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EVOLUTION AND BIOGEOGRAPHY OF WEST INDIAN FROGS OF THE GENUS *ELEUTHERODACTYLUS*: SLOW-EVOLVING LOCI AND THE MAJOR GROUPS

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Abstract

A new approach to electrophoretic analysis is presented in which only slow-evolving protein loci are examined, permitting large numbers of species to be compared in a single study. Using this method, 82 West Indian species of the leptodactylid frog genus *Eleutherodactylus* were compared with sequential electrophoresis at six loci. The initial number of alleles detected after one condition (113) was nearly doubled (223) after varied conditions were applied. Genetic distance analyses defined four major groups: 1) all native Jamaican species; 2) the majority of Hispaniolan South Island species; 3) most species previously placed in the *auriculatus* group from the Hispaniolan North Island, Puerto Rico, and the Lesser Antilles; and 4) species previously placed in the *inoptatus* group (Hispaniola). Variation in two morphological characters, liver shape and vocal sac condition, showed congruence with the allozyme groupings. Character analyses (using parsimony) of those four major groups defined subgroups, many of which were also supported by morphology and geography.

A revised classification is presented whereby four genera (*Ladailadne*, *Sminthillus*, *Syrrhophus*, and *Tomodactylus*) are placed in the synonymy of the genus *Eleutherodactylus* (ca. 450 sp.) and five subgenera are recognized: *Craugastor* (a Middle American clade of 68 sp.), *Eleutherodactylus* (presumably a paraphyletic taxon containing ca. 275 sp. distributed mostly in South America but with an eastern Caribbean clade), *Euhyas* (a western Caribbean clade of 78 sp.), *Pelorius* new subgenus (a Hispaniolan clade of six sp.), and *Syrrhophus* (a southern North American clade of 24 sp. previously placed in the genera *Syrrhophus* and *Tomodactylus*). Within the tribe Eleutherodactylini, which contains genera with direct development, the genus *Eleutherodactylus* is defined by a single synapomorphy: T-shaped terminal phalanges. Three subgenera, one section, five series, and 15 species groups are recognized for the West Indian species.

An hypothesized biogeographic history of West Indian *Eleutherodactylus* begins with dispersal from South America into a proto-Antillean land mass in the late Cretaceous or early Tertiary. The subsequent break-up of the proto-Antilles probably isolated the subgenus *Craugastor* on the Chortis Block and southern North America, the subgenus *Euhyas* on Cuba, and the subgenus *Eleutherodactylus* on the Hispaniolan North

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Island and/or Puerto Rico, although the latter group may have dispersed to the Antilles in the Paleocene or Eocene. Late Eocene or early Oligocene dispersal of Cuban *Euhyas* to southern North America apparently led to the subgenus *Syrrhophus*. Jamaica and the Hispaniolan South Island (separate tectonic blocks) were submerged until the Miocene, at which time they probably were colonized by *Euhyas* from Cuba. Collision of the South Island and the North Island in the late Miocene resulted in limited overland dispersal of the subgenus *Euhyas* to the North Island and the subgenus *Eleutherodactylus* to the South Island. The striking morphological similarity of many West Indian species is considered to be convergence as a result of independent island radiations, as in the anoline lizards. Ecomorphs (*sensu* Williams) of West Indian *Eleutherodactylus* are described for concordant variation in morphology and ecology of species on different islands.

Introduction

Over the past decade, attention has focused on two competing theories of Caribbean biogeography: vicariance and dispersal (Rosen 1976, 1978, 1985; MacFadden 1980, 1981; Pregill 1981; Armas 1982; Hedges 1982; Coney 1982; Savage 1982; Briggs 1984; Buskirk 1985). The vicariance theory suggests that the Greater Antilles once were part of a late Mesozoic/early Cenozoic land mass, and that the relationships of the present day biota reflect those ancient land connections (Rosen 1976, 1985). Dispersalists contend that the West Indian biota is the result of overwater transport from the mainland during the Cenozoic (Matthew 1918; Simpson 1956; Pregill 1981; Briggs 1984). Three critical elements are needed to test these theories: 1) a geological history; 2) the distribution of the groups; and 3) the phylogenetic history of the groups.

The geological history of the Caribbean region is becoming well known, and most recent syntheses are in agreement with a proto-Antillean land mass similar to that proposed by Rosen (Pindell and Dewey 1982; Sykes et al. 1982; Duncan and Hargraves 1984; Mann and Burke 1984; Buskirk 1985). Also, the geographic distributions of most major extant groups in the Caribbean are well documented, although paleo-distributions are poorly known due to the scant Tertiary fossil record (Williams this volume). A major obstacle now remaining to test these competing theories of Caribbean biogeography is the lack of accurate phylogenetic reconstructions for the groups. This study represents an effort at obtaining these phylogenetic data for a major vertebrate group in the Caribbean region, leptodactylid frogs of the genus *Eleutherodactylus*.

The genus *Eleutherodactylus*

With over 400 described species, *Eleutherodactylus* is the largest vertebrate genus. It is a Neotropical group with two major centers of species diversity: northwestern South America and the West Indies. Nearly all species share two characteristics: "T-shaped" terminal phalanges and direct development (Lynch 1971). The T-shaped terminal phalanx probably is an adaptation for climbing, since it is best developed in arboreal species with expanded digital pads. It is also present in terrestrial species (although reduced) indicating that the ancestral *Eleutherodactylus* likely was a species adapted for climbing. However, direct development, allowing for reproduction away from water and the subse-

quent exploitation of new and diverse habitats, probably is largely responsible for the enormous success of this genus (Lynch 1971; Bogart 1981b).

About one third (ca. 130) of *Eleutherodactylus* species occur in the West Indies, where they are the dominant amphibian group. No single species is naturally found on more than one of the four Greater Antillean Islands, and most are restricted to small areas within an island. Also, no species are endemic to the Bahamas, and only five are known from the Lesser Antilles (Schwartz 1978; Schwartz and Henderson 1985). The recent discovery of an Eocene *Eleutherodactylus* on Hispaniola (Poinar and Cannatella 1987) confirms that this group has been evolving for at least 40 million years in the West Indies. Its wide distribution, high endemism, and long period of residence in the West Indies makes *Eleutherodactylus* an ideal group for the study of Caribbean biogeography.

No comprehensive phylogenetic study has been done on the entire genus *Eleutherodactylus*, and only one unambiguous synapomorphy is known that defines a major division: the "E" condition of the mandibular ramus of the trigeminal nerve defining the Middle American Clade (Lynch 1986). Most other divisions of the genus have been assigned the rank species group, which are largely phenetic assemblages defined primarily by skin texture, digital pad size, finger length, and vomerine odontophore length (Lynch 1976; Schwartz 1978). Some species groups, such as the *unistrigatus* group (>155 species), have more taxa than most anuran families and contain species with considerable morphological diversity.

In the West Indies, about 130 species are placed in seven species groups (Schwartz 1978, 1985), mostly in the *auriculatus* and *ricordii* groups. This study examines the West Indian species using six slow-evolving allozyme loci in an attempt to identify the major lineages and their relationships. In turn, the phylogenetic data are used to develop a new hypothesis for the evolution and biogeography of West Indian *Eleutherodactylus*.

Slow-evolving loci

Soon after natural populations of organisms were examined at multiple electrophoretic loci (Hubby and Lewontin 1966; Lewontin and Hubby 1966), interlocus variation was found in the number of allelomorphs (hereafter referred to as alleles). Avise (1975) noted the usefulness of this variation for systematics, and Sarich (1977) introduced the terms "slow-" and "fast-evolving" loci. Sarich considered plasma proteins (albumin, esterases, hemoglobin, transferrin) to be fast-evolving and intracellular enzymes to be slow-evolving, with a tenfold difference in substitution rate. More recent studies have not supported a bimodality in allelic variation (Avise and Aquadro 1982; Hedges 1986:fig. 5). Instead, it appears that variability in protein loci spans a continuum, from slow-, through intermediate- to fast-evolving loci. Such a finding is not unexpected since variability in the amino acid substitution rate of proteins also spans a continuum (Dayoff 1978; Nei 1987). However, these terms have proven useful in describing loci that have relatively few (=slow-evolving) or many (=fast-evolving) alleles, a usage that is followed here.

The importance of electrophoresis in systematics and its widespread use is largely a result of this continuum of variability in protein loci. If all loci had the same electrophoretically detectable substitution rate, then the resolution of a phylogeny would be very limited. For example, if the average amino acid substitution rate for every locus was one in 20 million years, it would be difficult to resolve the relationships of a group of species resulting from a radiation in the late Pliocene, two million years before present (myBP),

since most species would appear identical in a set of 30 loci. Likewise, if the average substitution rate was one in two million years, then species that diverged in the Miocene (20 myBP) would not be expected to have any alleles in common. The systematic value of electrophoresis derives from variability in substitution rate: different loci often resolve different portions of a phylogeny. A suite of loci, with a continuum of variability, has the potential for resolving the relationships of a group spanning a considerable amount of evolutionary time (ca. 1-30 my).

Although the differential resolving power of electrophoresis has been known for some time (Avise 1975; Sarich 1977; Berlocher 1984), few systematists have taken advantage of it (e.g. Lanyon 1985). An exception is contact zone studies where fast-evolving loci are routinely examined (Barton and Hewitt 1983). One reason for this has been the strong reliance on the electrophoretic "clock" (Thorpe 1982) and the necessity to randomly sample as many loci as possible to obtain genetic distances that are comparable from study to study. Although many valuable studies have resulted, the full potential of electrophoretic loci as characters in a character analysis has not been fully realized. In addition, large amounts of time and effort have been expended comparing numerous alleles at fast-evolving loci only to find in the end that all of the species in the group have a different allele! The technical aspect of comparing large numbers of alleles at a particular locus also has limited the number of species that can be compared in any one study. Additional species require a disproportionately larger amount of laboratory work and thus electrophoretic studies rarely involve more than 25 species (Avise and Aquadro 1982). By using only slow-evolving loci, however, large numbers of species can be examined in one study because there usually are fewer alleles to compare.

Another advantage of using slow-evolving loci is that heterozygosity generally is much lower. Intraspecific polymorphism, a major problem in standard character analysis of electrophoretic data, is only rarely encountered at most slow-evolving loci. Differences between loci usually are "fixed" (with no heterozygotes) and thus the coding of alleles as character states is identical to the coding of morphological character states. Trees can then be generated by standard parsimony programs. Once the major groups have been identified by slow-evolving loci, individual studies can be conducted on each of those groups using faster-evolving loci.

In this study, I selected six slow-evolving loci to examine the major groups of West Indian *Eleutherodactylus*. These loci were selected by first running all species (84) at a large number of loci (>40) and choosing those loci that had the fewest number of alleles.

Materials and methods

Frogs were collected over a period of five years during 16 trips to the West Indies. A total of 84 species of *Eleutherodactylus* was obtained: all 17 native Jamaican species, 47 of 54 from Hispaniola, 12 of 15 from the Puerto Rican Bank, and four of five from the Lesser Antilles (Appendix 1). Access to Cuban species was available only through Guantanamo Bay Naval Station (*atkinsi*) and introduced populations in Jamaica (*planirostris*). Thus only two of the 33 Cuban *Eleutherodactylus* were obtained, a major limitation of the study. Two non-West Indian species were also included: *bransfordii* from Costa Rica, and *fenestratus* from Peru. If samples were available from multiple localities

within a species, the locality nearest to the type locality was used (for taxonomic purposes).

Specimens were processed in the field and tissue samples were transported to College Park in a liquid nitrogen tank, or live frogs were brought to the laboratory for processing. Processing included weighing and photographing each species, obtaining blood for microcomplement fixation studies, removing viscera (primarily heart, liver, and kidney) and leg muscle (or an entire leg) for electrophoresis, preparing intestines and testes for chromosome analysis (in specimens injected with colchicine), removing one finger and fixing in 2.5% glutaraldehyde for scanning electron microscopy of the digital pad, and preserving the carcass in 10% formalin (transferred later to 70% ethanol) as a voucher for deposition in the United States National Museum of Natural History (USNM). Tissue samples were stored in ultracold freezers (-75°C) in the laboratory until needed. Samples were homogenized in distilled water at a ratio of 5:1 (distilled water:tissue). Homogenates were then refrozen, thawed, and centrifuged at 2°C for 20 min and 10,000 rpm. The aqueous protein supernatants were stored again at -75°C until use.

Electrophoretic differences between species and species groups usually are "fixed" with no heterozygotes (Avise 1975; Gorman and Renzi 1979). Thus, for the purpose of this study, very little would be gained by having more than one individual per species and therefore the sample size used was one.

Sequential electrophoresis

For systematic purposes, it is important to know whether two or more alleles with the same mobility are homologous or convergent. Apparently, convergence of electromorphs is a technique problem, related to the efficiency of electrophoresis in detecting protein variants, and not a result of adaptation to similar environments. This efficiency has been examined in two proteins: hemoglobin (Ramshaw et al. 1979) and myoglobin (McLellan 1984). In both cases, standard electrophoresis (one condition) detected about 40% of the protein variants of known amino acid sequence. By using different electrophoretic conditions successively, a procedure termed "sequential electrophoresis" (Coyne 1982), 85-93% of the protein variants could be detected. Additional evidence from sequencing studies of natural populations suggests that sequential electrophoresis can detect all or nearly all amino acid substitutions (Lewontin 1985).

Despite the obvious implications for systematics in terms of increasing resolution and reducing homoplasy (Coyne et al. 1979), very few researchers (e.g. Aquadro and Avise 1982; Lanyon 1985) have used sequential electrophoresis in their systematic studies. Some use multiple conditions simultaneously but this is inefficient since an electrophoretic difference defined at one condition needs no additional confirmation. Also, unless alleles are characterized by the conditions under which they were detected, later comparisons (running samples side-by-side with known standards) are difficult or impossible since allelic differences detected under one condition may not be detected under another. Therefore, the use of multiple conditions simultaneously is usually not equivalent to sequential electrophoresis.

An even greater error in the estimate of allelic variation results if comparisons are not performed. Ratios of the distance travelled by an electromorph relative to a standard sometimes are used in place of side-by-side comparisons. However, this likely will result

in errors, such as missing small differences or in scoring differences when none exist, since no two electrophoretic runs are completely identical.

In order to reduce the amount of homoplasy (e.g. allelic convergence) in my data, I used sequential electrophoresis. The primary variable chosen was buffer type, since it has been shown to have substantial effects on mobility (Coyne 1982). After experimentation, I found that many loci were not resolvable on all buffer systems or in all taxa. Typically, only two or three buffer systems resulted in gels that were fully scorable at a particular locus. Thus, I used either one, two, or three conditions with the following six protein loci: *Acp*, *Ck*, *Icd-1*, *Lgl*, *Pgm*, and *Pt-3* (Table 1).

Horizontal starch gel electrophoresis was employed using Connaught starch at a concentration of 12.5%. Buffers were prepared following the methods of Selander et al. (1971). Assays and references for the proteins are given in Hedges (1986).

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 (e.g. Coyne 1982:fig. 1). This procedure was repeated for all pairs of samples representing the same presumed allele. Initial experimenting confirmed that more differences could be detected using this "alternating" method of comparison over one involving samples run side-by-side.

Alleles and multiple loci are ordered from cathode to anode. Alleles detected during the first electrophoretic run are assigned lower-case letters. If additional alleles were detected during the second and third runs, they are assigned numbers and upper-case letters, respectively. This is done in a "nested" fashion so that subdivided allelomorphs retain their initial designation, but are uniquely defined by their second and/or third additional designations (Appendix 2). 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 character analysis.

Genetic distance analyses

A UPGMA phenogram was produced using a modified Cavalli-Sforza distance (D_C; Nei et al. 1983), and a distance Wagner tree was generated with the Cavalli-Sforza and Edward's (1967) chord distance (D_A). A fuller discussion of the use of these distances and methods is presented elsewhere (Hedges 1986). The distance Wagner tree was rooted with *E. fenestratus* as the outgroup since that species is not believed to be phylogenetically close to any of the West Indian species (Lynch 1976). All trees using genetic distance data were produced with BIOSYS-I (Swofford and Selander 1981), modified to incorporate the Cavalli-Sforza distance used by Nei et al. (1983).

Character analyses

Character analyses were performed on the allelic data using PAUP (Phylogenetic Analysis Using Parsimony) computer software (Swofford 1985). Each locus was treated as a character and alleles as unordered character states. In cases where heterozygotes were encountered that had one allele shared with other species and another that was unique (autapomorphic), the unique allele was not considered since it was of no value in tree construction. In three cases, both alleles of the heterozygote were shared with two or more species. Since frequency coding was not possible, it was determined by outgroup

analysis, in two of those cases, which allele was derived and the species were coded as possessing only that allele, thus minimizing the loss of cladistic information. In the third case, (*Lgl*), the locus had to be omitted from the analysis of that group (IV).

Global branch-swapping was used to find the most-parsimonious tree (MPT) and in all cases more than one tree was found (in many cases, this was due to forced dichotomous resolution of polychotomies by PAUP). If a large number of MPT's exist, then PAUP only stores the first 100, which will be a biased sample dependent on the initial ordering of species in the data file. In order to eliminate or reduce this bias in those cases, I obtained 11 consensus trees (Adams 1972), each constructed from 100 MPT's generated by a random reordering of the species. A majority-rule consensus tree (Margush and McMorris 1981) was then constructed from those 11 initial consensus trees, thus representing 1100 MPT's.

Cladograms showing allelic changes were constructed using the topology of the final consensus tree except in some cases where aspects of one MPT were favored by data external to the study (e.g. morphology). In all cases, the character-state cladogram was slightly longer than any single MPT due to conflicting character state distributions generated in the consensus process.

Morphology

In an effort to find some morphological traits of systematic value in West Indian *Eleutherodactylus*, I examined preserved specimens in the United States National Museum of Natural History and in my own collection. Additional data were extracted from literature accounts. Emphasis was placed on traits that were not obviously correlated with environmental variables to reduce the likelihood of convergence. Three useful characters were identified that showed variation concordant with other sources of data and were thus surveyed in a majority of West Indian species: liver shape (small and/or with rounded lobes vs large and with a long pointed left lobe), testis color (black or pigmented vs white or unpigmented), and vocal sac condition (single, paired, or absent; internal or external).

In the case of liver shape, the lateral incision normally used to sex anurans was sufficient to allow scoring of that character. In some individuals, liver shape could be seen (without dissection) by holding the specimen in front of a strong light source. No vocal sac was ever found, upon dissection, in an adult male frog lacking vocal slits. Therefore, the absence of vocal slits in species not dissected was taken as evidence for the absence of a vocal sac. In the case of testis color, species polymorphic (usually >80% pigmented) for this character were treated as having pigmented testes since this method of coding resulted in a higher degree of concordance with other types of data.

Results

The number of alleles per locus ranged from 15 to 54 with an average of 37 and a total of 223 alleles detected (Appendix 2). Before sequential electrophoresis, only 113 alleles were detected and thus the use of additional buffer systems nearly doubled the total number of alleles. Heterozygosity averaged 5% (SE= ± 1%) among all loci (6) and species, which is about average for anurans and other amphibians and reptiles (Nevo 1984). However, since sequential electrophoresis significantly increases heterozygosity

estimates to the more correct value (Coyne 1982; Lewontin 1985), and since slow-evolving loci are expected to have lower heterozygosity, comparison with other studies may be misleading.

Genetic distance analyses

A UPGMA phenogram of 84 *Eleutherodactylus* species (Fig. 1) has a cophenetic correlation coefficient of 0.81, and a Prager and Wilson (1976) F-value of 4.73. Several large groups are defined. One contains all native Jamaican species (Group I), except for *nubicola*. Two others (Groups II and III) correspond, in general, to the *ricordii* and *auriculatus* groups of Dunn (1926a) and Schwartz (1958, 1969, 1978). Of two smaller groups, one (Group IV) is equivalent to the *inoptatus* group (Schwartz 1965, 1976; Hedges and Thomas 1987). The other is a cluster of six species morphologically allied to the *ricordii* group (Schwartz 1976), and which share an allele ($Pt\text{-}3^{i2}$) with Group II. The remaining six species (*counouspeus*, sp. nov. N, *glanduliferoides*, *richmondi*, *bransfordii*, and *fenestratus*) have either one or none of their alleles in common with other species at any of the loci and are therefore the most divergent.

Geographically, the species in Groups I and II are western Caribbean, occurring primarily on Jamaica, Cuba, and the South Island of Hispaniola. Species in Group III are eastern Caribbean, occurring primarily on the North Island of Hispaniola, Puerto Rico, and the Lesser Antilles. Group IV is restricted to Hispaniola.

A distance Wagner tree (Fig. 2) has a cophenetic correlation coefficient of 0.57 and a Prager and Wilson's (1976) F-value of 44.1 (0.80 and 5.77, respectively, after branch-length optimization). In general, the groupings are similar to those in the phenogram. The one Jamaican species omitted from Group I in the phenogram (*nubicola*) now associates with that group. Also, the two separate units of Group II in the phenogram form one cluster in the distance Wagner tree. However, Group III is broken into several units, Groups I and II do not associate, and Group IV clusters with Group I.

A character analysis of the entire group of 84 *Eleutherodactylus* species was not performed because of the absence of shared alleles between the ingroup and outgroup species (*bransfordii* and *fenestratus*), and the low levels of allelic similarity among the major subdivisions (Groups I-IV) of the ingroup. However, examination of the allelic data (Appendix II) reveals that each of the four groups is defined by one or more unique alleles (not necessarily possessed by all of the species in a group): Icd^{q2} (Group I), Pgm^{jB} (Group II), Icd^{f1} (Group III), and Icd^{p5}, Lgl^{a1}, and Pgm^{o} (Group IV). In a cladistic (character) analysis, only shared derived character states (synapomorphies) are used to cluster species whereas phenetic analyses use both synapomorphies and symplesiomorphies (shared primitive traits). Although some or all of the alleles defining Groups I-IV could be symplesiomorphic (i.e undesirable), the congruence with morphology (see below), immunology (Hass and Hedges, unpubl. MS), and geography suggests that they are synapomorphies defining monophyletic groups. For that reason, the four allozyme groups were treated separately in the following character analyses.

