



National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file *Votre référence*

Our file *Notre référence*

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

Canada

Systematics and Biogeography of Eastern Caribbean Frogs

Hinrich Kaiser

Department of Biology
McGill University, Montreal
September, 1993

A Thesis submitted to the Faculty of Graduate Studies and
Research in partial fulfilment of the requirements
of the degree of Doctor of Philosophy

© Hinrich Kaiser 1993



National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

The author has granted an irrevocable non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of his/her thesis by any means and in any form or format, making this thesis available to interested persons.

L'auteur a accordé une licence irrévocable et non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de sa thèse de quelque manière et sous quelque forme que ce soit pour mettre des exemplaires de cette thèse à la disposition des personnes intéressées.

The author retains ownership of the copyright in his/her thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without his/her permission.

L'auteur conserve la propriété du droit d'auteur qui protège sa thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

ISBN 0-315-94643-1

Canada

in memory of

Dorette Kaiser

Magdalene Kaiser

zum Andenken

dedicated to

Anita von Stösser

Karl von Stösser

gewidmet

TABLE OF CONTENTS

List of Tables	i
List of Figures	iv
Abstract	vii
Resumé	viii
Resumen	ix
Zusammenfassung	x
Preface	xi
Acknowledgments	xiv

GENERAL INTRODUCTION

General Introduction	1
Literature Cited	5

CHAPTER 1

The trade-mediated introduction of *Eleutherodactylus martinicensis* (Anura: Leptodactylidae) on St. Barthélemy, French Antilles, and its implications for Lesser Antillean biogeography

Preamble.....	10
Abstract	11
Introduction	11
Materials and Methods	13
Results	15
Discussion	19
Acknowledgments.....	22
Literature Cited	23
Appendix 1	28
Appendix 2	30

CHAPTER 2

The taxonomic status of Caribbean and South American frogs currently ascribed to *Eleutherodactylus urichi* (Anura: Leptodactylidae)

Preamble.....	39
Abstract	40
Introduction	40
Materials and Methods	41
Results	42
Discussion and Descriptions	46
<i>Eleutherodactylus euphronides</i> (Schwartz) <i>comb. nov.</i>	47
<i>Eleutherodactylus shrevei</i> (Schwartz) <i>comb. nov.</i>	49
<i>Eleutherodactylus urichi</i> (Boettger) <i>s. nov.</i>	52
Acknowledgments	58
Literature Cited	59
Appendix 1	63
Appendix 2	65
Appendix 3	66

CHAPTER 3

A new species of *Colostethus* (Anura: Dendrobatidae)
from Martinique, French Antilles

Preamble.....	81
Abstract	82
Introduction	82
Materials and Methods	83
<i>Colostethus chalcopis</i> <i>sp. nov.</i>	83
Discussion	91
Acknowledgments	94
Literature Cited	94
Appendix	99

CHAPTER 4

The atypical tadpole of the dendrobatid frog, *Colostethus chalcopis*, from Martinique, French Antilles

Preamble.....	105
Abstract	106
Introduction	106
Materials and Methods	107
Results and Discussion.....	107
Acknowledgments.....	113
Literature Cited	114

CHAPTER 5

Multivariate morphometrics of Eastern Caribbean *Eleutherodactylus* (Anura, Leptodactylidae): biogeography, divergence, and evolution

Preamble.....	120
Abstract	121
Introduction	122
Materials and Methods.....	127
Results	129
Discussion	134
Acknowledgments.....	138
Literature Cited	138
Appendix 1	146
Appendix 2	152

CHAPTER 6

Systematics and biogeography of Eastern Caribbean *Eleutherodactylus* (Anura: Leptodactylidae) with the description of a new species from Dominica

Preamble.....	177
Abstract	178
Introduction	179
Materials and Methods	180
Taxonomy	183
<i>Eleutherodactylus amplinympha</i> sp. nov.	183
Analysis of Phylogenetic Relationships.....	194
Discussion	195
Conclusions	201
Acknowledgments.....	202
Literature Cited	203
Appendix 1	211
Appendix 2	216
Appendix 3	218
Appendix 4	242

CHAPTER 7

Systematics and Biogeography of Eastern Caribbean frogs of the genus *Eleutherodactylus* (Anura: Leptodactylidae): evidence from allozymes

Preamble.....	255
Abstract	256
Introduction	256
Materials and Methods.....	258
Results	261
Discussion	264
Acknowledgments.....	269
Literature Cited	269
Appendix	275

Summary	292
---------------	-----

LIST OF TABLES

CHAPTER 1

TABLE 1. Protein loci and electrophoretic conditions.....	33
TABLE 2. List of measurements taken.....	34
TABLE 3. Allelic variation at thirteen allozyme loci diagnostic for <i>Eleutherodactylus johnstonei</i> and <i>E. martinicensis</i>	35

CHAPTER 2

TABLE 1. Protein loci and electrophoretic conditions.....	67
TABLE 2. List of measurements taken.....	68
TABLE 3. Group assignments from a discriminant analysis of <i>Eleutherodactylus johnstonei</i> , <i>E. shrevei</i> , and <i>E. euphronides</i>	69
TABLE 4. Discriminant loadings from a discriminant analysis of <i>Eleutherodactylus johnstonei</i> , <i>E. shrevei</i> , and <i>E. euphronides</i>	70
TABLE 5. Group assignments from a discriminant analysis of <i>Eleutherodactylus euphronides</i> , <i>E. shrevei</i> , <i>E. terraebolivaris</i> , and <i>E. urichi</i>	71
TABLE 6. Discriminant loadings from a discriminant analysis of <i>Eleutherodactylus euphronides</i> , <i>E. shrevei</i> , <i>E. terraebolivaris</i> , and <i>E. urichi</i>	72
TABLE 7. Means and extremes for six metric characteristics of <i>Eleutherodactylus euphronides</i> , <i>E. shrevei</i> , and <i>E. urichi</i>	73
TABLE 8. Allelic variation at twenty allozyme loci diagnostic of <i>Eleutherodactylus euphronides</i> , <i>E. shrevei</i> , and <i>E. urichi</i>	74

CHAPTER 5

TABLE 1. List of measurements taken.....	156
TABLE 2. Means and extremes for six metric characteristics of Eastern Caribbean <i>Eleutherodactylus</i>	157
TABLE 3. Discriminant loadings from a discriminant analysis of Eastern Caribbean <i>Eleutherodactylus</i>	167
TABLE 4. Group assignments from a discriminant analysis of Eastern Caribbean <i>Eleutherodactylus</i>	168
TABLE 5. Discriminant loadings from a discriminant analysis of northern vs. southern Eastern Caribbean <i>Eleutherodactylus</i>	169
TABLE 6. Group assignments from a discriminant analysis of northern vs. southern Eastern Caribbean <i>Eleutherodactylus</i>	170
TABLE 7. Discriminant loadings from a discriminant analysis of northern and southern populations of <i>Eleutherodactylus johnstonei</i>	171
TABLE 8. Group assignments from a discriminant analysis of northern and southern populations of <i>Eleutherodactylus johnstonei</i>	172

CHAPTER 6

TABLE 1. List of <i>Eleutherodactylus</i> species in the Eastern Caribbean.....	244
TABLE 2. Protein loci and electrophoretic conditions.....	245
TABLE 3. Means and extremes for eleven metric characteristics of <i>Eleutherodactylus amplynymphae</i> , <i>E. johnstonei</i> , and <i>E. martinicensis</i>	246
TABLE 4. Allelic variation at thirteen allozyme loci diagnostic of <i>Eleutherodactylus amplynymphae</i> , <i>E. johnstonei</i> , and <i>E. martinicensis</i>	247

CHAPTER 7

TABLE 1. Protein loci and electrophoretic conditions.....	279
TABLE 2. Allozyme frequencies of Eastern Caribbean <i>Eleutherodactylus</i> at twenty-one polymorphic loci	280
TABLE 3. Data matrices and character types for two cladistic analysis of allozyme data from Eastern Caribbean and Greater Antillean <i>Eleutherodactylus</i>	288

LIST OF FIGURES

INTRODUCTION

FIGURE 1. Map of the Eastern Caribbean, as defined in this study	9
--	---

CHAPTER 1

FIGURE 1. Distribution of <i>Eleutherodactylus martinicensis</i> and <i>E. johnstonei</i> in the Lesser Antilles	36
FIGURE 2. Audiospectrograms of the calls of <i>Eleutherodactylus martinicensis</i> and <i>E. johnstonei</i>	37
FIGURE 3. Plot of the first two principal components for populations of northern <i>Eleutherodactylus johnstonei</i> , southern <i>E. johnstonei</i> , and <i>E.</i> <i>martinicensis</i> from Guadeloupe, Martinique, and St-Barths.....	38

CHAPTER 2

FIGURE 1. Localities for populations of <i>Eleutherodactylus euphronides comb.</i> <i>nov.</i> , <i>E. shrevei comb. nov.</i> , and <i>E. urichi s. nov.</i>	75
FIGURE 2. Graphic representations of species clusters for <i>Eleutherodactylus</i> <i>euphronides comb. nov.</i> , <i>E. johnstonei</i> St. Vincent, <i>E. johnstonei</i> Grenada, and <i>E. shrevei comb. nov.</i>	76
FIGURE 3. Graphic representations of species clusters from multiple discriminant function analyses for <i>Eleutherodactylus euphronides comb.</i> <i>nov.</i> , <i>E. shrevei comb. nov.</i> , <i>E. terraebolivaris</i> , <i>E. urichi s. nov.</i> , and several unidentified specimens	77
FIGURE 4. Audiospectrograms of the calls of southern Eastern Caribbean <i>Eleutherodactylus</i>	78

FIGURE 5. Line drawings of hands and feet of <i>Eleutherodactylus euphronides</i> <i>comb. nov.</i> , <i>E. shrevei comb. nov.</i> , and <i>E. urichi s. nov.</i>	79
--	----

FIGURE 6. Photographs of <i>Eleutherodactylus euphronides comb. nov.</i> , <i>E.</i> <i>shrevei comb. nov.</i> , and <i>E. urichi s. nov.</i>	80
--	----

CHAPTER 3

FIGURE 1. Photograph of paratopotype of <i>Colostethus chalcopis sp. nov.</i>	100
---	-----

FIGURE 2. Photograph of the holotype of <i>Colostethus chalcopis sp. nov.</i> and a female paratopotype to show male-female differences in ventral coloration	101
--	-----

FIGURE 3. Line drawings of hand, foot, and right side of head of <i>Colostethus</i> <i>chalcopis sp. nov.</i>	102
--	-----

FIGURE 4. Photographs of paratopotypes of <i>Colostethus chalcopis sp. nov.</i> , showing variation in dorsal pattern	103
--	-----

FIGURE 5. Call of <i>Colostethus chalcopis sp. nov.</i>	104
---	-----

CHAPTER 4

FIGURE 1. Photograph of intact egg mass of <i>Colostethus chalcopis</i> , as collected in the field.....	117
---	-----

FIGURE 2. Line drawing of oral disc of <i>Colostethus chalcopis</i>	118
---	-----

FIGURE 3. Photographs of the tadpole of <i>Colostethus chalcopis</i> in dorsal, lateral, and ventral view.....	119
---	-----

CHAPTER 5

FIGURE 1. Distribution of the eight Eastern Caribbean <i>Eleutherodactylus</i>	173
--	-----

FIGURE 2. Discriminant score plots of multiple discriminant function analyses of Eastern Caribbean <i>Eleutherodactylus</i>	174
---	-----

FIGURE 3. UPGMA phenogram of Mahalanobis distances (D_M) between Eastern Caribbean <i>Eleutherodactylus</i>	175
---	-----

FIGURE 4. Degree of arboreality of Eastern Caribbean <i>Eleutherodactylus</i> as indicated by a plot of ln tibia length against ln total toepad area.....	176
---	-----

CHAPTER 6

FIGURE 1. Distribution of <i>Eleutherodactylus</i> in the Lesser Antilles.....	249
--	-----

FIGURE 2. Photograph of female holotype of <i>Eleutherodactylus amplinympha</i> sp. nov.	250
---	-----

FIGURE 3. Right hand and foot of <i>Eleutherodactylus amplinympha</i> sp. nov.	251
---	-----

FIGURE 4. Audiospectrograms of the calls of <i>Eleutherodactylus martinicensis</i> , <i>E. amplinympha</i> sp. nov., and <i>E. johnstonei</i>	252
---	-----

FIGURE 5. Strict consensus trees from a cladistic analysis of West Indian <i>Eleutherodactylus</i>	253
--	-----

FIGURE 6. Phylogram from a cladistic analysis of West Indian <i>Eleutherodactylus</i>	254
--	-----

CHAPTER 7

FIGURE 1. Distribution of Eastern Caribbean <i>Eleutherodactylus</i>	289
--	-----

FIGURE 2. Phenograms constructed from two genetic distance indices for Eastern Caribbean and Greater Antillean <i>Eleutherodactylus</i>	290
---	-----

FIGURE 3. Cladograms from a phylogenetic analysis of allozyme data for Eastern Caribbean <i>Eleutherodactylus</i>	291
---	-----

ABSTRACT

This study examines the systematics and biogeography of frogs in the Eastern Caribbean, a biogeographical province consisting of the Lesser Antilles, Trinidad, and Tobago. A comprehensive collection of specimens was subjected to an analysis incorporating morphometric, osteological, and biochemical approaches. An investigation of α -level taxonomy revealed the presence of four additional taxa: *Colostethus chalcopis* sp. nov. on Martinique, *Eleutherodactylus amplinympha* sp. nov. on Dominica, *E. euphronides* comb. nov. on Grenada, and *E. shrevei* comb. nov. on St. Vincent. Based on species distributions and detailed analyses of the largely congruent data sets, Eastern Caribbean frogs can be grouped into two major categories, those originating with South American stock and those of Greater Antillean ancestry. A South American origin is obvious for species which have no congeneric relatives in the Greater Antilles, e.g. *C. chalcopis*, *Leptodactylus fallax*, *L. wagneri*. Among the *Eleutherodactylus* species, northern Eastern Caribbean taxa form a monophyletic group within the *E. auriculatus* species group; the topology of relationships is ((*E. barlagnei*, *E. pinchoni*) ((*E. amplinympha*, *E. martinicensis*) *E. johnstonei*)). The southern Eastern Caribbean species may or may not form a monophyletic group, but *E. euphronides* and *E. shrevei* are sister taxa. The topology for these species is (*E. urichi* (*E. terraebolivaris* (*E. euphronides*, *E. shrevei*))). Thus, the Eastern Caribbean forms a biogeographic link between the large South American and Greater Antillean radiations of *Eleutherodactylus*; *Eleutherodactylus* is the only truly circum-Caribbean frog genus. Furthermore, historical evidence shows that the patchy, Caribbean-wide distribution of *E. johnstonei* is the direct result of accidental introduction mitigated by humans during the past three centuries.

RÉSUMÉ

Cette étude examine les relations systématiques et biogéographiques des anoures des Caraïbes de l'Est, une province biogéographique qui regroupe les Petites Antilles, Trinidad, et Tobago. Une collection représentative de spécimens a été soumise à une analyse incorporant des techniques morphométriques, ostéologiques, et biochimiques. Une investigation taxonomique de niveau α révèle la présence de quatre espèces additionnelles: *Colostethus chalcopis* sp. nov. de la Martinique, *Eleutherodactylus amplinympha* sp. nov. de la Dominique, *E. euphronides* comb. nov. de la Grenade, et *E. shrevei* comb. nov. du St-Vincent. Fondé sur la distribution des espèces et l'analyse détaillée des données majoritairement congruentes, on peut regrouper les anoures des Caraïbes de l'Est en deux grandes catégories, l'une d'origine sud-américaine et l'autre d'une lignée des Grandes Antilles. Il est évident que l'Amérique du Sud est le lieu d'origine des espèces dépourvues d'alliés congénériques aux Grandes Antilles, e.g. *C. chalcopis*, *Leptodactylus fallax*, *L. wagneri*. Parmi les espèces du genre *Eleutherodactylus*, les taxons de la partie septentrionale des Caraïbes de l'Est forment un ensemble monophylétique qui s'inscrit dans la section de l'espèce *E. auriculatus*; la topologie de ces relations phylogénétiques est ((*E. barlagnei*, *E. pinchoni*) ((*E. amplinympha*, *E. martinicensis*) *E. johnstonei*)). Dans la partie méridionale des Caraïbes de l'Est, les espèces de ce genre peuvent ou non former une groupe monophylétique, mais *E. euphronides* et *E. shrevei* représentent des groupe-frères. La topologie phylogénétique pour ces espèces est (*E. urichi* (*E. terraebolivaris* (*E. euphronides*, *E. shrevei*))). Ainsi, les Caraïbes de l'Est constituent le lien biogéographique des grandes radiations de l'Amérique du Sud et des Grandes Antilles; *Eleutherodactylus* est le seul genre d'anoures véritablement présent dans toutes les Caraïbes. De plus, les évidences historiques indiquent que la distribution discontinue de *E. johnstonei* sur tout le territoire caraïbien est le resultat d'introductions accidentelles dûes à l'activité humaine depuis les trois derniers siècles.

Translated by Michel Di Vergilio

RESUMEN

Este estudio revisa la sistemática y biogeografía de las ranas en el Caribe Este, una provincia biogeográfica que comprende las Antillas Menores, Trinidad, y Tobago. Una comprensiva colección de especímenes fue analizada bajo una perspectiva morfométrica, osteológica, y bioquímica. Una investigación de taxonomía alfa, revela la presencia de cuatro taxa adicionales: *Colostethus chalcopis* sp. nov. en Martinica, *Eleutherodactylus amplinympha* sp. nov. en Dominica, *E. euphronides* comb. nov. en Granada, y *E. shrevei* comb. nov. en San Vicente. Con base en las distribuciones de especies y detallados análisis de bases de datos congruentes, las ranas del Caribe Este pueden ser agrupadas en dos grandes categorías: aquellas originadas de un grupo sudamericano y aquellas con ancestría en las Antillas Mayores. Un origen sudamericano es obvio para las especies que no tienen parientes congénéricos en las Antillas Menores, e.g. *C. chalcopis*, *Leptodactylus fallax*, *L. wagneri*. Dentro de las especies de *Eleutherodactylus*, los taxa del noreste del Caribe conforman un grupo monofilético dentro del grupo *E. auriculatus*. La topología de las relaciones es ((*E. barlagnei*, *E. pinchoni*) ((*E. amplinympha*, *E. martinicensis*) *E. johnstonei*)). Las especies del sudeste del Caribe pueden o no formar un grupo monofilético, pero *E. euphronides* y *E. shrevei* son grupos hermanos. La topología de este grupo es (*E. urichi* (*E. terraebolivaris* (*E. euphronides*, *E. shrevei*))). De esta manera, el Caribe Este forma una unión biogeográfica entre las grandes radiaciones de *Eleutherodactylus* en América del Sur y las Antillas Mayores; *Eleutherodactylus* es la única verdadera rana circun-Caribea. Más aun, evidencia histórica muestra que la amplia distribución de *E. johnstonei* en el Caribe es resultado directo de la introducción accidental por el hombre durante los pasados tres siglos.

Translated by Victor Hugo Reynoso

ZUSAMMENFASSUNG

Diese Studie beschreibt die Systematik und Biogeographie von Fröschen der Ostkaribik, einer biogeographischen Provinz bestehend aus den Kleinen Antillen, Trinidad, und Tobago. Ich untersuchte eine gründliche Sammlung ostkaribischen Materials mittels morphometrischer, osteologischer, und biochemischer Methodik. Zwei bisher unbekannte Arten wurden entdeckt: *Colostethus chalcopis* sp. nov. auf Martinique und *Eleutherodactylus amplinympha* sp. nov. auf Dominica. Eine taxonomische Untersuchung von *E. urichi* zeigte, daß bis zu diesem Zeitpunkt als Unterarten behandelten Populationen tatsächlich die Spezies *E. euphronides* auf Grenada und *E. shrevei* auf St. Vincent sind. Sowohl aufgrund ihrer Verbreitung als auch mittels der Datenanalyse können ostkaribische Frösche in zwei Kategorien unterteilt werden: Arten mit Ursprung in Südamerika oder auf den Großen Antillen. Ein südamerikanischer Ursprung ist offensichtlich bei Arten, die keine verwandten Gattungsglieder auf den Großen Antillen haben, z. B. *Colostethus chalcopis*, *Leptodactylus fallax*, oder *L. wagneri*. Die *Eleutherodactylus*-Spezies der nördlichen Ostkaribik bilden eine monophyletische Gruppe in der *E. auriculatus* Artenserie mit der Verwandtschaftstopologie ((*E. barlagnei*, *E. pinchoni*) ((*E. amplinympha*, *E. martinicensis*) *E. johnstonei*)). Für die Arten der südlichen Ostkaribik konnte nicht bestimmt werden, ob sie monophyletisch verwandt sind; sicher ist jedoch, daß *E. euphronides* und *E. shrevei* eine Schwestergruppe bilden. Die Verwandtschaftstopologie für diese Spezies ist (*E. urichi* (*E. terraebolivaris* (*E. euphronides*, *E. shrevei*))). Die Ostkaribik ist also eine biogeographische Verbindung der Artenvielfalt Südamerikas und der Großen Antillen. *Eleutherodactylus* ist die einzige Froschgattung, die rund um das Karibische Meer angesiedelt ist. Außerdem konnte ich feststellen, daß wenigstens *E. johnstonei* durch menschliche Unachtsamkeit in den letzten dreihundert Jahren in mehrere neue, weit verbreitete Karibik-Lokalitäten eingeführt worden ist.

PREFACE

The study presented in this thesis is the first to use an interdisciplinary array of techniques to elucidate taxonomy, systematics, and biogeography of Eastern Caribbean anurans. It makes the following original contributions to our knowledge of these animals:

(1) *Eleutherodactylus urichi* (*sensu novo*) is a species indigenous only to Trinidad and Tobago. Frogs on Grenada and St. Vincent previously thought to be subspecies of *E. urichi* are recognized as the species *E. euphronides combinatio nova* and *E. shrevei comb. nov.*, respectively. All records of *E. urichi* from the South American mainland are due to misidentification.

(2) *Colostethus chalcopis* is described as a new species from Martinique, French Antilles. It is the only frog of the family Dendrobatidae endemic to an oceanic island. Its tadpoles are endotrophic and of unusual morphology, suggesting that heterochronic alterations of development may contribute to the phenotypes of anuran larvae.

(3) *Eleutherodactylus amplinympha* is recognized as a new species from Dominica. It is the sister taxon of *E. martinicensis*. The two species are most easily differentiated by vocalizations and by the presence of large females (SVL up to 50 mm) in *E. amplinympha*. Several diagnostic allozyme characters are identified. The species is most abundant at higher altitudes (> 500 m).

(4) Colonization of the Eastern Caribbean by frogs occurred from both northern South America and the Greater Antilles. *Eleutherodactylus euphronides*, *E. shrevei*, *E. terraebolivaris*, and *E. urichi* are of South American ancestry, while *E.*

amplinympha, *E. barlagnei*, *E. johnstonei*, *E. martinicensis*, and *E. pinchoni* are of Greater Antillean ancestry and form a monophyletic group within the *E. auriculatus* species group. Among these species, *E. amplinympha* and *E. martinicensis*, *E. barlagnei* and *E. pinchoni*, and *E. euphronides* and *E. shrevei* are sister taxa. At least three of the southern Eastern Caribbean *Eleutherodactylus* (*E. euphronides*, *E. shrevei*, *E. terraebolivaris*) have a close affinity with the South American *E. fitzingeri* group. The distribution of at least two species, *E. johnstonei* and *E. martinicensis*, has been influenced over the past three centuries by the activities of human settlers and traders.

(5) Although Eastern Caribbean *Eleutherodactylus* display four distinctive ecological life styles, their morphometric characteristics are relatively homogeneous. The inference from morphometric data indicates that the occurrence of morphological diversification may occur subsequent, or at least secondarily, to adaptive radiation.

Several chapters of this thesis have been submitted for publication as co-authored manuscripts. Each paper individually acknowledges the assistance of those who contributed their time, expertise, or materials. Each co-authored chapter was conceived and written by me alone. Co-authors' contributions were limited to editorial comments and parts of the technical descriptions in Chapters 3 and 4. The following statement is a mandatory addition to theses including co-authored papers.

"Candidates have the option, subject to the approval of their Department, of including, as part of their thesis, copies of the text of a paper(s) submitted for publication, or the clearly-duplicated text of a published paper(s), provided that these copies are bound as an integral part of the thesis. If this option is chosen, connecting texts, providing logical bridges between the different papers, are mandatory.

"The thesis must still conform to all other requirements of the "Guidelines Concerning Thesis Preparation" and should be in a literary form that is more than a mere collection of manuscripts published or to be published. The thesis must include, as separate chapters or sections: (1) a Table of Contents, (2) a general abstract in English and French, (3) an introduction which clearly states the rationale and objectives of the study, (4) a comprehensive general review of the background literature to the subject of the thesis, when this review is appropriate, and (5) a final overall conclusion and/or summary.

"Additional material (procedural and design data, as well as descriptions of equipment used) must be provided where appropriate and in sufficient detail (eg. in appendices) to allow a clear and precise judgment to be made of the importance and originality of the research reported in the thesis.

"In the case of manuscripts co-authored by the candidate and others, the candidate is required to make an explicit statement in the thesis of who contributed to such work and to what extent; supervisors must attest to the accuracy of such claims at the Ph.D. Oral Defense. Since the task of the examiners is made more difficult in these cases, it is in the candidate's interest to make perfectly clear the responsibilities of the different authors of co-authored papers."

ACKNOWLEDGMENTS

Although each chapter in this thesis contains its own particular acknowledgments, there are some that must be reiterated because the importance of some people has gone well beyond any single paper, or even the thesis as a whole. After all, over five odd years, seven field trips, and countless research adventures, there is much to be thankful for.

My time at the Redpath Museum has influenced me greatly and it has profoundly changed me. I have become attached to my research. Intellectual pursuit is exciting, and because learning never ceases in this business of academia, each new day can bring strings of new impressions, punctuated periodically by the achievement of a satisfying solution to one of many mystifying problems. I have also become very attached to frogs. So, first and foremost, I must acknowledge my debt to the animals I studied. May the understanding of the natural environment which I have gained through my specimens always let me keep in focus the responsibility we researchers have towards our study organisms. Finally, I have also grown attached to the Caribbean and its friendly populace. The spontaneous kindness which I so often encountered on my trips has been very humbling for one used to the rashness of our "progressive Western Civilization."

In writing this, I approach a threshold: the transition from student to academic. There is no one who has contributed more to my reaching this stage than my supervisor Dr. David M. Green. Over the years, David managed not only to tolerate me, the easily distracted, unfocused adolescent who liked to write in convoluted sentences (and still does!), but also helped transform me into someone progressing on the road to becoming a serious scientist. For that I respect him greatly and thank him profoundly. But David went beyond the call of professorial duty in serving as a personal confidant on many

occasions, and he periodically rebuilt my confidence when my spirit was down. I hope he will continue in that capacity far beyond this degree.

The members of my supervisory committee, Drs. Graham Bell, Derek Roff, and Kurt Sittmann, managed to keep me on my toes and prepare me for the worst. To them, and to others who contributed through discussions, in particular Drs. Robert Carroll, Donald Kramer, Robert Peters, Joe Rasmussen, and Henry Reiswig heartfelt thanks for jarring questions at appropriate times and for support throughout my experience at McGill. Kathy MacFarlane, Susan Gregus, and Kathryn Peterson were instrumental in keeping me administrated and financed when I became delinquent in one way or other; may your worst troubles be behind you! For supplying the most obscure information and the most elusive references on the facts of frogdom, heartfelt thanks to the staff at McGill's Blacker-Wood Library, in particular to Eleanor MacLean and Anne Habbick, with most special kudos to the queen of inter-library loans, Abena Mattocks.

Several of the manuscripts which make up this thesis have or will be submitted for publication in co-authorship with experts in the field, and I have frequently picked their brains when I reached the end of my tether. Through the experience of reading manuscripts and discussing approaches to anuran systematics, many have become friends. A very special thank you for their continued enthusiasm and patience to Ronn Altig, Luis Coloma, Bill Duellman, Linda Ford, Dave Hardy, John Simmons, and Linda Trueb. Here's to future collaborations!

This thesis owes a lot to the decades of work by Albert Schwartz, whose dedication to the West Indian herpetofauna has profoundly impressed me. His passing nearly a year ago left me in a void, as his commentaries on two of these chapters provided the type of checks and balances that could only come from someone as intimately familiar with these frogs on these islands as he. I am sad to have missed out on meeting him and talking shop.

Throughout my McGill years, I have been fortunate in living among fun and caring friends. For variously sharing insights into lab work, discussing topics too numerous to mention, having an open ear in times of need, visiting the hellish heat of the Redpath dungeon countless times, eliciting new and inspiring obscenities, I thank Mike Caldwell, Christèle du Souich, Pierre-Yves Gagnier, Courtney George, Heather Gray, Diane Harries, Rob Holmes, Les Lowcock, Jan MacDonald, Gary Mann, Rob Rishikof, and Tim Sharbel. A very special thanks to Christine Dwyer, whose support and care during the hectic months immediately preceding thesis submission made life so much more bearable.

Finally, I extend my deepest gratitude to my family, Caroline Blaß, Christopher Blaß, Constantin Blaß, Edith Blaß, Heinrich-Otto Kaiser, Anita von Stösser, and Karl von Stösser, whose support over the years never failed despite the ocean between us.

General Introduction

Previous work on the herpetofauna of the Lesser Antilles, Trinidad, and Tobago has centered on α -taxonomy, comparative morphology, and the publication of species lists (Barbour, 1914, 1916, 1930, 1935, 1937; Hardy, 1982; Kenny, 1969; Schwartz, 1967; Schwartz and Henderson, 1985, 1991; Schwartz and Thomas, 1975; Schwartz et al., 1978). Only rarely have attempts been made to investigate the relationships of taxa in this region or their biogeography either from a biochemical (Hardy, 1985; Hedges, 1989a) or biogeographical (Hardy, 1982; Hardy and Harris, 1979; Lescure, 1979a, 1983, 1987) viewpoint. In their comprehensive list of West Indian amphibians and reptiles (exclusive of Trinidad and Tobago), Schwartz and Henderson (1991:2) remarked on the cyclic nature of taxonomic work in the West Indies, suggesting that even as much work proceeded in the late 1980s, complete understanding of the herpetofauna of this diverse region was still elusive. Indeed, the late 1980s have seen the description of over 30 new amphibians and reptiles (Schwartz and Henderson, 1991), and discoveries continue. These discoveries have been facilitated by the development of tourism on each island, paralleled by the construction of better access roads and the manufacture of better maps. For the small islands with which this study is concerned, these developments hold especially true; logistics now permitted a new, more comprehensive investigation of systematic and biogeographic relationships of anurans on these islands.

This study was originally conceived as an investigation into population genetics of island *Eleutherodactylus* using biochemical means (see Weir, 1990), its purpose to determine how variable a small radiation of this genetically polymorphic genus (e.g., Hedges, 1989a, b; Miyamoto, 1983, 1984) was, and if the effect of isolation on islands might influence such variability in accordance with available theories (e.g., MacArthur and Wilson, 1967). An initial field trip to Barbados, Grenada, St. Lucia, and St. Vincent revealed, however, that any number of small

demes may have become isolated through the rugged, volcanically active topography on some islands, and that a more comprehensive survey was necessary to sample the variation I wanted to explore. As this secondary survey progressed, I became aware of some of the limitations imposed by the inadequate systematic and biogeographic information available to me. How could I estimate interspecific, let alone intraspecific variation without reliable information about species diversity or dispersal patterns? Thus, this study changed emphasis and turned towards systematic and biogeographic relationships in the hope of providing base line information on species diversity and dispersal patterns. With this information, studies of population genetics could be pursued later.

