Electrophoretic and Morphological Variation in Eleutherodactylus glaphycompus (Anura: Leptodactylidae) of Hispaniola

S. BLAIR HEDGES¹

Department of Zoology, University of Maryland, College Park, Maryland 20742, USA

ABSTRACT. – The distribution of the Haitian frog *Eleutherodactylus glaphycompus* is larger than previously believed due to confusion of museum specimens with *E. bakeri*. It occurs throughout the Tiburon Peninsula in areas of exposed limestone at elevations of 576-1480 m. Widely separated populations of *E. glaphycompus* have a similar advertisement call (an explosive "snap") not found in other Hispaniolan species, although some geographic variation is present. However, large genetic distances and considerable differences in body size between populations of *E. glaphycompus* on the northern and southern slopes of the Massif de la Hotte indicate that it may comprise more than one species. The habitat preference and elevational limits of *E. glaphycompus* may be factors responsible for limiting gene flow in this species. Two closely related species sympatric with *E. glaphycompus, E. bakeri* and *E. heminota,* occupy a wider range of elevations and show comparatively little geographic protein variation.

A large clade (ca. 80 sp.) of Eleutherodactylus inhabiting islands in the western Caribbean is characterized by ground and rock-dwelling species (Hedges, 1989a). Included are all native Jamaican species, most from Cuba, and most from the "South Island" of Hispaniola (areas south of the Cul de Sac/Valle de Neiba). Within this large clade (subgenus Euhyas, following Hedges, 1989a) is an unusual cohort of eight described species, the bakeri series, that have invaded primarily arboreal niches and have converged morphologically with species in the other large clade of West Indian Eleutherodactylus, the subgenus Eleutherodactylus. The bakeri series is restricted to the South Island of Hispaniola and most of the species are found only in the Haitian Massif de la Hotte. This series includes E. amadeus, E. bakeri, E. eunaster, E. glanduliferoides, E. glaphycompus, E. heminota, E. semipalmatus, and E. thorectes.

Species in the *bakeri* series are similar in several morphological features: most have enlarged digital tips, a wide thigh and shank bar, and similar dorsal pattern variants (e.g., Hedges et al., 1987, fig. 2). Distribution is of limited value in species identification because many species are sympatric in the Massif de la Hotte. The above factors have led to confusion in the literature and in museum collections regarding the definition and distribution of species in the *bakeri* series. My recent collections of Hispaniolan *Eleutherodactylus* and those of the Florida

¹ Present Address: Department of Biology, 208 Mueller Lab, Penn State University, University Park, Pennsylvania, 16802, USA. Museum of Natural History have provided enough freshly-preserved material, as well as biochemical and ecological data, to begin a reassessment of some species in the *bakeri* series. As a result, two new species have been described (Hedges et al., 1987; Hedges, 1988) and several other new taxa are under study.

Eleutherodactylus glaphycompus was described from the region of Castillon, Haiti (south of Marché Léon) based on material obtained by Richard Thomas (Schwartz, 1973). No additional localities or new information on this species have been published, although it has been reviewed several times (most recently, Schwartz, 1983; and Schwartz and Henderson, 1988). As will be shown, this species is widely distributed on the Tiburon Peninsula of Hispaniola and is represented by considerably more material, both old and new, in several museums. Most of these additional specimens of E. glaphycompus have been misidentified as E. bakeri, a closely related species, possibly as a result of geographic variation in body size in E. glaphycompus. In fact, the substantial difference in body size between specimens of E. glaphycompus from the north and south slopes of the Massif de la Hotte suggested that an undescribed species might be present. Therefore, I examined geographic variation in this species through analyses of electrophoretic, morphological, and call data.