Character analyses

Individual character analyses (using PAUP) were performed on the four groups defined in the genetic distance analyses. Each tree was rooted by using a composite outgroup of all West Indian species not present in the ingroup under consideration. This

composite outgroup was the same for all four ingroups, and consisted of alleles shared between those groups: Acp^{g}, Lgl^{g2B}, and $Pt\text{-}3^{k1}$. Primitive alleles were therefore those alleles present in both the ingroup and the outgroup. There were no shared alleles at the other three loci. In two cases (Acp^{o} and Lgl^{i3B}), ingroup/outgroup convergences were detected by examining outgroup topology, and those alleles were treated as apomorphies in their respective ingroups.

Group I.-- Numerous MPT's were generated, all with a length of 29 and a consistency index (CI) of 1.00 (i.e. no homoplasy). A majority rule consensus tree representing 1100 MPT's (Fig. 3) shows strong support for several clusters (*cavernicola* and *cundalli*; *fuscus* and *pentasyringos*; *luteolus*, *grabhami*, and *sisyphodemus*) and weaker support for others (*nubicola* and *andrewsi*; *cavernicola*, *cundalli* and *glaucoreius*; *junori*, *gossei*, *pantoni*, *fuscus*, and *pentasyringos*). These groupings are similar to those found in a more complete study of 29 loci in the Jamaican species (Hedges, in press). A cladogram of allelic changes (Fig. 4) has a length of 31 and a CI of 0.94. Allele $Icd\text{-}1^{q2}$ is a probable synapomorphy for the group, although the primitive state cannot be identified. It is present in 15 of the 17 species and is not found in any other West Indian species examined (Fig. 5). No ancestral allele could be determined for *Ck* and *Pgm*.

Several groups are indicated on the tree of allelic changes. A group of three species in western Jamaica (*grabhami*, *luteolus*, and *sisyphodemus*) is defined by alleles Pgm^{1B} (absent in *sisyphodemus*) and $Pt\text{-}3^{g}$. Another group, consisting of five morphologically similar terrestrial species (*fuscus*, *gossei*, *junori*, *pantoni*, and *pentasyringos*), has the allele $Pt\text{-}3^{k2}$. Three arboreal and rock-dwelling species with long limbs and large eyes (*cavernicola*, *cundalli*, and *glaucoreius*) form a group based on alleles Ck^{s2D} and Pgm^{fc}, and another trio of species (*alticola*, *andrewsi*, and *nubicola*) restricted to the Blue Mountains share alleles Ck^{s2B} (absent in *andrewsi*) and Pgm^{1a} (absent in *alticola*). The remaining three species (*griphus*, *orcutti*, and *jamaicensis*) do not show affinities with the other groups.

Group II.-- A majority-rule consensus tree representing 1100 MPT's of this group (Fig. 6) shows considerable resolution. All MPT's were of length 64 and had a CI of 0.95. A cladogram of allelic changes (Fig. 7) has a length of 65 and a CI of 0.94. Allele Pgm^{jB} (Fig. 8) is a probable synapomorphy for the group, although the primitive state cannot be identified. No ancestral allele could be determined for *Ck* and *Icd*.

A group of seven largely arboreal or rock-dwelling species (*amadeus*, *bakeri*, *eunaster*, *glanduliferoides*, *glaphycompus*, *heminota*, and sp. nov. P) is defined by $Pt\text{-}3^{l3}$. Eight species (*furcyensis*, *grahami*, *pictissimus*, *probolaeus*, *rhodesi*, *rufifemoralis*, *schmidti*, and *weinlandi*) form another group based on Ck^{m2A} (absent in *rufifemoralis* and *schmidti*). Within that group, two species with red flash marks and a dorsal pattern of reverse parentheses (*furcyensis* and *rufifemoralis*) also share allele Icd^{i}. Another subgroup is formed of five allopatric species (*grahami*, *pictissimus*, *probolaeus*, *rhodesi*, and *weinlandi*) that share allele Pgm^{s2A}.

Two species with a pattern of diagonal leg barring and restricted to the Massif de La Hotte (*glandulifer* and *sciagraphus*) also share allele Ck^{r}. Another pair of species (*apostates* and *oxyrhyncus*) have a similar robust appearance (stout-bodied with long thick legs), extreme sexual dimorphism in body size, and share allele Ck^{kC}. The remaining species in this assemblage do not associate into groups.

Group III.-- A majority-rule consensus tree representing 1100 MPT's (Fig. 9) re-

solves only one large group of Puerto Rican and Lesser Antillean species, and three small groups of Hispaniolan species. All MPT's were of length 71 and had a CI of 0.97. A cladogram of allelic changes (Fig. 10) has a length of 74 and a CI of 0.95. Allele Icd^{f1} (Fig. 5) is a probable synapomorphy for Group III (present in 25 species; absent only in *minutus*, *montanus*, *poolei*, *richmondi*, and *unicolor*) and not found in any other West Indian species, although the primitive state cannot be identified. No ancestral allele could be determined for *Ck* and *Pgm*.

Allele Acp^{d} defines the large group of Puerto Rican and Lesser Antillean species: *antillensis*, *barlagnei*, *cochranae*, *cooki*, *coqui*, *eneidae*, *johnstonei*, *martinicensis*, *pinchoni*, *portoricensis*, *richmondi*, *unicolor*, and *wightmanae* (the primitive allele is Acp^{g}). It is absent only in *richmondi*, but that species shares allele Ck^{g2} with three of those species (*antillensis*, *cochranae*, and *unicolor*). Within that group, three of the Lesser Antillean species (*johnstonei*, *martinicensis*, and *pinchoni*) form a subgroup defined by Ck^{g3A} and Pgm^{n2B} (absent in *johnstonei*). A fourth species, *barlagnei*, is also included in that subgroup based on the presence of dorsal chevrons and its morphological resemblance to *pinchoni*. Although data are included only for the introduced Jamaican *johnstonei*, specimens from Guadeloupe were also compared and found to be similar to the Jamaican sample at most loci examined.

All other species occur in Hispaniola and form a weakly defined group based on allele Ck^{f2B} (present in seven of 14 species). Within that group are three well-defined subgroups. One contains a trio of largely bromeliad-dwelling species (*fowleri*, *lamprotes*, and *wetmorei*) defined by alleles Acp^{o}, Lgl^{l5A} (absent in *wetmorei*) and Pgm^{u3B} (absent in *lamprotes*). Two species with notched digital pads, *poolei* and *flavescens*, share allele Lgl^{l2}, and two nearly identical montane species, *montanus* and *patricae*, share allele $Pt\text{-}3^{l2}$. A group of three, small high elevation species (*audanti*, *haitianus*, and *minutus*) share allele Ck^{f3B}.

Group IV.-- In this group, one locus (*Lgl*) had to be omitted from the parsimony analysis because it was polymorphic, with heterozygotes and homozygotes of both alleles present, and thus could not be coded for entry in PAUP. The parsimony analysis of five loci yielded three MPT's of length 10 and with a CI of 1.00. The cladogram of allelic changes (Fig. 11) also represents a strict consensus tree of the three MPT's (length = 11, CI = 0.91). Although not used in the parsimony analysis, *Lgl* is included on the tree.

Two groups of three species each are defined by unique alleles. The burrowing species (*hypostenor*, *parapelates*, and *ruthae*) form a group defined by alleles Acp^{b} and Ck^{j1A} (absent in *parapelates*). The three large terrestrial and arboreal species (*chlorophenax*, *inoptatus*, and *nortoni*) share alleles Ck^{j2} and $Pt\text{-}3^{j1}$.

Morphology

Variation in liver shape, testis color, and vocal sac condition was scored for 113 species of West Indian *Eleutherodactylus* (Appendix 3), although in many cases, data were unavailable for one or two of the characters. No information was available for the following 12 species: *albipes*, *cubanus*, *delacruzi*, *emiliae*, *guanahacabibes*, *gundlachi*, *intermedius*, *zeus*, *darlingtoni*, *lucioi*, *neodreptus*, and *warreni*.

Liver shape (Fig. 12) showed a strong correlation with the allozyme groupings. With few exceptions, species having livers with long and pointed left lobes belong to allozyme Groups I and II whereas species with short and rounded left lobes belong to Groups III

and IV. Exceptions are four Hispaniolan species (*abbotti*, *audanti*, *minutus*, and *parabates*) and one Puerto Rican species (*locustus*) belonging to Group III but which have long and pointed left lobes. The livers of five species (*poolei*, *cooki*, *karlschmidti*, *pinchoni*, and *wightmanae*) were intermediate in shape. In the case of two species, *johnstonei* (N=95, small liver with short and rounded left lobe) and *gossei* (N=31, large liver with long and pointed left lobe), large series were examined and no significant intraspecific variation in liver shape was found. Poorly preserved specimens or those with empty and contracted digestive tracts (indicating that the specimen was starved prior to preservation) were not scored for liver shape.

Of particular interest is the apparent lack of association between liver shape and ecology. Although Group III species are primarily arboreal, the arboreal species of Groups I and II (e.g. *jamaicensis*, *armstrongi*, *bakeri*, and *heminota*) have livers with long and pointed left lobes like other members of those allozyme groups. Also, the terrestrial Puerto Rican Bank species, *richmondi* and *lentus*, always associated with the *ricordii* group (Schwartz 1976), have a liver shape characteristic of the *auriculatus* group, thus in agreement with the allozyme data (no allozyme data were available for *lentus*). Also, there was no apparent correlation between liver shape and body size or altitude. Using liver shape, species for which allozyme data are unavailable can now be associated with allozyme groupings. Thus the Cuban species *Sminthillus limbatus*, associated with the *ricordii* group by Bogart (1981a) based on chromosomes, has a liver shape characteristic of that group (Groups I and II).

Testis color did not show the major geographic patterns that liver shape exhibited, except that all 17 species in Group I (Jamaica) and all six in Group IV (Hispaniola) had unpigmented testes whereas pigmented testes were found in all four species from Guadeloupe. Several of the smaller clades defined by allozyme data were supported by testis color (Fig. 7). There was no apparent association between testis color and either body size, altitude, or habitat.

Vocal sac condition showed a pattern similar to liver shape in exhibiting a dichotomy between Groups I & II and Group III. Nearly all Group III species have single external submandibular vocal sacs, as noted by Schwartz (1969) for the *auriculatus* group. Most species in Groups I and II either lack a vocal sac, or have an internal one. A clade of Hispaniolan (South Island) species have paired vocal sacs (Fig. 6). The condition of the vocal sac showed support for the allozyme data in several cases where the latter disagreed with previous species group allocations (e.g. *parabates* in Group III, and *armstrongi*, *bakeri*, and *heminota* in Group II). In two species, *amadeus* and *bakeri*, the vocal sac was absent in some adult males and present in others.

In an effort to establish polarity for the variation found in these three characters, preliminary information was obtained for several "outgroup" species from the mainland and from other leptodactylid genera. The same variation present in the ingroup was also found in the outgroup indicating that a more extensive survey of the genus *Eleutherodactylus* (and related genera) will be necessary to determine polarity for these characters.

Discussion

In comparison with other vertebrate groups, anurans are morphologically conservative (Wilson et al. 1977; Cherry et al. 1978) thus limiting the number of useful morpholog-

ical characters for phylogenetic analysis. In the speciose genus *Eleutherodactylus*, the problem is compounded in that similar morphologies have appeared in many unrelated lineages.

For example, both terrestrial and arboreal habits probably have evolved multiple times in the genus *Eleutherodactylus*. Since most terrestrial species have small digital pads and nearly all arboreal species have enlarged digital pads (presumably to aid in climbing), the use of such a highly adaptive trait as digital pad size may result in homoplasy in a phylogenetic analysis. Other characteristics that are correlated with the environment or ecology of the animal include ventral skin texture (rough or areolate in arboreal species) and interdigital webbing (present in aquatic species). All three of these characters have been used in previous systematic studies of *Eleutherodactylus* (Schwartz 1958; Shreve and Williams 1963; Lynch 1976).

In contrast, electrophoretic alleles (and most other types of molecular data) essentially are free from the problem of adaptive convergence, and therefore should be better indicators of phylogeny than morphology. Even if very strong directional selection for a specific enzyme function in two unrelated lineages existed, two identical convergent amino acid sequences would not likely result. Differences would nearly always occur at "functionally neutral" sites. Since electrophoresis, if properly applied using the sequential method (Coyne 1982), can detect most single amino acid substitutions, then in theory, alleles shared among taxa should be identical (or nearly so) in sequence. In practice, however, a small percentage of allelic differences likely will go undetected even using sequential electrophoresis (due to chance convergence), but this should not pose serious problems in a phylogenetic analysis.

In this study, slow-evolving electrophoretic loci provide useful phylogenetic information in West Indian *Eleutherodactylus*. Four major groups and many smaller clades are defined by allelic data. At present, the alleles defining the major groups can only be treated as "presumed synapomorphies" until mainland species (and other related genera) are surveyed at these loci and polarities are established. However, the general concordance of these allelic groups with morphology (liver shape and vocal sac condition, and to a lesser degree, external morphology) and geography suggests that they are monophyletic.

Systematics of the genus *Eleutherodactylus*

The basic systematic category within the genus *Eleutherodactylus* has been the species group, of which more than 30 are currently recognized (Lynch 1985; Schwartz 1985), if "assemblies" (Lynch 1980, 1981) are included. The first attempt at a higher-level organization of the genus was by Lynch (1971), who proposed an Alpha/Beta dichotomy on osteological grounds. The Alpha division included most of the West Indian species and "parts of the Andean system," *Syrrhophus*, and *Tomodactylus*. The Beta division included all other *Eleutherodactylus* examined. Later, Lynch (1976) proposed four "infrageneric units" for the South American species groups based on variation in the relative lengths of the two inner fingers, and ventral skin texture.

Recently, Lynch (1986) defined a Middle American clade of *Eleutherodactylus* based on a shared derived trait, the "E" condition of the mandibular ramus of the trigeminal nerve. This clade, which also extends into southern North America and northern South

America, comprises 68 species of *Eleutherodactylus* (including three species previously placed in the genus *Hylactophryne*). The defining character is the position of the mandibular ramus of the trigeminal nerve relative to the *M. adductor mandibulae externus superficialis* (jaw muscle). The nerve passes either lateral ("S") or medial ("E") to the muscle, with the former condition being primitive based on outgroup comparisons (Lynch 1986:fig. 1).

Lynch (1986) suggested that if the Middle American Clade were to be recognized taxonomically, it would take the generic or subgeneric name *Craugastor* Cope 1862. I propose that it be recognized as a subgenus (type species =*Hylodes fitzingeri* by subsequent designation [Dunn and Dunn 1940]).

Savage (1987) recently presented a phylogenetic scheme for *Eleutherodactylus* and closely related genera using variation in jaw musculature and chromosomes. His analysis, based primarily on the work of Starrett (1968) for jaw musculature, and Bogart (1970, 1981a) and Deweese (1976) for chromosomes, largely conflicts with the results of this study and previous morphological studies (Lynch, 1970, 1971, 1976; Heyer, 1975).

Savage (1987) recognized Lynch's Middle American Clade but also discussed data on variation in the depressor mandibulae muscle, which appears to define three lineages within that clade. However, only one condition of the depressor muscle (DFSQdAT) is present in species possessing the "S" condition of the trigeminal nerve. For those species and closely related eleutherodactyline genera outside of the Middle American Clade (ca. 80% of the genus *Eleutherodactylus*), Savage uses only chromosome number and chromosome arm number to define relationships, assuming 2n=26 is primitive and all other numbers (lower and higher) are derived. This approach resulted in the following three groups (Savage 1987:fig. 28): (I) one lineage containing *Tomodactylus* and *Ischnocnema* (sister genera), and a second lineage containing *Euparkerella* and *Holoaden* (sister genera), Cuban *E. auriculatus* group, and the *E. diastema* group (the most distant taxon of the second lineage); (II) *Syrrhophus* as a sister group to a lineage containing *Sminthillus* and the combined *E. ricordii* and *E. unistrigatus* groups); and (III) *E. altae* and Puerto Rican *E. auriculatus* group.

The genera *Tomodactylus* and *Syrrhophus* are very similar morphologically (osteology, external morphology) and have largely parapatric distributions in Mexico suggesting a close relationship (Lynch 1970). Previous workers have considered them to be sister genera (Dixon 1957; Lynch 1970, 1971; Heyer 1975) and related to West Indian *Eleutherodactylus* (Lynch 1971; Bogart 1981a). Specifically, they share with the West Indian species several osteological traits: fusion of the frontoparietals, degree of overlap of the parasphenoid alae and median rami of the pterygoids, and median separation of the prevomers (Lynch 1971). Therefore the placement of these two genera in different lineages by Savage (1987), and the grouping of *Tomodactylus* with *Ischnocnema* seems unlikely. The latter genus occurs in the upper Amazon basin and in southeastern Brazil, distant from the range of *Tomodactylus*. The placement of Cuban *auriculatus* group species with *Euparkerella* and *Holoaden*, two genera found in southeastern Brazil, seems even more improbable based on geography and morphology (Lynch 1971). Finally, the splitting of the Cuban and Puerto Rican *auriculatus* group species, which are similar in external morphology (Dunn 1926; Schwartz 1969) and osteology (Lynch 1971; Joglar 1986), and the clustering of the *ricordii* and *unistrigatus* groups, which differ considerably in external morphology and osteology (Lynch 1976; Joglar 1986), are also unlikely ar-

rangements. I suggest that these anomalous results can be explained by the use of too few data (karyotypes of 65 out of 400+ *Eleutherodactylus* species were used), and the finding that chromosome evolution in *Eleutherodactylus* apparently is too rapid (Bogart 1981a; Bogart and Hedges, in press) to be very useful in defining major groups due to the high probability of convergence in chromosome number.

Since only one condition of the depressor jaw musculature (DFSQdAT) appears to be present in 80% of *Eleutherodactylus* species (i.e. those outside of the Middle American Clade), that character is not very useful in defining major groups within the genus (although many species have yet to be examined). On the other hand, chromosome data appear to be too variable to be used for this purpose, except in conjunction with other types of data where they can be placed in a phylogenetic framework. Instead, the rapid rate of chromosome evolution in *Eleutherodactylus* is ideally suited for resolving lower-level relationships (species groups and smaller clades). Although slow-evolving electrophoretic loci have proven useful in defining major groups of West Indian *Eleutherodactylus*, they also may be too variable to establish relationships of major divisions within the genus. The technique of micro-complement fixation of albumin, which can be used to examine relationships extending into the Cretaceous (Maxson and Maxson 1986), shows promise for unravelling the phylogenetic history of the major groups of *Eleutherodactylus* (Hass and Hedges, unpubl. MS).

The genera *Sminthillus*, *Syrrhophus* and *Tomodactylus* have been recognized as offshoots of the *Eleutherodactylus* radiation for some time, based on osteology, but have been retained as genera in anticipation of further splitting of the genus *Eleutherodactylus* (Lynch 1971). If the major monophyletic groups within the genus *Eleutherodactylus* are treated as subgenera, as advocated here, then it becomes undesirable to retain those three as genera. To eliminate this paraphyletic situation, I place *Sminthillus*, *Syrrhophus*, and *Tomodactylus* in the synonymy of the genus *Eleutherodactylus*. A welcome result of this change is that it aids in defining the genus *Eleutherodactylus*, now comprising about 450 described species. Although other genera in the tribe Eleutherodactylini have direct development, only species of the genus *Eleutherodactylus* (including species previously placed in the genera *Sminthillus*, *Syrrhophus*, and *Tomodactylus*) possess T-shaped terminal phalanges (Lynch 1971). Nonetheless, several other eleutherodactyline genera lacking T-shaped terminal phalanges (*Adelophryne*, *Euparkerella*, *Ischnocnema*, *Phyllonastes*, *Phyzelaphryne*, and *Phrynopus*) are believed to be part of the *Eleutherodactylus* radiation (Lynch 1971, 1986; Savage 1987) and thus eventually may be synonymized in the genus *Eleutherodactylus* when additional information becomes available. I concur with Lynch's (1986) placement of *Hylactophryne* in the synonymy of the genus *Eleutherodactylus*.

Since the species previously placed in the genera *Syrrhophus* and *Tomodactylus* appear to form a monophyletic group united by several osteological characters (Lynch 1971; Joglar 1986), I propose that those species be placed in the subgenus *Syrrhophus* Cope 1878 (the older name), with the type species *Syrrhophus marnockii* Cope 1878 by monotypy. In so doing, it becomes necessary to erect two new categories to include the species previously placed in those two genera. For the 15 species (5 species groups) previously placed in the genus *Syrrhophus* (Lynch 1970), I propose the *longipes* series. This series includes the following species groups: *longipes*, *leprus*, *marnockii*, *modestus*, and *pipilans*. For the nine species (no recognized species groups) previously placed in

the genus *Tomodactylus* (Lynch 1971), I propose the *nitidus* series. However, one species in the *nitidus* series, *fuscus* Davis and Dixon 1955, becomes a junior secondary homonym of *Eleutherodactylus fuscus* Lynn and Dent 1943 and therefore a replacement name must be found. I suggest the name *Eleutherodactylus* (*Syrrhophus*) *maurus* (nomen novum) as a replacement, continuing allusion to the dark coloration of this species. Diagnoses and definitions for these two series are given in Lynch (1968, 1971) under their previous generic names. Albumin immunological distances (Hass and Hedges, unpubl. MS) suggest that the subgenus *Syrrhophus* is closer to West Indian Groups I and II (a separate subgenus defined below) than to III and IV (two additional subgenera), a finding which is concordant with their terrestrial habits, presence of glandular areas, and distribution (western Caribbean).

