l]/16[.9],7,2,8C, 4E. PUERTO RICO: *cooki*—1B,27,10,11, 8,3a[.83]/9b[.17],10,3A,7,17A,9,8,5,2J[.7]/ 3[.3],8,20,1,13,2[.1]/6[.9],5C,4,34,27,21,10C, 5B, 8C[.7]/11[.3], 5; *coqui*—1B[.8]/2A[23, 17,10,13,5,3a,8B[.5]/13A[.5],1,2,18,15,3,2,2J, 21,19[.1]/22[.9],1,12,4,5C,3[.9]/13[.1],35[.8]/ 39[.2],28[.1]/29[.2]/30[.7],18[.1]/21[.9],3,14C, 8A, 5; *richmondi*—1A,6[11[.5], 10[.12]/16[.88], 2A, 2c[.25]/6[.75], 8A, 3B,11,15,11A,12,7,2J,3[.88]/20[.12],7[.38]/ 11[.62]9,9B,7A[.38]/11[.62],8,1,19[.25]/ 26[.75],9,7[.88]/15[.12],8,1,5B,4F. LESSER ANTILLES: *johnstonei*—1B,26,9A, 15[.4],2B,2a[.17]/3a[.83],2,3C,12,21,11B,13,6, 2J,5,16,1,9A,3[.4]/14[.6],9A,3,36B[.1]/37[.9], 16,19,10C,11,3A,4F. COSTA RICA — *bransfordii*—3, 4[.5]/13B[.5], 6[.5]/12[.5], 13, 1, 9E, 16[.1]/5[.9], 8C[.75]/13B[.25], 7, 4, 2, 3, 7[.3]/ 21[.7]4,1,2,2,3,5,1,4[.8]/7[.2],19,30[.9]/38[.1], 7[.6]/13[.3]/26[.l],2,1,7,2A,4D.

APPENDIX III

Character-State Changes

The following are character-state changes on the cladogram of allelic data in Jamaican *Eleutherodactylus* (Fig. 3). Locus is given first (numbers correspond to loci listed in Table 1) followed by the new character state (allele or allelic combination; see Appendix II). Parentheses indicate retention of a primitive allele, and convergent alleles are underlined. Autapomorphies are not listed.

Clade A: 4-(2); 14-13a,(17B); 21-(10). Clade B: 2-2,8; 3-2; 7-13; 8-9B; 9-8D; 11-14; 12-13B, 14-17B; 15-(2D),2E; 16-14,16; 17-6,(13); 19-8; 21-(5A),10; 25-5D. Clade C: 6-9B; 24-10. Clade D: 7-12,(14C). Clade E: 3-(4); 6-9C; 25-11; 28-9B. Clade F: 4-2,(4); 12-10B; 15-2D; 23-8, (16A); 24-11B. Clade G: 11-20. Clade H: 6-13b; 12-10A; 15-2E; 23-7,(16A); 24-11A. Clade I: 4-(4); 13-(6B),14; 16-17; 26-10B. Clade J: 3-11A; 11-16B; 20-9B. Clade K: 1-2C; 7-14E. Clade L: 3-(11A),15; 4-3B; 16-13,(17); 28-3E. Clade M: 2-7A, (15C); 7-7; 12-17; 22-7; 25-10; 26-5. Clade N: 4-9B; 9-8D; 15-2F; 21-5B. Clade O: 2-15C; 3-4,(11B); 4-4,(8B); 5-3; 6-7; 7-14C; 8-7B; 9-8F; 10-8B; 11-16C; 13-6B; 14-10; 16-15B; 17-13; 19-7b; 20-8; 21-5A; 22-17; 23-16A; 25-5C; 27-17; 29-4C.