MATERIALS AND METHODS

Eleven populations of *Eleutherodactylus* were examined electrophoretically (see Appendix 1 for localities). The methods of tissue preparation and electrophoresis are described in detail elsewhere (Hedges, 1986, 1989*a*, *b*). The 21 pro-

		Enzyme (Flectrophoretic	
	Protein ^a	Locus	Number ^a	conditions ^b
1.	Acid phosphatase	Аср	3.1.3.2	5
2.	Aconitate hydratase	Acon-1	4.2.1.3	1
3.	Adenylate kinase	Ak	2.7.4.3	1
4.	Aspartate aminotransferase	Aat-1	2.6.1.1	1
5.	Aspartate aminotransferase	Aat-2	2.6.1.1	1
6.	Creatine kinase	Ck-1	2.7.3.2	6
7.	Creatine kinase	Ck-2	2.7.3.2	6
8.	Glucose-6-phosphate isomerase	Gpi	5.3.1.9	5
9.	Glutamate dehydrogenase	Glud	1.4.1.3	1
10.	Glycerol-3-phosphate dehydrogenase	Gpd	1.1.1.8	5
11.	Isocitrate dehydrogenase	Icd-1	1.1.1.42	1
12.	Isocitrate dehydrogenase	Icd-2	1.1.1.42	1
13.	L-lactate dehydrogenase	Ldh-1	1.1.1.27	3
14.	Malate dehydrogenase	Mdh-1	1.1.1.37	2
15.	Malate dehydrogenase	Mdh-2	1.1.1.37	2
16.	Mannose-6-phosphate isomerase	Mpi	5.3.1.8	5
17.	Peptidase	Pep	3.4.13.11	4
18.	Phosphoglucomutase	Pgm	5.4.2.2	3
19.	Protein 3	Pt-3	-	4
20.	Protein 4	Pt-4	-	3
21.	Pyruvate kinase	Pk	2.7.1.40	1

TABLE 1. Protein loci and electrophoretic conditions.

* Nomenclature Committee of the International Union of Biochemistry (1984).

^b(1) Tris-citrate pH 8.0, 130 v 6 h; (2) Tris-citrate pH 6.7, 150 v, 6 h; (3) Poulik, 400 v, ca. 7 h; (4) Lithium hydroxide, 400 v, ca. 8 h; (5) Tris-versene-borate, 250 v, 6 h; (6) Tris-HCl, 250 v, 4 h.

tein loci examined and buffer conditions used are listed in Table 1.

The allelic data were converted to genetic distances and analyzed by two different methods. A modified Cavalli-Sforza distance (Nei et al., 1983) and Nei's (1978) *D* were used with the UPGMA method (Sneath and Sokal, 1973), and the Cavalli-Sforza and Edwards (1967) chord distance was used with the distance-Wagner method (Farris, 1972) employing the multiple addition criterion (Swofford, 1981). A discussion of the rationale for choosing these distances and methods is presented elsewhere (Hedges, 1986). BIOSYS-1 (Swofford and Selander, 1981) was used to generate the genetic distances and trees.

The preserved specimens examined are listed in Appendix 2. Calls were recorded on a Sony TCM-5000 and analyzed with a Kay Digital Sona-Graph 7800.

RESULTS AND DISCUSSION

In addition to similar pattern features and large digital tips, most or all of the species in the *bakeri* series have a paired submandibular vocal sac, narrow vomerine odontophores, and a shared electrophoretic allele at Pt-3 (Hedges, 1989a). Eleutherodactylus glaphycompus can be distinguished from other species in the *bakeri* series by a combination of the following: (1) the paired vocal sac is external; (2) the venter is smooth; and (3) the vomerine odontophores are wide (long rows of teeth) rather than narrow. It also has a unique "snapping" advertisement call. The confusion with E. bakeri likely is due to shared pattern features (especially leg-barring) found in most species of the bakeri series (Hedges et al., 1987; Hedges, 1989a), and the similarity in body size of E. bakeri (both sexes) with most female E. glaphycompus. Upon closer examination, E. bakeri can be distinguished readily from E. glaphycompus by its internal vocal sac (or, in some cases, absence of a vocal sac in adult males), distinctly granular venter, relatively narrow vomerine odontophores (short rows of teeth), and whistled call. Also, E. bakeri is one of the few species in the genus that exhibits virtually no sexual dimorphism in body size (see also Hedges and Thomas, 1987:278). Eleutherodactylus glaphycompus is strongly sexually dimorphic in body size. Only species in the bakeri series are likely to be confused with E. glaphycompus; some detailed comparisons of other species in that series are found in Hedges et al. (1987).