The major taxonomic works on the frog fauna of the Lesser Antilles are those by Schwartz (1967, 1969) on species of *Eleutherodactylus* and by Lescure (1979b) on *Leptodactylus fallax*. The most important biogeographic comments related to the diversity and introduction of small vertebrates into the region were made by Lescure (1979a, 1983, 1987). Several other, less encompassing publications have continually added to that information (e.g., Hardy, 1985; Hardy and Harris, 1979). The major findings of the thorough evaluation done by Schwartz (1967, 1969) included the description of *E. pinchoni* and two subspecies of *E. urichi*, and placement of all of these taxa into the Greater Antilles-based *E. auriculatus* species group. Lescure (1979a, 1983, 1987) noted the stepwise reduction of faunal diversity between the South American mainland, Trinidad and Tobago, and again between Tobago and the Lesser Antilles, while recognizing that single-island endemism gained in relative importance to faunal composition. His suggestions also included some possible dispersal mechanisms between South America and the Lesser Antilles. However, his views were incongruent for *Eleutherodactylus*: whereas Schwartz's (1969)

assessment placed all species into a Greater Antillean context, Lescure (1987) favored a scenario including dispersal from South America.

The most comprehensive works on the anurans of Trinidad and Tobago, respectively, are those by Kenny (1969) and Hardy (1982). It is evident from the fauna described for these islands that a strong influx of South American species has helped define the present-day species composition. However, neither author considered possible faunal relationships between South America, Trinidad, Tobago, and the Lesser Antilles.

For the purposes of this study, I include in what I term the "Eastern Caribbean" parts of the Lesser Antilles (*sensu lato*) plus Trinidad and Tobago. Because the terminology of these former British, Dutch, and French colonies has fluctuated historically, it is necessary to clarify which islands are now included in the region termed "Lesser Antilles." Following Schwartz (1967) and Schwartz and Henderson (1991), my nomenclature defines the Lesser Antilles as those islands forming a volcanic arc at the eastern extreme of the Caribbean Basin, extending from the islands directly east of the Anegada Passage (Sombbrero and Anguilla) to Grenada and Barbados in the south (Fig. 1).

The reason for creating a more inclusive term by including Trinidad and Tobago in a new Eastern Caribbean unit lies not with paleogeology or tectonics but with geography and biogeography. The Lesser Antilles are disconnected from Puerto Rico and the Virgin Islands by one of the greatest sill depths in the Caribbean Sea (1900 m; Donnelly, 1989); the Lesser Antillean island arc has thus traditionally been considered an entity separate from the Greater Antilles (see Williams, 1989). Trinidad and Tobago, on the other hand are continental-shelf islands which at some point in their history were connected to each other and to northern South America (Hardy, 1982; see Perfit and Williams, 1989), thus strictly forming part of the South

American landmass. However, these two islands and the southern Lesser Antilles lie in the path of effluence from the Orinoco River in Venezuela. Fresh water in the surface layer is transported by currents from the Atlantic Ocean into the Caribbean Sea, enveloping island coasts; this phenomenon becomes particularly noticeable during the heavy annual fresh water expulsion in the rainy season. Furthermore, prevalent ocean currents, wind directions, and hurricane paths are generally headed due northwest from the South American Atlantic coast into the Caribbean Sea. Thus, Trinidad, Tobago, and the southern Lesser Antilles may be prone to receiving organisms periodically by rafting dispersal from South America via Orinoco flotsam or hurricane-uprooted debris, and should thus not be considered independently in questions of biogeography. My more inclusive approach is therefore conservative, and I hoped to be able to recognize relationships which the older, geographically more concentrated studies may have missed by being too exclusive.

My survey methodology is an outgrowth of the initial population genetic approach and my collection includes many localities which have never before been sampled. My choice of localities, aided by improvements in maps and roads over the past three decades, was island-wide in each case, incorporating searches at all prominent topographical features as well as at geographic extremes of each island, to ensure representation of possibly distinct peripheral isolates. Other important areas chosen for sampling were habitats near main harbours to seek potentially recent frog arrivals. The decision to return to Montréal with live frogs had been made in advance to optimize scientific use for each specimen taken. I also attempted to ease the pressure on anuran fauna caused by my intrusion and restricted my collection to between 10 and 20 specimens per locality, a number generally considered sufficient for both morphological and biochemical analyses.

After the change from questions of population genetics to those of systematics and biogeography, the primary foci of this investigation became to determine (1) how many species of frogs are extant in the Lesser Antilles; (2) how these species reached their respective islands; and (3) whether Eastern Caribbean *Eleutherodactylus* are of Greater Antillean or South American ancestry, or if both origins are represented. I had no reason to expect additions to the fauna, and I thought that the finite nature of islands, particularly those crowded perennially by hordes of tourists, would make this project straightforward. I was confident that in the time given to complete my doctoral degree I could answer all the above questions and remove any uncertainties about systematics and biogeography of Eastern Caribbean frogs. I did not anticipate nature's power to confuse and confound; instead of clearing up once and for all, my research raised new questions as more information became available. Although much of what I set out to do was accomplished, Schwartz and Henderson's (1991) "Age of Discovery" is still upon us in the Eastern Caribbean.

LITERATURE CITED

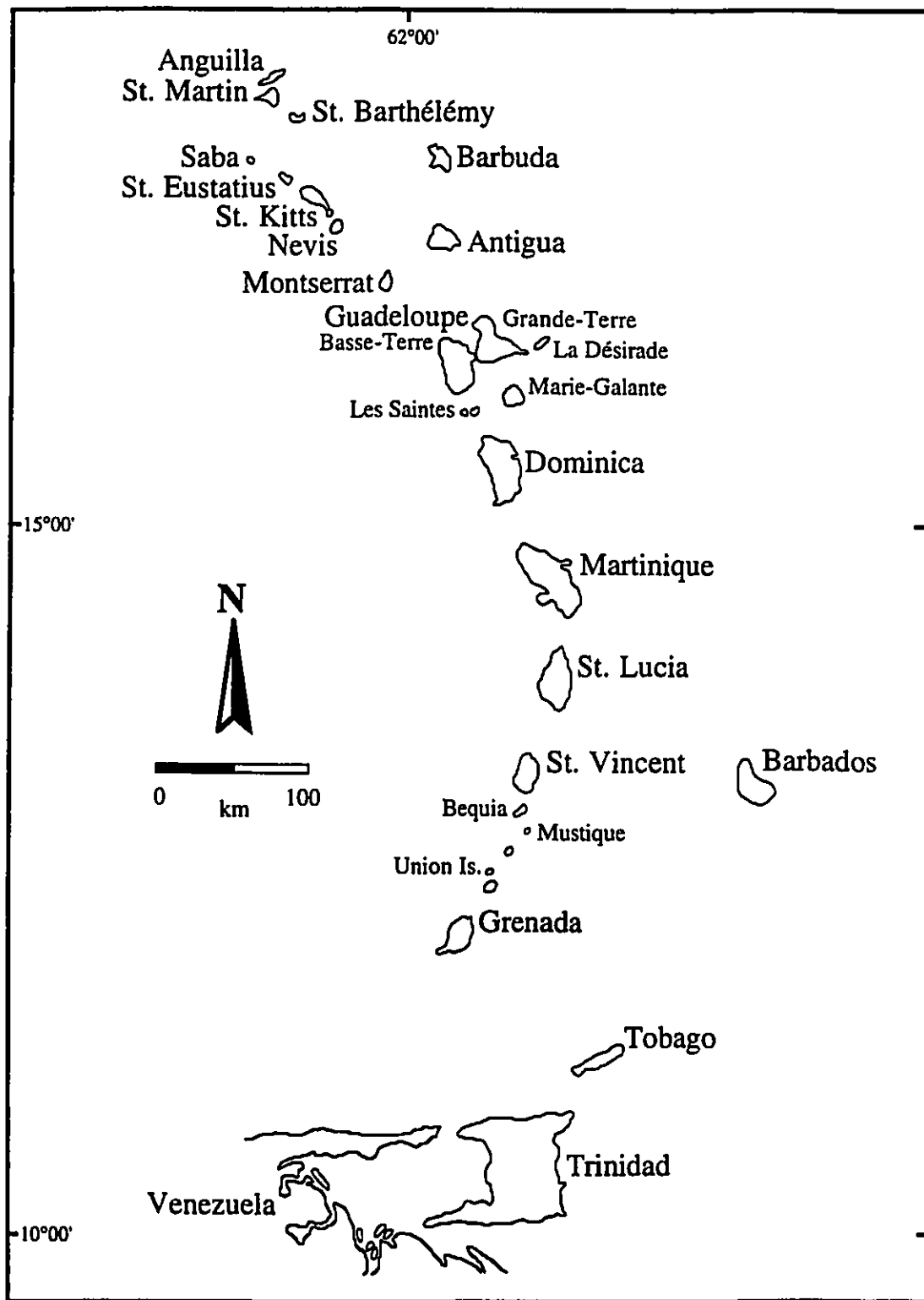
- BARBOUR, T. 1914. A contribution to the zoögeography of the West Indies, with especial reference to amphibians and reptiles. Mem. Mus. Comp. Zool. 44:209-359.
- _____. 1916. Amphibians and reptiles of the West Indies. Zool. Jahrb. Jena (4), Suppl. 11:437-442.
- _____. 1930. A list of Antillean reptiles and amphibians. Zoologica 11:61-116.
- _____. 1935. A second list of Antillean reptiles and amphibians. Zoologica 19:77-141.

- _____. 1937. Third list of Antillean reptiles and amphibians. Bull. Mus. Comp. Zool. 82:77-166.
- DONNELLY, T. W. 1989. History of marine barriers and terrestrial connections: Caribbean paleogeographic inference from pelagic sediment analysis. Pp. 103-118. In: C. A. Woods (Ed.). Biogeography of the West Indies: Past, Present, and Future. Sandhill Crane Press, Gainesville, Florida.
- HARDY, J. D., JR. 1982. Biogeography of Tobago, West Indies, with special reference to amphibians and reptiles: a review. Bull. Maryland Herpetol. Soc. 18:37-142.
- _____. 1985. Frog mountain: preliminary comments on the genus *Eleutherodactylus* on the island of Guadeloupe, West Indies. Bull. Maryl. Herpetol. Soc. 21:27-33.
- HARDY, J. D., JR., AND H. S. HARRIS. 1979. Occurrence of the West Indian frog, *Eleutherodactylus johnstonei*, in South America and on the island of Curaçao. Bull. Maryland Herpetol. Soc. 15:124-133.
- HEDGES, S. B. 1989a. Evolution and biogeography of West Indian frogs of the genus *Eleutherodactylus*: slow-evolving loci and the major groups. Pp. 305-370. In: C. A. Woods (Ed.). Biogeography of the West Indies: Past, Present, and Future. Sandhill Crane Press, Gainesville, Florida.
- _____. 1989b. An island radiation: allozyme evolution in Jamaican frogs of the genus *Eleutherodactylus* (Leptodactylidae). Carib. J. Sci. 25:123-147.
- KENNY, J. S. 1969. The Amphibia of Trinidad. Stud. Fauna Curaçao Carib. Isl. 29:1-78.
- LESCURE, J. 1979. Singularité et fragilité de la faune en vertébrés des Petites Antilles. C. R. Soc. Biogéogr. 482:93-109.

- _____. 1979b. Étude taxinomique et éco-éthologique d'un amphibien des petites Antilles: *Leptodactylus fallax* Müller, 1926 (Leptodactylidae). Bull. Mus. Natl. Hist. Nat., sect. A, Zool. Biol. Ecol. Anim., 4^e sér., 1:757-774.
- _____. 1983. Introductions passives et actives de reptiles et d'amphibiens dans les Antilles et les Guyanes. C. R. Soc. Biogéogr. 59:59-70.
- _____. 1987. Le peuplement en reptiles et amphibiens des Petites Antilles. Bull. Soc. Zool. France 112:327-342.
- MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Monogr. Pop. Biol. (1):1-203.
- MIYAMOTO, M. M. 1983. Frogs of the *Eleutherodactylus rugulosus* group: a cladistic study of allozyme, morphological and karyological data. Syst. Zool. 32:109-124.
- _____. 1984. Central American frogs allied to *Eleutherodactylus cruentus*: allozyme and morphological data. J. Herpetol. 18:256-263.
- PERFIT, M. R., AND E. E. WILLIAMS. 1989. Geological constraints and biological retrodictions in the evolution of the Caribbean Sea and its islands. Pp. 47-102. In: C. A. Woods (Ed.). Biogeography of the West Indies: Past, Present, and Future. Sandhill Crane Press, Gainesville, Florida.
- SCHWARTZ, A. 1967. Frogs of the genus *Eleutherodactylus* in the Lesser Antilles. Stud. Fauna Curaçao Carib. Isl. 24:1-62.
- _____. 1969. The Antillean *Eleutherodactylus* of the *auriculatus* group. Stud. Fauna Curaçao Carib. Isl. 30:99-115.
- SCHWARTZ, A., AND R. W. HENDERSON. 1985. A Guide to the Identification of the Amphibians and Reptiles of the West Indies Exclusive of Hispaniola. Milwaukee Public Museum, Milwaukee, Wisconsin.

- _____. 1991. *Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History*. University of Florida Press, Gainesville, Florida.
- SCHWARTZ, A., AND R. THOMAS. 1975. A check-list of West Indian amphibians and reptiles. *Carnegie Mus. Nat. Hist. Spec. Publ.* (1):1-216.
- SCHWARTZ, A., 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.
- WEIR, B. S. 1990. Intraspecific differentiation. Pp. 373-410. *In*: D. M. Hillis and C. Moritz (Eds.). *Molecular Systematics*. Sinauer Associates, Sunderland, Massachusetts.
- WILLIAMS, E. E. 1989. Old problems and new opportunities in West Indian biogeography. Pp. 1-46. *In*: C. A. Woods (Ed.). *Biogeography of the West Indies: Past, Present, and Future*. Sandhill Crane Press, Gainesville, Florida.

FIGURE 1. The Eastern Caribbean, as defined for this study.



1

**The Trade-Mediated Introduction of *Eleutherodactylus martinicensis*
(Anura: Leptodactylidae) on Saint-Barthélemy, French Antilles, and Its
Implications for Lesser Antillean Biogeography**

Published as: Kaiser, H. 1992. The trade-mediated introduction of *Eleutherodactylus martinicensis* (Anura: Leptodactylidae) on St. Barthélemy, French Antilles, and its implications for Lesser Antillean biogeography. *Journal of Herpetology* 26:264–273.

PREAMBLE CHAPTER 1

Since the development of this thesis was greatly influenced by the discovery of new species and the continuing process of manuscript preparation and refinement, chapters are basically organized in the order in which they were conceived. Thus these chapters not only present data analyses, results, and answers to scientific questions, but show how the larger project evolved and progressed. The first chapter thus deals with the first discovery made in the course of this project.

During my second collecting trip, I discovered populations of frogs on the island of St-Barthélemy in the French Antilles. There had previously been no record of frogs despite visits to the island by A. Schwartz in the 1960s, and the three populations seemed associated exclusively with relatively recent tourist developments. For my assessment of the anuran biogeography it was necessary to know the taxonomic identity of these frogs, and, if possible, to determine their origin. When it became apparent that these frogs were not *Eleutherodactylus johnstonei*, the species occurring on all neighboring islands, but *E. martinicensis*, a species occurring only in the central Lesser Antilles over 200 km distant, I returned to St-Barthélemy to investigate the history of this apparently recent introduction. The addition of historical and political information not only for *E. martinicensis* and St-Barthélemy but for *E. johnstonei* and rest of the Lesser Antilles was revealing.

ABSTRACT

Three topographically isolated populations of whistling frogs were discovered on the island of St-Barthélemy in the French Antilles. These are the first amphibians recorded on this island, and a morphometric and electrophoretic investigation shows that all three populations are members of the highly variable species *Eleutherodactylus martinicensis* (Tschudi). The data suggest further that the frogs on St-Barthélemy are most similar to populations on Guadeloupe, a geographically distant but commercially close island. This discovery, in combination with historical evidence and recent records of sudden whistling frog activity in other commercially linked locations, suggests that trade-mediated human introductions may have been the single most important factor in creating the present distribution of *Eleutherodactylus* in the Lesser Antilles. In the particular case of St-Barthélemy, introduction has most likely occurred via material transports to construction sites near each of the three localities.

INTRODUCTION

The Lesser Antilles (Fig. 1) are a tectonically cohesive group of islands on the eastern edge of the Caribbean Plate. They originated as a volcanic arc during the Late Cretaceous (Donnelly, 1989; Perfit and Williams, 1989) and were uplifted to their present locations only after the Early Oligocene (Malfait and Dinkelman, 1972). These islands support a great variety of endemic species of plants and animals despite their small sizes and oceanic position (Guyer and Savage, 1986; Jones, 1989; Schwartz and Henderson, 1985, 1991; Thomas, 1989; Williams, 1969; Woods, 1989a). Due to this faunal complexity, biogeography and speciation patterns of many Lesser Antillean taxa are still unresolved topics of active debate (Williams, 1989; see Woods, 1989b). In

particular, questions persist over whether vicariance or dispersal origins are more likely for the fauna of these islands (Briggs, 1984; Rosen, 1975; Savage, 1982).

In the case of the Lesser Antilles, dispersal would appear to be the more likely mechanism, in view of their recent origin and the small distances between them (Williams, 1989). Yet accidental "stepping stone island" and "waif" dispersals (Williams, 1989:4) by mechanisms such as random rafting (Heatwole and Levins, 1972; MacFadden, 1980) or hurricane transport of debris (Williams, 1969), must be regarded as rare due to the sensitivity of amphibians to salt (Duellman and Trueb, 1986). Despite the possible influence of extinctions, *in situ* speciation, or vicariant events on the island biotas, human introductions cannot be overlooked because of the considerable documentation available for accidental and purposive introductions of whistling frogs (Censky, 1989; Dunn and Conant, 1937; Günther, 1895; Hardy and Harris, 1979; Hedges and Thomas, 1989; Ibáñez and Rand, 1990; Lazell and Sinclair, 1990). Trade-mediated introductions in particular should have been an especially important dispersal mechanism in the Lesser Antilles, considering the long history of mercantilistic trade in the region and the strict division of the islands into French and British spheres of influence (Hall, 1982).

The amphibian fauna on the Lesser Antilles has been described by various authors (e.g., Barbour, 1914; Cochran, 1938; Cope, 1870; Schwartz, 1967). The whistling frogs, genus *Eleutherodactylus*, are the most diverse, most widely distributed, and most easily confused amphibians in the Lesser Antilles. Of the five species reported in the literature (Schwartz, 1967), *E. martinicensis* and *E. johnstonei* are the most widely distributed. These two species are generalists ecologically (Schwartz, 1967) and are widespread on the islands where they occur. The known distribution of *E. martinicensis* (Schwartz, 1967; Schwartz and Henderson, 1985, 1991; Schwartz and Thomas, 1975), is limited to the geographic center of the Lesser

Antilles (Fig. 1), suggesting that the species may have arisen in that area. The distribution of *E. johnstonei*, however, is discontinuous and enigmatic. Though present on Martinique, its range historically excluded the Guadeloupe archipelago and Dominica (Schwartz, 1967). It was only recently found on Guadeloupe (Hedges and Thomas, 1989; Schwartz et al., 1978).

Saint-Barthélemy, locally called "St-Barths," is a small, rugged, non-volcanic island of 21 km² surface area at the northern end of the Lesser Antilles (Fig. 1, inset). It lies on the Anguilla Bank with St-Martin and Anguilla. Politically and economically, though, it is part of the French Antilles, and lies 220 km to the north of the largest French Antillean island, Guadeloupe. Schwartz (1967:20) commented that the island "seems suitable ecologically" for amphibians, but that the "stillness of the nights on St. Barthélemy is startling to anyone who is accustomed to hearing tropical frog choruses."

During the course of a comprehensive systematic study of the Lesser Antillean *Eleutherodactylus* I visited St-Barths and discovered three frog populations of unknown origin. To determine the specific status of these populations, and to trace their probable origin, morphological and biochemical data were used for identification. The existence of *Eleutherodactylus martinicensis* and not *E. johnstonei* on St-Barths, provides evidence that accidental introductions of frogs during inter-island trade are important factors behind the present-day distribution of whistling frogs in the Lesser Antilles.

MATERIALS AND METHODS

Collections were made on St-Barths on 11 May, 1989, 3 January and 8–9 June, 1990, at Hotel Jean Bart in St. Jean, Hotel La Normandie in Lorient, and Anse aux Flamandes (Fig.1, inset). The rest of the island was surveyed by road for calling

frogs. A total of 25 specimens was captured and taken alive to the lab in Montréal. Tissue samples (liver, heart, kidney, muscle, spleen) were homogenized, centrifuged, and kept frozen at -80°C. Horizontal starch gel electrophoresis was used to obtain allozyme data (see Murphy et al. [1990] for a comprehensive description). Table 1 lists the protein loci and the electrophoretic conditions used. Other specimens used in this study were collected over a 2-yr period on all Lesser Antillean islands and treated as above.

Twenty length measurements (Table 2) were taken from 492 specimens (264 females, 228 males) to the nearest 0.1 mm using a dissecting microscope with digitizer attachment (Numonics 2200 digitizing tablet) and Jandel Scientific Sigma Scan (version 3.10) software. Principal components analysis (PCA) was performed using a variance-correlation matrix with Systat 5.1 on a Macintosh LC (4 RAM memory). Sound recordings were made on Grenada (1–2 August 1990), Guadeloupe (7–9 January 1990, 10–11 June 1990, 23–24 August 1990), Martinique (4–6 January 1990, 19–20 August 1990), Montserrat (25–26 August 1990), and St-Barths (3 January 1990, 8–9 June 1990) using a SONY professional walkman WM-D3. Audiospectrograms were made with a Kay Elemetrics Corp. digital sonagraph 7800.

The rationale for using such an array of comparative techniques lies with the great variation observed in the *Eleutherodactylus* populations studied. Previous morphological work by Schwartz (1967) conflicts in many variables with my preliminary data and is inadequate for aligning the St-Barths populations with either *E. johnstonei* or *E. martinicensis*. Consequently, it was necessary to employ PCA to obtain differences for all the measured variables combined, rather than for a few separate variables. Furthermore, to avoid problems with sexual dimorphism, artifacts of sample size, and to pinpoint the origin of the St-Barths populations, electrophoretic data were used to support the morphometric results. A second character independent of

sample size is provided by the vocalizations, which provide reliable identification for allopatric frog populations (Duellman and Trueb, 1986; Narins and Smith, 1986).

RESULTS

Habitat of frogs.—The localities immediately surrounding the sampling sites (Fig. 1, inset) are so far the only locations where whistling frogs are established on St-Barths. They are typical habitat for Lesser Antillean *Eleutherodactylus*. The smooth leaves of bromeliads, agava-types, and broad-leaved grasses provide meter-high calling perches for territorial males. A thick, humid layer of decaying plant material (typically old banana or palm foliage, but in the absence of plantation activity on St-Barths, the hotels' compost and windfalls in the vicinity) provides feeding grounds rich in insects and sites with high residual moisture well suited for terrestrially developing eggs (Townsend, 1989). Temperature varies only slightly during the year, averaging around 28°C during the day, and 24°C at night. Rainfall is sporadic, with more rain falling between August and December. Since there is no tropical forest, St-Barths is generally much drier than the volcanic islands to the south, and lush habitat suitable for amphibians is not abundant. Although there are many patches of the "ecologically suitable" vegetation *sensu* Schwartz (1967) on St-Barths, it has few locations where a regular water supply is ensured other than man-made irrigation systems such as those near hotels and other human habitations. This fact may prevent a continuous distribution for the frog population.

Introduction of frogs to St-Barths.—Information obtained from older local residents suggests that the frogs were not present at locality 1 (Fig. 1, inset) before the Jean Bart Hotel was built, and perhaps not when Schwartz surveyed the island in the

1960s. Consequently, the frogs have not yet entered into the local folklore as they have on other islands, an indication of their limited distribution and recent arrival. The frogs are elusive during daylight hours, and the local human populace was almost completely unaware that the frogs are responsible for some of the nightly noises. As on other islands, the frogs are known only as "crickets" by their sounds at night.

Vocalizations and morphology.—Audiospectrograms of *Eleutherodactylus* from St-Barths and of *E. martinicensis* from Guadeloupe and Martinique are shown in Figs. 2A, 2B and 2C, respectively. These two-note calls are almost identical in all characteristic features. Rise time, timing, frequency and intensity of both notes in the three calls shown match very well, with the first note at 2000 Hz, and the second note originating at 3200 Hz and increasing to 4200 Hz. The slight variation in signal strength is due to the variable distance from microphone to frog. Comparing these calls with those of *E. johnstonei* from Grenada and Montserrat (Fig. 2D, 2E, respectively), differences exist not only in timing, but also in frequency. *Eleutherodactylus johnstonei* has a shorter call, with a very rapid rise in the second note, and the maximum frequency barely reaches 4000 Hz.

The coloration and dorsal pattern of *Eleutherodactylus* on St-Barths are distinct from those found on neighboring islands, but identical, though less diverse, to those on Martinique and Guadeloupe. The ground color in life of *Eleutherodactylus* on St-Barths is a dark grayish brown with a silvery hue, easily distinguishable from the dull earthy brown color of *E. johnstonei*. Furthermore, dorsal patterns of *E. martinicensis* are generally less polymorphic than those of *E. johnstonei*. Dorsal patterns in *E. martinicensis* are formed of only two components, a single chevron and a thin middorsal line, whereas *E. johnstonei* has eight pattern components which assort to form at least fifteen dorsal patterns (unpubl. data).

Morphometrics.—Principal component (PC) 1 accounts for 37% of the total variance observed, with PC2–5 accounting for another 34%. Component loadings for PC1 are all positive, indicating that this component is a size index. The greatest loadings of PC1 are those determined from limb length, suggesting that in comparing these species, limb proportions are of great significance. The loadings of PC2–5 are indicative of shape, and the greatest loadings are those determined from head measurements. Fig. 3 shows a plot of PC1 against PC2, with centroids indicating the various test populations. The *Eleutherodactylus johnstonei* centroids overlap with each other, as do the St-Barths and Guadeloupe centroids. The Martinique centroid overlaps with the *E. johnstonei* populations and not with the *E. martinicensis* populations. The main conclusions from PCA are supported if sexes are analyzed separately as well.

Allozymes.—Among the thirteen investigated polymorphic loci, ten have no shared alleles between the St-Barths frogs and populations of *Eleutherodactylus johnstonei* (ADH-1, CE-1, CE-2, DDH, FBA, GP-1, MDH-1, PGDH, PEP [LGG], PEP [LLL]; Table 3), and therefore constitute fixed differences. Between St-Barths frogs and *E. martinicensis*, all loci have shared alleles, and there is only a single allele (MDH-1^a) on St-Barths that is not present in *E. martinicensis* populations on Guadeloupe or Martinique (Table 3). In two of the loci which are not fixed different between *E. johnstonei* and St-Barths populations (AAT-2, CA-2; Table 3), there are additional alleles present in *E. johnstonei* (AAT-2^d, CA-2^z, CA-2^a; Table 3). Allelic polymorphism is slightly greater in *E. johnstonei* (22 alleles present, compared with 19 in *E. martinicensis*).

Species designation.—*Eleutherodactylus martinicensis* was described originally from Martinique as *Hylodes martinicensis* (Tschudi, 1838), although both taxonomy and origin of the type series were subsequently altered, ascribing the type to *E. martinicensis* and Guadeloupe (Frost, 1985; Schwartz, 1967). This species has frequently been confused with *E. johnstonei* (Schwartz, 1967), and the differences between preserved specimens of these species are frequently minimal.

The morphometric and allozyme data clearly show that the St-Barths populations are not *Eleutherodactylus johnstonei*. However, identity with *E. martinicensis* on Guadeloupe or Martinique cannot be demonstrated unequivocally with morphometric data. The problem lies with the position of the St-Barths centroid (Fig. 3) vis-à-vis those of *E. martinicensis* from Guadeloupe and Martinique. While the Martinique and Guadeloupe centroids differ significantly from each other only in size (PC1), the St-Barths centroid is displaced because of shape, as indicated by the values of PC2 (Fig. 3). A size difference may easily be an artifact of sampling, reflecting the lack of large specimens, but the differences in shape are of uncertain origin and may reflect subtle morphological differences between the populations I sampled on Guadeloupe and those from which the introduced specimens were taken. However, since there is partial overlap of the St-Barths and Guadeloupe centroids (Fig. 3), the notion of close relationship between populations from these two islands is supported. The overlap between the Martinique centroid with the *E. johnstonei* centroids (Fig. 3) and the minor external morphological differences show how difficult an assessment of morphological differences between these species is. These results notwithstanding, part of the conundrum of the morphometric data may be a product of tremendous variation in limb proportions of *E. martinicensis* and *E. johnstonei*, as indicated previously in the data tables and descriptions of Schwartz (1967). However, the St-

Barths populations can still be recognized as *E. martinicensis* based on the combined evidence from vocalizations and allozymes.

DISCUSSION

The colonization of the Lesser Antilles in the early seventeenth century and the establishment of the mercantilistic trade system by Britain and France had a devastating influence on the endemic biotas. Extensive deforestation took place to make way for commercial crops (Ragatz, 1971), thus reducing the habitat for endemic frogs to remote and topographically inaccessible areas. Introductions of a variety of "such foreign plants as are worthy of being encouraged" (Ellis, 1770) as well as livestock and other animal species were undertaken by governments and plantation owners. Most notorious among these are the introductions of rats (*Rattus* spp.), sugar cane (*Saccharum officinarum*) and the Indian mongoose (*Herpestes auropunctatus*; see Hoagland et al., 1989; West and Agnelli, 1989), resulting in the subsequent eradication of agoutis, iguanas, most snakes, and ground nesting birds (West and Agnelli, 1989; see Bacon 1978). Monoculture (especially of sugar, coffee, cotton, and cocoa) was established rapidly on many islands, and left little room for other agricultural production. Since it required large numbers of slaves to tend the fields, food shortages resulted (Hall, 1982). Regular imports of large amounts of vegetables and fruits from other islands became necessary (Hall, 1982; West and Agnelli, 1989), providing many opportunities for whistling frogs to be transferred to a new island with part of their habitat.

The political organization of the Lesser Antilles in the seventeenth and eighteenth centuries (Fig. 1) prevented trade between French and English colonies by the Navigation Acts, the Molasses Act, and the Sugar Act on the British side, and by

reciprocating legislation by the French (Hall, 1982; Mitchell, 1973). Both sides sought to protect not only their trade opportunities in Europe by antagonistic policies in the Caribbean, but also their religious, political, and social integrity (Fortune, 1984; Hall, 1982). The strict separation of trade spheres, in combination with frequent inter-island transport of fruits and vegetables (capable of carrying frogs), can neatly explain the present distribution of whistling frogs. Although direct proof for actual introductions during the era of mercantilism is unlikely to surface, it is a fact that the present ranges of *Eleutherodactylus johnstonei* and *E. martinicensis* in the Lesser Antilles match the former boundaries of colonial trade exactly. Where monoculture reduced native habitat significantly, forcing endemic frogs to retreat to montane forests, introduced generalist "weed species," such as *E. johnstonei* and *E. martinicensis*, could radiate unimpeded from their points of introduction, resulting in the observed occurrence of these frogs: ubiquitous presence in lowland agricultural areas and around their periphery, absent from native forests at higher altitudes.

Bayley (1950) and Schwartz (1967) give anecdotal support for introductions of *E. johnstonei* from St. Lucia (or St. Vincent) to Barbados (in 1879) and on to Grenada (in 1885). In support of these reported introductions, Schwartz (1967) quotes T. Barbour and W. H. Fielden and the fact that these islands used to be British colonies, but raises doubts about the introduction sequence based on the lack of concrete evidence. A description by Ligon (1657) of an unseen but "lively, and chirping" animal, most likely a frog (Marsh, 1983), furthers Schwartz's doubts. Ligon's observation was made near the time of initial settlement and "in the woods," so that these animals might indeed have been present on Barbados when the island was colonized. Some islands, such as the Grenadines, Arguilla, and St-Barths, were not plantation islands, and not in need of fruit and vegetable imports. For those islands,

only recent touristic developments provided enough trade to introduce whistling frog populations.