A revised classification of West Indian *Eleutherodactylus*

The taxonomic framework for West Indian *Eleutherodactylus* initiated by Dunn (1926a) and developed extensively by Schwartz (1985) is largely supported by the electrophoretic data presented herein. In particular, the morphological division between two major assemblages, the *auriculatus* and *ricordii* groups, also is reflected in major allelic differences. However, some significant changes in taxonomy are suggested, and a more refined estimate of the relationships within the major groups is presented. Therefore, it is desirable to have a classification which more accurately reflects our current knowledge of the relationships of West Indian *Eleutherodactylus*.

A considerable body of molecular and chromosomal data now exist for the West Indian species, but comparable data are lacking for most of the mainland taxa. Therefore, the term "presumed synapomorphy" will be used in the systematic account below to refer to those shared derived characters (including those of morphology) in which polarity is suggested by only a limited sampling of mainland representatives and outgroups, or to those unique alleles which show concordance with other data sets. A summary of the following classification is presented in Table 2. Distributions do not include introduced populations.

Genus *Eleutherodactylus* Dumeril and Bibron 1841
Subgenus *Euhyas* Fitzinger 1843

TYPE SPECIES.-- *Hylodes ricordii* Dumeril and Bibron 1841

DEFINITION.-- Long vomerine odontophores, a large liver with a long and pointed left lobe, inguinal glands, and the absence of vocal slits (and vocal sac) are presumed synapomorphies, although not all of these traits are possessed by all species. Primarily terrestrial or rock-dwelling frogs with smooth or weakly rugose (or weakly areolate) ventral skin.

CONTENT.-- 78 species, 11 species groups, and 3 series.

DISTRIBUTION.-- Cuba and Bahamas (27 sp.), Jamaica (17 sp.), Hispaniola (33 sp.), and Mona Island (1 sp.).

REMARKS.-- This subgenus corresponds to allozyme Groups I and II defined in this study, and largely contains species previously placed in the *ricordii* group (Dunn 1926a; Schwartz 1958, 1965b, 1973, 1976, 1985). Although long vomerine odontophores are

believed to be a synapomorphy (Joglar 1986), species with short vomerine odontophores can be placed confidently in this subgenus based on a combination of other characteristics (morphological and molecular; see below) indicating that there have been multiple reversals in this character. Those species are *amadeus*, *bakeri*, *brevirostris*, *cubanus*, *delacruzi*, *eunaster*, *glanduliferoides*, *heminota*, *orcutti*, sp. nov. P (Hedges, unpubl. MS), *rufifemoralis*, *sciagraphus*, *semipalmatus*, *symingtoni*, *thorectes* (Hedges 1988), *turquinensis*, *varleyi*, *ventrilineatus*, and *zeus*. It is possible that the size of the vomerine odontophores (and hence number of vomerine teeth) is correlated with feeding habits: short for soft-bodied prey such as Diptera and Lepidoptera, long for hard-bodied prey such as Orthoptera and Coleoptera. This would explain why most arboreal species (those that would encounter prey such as Diptera and Lepidoptera more frequently) have short odontophores and most terrestrial species (which would encounter hard-bodied prey more often) have long odontophores. Preliminary data on stomach contents lends initial support to that hypothesis but a much more extensive survey is warranted.

Of 46 species in this subgenus that have been karyotyped, 35 are either 2N=30 or 32 (Bogart 1981a; Bogart and Hedges, in press; and J. Bogart, pers. comm.). Diploid chromosome numbers in the other major West Indian assemblage, the *auriculatus* section of the subgenus *Eleutherodactylus*, are 2N=28 or fewer except for three Puerto Rican species which are 2N=30 (*karlschmidti*, *richmondi*, and *unicolor*). A few mainland species are 2N=32 and *marnockii* is 2N=30 (Bogart 1970, 1981a), although, except for the latter species, none appear to be close to the subgenus *Euhyas*. Bogart's (1981a) inclusion of *Sminthillus limbatus* in the *ricordii* group (=subgenus *Euhyas*) of *Eleutherodactylus* based on chromosome data is supported by its liver shape (long and pointed left lobe).

luteolus series

DEFINITION.-- Allele *Icd-1*^{q2} (absent in *fuscus* and *nubicola*) is a presumed synapomorphy (there are no known morphological synapomorphies). These are primarily terrestrial species but are morphologically and ecologically diverse. This series includes all native Jamaican *Eleutherodactylus*.

CONTENT.-- 17 species; 5 species groups.

DISTRIBUTION.-- Jamaica

REMARKS.-- Additional synapomorphic alleles are presented elsewhere (Hedges, in press). All species possess relatively large, white testes and lack vocal slits (and vocal sacs), but these probably are plesiomorphic traits within the subgenus *Euhyas*. Diploid chromosome numbers in this series are 24, 26, 28, 30, and 32 (Bogart and Hedges, unpubl. MS). Albumin immunological distance data support the monophyly of this series (Hass and Hedges, in press), although an analysis of morphological variation in the Jamaican species by Flores (1984) does not.

luteolus group
Figure 13

DEFINITION.-- Alleles *Pgm*^{1B} (absent in *sisyphodemus*) and *Pt-3*^{g} are synapomorphies.

CONTENT.-- 3 species: *grabhami*, *luteolus*, and *sisyphodemus*.

DISTRIBUTION.-- Western Jamaica.

REMARKS.-- Dunn (1926b) used the "*luteolus* group" in a broader sense, referring to most Jamaican species known at the time. The group defined here is a restricted version primarily based on allozyme characters but with a geographic cohesiveness: all three species occur in karst areas of Western Jamaica. They appear to be morphologically dissimilar, although *luteolus* and *sisyphodemus* are both very small (13-16 mm SVL, males). There is chromosomal evidence for a relationship between *grabhami* and *sisyphodemus* (Bogart and Hedges, in press).

gossei group
Figure 14

DEFINITION.-- Allele $Pt\text{-}3^{k2}$ is a synapomorphy for the group. Stout-bodied and short-legged terrestrial frogs with a smooth dorsum and small digital pads.

CONTENT.-- 5 species: *fuscus*, *gossei*, *junori*, *pantoni*, and *pentasyringos*.

DISTRIBUTION.-- Jamaica.

REMARKS.-- Goin (1954) constructed the *gossei* group to accommodate most Jamaican species previously placed in Dunn's *luteolus* group (excluding *luteolus*), and it has been used in a similar manner since that time (Goin 1960; Schwartz and Fowler 1973; Crombie 1977, 1986). It is used here in a restricted sense to define a monophyletic subset of those species. Schwartz and Fowler (1973) described *pentasyringos* as a subspecies of *pantoni*, but I regard it as a distinct species based on call differences (Crombie 1986), a different chromosome number (Bogart and Hedges, in press), allozyme differences (Hedges, in press), and an apparent lack of intergradation (R. Crombie, pers. comm.).

This is a morphologically well-defined group (Flores 1984). Chromosome, immunological, and additional allozyme data supporting this group will be presented elsewhere (Bogart and Hedges, in press; Hass and Hedges, unpubl. MS; Hedges, in press).

cundalli group
Figure 15

DEFINITION.-- Alleles Ck^{s2D} and Pgm^{fC} are synapomorphies. Long-limbed species with large eyes, a rugose or tuberculate dorsum, and large digital pads.

CONTENT.-- 3 species: *cavernicola*, *cundalli*, and *glaucoreius*.

DISTRIBUTION.-- Jamaica

REMARKS.-- Synapomorphic alleles at six additional loci will be presented elsewhere (Hedges, in press). The species *glaucoreius* was described as an eastern subspecies of *cundalli* by Schwartz and Fowler (1973) based on smaller body size and shorter vomerine odontophores. It can be distinguished from both *cavernicola* and *cundalli* by electrophoretic (Hedges in press) and chromosomal (Bogart and Hedges, in press) differences. All three taxa are allopatric with non-adjoining ranges. Since *glaucoreius* has differentiated to at least the same degree as *cavernicola* (from *cundalli*), I regard it as a distinct species. All previous workers on Jamaican *Eleutherodactylus* have considered *cundalli* (and by association, *cavernicola* and *glaucoreius*) and *grabhami* to be closer to Cuban and Hispaniolan species of the *ricordii* group (=subgenus *Euhyas*) than to other Jamaican

species based on external morphology and osteology (Dunn 1926b; Lynn 1940; Goin 1954; Schwartz and Fowler 1973; Crombie 1977; Flores 1984). However, one morphological trait is in agreement with the molecular data showing a relationship between the *cundalli* group and other Jamaican *Eleutherodactylus*. The "picket" dorsal pattern apparently is a rare variant only known in seven Jamaican species (*cundalli*, *glaucoreius*, *fuscus*, *gossei*, *pantoni*, *pentasyringos*, and *sisyphodemus*) and one Middle American species of *Eleutherodactylus* (Goin 1960; Schwartz and Fowler 1973; Crombie 1977).

jamaicensis group
Figure 16

DEFINITION.-- Allele Ck^{s2f}, and an areolate venter are autapomorphies for the single bromeliad-dwelling species in this group.

CONTENT.-- 1 species: *jamaicensis*.

DISTRIBUTION.-- Jamaica.

REMARKS.-- Dunn (1926b) and Schwartz (1969) associated *jamaicensis* with the *auriculatus* group (=*auriculatus* section). Schwartz and Fowler (1973) considered it an aberrant *gossei* group (=*luteolus* series) species, and Crombie (1977) placed it in its own group (as a separate invasion to Jamaica). Flores (1984) considered it distant from all other Jamaican species based on osteological characters. Although considered here to be part of the Jamaican radiation (*luteolus* series), it is retained in a separate group.

nubicola group
Figure 17

DEFINITION.-- A diploid chromosome number of 32 (Bogart and Hedges, in press) and absence of inguinal glands are synapomorphies. Stout-bodied terrestrial species with small digital pads (except *orcutti*) and a smooth dorsum (except *alticola*).

CONTENT.-- 5 species: *alticola*, *andrewsi*, *griphus*, *nubicola*, and *orcutti*.

DISTRIBUTION.-- Jamaica.

REMARKS.-- Except for *griphus* (Crombie 1986), all are restricted to the Blue Mountains of eastern Jamaica. Flores (1984) considered the absence of inguinal glands in this group to be a synapomorphy. Although no allelic synapomorphies were detected in this study, chromosome and allozyme data to be presented elsewhere support the monophyly of this group (Bogart and Hedges, in press; Hedges, in press).

bakeri series
Figure 18

DEFINITION.-- Allele $Pt\text{-}3^{13}$ (absent in *glaphycompus*; unknown in *semipalmatus* and *thorectes*), a paired vocal sac (vocal sac absent in *glanduliferoides* and *semipalmatus*), and enlarged digital pads (reduced in *glanduliferoides*) are synapomorphies. Primarily arboreal and rock-dwelling species with rugose or areolate venters.

CONTENT.-- 9 species: *amadeus* (Hedges et al. 1987), *bakeri*, *eunaster*, *glandulife-*

roides, *glaphycompus*, *heminota* (Fig. 18), sp. nov. P (Hedges, unpubl. MS), *semipalmatus* and *thorectes* (Hedges 1988).

DISTRIBUTION.-- Hispaniola (South Island).

REMARKS.-- This series has invaded the arboreal adaptive zone normally occupied by species of the *auriculatus* section of the subgenus *Eleutherodactylus* (see below). The paired vocal sac is internal in *heminota*, external in *eunaster*, *glaphycompus*, and sp. nov. P, absent in *glanduliferoides*, *semipalmatus*, and *thorectes*, and either internal or absent (i.e. polymorphic) in *amadeus* and *bakeri*. Most are climbing species (*amadeus*, *bakeri*, *eunaster*, and *heminota* are arboreal; *glaphycompus* and sp. nov. P are rock-dwelling) although two species (*glanduliferoides* and *thorectes*) are found on or near the ground. The poorly known *semipalmatus* is believed to inhabit streams based on its digital fringe and webbing, although some examples of the bromeliad-dwelling *heminota* also possess these traits (to a lesser extent). Several additional undescribed species belonging to this series are present in collections from the Massif de la Hotte (Hedges, unpubl. MS).

pictissimus series

DEFINITION.-- Allele Ck^{m2A} (absent in *rufifemoralis* and *schmidti*) is a synapomorphy. Terrestrial species with reduced digital pads and a common dorsal pattern of mottling and/or dorsolateral stripes (or reverse parentheses).

CONTENT.-- 12 species; 3 species groups.

DISTRIBUTION.-- Hispaniola and Mona Island.

REMARKS.-- Aside from the co-occurrence of *paulsoni* and *pictissimus*, and possibly *schmidti* and *weinlandi*, all of the species in this series are allopatric.

rufifemoralis group
Figure 19

DEFINITION.-- Allele *Icd-1*^{i}, red "flash" marks on the concealed portions of the thigh and groin, and a "reverse parentheses" dorsal pattern are synapomorphies.

CONTENT.-- 2 species: *furcyensis* and *rufifemoralis* (Fig. 19).

DISTRIBUTION.-- Hispaniola (South Island), in the Sierra de Baoruco and Massif de la Selle.

REMARKS.-- These two allopatric species differ greatly in body size: *furcyensis* = 20 mm (male), 37 mm (female) SVL; *rufifemoralis* = 15 mm (male), 19 mm (female) SVL.

schmidti group
Figure 20

DEFINITION.-- Allele Ck^{kA}, webbing (slight) on hind feet, and large body size (to 58 mm SVL) are autapomorphies.

CONTENT.-- 1 species: *schmidti*.

DISTRIBUTION.-- Hispaniola (North Island).

REMARKS.-- Geographic variation in this stream-associated species was detailed by Schwartz (1971).

pictissimus group
Figure 21

DEFINITION.-- Allele Pgm^{s2A} (unknown in *lucioi*, *monensis*, and *warreni*) is a synapomorphy. Most species possess vocal slits and an internal submandibular vocal sac (absent in *lucioi*, *monensis*, and *probolaeus*). Dorso-ventrally flattened terrestrial species with a dorsal pattern of mottling or dorsolateral stripes.

CONTENT.-- 8 species: *grahami*, *lucioi*, *monensis*, *pictissimus*, *probolaeus*, *rhodesi*, *warreni*, and *weinlandi* (Fig. 21).

DISTRIBUTION.-- Hispaniola and Mona Island.

REMARKS.-- Morphological variation in this complex of allopatric species was discussed by Schwartz (1976), who proposed a phylogeny based on the presence or absence of glandular areas and digital pad size. Two species considered by Schwartz to be closely related to this assemblage (*richmondi* and *alcoae*) were not found to be close based on allozyme data.

Species unassigned to species group:

A single species, *paulsoni*, is placed in the *pictissimus* series based on its morphological resemblance to those species (Schwartz 1964), but is unassignable to species group (no allozyme data are available). It is restricted to the Tiburon peninsula of Hispaniola (South Island) and adjacent areas.

Species groups unassigned to series:
emiliae group

DEFINITION.-- A smooth dorsum, vocal slits (unknown in *emiliae*), and an absence of glandular areas are presumed synapomorphies.

CONTENT.-- 3 species: *albipes*, *emiliae*, and *intermedius*.

DISTRIBUTION.-- Cuba.

REMARKS.-- This group originally was designated as the *dimidiatus* group by Dunn (1926a), but Schwartz and Fowler (1973) removed *dimidiatus* (which they considered close to Jamaican species) and erected the *emiliae* group for the remainder of the species. Of the three Hispaniolan species previously placed in this group, I consider one (*parabates*) to belong to the *auriculatus* section (subgenus *Eleutherodactylus* [discussed below]) and the other two (*jugans* and *ventrilineatus*) to be unassigned to a series or group. Both *jugans* and *ventrilineatus* have a rugose and tuberculate (not smooth) dorsum, and at least *jugans* has glandular areas (supraxillary and inguinal). Also, both species lack vocal slits whereas at least two of the three Cuban members of the *emiliae* group possess vocal slits (not examined in *emiliae*). Thus, the two Hispaniolan species, although morphologically similar to one another, do not agree with the *emiliae* group characteristics as defined by Shreve and Williams (1963) or here, and are therefore removed from that group. No allozyme data are available for this group of Cuban species.

symingtoni group

DEFINITION.-- Short vomerine odontophores (a reversal), large body size, and a very rugose and tuberculate dorsum are synapomorphies.

CONTENT.-- 3 species: *delacruzi*, *symingtoni*, and *zeus*.

DISTRIBUTION.-- Cuba; the western province of Pinar del Rio (and possibly Matanzas).

REMARKS.-- This group recently was reviewed by Estrada et al. (1986). Although no allozyme data are available, I place the *symingtoni* group in the subgenus *Euhyas* based on the absence of vocal slits (in at least *symingtoni*), and the presence of a rugose dorsum and smooth venter (weakly rugose in *delacruzi* and *zeus*). Also, the species appear to have terrestrial or rock-dwelling habits, characteristic of species in this subgenus. Joglar (1986) places *symingtoni* and *zeus* in the *unistrigatus* group (=*auriculatus* section) based on short vomerine odontophores. I interpret the short vomerine odontophores in this group as a reversal to the plesiomorphic state.

varleyi group

DEFINITION.-- Short vomerine odontophores (a reversal), and small body size are presumed synapomorphies.

CONTENT.-- 2 species: *cubanus* and *varleyi*.

DISTRIBUTION.-- Cuba.

REMARKS.-- I place the Hispaniolan species *eunaster* and *glanduliferoides* in the *bakeri* series, rather than in this group (Schwartz 1985), based on morphology. The two Cuban species lack glandular areas (Shreve and Williams 1963) whereas both Hispaniolan species possess supraxillary, inguinal, and postfemoral glands. Also, *eunaster* has a paired vocal sac like most other species in the *bakeri* series whereas *varleyi* possesses a single pectoral vocal sac (vocal sac is absent in *glanduliferoides* and no information is available for *cubanus*). It is possible that the *varleyi* group belongs in the *bakeri* series, but there is little morphological justification, aside from short vomerine odontophores, and no allozyme data are available for the Cuban species.

Species unassigned to series:

The following species are placed in the subgenus *Euhyas* but are unassignable to series: Cuba (19) - *acmonis*, *atkinsi*, *bresslerae*, *cuneatus*, *dimidiatus*, *etheridgei*, *greyi*, *guanahacabibes*, *gundlachi*, *klinikowskii*, *limbatus*, *pezopetrus*, *pinarensis*, *planirostris*, *ricordii*, *sierramaestrae*, *thomasi*, *turquinensis*, and *zugi*; Hispaniola (13) - *alcoae*, *apostates*, *armstrongi*, *brevirostris* (Fig. 22), sp. nov. C (Hedges unpubl. MS), *darlingtoni*, *glandulifer*, *jugans*, *leoncei*, *neodreptus*, *oxyrhyncus* (Fig. 23), *sciagraphus*, and *ventrilineatus*).

Subgenus *Eleutherodactylus* Dumeril and Bibron 1841

TYPE SPECIES.-- *Hylodes martinicensis* Tschudi 1838

CONTENT.-- ca. 275 species.

DISTRIBUTION.-- South America, Middle America, and the West Indies (excluding Jamaica).

REMARKS.-- Presumably a paraphyletic assemblage which includes more than half of the named species in the genus, mostly distributed in northwestern South America. Only one division of this subgenus will be considered here: the *auriculatus* section. The South American species groups are reviewed by Lynch (1976), and the current composition of these groups can be found in Lynch (1985), with some recent changes (Lynch 1986).

auriculatus section

DEFINITION.-- Allele *Icd-1*^{f1} (Fig. 5) is a presumed synapomorphy, present in 25 of 32 species examined (absent in *counouspeus*, *minutus*, *montanus*, sp. nov. N, *poolei*, *richmondi*, and *unicolor*; 12 species not examined electrophoretically). Primarily an arboreal group distinguished from other West Indian species of the genus *Eleutherodactylus* by a combination of short vomerine odontophores, areolate venter, external submandibular vocal sac, and enlarged digital pads.

CONTENT.-- 44 species, 2 series.

DISTRIBUTION.-- Cuba (6 sp.), Hispaniola (16 sp.), Puerto Rican Bank (17 sp.), and the Lesser Antilles, Trinidad, and northeastern South America (5 sp.).

REMARKS.-- Previously referred to as the *auriculatus* group (Dunn 1926a; Schwartz 1969), this section is morphologically similar to the *unistrigatus* group (Lynch 1976; Joglar 1986). However, in the *auriculatus* section, the frontoparietal and otoccipital bones normally are fused (not fused in most *unistrigatus* group species) and the median ramus of the pterygoid does not overlap the parasphenoid alae (usually overlaps in *unistrigatus* group species) (Lynch 1976). Also, some differences exist in the tympanum, hyoid processes, and presence or absence of nuptial pads, but none are diagnostic (Joglar 1986). Until a critical examination of the mainland *Eleutherodactylus* (especially the *unistrigatus* group) reveals that the *auriculatus* section is not monophyletic, I prefer to continue regarding it as such given the limited data available. Considering the close association between geography and phylogeny in other *Eleutherodactylus* groups, and the relatively high degree of morphological similarity among most *auriculatus* section species, it is likely that this geographic unit is monophyletic. Since *counouspeus* has a small liver with rounded lobes and an external submandibular vocal sac, it tentatively is placed in this section, but its chromosome number (2N=32; J. Bogart, pers. comm.), rock-dwelling habits, and distribution (South Island) would otherwise associate it with the subgenus *Euhyas*.

martinicensis series
Figures 24-25

DEFINITION.-- Allele *Acp*^{d} (absent in *brittoni*, *gryllus*, *locustus*, and *richmondi*) is a synapomorphy. There are no known morphological synapomorphies.

CONTENT.-- 22 species; 1 species group.

DISTRIBUTION.-- The Puerto Rican Bank, Lesser Antilles, and northeastern South America.

REMARKS.-- Although allele Acp^{d} is absent in *brittoni*, *gryllus*, *locustus*, and *richmondi*, other data suggest that these species are associated with the *martinicensis* series. Allele Pgm^{u4B} is unique to *locustus* and a species in the *martinicensis* series, *antillensis*. Also, *richmondi* has an allele, Ck^{g2}, found only in species of this series. In an electrophoretic study of eight proteins in seven Puerto Rican *Eleutherodactylus*, Smith et al. (1981) found *brittoni* and *locustus* to be close to other species on the island (*antillensis* and *eneidae*, respectively). Since the synapomorphic allele Acp^{d} is polymorphic in at least two species (*coqui* and *portoricensis*), then it is possible that it was not found in those four species due to the small sample size (one).