Morphological Variation.—Eleutherodactylus glaphycompus is invariant in the three defining morphological characters noted above. I have been unable to identify any non-mensural characters that show geographic variation. However, geographic variation in body size is so great that virtually no overlap exists between mature females from the north and south slopes of the Massif de la Hotte: those from the south



FIG. 1. Eleutherodactylus glaphycompus, from the vicinity of Plaines Formon, Dépt. de Sud, Haiti.

slope are considerably larger. Frogs from other localities are intermediate between these two extremes and there are no clear geographic patterns (Fig. 2). Variation in other mensural characters (not shown) is strongly correlated with body size.

Electrophoretic Variation.—The following loci were monomorphic: *Ak*, *Ck-1*, *Ck-2*, *Ldh-1*, and *Pt-4*. Allele frequencies at the 16 variable loci are given in Table 2, and genetic distances (Nei, 1978; Cavalli-Sforza and Edwards, 1967) are presented in Table 3. In a computer simulation study (Nei et al., 1983), a modified Cavalli-Sforza distance was found to give the best estimate of phylogeny. In this study, the modified Cavalli-Sforza distance and Nei's (1978) distance both resulted in the same UPGMA topology (Fig. 3). The tree of Nei's distances is shown here so that comparison can be made with other studies re-



FIG. 2. Body size variation in seven populations of *E. glaphycompus*. The areas sampled (nearby localities pooled), arranged from west to east along the Tiburon Peninsula, are: (A) region of Castillon; (B) region of Plaines Formon; (C) Les Platons; (D) 13.5 km N Camp Perrin; (E) vicinity of Beaumont; (F) 18.2-20.6 km N Cavaillon; and (G) 0.6 km E Blockauss. Shown are mean (horizontal line), ± 2 standard errors (vertical bar), range (vertical line), and sample size (in parentheses).



FIG. 3. Phylogenetic tree of Nei's (1978) genetic distances constructed by the UPGMA method. Prager and Wilson's (1976) F-value = 18.4. See Appendix 1 for localities. The "new species" refers to a morphologically distinctive form currently under investigation and not treated in this paper.

garding taxonomic level of differentiation (Thorpe, 1983).

All five populations of *E. heminota* and both populations of E. bakeri cluster at a level of differentiation (D < 0.10) typical of populations within a species (Thorpe, 1983). Two of the E. glaphycompus samples (Castillon and Camp Perrin) also cluster closely, but the sample from Plaines Formon clusters more closely with the three other species. Those E. glaphycompus populations are separated by a D of 0.43, a level characteristic of different species within a genus (Thorpe, 1983). A distance-Wagner analysis of Cavalli-Sforza and Edwards chord distances (Fig. 4) differs slightly from Fig. 3. The three populations of E. glaphycompus form a group in that tree which includes the new species. In another study using only one individual per species but with the greater resolving power of sequential electrophoresis (Hedges, 1989a), some additional "hidden" alleles were detected at five loci (Acp, Ck-1, Icd, Pgm, and Pt-3).

These protein data indicate that the south slope population (3) of *E. glaphycompus* could be recognized as a separate species based on its large genetic distance to the other two populations of *E. glaphycompus* examined. However, the morphological data (Fig. 2) are discordant with the protein data: individuals from population 2 (Fig. 2D) are intermediate in body size between population 1 (Fig. 2A) and population 3 (Fig. 2B), rather that being close to population 1. This poses a problem, in that the only morphological character showing geographic variation, body size, can not be used reliably to allocate populations to one or the other of the two electrophoretic groups.