Anecdotal accounts or brief communications are also available to document a variety of introductions of *Eleutherodactylus* into Anguilla (Censky, 1989), Bequia (Lazell and Sinclair, 1990), Bermuda (Dunn and Conant, 1937), Caracas, Venezuela (Hardy and Harris, 1979), Cumaná, Venezuela (Hardy and Harris, 1979), Curaçao (Hardy and Harris, 1979), England (Günther, 1895), Guyana (Hardy and Harris, 1979), Jamaica (Dunn and Conant, 1937) and Panamá (Ibáñez and Rand, 1990). Whether they are purposive, as in Bermuda, Cumaná, Venezuela, or Curaçao, or accidental, such as a barely thwarted escape attempt by six *E. johnstonei* during research on Trinidad (Hardy and Harris, 1979), human introductions often provide the appropriate habitat for the animals on top of providing safe passage to the new location (Ibáñez and Rand, 1990).

Most recently, with the independence of many Caribbean islands and the formation of strong economic ties, especially among the Eastern Caribbean members of the British Commonwealth, inter-island trade has increased drastically, and some accidental introductions have already been reported. On Guadeloupe, *Eleutherodactylus johnstonei* is now known from both the Basse-Terre and Grande-Terre portions, but is still limited to two main traffic centers (R. I. Crombie, in litt.). Both these areas, near the port city of Basse-Terre and near Le Raizet International Airport (R. I. Crombie, in litt.), should be considered prime points of entry for stowaway frogs. R. I. Crombie (in litt.) also reports that *E. johnstonei* may have been present near the Canari River on Dominica right after Hurricane David devastated the island in 1979. He suggests that in the aftermath of the hurricane, frogs may have arrived with emergency supplies from a variety of islands. However, during my recent visits to Dominica, I never heard *E. johnstonei* in that area, and I think that the

introduction may have been unsuccessful. On St. Vincent and Grenada, I found native *Eleutherodactylus* almost perfectly parapatric to *E. johnstonei* along altitudinal boundaries, a situation similar to that of Guadeloupe populations of *E. martinicensis*, which are less populous in the higher altitude habitats occupied by the two native species, *E. barlagnei* and *E. pinchoni*. A common Caribbean species, *E. planirostris*, has now been documented from Grenada and some of the Grenadines (Crombie and Wynn, 1993; Hedges, pers. comm.).

With all these changes in species distribution through the agency of *Homo sapiens*, the discovery of three small anuran populations on St-Barths is interesting beyond the level of a mere geographic range extension. It seems clear that a recent introduction has occurred, probably since Schwartz surveyed St-Barths in the 1960s. Because St-Barths is surrounded by *Eleutherodactylus johnstonei* islands, it seems also clear that an introduction took place from a commercially linked French Antillean island, most likely Guadeloupe. The case of the St-Barths frogs serves as a good recent example to document the historical role of human-mitigated inter-island migration of whistling frogs, a factor that has not been appreciated to the extent it deserves.

ACKNOWLEDGMENTS

I am grateful to C. A. George, H. M. Gray, and H. H. Schwarten for field assistance, and to M. Chandler and T. F. Sharbel for laboratory help. Thanks to R. E. Lemon for the use of the sonagraph, and to D. J. Mountjoy for teaching me how to use the machine. H. M. Reiswig is gratefully acknowledged for setting up his digitizing apparatus for frog size and for instructing me on the pitfalls of the scan software. I very much appreciate the assistance of F. R. Cook and R. M. Rankin for making some of the DMG specimens available from the Canadian Museum of Nature. Discussions

with R. I. Crombie, D. A. Good, and D. M. Green provided some interesting new perspectives. M. W. Caldwell, D. M. Green, T. F. Sharbel, and C. W. Zeyl made valuable comments on the manuscript. This research was supported by grants from the Hans-Krüger-Stiftung and the Studienstiftung des Deutschen Volkes, Germany, and by an NSERC Canada operating grant to D. M. Green.

LITERATURE CITED

- BACON, P. R. 1978. Flora and Fauna of the Caribbean. Key Caribbean Publications, Port-of-Spain, Trinidad.
- BARBOUR, T. 1914. A contribution to the zoögeography of the West Indies, with especial reference to amphibians and reptiles. Mem. Mus. Comp. Zool. 44:209–359.
- BAYLEY, I. 1950. The whistling frogs of Barbados. J. Barbados Mus. Nat. Hist. Soc. 17:161–170.
- BRIGGS, J. C. 1984. Freshwater fishes and biogeography of Central America and the Antilles. Syst. Zool. 24:428–435.
- CENSKY, E. J. 1989. *Eleutherodactylus johnstonei* (Salientia: Leptodactylidae) from Anguilla, West Indies. Carib J. Sci. 25:229–231.
- CLAYTON, J. W., AND D. N. TRETIK. 1972. Amine citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Bd. Canada 29:1169–1172.
- COCHRAN, D. M. 1938. Reptiles and amphibians from the Lesser Antilles collected by Dr. S. T. Danforth. Proc. Biol. Soc. Washington 51:147–156.
- COPE, E. D. 1870. Seventh contribution to the herpetology of tropical America. Proc. Amer. Phil. Soc. II:147–169.

- CROMBIE, R. I., AND A. H. WYNN. 1993. *Eleutherodactylus planirostris*, a recently introduced frog on Grenada. Carib. J. Sci. *In press*.
- DONNELLY, T. W. 1989. History of marine barriers and terrestrial connections: Caribbean paleogeographic inference from pelagic sediment analysis. Pp. 103–118. *In*: C. A. Woods (Ed.). Biogeography of the West Indies: Past, Present, and Future. Sandhill Crane Press, Gainesville, Florida.
- DUELLMAN, W. E., AND L. TRUEB. 1986. The Biology of Amphibians. McGraw-Hill, New York, New York.
- DUNN, E. R., AND R. CONANT. 1937. The herpetological fauna of Bermuda. Herpetologica 1:78–80.
- ELLIS, J. 1770. Directions for Bringing Over Seeds and Plants, From the East Indies and Other Distant Countries, in a State of Vegetation: Together With a Catalogue of Such Foreign Plants as are Worthy of Being Encouraged in Our American Colonies. London.
- FORTUNE, S. A. 1984. Merchants and Jews: The Struggle for British West Indian Commerce, 1650–1750. University of Florida Press, Gainesville, Florida.
- FROST, D. R. 1985. Amphibian Species of the World. A Taxonomic and Geographical Reference. Allen Press, Inc., and The Association of Systematics Collections, Lawrence, Kansas.
- GÜNTHER, A. 1895. Introduction of a West Indian frog into the Royal Gardens, Kew. Nature 52:643.
- GUYER, C., AND J. M. SAVAGE. 1986. Cladistic relationships among anoles (Sauria: Iguanidae). Syst. Zool. 35:509–531.
- HALL, D. 1982. The Caribbean Experience: An Historical Survey 1450–1960. Heinemann Educational Books, London.

- HARDY, J. D., JR., AND H. S. HARRIS. 1979. Occurrence of the West Indian frog, *Eleutherodactylus johnstonei*, in South America and on the island of Curaçao. Bull. Maryland Herpetol. Soc. 15:124–133.
- HEATWOLE, H., AND R. LEVINS. 1972. Biogeography of the Puerto Rican bank: flotsam transport of terrestrial animals. Ecology 53:112–117.
- HEDGES, S. B., AND R. THOMAS. 1989. Supplement to West Indian amphibians and reptiles: a check-list. Milwaukee Publ. Mus. Contr. Biol. Geol. (77):1–11.
- HOAGLAND, D. B., G. R. HORST, AND C. W. KIRKPATRICK. 1989. Biogeography and population biology of the mongoose in the West Indies. Pp. 611–634. In: C. A. Woods (Ed.). Biogeography of the West Indies: Past, Present, and Future. Sandhill Crane Press, Gainesville, Florida.
- IBÁÑEZ, D. R., AND A. S. RAND. 1990. Geographic distribution: *Eleutherodactylus johnstonei*. Herpetol. Rev. 21:37.
- JONES, J. K., JR. 1989. Distribution and systematics of bats in the Lesser Antilles. Pp. 645–660. In: C. A. Woods (Ed.). Biogeography of the West Indies: Past, Present, and Future. Sandhill Crane Press, Gainesville, Florida.
- LAZELL, J., AND T. SINCLAIR. 1990. Geographic distribution: *Eleutherodactylus johnstonei*. Herpetol. Rev. 21:95.
- LIGON, R. 1657. A True and Exact History of the Island of Barbados. London.
- MACFADDEN, B. 1980. Rafting mammals or drifting islands: biogeography of the Greater Antillean insectivores *Nesophontes* and *Solenodon*. J. Biogeogr. 7:11–22.
- MALFAIT, B. T., AND M. G. DINKELMAN. 1972. Circum-Caribbean tectonic and igneous activity and the evolution of the Caribbean Plate. Geol. Soc. Am. Bull. 83:251–272.

- MARSH, R. E. 1983. Unquestionable evidence that the whistling frog of Barbados is indigenous. *J. Barbados Mus. Hist. Soc.* 50:68-71.
- MITCHELL, H. 1973. *Europe in the Caribbean: The Policies of Great Britain, France and the Netherlands Towards Their West Indian Territories.* Cooper Square Publ. Inc., New York.
- MURPHY, R. W., J. W. SITES, D. G. BUTH, AND C. H. HAUFLE. 1990. Proteins I: isozyme electrophoresis. Pp. 45-126. *In:* D. M. Hillis and C. Moritz (Eds.). *Molecular Systematics.* Sinauer Associates, Sunderland, Massachusetts.
- NARINS, P. M., AND D. D. HURLEY. 1982. The relationship between call intensity and function in the Puerto Rican Coqui (Anura: Leptodactylidae). *Herpetologica* 38:287-295.
- NARINS, P. M., AND S. L. SMITH. 1986. Clinal variation in anuran advertisement calls: basis for acoustic isolation? *Behav. Ecol. Sociobiol.* 19:135-141.
- NOMENCLATURE COMMITTEE OF THE INTERNATIONAL UNION OF BIOCHEMISTRY. 1984. *Enzyme Nomenclature 1984.* Academic Press, New York, NY.
- PERFIT, M. R., AND E. E. WILLIAMS. 1989. Geological constraints and biological retrodictions in the evolution of the Caribbean Sea and its islands. Pp. 47-102. *In:* C. A. Woods (Ed.). *Biogeography of the West Indies: Past, Present, and Future.* Sandhill Crane Press, Gainesville, Florida.
- PREGILL, G. K., D. W. STEADMAN, S. L. OLSON, AND F. V. GRADY. 1988. Late Holocene fossil vertebrates from Burma Quarry, Antigua, Lesser Antilles. *Smithson. Contr. Zool.* (463):1-27.
- RAGATZ, L. J. 1971. *The Fall of the Planter Class in the British Caribbean, 1763-1833.* Octagon Books, New York.

- ROSEN, D. E. 1975 [1976]. A vicariance model of Caribbean biogeography. *Syst. Zool.* 24:431–464.
- SAVAGE, J. M. 1982. The enigma of the Central American herpetofauna: dispersals or vicariance? *Ann. Miss. Bot. Garden* 69:464–457.
- SCHWARTZ, A. 1967. Frogs of the genus *Eleutherodactylus* in the Lesser Antilles. *Stud. Fauna Curaçao Carib. Isl.* 23:1–62.
- SCHWARTZ, A., AND R. W. HENDERSON. 1985. A Guide to the Identification of the Amphibians and Reptiles of the West Indies Exclusive of Hispaniola. Milwaukee Pub. Mus., Milwaukee, Wisconsin.
- _____. 1991. Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History. University of Florida Press, Gainesville, Florida.
- SCHWARTZ, A., AND R. THOMAS. 1975. A check-list of West Indian amphibians and reptiles. *Carnegie Mus. Nat. Hist. Spec. Publ.* (1):1–216.
- SCHWARTZ, A., 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.
- THOMAS, R. 1989. The relationships of Antillean *Typhlops* (Serpentes: Typhlopidae) and the description of three new Hispaniolan species. Pp. 409–432. *In*: C. A. Woods (Ed.). *Biogeography of the West Indies: Past, Present, and Future*. Sandhill Crane Press, Gainesville, Florida.
- TOWNSEND, D. S. 1989. The consequences of microhabitat choice for male reproductive success in a tropical frog (*Eleutherodactylus coqui*). *Herpetologica* 45:451–458.
- TSCHUDI, J. J. 1838. Classification der Batrachier, mit Berücksichtigung der Fossilien Thiere dieser Abteilung der Reptilien. Neuchatel, Switzerland.

- WEST, R. C., AND J. P. AGNELLI. 1989. Middle America: Its Lands and Peoples. Prentice Hall, Englewood Cliffs, New Jersey.
- WILLIAMS, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *Quart. Rev. Biol.* 44:345-389.
- _____. 1989. Old problems and new opportunities in West Indian biogeography. Pp. 1-46. *In*: C. A. Woods (Ed.). *Biogeography of the West Indies: Past, Present, and Future*. Sandhill Crane Press, Gainesville, Florida.
- WOODS, C.A. 1989a. The biogeography of West Indian rodents. Pp. 741-798. *In*: C. A. Woods (Ed.). *Biogeography of the West Indies: Past, Present, and Future*. Sandhill Crane Press, Gainesville, Florida.
- _____. (Ed.). 1989b. *Biogeography of the West Indies: Past, Present, and Future*. Sandhill Crane Press, Gainesville, Florida.

APPENDIX 1

Localities for electrophoretic analysis

The following populations were sampled in the electrophoretic analysis: (1) *Eleutherodactylus martinicensis*, Guadeloupe, Basse-Terre, Chutes du Carbet, path to lower falls, alt. ca. 700 m, $n = 2$; (2) *E. martinicensis*, Guadeloupe, Basse-Terre, Rivière Moreau, ca. 7 km SW Douville, alt. ca. 300 m, $n = 2$; (3) *E. martinicensis*, Guadeloupe, Grande-Terre, 1.7 km S Espérance, alt. ca. 75 m, $n = 2$; (4) *E. martinicensis*, Martinique, 100 m below top of Morne Bigot road, $n = 2$; (5) *E. martinicensis*, Martinique, Fort-de-France, Vieux Fort Park, $n = 4$; (6) *E. martinicensis*, St. Barthélemy, St. Jean, Jean Bart Hotel, $n = 9$; (7) *E. martinicensis*, St. Barthélemy, Anse aux Flamandes, $n = 3$; (8) *E. martinicensis*, St. Barthélemy, Lorient, Hotel La Normandie, $n = 3$; (10) *E. johnstonei*, Antigua, Parish of St. Mary,

End of road in Christian Valley, alt. 35 m, $n = 4$; (11) *E. johnstonei*, Antigua, Parish of St. Philip, Gaynor's Mill, sea level, $n = 4$; (12) *E. johnstonei*, Barbados, Parish of St. James, Garden of Bellairs Research Institute, sea level, $n = 2$; (13) *E. johnstonei*, Barbados, Parish of St. Andrew, Turner's Hall Woods, 0.6 km S St. Simon's, alt. ca. 50 m, $n = 3$; (14) *E. johnstonei*, Barbados, Parish of St. Michael, Bridgetown, Parking lot of Grand Barbados Beach Hotel, sea level, $n = 3$; (15) *E. johnstonei*, Grenada, Parish of St. Patrick, 2.4 km SW Sauteurs, alt. ca. 150 m, $n = 5$; (16) *E. johnstonei*, Grenada, Parish of St. Andrew, Grand Etang Lake parking lot, $n = 3$; (17) *E. johnstonei*, Nevis, St. George Gingerland Parish, Golden Rock Estate, $n = 2$; (18) *E. johnstonei*, Nevis, St. James Windward Parish, Nesbitt Plantation, $n = 2$; (19) *E. johnstonei*, Saba, 1 km N The Gap, $n = 3$; (20) *E. johnstonei*, Saba, 1 km N Windwardside beyond English Quarter, $n = 3$; (21) *E. johnstonei*, Saba, Windwardside, beginning of Mt. Scenery steps, $n = 2$; (22) *E. johnstonei*, St. Eustatius, The Quill, $n = 16$; (23) *E. johnstonei*, St. Kitts, St. Thomas Middle Island Parish, Romney Manor, 0.8 km N Old Road Town, $n = 2$; (24) *E. johnstonei*, St. Kitts, St. Peter Basseterre Parish, Bayford's TV mast, 1 km N Ogee's, $n = 2$; (25) *E. johnstonei*, St. Kitts, Christ Church Nichola Town Parish, St. George's Ghut, 0.5 km S Tabernacle, $n = 2$; (26) *E. johnstonei*, St. Martin, Pic Paradis summit, $n = 6$; (27) *E. johnstonei*, St. Martin, Terres Basses, $n = 6$; (28) *E. johnstonei*, Barbuda, Codrington, $n = 1$; (29) *E. johnstonei*, Montserrat, Parish of St. Anthony, Richmond Hill, $n = 1$. Voucher specimens will be deposited in the Canadian Museum of Nature.

APPENDIX 2

Specimens examined

The following are the specimens of *Eleutherodactylus* which were examined in this study. All specimens were used in the morphometric analysis. Populations used in the electrophoretic analysis are marked with an asterisk. All distances given are road distances. Specimens are designated by DMG (David M. Green) field numbers and will be deposited in the Canadian museum of Nature, Ottawa.

Eleutherodactylus johnstonei (371).—ANTIGUA: Parish of St. John—Roslyn's Guest House, 1.8 km N St. John's Cathedral, DMG 3141–43, 3146–49, 3152–60. Parish of St. Mary—End of road in Christian Valley, alt. 35 m*, DMG 3221–23, 3225–29, 3234. Parish of St. Philip—Gaynor's Mill, sea level*, DMG 3217–19. BARBADOS: Parish of St. John—0.2 km W Conset Bay, sea level, DMG 2885–2891, 2893–98, 3059. Parish of St. James—Garden of Bellairs Research Institute, sea level, DMG 2899–2911, 3010–11, 3057–58. Parish of St. Andrew—Turner's Hall Woods, 0.6 km S St. Simon's, alt. ca. 50 m*, DMG 2913–34. Parish of St. Michael—Bridgetown, Parking lot of Grand Barbados Beach Hotel, sea level*, DMG 3004, 3009, 3012, 3015, 3061. BARBUDA: Codrington, yard of Nedd's supermarket, sea level*, DMG 3275; Sunset View Hotel, sea level, DMG 3593, 3624, 3633, 3654, 3667–69, 3695, 3716–17, 3721, 3729. MONTSERRAT: Parish of St. Anthony—Richmond Hill, DMG 3161–65, 3167–75, 3177–78; End of Galways Soufriere road*, DMG 3350–52, 3354–55, 3357–59, 3380–88. Parish of St. Peter—Fogarty's, Soldier's Ghaut, DMG 3360–63, 3365–67, 3370–71, 3373–78. NEVIS: St. George Gingerland Parish—Golden Rock Estate*, DMG 3122–36, 3139–40. St. James Windward Parish—Nesbitt Plantation*, DMG 3180–85, 3187–97. SABA: 1 km N The Gap*, DMG 3235, 3239–40, 3246, 3249–50, 3252–53; 1 km N

Windwardside beyond English Quarter*, 3255–61, 3263, 3268–74; Windwardside, beginning of Mt. Scenery steps*, 3285–94, 3296–3304. ST. EUSTATIUS: The Quill*, DMG 3335, 3337–39, 3341–49. ST. KITTS: St. Thomas Middle Island Parish—Romney Manor, 0.8 km N Old Road Town*, DMG 3094–3105, 3107–13. Christ Church Nichola Town Parish—St. George's Ghut, 0.5 km S Tabernacle*, DMG 3198, 3200, 3202–03, 3205–08, 3210–11, 3214–16. St. Peter Basseterre Parish—Bayford's TV mast, 1 km N Ogee's*, DMG 3389–90, 3392–99, 3401–03, 3405–06. ST. LUCIA: 1.4 km NW Dennery, DMG 2782–91, 2846–48; Sans Souciss, Castries*, DMG 2850–68, 3062; 2.5 km SE Ravine Poisson Village, 2869–72, 2874–82, 3067; 3 km N Gros Islet (Le Sport Hotel)*, 2982–94, 3060. ST-MARTIN: Pic Paradis summit*, DMG 3090–93, 3305–18; Terres Basses*, DMG 3319–34.

Eleutherodactylus martinicensis (121).—GUADELOUPE: Basse-Terre—Chutes du Carbet, path to lower falls, alt. ca. 700 m*, DMG 3545, 3600, 3628–29, 3639, 3651–52, 3876–77, 3902–03; Rivière Moreau, ca. 7 km SW Douville, alt. ca. 300 m, DMG 3531–37, 3582, 3638, 3640–41, 3720, 3740; Rivière des Vieux Habitants, 2 km NE Maison du Café, DMG 3518, 3544, 3594, 3719, 3747; Rivière des Vieux Habitants, 1 km N Maison du Café*, DMG 3554, 3580, 3731, 3750, 3819–21; Rivière Petit David, 400 m SE Les Mamelles, along road D23, alt. ca. 700 m, DMG 3597–98, 3736, 3742; Sofaïa, Rivière Salée, end of road D19, alt. ca. 300 m, DMG 3542, 3571, 3584, 3586, 3653, 3693, 3727, 3735; Rivière du Vieux Fort, 1 km SW Desbonnes, DMG 3511, 3540, 3601. Grande-Terre—1.7 km S Espérance, alt. ca. 75 m*, DMG 3512–13, 3553, 3660. MARTINIQUE: Morne Rouge, 600 m SE Montagne Pelée, along road D39, DMG 3634, 3826; Deux Choux, 100 m N intersection of roads N3 and D1, DMG 3541, 3684, 3692, 3728, 3823–24; Croix

Blanche, DMG 3557, 3648–49, 3827; 1 km W Morne Pavillon, DMG 3630, 3644, 3690, 3754; 100 m below top of Morne Bigot road*, DMG 3505, 3602, 3612, 3647, 3661–62, 3828–30; Montagne du Vauclin, DMG 3696, 3722, 3739, 3758, 3816; Grand Fond, DMG 3608, 3645–46, 3723–34, 3757, 3817; Fort-de-France, Vieux Fort Park*, DMG 3508–10, 3664–65, 3691, 3748. ST-BARTHÉLEMY: St. Jean, Jean Bart Hotel*, DMG 3276–84; Lorient, Hotel La Normandie*, DMG 3519, 3558–61; Anse aux Flamandes*, DMG 3566–67, 3847, 3851, 3884, 3888–91, 3897–98.

TABLE 1. Protein loci and electrophoretic conditions.

Protein ^a	Enzyme Commission		Electrophoretic conditions ^c
	Locus ^a	Number ^b	
1. Alcohol Dehydrogenase	ADH-1	1.1.1.1	1
2. Aspartate Aminotransferase	AAT-2	2.6.1.1	3
3. Carbonic Anhydrase	CA-2	4.2.1.1	4
4. Choline Esterase	CE-1	3.1.1.8	4
5. Choline Esterase	CE-2	3.1.1.8	4
6. Dihydrolipoamide Dehydrogenase	DDH	1.8.1.4	1
7. Fructose-biphosphate Aldolase	FBA	4.1.2.13	2
8. General Protein	GP-1	-	2
9. L-Iditol Dehydrogenase	IDDH-2	1.1.1.14	1
10. Malate Dehydrogenase	MDH-1	1.1.1.37	3
11. Peptidase-B (L-leucylglycylglycine)	PEP (LGG)	3.4.11.4	4
12. Peptidase-F (L-leucyl-L-leucyl-L-leucine)	PEP (LLL)	3.4.11.4	4
13. Phosphogluconate Dehydrogenase	PGDH	1.1.1.44	3

^aNomenclature Committee of the International Union of Biochemistry (1984), modified according to Murphy et al. (1990).

^bNomenclature Committee of the International Union of Biochemistry (1984).

^c(1) Tris-citrate pH 8.0, 130 V, 4 h; (2) Poulik pH 8.7, 75mA, 3 h; (3) Amine Citrate pH 6.1 (Clayton and Tretiak 1972), 75 mA, 4 h; (4) Lithium Hydroxide, 325 V, 3 h.

TABLE 2. List and description of twenty measurements taken from 492 specimens of Lesser Antillean *Eleutherodactylus* (see Appendix 2). Measurements were taken from the right side of adult specimens where applicable. All measurements were divided by snout–vent length to normalize the data and to minimize the influence of size on the principal components.

	Measurement	Description
1.	Head width	measured at level of tympana
2.	Eye diameter	greatest distance from anterior to posterior
3.	Eye–Naris distance	taken from posterior edge of naris to anterior edge of eye
4.	Tympanum diameter	taken from anterior to posterior
5.	Tympanum–Eye distance	shortest distance from posterior edge of eye to anterior edge of tympanum
6.	Interorbital distance	shortest distance between eyes across the skull
7.	Snout length	from tip of snout to intersection with interorbital distance
8.	Internarial distance	measured between medial edges of nares
9.	Naris–Tympanum distance	from posterior edge of naris to anterior edge of tympanum
10.	Snout–Vent length	–
11–14.	Finger lengths	–
15.	Hand length	from tip of third finger to wrist
16.	Length of longest toe	–
17.	Foot length	from tip of longest toe to back of heel
18.	Femur length	from groin to knee
19.	Tibia length	from knee to heel
20.	Radioulnar length	from wrist to elbow

TABLE 3. Allelic variants at thirteen indicator loci of *Eleutherodactylus johnstonei* and *E. martinicensis* (Appendix 1). There are ten loci which have fixed differences between *E. johnstonei* and St-Barths frogs, while there are none to distinguish the latter from *E. martinicensis*.

Locus	<i>E. johnstonei</i>	St-Barths	<i>E. martinicensis</i>
AAT-2	c,d	b,c	b,c
ADH-1	a,c	b	b
CA-2	z,a,b	b,c	b,c
CE-1	c,d	a,b	a,b
CE-2	b	c	c
DDH	a,b	c	c
FBA	b	c	c
GP-1	a,b	c	c
IDDH-2	b	b,c	b,c
MDH-1	c	a,b	b,c
PEP (LGG)	b	c	c
PEP (LLL)	b	a	a
PGDH	a,b,c	d	d

FIGURE 1. Distribution of *Eleutherodactylus martinicensis* (solid circles) and *E. johnstonei* (open circles) in the Lesser Antilles. Stippled islands were French colonies at the time when whistling frogs may have been redistributed in the Lesser Antilles. It is notable that during the past few years no *E. martinicensis* have been caught or heard in the localities listed by Schwartz (1967) on Antigua (Pregill et al., 1988; personal observation). Hence I have excluded the island from the range of that species. The inset shows the island of St-Barthélemy with the collection sites indicated: (1) Jean Bart Hotel, St. Jean; (2) Hotel La Normandie, Lorient; (3) Anse aux Flamandes.

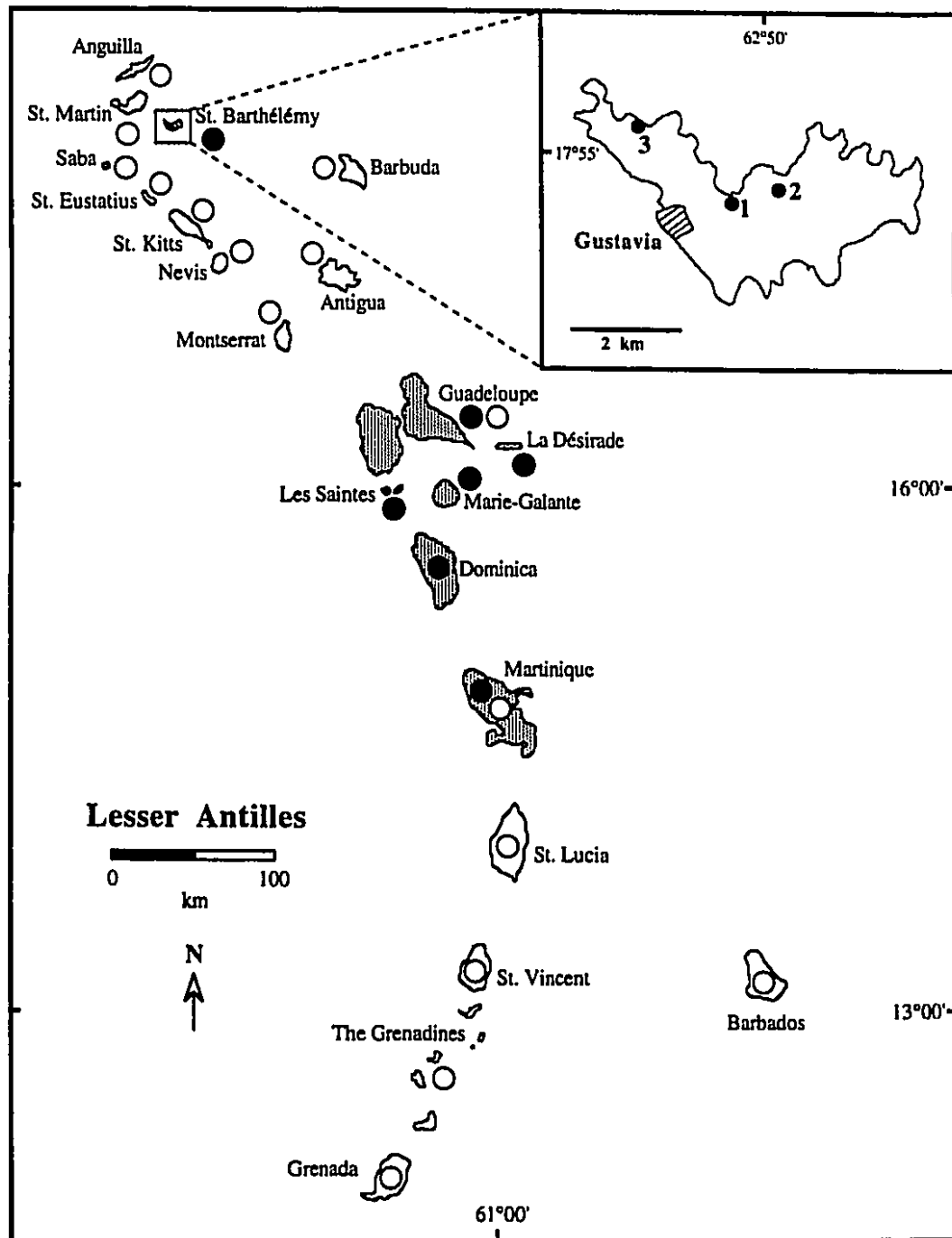


FIGURE 2. Audiospectrograms of the calls of *Eleutherodactylus martinicensis* from (A) St-Barths, (B) Guadeloupe, (C) Martinique, and of *E. johnstonei* from (D) Montserrat and (E) Grenada. Horizontal axis is time, and call (A) is 0.35 seconds long. Recordings were made at temperatures around 24°C ($\pm 2^\circ\text{C}$). All calls consist of two notes: a first short note to deter competitors, and a second, extended component to attract mates (Narins and Hurley, 1982).