No allozyme data are available for *hedricki* and *karlschmidti*, but chromosomal data suggest an association with other Puerto Rican species (Bogart 1981a). The inclusion of *karlschmidti* and *unicolor* in the *ricordii* group (=subgenus *Euhyas*) by Savage (1987:table 3) based on chromosome number (2N=30) apparently was an error.

The ovoviviparous species *jasperi* recently was placed in a separate genus, *Ladailadne* (Dubois 1986) primarily based on its unique mode of reproduction. However, ovoviviparity has not been found in any other *Eleutherodactylus* species and is a derived trait. Since it is therefore an autapomorphy, it conveys no information concerning the relationship of *jasperi* to other *Eleutherodactylus* species. No electrophoretic data are available for *jasperi*, but it has a small liver with a rounded left lobe and an external submandibular vocal sac, two traits which associate it with the *auriculatus* section of the subgenus *Eleutherodactylus*. Additionally, it has a diploid chromosome number of 26 (Drewry and Jones 1976) like most other Puerto Rican species (Bogart 1981a), although a few Hispaniolan species in the *auriculatus* section also have that number (Bogart and Hedges, unpubl. data). There is no indication that *jasperi* is other than a member of the *auriculatus* section (based on morphology, geography, and chromosome number) and thus I place the genus *Ladailadne* in the synonymy of the genus *Eleutherodactylus*.

martinicensis group

DEFINITION.-- Alleles Ck^{g3A} (absent in *barlagnei*), Pgm^{n2B} (absent in *barlagnei* and *johnstonei*), and a common pattern of dorsal chevrons are synapomorphies.

CONTENT.-- 4 species: *barlagnei*, *johnstonei*, *martinicensis*, and *pinchoni*.

DISTRIBUTION.-- Lesser Antilles.

REMARKS.-- Schwartz (1967:58) suggested that these four Lesser Antillean species might share a common ancestor based on a pattern variant of one or two dorsal chevrons present in all. Two of the four, *barlagnei* and *pinchoni*, are endemic to Guadeloupe and all four occur on that island (*johnstonei* recently was introduced). Based on geography, *urichi*, which occurs in the southern Lesser Antilles and northern South America, may also be a member of this group, although no allozyme data are available for that species.

Species unassigned to species group:

The following species in the *martinicensis* series are unassignable to species group: *antillensis*, *brittoni*, *cochranae*, *cooki* (Fig. 24), *coqui* (Fig. 25), *eneidae*, *gryllus*, *hedricki*, *jasperi*, *karlschmidti*, *lentus*, *locustus*, *portoricensis*, *richmondi*, *schwartzi*, *unicolor*, *urichi*, and *wightmanae*.

montanus series
Figures 26-27

DEFINITION.-- Alleles Icd^{f2B}, Lgl^{l3A}, and Pgm^{p3B} are presumed synapomorphies, but see remarks below.

CONTENT.-- 15 species; 1 species group.

DISTRIBUTION.-- Hispaniola.

REMARKS.-- This series is weakly defined since out of 14 species examined, only seven have allele Icd^{f2B}, only five have Lgl^{l3A}, and only two have allele Pgm^{p3B} (9 species have at least one of the three). However, all occur on Hispaniola and most have chromosome numbers that are lower than those in the *martinicensis* series (Bogart 1981a; Bogart and Hedges, unpubl. data). It is possible that the six Cuban *auriculatus* section species are associated with this series since the two species that have been karyotyped (*auriculatus* and *varians*; Bogart 1981a) also have a low number, 2N=18, which is the modal number in the *montanus* series.

Among the unassigned species, several groups are suggested by the allelic data. Two species with "notched" digital pads, *flavescens* and *poolei*, share the unique allele Lgl^{i2} and are allopatric in distribution. Also, two virtually identical species, *montanus* (Fig. 26) and *patricae* (Schwartz 1965c), share the unique allele $Pt\text{-}3^{l2}$. Three small high elevation species, *audanti*, *haitianus*, and *minutus*, share the unique allele Ck^{f3B}.

wetmorei group
Figure 27

DEFINITION.-- Alleles Acp^{o}, Lgl^{l5A} (absent in *wetmorei*), and Pgm^{u3B} (absent in *lamprotes*) are synapomorphies. Moderate to large-sized bromeliad-dwelling species with large circular digital pads.

CONTENT.-- *fowleri*, *lamprotes*, and *wetmorei* (Fig. 27).

DISTRIBUTION.-- Hispaniola.

REMARKS.-- Allele Acp^{o} also occurs in *glanduliferoides* (subgenus *Euhyas*, *bakeri* series), but is interpreted as a convergence based on other allelic data, chromosomes, and morphology (see discussion of *bakeri* series above). The two allopatric South Island species, *fowleri* and *lamprotes*, are relatively large, have greatly expanded digital pads, and live almost exclusively in bromeliads. The third species, *wetmorei*, occurs on both the North and South Islands and is ecologically more variable, but is also commonly found in bromeliads.

Species unassigned to species group:

The following species in the *montanus* series are unassignable to species group: *abbotti*, *audanti*, *auriculatoides*, *flavescens*, *haitianus*, *minutus*, *montanus*, *parabates*, *patricae*, *pituinus*, *poolei*, and sp. nov. N (Sierra de Neiba).

Species unassigned to series:

The following species of the *auriculatus* section are unassignable to series: *auriculatus*, *bartonsmithi*, *counouspeus* (Fig. 28), *eileenae*, *leberi*, *ronaldi*, and *varians*.

***Pelorius* new subgenus**

Cornufer Tschudi 1838 [Type species by monotypy, *Cornufer unicolor* Tschudi 1838 (=*Eleutherodactylus inoptatus* Barbour 1914; see Zweifel 1967). The specific name *Cornufer unicolor* Tschudi 1838 was placed on the Official Index of Rejected and Invalid Specific Names in Zoology (Bulletin of Zoological Nomenclature 34:267).]

TYPE SPECIES.-- *Leptodactylus inoptatus* Barbour 1914

DEFINITION.-- Alleles Icd^{pS} (absent in *inoptatus*), Lgl^{a1} (absent in *parapelates*), and Pgm^{o} (absent in *chlorophenax* and *nortoni*), a relatively long first finger (longer than second finger in *inoptatus*, *parapelates*, and *ruthae*), and large body size (50-90 mm SVL) are presumed synapomorphies. These are robust species with a relatively wide head and a smooth to weakly areolate venter.

CONTENT.-- 6 species; 2 species groups.

DISTRIBUTION.-- Hispaniola.

ETYMOLOGY.-- From the Greek, *Pelorios*, meaning huge, prodigious, awe-inspiring; referring to the large size of the species in this group, and the striking appearance of some (e.g. *nortoni*).

REMARKS.-- Schwartz (1965a) separated the *inoptatus* group (=subgenus *Pelorius*) from the *auriculatus* group (=*auriculatus* section) citing differences in size (larger in the *inoptatus* group), vomerine odontophore length (short, but not "patch-like"), vocal sac (not external), vocalization, and calling site (low to the ground or underground). Hedges and Thomas (1987) found that all six species have a single, internal, submandibular vocal sac and discussed species differences in vocalization and calling sites.

***inoptatus* group**
Figure 29

DEFINITION.-- Alleles Ck^{j2} and $Pt\text{-}3^{l1}$, and very large body size (66-90 mm SVL) are synapomorphies.

CONTENT.-- 3 species - *chlorophenax* (Fig. 29), *inoptatus*, and *nortoni*.

DISTRIBUTION.-- Hispaniola.

REMARKS.-- Two of the three species, *chlorophenax* and *nortoni*, form a subgroup based on synapomorphic allele Pgm^{q}. Both species also have greatly enlarged digital pads and a similar rising call (Hedges and Thomas 1987).

***ruthae* group**
Figure 30

DEFINITION.-- Alleles Acp^{b} and Ck^{j1A} (absent in *parapelates*), a protruding snout with cornified skin at tip, chevron-shaped shank bars, and a laterally extended vocal sac are synapomorphies. Moderate-sized (ca. 50 mm SVL) burrowing species.

CONTENT.-- 3 species - *hypostenor*, *parapelates*, and *ruthae* (Fig. 30).

DISTRIBUTION.-- Hispaniola.

REMARKS.-- In addition to a cornified snout, these three allopatric species have unusually large subarticular tubercles, both probably adaptations for burrowing (I have observed captive *ruthae* use all four limbs and snout while burrowing). Considerable geographic call variation in *ruthae* (Schwartz 1965a; Hedges and Thomas 1987) may indicate that there are additional undescribed species.

BIOGEOGRAPHY

The results of this study indicate that overwater dispersal has not been a major factor in the recent evolutionary history of the genus *Eleutherodactylus* in the West Indies. This is suggested by the high degree of intra-island similarity, and the nearly complete absence of shared alleles between species on different islands. Others have assigned a more important role to dispersal, based on the morphological resemblance of species on different islands (Shreve and Williams 1963; Schwartz 1978). However, the allelic data indicate that intra-island radiations accompanied by morphological convergence, as in the anoline lizards (Williams 1969, 1983), has been the major theme in West Indian *Eleutherodactylus* evolution and biogeography.

The relevance of vicariance to *Eleutherodactylus* evolution in the Caribbean region depends strongly on the time frame involved. If the times of divergence of the major groups in the West Indies post-date the early Tertiary breakup of the proto-Antilles, then the vicariance theory (Rosen 1976, 1985) is not supported for this genus, and dispersal must have occurred. Information on times of divergence can come from fossil data, or from molecular data such as albumin immunological distances calibrated with geological time.

FOSSIL RECORD.-- An Upper Eocene *Eleutherodactylus* recently was discovered in Dominican Republic amber (Poinar and Cannatella 1987). It is the only unquestionable pre-Quaternary fossil *Eleutherodactylus* (Lynch 1971). This important find establishes the presence of the genus (in addition to *Anolis* and *Sphaerodactylus*; see Williams, this volume) in the Antilles 35-40 myBP. However, the description of the frog is insufficient to associate it with one of the five subgenera of *Eleutherodactylus*, making any other biogeographic interpretations difficult.

Notwithstanding, Poinar and Cannatella (1987) asserted that the presence of the Eocene amber fossils supports the vicariance model (Rosen 1976, 1985) in that they occur at a much earlier time than predicted by the dispersal model (Oligocene or Miocene at earliest). However, the mid-Tertiary arrival of Antillean groups in the dispersal model was based on the earliest known fossils of those groups, all from the mainland (Pregill 1981). That some of the earliest fossils are now from Hispaniola does not counter the dispersal model but simply extends the minimum age for these groups. Dispersal may have occurred during the Eocene or before.

Also, Poinar and Cannatella suggested that the relationships of the amber *Anolis* (Rieppel 1980), also from the North Island, supports the vicariance model, since it belongs to a subgroup of the genus which is distributed primarily on Cuba and Hispaniola (Williams 1976). However, this in fact supports dispersal, since most of the twenty Hispaniolan species of the subgroup (*carolinensis* subsection) occur on the South Island of Hispaniola (Schwartz 1980, Henderson and Schwartz 1984), which was separated from the North Island by over 1000 km of ocean in the Upper Eocene (Buskirk 1985).

Finally, a test was proposed by Poinar and Cannatella whereby vicariance is disproven if the fossil *Eleutherodactylus* (North Island) eventually is found to be more closely related to present-day South Island *Eleutherodactylus* than to North Island *Eleutherodactylus*. One difficulty with this test is the extremely low probability of rejecting the vicariance hypothesis. Only a complicated and unlikely biogeographic scenario would result in the Eocene North Island species being more closely related to present-day South Island species than to North Island species. Secondly, geologic data (Buskirk 1985) suggest that Jamaica and the South Island of Hispaniola were submerged during the mid-Tertiary. If true, then the present biota of those two islands must have arrived by dispersal. Although the Eocene amber fossils from Hispaniola establish the antiquity of those lineages in the West Indies, they do not presently favor one model over the other.

DISTRIBUTION.-- The five subgenera of *Eleutherodactylus* (*Craugastor*, *Eleutherodactylus*, *Euhyas*, *Pelorius*, and *Syrrhophus*) all occur in the Caribbean region (including adjacent mainland areas) and have largely allopatric distributions (Figs. 31-32). Although both subgenera *Eleutherodactylus* and *Euhyas* occur on Cuba and Hispaniola, the number of species per island of each subgenus indicates that the former taxon primarily is an eastern Caribbean group whereas the latter taxon is a western Caribbean group (Fig. 33). All Jamaican *Eleutherodactylus* belong to the subgenus *Euhyas* whereas all Puerto Rican Bank and Lesser Antillean species are in the subgenus *Eleutherodactylus*. The subgenus *Pelorius* is restricted to Hispaniola where it occurs with both subgenera (*Eleutherodactylus* and *Euhyas*).

In Middle America, the subgenus *Syrrhophus* has a northern distribution, occurring in Mexico, Belize, and northern Guatemala. Although the subgenus *Craugastor* is sympatric with *Syrrhophus* in northern Middle America, it is more widely distributed and has its highest diversity on the Chortis Block (southern Guatemala, Honduras, Nicaragua, and northern Costa Rica). The subgenus *Eleutherodactylus* (excluding the *auriculatus* section) extends into southern Middle America but has its highest diversity in South America.

BIOGEOGRAPHIC HISTORY.-- The distribution and relationships of the major groups of the genus *Eleutherodactylus* in the Caribbean region suggest a biogeographic history that includes both vicariance and dispersal. The timing of the events is inferred from albumin immunological data (Hass and Hedges, unpubl. MS, unpubl. data) using the albumin clock (Wilson et al. 1977). Since molecular data are lacking for most mainland species, the following biogeographic scenario focuses primarily on Antillean events.

The genus *Eleutherodactylus* likely arose in South America (Lynch 1971) and dispersed across the proto-Antilles to reach southern North America and the Chortis Block in the late Cretaceous. Perfit and Williams (this volume) argue that the proto-Antilles was a discontinuous chain of islands and not a continuous land mass. Geologic data are insufficient to distinguish clearly between these two alternatives, although in contrast to Williams, I believe that the latter is more likely. First, the proto-Antillean volcanic arc was already about 50-60 million years old by the late Cretaceous (Donnelly 1985). It is possible that this long period of activity resulted in a larger accretion of land than would a newly formed island arc system, although this has not been reflected in the sedimentary strata (T.W. Donnelly pers. comm.). Also, the poor overwater dispersal ability of *Eleutherodactylus* indicated by this study suggests that the connection between North and South

America at the end of the Cretaceous was relatively continuous for the South American *Eleutherodactylus* to have reached the Chortis block and southern North America.

The breakup of the proto-Antilles probably was the vicariant event that isolated the subgenus *Craugastor* on the Chortis block (and possibly southern North America) in the early Tertiary (60 myBP). Likewise, the subgenus *Euhyas* became isolated on Cuba. Jamaica and the South Island of Hispaniola may have carried an *Eleutherodactylus* fauna at this time but these islands later were completely submerged in the Oligocene (Buskirk 1985). It is unclear when the subgenera *Eleutherodactylus* and *Pelorius* entered the West Indies, or what vicariant event (if any) led to their divergence. If they diverged in the Oligocene as suggested by immunological data (Hass and Hedges, unpubl. data), then the Eocene amber frog (Poinar and Cannatella 1987) likely was a member of the ancestral stock of those two groups, based on their current distributions (Figs. 32-33). This ancestral stock may have been present on the North Island of Hispaniola and/or Puerto Rico during the initial breakup of the proto-Antilles, or dispersed there from South America sometime before the late Eocene.

Following the breakup of the proto-Antilles, Cuba, the North Island of Hispaniola, and Puerto Rico moved northeastward relative to North and South America, eventually colliding with the Bahamas platform in the Eocene (Pindell and Dewey 1982; Sykes et al. 1982; Duncan and Hargraves 1984). In the late Eocene or early Oligocene (35-40 myBP), dispersal from Cuba (subgenus *Euhyas*) to nearby southern North America may have led to the establishment of the subgenus *Syrrhophus* in what is now southern Mexico, Guatemala, and Belize. Since all species of that subgenus lack vomerine teeth (Joglar 1986), the dispersal event probably was from Cuba to North America and not in the other direction, as most Cuban *Eleutherodactylus* have vomerine teeth and it is less likely that this trait would reappear after being lost. A resident North American *Eleutherodactylus* fauna (the subgenus *Craugastor*) may have posed an ecological barrier (e.g. Williams 1969) to dispersal. However, species of the subgenera *Euhyas* and *Syrrhophus* are more terrestrial than those of the subgenus *Craugastor* and thus less likely to compete. Also, the subgenus *Craugastor* may have been restricted to the Chortis Block at that time, in which case the proto-*Syrrhophus* colonist would not have faced a potential competitor.

At about this time (late Eocene), a fault zone developed in the northern Caribbean, extending from southern Mexico and northern Guatemala and through the present day Cayman Trough (Burke et al. 1978; Pindell and Dewey 1982; Sykes et al. 1982). Jamaica and the South Island of Hispaniola since have moved eastward along this fault zone.

Thick limestone sequences lacking terrestrial sediments were deposited throughout Jamaica during the Oligocene indicating that it was completely submerged (Robinson et al. 1970; Horsfield 1973; Comer 1974; Horsfield and Roobol 1974; Arden 1975; Kashfi 1983; Wadge and Dixon 1984). Since limestone does not presently cover the Blue Mountains, presumably having been eroded away, it cannot be proven that all of Jamaica was submerged. However, the purity of the limestone immediately adjacent to the Blue Mountains argues against emergence even in that region (Horsfield and Roobol 1974). Also, there was no orogenic activity (uplift) occurring in Jamaica during most of the Oligocene. Instead, up to 3650 m of subsidence (Kashfi 1983) further suggests that there was no emergent land other than coral atolls, unlikely to support a continuous lineage of *Eleutherodactylus*. The South Island of Hispaniola also apparently was submerged at that

time (Bowin 1975; Maurrasse 1982), although the geological evidence is not as strong due to extensive late Cenozoic uplift and erosion of mid-Tertiary limestones.

During the Oligocene, the subgenus *Euhyas* probably was restricted to Cuba where it was evolving in isolation. This is suggested by its present distribution and the fact that Jamaica and the South Island of Hispaniola probably were submerged at the time.

By the early Miocene (20 myBP), Jamaica and the South Island had moved further eastward relative to Cuba, and were now emergent (Fig. 34:top). Dispersal of the subgenus *Euhyas* from Cuba to Jamaica and the South Island of Hispaniola probably occurred at this time, based on albumin immunological distances (Hass and Hedges, unpubl. data). The latter two islands initially were low and flat with a blanket of highly dissected limestone (Comer 1974: fig. 5). Major uplift since the late Miocene (10 myBP) resulted in the Blue mountains in Jamaica and the three South Island ranges: the Massif de la Hotte, Massif de la Selle, and the Sierra de Baoruco (Horsfield 1973; Burke et al. 1980). It was during this geologically active time that most of the speciation on Jamaica and the South Island probably occurred. This can be inferred by the fact that many species from these two islands presently are restricted to upland areas, where they presumably evolved.

Pregill and Olson (1981) suggested that the large radiation of South Island *Eleutherodactylus* mainly was the result of Pleistocene sea level and climatic changes. However, the levels of allozyme divergence among South Island species examined in this study (some with different alleles at most of the six slow-evolving loci) indicate a longer period of evolution. This is also supported by the high degree of morphological and ecological differentiation of the species, with at least 20 sympatric at one site in the Massif de la Hotte (Schwartz 1973; Hedges and Thomas 1987).

After the South Island collided with the North Island in the late Miocene (10 myBP; Sykes et al. 1982), one lineage of the subgenus *Euhyas* (*pictissimus* series) dispersed northward and one lineage of the *auriculatus* section of the subgenus *Eleutherodactylus* (*wetmorei* group) dispersed southward (Fig. 34:bottom). These overland dispersal events probably occurred relatively recently (late Pliocene) since each led to a small radiation of closely related species, mostly allopatric and morphologically similar. The origin of the Cuban *auriculatus* section species is less clear, although their morphological and chromosomal similarity to North Island species suggests a relatively recent (late Miocene or Pliocene) overwater dispersal from the North Island.

Two *auriculatus* section species which are islandwide on Hispaniola, *abbotti* and *audanti*, probably dispersed from the North Island to the South Island in the Quaternary. The spotty distribution of *audanti* on the South Island (absent from many undisturbed areas in the Massif de la Hotte) further suggests it is a recent arrival.

The present distribution of the subgenus *Pelorius* throughout Hispaniola implies that it dispersed from the North to the South Island after the collision. Another possibility is that it dispersed to the South Island soon after the emergence of that island (late Oligocene?), evolved along with the subgenus *Euhyas* during the Miocene, and dispersed (*inoptatus* and *ruthae*) back to the North Island after collision. That would provide a vicariance explanation for the origin of *Pelorius*. There are other possibilities, but whichever is correct, the large body size characteristic of the subgenus *Pelorius* probably has facilitated coexistence with the other two subgenera (*Eleutherodactylus* and *Euhyas*) on Hispaniola.

The preceeding scenario differs substantially from previous explanations for North vs

South Island faunal distribution patterns (Mertens 1939; Williams 1961, 1965; Schwartz 1978, 1980; Pregill and Olson 1981). Those authors suggested that sea level and climatic changes, especially those that occurred during the Pleistocene, were responsible for the isolation of populations on either side of the Cul de Sac/Valle de Neiba trough. While such a mechanism may explain North vs South Island species pairs (e.g. the *Anolis chlorocyanus* species group; Williams 1965), the more trenchant differences between the North and South Island *Eleutherodactylus* faunas revealed by this study are better explained by the tectonic history of the two islands outlined above.