Vocalization.—The advertisement call of *E.* glaphycompus shows some geographic variation (Fig. 5). At the type locality, Richard Thomas

	Population										
	1.1						······			new	
_	8	apnycompus	; •	bak	eri –	,	ne T	minota	•	10	species
Locus	1	2	3	4	5	6	7	8	9	10	11
Аср	b	b	b	а	а	b	b	b	b	b	b
Acon-1	b	b	b	b (0.88) c (0.12)	a (0.12) b (0.88)	b	a (0.75) b (0.25)	a (0.83) b (0.17)	а	а	b
Aat-1	b (0.17) c (0.83)	b	a (0.1) b (0.9)	b	b	b	b	b	b	b	b
Aat-2	a (0.06) c (0.89) d (0.05)	a (0.17) c (0.83)	b	a (0.13) b (0.75) c (0.12)	a	b	b	b	b	b	b
Gpi	b	b	a (0.1) c (0.9)	с	с	с	с	с	с	с	b
Glud	a (0.94) b (0.06)	а	а	а	a	а	a	a	a	а	а
Gpd	a (0.94) c (0.06)	a (0.83) c (0.17)	а	а	a (0.88) b (0.12)	а	a	а	а	а	а
Icd-1	с	с	b (0.7) c (0.3)	b	b	b	b	a (0.33) b (0.67)	b	а	с
Icd-2	а	а	с	b	b	b	b	b	b	b	d
Mdh-1	c (0.39) e (0.61)	c (0.08) e (0.92)	с	а	a (0.44) b (0.56)	f (0.75) g (0.25)	f	f	f	f	d
Mdh-2	b	b	b	b	Ь	a (0.25) b (0.75)	b	b (0.67) c (0.33)	b	b	b
Mpi	с	c	b (0.7) c (0.3)	a (0.38) b (0.62)	a (0.06) c (0.94)	a (0.5) b (0.5)	с	a (0.33) b (0.67)	a (0.67) b (0.33)	c	b
Pep	b	b	b	a (0.38) b (0.62)	с	b	b	b	b	b	b
Pgm	b	b	b	b (0.63) c (0.37)	b	b (0.5) c (0.5)	a (0.75) b (0.25)	b	a (0.67) b (0.33)	b	b
Pt-3	e	d	с	b (0.75) c (0.25)	a (0.06) b (0.94)	с	с	с	с	с	с
Pk	b	Ъ	Ъ	Ъ	b	a (0.75) b (0.25)	а	Ь	b	b	Ъ

TABLE 2. Allelic Variation in 11 populations of Hispaniolan *Eleutherodactylus* (four species) at 16 polymorphic loci. See Appendix 1 for localities.

(in Schwartz, 1973) described the call as "somewhat like two ball-bearings clicking together but lacks the metallic quality and is explosive in nature." My recordings made more recently from the region of Castillon (1000-1100 m) match that verbal description of the call. The call recorded in this region (Fig. 5A), consists of a single note ("snap") containing two sharp pulses at 2.52 \pm 0.05 kHz and 3.28 \pm 0.02 kHz (N = 10 calls). At the second locality, 13.5 km

TABLE 3. Cavalli-Sforza and Edwards (1967) chord distances above diagonal, Nei (1978) unbiased genetic distances below diagonal, and mean heterozygosities along diagonal. See Appendix 1 for localities.

	Population										
	1	2	3	4	5	6	7	8	9	10	11
1.	(0.06)	0.26	0.48	0.58	0.58	0.55	0.58	0.54	0.57	0.54	0.47
2.	0.09	(0.04)	0.47	0.56	0.55	0.53	0.56	0.52	0.55	0.52	0.44
3.	0.34	0.33	(0.06)	0.47	0.52	0.38	0.43	0.38	0.41	0.42	0.38
4.	0.52	0.46	0.29	(0.12)	0.27	0.41	0.48	0.43	0.45	0.48	0.55
5.	0.52	0.45	0.38	0.07	(0.07)	0.49	0.51	0.47	0.50	0.51	0.60
6.	0.45	0.40	0.16	0.20	0.32	(0.12)	0.27	0.28	0.30	0.36	0.48
7.	0.54	0.49	0.26	0.31	0.40	0.05	(0.05)	0.28	0.25	0.32	0.52
8.	0.44	0.39	0.17	0.24	0.32	0.07	0.09	(0.08)	0.19	0.18	0.47
9.	0.53	0.47	0.22	0.26	0.37	0.09	0.07	0.03	(0.06)	0.27	0.50
10.	0.45	0.40	0.23	0.32	0.38	0.15	0.13	0.03	0.09	(0.00)	0.48
11.	0.30	0.26	0.18	0.45	0.55	0.30	0.42	0.30	0.31	0.29	(0.00)