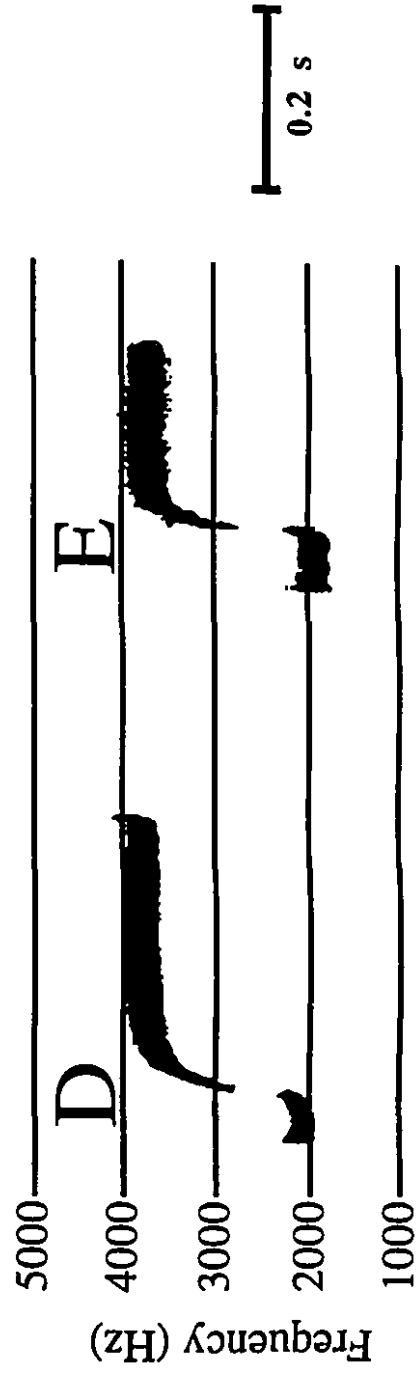
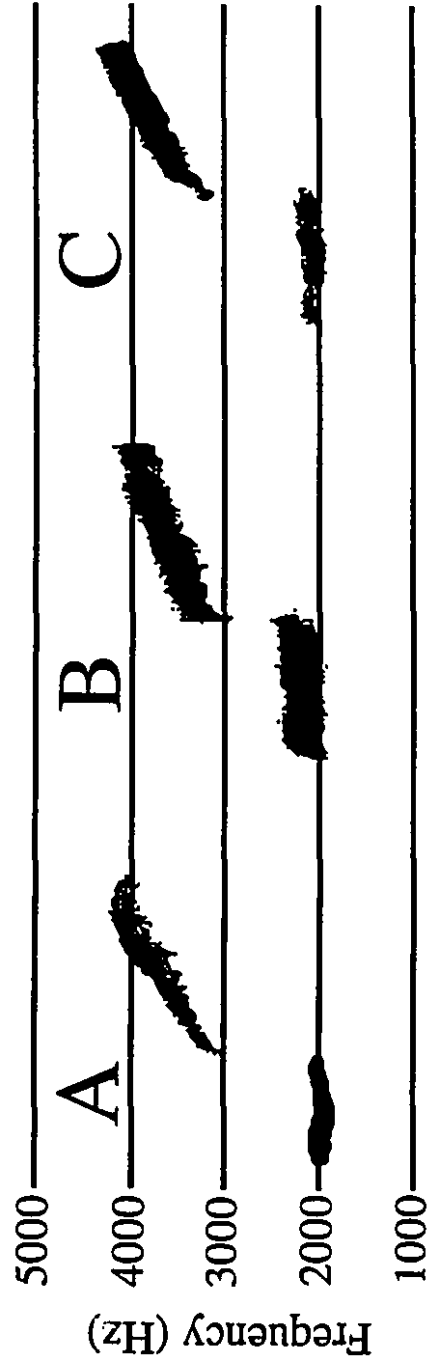
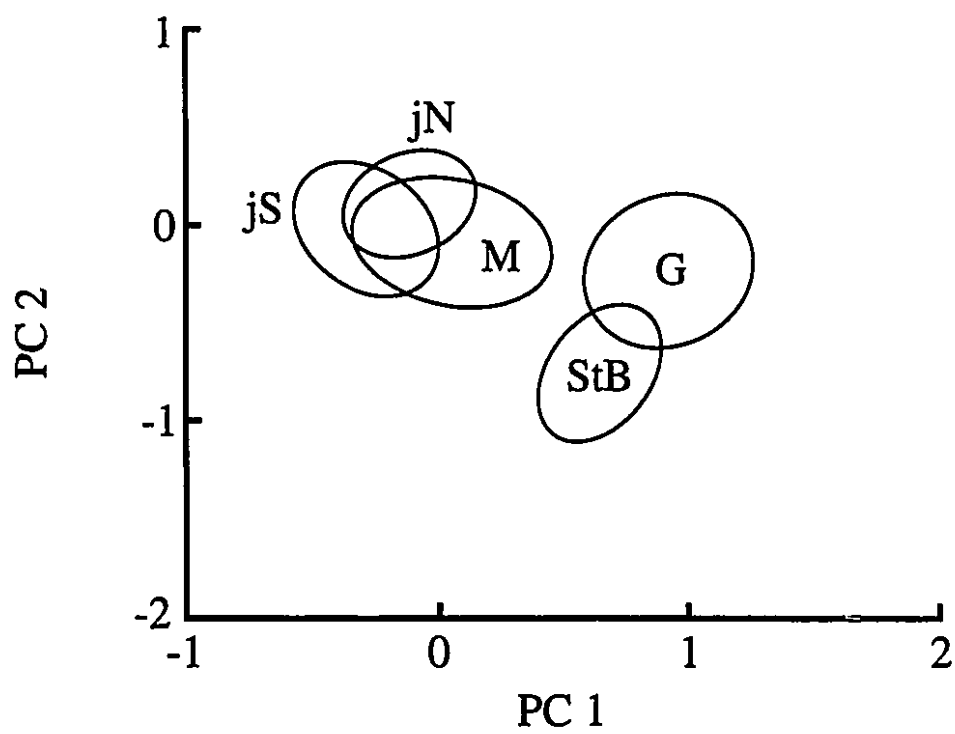


FIGURE 3. Plot of the first two principal components (PC) for populations of northern *Eleutherodactylus johnstonei* (jN, from Antigua, Barbuda, Montserrat, Nevis, Saba, St. Eustatius, St. Kitts and St-Martin; $n = 250$), southern *E. johnstonei* (jS, from Barbados and St. Lucia; $n = 121$), and *E. martinicensis* from Guadeloupe (G; $n = 56$), Martinique (M; $n = 43$), and St-Barths (StB; $n = 22$). The ellipsoids are the centroids of each distribution.



2

The Taxonomic Status of Caribbean and South American Frogs Currently Ascribed to *Eleutherodactylus urichi* (Anura: Leptodactylidae)

Published as: Kaiser, H., J. D. Hardy, Jr., and D. M. Green. The taxonomic status of Caribbean and South American frogs currently ascribed to *Eleutherodactylus urichi* (Anura: Leptodactylidae). *Copeia*. *In press*.

PREAMBLE CHAPTER 2

Schwartz (1967, Stud. Fauna Curaçao Carib. Isl. 23:1–62) described two nominal subspecies of *E. urichi* from Grenada and St. Vincent. While collecting these taxa, as well as *E. urichi* on Trinidad and Tobago, for my systematics research, I began to question Schwartz's taxonomic decision. My knowledge of the taxa was then based on more specimens than Schwartz had had available, as well as on recordings of vocalizations and behavioral observations in the field. To allay my doubts, and in view of the larger systematic study, it was necessary to conduct a detailed investigation to ascertain how many species I was actually dealing with.

ABSTRACT

Phenotypic characters, body proportions, allozyme polymorphisms, and calls of populations of the frog *Eleutherodactylus urichi* (Boettger) from the southeastern Caribbean and northern South America indicate that forms from Grenada and St. Vincent are distinct from other populations and from each other at the species level. These populations are thus elevated to full species status as *E. euphronides* and *E. shrevei*, respectively. All South American records for *E. urichi* are due to misidentification, and *E. urichi s. nov.* is redescribed to prevent further confusion. A key to Eastern Caribbean *Eleutherodactylus* is included.

INTRODUCTION

The Eastern Caribbean frog, *Eleutherodactylus urichi* (Boettger), has been recorded from forested highland areas on the islands of Grenada, St. Vincent, Tobago, and Trinidad, and there are several reports of its existence in South America (e.g., Barbour, 1914, 1916; Rivero, 1961, 1964; Schwartz, 1967; Hardy, 1970, 1982, 1984; Schwartz and Henderson, 1991). With the exception of the widely introduced *E. johnstonei* (Kaiser, 1992; Chapter 1), *E. urichi* is the only frog that occurs on Eastern Caribbean islands as well as the South American mainland, and which has recognized subspecies. *Eleutherodactylus u. euphronides* Schwartz is known from Grenada, *E. u. shrevei* Schwartz from St. Vincent, and *E. u. urichi* Schwartz (or "*E. urichi* subsp.") from Tobago, Trinidad, and northern South America (Schwartz, 1967; Hardy, 1970, 1982; Lescure, 1979, 1983, 1987). Because *E. urichi*, as presently recognized, has narrow ranges in each of its native habitats and is restricted to primary forests, it cannot be considered a colonizing species, such as the widespread *E. johnstonei*. I resolved to

clarify the scattered reports for the sporadic occurrences of *E. urichi* by investigating the systematic relationships of all known *E. urichi*-populations with each other and with the sympatric species *E. johnstonei* and *E. terraebolivaris*.

MATERIALS AND METHODS

Specimen collections and observations of vocalizations and general ecology of *Eleutherodactylus* populations were made during January (1989) and during the month of August in 1990–92 on Grenada and St. Vincent, and during May (1990) and the months of August and September in 1990–92 on Tobago and Trinidad, at a variety of localities (Fig. 1). Seventy-seven specimens (Appendix 1) were collected and taken to the lab in Montréal. For electrophoresis, tissue samples (liver, heart, kidney, muscle, spleen) were homogenized, centrifuged, and stored at -80°C prior to horizontal starch gel electrophoresis (see Murphy et al., 1990) exploring 26 loci (Table 1). All procedures with animals, including captive care, conformed to guidelines established by the Canadian Council on Animal Care (1980–84) and were approved by the Animal Care Committee of McGill University. Preserved specimens have been deposited in the Canadian Museum of Nature. For morphometric comparisons, an additional 261 museum specimens were used, including the type specimens of *E. johnstonei*, *E. urichi euphronides*, *E. u. shrevei*, and *E. terraebolivaris*. Institutional abbreviations used are listed in Leviton et al. (1985).

Twenty length measurements (Table 2) were taken to the nearest 0.1 mm using a dissecting microscope with a Numonics 2200 digitizing tablet and Jandel Scientific Sigma Scan (version 3.10) software. Use of this digitizing setup minimized measurement error within characters as well as specimens (< 3% error for ten repetitive measurements). Log-transformed data were analyzed using Systat software (version

5.2) on an Apple Macintosh LC computer (expanded memory) to perform multiple discriminant function analyses (MDAs) on specimen groupings determined by locality. To stabilize the statistical terminology, the recommendations of Hair et al. (1992) were followed. Two known and distinct species occurring sympatrically with *E. urichi* over part of its range, *E. johnstonei* and *E. terraebolivaris*, were used as comparative groups in building the discriminant functions (DFs). Groupings of South American specimens were tested using the derived discriminant functions.

Sound recordings were made with a SONY professional walkman WM-D3. Audiospectrograms were produced using a Kay Elemetrics Corp. digital sonagraph model 7800.

RESULTS

Morphometrics.—Populations of *Eleutherodactylus johnstonei* from Grenada and St. Vincent were statistically distinct from both *E. urichi euphronides* and *E. u. shrevei* (Pearson chi-square $P \leq 0.001$). However, there was some overlap in group assignments between the *E. johnstonei*-populations, as well as between *E. u. euphronides* and *E. u. shrevei* (Table 3). Plots of discriminant scores (DS) 1 and DS2 (Figs. 2A, B) failed to distinguish *E. u. euphronides* from *E. u. shrevei*, but plots of DS1 or DS2 against DS3 (Figs. 2C, D) provided partial separation along DS3 due to the relatively greater discriminating power of head characters in the discriminant loadings of DF3 (Table 4).

Results of an MDA including *E. u. urichi* and *E. terraebolivaris* confirmed the distinctiveness of both *E. u. euphronides* and *E. u. shrevei* from *E. u. urichi* and from each other (Wilks' lambda, Pillai trace, Hotelling-Lawley trace F-statistics and theta $P \leq 0.001$). The group assignment for *E. u. urichi* from Trinidad or Tobago was always

correct, with some overlap between *E. u. euphronides* and *E. u. shrevei* (Pearson chi-square $P \leq 0.001$; Table 5). Likewise, overlap with *E. terraebolivaris* was very minor, at 9% for *E. u. shrevei* and 4% for *E. u. euphronides* (Table 5). *Eleutherodactylus u. euphronides* and *E. u. shrevei* were clearly separable from *E. u. urichi* on the basis of DS1 and DS2 (Figs. 3A–C) while DS3 and DS4 distinguished them from each other (Figs. 3D, E). Three MCZ-specimens from Tobago (86950, 86952–53), included in the analysis to verify their tentative identification as *E. cf. rozei* (Hardy, 1982), did not fall within the boundary of any particular species (Fig. 3A). Tests for species affinities of South American specimens incorporating all species under investigation into the analysis allowed no resolution (Fig. 3F). However, when testing against a discriminant function created by using the affinities proposed by Hardy (1970) and Lescure (1981) for *E. johnstonei* and by Rivero (1961) for *E. terraebolivaris* (Fig. 3G) some of the specimens (AMNH 18981, 21403-04, 21413) could be identified unequivocally (group assignment probabilities 0.999, 1.000, 1.000, and 0.969, respectively) as *E. johnstonei*. All other specimens were not morphometrically aligned with any Eastern Caribbean species, although two specimens (AMNH 43669, 46247) were well aligned (group assignment probability 1.000 in each case) with the FMNH-specimens from Venezuela (Fig. 3G).

Discriminant loadings for DF1 were greatly influenced by size differences between taxa (Tables 4 and 6), indicating that size differences alone have significant discriminating power in comparisons of these species. Hand and lower limb characteristics made the greatest relative contributions to DF1 and DF2, and, in the case of DF2, some head characters also contributed (Table 6). Head characters also made the greatest contribution to DF3, whereas both head and limb characters contributed to DF4 (Table 6).

Basic statistics (Table 7) for snout-vent length (SVL), head width (HW), eye-naris distance (EN), and tibia length (TIB) showed significant size differences between *E. u. urichi*, *E. u. euphronides*, and *E. u. shrevei* (independent samples t-test, $P \leq 0.001$). The Lesser Antillean populations had a slightly longer tibia and a slightly wider head than Trinidad and Tobago populations, as seen in body proportion ratios (Table 7). There was no significant difference in sexual size dimorphism between the three subspecies. Values for average female-male SVL ratio are 1.20 for *E. u. shrevei*, 1.25 for *E. u. euphronides*, and 1.26 for *E. u. urichi*. Analyses for sexes combined yielded very similar results to sexes treated separately; data for separate analyses by sex were thus omitted.

Electrophoresis.—Of the twenty-six investigated loci, twenty were polymorphic, and fourteen provided diagnostic information (Table 8). There were thirteen fixed differences between *E. u. urichi* and the Lesser Antillean species. Between *E. u. euphronides* and *E. u. shrevei*, there were four fixed differences, each species having several unique alleles. There were 43 alleles present at the diagnostic loci (Table 8). Of these, nine were identifiers for *E. u. euphronides* (AAT-2^a, CK-1^{a,c}, CK-2^{a,b,c}, DDH^{c,d}, PEP [LA]^a), and nine for *E. u. shrevei* (AAT-1^a, CK-1^b, DDH^{a,b}, GPI^c, HK^a, IDH-1^a, MDH-1^c, PEP [LA]^b).

Vocalizations.—Calls of *E. u. urichi*, *E. u. shrevei*, and *E. u. euphronides* (Fig. 4) were distinct from each other both quantitatively and qualitatively. *Eleutherodactylus u. urichi* calls (Fig. 4A) consisted of a single note in a frequency range of 2900–3600 Hz; these individual notes were issued repeatedly during bouts of calling. The length of each note and the spacing between notes varied slightly among individuals, averaging 70 ms and 225 ms, respectively ($n = 10$). During three

observed agonistic encounters, *E. u. urichi* males produced a series of clicks (frequency range 2700–3800 Hz, \bar{x} = 25 ms; Fig. 4B).

The call of *E. u. euphronides* consisted of a series of clicks (Fig. 4C; Barbour, 1914). These were given at a dominant frequency of 4000 Hz (with a 3000–4700 Hz range) at a rate of 12–14 clicks per call (n = 10). The average total time elapsed for a complete set of clicks was 2.27 s (n = 10), with lengths of individual clicks less than 20 ms. Spacing between the first two clicks was long (260 ms; n = 10), with the following clicks spaced apart fairly evenly (170 ± 20 ms; n = 26), and with a slight increase in interval towards the end of the call up to a maximum of 310 ms (Fig. 4C).

As in *E. u. euphronides*, the predominant component of *E. u. shrevei* calls were clicks of great intensity (Fig. 4D), with very few longer calls (Fig. 4E) issued intermittently in rapid succession. The clicks were produced at a dominant frequency of 3700 Hz (with a 2700–4500 Hz range) and were all under 20 ms long. They were issued in groups of 9 or 10 (n = 10), with a spacing of 330 ms (n = 10) between the two first clicks, and increasing gradually from a minimum of 150 ms to a maximum of 270 ms during observed call groupings. Total length of a typical call was 1.83 s (n = 10). The longer calls had a starting frequency close to 3000 Hz, rising rapidly to a dominant frequency of 3700 Hz. During my observations, these were issued only rarely. They were 270 ms apart on average in a series of four or five calls, with no individual issuing more than five calls in sequence.

General morphology.—Identification of living or unfixed specimens of island populations of *E. urichi* is generally easy since *E. u. urichi* is unique among all Eastern Caribbean frogs in having a distinctly greenish blue upper portion of the iris (Johnson, 1946). All three subspecies were distinguishable from *E. johnstonei* by the coloration

of the hidden portions of the femur, which is a brown orange in *E. u. euphronides*, bright red in *E. u. shrevei* and *E. u. urichi*, and cream in *E. johnstonei*.

In preservative, the three species can be differentiated from *E. johnstonei* by the presence of some degree of mottling of the labial area, the presence of a second palmar tubercle (Figs. 5A, C, E), and the absence of large areolae in the groin. The palmar tubercles of *E. u. urichi* are small and almost indistinct because this species has relatively fleshy palms (Fig. 5A). In both *E. u. euphronides* and *E. u. shrevei*, the palmar tubercles are large (Figs. 5C and 5E, respectively). The thenar tubercle of *E. u. urichi* (Fig. 5A) covers the entire basal portion of digit I, while it covers only the distal edge of that digit in *E. u. euphronides* and *E. u. shrevei* (Figs. 5C and 5E, respectively). The disc on the first finger of *E. u. urichi* is much reduced (Fig. 5A). In both *E. u. urichi* and *E. johnstonei*, the canthus rostralis is concave, while it is straight in the other two taxa. A supratympanic fold is absent in *E. johnstonei* and *E. u. urichi*, but is clearly discernible in *E. u. shrevei* and *E. u. euphronides*.

DISCUSSION AND DESCRIPTIONS

In recognizing different subspecies of *Eleutherodactylus urichi* on Grenada and St. Vincent, Schwartz (1967) taxonomically flagged two biogeographically interesting populations, and in so doing confirmed an impression first verbalized by Barbour (1935). However, Schwartz's decision was conservative because it was based on relatively little comparative material, and he took an approach consistent with the frequently used practice of labelling as subspecies what may be considered geographic morphs. Given that the subspecies of *E. urichi* clearly represent independently evolving lineages (see papers in Otte and Endler, 1989), my data necessitate a revision of *E. urichi*.

The position of distribution polygons from MDA data provides conclusive evidence for the distinction of *E. u. euphronides* and *E. u. shrevei* from *E. johnstonei*, mainly due to limb proportions (DS1, Fig. 2A; DF1, Table 4), as well as from *E. u. urichi*, based upon both limb proportions and general size (DS1 and DS2, Figs. 3A–C; DF1–4, Table 6). As Schwartz (1967) remarked, the differences between *E. u. shrevei* and *E. u. euphronides* are difficult to assess, and neither morphometric representations (Figs. 2B–D) nor general morphology may be convincing. However, allozyme differences (Table 8) and vocalizations (Figs. 4C–F) provide conclusive evidence for distinctiveness at the species level.

In order to best summarize the taxonomy of these three species and to facilitate future comparisons, I am including diagnoses for morphological characters, as well as additional comments on the natural history of each species and a full redescription of *E. urichi s. nov.* The original description of that species (Boettger, in Mole and Urich, 1894) is quite limited and warrants emendation. The diagnosis format recommended by Lynch (1979) is followed, but the disk terminology of Savage (1987) is used.

Eleutherodactylus euphronides (Schwartz) *comb. nov.*

Figs. 5C, D and 6A

Eleutherodactylus urichi euphronides Schwartz, 1967, Stud. Fauna Curaçao Carib. Isl. 24:6. Holotype MCZ 43229, an adult female from Grand Etang, Grenada, West Indies (61° 42' 00" W, 12° 05' 45" N, elev. 519 m), collected on 25 February 1961 by D. C. Leber and A. Schwartz.

Diagnosis.—A forest-dwelling species of *Eleutherodactylus* with the following diagnostic characters: (1) skin on dorsum of body smooth with few minute tubercles

on the posterior third; dorsolateral folds absent; skin on venter with few minute colorless areolae between pectoral and pelvic areas; (2) tympanum round, distinct, 1/3 diameter of eye, partly obscured posterodorsally by weak supratympanic fold; (3) snout round in dorsal view and in profile, $EN < \text{length of eye}$; nares protruding slightly; canthus rostralis sharply angled; canthal ridge straight with a slight lateral inflection and a dark line along its length; (4) supraocular tubercles present; interorbital distance equal to the width of upper eyelid upper eyelid darkly pigmented; cranial crests absent; (5) vomerine odontophores triangular and slightly oblique; choanae triangular; (6) males with vocal slits and single median subgular vocal sac; (7) size of fingers $I = II < IV < III$, III about one third longer than I; finger disks III and IV wider than fingers, disks I and II only slightly so, all oval in shape; finger disk size ($I = II$) $< (III = IV)$, with I not reduced; ventral surface of finger disks unpigmented; number of subarticular tubercles 2-2-3-2 for fingers I-IV, respectively; all subarticular tubercles oval; two large confluent palmar tubercles covering almost entire lower half of palm; one large basal thenar tubercle; (8) fingers lacking lateral fringes; (9) ulnar tubercles indistinct, with several small tubercles on elbow; (10) several small, flat heel tubercles present; inner tarsal fold indistinct; (11) two ovoid metatarsal tubercles, inner about twice the size of outer; several supernumerary plantar tubercles present; (12) number of subarticular tubercles 1-2-3-3-2 for toes I-V, respectively; lateral fringes and webbing absent; (13) dorsum dark brown, venter cream; labial areas mottled; posterior surfaces of thighs orange-brown; never with a cream interocular bar; dark supratympanic stripe present, extending from corner of eye to armpit; upper iris color bronze; (14) SVL of males 17.7–27.0 mm ($\bar{x} = 22.7$, $n = 41$), of females 19.4–39.4 mm ($\bar{x} = 28.3$, $n = 31$).

Variation.—see Schwartz (1967).

Distribution and ecology.—This species is known only from the island of Grenada, West Indies (Fig. 1C). On three visits to the type locality during the month of August (1990–92), I could not find or even hear *E. euphronides*, although *E. johnstonei* was very common. During the first visit to the Cable and Wireless site near Mt. St. Catherine on Grenada (August 1990), there were very few calling *E. johnstonei*, but many *E. euphronides*. In August 1991 and 1992, very few *E. euphronides* were present but many *E. johnstonei*, and the intense calls of that species (Fig. 4D) drowned out calls of *E. euphronides*. It seems that populations of *E. euphronides* are becoming more and more restricted in distribution. This may in some instances have split a previously continuous range, dividing the frogs into a northern population near Mt. St. Catherine and a southern one in the mountains forming the southern boundary of Grand Etang Forest Reserve.

Males of *E. euphronides* called from elevated perches, such as branches and large-leafed shrubs. Calling activity of *E. euphronides* is limited to the period right around dusk and seemed generally very sparse during observations in August. There was no significant increase in calling activity of *E. euphronides* during and just after a brief rain near dusk, while chorusing of *E. johnstonei* increased markedly. Females were encountered most frequently crouching at and near ground level.

Eleutherodactylus shrevei (Schwartz) *comb. nov.*

Figs. 5E, F and 6B

Eleutherodactylus urichi shrevei Schwartz, 1967, Stud. Fauna Curaçao Carib. Isl. 24:13. Holotype MCZ 43230, an adult female from Lowrey, St. Vincent, West Indies (61° 12' 55" W, 13° 12' 40" N), collected on 7 March 1961 by D. C. Leber and A. Schwartz.

Diagnosis.—A forest-dwelling species of *Eleutherodactylus* with the following diagnostic characters: (1) skin on dorsum of body smooth with a few minute tubercles on the posterior third; dorsolateral folds absent; venter with few minute colorless areolae between pectoral and pelvic areas; (2) tympanum round, distinct, $1/4$ diameter of eye, partly obscured posterodorsally by pronounced supratympanic fold; (3) snout round in dorsal view and in profile, $EN < \text{length of eye}$; nares protruding slightly; canthus rostralis sharply angled; canthal ridge straight with a slight lateral inflection and a dark line along its length; (4) supraocular tubercles present; interorbital distance equal to the width of upper eyelid; upper eyelid darkly pigmented; cranial crests absent. (5) vomerine odontophores triangular and straight; choanae triangular; (6) males with vocal slits and single median subgular vocal sac; (7) size of fingers $I = II < IV < III$, III about one third longer than I; finger disks III and IV wider than fingers, disks I and II only slightly so, all oval in shape; finger disk size $I < II < III < IV$, with I not reduced; ventral surface of finger disks darkly pigmented; number of subarticular tubercles 2-2-3-2 for fingers I–IV, respectively; two large subarticular tubercles side-by-side on finger I; all subarticular tubercles oval; two confluent but distinct palmar tubercles covering palm; one large basal thenar tubercle; (8) fingers lacking lateral fringes; (9) ulnar tubercles indistinct, with several small tubercles on elbow; (10) several small, flat heel tubercles present; inner tarsal fold indistinct; (11) two large ovoid metatarsal tubercles, equal in size; several supernumerary plantar tubercles present; (12) number of subarticular tubercles 1-2-3-3-2 for toes I–V, respectively; subarticular tubercle on I enlarged, most proximal tubercle on III reduced; lateral fringes and webbing absent; (13) dorsum dark brown, venter lighter brown; labial areas mottled; posterior surfaces of thighs carmine red; dark supratympanic stripe present, extending from corner of eye to armpit; upper iris color usually bronze.

sometimes gray in specimens from Soufriere summit; (14) SVL of males 21.0–28.0 mm (\bar{x} = 24.9, n = 16), of females 19.0–40.1 mm (\bar{x} = 30.0, n = 17).

Variation.—see Schwartz (1967).

Distribution and ecology.—This species is known only from the island of St. Vincent, West Indies (Fig. 1A). On visits to the type locality during the month of August 1990–92, few *E. shrevei* could be found or heard, although *E. johnstonei* was present in abundance. R. I. Crombie (in litt.) reported that *E. shrevei* was common after rains in September 1991 in the Columbian and Layou valleys, but only in forested areas at higher altitudes. It seems that *E. shrevei*, like *E. euphronides*, has become more restricted in range, and now inhabits mainly pristine montane forests. At Soufriere volcano, *E. shrevei* occurs sympatric with *E. johnstonei* on the bare slopes near the crater and along the sparsely vegetated lava flows reaching down the mountain, but only *E. shrevei* inhabits the densely forested areas. *Eleutherodactylus johnstonei* is the sole inhabitant of the coconut groves on the lower slopes of the mountain. When ascending the mountain at dusk through the forest, the deafening calling of *E. johnstonei* ceased abruptly at cloud level (usually at an altitude of ca. 600–650 m). The characteristic clicking of *E. shrevei* could then be heard at higher altitudes. The habitat near the summit of Soufriere crater lake where specimens were collected in the early 1960s (Fig. 1A) suffered a major volcanic eruption in 1979, but the frog population now seems to have recovered, with the addition of *E. johnstonei*.

The Soufriere observation site used for my behavioral observations is in dense montane rain forest, with much decaying foliage, rotting logs, and a multitude of smooth-leafed plants. Males of *E. shrevei* were observed calling from far above ground, usually perched sideways on small branches, except on the bare slopes in the

vicinity of the crater, where ground bromeliads provide the only perches (Hardy and Harris, 1979). Clicking began suddenly just before the sun set, and remained the most common call component heard. Females and non-calling males were encountered mainly on the decaying plant material or on leaves. *Eleutherodactylus shrevei* is an extremely cryptic species, and males stopped calling and fled when approached with artificial light.

Eleutherodactylus urichi (Boettger) *s. nov.*

Figs. 5A, B and 6C

Hylodes urichi: Boettger, 1894:88 (in Mole and Urich, 1894).

Eleutherodactylus urichi: Barbour, 1914:251.

Eleutherodactylus urichii: Barbour, 1914:347.

Eleutherodactylus urichi euphronides: Schwartz, 1967:6.

Eleutherodactylus urichi shrevei: Schwartz, 1967:13.

Eleutherodactylus urichi urichi x *euphronides*: Schwartz, 1967:13.

Eleutherodactylus ulrichi ulrichi: Maclean et al., 1977:45.

Syntypes.—lost.

Lectotype.—Senckenberg-Museum, Frankfurt, 3818 (designated by Mertens, 1967).

Diagnosis.—A small forest-dwelling species of *Eleutherodactylus* with the following diagnostic characters: (1) skin on dorsum of body smooth with a few tubercles on the posterior third; dorsolateral folds absent; venter smooth; (2) tympanum round, indistinct, 2/5 diameter of eye; supratympanic fold absent; (3)

snout round in dorsal view and in profile, $EN < \text{length of eye}$; nares protruding slightly; canthus rostralis rounded; canthal ridge slightly concave; (4) minute supraocular tubercles present; interorbital distance equal to the width of upper eyelid; upper eyelid darkly pigmented; dark interocular triangle often present with apex pointing posteriorly; (5) vomerine odontophores oval and oblique; choanae teardrop-shaped; (6) males with vocal slits and single median subgular vocal sac; (7) size of fingers $I < (II = IV) < III$, III about one third longer than I; finger disks only slightly wider than fingers, oval in shape; finger disk size $I < (II = III = IV)$, with I reduced; ventral surface of finger disks darkly pigmented; number of subarticular tubercles 1-2-3-2 for fingers I-IV, respectively; tubercle on I oval and enlarged, proximal tubercle on II enlarged; two palmar tubercles; one thenar tubercle covering entire lower part of digit I; palms fleshy; (8) fingers lacking lateral fringes; (9) few indistinct ulnar tubercles, tubercles on elbow absent; (10) one cornified heel tubercle present; inner tarsal fold absent; (11) two metatarsal tubercles present, inner large and ovoid, outer small and conical; supernumerary plantar tubercles absent; (12) number of subarticular tubercles 1-1-2-3-2 for toes I-V, respectively; lateral fringes and webbing absent; (13) dorsum dark brown, venter cream with minute dark pigment spots; two dark suprascapular spots present; labial areas mottled; posterior surfaces of thighs carmine red; two dark spots in groin region; short, boomerang-shaped supratympanic stripe present, extending from near corner of eye to lower edge of tympanum; upper iris color greenish blue. (14) SVL of males 17.5–22.6 mm ($\bar{x} = 19.1$, $n = 22$), of females 23.1–25.0 mm ($\bar{x} = 24.1$, $n = 2$).

Description.—The specimen used in this description is an adult female, NMC 35032-3, from Simla, Arima Valley, Trinidad. Head wider than body, longer than wide. Snout marginally rounded in ventral view and in profile, trapezoid in dorsal

view. Lower lip bearing a small ill-defined papilla. Weakly protruding nostrils, directed dorsolaterally. Slightly concave canthal ridge with minor lateral inflection. Indistinct tympanum, partly obscuring the dorsoposterior edge of tympanic annulus. Boomerang-shaped dark supratympanic stripe from near orbit to lower edge of tympanic annulus. Choanae round, unobstructed by maxillary arch when viewed from above. Vomerine teeth small, less than one half size of a choana, lying medial and posterior to choanae, aligned in a posteriorly elevated transverse row with a slightly posteriorly angled medial aspect, about same size as a choana. Tongue slightly longer than wide, with free posterior margin forming a straight edge. Skin of dorsum smooth. Venter smooth medially, but with many small areolae laterally and on posterior third.

Measurements of described specimen in mm.—SVL 23.1; TIB 11.8; HW 9.1; IOD 2.7; EL 3.2; EN 2.9; ID 1.7.