Island radiations and convergence

Broadly defined, almost any monophyletic group of organisms can be referred to as an evolutionary radiation. When most or all of the species of a taxon inhabiting an island form a monophyletic group, it can be referred to as an island radiation (Williams 1983). An adaptive radiation (Osborn 1902) is an evolutionary radiation believed to be the result of the filling of newly available ecological niches through adaptation (Romer 1966).

Raup (1984) considers the term adaptive radiation to be a tautology because "a group that suddenly increases in diversity does so for reasons of adaptive success," and therefore he prefers the term evolutionary radiation. I maintain the distinction here since I believe that cladogenesis and diversity can increase without "adaptive success". This could occur when a widespread species is fragmented into geographical isolates, each resulting in a new species (vicariance) but with similar ecologies.

An example of such a nonadaptive radiation is the *pictissimus* group of *Eleutherodactylus* (subgenus *Euhyas*). It includes eight allopatric Hispaniolan species similar in habitus and ecology. In this case, cladogenesis probably was caused by Pleistocene climatic changes (Pregill and Olson 1981) resulting in range fragmentation of a widespread ancestral species. Over time, a nonadaptive radiation may lead to an adaptive radiation if species become sympatric and develop morphological and ecological differences. Thus, evolutionary radiations (or island radiations) may include both adaptive and nonadaptive radiations.

One of the best known examples of island radiations involves the West Indian anoline lizards of the family Iguanidae. Although the systematics of the Cuban and Hispaniolan species are not well known, island radiations probably occurred on each of the four Greater Antilles (Williams 1976, 1983). This has resulted in numerous cases of morphological and ecological convergence, and formed the basis for the concept of ecomorph (Williams 1972, 1983).

In contrast, the morphological and ecological diversity of West Indian *Eleutherodactylus* are not equally represented among the major lineages (subgenera). The frogs of the subgenus *Euhyas* generally are terrestrial in habits whereas the subgenus *Eleutherodactylus* (*auriculatus* section) mainly is composed of arboreal species. The six species in the subgenus *Pelorius* span a variety of ecological types, although burrowing species are unique to this group. Thus it appears that the ecological habits of the ancestors of these groups have been largely maintained in the descendants, which may explain why the correlated morphological traits (small digital pads and smooth venter in terrestrial species; large digital pads and areolate or rugose venter in arboreal species) generally have proven to be useful diagnostic characters.

Nonetheless, island radiations have occurred in West Indian *Eleutherodactylus*, but within the phylogenetic and ecological context of the two major subgenera. Thus, the radiations on Cuba, Jamaica, and the South Island of Hispaniola largely involve terrestrial species (subgenus *Euhyas*), whereas arboreal species dominate the radiations on the North Island of Hispaniola, Puerto Rico, and the Lesser Antilles (subgenus *Eleutherodactylus*).

One example of convergence that has resulted from these independent island radiations involves the aquatic or semiaquatic species found on Cuba (*cuneatus*, *sierramaestrae*, and *turquinensis*), Jamaica (*orcutti*), Hispaniola (*semipalmatus*), and Puerto Rico (*karlschmidti*). Shreve and Williams (1963) erected the *orcutti* group for this assemblage based on the presence of toe webbing, but subsequent authors (Schwartz and Fowler 1973; Schwartz 1967; Crombie 1977) have considered those species (and *barlagnei* of Guadeloupe) to be convergent. Although only *barlagnei* and *orcutti* were examined in this study, the results also indicate convergence in morphology, with toe webbing being an adaptation to an aquatic lifestyle.

In addition to the aquatic ecomorph, at least two other widespread ecomorphs of West Indian *Eleutherodactylus* can be recognized: rock/cave and bromeliad. The rock/cave ecomorph includes species with long limbs, large eyes, and large, truncated (or notched) digital pads. Those species are: *greyi*, *guanahacabibes*, *thomasi*, and *zeus* (Cuba); *cavernicola* and *cundalli* (Fig. 15; Jamaica); *counouspeus* (Fig. 28), *glaphycompus*, and sp. nov. P (Hispaniola-South Island); *pituinus* (Hispaniola-North Island), and *cooki* (Fig. 24; Puerto Rico). The bromeliad ecomorph includes dorsoventrally flattened species with an areolate venter (smooth in *heminota*) and with large, rounded or circular digital pads. They are: *jamaicensis* (Fig. 16; Jamaica); *fowleri*, *heminota* (Fig. 18), and *lamprotes* (Hispaniola-South Island); *auriculatoides* (Hispaniola-North Island); and *gryllus* and *jasperi* (Puerto Rico).

In Hispaniola, the largely independent evolution of the North Island (subgenus *Eleutherodactylus*) and South Island (subgenus *Euhyas*) *Eleutherodactylus* faunas has led to some striking examples of convergence (Fig. 35; Table 3). At least seven ecomorphs can be recognized, six of which involve species from both subgenera and presumably separated for most of the Cenozoic (60 my) based on albumin immunological distance data (Hass and Hedges unpubl. MS).

One example of the remarkable similarity in some of these convergent species pairs involves *jugans*, *ventrilineatus*, and *parabates*. Schwartz (1964) gave the North Island species its name, *parabates* (meaning "transgressor"), in allusion to its resemblance to South Island *jugans* and *ventrilineatus*, presuming that *parabates* had transgressed the Valle de Neiba from the South. However, allozyme data (Fig. 1) and ecological observations suggest that *parabates* is a North Island *auriculatus* section member, convergent with *jugans* and *ventrilineatus*. The latter two species are terrestrial in habits as are most species in the subgenus *Euhyas*. Despite its very stocky and short-legged appearance (Fig. 35), *parabates* males call from arboreal sites, like nearly all other species in the *auriculatus* section (Hedges and Thomas, unpubl. data).

Very little is known about the ecology and behavior of most West Indian *Eleutherodactylus* and thus the ecomorph categories described here are likely to change in definition and composition. Also, the underlying assumption with the concept of ecomorph,

that island radiations are also adaptive radiations, is a difficult hypothesis to test but one which agrees with the nonrandom associations between morphology and ecology.

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Table 1. Protein loci and electrophoretic conditions.

Protein[1]	Locus	Enzyme Commission[1] Number	Electrophoretic Conditions[2] First	Second	Third
1. Acid phosphatase	*Acp*	3.1.3.2	E	-	-
2. Creatine kinase	*Ck*	2.7.3.2	C	D	E
3. Isocitrate dehydrogenase ($NADP^+$)	*Icd-1*	1.1.1.42	A	B	-
4. Lactoylglutathione lyase	*Lgl*	4.4.1.5	F	D	C
5. Phosphoglucomutase	*Pgm*	5.4.2.2	B	C	A
6. Protein 3	*Pt-3*	-	C	D	-

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

[2] (A)Tris-citrate pH 8.0, 130v, 6h; (B)Tris-citrate pH 6.7, 150v, 6h; (C)Poulik, 300v, ca. 7h; (D)Lithium hydroxide, 400v, ca. 8h; (E)Tris-versene-borate, 250v, 6h; (F)Tris-HCl, 250v, 4h.

Table 2. A revised classification of West Indian *Eleutherodactylus* (summary).

Genus *Eleutherodactylus* (ca. 450 sp.; 128 sp. in West Indies) - South America, Central America, North America, West Indies

- Subgenus *Euhyas* (78 sp.) - Bahamas, Cuba, Jamaica, Hispaniola, Mona Island
  - *luteolus* series (17 sp.) - Jamaica
    - *luteolus* group (3 sp.) - Jamaica
    - *gossei* group (5 sp.) - Jamaica
    - *cundalli* group (3 sp.) - Jamaica
    - *jamaicensis* group (1 sp.) - Jamaica
    - *nubicola* group (5 sp.) - Jamaica
  - *bakeri* series (9 sp.) - Hispaniola (South Island)
  - *pictissimus* series (12 sp.) - Hispaniola
    - *rufifemoralis* group (2 sp.) - Hispaniola (South Island)
    - *schmidti* group (1 sp.) - Hispaniola (North Island)
    - *pictissimus* group (8 sp.) - Hispaniola
    - unassigned species (1) - Hispaniola (South Island)
  - unassigned groups:
    - *emiliae* group (3 sp.) - Cuba
    - *symingtoni* group (3 sp.) - Cuba
    - *varleyi* group (2 sp.) - Cuba
  - unassigned species (32) - Bahamas, Cuba, Hispaniola
- Subgenus *Eleutherodactylus* (ca. 275 sp.) South America, Central America, West Indies
  - *auriculatus* section (44 sp.) - Cuba, Hispaniola, Puerto Rican Bank, Lesser Antilles, NE South America
  - *martinicensis* series (22 sp.) - Puerto Rican Bank, Lesser Antilles, NE South America
    - *martinicensis* group (4 sp.) - Lesser Antilles
    - unassigned species (18) - Puerto Rican Bank, Lesser Antilles, NE South America
  - *montanus* series (15 sp.) - Hispaniola
    - *wetmorei* group (3 sp.) - Hispaniola
    - unassigned species (12) - Hispaniola
  - unassigned species (7) - Cuba, Hispaniola (South Island)
- Subgenus *Pelorius* (6 sp.) - Hispaniola
  - *inoptatus* group (3 sp.) - Hispaniola
  - *ruthae* group (3 sp.) - Hispaniola

Table 3. Convergence in Hispaniolan *Eleutherodactylus*. North and South Island refer to paleoislands presently separated by the arid Cul de Sac (Haiti) and Valle de Neiba (Dominican Republic). Species are listed in order of increasing body size (maximum female snout-vent length in mm), indicated in parentheses.

ECOMORPH	SOUTH ISLAND[1]	NORTH ISLAND[2]	MORPHOLOGY	ECOLOGY
Small Terrestrial Montane	*thorectes* (17)	sp. nov. N (15) *haitianus* (17)	short limbs; small digital pads; rugose dorsum	high elevation; ground and leaf litter
Small Arboreal Montane	*amadeus* (25)	*minutus* (19) *audanti*[3] (25)	moderately developed digital pads	high elevation; low vegetation
Intermediate Terrestrial Montane	*ventrilineatus* (25) *jugans* (33)	*parabates* (24)	short snout; stocky habitus; small digital pads	moderate to high elevation; ground and low vegetation
Rock/cave	*glaphycompus* (29) sp. nov. P (33)	*pituinus* (29)	long limbs; large, notched digital pads; large eyes	rock- and cave-dwelling
Bromeliad	*lamprotes* (28) *heminota* (30) *fowleri* (33)	*auriculatoides* (33)	dorsoventrally flattened; large, rounded digital pads	bromeliad-dwelling

Table 3. Convergence in Hispaniolan *Eleutherodactylus* (concluded).

ECOMORPH	SOUTH ISLAND[1]	NORTH ISLAND[2]	MORPHOLOGY	ECOLOGY
Large Arboreal Montane	*bakeri* (37) *armstrongi* (43)	*patricae* (35) *montanus* (45)	large digital pads; little or no sexual dimorphism in size[4]	arboreal generalists; whistle call
Large Terrestrial Montane	*apostates* (44) *oxyrhyncus* (55)	*schmidti* (58)	robust habitus; large limbs; small digital pads	terrestrial; ravine and stream associated

[1] subgenus *Euhyas*, except *fowleri* and *lamprotes* (subgenus *Eleutherodactylus*).
[2] subgenus *Eleutherodactylus*, except *schmidti* (subgenus *Euhyas*).
[3] also occurs on the South Island.
[4] except *armstrongi*.

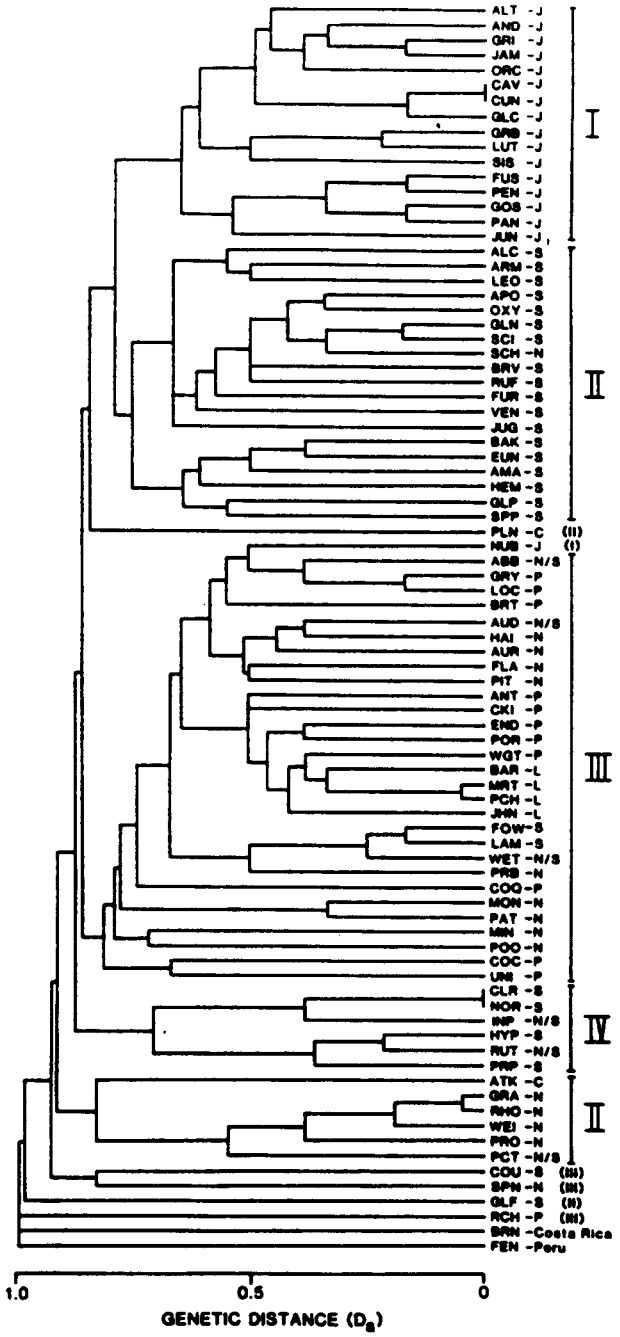


Figure 1.-- Phylogenetic tree of 84 *Eleutherodactylus* species constructed by UPGMA clustering of modified Cavalli-Sforza distances. Prager and Wilson's F value = 4.73. Species abbreviations defined in Appendix 1, island abbreviations are: C, Cuba; N, Hispaniola - North Island; S, Hispaniola - South Island; J, Jamaica; L, Lesser Antilles; P, Puerto Rico.

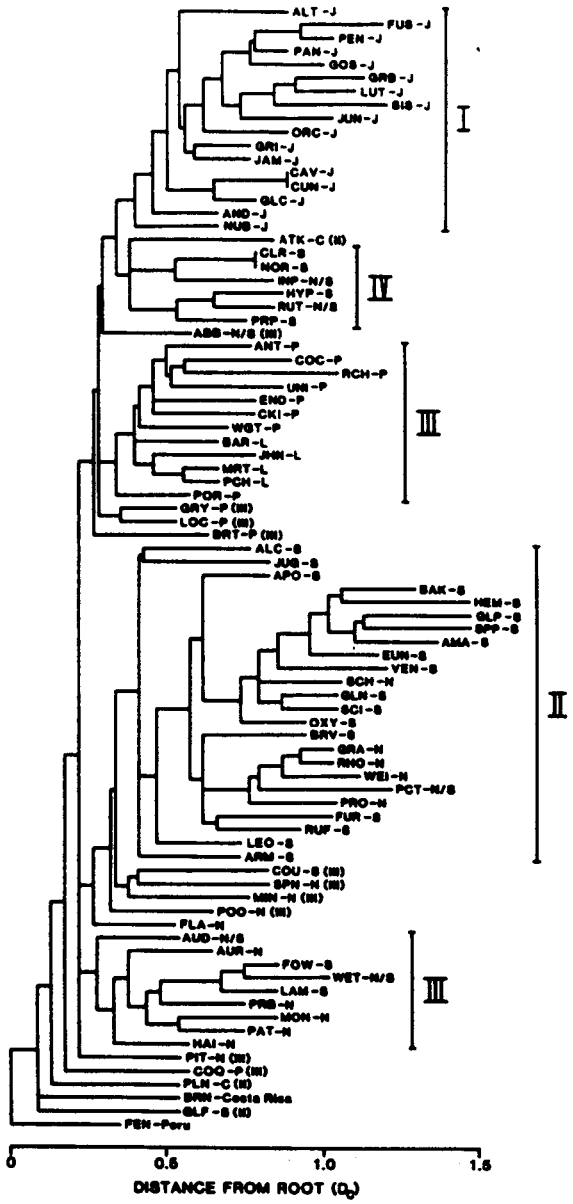


Figure 2.-- Phylogenetic tree of 84 *Eleutherodactylus* species constructed by the distance Wagner method using Cavalli-Sforza and Edwards (1967) chord distance and rooted with *fenestratus* (FEN). Prager and Wilson's F value = 44.1 (5.77 with branch-length optimization).

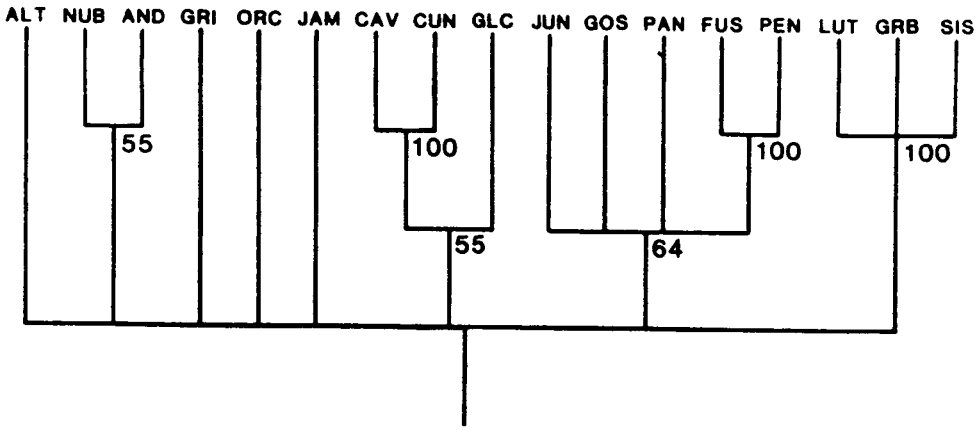


Figure 3.-- Majority-rule consensus tree representing 1100 most-parsimonious trees (each of length = 29, CI = 1.00) of Group I (subgenus *Euhyas*, *luteolus* series; = all 17 native Jamaican species). Numbers refer to percent of trees defining a particular group.

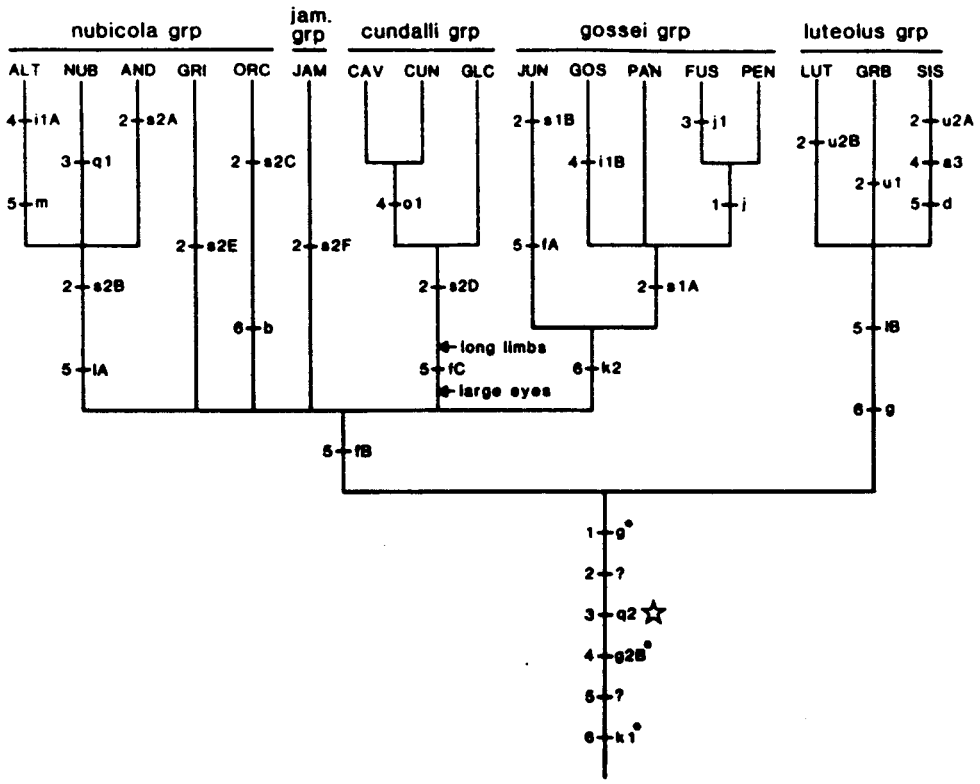


Figure 4.-- Cladogram of Group I showing allelic changes (length = 31, CI = 0.94). Number at left of tick mark is locus: 1) *Acp*, 2) *Ck*, 3) *Icd-1*, 4) *Lgl*, 5) *Pgm*, and 6) *Pt-3*. The combination of number and letters at right identifies the allele (Appendix 2) possessed by all taxa above the tick mark (unless additional changes at that locus are indicated). The tree is rooted by a composite outgroup (see text). A star indicates a presumed synapomorphy for the group, asterisks are plesiomorphic alleles (shared with outgroup), and loci where the primitive allele cannot be determined are indicated by question marks. Morphological changes are also indicated but were not used in the analysis.