FIG. 4. Phylogenetic tree of Cavalli-Sforza and Edwards (1967) chord distances constructed by the distance Wagner method using the multiple addition criterion, branch length optimization (Swofford, 1981), and rooted at the midpoint of the longest path. Prager and Wilson's *F*-value = 3.58.

north of Camp Perrin (680 m), the call is similar, but has an additional "whistle" note (3.93 \pm 0.04 kHz; N = 4 calls) immediately following the snap (Fig. 5B). At Plaines Formon (1000 m), the call again is similar (Fig. 5C) but with a more well-developed trailing whistle at a frequency of 4.18 \pm 0.15 kHz (N = 16 calls).

The only other population of *E. glaphycompus* where the call has been reported is 0.6 km E Blockauss. In his field notes, Thomas described the call at this locality as a "single, high-pitched, fairly intense note (=whistle) of about one-second duration," as quoted by Schwartz (1980) in his account of *E. bakeri*. However, immediately following that description, Thomas's notes

mention that the "call sometimes has an almost snapping or clicking quality when hearer is in close proximity" (R. Thomas, pers. comm.). Therefore, that "snapping" quality is present in all four widely spaced populations of E. glaphycompus where the call has been noted, and it appears to be a unifying trait for the species. Nonetheless, the call at the type locality appears to be unique in that it lacks the trailing whistle. The only other species of Hispaniolan Eleutherodactylus that has a similar snap-like call is E. glanduliferoides, also a member of the bakeri series but much smaller in body size and not obviously a close relative based on allozyme and morphological data (Hedges, 1989a). The call of that species restricted to the Massif de la Selle in Haiti can be described as a single, faint, highpitched snap (pers. obs.). Four species in the bakeri series (E. amadeus, E. bakeri, E. eunaster, and E. heminota) have "whistle-like" calls that differ in frequency and number of notes per call (Schwartz, 1973; Hedges et al., 1987; Hedges, unpubl. data). No call information is available for E. semipalmatus or E. thorectes. Additional individuals and populations of E. glaphycompus need to be sampled for variation in call characteristics in order to obtain a more complete picture of geographic variation.

Natural History.—Eleutherodactylus glaphycompus is a rock-dwelling species. Other species in the bakeri series are associated with vegetation, although no ecological information is available for the presumably aquatic *E. semipalmatus*. My field observations of *E. glaphycompus* at the region of the type-locality (region of Castillon),



time in seconds

FIG. 5. Audiospectrograms of *E. glaphycompus* from three localities: (A) Dépt. de la Grand'Anse, region of type-locality (Castillon); (B) Dépt. du Sud, 13.5 km N Camp Perrin; and (C) Dépt. du Sud, vicinity of Plaines Formon. In each case, the call is shown first with a 45 Hertz filter, and then with a 300 Hertz filter. The call consists of a "snap" component (vertical lines with 300 Hertz filter), followed by a whistle (horizontal or slightly rising bar with 300 Hertz filter), except at locality A where the trailing whistle is absent.



FIG. 6. The Tiburon Peninsula of Hispaniola (Haiti), showing the distribution of *Eleutherodactylus glaphy-compus*. The numbers indicate electrophoretic localities as given in Appendix 1.

at 13.5 km N Camp Perrin, and the region of Plaines Formon agree with observations made by Richard Thomas in collecting the type series (Schwartz, 1973). Males characteristically call from small, spoon-sized pockets on limestone rock outcrops. Females also are found on limestone rock, although some have been taken on the ground and vegetation, but always near a limestone rock outcrop. Specimens from near Blockauss were taken from a rock face with trickling water (R. Thomas, in Schwartz, 1973), as were two females collected by Thomas and myself from the region of the type-locality. The relatively short and "explosive" call of this species, combined with its cryptic coloration and calling site, make it difficult to trace and collect.