Variation.—The variation in this species is due to ground color, dorsal patterns, and limb stripes. Most specimens have a pair of dark suprascapular dots, a dark interocular triangle, and a pair of dark blotches in the groin area. Two specimens (NMC 35031-9, 35032-1) have a distinct dorsal chevron. Three specimens (NMC 35030-1, 35031-4, 35032-4) have a wide, dark middorsal stripe, paired dark spots in sacral or groin area, a dark line along the canthal ridge and a dark anal area. Tibia and radioulna may have one or two dark stripes, the femur may have a single dark stripe. The dorsum itself varies in darkness of the ground color, from a light grayish brown to a deep earthy brown. Specimens with a lighter brown ground color frequently have a dark line along the canthal ridge extending onto the eyelid at the eye-eyelid interface.

Distribution and ecology.—The species has been confirmed only on Trinidad and Tobago (Figs. 1B, D). The species is ubiquitous in the forested areas of the Northern and Central Range mountains in Trinidad. During multiple visits, I was unable to confirm the presence of *E. urichi* in the lowland habitats described by Kenny (1969). On Tobago, the species seems restricted to the forests of the Main Ridge (Hardy, 1982, and personal observation).

Males usually began calling well after dusk. Very little calling was heard before complete darkness, and calling activity peaked before midnight. They were observed calling from slightly elevated perches in the vegetation, and most males called from smooth leaves or old dried foliage close to the ground. They were wary of artificial light and retreated quickly into the dense undergrowth when disturbed by movement. During periods of rain, calling activity increased drastically, and a ramping pattern (*sensu* Drewry and Rand, 1983) was observed. During observed agonistic encounters, clicks were issued synchronously before and between bouts of physical combat (as described by Wells, 1981). I have also observed frequent rapid clicking while one male clasped another, with the bottom male issuing calls at a higher rate. Interestingly, several observed interactions involved multiple males and occurred in transparent plastic collecting bags. Despite the bright illumination of a video camera lamp on one occasion, the males continued to fight in their “arena” until they were transferred to separate containers.

Etymology.—The species was named for F. W. Urich, who collected the first specimens.

Tobago specimens of *E. urichi* fall within the morphospace boundaries of Trinidadian specimens (Figs. 3A–C), and the notion of Schwartz (1967) that Tobago

individuals of *E. urichi* are intermediate between *E. urichi* and *E. euphronides* (*E. u. urichi* \times *euphronides* in Schwartz's terminology) is not supported. However, the paucity of *E. urichi* specimens from Tobago (Schwartz's comments are based on three specimens, my morphometric analysis includes only four) leaves a final decision on Tobago frogs beyond the reach of my data. One of Schwartz's specimens (KU 265455), considered by him to be at the upper size extreme for *E. urichi* (Schwartz, 1967:5), is identified unequivocally as *E. terraebolivaris* by its morphometric position (Fig. 3A). Taxonomic uncertainty about Tobago frogs is compounded by the presence of a third *Eleutherodactylus* species (Hardy, 1982), *E. cf. rozei*. The only collection of the latter available for this study was the three small Tobago specimens from the MCZ (Fig. 3A), collected by JDH in the 1960s.

Records for *E. urichi* in northern South America are based on few specimens, all of which are now in poor condition. I have seen all specimens available at North American institutions and found that these records must all be attributed to misidentification. I concur with Schwartz (1967) and Hardy (1982) in questioning Rivero's (1961, 1964) records for *E. urichi* from the South American mainland (FMNH 17777-87). Despite the poor degree of preservation, morphological comparison allows easy distinction of these specimens from *E. urichi* (or *E. euphronides* and *E. shrevei*) due to pronounced differences in dorsal and ventral color pattern, aspect of canthus rostralis and tympanum, and limb characteristics. Identifications provided in the FMNH specimen catalogue by K. P. Schmidt are given as *Pleurodema brachyops* (FMNH 17783), *E. bicumulus* (FMNH 17784), and *E. gollmeri*. The identity of the *Pleurodema* specimen has been confirmed (A. Resetar, pers. comm.). The scope of this paper does not permit specific identification for the other specimens, although clear differences exist between FMNH 17784 and the

remaining individuals. These specimens should be considered as *Eleutherodactylus* spp. pending further research (Appendix 2).

The specimens I have examined from the Guyanas (AMNH 13534–36, 18981, 21403–04, 21413, 43669, 46247) are also small and in poor condition. Based on my morphometric data, four Guyana specimens (AMNH 18981, 21403–04, 21413) are referable to *E. johnstonei* (Fig. 3G), a species introduced to Guyana before 1923 (Hardy and Harris, 1979). Two specimens (MCZ 44557–58) have previously been identified as *E. marmoratus* (Lescure, 1981), while AMNH 4221 is a specimen of *Adenomera andreae*, and AMNH 18982 and 23129 have been aligned with *E. johnstonei* (P. Damiani, in litt.). The remaining AMNH specimens (13534–36, 43669, 46247) are not referable to any Eastern Caribbean taxon. Two of these (AMNH 43669, 46247) align with Schmidt's (1932) specimens of "*E. gollmeri*" in my analysis (Fig. 3G), a species not found in northern South America. The remaining two are juveniles and, though not referable to *E. urichi* or *E. johnstonei*, cannot be aligned with any other taxon based on my data. The only described species whose range includes both the Venezuelan and the Guyanan locality is *E. marmoratus* (Hoogmoed, 1979; Frost, 1985). I thus propose to remove references to *E. urichi* from these records in favor of the suggested taxonomic realignments (Appendix 2).

Eleutherodactylus euphronides, *E. shrevei*, and *E. urichi* are all forest-dwellers, in contrast to *E. johnstonei*, which is an ecological generalist (Pough et al., 1977; Stewart, 1977). On St. Vincent and Grenada, *E. johnstonei* is by far the more abundant species. The ranges of *E. euphronides* and *E. shrevei* observed in 1990, 1991, and 1992 seemed much reduced from those given by Schwartz (1967), with *E. johnstonei* almost exclusively occupying those areas where type specimens for both subspecies were collected in the 1960s (Schwartz, 1967). These observations are consistent with the hypothesis that *E. johnstonei* is a recent introduction to these islands

(Kaiser, 1992; Chapter: 1) and may be able to outcompete the native species (Pough et al., 1977; Stewart, 1977; Hardy and Harris, 1979; Stewart and Martin, 1980). The apparently continuing advance of *E. johnstonei* into the habitats of endemic *Eleutherodactylus* on St. Vincent and Grenada may be due to direct territorial competition (Pough et al., 1977; Stewart, 1977). The ranges of *E. urichi* on both Trinidad and Tobago, where *E. johnstonei* is still limited to very few individuals in the harbor area (Boos, 1979; Kenny [1980] reports these as *E. martinicensis* in error), have not changed since they were described by Schwartz (1967) and Kenny (1969).

ACKNOWLEDGMENTS

I am very grateful to C. A. George, G. Schäfer, H. H. Schwarten, T. F. Sharbel, D. von Stösser, and A. Werres for their help and companionship in the field. Most sincere thanks to H. M. Gray for memorable discussions, some inspired video work, and unfailing good humor throughout three field trips. The laboratory assistance of T. F. Sharbel is gratefully acknowledged. I thank W. R. Heyer, R. E. Lemon, D. J. Mountjoy, and H. M. Reiswig for use of equipment and technical advice. J. Ramsay shared his insights into multivariate morphometrics and rescued the statistical terminology used in this paper from the jaws of jargon. F. R. Cook, R. I. Crombie, P. Damiani, W. E. Duellman, W. R. Heyer, C. W. Myers, C. Parker, R. M. Rankin, A. Resetar, J. P. Rosado, and J. E. Simmons authorized loans of specimens or helped with identifications. Thanks to D. R. Frost for providing an electronic manuscript version of his *Amphibian Species of the World*, Second Edition. Discussions with R. Altig, R. I. Crombie, W. E. Duellman, D. M. Green, J. D. Hardy, Jr., L. A. Lowcock, and R. W. McDiarmid provided some interesting new perspectives. D. M. Green, J. D. Hardy, Jr., W. R. Heyer, L. A. Lowcock, and the late A. Schwartz made

valuable comments on the manuscript during its development. This research was supported by grants from the Hans-Krüger-Stiftung and the Studienstiftung des Deutschen Volkes, Germany, and by an NSERC Canada operating grant to D. M. Green.

LITERATURE CITED

- BARBOUR, T. 1914. A contribution to the zoögeography of the West Indies, with especial reference to amphibians and reptiles. *Mem. Mus. Comp. Zool.* 44:209–359.
- _____. 1916. The reptiles and amphibians of Grenada. *Grenada Handbook* 1916:236–243.
- _____. 1935. A second list of Antillean reptiles and amphibians. *Zoologica* 19:77–141.
- BOOS, H. 1979. The Status and Distribution of Important Reptiles and Amphibians in Trinidad and Tobago. Ministry of Agriculture, Lands, and Food Production, Port-of-Spain.
- CANADIAN COUNCIL ON ANIMAL CARE. 1980–84. Guide to the Use and Care of Experimental Animals. 2 Vols. CCAC, Ottawa.
- CLAYTON, J. W., AND D. N. TRETIK. 1972. Amine citrate buffers for pH control in starch gel electrophoresis. *J. Fish. Res. Bd. Canada* 29:1169–1172.
- DREWRY, G. E., AND A. S. RAND. 1983. Characteristics of an acoustic community: Puerto Rican frogs of the genus *Eleutherodactylus*. *Copeia* 1983:941–953.
- FROST, D. R. 1985. Amphibian Species of the World. A Taxonomic and Geographical Reference. Allen Press, Inc., and The Association of Systematics Collections, Lawrence, Kansas.

- HAIR, J. F., JR., R. E. ANDERSON, R. L. TATHAM, AND W. C. BLACK. 1992. Multivariate Data Analysis. Third Edition. Macmillan Publishing Company, New York.
- HARDY, J. D., JR. 1970. A review of recent studies of the frog, *Eleutherodactylus urichi*, with recommendations for continued research. Chesapeake Biol. Lab. Report 70-49.
- _____. 1982. Biogeography of Tobago, West Indies, with special reference to amphibians and reptiles: a review. Bull. Maryland Herpetol. Soc. 18:37-142.
- _____. 1984. Frogs, egg teeth, and evolution: preliminary comments on egg teeth in the genus *Eleutherodactylus*. Bull. Maryland Herpetol. Soc. 20:1-11.
- HARDY, J. D., JR., AND H. S. HARRIS. 1979. Occurrence of the West Indian frog, *Eleutherodactylus johnstonei*, in South America and on the island of Curaçao. Bull. Maryland Herpetol. Soc. 15:124-133.
- HOOGMOED, M. S. 1979. The herpetofauna of the Guianan Region. Pp. 241-279. In: W. E. Duellman (Ed.). The South American Herpetofauna: Its Origin, Evolution, and Dispersal. Museum of Natural History, University of Kansas, Lawrence.
- JOHNSON, M. L. 1946. Herpetological notes from Trinidad. Copeia 1946:108.
- KAISER, H. 1992. The trade-mediated introduction of *Eleutherodactylus martinicensis* (Anura: Leptodactylidae) on St. Barthélemy, French Antilles, and its implications for Lesser Antillean biogeography. J. Herpetol. 26:264-273.
- KENNY, J. S. 1969. The Amphibia of Trinidad. Stud. Fauna Curaçao Carib. Isl. 29:1-78.
- _____. 1980. Some recent animal colonizations. Living World 1979-80:27.
- LESCURE, J. 1979. Singularité et fragilité de la faune en vertébrés des Petites Antilles. C. R. Soc. Biogéogr. 482:93-109.

- _____. 1981. Contribution à l'étude des amphibiens de Guyane française. VII. *Les Eleutherodactylus* (Anura, Leptodactylidae). Rev. fr. Aquariol. 8:25-32.
- _____. 1983. Introductions passives et actives de reptiles et d'amphibiens dans les Antilles et les Guyanes. C. R. Soc. Biogéogr. 59:59-70.
- _____. 1987. Le peuplement en reptiles et amphibiens des Petites Antilles. Bull. Soc. Zool. France 112:327-342.
- LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802-832.
- LYNCH, J. D. 1979. The frogs of the genus *Eleutherodactylus* in the Andes of southern Ecuador. Misc. Publ. Mus. Nat. Hist. Univ. Kansas (66):1-62.
- MACLEAN, W. P., R. KELLNER, AND H. DENNIS. 1977. Island lists of West Indian Amphibians and Reptiles. Smithson. Herpetol. Info. Serv. (40):1-47.
- MERTENS, R. 1967. Die herpetologische Sektion des Natur-Museums und Forschungs-Institutes Senckenberg in Frankfurt a. M. nebst einem Verzeichnis ihrer Typen. Senckenb. Biol. 48A:1-39.
- MOLE, R. R., AND F. W. URICH. 1894. A preliminary list of reptiles and batrachians of the island of Trinidad. J. Trinidad Field Nat. Club 2:87-89.
- MURPHY, R. W., J. W. SITES, D. G. BUTH, AND C. H. HAUFLE. 1990. Proteins I: Isozyme electrophoresis. Pp. 45-126. In: D. M. Hillis and C. Moritz (Eds.). Molecular Systematics. Sinauer Associates, Sunderland, Massachusetts.
- NOMENCLATURE COMMITTEE OF THE INTERNATIONAL UNION OF BIOCHEMISTRY. 1984. Enzyme Nomenclature 1984. Academic Press, New York.

- POUGH, F. H., M. M. STEWART, AND R. G. THOMAS. 1977. Physiological basis of habitat partitioning in Jamaican *Eleutherodactylus*. *Oecologia* 27:285–293.
- OTTE, D., AND J. A. ENDLER (EDS.). 1989. Speciation and Its Consequences. Sinauer Associates Inc., Sunderland, Massachusetts.
- RIVERO, J. A. 1961. Salientia of Venezuela. *Bull. Mus. Comp. Zool.* 126:1–207.
- _____. 1964. The distribution of Venezuelan frogs. *Carib. J. Sci.* 4:397–405.
- SAVAGE, J. M. 1987. Systematics and distribution of the Mexican and Central American rainfrogs of the *Eleutherodactylus gollmeri* group (Amphibia: Leptodactylidae). *Fieldiana Zool., N. Ser.* (33):1–57.
- SCHMIDT, K. P. 1932. Reptiles and amphibians of the Mandel Venezuelan expedition. *Pub. Field Mus. Nat. Hist., Zool. Ser.* 18:159–163.
- SCHWARTZ, A. 1967. Frogs of the genus *Eleutherodactylus* in the Lesser Antilles. *Stud. Fauna Curaçao Carib. Isl.* 23:1–62.
- SCHWARTZ, A., AND R. W. HENDERSON. 1991. Amphibians and Reptiles of the West Indies: Description, Distribution and Natural History. University of Florida Press, Gainesville, Florida.
- STEWART, M. M. 1977. The role of introduced species in a Jamaican frog community. *Actas IV Simpos. Int. Ecol. Trop.* 1:110–146.
- STEWART, M. M., AND G. E. MARTIN. 1980. Coconut-husk piles—a unique habitat for Jamaican terrestrial frogs. *Biotropica* 12:107–116.
- WELLS, K. D. 1981. Territorial behavior of the frog *Eleutherodactylus urichi* in Trinidad. *Copeia* 1981:726–728.

APPENDIX 1

Specimens examined

This list excludes those specimens whose identities have been questioned. New taxonomic alignments and locality data for these is in Appendix 2. Localities from which specimens were examined electrophoretically are indicated by asterisks (*).

Eleutherodactylus euphronides (84).—GRENADA: Parish of St. Andrew—Grand Etang, AMNH 74536–44, KU 93337–38, 265429–44, MCZ 43229 (holotype), MCZ 2910–30, 2932–35, 2961–62, 2976, 31560, 51762–64, 51766–67, UIMNH 61641–43; *Cable and Wireless station near Mt. St. Catherine, ca. 4 km NW Paraclete, alt ca. 650 m, NMC 35009–1–8, 35010–1–10. Parish of St. David—Les Avocats waterworks, alt. ca. 400 m, NMC 35008; 1 mi N Vincennes, KU 265441. Parish of St. George—8 mi NE St. George's, KU 265442–44.

Eleutherodactylus johnstonei (136).—GRENADA: Parish of St. George—St. George's, MCZ 2759 (syntypes); St. George's, St. Ann's Guest House, alt. ca. 60 m, NMC 35011–1–15. Parish of St. Patrick—2.4 km SW Sauteurs, alt. ca. 150 m, NMC 35012–1–5. Parish of St. David—Bacolet Estate, 450 m beyond Petit Bacaye intersection, alt. ca. 30 m, NMC 35013–1–9; Les Avocats Waterworks, alt. ca. 400 m, NMC 35014–1–17. Parish of St. Andrew—Grand Etang Lake parking lot, alt. ca. 500 m, NMC 35015–1–20, 35016–1–5; 1.2 km W Nianganfoix Estate, alt. ca. 300 m, NMC 35017–1–5; Cable and Wireless station near Mt. St. Catherine, ca. 4 km NW Paraclete, alt ca. 650 m, NMC 35018–1–2, 35019. ST. VINCENT: Parish of St. George—Kingstown, Kingstown Park Guest House, NMC 35020–1–14. Parish of St. Andrew—Lowrey, 1.5 km NE Vermont, NMC 35021–1–19. Charlotte Parish—

ca. 4 km W Orange Hill at end of Soufriere jeep track, NMC 35022-1-19; Mt. William, 800 m W Byera Hill tunnel, NMC 35023-1-12.

Eleutherodactylus marmoratus (2).—GUIANE FRANÇAISE: "between Sophie and La Grève," MCZ 44557-58.

Eleutherodactylus cf. *rozei* (3).—TOBAGO: Parish of St. John—mile marker 27 3/4 on Charlotteville-Bloody Bay road, MCZ 86950, 86952-53.

Eleutherodactylus shrevei (42).—ST. VINCENT: Parish of St. Andrew—Lowrt [sic], 1000 ft, KU 265445-54, MCZ 43230 (holotype), UIMNH 61644-46. Charlotte Parish—*ca. 5.5 km W Orange Hill on La Soufriere summit track, alt. ca. 750 m, NMC 35027-1-19; Edge of Soufriere crater, alt. ca. 950 m, MCZ 19814-17, 51452-54, 51456.

Eleutherodactylus terraebolivaris (36).—COLOMBIA: Amazonas State, Rio Sencella, tributary of the Upper Caqueta [River], USNM 144737; Amazonas State, Rio Caqueta, Araracuara, USNM 144738. TOBAGO: Hills above Man-of-War Bay, 1.5-3.5 km ENE Charlotteville, AMNH 87408, 87412, 87427-28, 87431, KU 265455; Parish of St. John, mile marker 27 3/4 on Charlotteville-Bloody Bay road, USNM 167609-13; ca. 7 km N Roxborough, NMC 35024, 35025-1-5, 35026-1-16. VENEZUELA: Rancho Grande, MCZ 31062 (holotype); Miranda State, Los Canales, Planta Electrica de Naiduata, USNM 128807-08, 128812-14 (paratypes).

Eleutherodactylus urichi (24).—TOBAGO: *Main Ridge, ca. 7 km N Roxborough, NMC 35028, 35029-1-2, KU 265456. TRINIDAD: *N Arima Valley, NMC 35030-1-2, 35031-1-10, 35032-1-6, KU 265457-58.

APPENDIX 2

Hitherto problematic specimens

referred to *Eleutherodactylus johnstonei*.—GUYANA: Georgetown, AMNH 18981, 21413; Kamakusa, 21403-04.

referred to *Eleutherodactylus* sp. A.—VENEZUELA: Mt. Turumiquire, 7000-8000 ft, FMNH 17777-82, 17785-87. GUYANA: Onora Creek, AMNH 43669; Shudikarwan, AMNH 46247.

referred to *Eleutherodactylus* sp. B.—VENEZUELA: Mt. Turumiquire, 7000-8000 ft, FMNH 17784.

referred to *Eleutherodactylus* sp. C.—GUYANA: Demerara River, AMNH 13534-36.

referred to *Pleurodema brachyops*.—VENEZUELA: Mt. Turumiquire, 7000-8000 ft, FMNH 17783.

APPENDIX 3

Key to Eleutherodactylus species native to the Eastern Caribbean.

- 1a Hind feet unwebbed.....2
- 1b Hind feet webbed.....*E. barlagnei*
- 2a Disks on fingers III and IV \geq twice as wide as digit3
- 2b Disks on fingers III and IV $<$ twice as wide as digit5
- 3a Disks on toes \geq twice as wide as digit4
- 3b Disks on toes $<$ twice as wide as digit*E. terraebolivaris*
- 4a Palmar tubercles distinct from each other, ventral surface of finger disks darkly pigmented, supratympanic fold pronounced *E. shrevei*
- 4b Palmar tubercles confluent, ventral surface of finger disks unpigmented, weak supratympanic fold..... *E. euphronides*
- 5a Disk on finger I reduced.....6
- 5b Disc on finger I not reduced.....7
- 6a Disk of finger III much smaller than tympanum, upper portion of iris blue in life*E. urichi*
- 6b Disk of finger III equal or smaller in size to tympanum, upper portion of iris bronze in life*E. cf. rozei*
- 7a Posterior part of venter replete with areolae..... *E. johnstonei*
- 7b Few areolae on venter.....8
- 8a Interorbital distance \geq length of eye.....9
- 8b Interorbital distance about 4/5 length of eye..... *E. pinchoni*
- 9a Toe V reaches distal tubercle on toe IV*Eleutherodactylus* sp. (Dominica)
- 9b Toe V does not reach distal tubercle on toe IV *E. martinicensis*

TABLE 1. Protein loci and electrophoretic conditions.

Protein ^a	Enzyme Commission		Electrophoretic conditions ^c
	Locus ^a	Number ^b	
1. Aconitate Hydratase	ACOH	4.2.1.3	1
2. Aspartate Aminotransferase (2 loci)	AAT	2.6.1.1	2
3. Creatine Kinase (2 loci)	CK	2.7.3.2	2
4. Dihydrolipoamide Dehydrogenase	DDH	1.8.1.4	2
5. Dipeptidase (leucylalanine)	PEP (LA)	3.4.13.11	1
6. Fumarate Hydratase	FUMH	4.2.1.2	2
7. Glucose Dehydrogenase	GCDH	1.1.1.118	1
8. Glucose-6-phosphates Isomerase	GPI	5.3.1.9	2
9. Glyceraldehyde-3-phosphate Dehydrogenase	GAPDH	1.2.1.12	2
10. Glycerol-3-phosphate Dehydrogenase	G3PDH	1.1.1.8	2
11. Hexokinase	HK	2.7.1.1	1
12. L-Iditol Dehydrogenase	IDDH	1.1.1.14	1
13. Isocitrate Dehydrogenase (2 loci)	IDH	1.1.1.42	1
14. L-Lactate Dehydrogenase (2 loci)	LDH	1.1.1.27	2
15. Malate Dehydrogenase (2 loci)	MDH	1.1.1.37	1
16. Mannose-6-phosphate Isomerase (2 loci)	MPI	5.3.1.8	1
17. Peptidase-B (L-leucylglycylglycine)	PEP (LGG)	3.4.11.4	1
18. Phosphoglucomutase	PGM	2.7.5.1	1
19. Phosphogluconate Dehydrogenase	PGDH	1.1.1.44	1
20. Superoxide Dismutase	SOD	1.15.1.37	1

^aNomenclature Committee of the International Union of Biochemistry (1984), modified according to Murphy et al. (1990).

^bNomenclature Committee of the International Union of Biochemistry (1984).

^c(1) Tris-citrate pH 8.0, 80 mA, 6 h; (2) Amine citrate pH 6.1 (Clayton and Tretiak, 1972), 65 mA, 6 h.

TABLE 2. List and description of twenty measurements taken from 334 specimens of Eastern Caribbean *Eleutherodactylus*. All measurements were log-transformed before discriminant function analysis.

	Measurement	Abbreviation	Description
1.	Head width	HW	measured across head between anterior edges of tympana
2.	Eye diameter	ED	greatest distance from anterior to posterior
3.	Eye–Naris distance	EN	anterior edge of eye to posterior edge of naris
4.	Tympanum diameter	TD	from anterior to posterior extreme
5.	Tympanum–Eye distance	TE	shortest distance from anterior edge of tympanum to posterior edge of eye
6.	Interorbital distance	IOD	shortest distance between eye sockets across the skull
7.	Snout length	SL	tip of snout to intersection with interorbital distance
8.	Internarial distance	IN	measured between medial edges of nares
9.	Tympanum–Naris distance	TN	anterior edge of tympanum to posterior edge of naris
10.	Snout–Vent length	SVL	-
11-14.	Finger lengths	F1-4	-
15.	Hand length	HL	tip of third finger to wrist
16.	Length of longest toe	LT	-
17.	Foot length	FL	tip of longest toe to back of heel
18.	Femur length	FL	anus to knee
19.	Tibia length	TL	knee to heel
20.	Radioulnar length	RU	wrist to elbow

TABLE 3. Group assignments for 259 specimens of *Eleutherodactylus johnstonei* from Grenada (jGRE), St. Vincent (jVIN), *E. euphronides comb. nov.* (EUP), and *E. shrevei comb. nov.* (SHR), from a multiple discriminant function analysis (MDA) of 20 metric characters. Rows are MDA predictions, columns are actual groupings. Differences between groupings tested significant at $P \leq 0.001$ (Pearson chi-square).

	jGRE	jVIN	EUP	SHR	Total
jGRE	58	11	0	0	69
jVIN	13	51	0	0	64
EUP	0	0	65	7	72
SHR	0	0	19	35	54
Total	72	62	84	42	259

TABLE 4. Discriminant loadings from a multiple discriminant function analysis of twenty length measurements of *Eleutherodactylus euphronides comb. nov.*, *E. shrevei comb. nov.*, and two populations of *E. johnstonei* from the southern Lesser Antilles. Characters with the relatively greatest discriminating power for each discriminant function (DF) are marked with asterisks (*). Cutoff values were arbitrarily assigned at 0.800 (DF1), and + or - 0.100 (DF2 and DF3). Abbreviations of measurements are listed in Table 2.

	DF 1	DF 2	DF 3
log HW	0.679	0.035	0.096
log ED	0.859*	0.113*	0.123*
log EN	0.651	0.159*	0.157*
log TD	0.528	0.048	-0.206*
log TE	0.491	-0.224*	-0.003
log IOD	0.545	0.167*	0.033
log SL	0.763	0.084	0.147*
log ID	0.782	0.005	0.128*
log TN	0.788	0.093	0.144*
log SVL	0.567	0.048	0.221*
log F1	0.823*	-0.064	-0.021
log F2	0.796	-0.038	-0.006
log F3	0.811*	0.056	-0.058
log F4	0.779	0.021	0.005
log HL	0.828*	0.057	0.006
log LT	0.847*	-0.083	0.064
log FL	0.810*	0.064	0.066
log FEM	0.803*	0.072	0.113*
log TIB	0.835*	0.047	0.117*
log RU	0.587	0.162*	0.071

TABLE 5. Group assignments for 186 specimens of *Eleutherodactylus euphronides* comb. nov. (EUP), *E. shrevei* comb. nov. (SHR), *E. terraebolivaris* (TER), and *E. urichi* s. nov. (URI) from a multiple discriminant function analysis (MDA) of 20 metric characters. Rows are MDA predictions, columns are actual groupings. Differences between groupings tested significant at $P \leq 0.001$ (Pearson chi-square).

	TER	URI	EUP	SHR	Total
TER	34	0	2	3	39
URI	0	21	0	0	21
EUP	1	0	62	6	69
SHR	4	0	20	33	57
Total	39	21	84	42	186

TABLE 6. Discriminant loadings from a multiple discriminant function analysis of twenty length measurements of *Eleutherodactylus euphronides comb. nov.*, *E. shrevei comb. nov.*, *E. terraebolivaris*, and *E. urichi s. nov.* from the southeastern Caribbean. Characters with the relatively greatest discriminating power for each discriminant function (DF) are marked with asterisks (*). Cutoff values were arbitrarily assigned at -0.400 (DF1), 0.600 (DF2), and + or - 0.300 (DF3 and DF4). The negative value of the size function DF1 in this analysis due to the input of log-transformed data in the building of the discriminant functions. The relative contribution of size is still the most powerful in discriminating between the studied taxa; however, the contributions are affecting the function in the opposite way as, for example, DF1 in Table 2. Abbreviations of measurements are listed in Table 2.

	DF 1	DF 2	DF 3	DF 4
log HW	-0.340	0.471	0.190	-0.371
log ED	-0.382	0.525	0.059	-0.329
log EN	-0.104	0.667	0.146	-0.269
log TD	0.018	0.512	0.486	-0.035
log TE	-0.092	-0.249	-0.368	-0.375
log IOD	-0.177	0.406	0.314	-0.392
log SL	-0.193	0.631	0.144	-0.321
log ID	-0.279	0.560	0.146	-0.343
log TN	-0.270	0.624	0.079	-0.275
log SVL	-0.209	0.577	0.140	-0.412
log F1	-0.512	0.600	0.255	-0.242
log F2	-0.473	0.551	0.249	-0.267
log F3	-0.478	0.531	0.284	-0.217
log F4	-0.507	0.486	0.241	-0.321
log HL	-0.422	0.566	0.259	-0.287
log LT	-0.392	0.646	0.245	-0.327
log FL	-0.311	0.630	0.274	-0.360
log FEM	-0.204	0.666	0.213	-0.330
log TIB	-0.263	0.674	0.240	-0.380
log RU	-0.213	0.499	0.224	-0.318

TABLE 7. Means and extremes (in mm) of snout-vent length (SVL), head width (HW), eye-naris distance (EN), tibia length (TIB), and two ratios indicative of body proportion for male and female specimens of *Eleutherodactylus euphronides* comb. nov., *E. shrevei* comb. nov., and *E. urichi* s. nov.

Males	<i>n</i>	SVL	HW	EN	TIB	TIB/SVL	HW/SVL
<i>E. euphronides</i> (Grenada)	41	22.7 (17.7–27.0)	9.5 (7.2–11.5)	2.7 (1.8–4.2)	12.6 (10.1–14.7)	0.557 (0.493–0.613)	0.419 (0.377–0.470)
<i>E. shrevei</i> (St. Vincent)	16	24.9 (21.0–28.0)	10.0 (8.2–15.7)	2.9 (1.9–4.1)	13.4 (11.2–19.5)	0.540 (0.489–0.595)	0.402 (0.376–0.441)
<i>E. urichi</i> (Tobago)	3	19.3 (17.8–22.6)	7.4 (6.7–8.7)	2.2 (1.7–2.6)	10.4 (8.9–12.0)	0.539 (0.500–0.569)	0.382 (0.373–0.394)
<i>E. urichi</i> (Trinidad)	17	19.1 (17.5–20.7)	7.5 (7.0–8.4)	2.3 (1.9–2.7)	9.4 (8.4–10.5)	0.493 (0.415–0.535)	0.394 (0.360–0.447)
Females	<i>n</i>	SVL	HW	EN	TIB	TIB/SVL	HW/SVL
<i>E. euphronides</i> (Grenada)	31	28.3 (19.4–39.4)	12.1 (8.0–17.4)	3.4 (1.9–5.1)	15.4 (10.1–21.2)	0.545 (0.491–0.594)	0.427 (0.400–0.454)
<i>E. shrevei</i> (St. Vincent)	17	30.0 (19.0–40.1)	12.6 (7.6–17.5)	3.6 (2.3–5.3)	16.2 (10.4–21.7)	0.543 (0.494–0.571)	0.417 (0.376–0.454)
<i>E. urichi</i> (Tobago)	1	25.0	9.3	2.8	12.1	0.486	0.370
<i>E. urichi</i> (Trinidad)	1	23.1	9.1	2.9	11.8	0.511	0.394

TABLE 8. Allelic variants at 20 polymorphic allozyme loci diagnostic for *Eleutherodactylus euphronides* comb. nov., *E. shrevei* comb. nov., and *E. urichi* s. nov. Four loci have fixed differences between *E. euphronides* and *E. shrevei*, and thirteen are fixed different between these species and *E. urichi*. Six other investigated loci (ACOH, G3PDH, IDDH, LDH-2, PEP[LGG], SOD) were found to be monomorphic. Differences fixed between *E. urichi* and the Lesser Antilles are indicated by asterisks (*), between *E. euphronides* and *E. shrevei* by daggers (†).