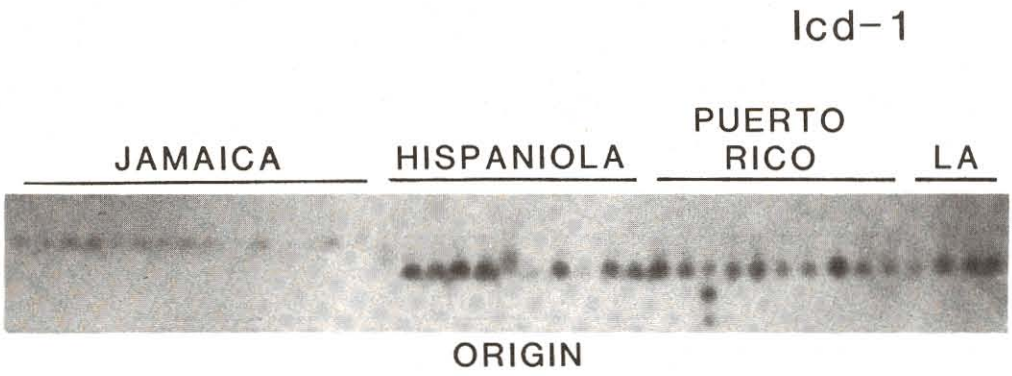


Figure 5.-- Allelic differences at a slow-evolving locus, isocitrate dehydrogenase (*Icd*) illustrating the separation of Jamaican species of the genus *Eleutherodactylus* (allele q2) from species on other islands (allele f1). The species (one per slot) are arranged in the following order (see Appendix 1 for abbreviations): Jamaica - ALT, AND, CAV, GLC, CUN, GOS, GRB, GRI, JAM, JUN (h/q2 heterozygote), LUT, ORC, PAN, PEN, SIS; Hispaniola - ABB (f1/m2 heterozygote), AUD, AUR, FLA, FOW, HAI (f1/m1 heterozygote), LAM, PRB, PAT, PIT, WET; Puerto Rico - ANT, BRT, COC (a/f1 heterozygote), CKI, COQ, END, GRY, LOC, POR, WGT; Lesser Antilles - BAR, JHN, MRT, and PCH. Note that no alleles are shared between the Jamaican species and species from other islands (species possessing other alleles are not shown). In addition to the mobility difference, note the difference in intensity: the Jamaican species are more weakly staining. (Gel BH-1165; Tris-citrate pH 8.0.)

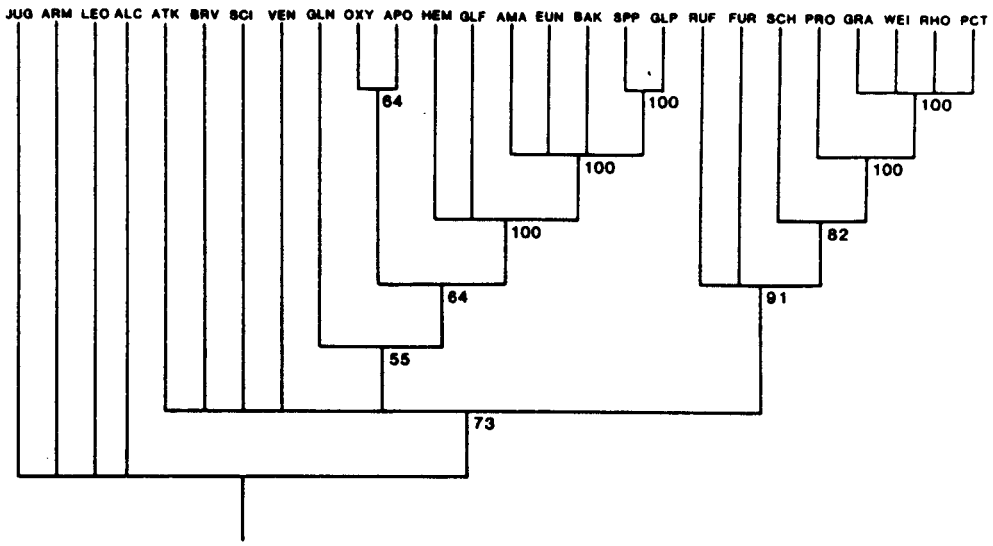


Figure 6.-- Majority-rule consensus tree representing 1100 most-parsimonious trees (each of length = 64, CI = 0.95) of Group II (subgenus *Euhyas*, part; = 25 Hispaniolan and one Cuban species, ATK).

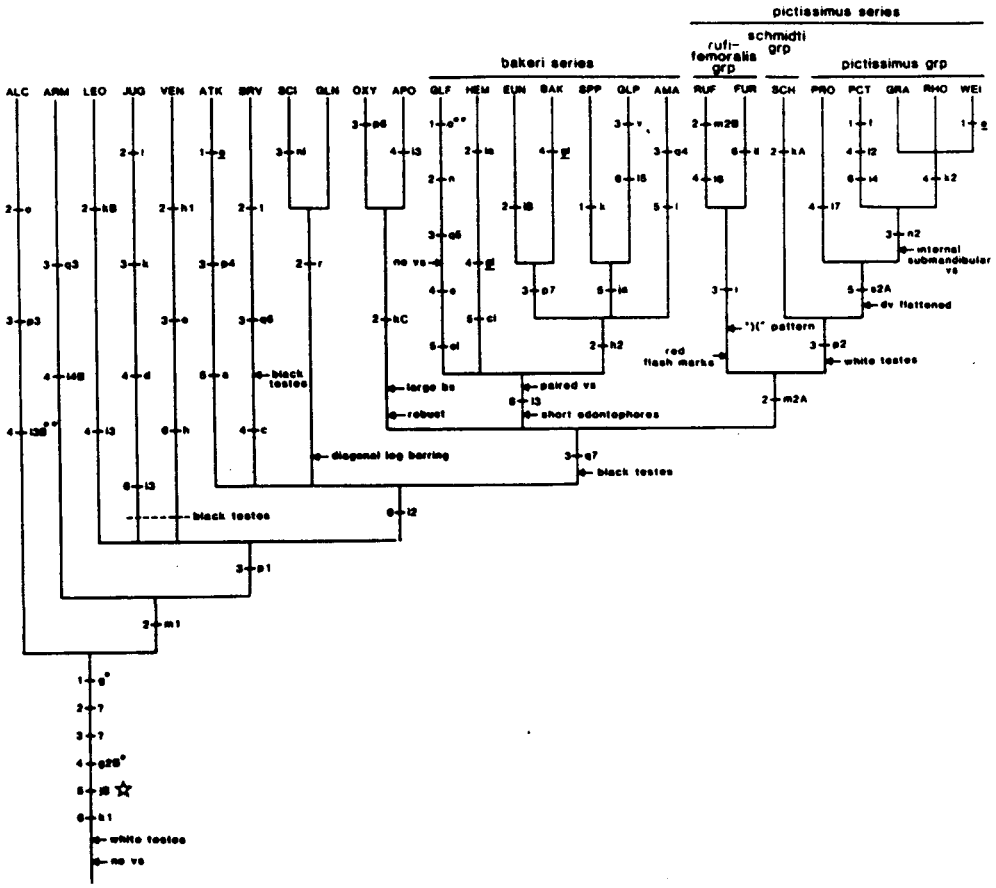


Figure 7.-- Cladogram of Group II showing allelic changes (length = 65, CI = 0.94). Morphological changes are also indicated but were not used in the analysis (BS = body size, DV = dorsoventrally, VS = vocal sac). Underlined alleles are those convergent within the group; two asterisks indicate allelic convergence with species outside of the group. Other symbols as in Fig. 4.

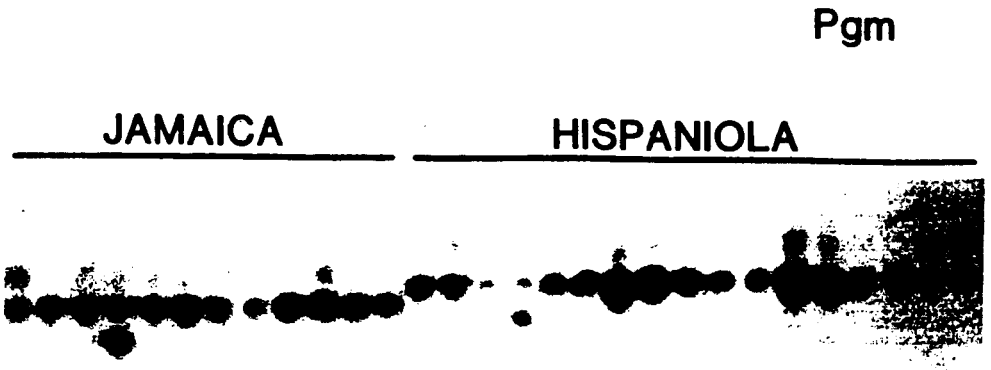


Figure 8.-- Allelic differences at a slow-evolving locus, phosphoglucomutase (*Pgm*), illustrating the separation of Jamaican and Hispaniolan (South Island, except SCH) species of the genus *Eleutherodactylus*. Although only two major allelic classes (f and j) are resolved on this gel, tris-citrate pH 6.7, additional hidden allelic variation within these classes (fA, fB, fC; jA, jB) was detected on tris-citrate pH 8.0. The species are arranged in the following order: Jamaica - ALT (fB/m heterozygote), CAV (fC), CUN (fC), FUS (a1/fB heterozygote), GLC (fC), GOS (fB), GRI (fB), JAM (fB), JUN (fA), ORC (fB), PAN (fB), PEN (fB); Hispaniola - ALC (jB), APO (jB), ARM (jB), BAK (c2/jB heterozygote), BRV (jB), EUN (jB), FUR (g1/jB heterozygote), GLN (jB), GLP (jA), JUG (jB), LEO (jB), OXY (jB), SPP (h/jA heterozygote), RUF (jB), SCI (jB), VEN (jB/s2B heterozygote), and SCH (jB). Note that no alleles are shared between Jamaican and Hispaniolan species (species possessing other alleles are not shown). (Gel BH-1164.)

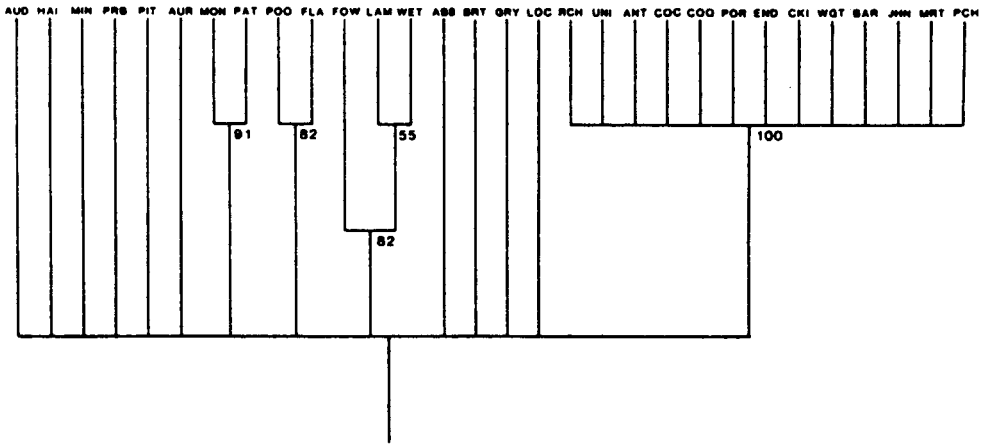


Figure 9.-- Majority-rule consensus tree representing 1100 most-parsimonious trees (each of length = 71, CI = 0.97) of Group III (subgenus *Eleutherodactylus*, *auriculatus* section).

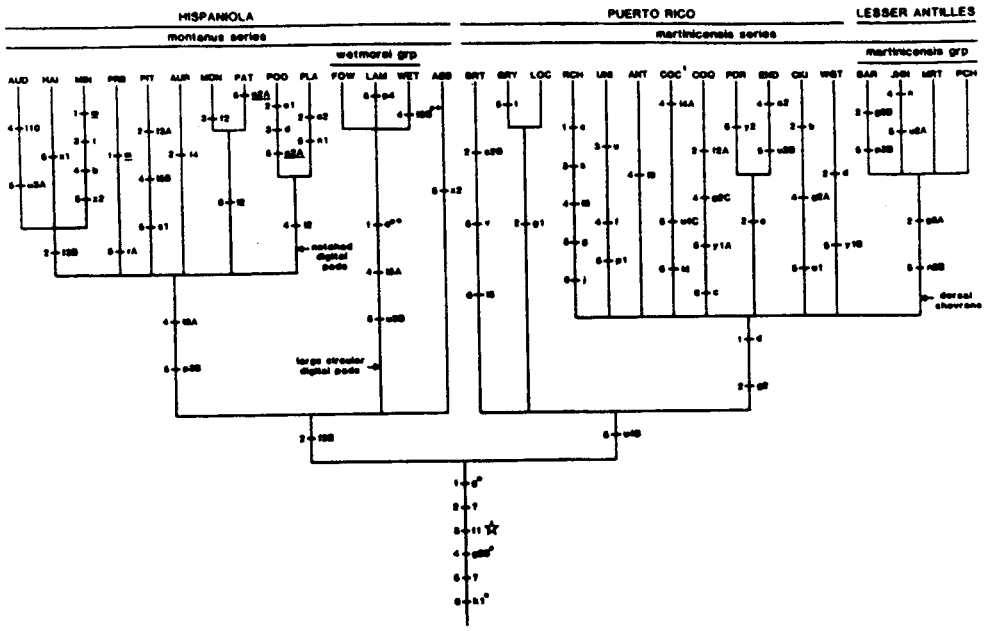


Figure 10.-- Cladogram of Group III showing allelic changes (length = 74, CI = 0.95). Morphological changes and geographic associations are also indicated but were not used in the analysis. Symbols as in Figures 4 and 6.

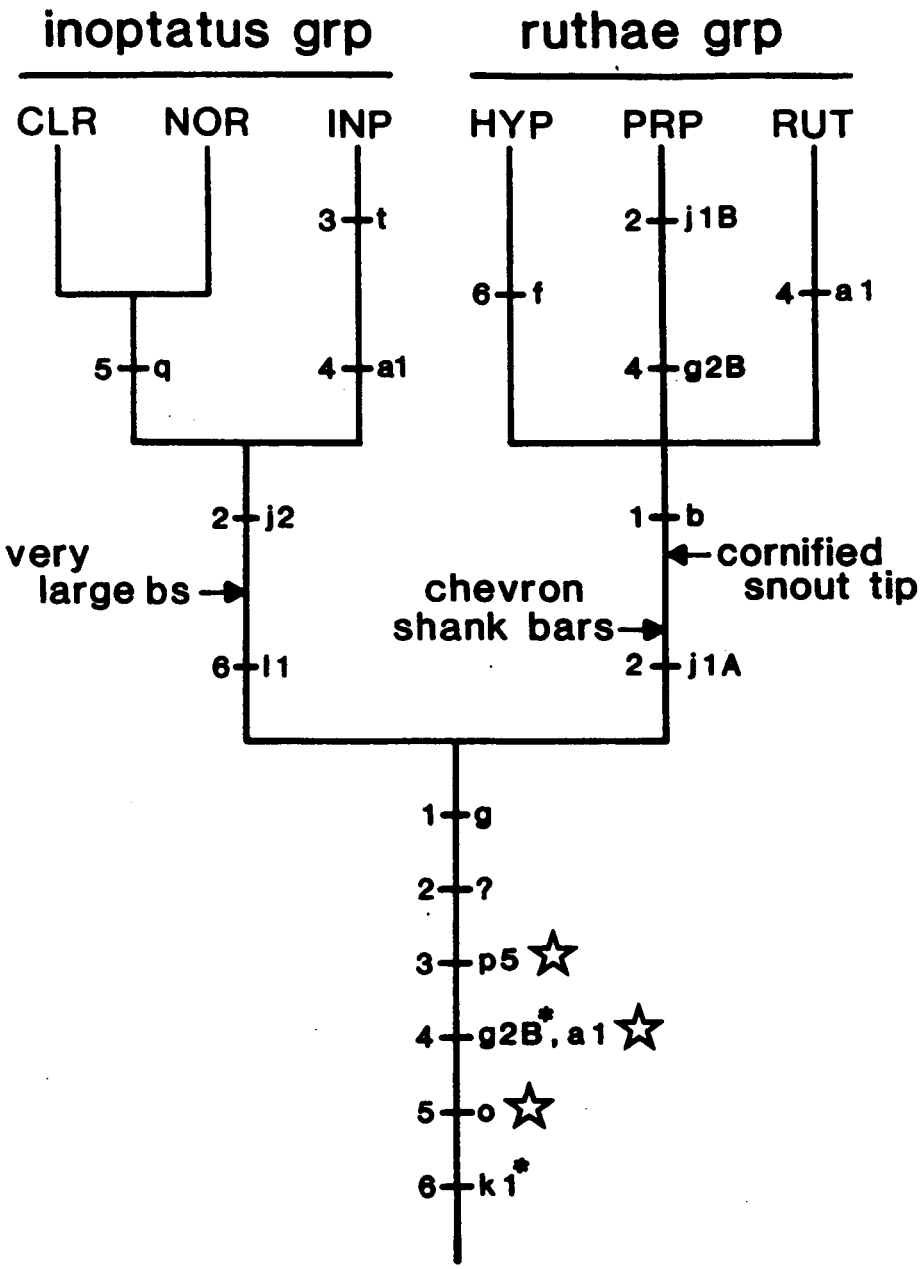


Figure 11.-- A strict consensus tree (length = 11, CI = 0.91) of the three most-parsimonious trees (length = 10, CI = 1.00) of Group IV (subgenus *Pelorius*; = six Hispaniolan species) showing allelic changes. Morphological changes are also indicated but were not used in the analysis. Symbols as in Figures 4 and 6.

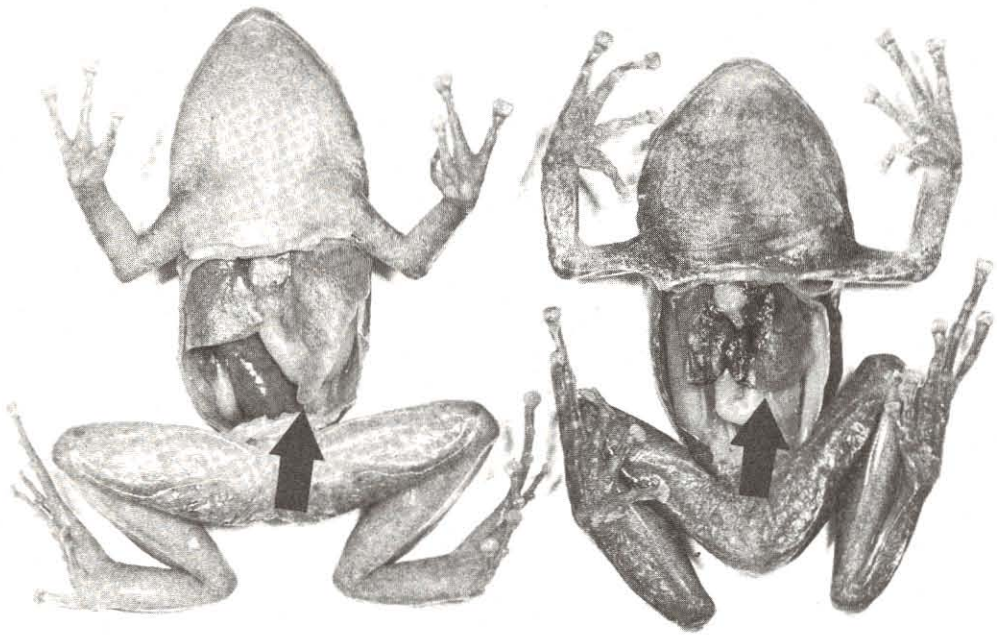
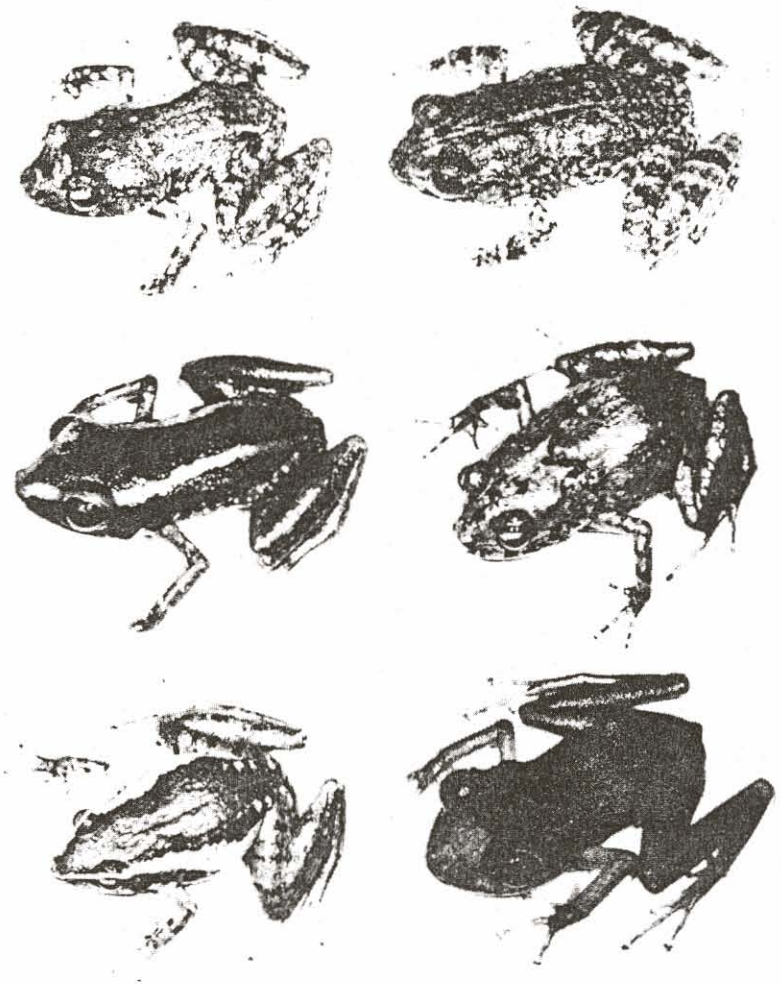
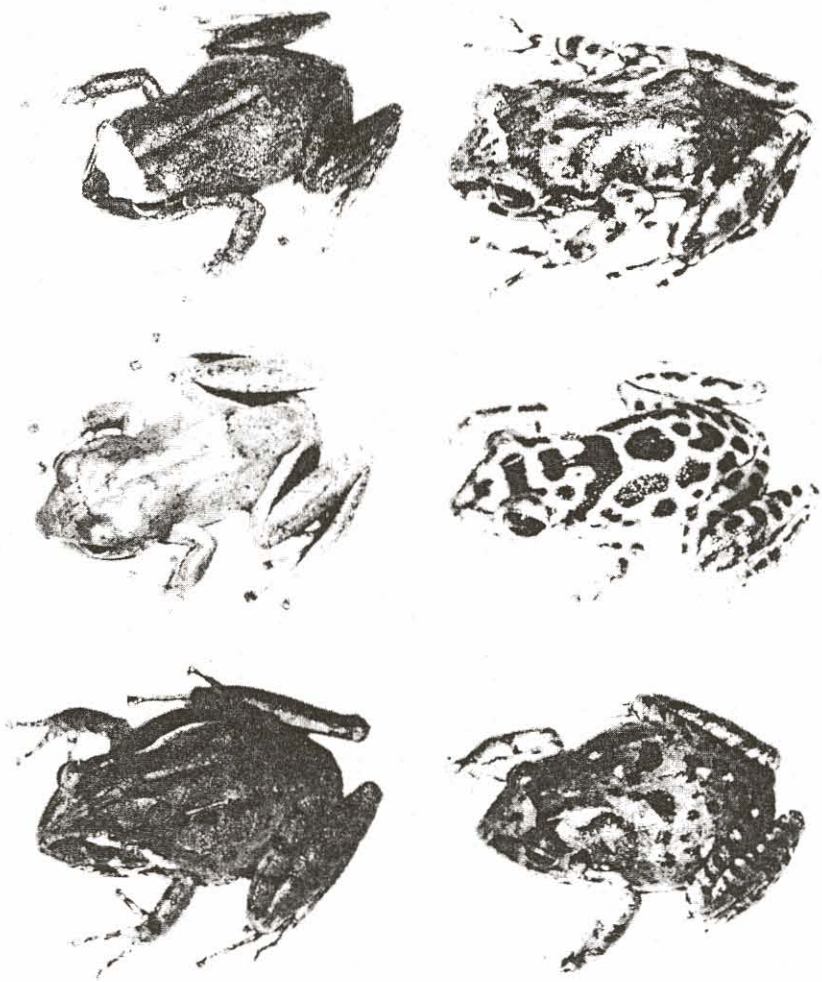


Figure 12.-- *Eleutherodactylus armstrongi* (left) and *Eleutherodactylus montanus* (right) with venters dissected away to show two major differences in liver shape among West Indian *Eleutherodactylus*: long and pointed left lobe (*armstrongi*) vs short and rounded left lobe (*montanus*). Arrows point to left lobe of liver. Although both species have been placed in the same species group based on similarities in large digital pad size, arboreality, and call, allozyme data and liver shape show that each belongs to one of two major West Indian groups and that the external morphological similarities are due to convergence.