Distribution.—Eleutherodactylus glaphycompus is widely distributed on the Tiburon Peninsula (Fig. 6), although all localities are interior and intermediate in elevation (576–1480 m). Two unverified literature records (no specimens available) for *E. bakeri*, Sources Chaudes and St.-Cyr (Schwartz et al., 1978), likely represent *E.* glaphycompus based on elevation. If correct, the lower elevational limit for *E. glaphycompus* would be 212 m (Sources Chaude).

Biogeography.—The geographic variation seen in *E. glaphycompus* contrasts with two sympatric species, *E. bakeri* and *E. heminota*, which show little geographic protein variation (Fig. 3). The altitudinal distribution of these three species may provide an explanation for the difference. *Eleutherodactylus bakeri* appears to be continuously distributed in the high elevations of the Massif de la Hotte (ca. 900–2340 m), thus providing an opportunity for gene flow between the south slope (Morne Formon) and north slope (Castillon) populations. However, despite extensive collecting in the southern and central Massif de la Hotte (Formon and Macaya regions), *E. glaphycompus* has not been found above 1305 m, and 1480 m is the highest recorded locality on the north slope. This upper elevational limit may be tied to the ecological habits of E. glaphycompus and its association with limestone rock outcrops. Igneous and metamorphic rock form the core of the Massif de la Hotte, and it is these rock types (and associated vegetation) that usually are exposed in the highest elevations. This probably poses a barrier to gene flow between the south and north slope populations of E. glaphycompus, except in lower elevations of the Massif de la Hotte (e.g., Camp Perrin) where there is suitable limestone habitat. Eleutherodactylus heminota has not been recorded from the highest elevations in the Massif de la Hotte (Pic Formon and Pic Macaya), but it has a wider elevational distribution (0-1700 m) than E. glaphycompus and does not appear to be restricted to any rock or forest type.

The Blockauss locality lies at the eastern edge of the Massif de la Hotte physiographic province, which is separated from the Massif de la Selle by the Jacmel-Fauche depression (Maurrassee, 1982). Collections from suitable habitat southwest of Seguin on the south slope of the Massif de la Selle have failed to produce specimens of *E. glaphycompus*. Thus, the Jacmel-Fauche depression, possibly a narrow seaway during times of higher sea level in the Pliocene and Pleistocene, may also form the eastern boundary of the range of *E. glaphycompus*. More collecting on the Tiburon Peninsula will be necessary before the distributions of *E. glaphycompus* and other South Island species are well known.

It is possible that some populations of *E. glaphycompus*, especially those from the region of Plaines Formon, represent an undescribed species. On the other hand, additional collecting and molecular analyses may demonstrate clinal geographic variation among the differentiated populations of *E. glaphycompus*. Until more data become available, *E. glaphycompus* is best recognized as a geographically variable species with a larger range than previously thought.

This reassessment of *E. glaphycompus* does not affect the distributions of other species in the *bakeri* series, except for *E. bakeri*. That latter species now has a smaller range than indicated in Schwartz (1980) and Schwartz and Henderson (1988). It is restricted to the upper elevations of the Massif de la Hotte (ca. 900–2340 m), from the Morne Formon and Morne Macaya regions to the vicinity of Castillon (south of Marché Léon) on the north slope (see comment above concerning the Sources Chaudes and St.-Cyr literature records).

Acknowledgments.—I thank Richard Thomas for assisting me on the Haitian expeditions; Richard Franz and Charles Woods for access to the Florida Museum of Natural History herpetological collections from Haiti; Walter Auffenberg, David Auth, Ronald Crombie, William Duellman, Jack McCoy, Jose Rosado, Albert Schwartz, and George Zug for loan of specimens; Ronald Heyer for access to the sound analysis laboratory of the Division of Amphibians and Reptiles (Smithsonian Institution); Gaston Hermatin, Edmond Magny, Paul Paryski, and Florence Sergile for collecting and export permits in Haiti; and Richard Highton for providing laboratory facilities and support. David Cannatella and Linda Maxson offered helpful comments on the manuscript. Supported in part by grants from the National Science Foundation (BSR 8307115 to Richard Highton and BSR 8906325 to SBH) and a USAID/HAITI grant to Charles Woods (521-0169-C-00-3083).