Locus	<i>E. euphronides</i>	<i>E. shrevei</i>	<i>E. urichi</i>
AAT-1	b	a,b	b,c
AAT-2	a,b	b	c*
CK-1	a,c	b†	d*
CK-2	a,b,c,d	d	e*
DDH	c,d	a,b†	e*
FUMH	a	a	b*
GAPDH	b	b	a*
GCDH	a,b	b	a
GPI	b	b,c	a*
HK	c	a,c	b*
IDH-1	b,c	a,b,c	d*
IDH-2	a	a	b*
LDH-1	b	b	a*
MDH-1	a	c†	a,b
MDH-2	a	a,b	b
MPI-1	a	a,b	b
MPI-2	b	a,b	b
PEP (LA)	a	b†	c*
PGDH	b	b	a*
PGM	a,b	a	b

FIGURE 1. Localities for populations of *Eleutherodactylus euphronides* comb. nov., *E. shrevei* comb. nov., and *E. urichi* s. nov. Open circles are localities for which we have confirmed the presence of the species. Filled circles are records of other workers, as reported in the literature. Type localities are marked with an asterisk (*). No exact type locality is given in the original description of *E. urichi*. (A) St. Vincent. The Soufriere locality of Schwartz (1967) is marked with an arrow. The stippled line indicates the present extent of the crater and surrounding area, which in 1992 supported only sparse primary growth on volcanic rubble. (B) Tobago. (C) Grenada. (D) Trinidad.

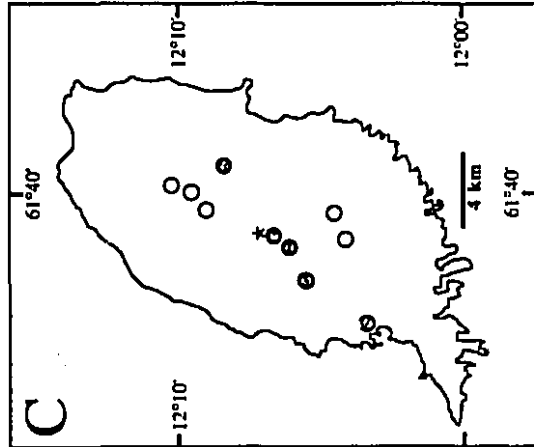
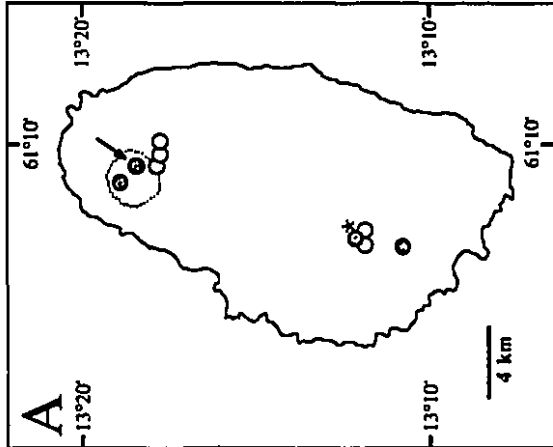
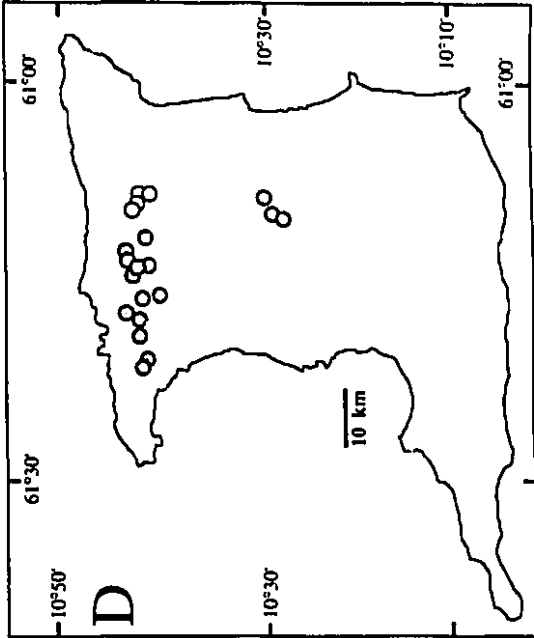
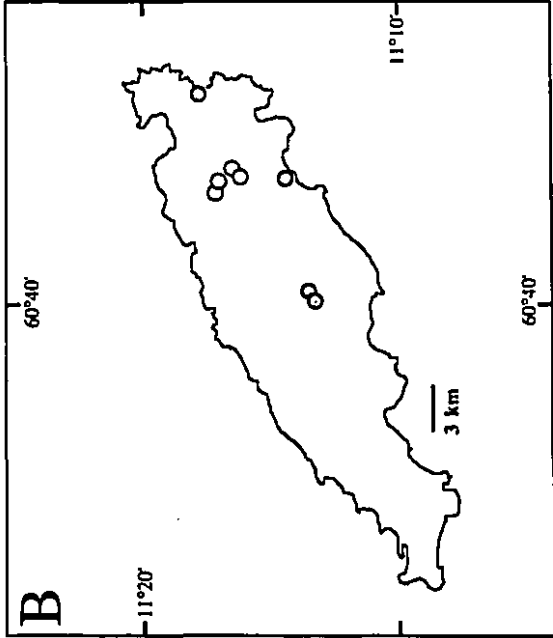


FIGURE 2. Graphic representations of species clusters for *Eleutherodactylus euphronides* *comb. nov.* (circles), *E. johnstonei* St. Vincent (dark dotted squares), *E. johnstonei* Grenada (light dotted squares), and *E. shrevei* *comb. nov.* (squares). Graphs (B) to (D) depict plots of discriminant scores for populations of *E. euphronides* and *E. shrevei*. Holotypes for *E. euphronides* (H_{eup}) and *E. shrevei* (H_{shr}) are indicated. (A) Plot of discriminant scores (DS) 2 against DS1 of a combined discriminant function analysis (DFA) for populations of three species, from Grenada and St. Vincent. (B) Plot of DS2 against DS1. (C) Plot of DS3 against DS1. (D) Plot of DS3 against DS2.

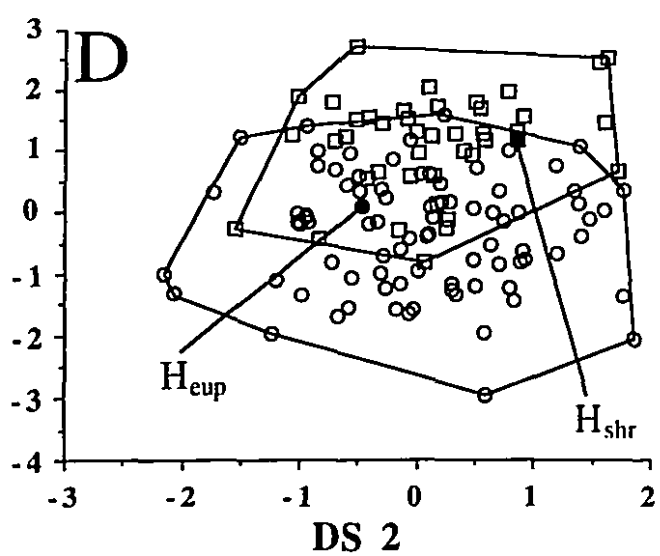
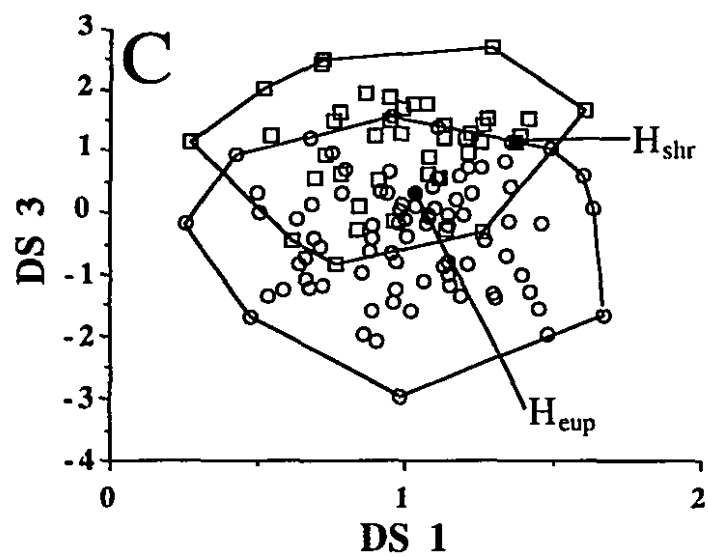
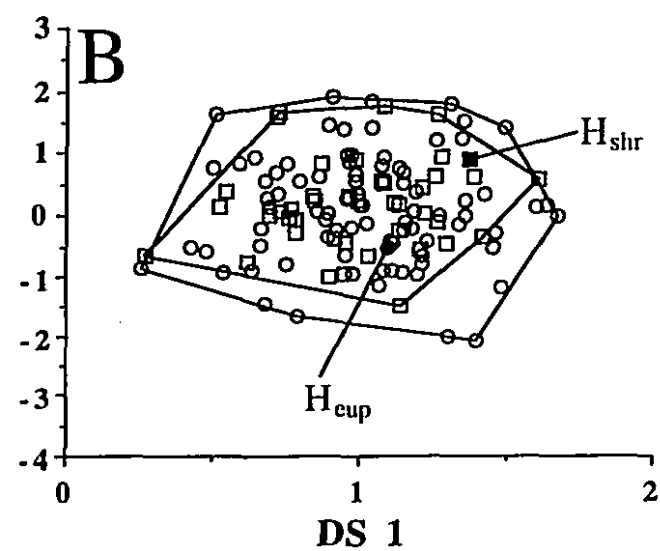
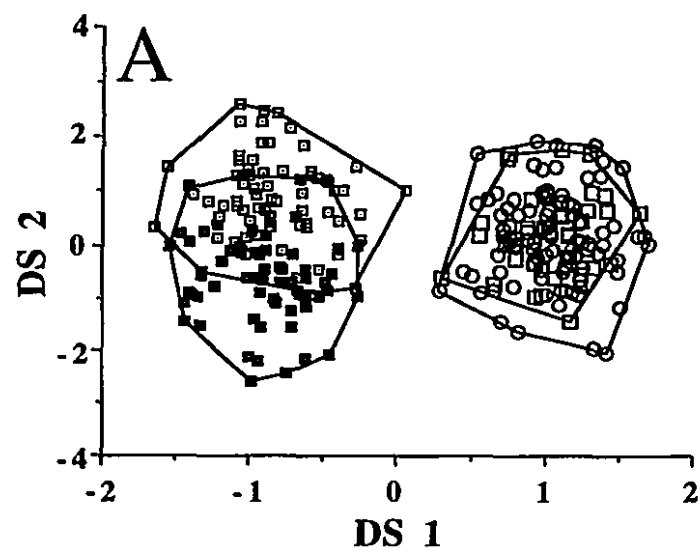


FIGURE 3. Graphic representations of species clusters from multiple discriminant function analyses (MDAs) for *Eleutherodactylus euphronides* comb. nov. (circles), *E. shrevei* comb. nov. (squares), *E. terraebolivaris* (grey triangles), *E. urichi* s. nov. (Trinidad: open triangles; Tobago: solid triangles), and several unidentified specimens. Species morphospace is enclosed by polygons. (A) Plot of discriminant scores (DS) 2 against DS1. Specimens denoted by small crosses and labeled "MCZ specimens" do not align with any other taxon; they may be referable to *E. cf. rozei* (Hardy, 1982). The labeled open triangle among the cluster of *E. terraebolivaris* denotes Schwartz's misidentified Tobago specimen. (B) Plot of DS2 against DS1 for populations of *E. euphronides* and *E. urichi*. (C) Plot of DS2 against DS1 for populations of *E. shrevei* and *E. urichi*. (D) Plot of DS3 against DS2 for populations of *E. euphronides* and *E. shrevei*. (E) Plot of DS4 against DS3 for populations of *E. euphronides* and *E. shrevei*. (F) Plot of DS2 against DS1 for Eastern Caribbean *Eleutherodactylus*. Only polygons are shown to clarify the positions of specimens from Guyana (x) and Venezuela (+). (G) Plot of DS2 against DS 1 for populations of *E. johnstonei* and *E. terraebolivaris*, with controversial South American specimens identified by numbers (AMNH: black squares; FMNH: grey circles). Four specimens are identified as *E. johnstonei*. The cluster of grey circles presumably denotes a distinct species, possibly *E. marmoratus*.

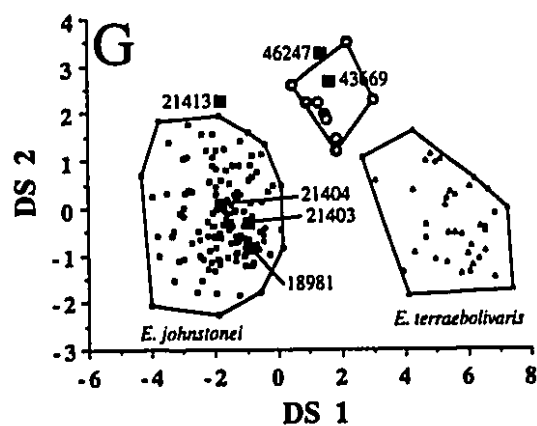
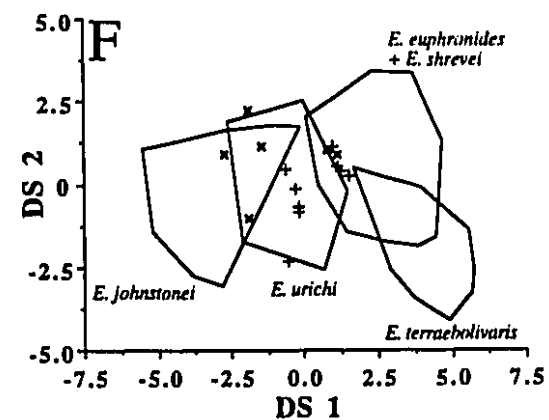
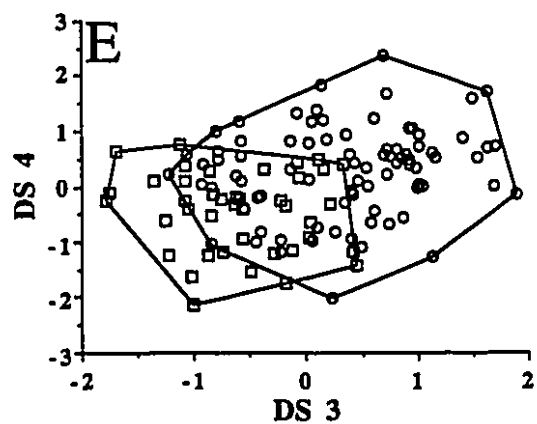
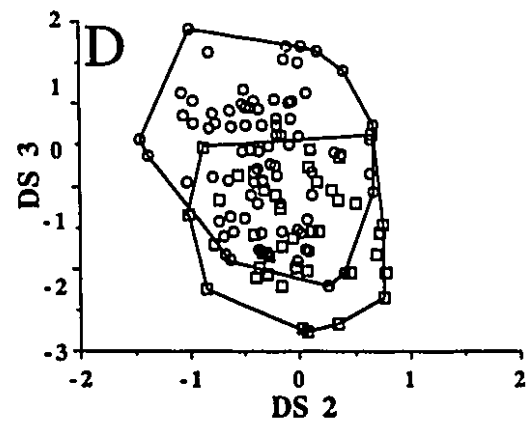
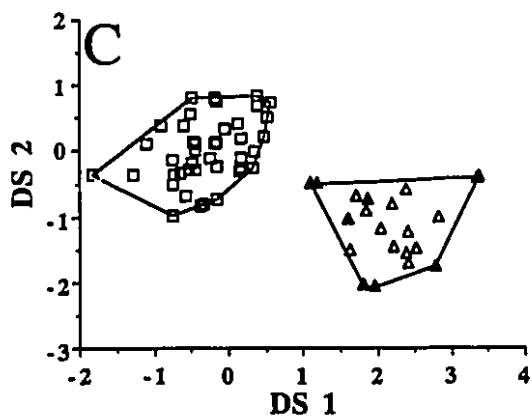
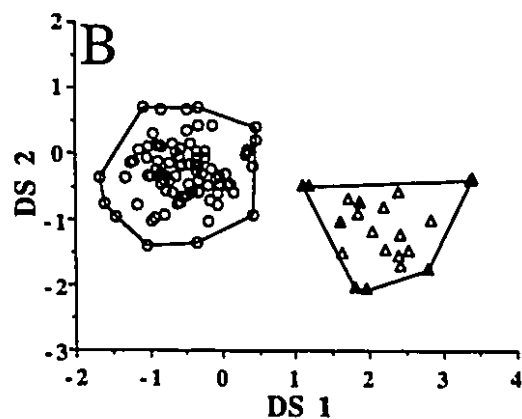
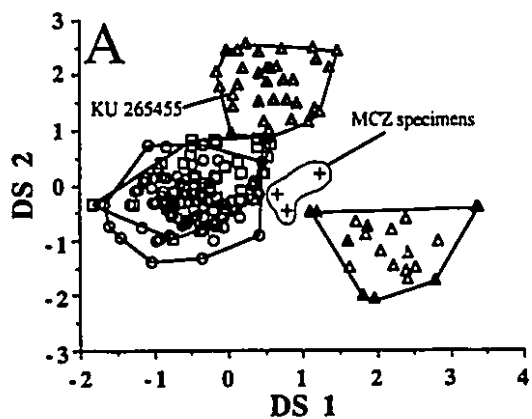


FIGURE 4. Audiospectrograms of the calls of *Eleutherodactylus* from the Eastern Caribbean, shown at identical scales. Horizontal axis is time, and call (F) is 0.33 seconds long. Recordings were made at temperatures around 24°C (\pm 2°C). Calls shown in (A) and (B) are of *E. urichi* s. nov. from Trinidad. The single notes shown in A serve as this species' universal advertisement call. The calls in (B) are part of an extended interchange of agonistic calls between two *E. urichi* males (M_1 , M_2). These clicks can be considered territorial as well as agonistic (Wells, 1981). Both males called rhythmically and sequentially until a physical confrontation ensued. Calls of *E. euphronides* comb. nov. from Grenada and of *E. shrevei* comb. nov. from St. Vincent are shown in (C) and (D), respectively. In both calls, clicks are the dominant component, but *E. shrevei* also sometimes issues a second, extended call at higher frequency (E). *Eleutherodactylus johnstonei* has an entirely different two-note call (F).

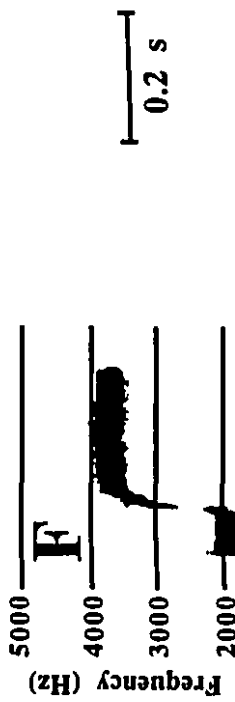
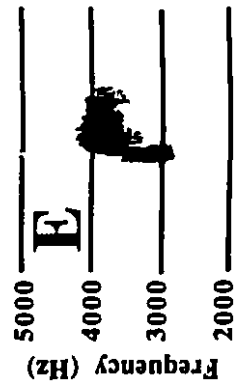
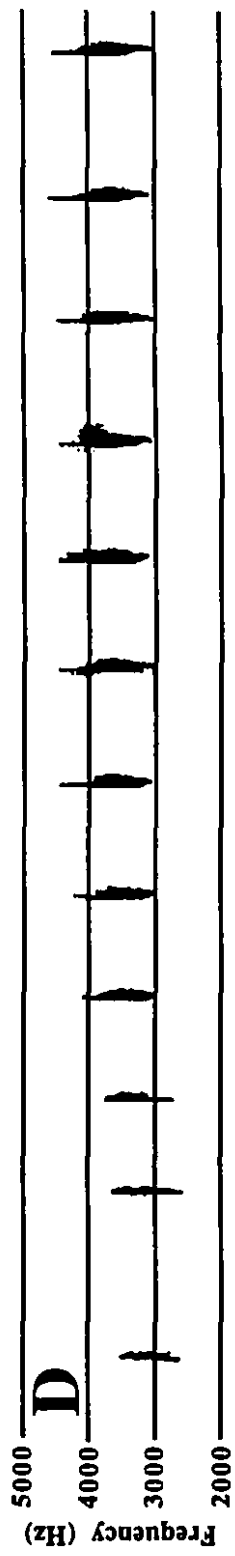
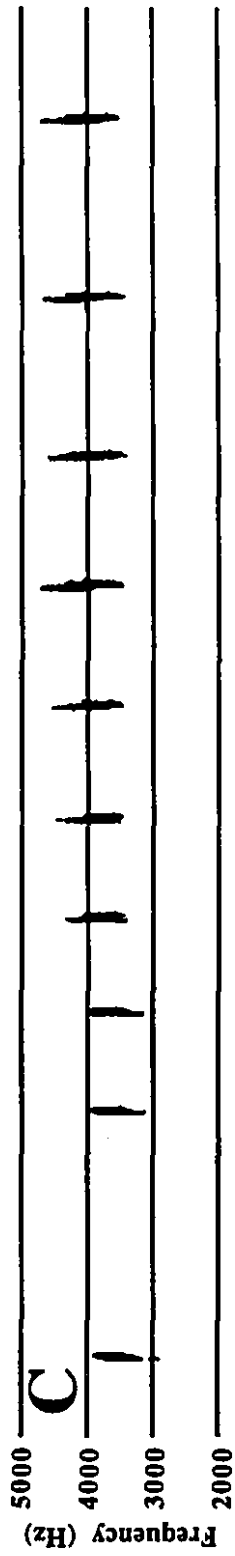
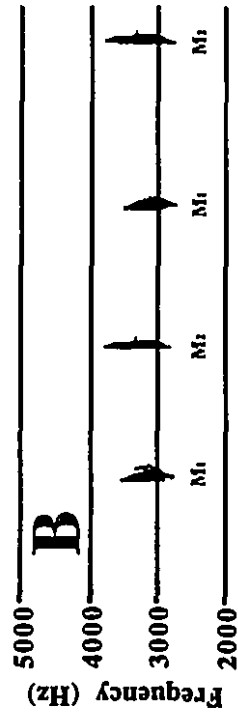
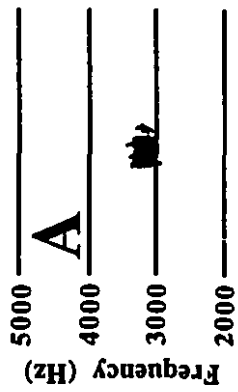


FIGURE 5. (A) Right hand of male *Eleutherodactylus urichi* s. nov. (NMC 35032-5), and (B) left foot of male *E. urichi* (NMC 35032-6). Scale bars = 1 mm. (C) Right hand and (D) left foot of female *E. euphronides* comb. nov. (NMC 35010-3). Scale bars = 2 mm. (E) Right hand and (F) left foot of female *E. shrevei* comb. nov. (NMC 35027-3). Scale bars = 2 mm.

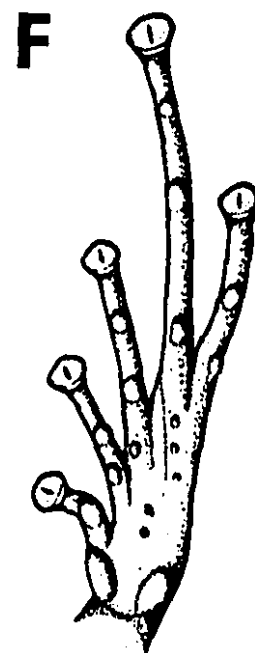
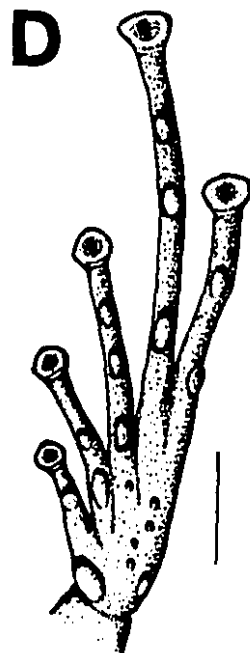
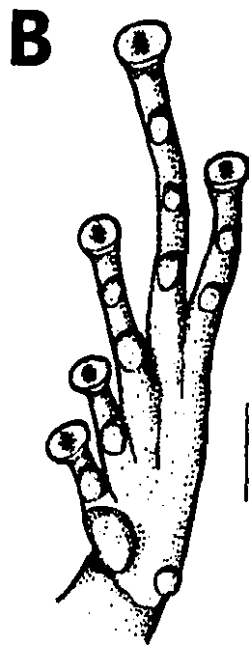
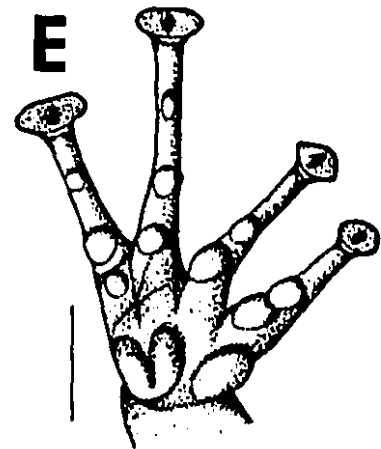
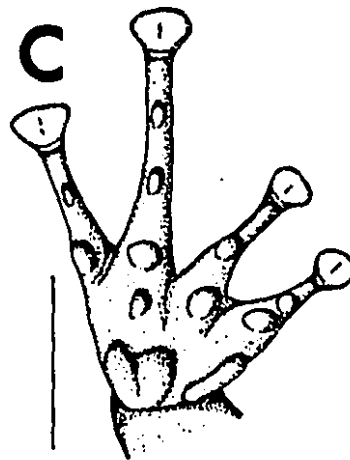
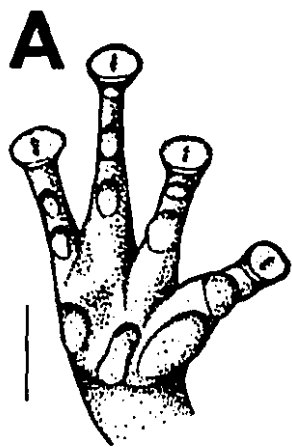


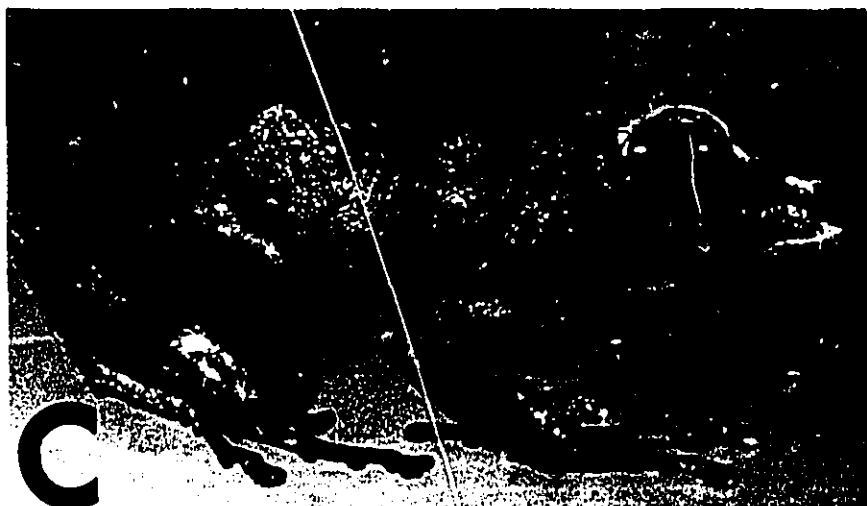
FIGURE 6. (A) Male specimen of *Eleutherodactylus urichi* s. nov. (NMC 35032-1), SVL 20.7 mm. (B) Female specimen of *E. euphronides* comb. nov. (NMC 35010-3), SVL 29.7 mm. (C) Female specimen of *E. shrevei* comb. nov. (NMC 35027-5), SVL 40.1 mm.



A



B



C

3

A New Species of *Colostethus* (Anura: Dendrobatidae) from Martinique, French Antilles

Published as: Kaiser, H., L. A. Coloma, and H. M. Gray. A new species of *Colostethus* (Anura: Dendrobatidae) from Martinique, French Antilles. *Herpetologica*. *In press*.

PREAMBLE CHAPTER 3

During a visit to Martinique in 1990, I recorded a call which was not identifiable as either *Eleutherodactylus johnstonei* or *E. martinicensis*. Having looked at the audiospectrogram in the lab, it became necessary to return and investigate so that I would not miss any unknown species of *Eleutherodactylus* in the systematic study. After an unsuccessful evening's search near the site where the initial recording had been made, I resolved to see if the call could be heard elsewhere. Further searching over a two-day period resulted in the capture of two tiny frogs, obviously non-*Eleutherodactylus*.

ABSTRACT

Field work on Martinique, French Antilles, in the summer of 1990 led to the discovery of an undescribed species of *Colostethus* (Anura: Dendrobatidae). The species is a small (snout-vent length < 20 mm), brown frog which can easily be identified by its distinct ventral coloration. The venter is a uniform pale orange in life, with males having a dark throat and a black collar covering the entire hyoid region. Toe webbing is reduced to barely perceptible vestigial webbing between toes III and IV. The species has a crepuscular activity cycle and a distinctive, high-pitched call. Its habitat is restricted to the upper slopes of Montagne Pelée on the island of Martinique in the central Lesser Antilles. Its discovery is remarkable because it was not recognized previously on this otherwise herpetologically well-known island, and because it is the only known member of the frog family Dendrobatidae endemic to an oceanic island.

INTRODUCTION

Studies of Lesser Antillean frogs and amphibian check-lists (Hedges and Thomas, 1989; Schwartz, 1967, 1969; Schwartz and Henderson, 1985, 1991; Schwartz and Thomas, 1975; Schwartz et al., 1978) have previously identified only five species of *Eleutherodactylus*, two species of *Leptodactylus*, and the introduced *Bufo marinus* and *Scinax rubra* on these islands. In January 1990, during field work looking for *Eleutherodactylus*, I recorded a peculiar call near sunset on the slopes of Montagne Pelée in the northern part of Martinique, but was at the time unable to find the animal responsible. A further investigation six months later led to the fortuitous discovery of a previously undescribed dendrobatid frog in the genus *Colostethus*.

MATERIALS AND METHODS

Specimens reported here are deposited in the Canadian Museum of Nature (NMC), University of Kansas Museum of Natural History (KU), the American Museum of Natural History (AMNH), the Museum of Comparative Zoology (MCZ), the United States National Museum of Natural History (USNM), and the Museo de Zoología de la Pontifica Universidad Católica del Ecuador (QCAZ). Snout-vent length (SVL) and other metric characters were measured with Vernier calipers from specimens fixed in formalin and preserved in 70% ethanol. Sound recordings were made using a SONY professional walkman WM-D3. Audiospectrograms were made with a Kay Elemetrics Corp. digital sonagraph 7800. Diagnosis and description follow the standard established for *Colostethus* by Duellman and Simmons (1988), with the addition of the potentially phylogenetically important larval characterization. Degree of toe webbing was assessed using the toe webbing formula of Savage and Heyer (1967), as modified by Myers and Duellman (1982).

Colostethus chalcopis sp. nov.

Figs. 1–5

Holotype.—NMC 33675, an adult male from a ravine, approx. 3 km (by road) NE Morne Rouge, Martinique, French Antilles (ca. 14° 48' N, 61° 8' W, approx. elev. 500 m). The specimen was collected on 20 August 1990 by H. Kaiser and H. M. Gray.

Paratypes.—NMC 33674, a female topotype collected on 19 August 1990 by H. Kaiser and H. M. Gray. Fourteen other paratopotypes (NMC 33902-1-9 [seven females, two juveniles], AMNH A135397-99 [two females, one juvenile], KU 218528-29 [one female, one juvenile]) were collected on 9 August 1991 by H. Kaiser and H. M. Gray.

Distribution.—Known only from ravines on the slopes of Montagne Pelée, Martinique, French Antilles.