Figures 13-18: West Indian frogs of the genus *Eleutherodactylus*. Figure 13 (upper left).-- *Eleutherodactylus* (*Euhyas*) *luteolus* of the *luteolus* group and *luteolus* series (Jamaica: St. James; 2.4 km W Mocho). Figure 14 (upper right).-- *Eleutherodactylus* (*Euhyas*) *gossei* of the *gossei* group and *luteolus* series (Jamaica: St. James; 3.2 km W Mocho). Figure 15 (middle left).-- *Eleutherodactylus* (*Euhyas*) *cundalli* of the *cundalli* group and *luteolus* series (Jamaica: Trelawny; 0.8 km N Burnt Hill). Figure 16 (middle right).-- *Eleutherodactylus* (*Euhyas*) *jamaicensis* (dark phase) of the *jamaicensis* group and *luteolus* series (Jamaica: Trelawny; 0-11 km NNW Quick Step). Figure 17 (lower left).-- *Eleutherodactylus* (*Euhyas*) *nubicola* of the *nubicola* group and *luteolus* series (Jamaica: St. Andrew; 1.3 km W Hardwar Gap). Figure 18 (lower right).-- *Eleutherodactylus* (*Euhyas*) *heminota* of the *bakeri* series (Haiti: Grande Anse; 17.6 km N Camp Perrin).



Figures 19-24: West Indian frogs of the genus *Eleutherodactylus*. Figure 19 (upper left).-- *Eleutherodactylus* (*Euhyas*) *rufifemoralis* of the *rufifemoralis* group and *pictissimus* series (Dominican Republic: Barahona; 15 km SSW La Guazara). Figure 20 (upper right).-- *Eleutherodactylus* (*Euhyas*) *schmidti* of the *schmidti* group and *pictissimus* series (Dominican Republic: Elias Piña; Loma Nalga de Maco). Figure 21 (middle left).-- *Eleutherodactylus* (*Euhyas*) *weinlandi* of the *pictissimus* group and *pictissimus* series (Dominican Republic: El Seibo; 22 km WNW El Valle). Figure 22 (middle right).-- *Eleutherodactylus* (*Euhyas*) *brevirostris* (Haiti: Grande Anse; 11.2 km S, 1.9 km E Marché Léon). Figure 23 (lower left).-- *Eleutherodactylus* (*Euhyas*) *oxyrhyncus* (Haiti: Grande Anse; 9.0-9.7 km S Marché Léon). Figure 24 (lower right).-- *Eleutherodactylus* (*Eleutherodactylus*) *cooki* of the *martinicensis* series and *auriculatus* section (Puerto Rico: 2.3 km SW Yabucoa).



Figures 25-30: West Indian frogs of the genus *Eleutherodactylus*. Figure 25 (upper left).-- *Eleutherodactylus* (*Eleutherodactylus*) *coqui* of the *martinicensis* series and *auriculatus* section (Puerto Rico: El Yunque peak). Figure 26 (upper right).-- *Eleutherodactylus* (*Eleutherodactylus*) *montanus* of the *montanus* series and *auriculatus* section (Dominican Republic: La Vega; 13 km NW La Horma). Figure 27 (middle left).-- *Eleutherodactylus* (*Eleutherodactylus*) *wetmorei* of the *wetmorei* group and *auriculatus* section (Haiti: Grande Anse; 9.0-9.7 km S Marché Léon). Figure 28 (middle right).-- *Eleutherodactylus* (*Eleutherodactylus*) *counouspeus* (Haiti: Sud; 13.5 km N Camp Perrin). Figure 29 (lower left).-- *Eleutherodactylus* (*Pelorius*) *chlorophenax* of the *inoptatus* group (Haiti: Sud; Plain Formon). Figure 30 (lower right).-- *Eleutherodactylus* (*Pelorius*) *ruthae* of the *ruthae* group (Haiti: Sud; ca. 5-6 km NW Les Platons).

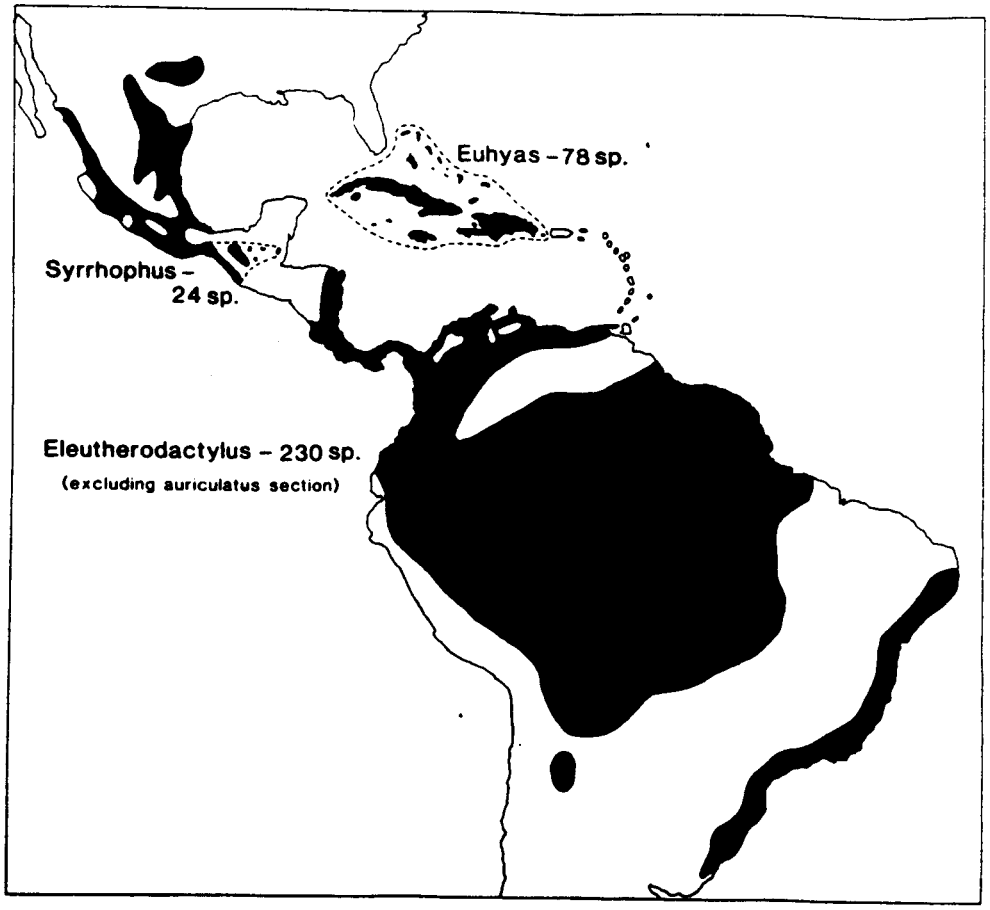


Figure 31.-- Map showing the distribution of the subgenera *Syrrhophus*, *Euhyas*, and *Eleutherodactylus* (excluding *auriculatus* section) based on Lynch (1970, 1976), Schwartz and Thomas (1975), Henderson and Schwartz (1984), and Schwartz and Henderson (1985).

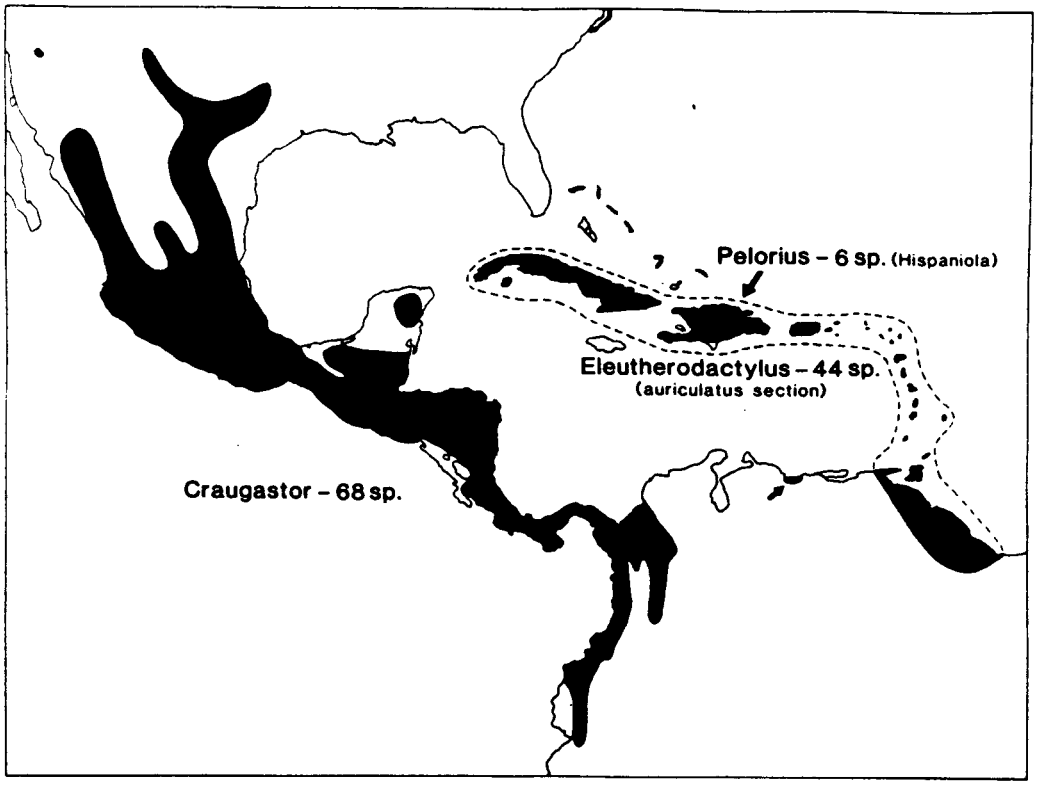


Figure 32.-- Map showing the distribution of the subgenera *Craugastor*, *Eleutherodactylus* (*auriculatus* section), and *Pelorius* based on Lynch (1986), Schwartz and Thomas (1975), Schwartz et al. (1978), Henderson and Schwartz (1984), and Schwartz and Henderson (1985).

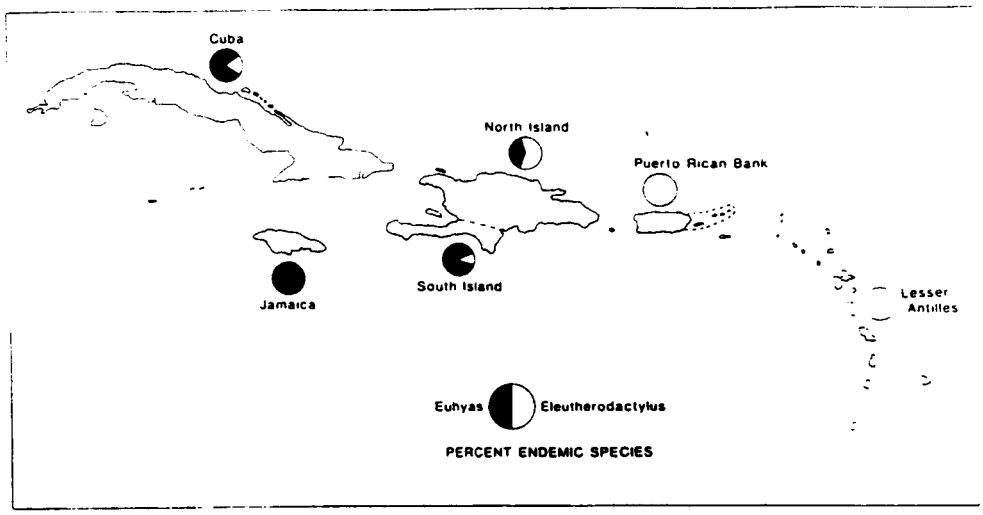


Figure 33.-- Map showing the percentage of species of the subgenera *Eleutherodactylus* and *Euhyas* endemic to each island or island group in the West Indies. The number of species (*Euhyas/Eleutherodactylus*) are: 27/6 (Cuba); 17/0 (Jamaica); 25/3 (South Island); 7/10 (North Island); 0/17 (Puerto Rican Bank); and 0/5 (Lesser Antilles). Four islandwide Hispaniolan species (*abbotti*, *audanti*, *pictissimus*, and *wetmorei*) and one species from Mona Island (*monensis*) are not included.

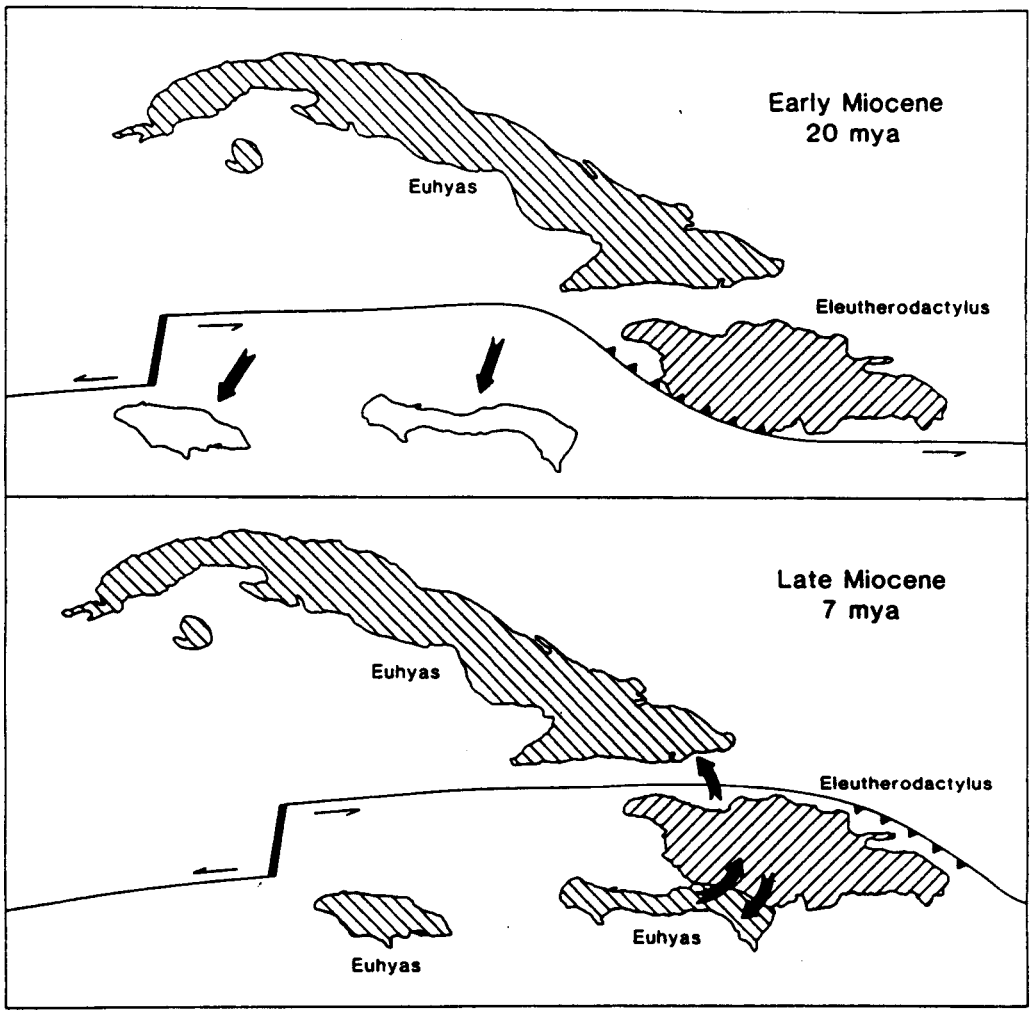


Figure 34.-- Hypothesized biogeographic history of *Eleutherodactylus* (subgenera *Euhyas* and *Eleutherodactylus*) in the Western Caribbean during the Miocene. Paleoreconstructions are based on Sykes et al. (1982). Spreading zone is indicated by wide line, narrow lines are plate boundaries, small arrows show relative direction of plate movement, large arrows indicate dispersal, and subduction is indicated by tooth marks on overriding plate. Early Miocene - Jamaica and the South Island arise above water and are colonized by Cuban frogs of the subgenus *Euhyas* while the North Island is occupied by the subgenus *Eleutherodactylus*. Late Miocene - The South Island has collided with the North Island, halting subduction, and a new fault zone forms to the North of Hispaniola. Overland dispersal of one South Island lineage (subgenus *Euhyas*, *pictissimus* series) to the North Island and one North Island lineage (subgenus *Eleutherodactylus*, *wetmorei* group) to the South Island occurs. Overwater dispersal of North Island *Eleutherodactylus* to Cuba may have occurred at this time.

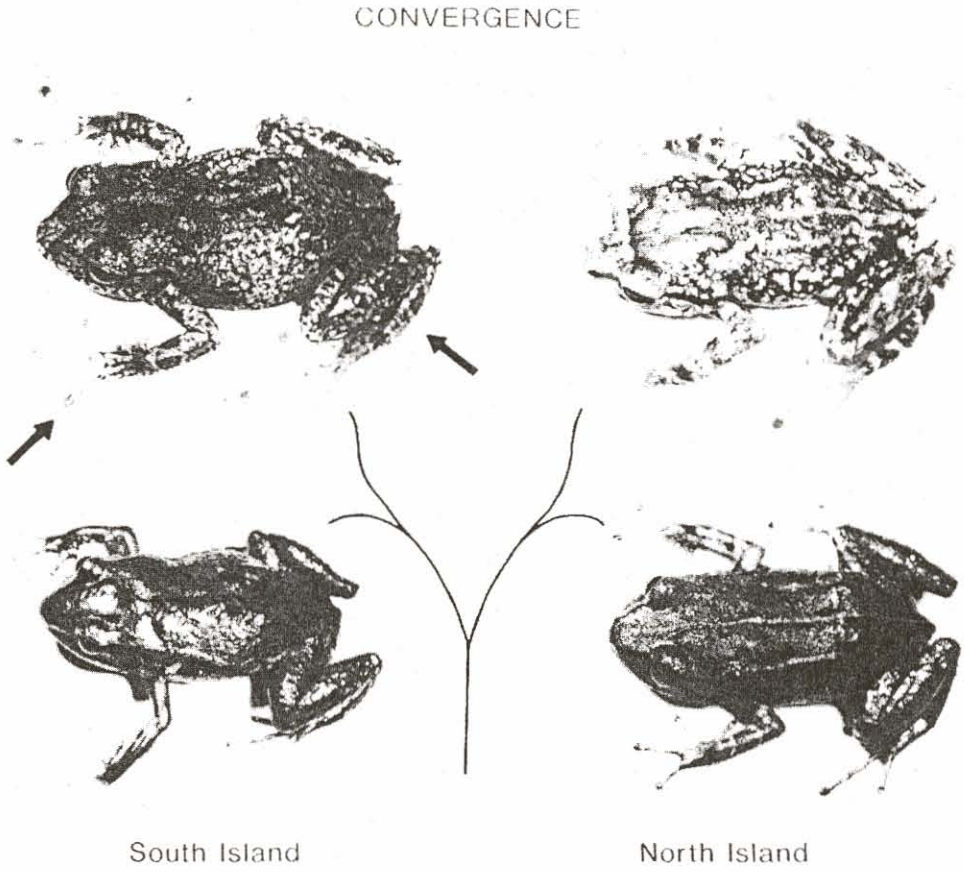


Figure 35.-- Morphological convergence in Hispaniolan *Eleutherodactylus*. Shown are two examples of apparent convergence between North and South Island species. TOP: species of the large arboreal montane ecomorph (*bakeri*, South Island; *patricae*, North Island) show convergence in digital pad size (large) and relative leg length (long). BOTTOM: species of the intermediate terrestrial montane ecomorph (*jugans*, South Island; *parabates*, North Island) have small digital pads and relatively short legs.