LITERATURE CITED

- AUTH, D. L. 1989. Florida State Museum changes its name but keeps its acronym. Herpetol. Review 20(2):38.
- CAVALLI-SFORZA, L. L., AND A. W. F. EDWARDS. 1967. Phylogenetic analysis: models and estimation procedures. Evolution 21(3):550–570.
- FARRIS, J. S. 1972. Estimating phylogenetic trees from genetic distance matrices. Amer. Natur. 106(951): 645–668.
- HEDGES, S. B. 1986. An electrophoretic analysis of Holarctic hylid frog evolution. Syst. Zool. 35(1): 1-21.

- ——. 1988. A new diminutive frog from Hispaniola (Leptodactylidae, Eleutherodactylus). Copeia 1988(3):636-641.
- ——. 1989a. Evolution and biogeography of West Indian frogs of the genus *Eleutherodactylus*: slowevolving loci and the major groups. *In* C. A. Woods (ed.), Biogeography of the West Indies: Past, Present, and Future, pp. 305–370. Sandhill Crane Press, Gainesville, Florida.
- ——. 1989b. An island radiation: allozyme evolution in Jamaican frogs of the genus Eleutherodactylus (Leptodactylidae). Caribbean J. Sci. 25(3– 4):123–147.
- ——, AND R. THOMAS. 1987. A new burrowing frog from Hispaniola with comments on the *inoptatus* group of the genus *Eleutherodactylus* (Anura, Leptodactylidae). Herpetologica 43(3):269–279.
- —, —, AND R. FRANZ. 1987. A new species of *Eleutherodactylus* (Anura, Leptodactylidae) from the Massif de La Hotte, Haiti. Copeia 1987(4):943– 949.
- LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: part 1, standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985(3):802-832.
- MAURRASSEE, F. J. 1982. Survey of the geology of Haiti. Miami Geol. Soc., Miami, 103 pp.
- NEI, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89(3):583–590.
- —, F. TAJIMA, AND Y. TATENO. 1983. Accuracy of estimated phylogenetic trees from molecular data. II. Gene frequency data. J. Mol. Evol. 19(2): 153-170.
- NOMENCLATURE COMMITTEE OF THE INTERNATIONAL UNION OF BIOCHEMISTRY. 1984. Enzyme Nomenclature 1984. Academic Press, New York.
- PRAGER, E. M., AND A. C. WILSON. 1976. Congruency of phylogenies derived from different proteins. A molecular analysis of the phylogenetic position of cracid birds. J. Mol. Evol. 9(1):45–57.
- SCHWARTZ, A. 1973. Six new species of Eleutherodactylus (Anura: Leptodactylidae) from Hispaniola. J. Herpetol. 7(3):249-273.
- ——. 1980. Eleutherodactylusbakeri. Cat. Amer. Amphib. Rept. 247.1.
- ——. 1983. Eleutherodactylus glaphycompus. Cat. Amer. Amphib. Rept. 323.1.
- —, AND R. W. HENDERSON. 1988. West Indian amphibians and reptiles: a checklist. Milwaukee Public Mus. Contr. Biol. Geol. 74:1–264.
- ——. R. THOMAS, AND L. D. OBER. 1978. First supplement to a check-list of West Indian amphibians and reptiles. Carnegie Mus. Nat. Hist., Spec. Publ. 5:1–35.
- SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical Taxonomy. W. H. Freeman, San Francisco. 573 pp.
- SWOFFORD, D. L. 1981. On the utility of the distance Wagner procedure. In V. A. Funk and D. A. Brooks (eds.), Advances in cladistics, proceedings of the first meeting of the Willi Hennig Society, pp. 25– 43. New York Bot. Garden, New York.
 - , AND R. B. SELANDER. 1981. Biosys-1: a FOR-TRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Heredity 72(4):281–283.