Diagnosis.—A very small species of *Colostethus* with the following diagnostic characters: (1) SVL, male 17.4 mm, females 16.1–18.4 mm ($\bar{x} = 17.5$, $n = 7$); (2) disc on Finger III expanded; (3) Finger I equal in length or slightly shorter than Finger II; (4) fringe absent on Finger II; (5) disc on Toe IV expanded; (6) fringe absent on Toe IV; (7) outer tarsal fold absent; (8) toe webbing formula III3-4I/2IV, with webbing vestigial and barely perceptible (Fig. 3B); (9) dorsolateral stripe absent; (10) oblique lateral stripe absent; (11) ventrolateral stripe absent; (12) markings on throat and chest present in some animals; (13) belly uniformly pale orange; (14) darkly pigmented throat with black collar covering entire hyoid region only present in males, in addition to faint reticulation on abdomen, discrete marks absent on gular-chest region in females (Fig. 2); (15) third finger not swollen in males; (16) nidicolous (Altig and Johnston, 1989) endotrophic larvae (Chapter 4).

At the type locality, this species can only be confused with *Eleutherodactylus johnstonei* and *E. martinicensis*. In particular, juveniles of those species and young *Colostethus chalcopis* (SVL < 10 mm) with not yet fully developed ventral coloration

are remarkably similar in color and habit. However, the presence of digital scutes (Fig. 1) will readily allow differentiation. In addition, an inspection of head shape may facilitate identification in the field, because the snout is more elongate in *Eleutherodactylus*.

La Marca (1984a, b, 1989) and Myers et al. (1991) attempted to determine phylogenetically close taxa using the presence of a throat collar. Although Myers et al. (1991) cautioned against the use of color patterns because of the problems with determining homology, La Marca (1992) nevertheless defined the genus *Mannophryne* for the collared *Colostethus* using a variety of pattern and behavioral characters in addition to several conventional morphological features. Clearly, until a greater body of evidence is available to determine actual synapomorphies of monophyletic subsets within this genus, generic recognition of any particular subgroup, such as the collared morphotypes, is likely premature (see discussion). We therefore compare *C. chalcopis* to congeneric species possessing a throat collar as well as to those displaying a majority of its characteristics.

Among the collared *Colostethus*, only *C. oblitteratus* has extensive webbing (*C. guatapoensis* and *C. oblitteratus* were synonymized by Rivero [1988]). The rest have clearly different toe webbing formulae (La Marca, 1984a), extending much beyond the barely perceptible webbing between toes III and IV of *C. chalcopis*. Furthermore, the collar is quite distinct in females of other collared *Colostethus*; it is sometimes obscured in males due to the dark throat pigmentation (La Marca, 1984a), which also occurs in *C. chalcopis* (Fig. 2). Only in the monotypic *Aromobates nocturnus* is the collar sometimes absent in females (Myers et al., 1991). *Colostethus chalcopis* also differs from other collared *Colostethus* by its diminutive size. There are three species which

by size, body aspect, and general morphology come close to *C. chalcopis*: *C. alagoanus*, *C. mystax*, and *C. pumilus*. These all have unwebbed toes, but neither has a throat collar, and none share the peculiar dorsal pattern found in *C. chalcopis*: occurrence of dark, diamond-shaped patterns (Fig. 4).

Colostethus chalcopis is only the third dendrobatid frog for which a non-feeding tadpole has been documented (Chapter 4). The other two, *C. degranvillei* and *C. stepheni* are more highly modified (Juncá et al., in press; Chapter 4), and neither species is collared or morphologically similar to *C. chalcopis*. In addition, other collared *Colostethus* have much larger clutch sizes than *C. chalcopis* (mean clutch size = 2.9 eggs; Chapter 4), with the possible exception of *C. yustizi* (La Marca, 1984a).

Description of holotype.—An adult male 17.4 mm SVL; body moderately slender; head slightly wider than long; head length 34.4% of SVL, head width 35.8% of SVL; snout short, bluntly rounded in dorsal view, truncate in profile; loreal region barely concave; nostrils slightly protuberant laterally; eye–nostril distance 43% length of eye; supratympanic fold weak, diffuse, obscuring posterodorsal part of tympanum; length of tympanum 40% length of eye, separated from eye by distance equal to about two fifths length of eye.

Forelimbs moderately long, slender; first finger slightly shorter than second; fingers unwebbed, lacking fringes; third finger not swollen; terminal discs moderately expanded, third finger disc about 1.4 times wider than distal end of adjacent phalange; subarticular tubercles low, oval; palmar tubercle about twice size of thenar, moderately rounded, barely elevated; thenar tubercle rounded and large (Fig. 3A). Hind limbs moderately slender; tibia length 47.5% of SVL; foot length 41.6% of SVL; outer tarsal

fold absent; inner tarsal fold absent; small, low tubercle on proximal half of tarsus; outer metatarsal tubercle rounded to elliptical, about three-fourths size of round inner metatarsal tubercle; toe webbing formula **III**3-41/2**IV**, skin-like remnant webbing barely perceptible, toes without lateral fringes; terminal discs only very slightly expanded, about 1.2 times width of digits; 1-1-2-3-2 subarticular tubercles on Toes I–V respectively, very small, rounded (Fig. 3B).

Skin on dorsum, venter and flanks smooth; anal opening directed posteroventrally at upper level of thighs with some ill-defined tubercles anterior to it; anal sheath short. Testes white, mean length 0.9 mm. Tongue elongately elliptical, narrow proximally, free posteriorly for about three-fourths of its length; vocal slits present; vomerine odontophores absent.

Color of holotype in preservative.—Dorsum grayish brown with darker marks; head with dark stripe along canthus rostralis from eyes to nostril, and a less well defined, narrow dark line along upper lip parallel to canthus rostralis (Fig. 3C); dark “U”-shaped mark between nostrils, with bottom of “U” at upper lip; a triangular mark between eyes, with apex of triangle pointing posteriorly; dark supratympanic stripe extending from eye to just beyond tympanum, connected to a dark postorbital wedge (Fig. 3C); two bilateral small dark round marks with pale center at scapular level, a diffuse dark mark on the sacral region anteriorly, two bilateral black spots at the posterior lateral sacral region; anal region dark brown bordered by a diffuse paler band that extends transversally across the thighs; flanks gray with two oblique dark brown bands across the flank, one anterior to the forelimbs covering the upper border of the tympanic region, and the other posterior to the forelimbs. Dorsal surfaces of forelimbs

light brown with gray shading, diffuse, darker longitudinal stripes anteriorly and posteriorly on surface of upper arm; two transverse dark stripes across the lower arm and more diffuse ones across fingers; digital discs of Fingers I and II white, Fingers III and IV bearing slightly darker discs; dorsal surfaces of hind limbs light brown, bearing transverse dark brown bars along the entire length, each limb displaying one narrow bar on thighs, one on shank, one on tarsus and one across base of toes. Toe pads and digital scutes pigmented. Throat uniform dark gray with a black collar covering entire hyoid region; chest and abdomen speckled pale gray with a faint reticulate pattern on abdomen distally; ventral surfaces of limbs grayish white, tubercles with less pigmentation.

Color in life and variation.—Dorsum light brown, darker brown markings present (brown and dark brown markings are turned gray and dark gray in preservative, respectively). Eye color is brown, upper portion of iris with a distinctive copper-colored hue. In most of the paratopotypes, the triangle mark between the eyes is not well defined. One paratopotype (NMC 33902-1) displays three diamond-shaped dark areas from the interorbital space to the anal region (Fig. 4). The bottom of the “U”-shaped mark on the snout is indistinct in NMC 33674–75, 33902-1 and 33902-2, and AMNH A135398. Four paratopotypes (NMC 33902-1, 33902-3, 33902-8, and AMNH A135398) have a second dark stripe, parallel to the supratympanic stripe but ventrally. The four juveniles (< 10 mm; KU 218529, AMNH A135399, NMC 33902–7, and 33902-8) vary considerably in pattern development, with one (NMC 33902-8) already displaying a complete adult pattern, with all the stripes and markings visible, while two vary and one (AMNH A135399) has uniform coloration with no markings.

Throat color in males is black, tapering off to a dark gray anteriorly. In females, throat and venter are of identical pale orange color. A small number of tubercles may or may not be present at the scapular level, on antebrachia, lower back, shanks, and on the tarsi (Fig. 1); these are not easily noticeable in preservative.

Dimensions of the holotype (in mm).—SVL 17.4, tibia length 8.3, foot length 7.2, head length 6.0, head width 6.2, eye diameter 2.9, eye–nostril distance 1.24.

Distribution and Ecology.—All specimens of *Colostethus chalcopis* were found on the ground in and near a deep ravine on the southeastern slope of Montagne Pelée, Martinique, at an altitude of approximately 500 m. This area was formed by an ancient lava flow and is part of the Mne. Pelée rain forest system surrounding the still active volcano (Johnson, 1988). The montane rain forest vegetation at this elevation consists mainly of a few tall trees (up to 30 m), shrub thickets, palm brakes and ferns (Davis et al., 1986; Nicolson, 1991); some stands of giant bamboo (Bambusoideae) are present as well. A few *C. chalcopis* also called from smaller ravines along the upper slopes of the mountainside, beyond the rain forest, in elfin woodland. The low thicket-like forest with its cover of epiphyllous hepatics and dripping moss mats (Nicolson, 1991) is an ideal refugium for anurans; it is impenetrable without destructive bush-whacking.

This species appears to follow a crepuscular daily activity pattern, judged by the observed peaks in calling and the difficulty in finding active specimens both during mid-day and at night. Calling peaks occur at dawn and dusk, with the latter being the more intense period. However, some calling was heard throughout the day. Despite the fact that there were dozens of calling males along the sides of the ravine, only very

few were actually seen because of the dense vegetation. Active pursuit of these into the thickets was not seriously attempted for fear of the Martinique fer-de-lance (*Bothrops lanceolata*) which also inhabit the ravines on Mne. Pelée. No calling was heard immediately adjacent to the small stream in the bottom of the ravine.

The frogs were very secretive and retreated under dry leaves or rocks when approached; they blend in perfectly with old decaying foliage. Most animals were discovered during the day by turning large leaves and rocks in the ravine, sometimes even in the small stream. Not one frog was caught without considerable pursuit, often over distances in excess of 10 m. When a frog was discovered under a rock or leaf, the frog escaped immediately by making a rapid succession of jumps, and changing direction quickly and randomly. Some jumped into small pools of water and attempted to swim away, but they are relatively slow swimmers and easily captured in the water. All animals observed were extremely shy of artificial light. A light source shone directly into a frog's eyes did not, as in many other species, prevent immediate escape; however, keeping a light on a frog from jump to jump did seem to disorient or distract, and aided capture.

Vocalizations.—The call (Fig. 5) is a single note, which rises rapidly from 4000 Hz to 5200 Hz. The duration of each note is approximately 60 ms, with an interval of 0.6–0.7 s. There is no voucher specimen, but some calls were recorded directly from a calling frog in August 1990, which escaped during the attempt to capture it.

Etymology.—The specific name *chalcopis* (= copper-eyed) is a Latinized composite of the Greek “chalkos” and “ops.” It was chosen to characterize the species by the distinctive hue of the upper portion of the iris.

DISCUSSION

Taxonomic Comments.—It has been suggested repeatedly that *Colostethus* is in need of revision because it is likely paraphyletic (Frost, 1985; La Marca, 1984a; Lynch, 1982; W. E. Duellman, pers. comm.; L. S. Ford, pers. comm.). The phylogenetic relationships of genera within the family Dendrobatidae are generally problematic because reliable synapomorphies and symplesiomorphies have not been identified for each genus, a problem particularly pressing in the case of *Colostethus* (Lynch, 1982). One consequence of such uncertainty is that several attempts to modify the classification have not been comprehensive enough (La Marca, 1992; Myers et al., 1991; Zimmermann and Zimmermann, 1988).

In the specific case of *Colostethus*-type morphologies, Cope's (1866) original definition of *Colostethus* in the description of *C. latinasus* is much too vague to unequivocally demarcate generic synapomorphies. Definitions of *Colostethus* given by Edwards (1971, 1974), Lynch (1982), Myers (1991), Myers et al. (1991), and Savage (1968) are more encompassing, but fall short of providing definitive generic characteristics. Lynch (1982) noted that the generic status of two new species was questionable because of the probable paraphyly of *Colostethus*, but placed them in *Colostethus* in expectation of a systematic revision. Likewise, I have found it problematic to accommodate the species I describe here in an available genus. Lack of toxins or noxious secretions, as determined by taste and smell (C. W. Myers, pers.

comm.), places this frog near the base of the lipophilic alkaloid-producing dendrobatids (Myers, 1987) and precludes its inclusion in *Aromobates*, *Dendrobates*, *Epipedobates*, *Minyobates*, or *Phyllobates*. Although La Marca (1992) proposed the genus *Mannophryne* for collared *Colostethus*-morphotypes, the Martinique dendrobatid is clearly distinct from all species assigned to *Mannophryne* by virtue of its unique larval characteristics (Chapter 4), dorsal patterning, webbing formula, and sexual dimorphism with respect to the collar.

Considering the defining features of *Mannophryne* (La Marca, 1992) and the known variability within the species assemblage currently classified as *Colostethus*, *C. chalcopis* may either be regarded as a sister taxon to *Mannophryne*, or *Mannophryne* itself may be an artifact of classification. In lieu of a comprehensive systematic analysis, which is beyond the scope of this species description, I see the precedent set by Lynch (1982), choosing a questionable generic assignment over creating a potentially useless name, as my only possible choice for generic placement at this time. Awaiting the comprehensive study of dendrobatid relationships announced by Myers (1987), I conclude that *chalcopis* lies within *Colostethus* as currently understood, but as a species *incertae sedis* within that assemblage.

Biogeography.—The occurrence of *Colostethus chalcopis* in the Lesser Antilles is peculiar for two reasons: no other member of the family Dendrobatidae is autochthonous to an oceanic island (although *Dendrobates auratus* was introduced on Oahu, Hawaii), and the locality of *C. chalcopis* is a small isolate, quite removed from the known range of the family. The amphibian fauna of the Lesser Antilles has been described by various authors (Barbour, 1914; Cochran, 1938; Cope, 1870; Schwartz

and Henderson, 1985, 1991), and there have never been any previous reports of dendrobatid frogs (the type locality of *Phyllobates bicolor*, given as "Cuba," is obviously in error, probably caused by poor record-keeping, and was corrected to "Colombia" by Silverstone [1976]).

There are two species of collared *Colostethus* on islands just to the south of the Lesser Antilles. However, both *C. trinitatis* from Trinidad and *C. olmonae* from Tobago should be considered part of the South American herpetofauna, because geologically, Trinidad and Tobago once were a part of the South American land mass and may only have separated from it in recent geological times (Hardy, 1982; Perfit and Williams, 1989). Martinique, on the other hand, is part of the Lesser Antillean island arc and is truly oceanic. Like most of its neighbors, it is the result of geological uplift and subsequent volcanism at the edge of the Caribbean Plate (Perfit and Williams, 1989). Because of the distance of Martinique from the South American mainland, the biogeographic origin for *C. chalcopis* is mystifying. In the eastern Caribbean, introductions through the agency of humans are documented for *Bufo marinus* (Frost, 1985; Schwartz and Thomas, 1975) and frogs of the genus *Eleutherodactylus* (Kaiser, 1992; Chapter 1), but human trade is not an appropriate means of transport for a species as secretive and localized as *C. chalcopis*. A scenario of stepping-stone dispersal (Williams, 1989) with subsequent extinctions on the stopover islands is possible, but, without fossil evidence, highly speculative. At this time, it is not possible to offer a satisfactory answer to the biogeographic enigma posed by *C. chalcopis*.

ACKNOWLEDGMENTS

I extend my sincere gratitude to H. M. Gray, H. H. Schwarten, and T. F. Sharbel for assistance in the field. I thank R. E. Lemon and D. J. Mountjoy for the use of the sonagraph and for technical assistance. M. W. Caldwell, D. C. Cannatella, L. A. Coloma, W. E. Duellman, L. S. Ford, H. M. Gray, D. M. Green, E. La Marca, C. W. Myers, and T. F. Sharbel shared their thoughts on problems with and approaches to *Colostethus*-systematics with me, contributing some very useful comments to the manuscript throughout its development. The assistance of A. Schachter in finding an appropriate name is gratefully acknowledged. J. P. Rosado, W. R. Heyer, and C. W. Myers are gratefully acknowledged for authorizing specimen loans. This research was supported by grants from the Hans-Krüger-Stiftung and the Studienstiftung des Deutschen Volkes, Germany, and by an NSERC Canada operating grant to D. M. Green.

LITERATURE CITED

- ALTIG, R., AND G. F. JOHNSTON. 1989. Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. *Herpetol. Monogr.* (3):81–109.
- BARBOUR, T. 1914. A contribution to the zoögeography of the West Indies, with especial reference to amphibians and reptiles. *Mem. Mus. Comp. Zool.* 44:209–359.
- COCHRAN, D. M. 1938. Reptiles and amphibians from the Lesser Antilles collected by Dr. S. T. Danforth. *Proc. Biol. Soc. Washington* 51:147–156.

- COPE, E. D. 1866. Fourth contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia 18:123-132.
- _____. 1870. Seventh contribution to the herpetology of tropical America. Proc. Amer. Phil. Soc. II:147-169.
- DAVIS, S. D., S. J. M. DROOP, P. GREGERSON, L. HENSON, C. J. LEON, J. LAMLEIN VILLA-LOBOS, H. SYNGE, AND J. ZANTOVSKA. 1986. Plants in Danger. What do we know? IUCN, Cambridge, United Kingdom.
- DUELLMAN, W. E., AND J. E. SIMMONS. 1988. Two new species of dendrobatid frogs, genus *Colostethus*, from the Cordillera del Cóndor, Ecuador. Proc. Acad. Nat. Sci. Philadelphia 140:115:124.
- EDWARDS, S. R. 1971. Taxonomic notes on South American *Colostethus* with descriptions of two new species (Amphibia, Dendrobatidae). Proc. Biol. Soc. Wash. 84:147-162.
- _____. 1974. A phenetic analysis of the genus *Colostethus* (Anura: Dendrobatidae). Unpubl. Ph.D. Thesis, Univ. of Kansas, Lawrence.
- FROST, D. R. (Ed.). 1985. Amphibian Species of the World. A Taxonomic and Geographical Reference. Allen Press, Inc., and the Association of Systematics Collections, Lawrence, Kansas.
- HARDY, J. D., JR. 1982. Biogeography of Tobago, West Indies, with special reference to amphibians and reptiles: a review. Bull. Maryland Herpetol. Soc. 18:37-91.
- HEDGES, S. B., AND R. THOMAS. 1989. Supplement to West Indian amphibians and reptiles: a check-list. Milwaukee Publ. Mus. Contr. Biol. Geol. (77):1-11.

- JOHNSON, T. H. 1988. Biodiversity and conservation in the Caribbean: profiles of selected islands. Int. Council Bird Preserv. Monogr. (1):1-144 .
- JUNCÁ, F. A., R. ALTIG, AND C. GASCON. 1993. Breeding biology of *Colostethus stepheni*: a dendrobatid with a non-transported nidicolous tadpole. Copeia (in press).
- KAISER, H. 1992. The trade-mediated introduction of *Eleutherodactylus martinicensis* (Anura: Leptodactylidae) on St. Barthélémy, French Antilles, and its implications for Lesser Antillean biogeography. J. Herpetol. 26:264-273.
- LA MARCA, E. 1984a. A taxonomic and systematic revision of the frogs of the *Colostethus collaris* group (Anura: Leptodactylidae: Dendrobatinae). Unpubl. M.Sc. Thesis, Univ. of Nebraska, Lincoln.
- _____. 1984b. Sistemática de las ranas con collar del género *Colostethus* (Anura: Dendrobatidae). Acta Cient. Venezol. 35, Supl. 1:478.
- _____. 1989. A new species of collared frog (Anura: Dendrobatidae: *Colostethus*) from Serrania de Portuguesa, Andes of Estado Lara, Venezuela. Amphib.-Rept. 10:175-183.
- _____. 1992. Catálogo taxonómico biogeográfico y bibliográfico de las ranas de Venezuela. Cuad. Geog. Univ. Los Andes, Mérida (9):1-197.
- LYNCH, J. D. 1982. Two new species of poison-dart frogs (*Colostethus*) from Colombia. Herpetologica 38:366-374.
- MYERS, C. W. 1987. New generic names for some neotropical poison frogs (Dendrobatidae). Papéis Avulsos Zool., S. Paulo 36:301-306.

- _____. 1991. Distribution of the dendrobatid frog *Colostethus chocoensis* and description of a related species occurring macrosympatrically. *Am. Mus. Novitates* (3010):1-15.
- MYERS, C. W., AND W. E. DUELLMAN. 1982. A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. *Am. Mus. Novitates* (2752):1-32.
- MYERS, C. W., A. PAOLILLO O., AND J. W. DALY. 1991. Discovery of a defensively malodorous and nocturnal frog in the family Dendrobatidae: phylogenetic significance of a new genus and species from the Venezuelan Andes. *Am. Mus. Novitates* (3002):1-33.
- NICOLSON, D. H. 1991. Flora of Dominica, part 2: Dicotyledoneae. *Smithson. Contr. Bot.* (77):1-274.
- PERFIT, M. R., AND E. E. WILLIAMS. 1989. Geological constraints and biological retrodictions in the evolution of the Caribbean Sea and its islands. Pp. 47-102. *In:* C. A. Woods (Ed.). *Biogeography of the West Indies: Past, Present, and Future*, Sandhill Crane Press, Gainesville, Florida.
- RIVERO, J. A. 1988. Sobre las relaciones de las especies del género *Colostethus* (Amphibia, Dendrobatidae). *Mem. Soc. Cien. Nat. La Salle* 48:3-32.
- SAVAGE, J. M. 1968. The dendrobatid frogs of Central America. *Copeia* 1968:745-776.
- SAVAGE, J. M., AND W. R. HEYER. 1967. Variation and distribution in the treefrog genus *Phyllomedusa* in Costa Rica, Central America. *Beitr. Neotrop. Fauna* 5:111-131.

- SCHWARTZ, A. 1967. Frogs of the genus *Eleutherodactylus* in the Lesser Antilles. Stud. Fauna Curaçao Carib. Isl. 23:1-62.
- _____. 1969. The Antillean *Eleutherodactylus* of the *auriculatus* group. Stud. Fauna Curaçao Carib. Isl. 30:99-115.
- SCHWARTZ, A., AND R. W. HENDERSON. 1985. A Guide to the Identification of the Amphibians and Reptiles of the West Indies Exclusive of Hispaniola. Milwaukee Public Museum, Milwaukee, Wisconsin.
- _____. 1991. Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History. University of Florida Press, Gainesville, Florida.
- SCHWARTZ, A., AND R. THOMAS. 1975. A check-list of West Indian amphibians and reptiles. Carnegie Mus. Nat. Hist. Spec. Publ. (1):1-216.
- SCHWARTZ, A., AND 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.
- SILVERSTONE, P. A. 1976. A revision of the poison-arrow frogs of the genus *Phyllobates* Bibron. Nat. Hist. Mus. Los Angeles Co. Sci. Bull. (27):1-53.
- WILLIAMS, E. E. 1989. Old problems and new opportunities in West Indian biogeography. Pp. 1-46. In: C. A. Woods (Ed.). Biogeography of the West Indies: Past, Present, and Future, Sandhill Crane Press, Gainesville, Florida.
- ZIMMERMANN, H., AND E. ZIMMERMANN. 1988. Ethno-Taxonomie und zoogeographische Artengruppenbildung bei Pfeilgiftfröschen (Anura: Dendrobatidae). Salamandra 24:125-160.

APPENDIX

Specimens examined

Colostethus chalcopis.—AMNH A135397–99, KU 218528–29, NMC 33674–75, 33902–1–9; *C. collaris*.—MCZ 3886–87, 10723–24; *C. degranvillei*.—AMNH 90874, 90879–80, 90890, 90894, MCZ 97313–14, 97318–20; *C. mystax*.—KU 147094, 147095 (holotype), 147096–98, 147105; *C. nexipus*.—QCAZ 1431–32; *C. pumilus*:s—USNM 282812–13. *C. trinitatis*.—AMNH 73769, 73771–72, 60308–09, 135312, MCZ 21404–06, 3963–66.

FIGURE 1. Paratopotype of *Colostethus chalcopis* *sp. nov.*, NMC 33902-9, female, 17.9 mm SVL.



FIGURE 2. Photograph of the holotype of *Colostethus chalcopis* sp. nov., male, NMC 33675 (right), 17.4 mm SVL, and a female paratopotype, NMC 33902-3 (left), 18.3 mm SVL, to show male-female differences in ventral coloration. The holotype has a black throat collar, covering the entire hyoid region. Its venter is densely pigmented to the pelvic region, while there is no skin pigmentation evident in the female.

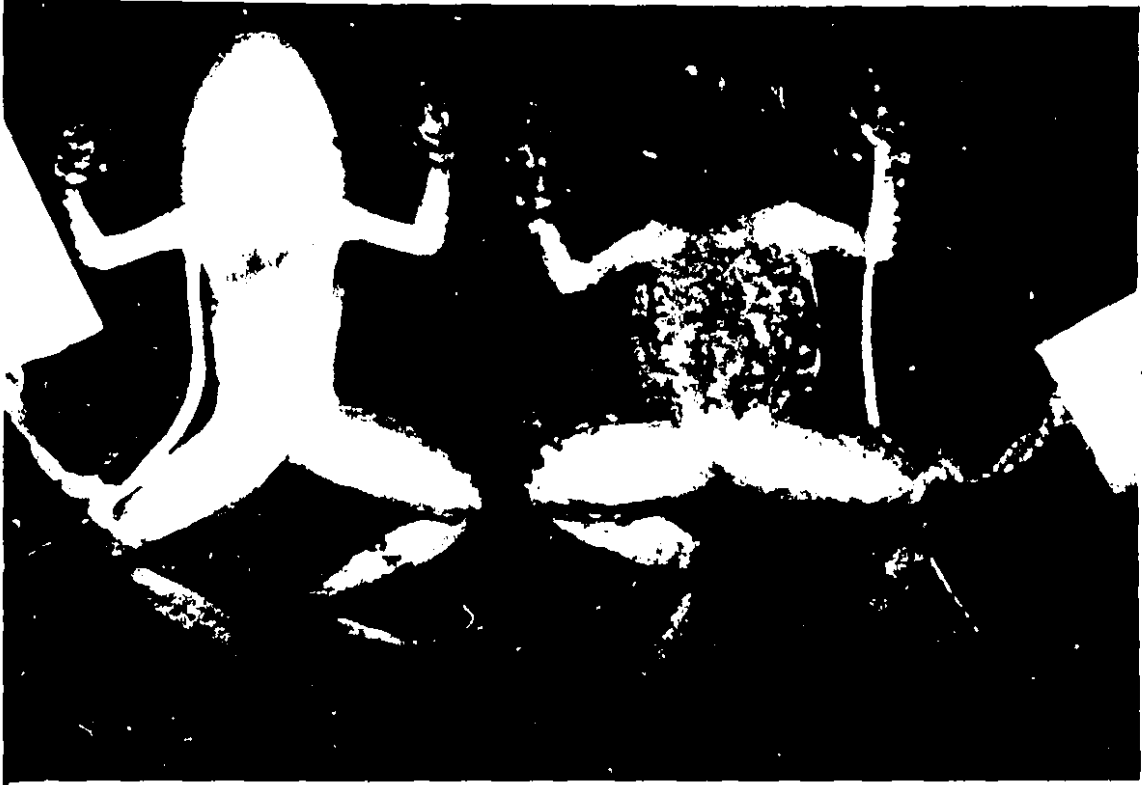


FIGURE 3. (A) Right hand of a paratopotype of *Colostethus chalcopis* sp. nov., NMC 33902-4. (B) Left foot of a paratopotype of *C. chalcopis* sp. nov., NMC 33902-1. Arrow indicates the position of the skin-like webbing. (C) Side of head of *C. chalcopis* sp. nov., NMC 33675 (holotype).

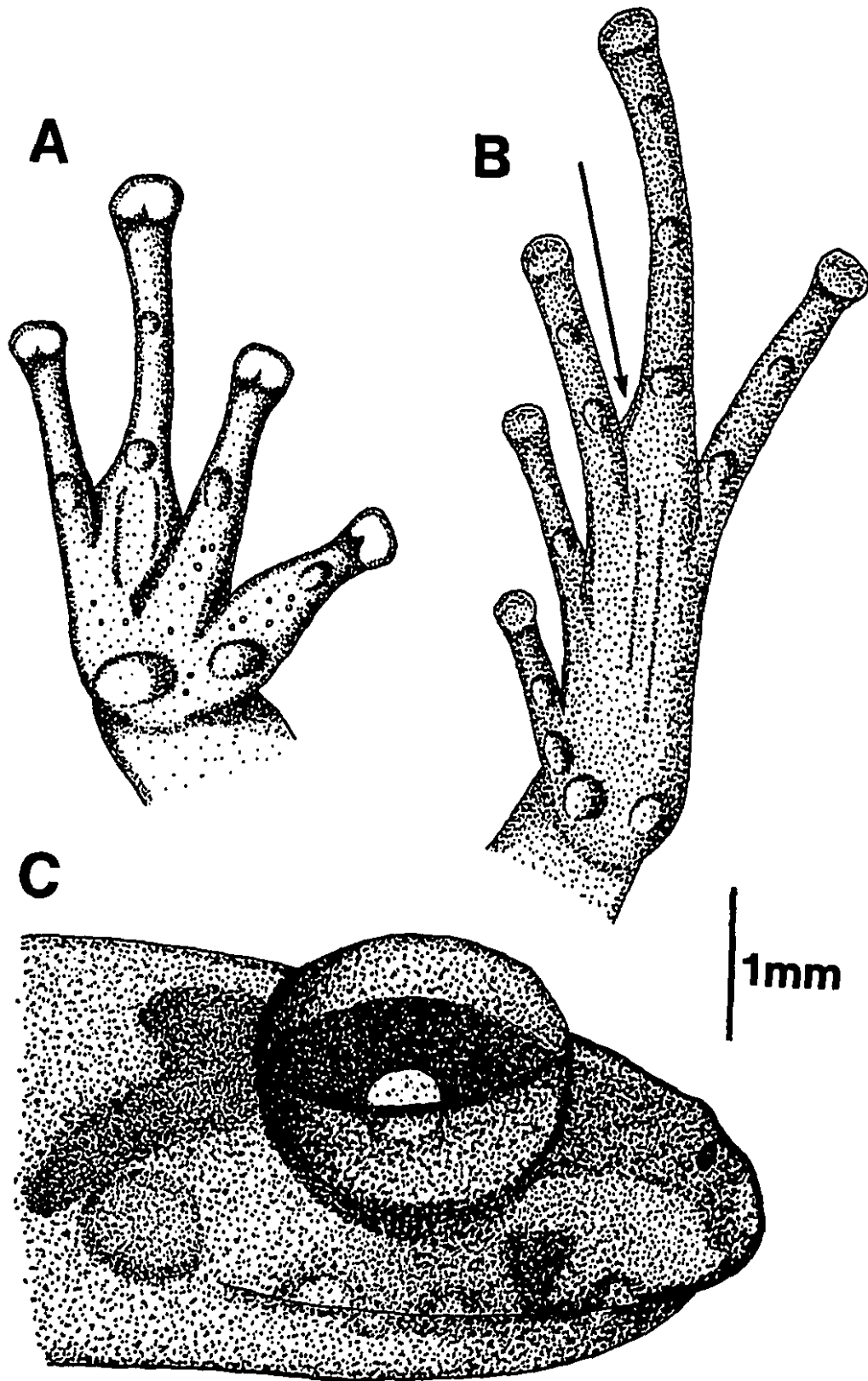
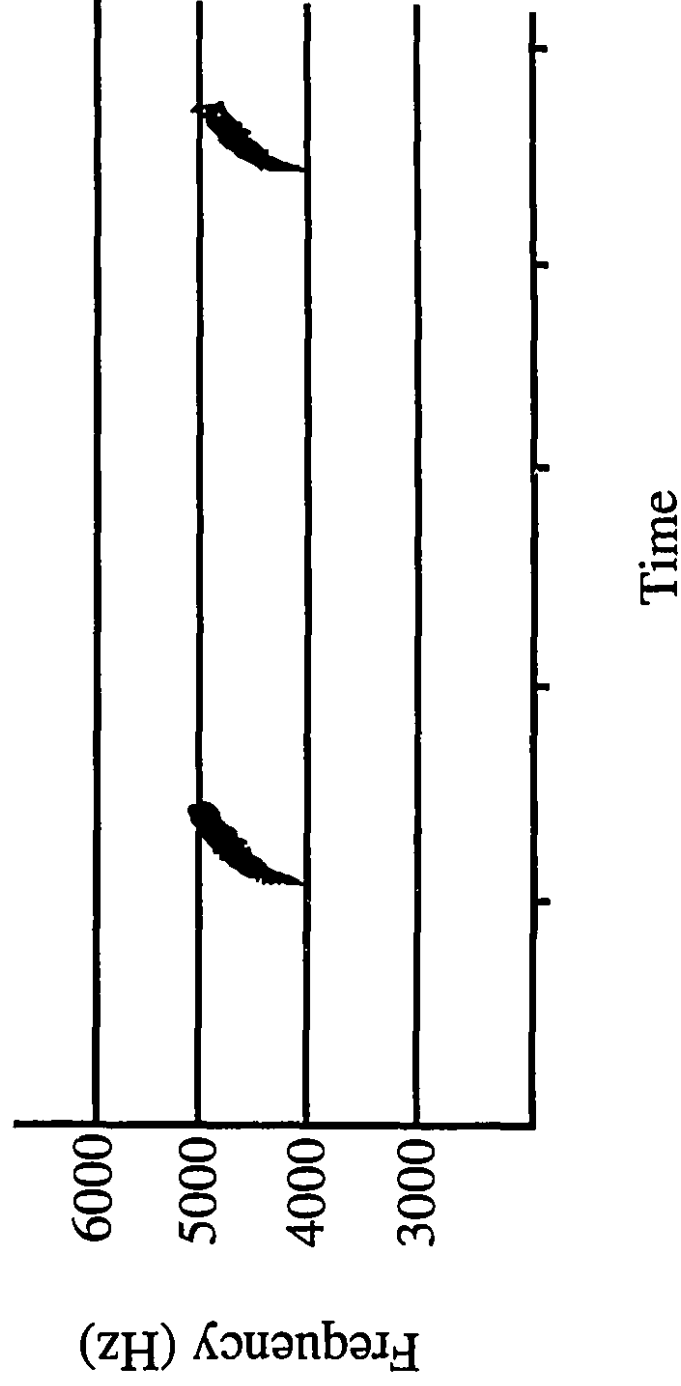


FIGURE 4. Photographs of paratopotypes of *Colostethus chalcopis* *sp. nov.* (clockwise from upper left NMC 33902-2, 33902-1, 33902-4 and KU 218528), showing variation in dorsal pattern.