APPENDIX 1
Localities and Voucher Specimens

CUBA.-- *atkinsi* (ATK) - Guantanamo Bay Naval Station (University of Southern California 7516); *planirostris* (PLN) - Jamaica (introduced), St. Mary, 2.9 km NW Port Maria (tissue voucher only, but from same population as USNM 266461-465).

JAMAICA.-- *alticola* (ALT) - St. Thomas, Blue Mountain Peak, 1980-2256 m (USNM 269234); *andrewsi* (AND) - St. Andrew, 1.3 km W Hardwar Gap, ca. 1200 m (USNM 269235); *cavernicola* (CAV) - Clarendon, ca. 1.6 km ESE Jacksons Bay, 15 m (USNM 266359); *cundalli* (CUN) - Trelawny, ca. 11 km NNW Quick Step, ca. 450 m (USNM 266362); *fuscus* (FUS) - St. James, 3.2 km W Mocho (USNM 266381); *glaucoreius* (GLC) - St. Andrew, 1.3 km W Hardwar Gap, ca. 1200 m (tissue voucher only, but from same population as USNM 266374-375); *gossei* (GOS) - St. James, 3.2 km W Mocho (USNM 269236); *grabhami* (GRB) - Trelawny, ca. 11 km NNW Quick Step, ca. 450 m (USNM 269237); *griphus* (GRI) - Trelawny, ca. 11 km NNW Quick Step, ca. 450 m (USNM 269238); *jamaicensis* (JAM) - St. Andrew, ca. 2.4 km NW Hardwar Gap, ca. 1200 m (tissue voucher only); *junori* (JUN) - Trelawny, 7.7 km WNW Troy, 625 m (USNM 269239); *luteolus* (LUT) - St. James, 2.4 km W Mocho, 640 m (USNM 269246); *nubicola* (NUB) - St. Andrew, vicinity of Hardwar Gap, 1220 m (USNM 269247); *orcutti* (ORC) - Portland, 0.8 km S Section (USNM 269248); *pantoni* (PAN) - Trelawny, 10.1 km NW Troy (USNM 269254); *pentasyringos* (PEN) - Portland, 2.3 km S Fellowship (USNM 266460); *sisyphodemus* (SIS) - Trelawny, ca. 11 km NNW Quick Step, ca. 450 m (USNM 266468).

HISPANIOLA.-- *abbotti* (ABB) - Dom. Rep., El Seibo, ca. 10 km W Sabana de la Mar (airline), 5 m (USNM 269255); *alcoae* (ALC) - Dom. Rep., Barahona, Los Patos, 0 m (USNM 269256); *amadeus* (AMA) - Haiti, Sud, N slope of Morne Formon, 1700 m (USNM 258691); *apostates* (APO) - Haiti, Grande Anse, 11.7 km S, 1.7 km E Marché Léon (airline), 1480 m (USNM 269257); *armstrongi* (ARM) - Dom. Rep., Barahona, 15.3 km S, 3.2 km E Cabral (by road), 1220 m (USNM 269258); *audanti* (AUD) - Haiti, Ouest, 5 km S Furcy, 1520 m (USNM 269259); *auriculatoides* (AUR) - Dom. Rep., La Vega, 19 km E El Río, 1140 m (USNM 269260); *bakeri* (BAK) - Haiti, Sud, crest of Formon Ridge, 1840-1880 m (USNM 269261); *brevirostris* (BRV) - Haiti, Sud, 2.6 km N, 15.1 km W Camp Perrin (airline), 1650 m (USNM 269262); *chlorophenax* (CLR) - Haiti, Sud, vic. of Plain Formon, 1000 m (USNM 257729); *counouspeus* (COU) - Haiti, Sud, 13.5 km N Camp Perrin, 750 m (USNM 269263); *eunaster* (EUN) - Haiti, Grande Anse, 9.0-9.7 km due S of Marché Léon (airline), 1030-1090 m (USNM 269264); *flavescens* (FLA) - Dom. Rep., Altagracia, ca. 2 km N Boca de Yuma (on new road), (USNM 269265); *fowleri* (FOW) - Dom. Rep., Pedernales, Los Arroyos, 1180 m (USNM 269266); *furcyensis* (FUR) - Haiti, Sud Est, 8.4 km SW Seguin, 1040 m, (USNM 269267); *glandulifer* (GLN) - Haiti, Sud, 2.6 km N, 15.1 km W Camp Perrin (airline), 1650 m (USNM 269268); *glanduliferoides* (GLF) - Haiti, Ouest, 5 km S Furcy, 1520 m (USNM 269269); *glaphycompus* (GLP) - Haiti, Grand Anse, 9.0-9.7 km due S of Marché Léon (airline), 1030-1090 m (USNM 269270); *grahami* (GRA) - Haiti, Artibonite, 10.4 km NW Ça Soleil, 130 m (USNM 269272); *haitianus* (HAI) - Dom. Rep., La Vega, ca. 37 km SE Constanza (via new road), 2300 m (USNM 269273); *heminota* (HEM) - Haiti, Ouest, Furcy (USNM 269274); *hypostenor* (HYP) - Dom. Rep., Barahona, 19.5 km SW Barahona, 880 m (USNM 257734); *inoptatus* (INP) - Dom. Rep., Pedernales, Los Arroyos, 1180 m (USNM 269275); *jugans* (JUG) - Haiti, Sud'Est, 8 km NW Seguin, 1850 m (USNM 269276, 269279); *lamprotes* (LAM) - Haiti, Grande Anse, 9.0-9.7 km due S of Marché Léon (airline), 1030-1090 m (USNM 269280); *leoncei* (LEO) - Haiti, Sud'Est, 8.0 km NW Seguin, 1850 m (USNM 269281); *minutus* (MIN) - Dom. Rep., La Vega, 14.2 km SE Constanza (via new road), 2000 meters (USNM 269282); *montanus* (MON) - Dom. Rep., La Vega, 18 km SE Constanza, 1770 m (USNM 269283); sp. nov. N (SPN) - Dom. Rep., Independencia, 7 km N Cacique Enriquillo, 1640 m (USNM 269316); *nortoni* (NOR) - Haiti, Sud, vic. of Plain Formon, 1000 m (USNM 257744); *oxyrhyncus* (OXY) - Haiti, Grande Anse, 9.5 km S, 0.6 km W Marché Léon (airline), 1030 m (USNM 269284); sp. nov. P (SPP) - Haiti, Sud, vicinity of Plain Formon, 1000 m (USNM 269271); *parabates* (PRB) - Dom. Rep., Elias Piña, 13 km N Cacique Enriquillo, 1870 m (USNM 269285); *parapelates* (PRP) - Haiti, Grande Anse, 7.8 km S, 0.3 km E Marché Léon (airline), 960 m (USNM 257726); *patricae* (PAT) - Dom. Rep., La Vega, ca. 37 km SE Constanza, 2300 m (USNM 269286); *pictissimus* (PCT) - Dom. Rep., Barahona, Los Patos, 0 m (tissue voucher only, but from same population as USNM 266310-314); *pituinus* (PIT) - Dom. Rep., Peravia, 10.5 km NW La Horma, 1645 m (USNM 269287); *poolei* (POO) - Haiti, Nord, Citadel of King Christophe, 600 m (USNM 269288); *probolaeus* (PRO) - Dom. Rep., Altagracia, 2 km N Boca de Yuma (on old road) (USNM 269290); *rhodesi* (RHO) - Haiti, Nord Ouest, 1.0 km N Balladé, (USNM 269291); *rufifemoralis* (RUF) - Dom. Rep., Barahona, ca. 15 km SSW La Guazara, 1036-1219 m, (USNM 269292); *ruthae* (RUT) - Haiti, Sud, ca. 5-6 km NW Les Platons, ca. 900 m (USNM 257751); *schmidti* (SCH) - Dom. Rep., Elias Piña, 3.2 km S, 4.0 km E Rio Limpio (CREAR), ca. 1270 m (USNM 269293); *sciagraphus* (SCI) - Haiti, Grande Anse, 10.7 km S, 1.6 km E Marché Léon (airline), 1270 m (USNM 269294); *ventrilineatus* (VEN) - Haiti, Sud, crest of Formon Ridge, 1840-1880 m (USNM 269295); *weinlandi* (WEI) - Dom. Rep., El Seibo, 22 km WNW El Valle, 76 m (USNM 269296); *wetmorei* (WET) - Haiti, Grande Anse, 9.0-9.7 km due S of Marché Léon (airline), 1030-1090 m (USNM 269297).

PUERTO RICO.-- *antillensis* (ANT) - 2.2 km S Palmer on route 191, (USNM 269298); *brittoni* (BRT) - 4.2 km E Catalina in Luquillo National Forest, (USNM 269299); *cochranae* (COC) - 2.2 km S Palmer on route 191, (USNM 269300); *cooki* (CKI) - 2.3 km SW Yabucoa (USNM 269301); *coqui* (COQ) - El Yunque (near peak), 1000 m (USNM 269302); *eneidae* (END) - El Yunque (near peak), 1000 m (USNM 269303); *gryllus* (GRY) - El Yunque (near peak), 1000 m (USNM 269304); *locustus* (LOC) - El Yunque (near peak), 1000 m (USNM 269305); *portoricensis* (POR) - El Yunque (near peak), 1000 m (USNM 269306); *richmondi* (RCH) - 3.2 km S Campamento Guavate, (USNM 269307); *unicolor* (UNI) - El Yunque (near peak), 1040 m (USNM 269308); *wightmanae* (WGT) - 1.3 km S, 1.1 km E of El Yunque peak, (USNM 269309).

LESSER ANTILLES.-- *barlagnei* (BAR) - Guadeloupe, Basse Terre, 4 km E Marigot, 120 m (USNM 269310); *martinicensis* (MRT) - Guadeloupe, Basse Terre, 5 km W St. Sauveur, 390 m (USNM 269313-314); *pinchoni* (PCH) - Guadeloupe, Basse Terre, 5 km W St. Sauveur, 390 m (USNM 269318); *johnstonei* (JHN) - Jamaica (introduced), Trelawny, 8.0-8.9 km NW Troy, 610-640 m (USNM 269312), and Guadeloupe, Basse Terre, Pointe de la Grande Anse (near Trois Rivieres), 5 m (USNM 269311).

COSTA RICA.-- *bransfordii* (BRN) - Heredia, Finca La Selva, 60 m (USNM 266332).

PERU.-- *fenestratus* (FEN) - Madre de Dios, Tambopata, near Puerto Maldonado (USNM 268941).

APPENDIX 2
Allelic Variation

Allelic variation is presented for 84 *Eleutherodactylus* species at six slow-evolving protein loci: *Acp*, *Ck*, *Icd-1*, *Lgl*, *Pgm*, and *Pt-3* (alleles listed in that order). In all cases, sample size is one and heterozygotes are indicated by parentheses. Alleles are designated by the conditions under which they were detected (Table 1): lower-case letters, numbers, and upper-case letters refer to first, second, and third conditions, respectively. The total number of alleles at each locus and each condition (cumulative) are: *Acp* (15), *Ck* (21,33,49), *Icd-1* (24,41), *Lgl* (15,33,41), *Pgm* (26,41,54) and *Pt-3* (12,23); total = 223 alleles.

CUBA.-- *atkinsi* - e,m1,p4,g2B,a2,i2; *planirostris* - g,p,j2,o2,e2,i5.

JAMAICA.-- *alticola* - g,s2B,q2,i1A,(fB,m),k1; *andrewsi* - g,s2A,q2,g2B,1A,k1; *cavernicola* - g,s2D,q2,o1,fC,k1; *cundalli* - g,s2D,q2,o1,fC,k1; *fuscus* - j,s1A,j1,g2B,(a1,fB),k2; *glaucoreius* - g,s2D,q2,g2B,fC,k1; *gossei* - g,s1A,q2,i1B,fB,k2; *grabhami* - g,u1,q2,(g2B,j),lB,g; *griphus* - g,s2E,q2,g2B,fB,k1; *jamaicensis* - g,s2F,q2,g2B,fB,k1; *junori* - g,s1B,(h,q2),g2B,fA,k2; *luteolus* - g,u2B,q2,g2B,lB,g; *nubicola* - g,s2B,q1,g2B,1A,k1; *orcutti* - g,s2C,q2,g2B,fB,b; *pantoni* - g,s1A,q2,g2B,fB,k2; *pentasyringos* - j,s1A,q2,g2B,fB,k2; *sisyphodemus* - g,u2A,q2,(a3,g3),d,g.

HISPANIOLA.-- *abbotti* - g,f2B,(f1,m2),g2B,(x2,z1),k1; *alcoae* - g,o,p3,l3B,jB,(k1,m); *amadeus* - g,h2,q4,g2B,i,l3; *apostates* - g,kC,q7,i3,jB,i2; *armstrongi* - g,m1,q3,l4B,jB,k1; *audanti* - g,f3B,f1,l10,u3A,k1; *auriculatoides* - g,f4,f1,l3A,p3B,k1; *bakeri* - g,h2,p7,g1,(c2,jB),l3; *brevirostris* - g,t,q6,c,jB,i2; *chlorophenax* - g,j2,p5,(a1,g2B),q,l1; *counouspeus* - a,f5,j3,l5C,p2,k1; *eunaster* - g,iB,p7,g2B,jB,l3; *flavescens* - g,e2,f1,(b,i2),n1,k1; *fowleri* - o,f2B,f1,l5A,u3B,k1; *furcyensis* - g,m2A,i,(g2B,k1),(g1,jB),i1; *glandulifer* - g,r,p1,g2B,jB,i2; *glanduliferoides* - o,n,q5,e,e1,l3; *glaphycompus* - g,h2,v,g2B,jA,l5; *grahami* - g,m2A,(n2,w),k2,s2A,i2; *haitianus* - g,f3B,(f1,m1),l3A,x1,k1; *heminota* - g,iA,q7,g1,c1,l3; *hypostenor* - b,j1A,p5,(a1,g2B),o,f; *inoptatus* - g,j2,t,a1,o,l1; *jugans* - g,l,k,d,jB,i3; *lamprotes* - o,f2B,f1,l5A,p4,k1; *leoncei* - g,kB,p1,i3,jB,k1; *minutus* - m,f3B,l,b,z2,k1; *montanus* - g,f2B,f2,l3A,p3B,l2; sp. nov. N - i,f1,(b,e),l1,rB,k1; *nortoni* - g,j2,p5,(a1,g2B),q,l1; *oxyrhyncus* - g,kC,p6,g2B,jB,i2; sp. nov. P - k,h2,q7,g2B,(h,jA),l3; *parabates* - m,f2B,f1,l3A,rA,k1; *parapelates* - b,j1B,p5,g2B,o,k1; *patricae* - g,f2B,f1,l3A,n2A,l2; *pictissimus* - f,m2A,n2,l2,s2A,i4; *pituinus* - g,f3A,f1,l5B,s1,k1; *poolei* - g,e1,(d,r),(b,i2),n2A,k1; *probolaeus* - g,m2A,p2,l7,s2A,i2; *rhodesi* - g,m2A,n2,k2,s2A,i2; *rufifemoralis* - g,m2B,i,l6,jB,i2; *ruthae* - b,j1A,p5,a1,o,k1; *schmidti* - g,kA,p2,g2B,jB,i2; *sciagraphus* - g,r,n1,g2B,jB,i2; *ventrilineatus* - g,h1,o,g2B,(jB,s2B),h; *weinlandi* - e,m2A,n2,k2,s2A,i2; *wetmorei* - o,f2B,f1,l3B,u3B,k1.

PUERTO RICO.-- *antillensis* - d,g2,f1,l9,u4B,k1; *brittoni* - g,s2G,f1,g2B,v,l6; *cochranae* - d,g2,(a,f1),l4A,u4C,l4; *cooki* - d,b,f1,g2A,u1,k1; *coqui* - (d,g),f2A,f1,g2C,y1A,c; *eneidae* - d,c,f1,a2,u2B,k1; *gryllus* - g,g1,f1,g2B,t,k1; *locustus* - g,g1,f1,g2B,u4B,k1; *portoricensis* - (d,g),c,f1,g2B,y2,k1; *richmondi* - c,g2,s,l8,g2,j; *unicolor* - d,g2,u,f,p1,k1; *wightmanae* - d,d,f1,(g2B,i4),y1B,k1.

LESSER ANTILLES.-- *barlagnei* - d,g3B,f1,g2B,p3A,k1; *martinicensis* - d,g3A,f1,g2B,(n2B,u4A),k1; *pinchoni* - d,g3A,f1,g2B,n2B,k1; *johnstonei* - d,g3A,f1,n,u2A,k1.

COSTA RICA.-- *bransfordii* - l,q,j4,h,b,a.

PERU.-- *fenestratus* - (h,n),a,g,m,k,(d,e).

APPENDIX 3
Morphological Variation

Variation in liver shape, testis color, and vocal sac condition (in that order) is presented for 113 species of West Indian frogs of the genus *Eleutherodactylus*. Abbreviations are as follows: liver shape (L = long and pointed left lobe, S = short and rounded left lobe, I = intermediate condition), testis color (U = unpigmented, P = pigmented or polymorphic for pigmented and unpigmented), and vocal sac (I = internal, X = external, A = absent; P = paired, S = single). A question mark ("?") indicates that no data were available.

Cuba.-- *acmonis* - L,?,A; *atkinsi* - L,U,IS; *auriculatus* - S,P,XS; *barlonsmithi* - ?,?,XS; *bresslerae* - ?,?,A; *cuneatus* - L,U,IS; *dimidiatus* - L,U,A; *eileenae* - ?,?,XS; *etheridgei* - ?,U,IS; *greyi* - L,?,A; *klinikowskii* - ?,P,?; *leberi* - ?,?,XS; *limbatus* - L,?,?; *pezopetrus*-?,?,A; *pinarensis* - L,P,A; *planirostris* - L,U,A; *ricordii* - ?,?,A; *ronaldi* - ?,?,XS; *sierramaestrae* - L,P,A; *symingtoni* - ?,?,A; *thomasi* - L,U,IS; *turquinensis* - L,P,A; *varians* - S,?,XS; *varleyi* - L,U,XS; *zugi* - ?,P,A.

Jamaica.-- *alticola* - L,U,A; *andrewsi* - L,U,A; *cavernicola* - L,U,A; *cundalli* - L,U,A; *fuscus* - L,U,A; *glaucoreius* - L,U,A; *gossei* - L,U,A; *grabhami* - L,U,A; *griphus* - L,U,A; *jamaicensis* - L,U,A; *junori* - L,U,A; *luteolus* - L,U,A; *nubicola* - L,U,A; *orcutti* - L,U,A; *pantoni* - L,U,A; *pentasyringos* - L,U,A; *sisyphodemus* - L,U,A.

Hispaniola.-- *abbotti* - L,P,XS; *alcoae* - ?,U,A; *amadeus* - L,P,IP; *apostates* - L,P,A; *armstrongi* - L,U,A; *audanti* - L,P,XS; *auriculatoides* - S,U,XS; *bakeri* - L,P,IP; *brevirostris* - L,P,A; *chlorophenax* - ?,U,IS; *counouspeus* - S,U,XS?; *eunaster* - L,P,XP; *flavescens* - S,U,XS; *fowleri* - ?,U,XS; *furcyensis* - L,P,A; *glandulifer* - L,U,?; *glanduliferoides* - L,P,A; *glaphycompus* - L,P,XP; *grahami* - L,U,IS; *haitianus* - S,P,XS; *heminota* - L,P,IP; *hypostenor* - ?,U,IS; *inoptatus* - S,U,IS; *jugans* - L,P,A; *lamprotes* - ?,U,XS; *leoncei* - L,U,A; *minutus* - L,P,XS; *montanus* - S,U,XS; sp. nov. "N" - ?,P,XS; *nortoni* - S,U,IS; *parabates* - L,P,XS; *parapelates* - ?,U,IS; *patricae* - S,U,XS; *paulsoni* - L,?,A; *pictissimus* - L,U,IS; *pituinus* - ?,U,XS; *poolei* - I,P,XS; *probolaeus* - L,U,A; *rhodesi* L,U,IS; *rufifemoralis* - L,P,A; *ruthae* - S,U,IS; *schmidti* - L,U,A; *sciagraphus* - ?,U,A; *semipalmatus* - L,P,A; *thorectes* - L,P,A; *ventrilineatus* - L,P,A; *weinlandi* - L,U,IS; *wetmorei* - S,P,XS.

Mona Island.-- *monensis* - L,U,A.

Puerto Rican Bank.-- *antillensis* - S,P,XS; *brittoni* - S,P,XS; *cochranae* - S,P,XS; *cooki* - I,U,XS; *coqui* - S,U,XS; *eneidae* - S,P,XS; *gryllus* - ?,P,?; *hedricki* - ?,?,XS; *jasperi* - S,P,XS; *karlschmidti* - I,U,XP?; *lentus* - S,U,IS; *locustus* - L,P,XS; *portoricensis* - S,P,XS; *richmondi* - S,U,XS; *schwartzi* - S,U,XS; *unicolor* - ?,U,?; *wightmanae* - I,U,XS.

Lesser Antilles.-- *barlagnei* - S,P,XS; *johnstonei* - S,P,XS; *martinicensis* - S,P,XS; *pinchoni* - I,P,XS; *urichi* - S,U,XS.