THORPE, J. P. 1983. Enzyme variation, genetic distance and evolutionary divergence in relation to levels of taxonomic separation. *In* G. S. Oxford and D. Rollinson (eds.), Protein Polymorphism: Adaptive and Taxonomic Significance, pp. 131–152. Academic Press, New York.

Accepted: 10 July 1990.

Appendix 1

Electrophoretic Localities

The following 11 populations were sampled in the electrophoretic analysis: (1) E. glaphycompus, Haiti, Grand'Anse, region of Castillon, N = 9; (2) E. glaphycompus, Haiti, Grand'Anse, 13.5 km N Camp Perrin, N = 6; (3) E. glaphycompus, Haiti, Sud, vicinity of Plaines Formon, N = 5; (4) E. bakeri, Haiti, Sud, Morne Formon, N = 4; (5) E. bakeri, Haiti, Grand'Anse, region of Castillon, N = 8; (6) E. heminota, Haiti, Grand'Anse, region of Castillon, N = 2; (7) E. heminota, Haiti, Sud, 17.6 km N Camp Perrin, N = 2; (8) E. heminota, Haiti, Sud'Est, 8.4 km SW Seguin, N = 3; (9) E. heminota, Haiti, L'Ouest, Furcy, N = 3; (10) E. heminota, Republica Dominicana, Pedernales, Los Arroyos, N = 2, and (11) one specimen of an undescribed species (Hedges, unpubl. data), Haiti, Sud, Morne Formon, N = 1. Voucher specimens are in the United States National Museum.

APPENDIX 2

Specimens Examined

Museum abbreviations follow Leviton et al. (1985) except for the Florida Museum of Natural History (UF), which is reported incorrectly in Leviton et al. (Auth, 1989). Asterisks refer to specimens used in the electrophoretic analysis.

Eleutherodactylus glaphycompus (169).-HAITI. Dépt. de la Grand'Anse: Castillon, ca. 763 m, CM 54092 (holotype), KU 232252-267 (paratypes), KU 232271; 9.0-9.7 km due S Marché Léon, 1030-1090 m, USNM 269270*, USNM 292236-241*, 292242-246; 9.2 km S, 0.2 km W (airline) Marché Léon, 1030 m, USNM 292247-248*; 10.7 km S, 1.6 km E (airline) Marché Léon, 1270 m, USNM 292249-256; 11.2 km S, 1.9 km E (airline) Marché Léon, 1360 m, USNM 292259; 11.7 km S, 1.7 km E (airline) Marché Léon, 1480 m, USNM 292257-258; 0.4 km NE Beaumont, MCZ 88848-849; ca. 6.4 km NE Beaumont, MCZ 888543-546. Dépt. du Sud: between Plaines Formon and Morne Formon, 1200-1260 m, UF 64224, 64430; 3 km W "Formon" (=Plaines Formon?), 1250 m, UF 64208; ca. 2.5 km NW Plaines Formon, 1240-1260 m, UF 58361, 64453-454, 64456, 64469-470; ca. 2 km NW Plaines Formon, 1108-1285 m, UF 56811, 58367, 58373, 60455, 64033-034, 64409, 64433, 64451, 64484, 64487; vic. of Plaines Formon, 1000 m, USNM 269271*, USNM 292231-234*, 292235; near Plaines Formon, 1305 m, UF 64183; ca. 1 km NNE Plaines Formon, 950 m, UF 64395-396; Grand Ravine du Sud, 1090 m, UF 64287; Les Platons, 720 m, MCZ 88994-995; 13.5 km N Camp Perrin, 680 m, USNM 292222-227*, 292228-230; 18.2 km N Cavaillon, "1900 ft." (576 m), KU 232338-347; 19.8 km N Cavaillon, "2000 ft." (606 m), KU 232276-309; 20.2 km N Cavaillon, "2000 ft." (606 m), KU 232314-337; 20.5 km N Cavaillon, "2000 ft." (606 m), KU 232310-313; 20.6 km N Cavaillon, KU 232272-275. Dépt. de Sud'Est: 0.6 km E "Blockhaus" (=Blockauss on topographic map), "1900 ft." (576 m), KU 232268-270.