FIGURE 5. Call of *Colostethus chalcopis* sp. nov., recorded on the slopes of Mne. Pelée, Martinique, on 9 August 1991. Temperature 20°C. Time scale marked in intervals of 0.2 s.



4

The Atypical Tadpole of the Dendrobatid Frog, *Colostethus chalcopis*, from Martinique, French Antilles

Published as: Kaiser, H., and R. Altig. The atypical tadpole of the dendrobatid frog, *Colostethus chalcopis*, from Martinique, French Antilles. *Journal of Herpetology*. *In press*.

PREAMBLE CHAPTER 4

Additional searches for specimens of *Colostethus chalcopis* on Martinique in 1992 resulted in the discovery of an unattended egg mass. After hatching, the tiny tadpoles could be identified as belonging to *C. chalcopis*, and I decided to describe the tadpole to see if its characteristics could be used to infer a relationship with any other *Colostethus*.

ABSTRACT

The discovery of a small clutch of eggs from the recently described species *Colostethus chalcopis* from Martinique, French Antilles, provides insights into the natural history of this secretive species. The larvae are unusual for dendrobatids because they do not feed and are morphologically primitive. Only two other described dendrobatid larvae are nonfeeding but both of these have much modified oral morphologies, unlike *C. chalcopis* which has normal mouth parts. In light of such fundamental differences even within a single presumptive genus, the congruence of phylogenies for dendrobatid genera may have to be reconsidered.

INTRODUCTION

The well-known herpetofauna of Martinique, French Antilles, includes only three anurans: *Bufo marinus*, *Eleutherodactylus johnstonei*, and *E. martinicensis* (Schwartz and Henderson, 1991). Several searches during 1990–92 resulted in the discovery of the dendrobatid *Colostethus chalcopis* (Kaiser et al., 1994; Chapter 3). In the summer of 1992, six tadpoles were reared from a terrestrial egg mass collected near calling males of *C. chalcopis*. Based on number of eggs, egg pigmentation, deposition site, and developmental mode, these eggs could not have been laid by *B. marinus* (many small, darkly pigmented eggs in strings in lentic water which develop into exotrophic tadpoles) or by *Eleutherodactylus* spp. (few large non-pigmented, terrestrial eggs which develop directly). Based on tadpole morphology, general breeding biology, presence of adult *C. chalcopis*, and assuming the absence of any unknown taxa, we assign these eggs to *C. chalcopis*, even though the death of the larvae prevented examination of post-metamorphic material. These free-living, nonfeeding

larvae ("nidicolous" *fide* Altig and Johnston, 1989) differ from all known tadpoles of the genus *Colostethus* as presently diagnosed (e.g., Lynch, 1982; Frost, 1985; Myers et al., 1991; Kaiser et al., 1994; Chapter 3).

MATERIALS AND METHODS

Six eggs of *Colostethus chalcopis*, found on 29 August 1992 by HK and T. F. Sharbel at the type locality (Rivière Cloche, ca. 3 km by road NE Morne Rouge, altitude ca. 500 m; ca. 25 C) hatched 6 days after collection. Within 48 h of hatching, four tadpoles died; the remaining two larvae were preserved in 10% buffered formalin. The oral terminology of Altig (1970) and the staging system of Gosner (1960) were followed in the description. All measurements are in millimeters unless otherwise stated; measurements involving the spiracle aperture, eyes, and nares were made to the centers of those structures. Tadpoles were deposited in the United States National Museum of Natural History (USNM 319989–90). Adult specimens used for comparisons were deposited in the American Museum of Natural History (AMNH A135397–99), the Canadian Museum of Nature (NMC 33674 [paratype], 33675 [holotype], 33902–1–9), and the Museum of Natural History, The University of Kansas (KU 218528–29). Information for *C. degranvillei* was obtained from Lescure (1984), who did not provide specimen numbers. Specimen numbers for *C. stephensi* are given in Juncá et al. (in press).

RESULTS AND DISCUSSION

Eggs.—The egg mass (Fig. 1A) was found on a decaying palm leaf hidden among layers of decomposing foliage on a steep slope, about 1.5 m from a broad seepage of surface water entering a stream at the bottom of the deeply shaded ravine.

No adult was in attendance, but males of *Colostethus chalcopis* were calling within 3 m of the nest site. Upon collection, the leaf was folded and placed on paper towels in a small plastic container. When the first larva hatched 6 days later, ca. 1 cm of tap water was added to the container. All larvae hatched within 36 h.

Based on egg placement and the asynchronous development of the embryos (Fig. 1), I conclude that the egg mass consisted of two clutches of three eggs each laid a short time apart. At collection, three embryos (Fig. 1A) were at ca. stage 22 and three at ca. early stage 25; 3 days later (Fig. 1B), the younger embryos had developed to early stage 25, while the other embryos had reached about stage 26 or 27. Embryos were surrounded by a gelatinous, transparent jelly (Fig. 1) when collected. After 3 days, the jelly of the older clutch became cloudy (Fig. 1B). I estimated clutch size based on the number of large, yellow ovarian eggs in all female specimens of *Colostethus chalcopis* collected to date. Large ovarian ova in 20 females ranged from 1–4 ($\bar{x} = 2.9$) and 66% were in the left ovary. The mean diameter of ovarian eggs was 2.7 mm.

The presence of two clutches of similar age at the same location may indicate multiple use of an appropriate site by females or males (site fidelity), or communal nesting by multiple pairs (Wells, 1977). Male territoriality is quite common among the Dendrobatidae (Wells, 1977; Duellman and Trueb, 1986) and a single, calling territorial male may attract or lead more than one female to a defended oviposition site (Crump, 1972; Wells, 1977).

Tadpole.—Measurements of a stage-32 specimen (USNM 319990) are: 12.0 total length, 4.4 body length, 7.6 tail length, 1.3 tail muscle height at base, 0.9 tail muscle width at base, 0.8 maximum dorsal fin height located 5.4 from the body terminus, 0.8 maximum ventral fin height located 5.8 from body terminus, 2.7 body

width located 2.7 from snout, 1.5 body height located 2.3 from snout, 0.6 eye diameter, 0.2 pupil diameter, 1.2 interorbital distance, 0.1 narial diameter, 0.8 internarial distance, 0.2 snout-naris, 0.8 snout-eye, 2.3 snout-spiracle, 0.6 naris-eye, and 0.9 transverse diameter of oral disc. Other major characteristics are: almost ventral, non-emarginate oral disc with a wide dorsal gap in the reduced marginal papillae, dorsal eyes, sinistral spiracle, medial vent, dorsal fin terminates 1.4 posterior to dorsal tail-body junction, ventral fin terminates at the body, neuromasts not visible, and labial tooth row formula (LTRF) 2/3.

The translucent, non-emarginate oral disc (Fig. 2) is almost invisible without staining. Marginal papillae are present as indistinct crenulations around the disc except for a wide dorsal gap, and submarginal papillae are absent. Both weakly keratinized jaw sheaths are narrow (ca. 0.02 mm) and coarsely serrate. The edge of the upper sheath forms a uniform, wide arc, and the lower sheath is widely U-shaped. Light staining with methylene blue was required to discern the LTRF. About 10 weakly keratinized teeth with no visible replacements make up row A-1. Row A-2 has a few teeth set far laterally (i.e., with a wide medial gap between sections), and rows P-1 and P-2 each have a few teeth. A ridge without teeth is in the position of P-3.

The depressed body (Fig. 3) is ventrally flattened. Eyes and nares are placed well forward on the head in positions typical of embryos of exotrophic larvae, but also characteristic of nidicolous larvae even at this more advanced stage. The round nares face anterolaterally and are visible as a slight bulge in the dorsal silhouette. The spiracle tube emerges on the venter and the aperture is just above the abrupt angle between the flattened ventral surface of the body and the sides; the tube is not visible in dorsal view, and the small, round aperture faces posteriorly. The medial vent tube narrows as a funnel-shaped extension of the body wall that originates even with the ventral margin of the limb buds. The tube is attached to the ventral fin at about midlength of the limb

buds. As is typically the case in nidicolous larvae, the hind-limb buds are both absolutely and proportionally large relative to the size of the body: 1.2 vs. 1.0 in length and 27.3 vs. 12.7% of body length when compared with the exotrophic tadpole of *Bufo woodhousii* of the same stage (used as an example of a typical nonspecialized larva). The low fins terminate in a broadly rounded tip. The dorsal fin begins as a ridge well posterior of the dorsal tail-body junction and attains appreciable height only further posteriorly. The large gut (2.8 diameter at the wall of the buccopharyngeal cavity) is full of yolk and makes only two turns as it diminishes in size. Yolk platelets removed from the gut are oval or slightly rounded rectangles (mean of largest platelets = $10.9 \times 8.4 \mu\text{m}$; $n = 10$).

The body is uniformly dark brown above with closely spaced, platelike melanophores. The outlines of large vitelline vessels are obvious laterally and dorsolaterally on the abdomen. The throat and belly, except for the center of the abdomen, is sparsely pigmented with large stellate melanophores in both dermal and subdermal layers. The fins are unpigmented except for a few small melanophores in the dorsal fin near midlength of the tail.

Characteristics of the smallest larva available (9.3 TL, ca. stage 27; in lot USNM 319989) cannot be evaluated because of deterioration before the dead tadpole was preserved. The jaw sheaths resemble the older larva, but conditions of the spiracle and vent prevent evaluations. The pigment looks like irregular granules arranged uniformly but more sparsely than in later stages.

Behavior in captivity.—Larvae were usually found hiding together under the palm leaf during the day. On several occasions, one of the older tadpoles was observed using rapid tail undulations to move up the wall of the container, a distance of ca. 8 cm. No obvious movements of the oral disc were seen, and it appears that cohesion

between the wet tadpole and the container wall, perhaps enhanced by the flattened venter, was the only means of maintaining position. Upon reaching the upper lip of the container, the larva would stop moving and rest with the tail curled around the body. When a tadpole was gently pushed downwards, it would start rapid tail undulations and move in a downward arc. The rapid and exaggerated tail undulations of tadpoles when placed in water resulted in little progress and was accompanied by anterior lateral displacement (see Wassersug and Hoff, 1985). Tadpoles were never seen moving into free water of their own volition.

Morphology, Ecology, and Life History.—Altig and Johnston (1989) recognized a continuum of developmental patterns within a guild of free-living, non-feeding (i.e., nidicolous) tadpoles. Nidicolous larvae are small, and the developmental patterns and resultant morphology range from a typical, morphologically unmodified tadpole at one end of the continuum to a highly modified larva at the other extreme. The stage-32 larva of *Colostethus chalcopis* represents the unmodified end of the nidicolous continuum, and is probably as big as this tadpole gets considering the larval development of congeners (La Marca, 1984; pers. obs.); metamorphs likely have a SVL of about 4.0. Juveniles (SVL 6.0–8.0) collected at the type locality (AMNH A135399, KU 218529, NMC 33902-7 and 33902-8) have incompletely developed dorsal patterns (Kaiser et al., 1994; Chapter 3).

Although no tadpoles beyond stage 32 were available, it is very likely that tadpoles of *Colostethus chalcopis* remain endotrophic beyond that stage. At stage 32, other known *Colostethus* larvae are feeding (La Marca, 1984; La Marca and Mijares U., 1988), and no other exotrophic tadpoles retain as much yolk this late in larval development. The clouding of the jelly surrounding the older embryos 3 days after collection may have been caused by some fungal or bacterial infection. The fact that

hatching commenced very soon after onset of egg clouding can be considered consistent with hatching plasticity (i.e., tadpoles avoiding infection by hatching early).

Systematics.—Of all other known dendrobatid larvae only two, putatively unrelated to *Colostethus chalcopis*, are endotrophs: *C. degranvillei* from French Guyana (Lescure, 1975, 1984) and *C. stepheni* (Juncá et al., in press) from Brazil. *Colostethus degranvillei* has a small vestige of the upper labium and lacks keratinized mouth parts and a vent tube; these pigmented larvae ride the back of the parent until they metamorphose. Larvae of *C. stepheni* are also pigmented, lack all mouth parts, but have a vent tube and spiracle; larvae remain in the nest site until metamorphosis. Tadpoles of species in the putatively monophyletic *C. collaris* group (La Marca, 1984), an assemblage of geographically close and also collared species, are all transported, and have pointed tail tips and more strongly keratinized, V-shaped lower jaw sheaths than *C. chalcopis* tadpoles [La Marca (1992) proposed the new genus *Mannophryne* for these taxa without identifying reliable synapomorphies. I follow the more conservative taxonomy and retain these taxa in *Colostethus*]. *Colostethus chalcopis* is unusual in having only about three eggs per clutch, a number more consistent with clutch sizes of *Dendrobates*, *Epipedobates*, or *Phyllobates*. The only other *Colostethus* with such a small clutch size is *C. yustizi* (La Marca, 1984).

Morphologically, the tadpoles of *Colostethus chalcopis*, *C. degranvillei*, and *C. stepheni* resemble embryological stages of younger exotrophic tadpoles. Furthermore, differences in morphological detail, such as those in the oral region, seen even in three congeneric endotrophic larvae, may be attributable to changes in developmental patterns. Thus, in a strictly developmental context, we raise the question of whether our observations are representative of heterochronic alterations similar to those seen in some salamanders (i.e., paedomorphosis, peramorphosis; see McKinney and

McNamara, 1991). The absence of a definite sequence in which character alterations are manifested in these *Colostethus* tadpoles provides additional evidence for the notion that developmental patterns of many larval characters are uncoupled (Nodzenski and Inger, 1990).

Although about a quarter of the tadpoles of the 90 known species of *Colostethus* (Duellman, 1993) have been described, there is minimal information available on their eggs, clutch sizes, and egg deposition sites. These data may be crucial in investigations of phylogenetic relationships between or within any of the dendrobatid genera (e.g., Edwards, 1974; Silverstone, 1976; La Marca, 1984; Zimmermann and Zimmermann, 1988; Myers et al., 1991). The occurrence of three kinds of nidicolous endotrophic development within a single presumptive genus of dendrobatid frogs adds to the complexity of group systematics and may need to be considered when constructing phylogenetic relationships for species currently placed in *Colostethus*.

ACKNOWLEDGMENTS

The enthusiastic assistance of H. M. Gray, H. H. Schwarten, and T. F. Sharbel during climbs into *sérpent*-territory is gratefully acknowledged. I thank R. Altig for writing the technical description, and T. Kahn for preparing the illustration of mouthparts. R. Altig, M. W. Caldwell, L. A. Lowcock, R. W. McDiarmid, and L. Trueb offered editorial clarification to the manuscript. Thanks go to D. M. Green for comments and extensive discussions on all things dendrobatid. This research was funded in part by grants from the Hans-Krüger-Stiftung and the Studienstiftung des Deutschen Volkes and by an NSERC Canada operating grant to D. M. Green.

LITERATURE CITED

- ALTIG, R. 1970. A key to the tadpoles of the continental United States and Canada. *Herpetologica* 26:180–207.
- ALTIG, R., AND G. F. JOHNSTON. 1989. Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. *Herpetol. Monogr.* (3):81–109.
- CRUMP, M. L. 1972. Territoriality and mating behavior in *Dendrobates granuliferus* (Anura: Dendrobatidae). *Herpetologica* 28:195–198.
- DUELLMAN, W. E. 1993. Amphibian species of the world: additions and corrections. *Univ. Kansas Mus. Nat. Hist. Spec. Publ.* (21):1–372.
- DUELLMAN, W. E., AND L. TRUEB. 1986. *Biology of Amphibians*. McGraw-Hill, New York.
- EDWARDS, S. R. 1974. A phenetic analysis of the genus *Colostethus* (Anura: Dendrobatidae). Unpubl. Ph.D. Thesis, Univ. of Kansas, Lawrence.
- FROST, D. R. (Ed.). 1985. *Amphibian Species of the World. A Taxonomic and Geographical Reference*. Allen Press, Inc., and The Association of Systematics Collections, Lawrence, Kansas.
- GOSNER, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16:183–190.
- JUNCÁ, F. A., R. ALTIG, AND C. GASCON. 1994. Breeding biology of *Colostethus stepheni*: a dendrobatid with a non-transported nidicolous tadpole. *Copeia*. *In press*.
- KAISER, H., L. A. COLOMA, AND H. M. GRAY. 1994. *Colostethus chalcopis* (Anura: Dendrobatidae), a new species from Martinique, French Antilles. *Herpetologica*. *In press*.

- LA MARCA, E. 1984. A taxonomic and systematic revision of the frogs of the *Colostethus collaris* group (Anura: Leptodactylidae: Dendrobatinae). Unpubl. M.S. Thesis, Univ. of Nebraska, Lincoln.
- _____. 1992. Catálogo taxonómico biogeográfico y bibliográfico de las ranas de Venezuela. Cuad. Geog. Univ. Los Andes, Mérida (9):1-197.
- LA MARCA, E., AND A. MUJARES U. 1988. Description of the tadpole of *Colostethus mayorgai* (Anura: Dendrobatidae) with preliminary data on the reproductive biology of the species. Bull. Maryland Herpetol. Soc. 24:47-57.
- LESCURE, J. 1975. Contribution à l'étude des amphibiens de Guyane française. III. Une nouvelle espèce de *Colosthetus* [sic] (Dendrobatidae): *Colosthetus* [sic] *degranvillei* nov. sp. Bull. Mus. Natn. Hist. Nat., Paris, 3e Sér., Zool. 203:413-420.
- _____. 1984. Las larvas de dendrobatidae [sic]. [Proc.] II. Reunión Iberoamer. Cons. Zool. Vert. pp. 37-45.
- LYNCH, J. D. 1982. Two new species of poison-dart frogs (*Colostethus*) from Colombia. Herpetologica 38:366-374.
- MCKINNEY, M. L., AND K. J. MCNAMARA. 1991. Heterochrony: the Evolution of Ontogeny. Plenum Press, New York.
- MYERS, C. W., A. PAOLILLO O., AND J. W. DALY. 1991. Discovery of a defensively malodorous and nocturnal frog in the family Dendrobatidae: phylogenetic significance of a new genus and species from the Venezuelan Andes. Amer. Mus. Nov. (3002):1-33.
- NODZENSKI, E., AND R. F. INGER. 1990. Uncoupling of related structural changes in metamorphosing torrent-dwelling tadpoles. Copeia 1990:1047-1054.
- SILVERSTONE, P. A. 1976. A revision of the poison-arrow frogs of the genus *Phyllobates* Bibron. Nat. Hist. Mus. Los Angeles Co. Sci. Bull. (27):1-53.

- WASSERSUG, R. J., AND K. V. S. HOFF. 1985. The kinematics of swimming in anuran larvae. *J. exp. Biol.* 119:1-30.
- WELLS, K. D. 1977. The social behaviour of anuran amphibians. *Anim. Behav.* 25:666-693.
- ZIMMERMANN, H., AND E. ZIMMERMANN. 1988. Ethno-Taxonomie und zoogeographische Artengruppenbildung bei Pfeilgiftfröschen (Anura: Dendrobatidae). *Salamandra* 24:125-160.

FIGURE 1. (A) Intact egg mass of *Colostethus chalcopis*, as collected in the field. The three embryos at the upper left are at about Gosner (1960) stage 22, and the embryos at the lower right are at about early stage 25. (B) Intact egg mass, photographed three days after collection. Three embryos (upper left) have developed to early stage 25, and the others are in stage 26 or 27.



FIGURE 2. Oral disc of *Colostethus chalcopis* (actual width = 0.9 mm).

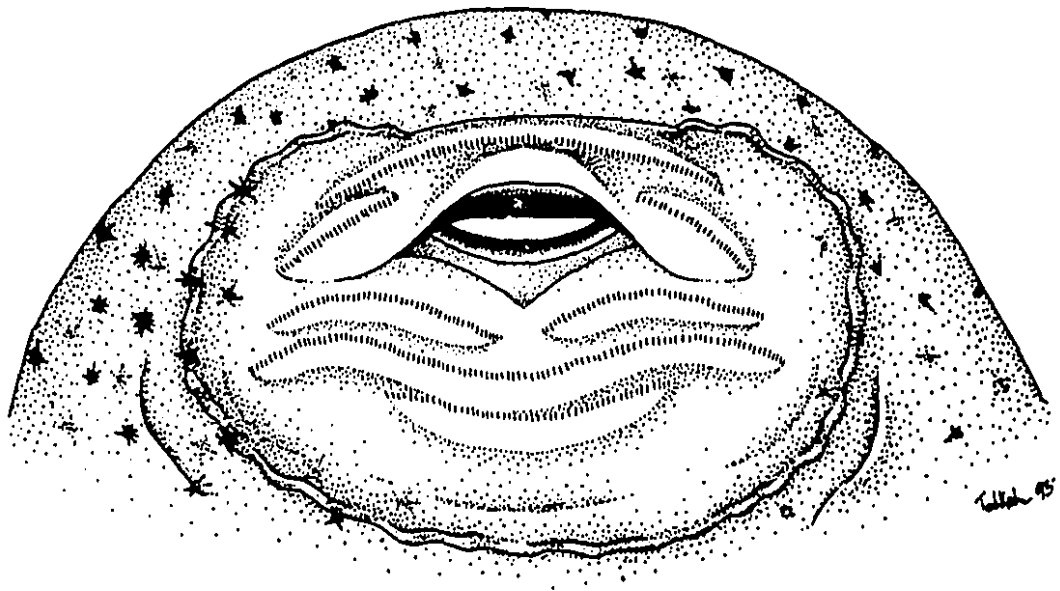
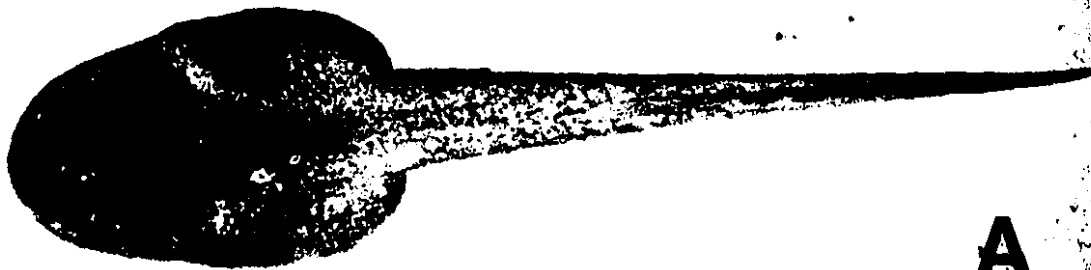
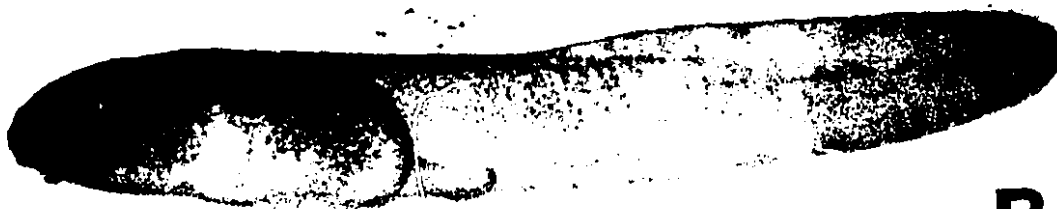


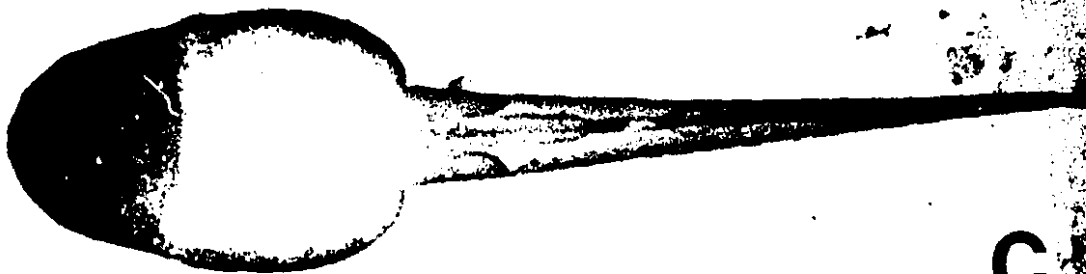
FIGURE 3. Tadpole of *Colostethus chalcopis*: (A) dorsal, (B) lateral, and (C) ventral views (actual length = 12.0 mm).



A



B



C

5

Multivariate Morphometrics of Eastern Caribbean *Eleutherodactylus* (Anura, Leptodactylidae): Biogeography, Divergence, and Evolution

To be published as: Kaiser, H. Multivariate morphometrics of Eastern Caribbean *Eleutherodactylus* (Anura, Leptodactylidae): biogeography, divergence, and evolution. *Herpetologica*. *Submitted*.

PREAMBLE CHAPTER 5

Having collected specimens of *Eleutherodactylus* on all Eastern Caribbean islands, it became apparent that these taxa would be the most challenging from a systematics point of view due to their great morphological similarity. In order to make the systematic study as comprehensive as possible, I began investigating species relationships phenetically using multivariate morphometrics. This type of analysis is state-of-the-art and has recently earned considerable attention, for example in the journal *Evolution*, when used in studies of divergence and evolution. During the research for Chapters 1 and 2, these techniques had been useful in assigning taxa to species, confirming the results of allozyme data. I wanted to see whether they could also be used to find and define species groups within the taxa studied.

ABSTRACT

Morphometric analyses of 20 metric characters for eight Eastern Caribbean species of *Eleutherodactylus* provide evidence that the anuran fauna of this area contains both South American and Lesser Antillean elements. Statistical assignments using individual canonical factors of all measured individuals assigned species correctly in only 63.9% of all cases, indicating that overall linear morphologies of species are quite similar. However, a comparison of northern with southern species groups identified groups correctly in 92.5% of all cases and aligns southern taxa with *E. terraebolivaris*, a species native to Tobago and Venezuela. There were also significant differences between northern and southern populations of *E. johnstonei*, a species which has become widespread through human introductions. The most important factors in consistently differentiating southern and northern species were those related to limb proportions. Three conclusions emerge from this approach: (1) Colonization of the Eastern Caribbean by anurans occurred at least twice; (2) Rapid adaptive diversification of colonizing ancestors led to the evolution of at least four species that can be recognized as Antillean stock, and three species of South American stock; (3) Morphological divergence lags behind adaptive diversification among Eastern Caribbean *Eleutherodactylus*, as evidenced by the presence of four different modes of life among frogs with very similar morphologies: generalists (*E. johnstonei*, *E. martinicensis*), a semi-aquatic specialist (*E. barlagnei*), arboreal forest-dwellers (*E. euphronides*, *E. shrevei*), and two miniaturized ecomorphs (*E. pinchoni*, *E. urichi*). The close connection between adaptation to specific life-styles and morphology among these taxa is convincingly demonstrated by the clear relationship of tibia length, the most important variable in the morphometric assessment, with total toepad area, an indicator of species arboreality.

INTRODUCTION

Neotropical frogs of the genus *Eleutherodactylus* range throughout much of South and Central America and most of the Caribbean islands. With over 500 species (Duellman, 1993), it is the most speciose vertebrate genus. Although several species groups within the genus have been identified through morphological and biochemical means (e.g., Lynch, 1975, 1979, 1980, 1981; Lynch and Myers, 1983; Miyamoto, 1983, 1984, 1986; Savage, 1975, 1987), adjustments of internal classification continue to be made (e.g., Hedges, 1989; Joglar, 1989). Morphologically, *Eleutherodactylus* is a difficult genus; frogs are typically small, with high phenotypic variability within and between species. However, this variability occurs within a morphologically conservative bauplan. Furthermore, unequivocal identification is often complicated by color polymorphisms and sexual dimorphism. Although the Eastern Caribbean *Eleutherodactylus* also display a high degree of dorsal pattern polymorphism (Kaiser, 1992; Schwartz, 1967; Chapter 1), their discrete island distributions (Fig. 1) and our knowledge of the fauna (Hardy, 1982; Hedges and Thomas, 1989; Kaiser, 1992; Kaiser et al., 1993a; Lescure, 1979, 1987; Schwartz, 1967, 1969; Schwartz and Henderson, 1985, 1991; Schwartz and Thomas, 1975; Schwartz et al., 1978; Chapters 1, 2) make them a manageable study group, in contrast to the large, unwieldy assemblages occurring elsewhere.

In the Eastern Caribbean (i.e., the Lesser Antilles plus Trinidad and Tobago; Fig. 1), a small assemblage of eight *Eleutherodactylus* species is found on a group of small oceanic and continental-shelf islands, geographically located between the diverse *Eleutherodactylus* faunas of the Greater Antilles and northern South America. Schwartz's (1967) review of the frog fauna of the Lesser Antilles listed five species: *E. barlagnei*, *E. johnstonei*, *E. martinicensis*, *E. pinchoni*, and *E. urichi*. A systematic

investigation ascertained the full species status of *E. euphronides* from Grenada and *E. shrevei* from St. Vincent (Kaiser et al., 1993a; Chapter 2), which Schwartz (1967) originally described as subspecies of *E. urichi*. *Eleutherodactylus terraebolivaris*, the only species whose range extends from northern South America into the Eastern Caribbean (Tobago; Fig. 1), is an important link between mainland and island species, making it a *quasi* outgroup to the island taxa.

Despite the relatively low diversity of *Eleutherodactylus* in the Eastern Caribbean, four adaptive life-styles are exploited by these species. *Eleutherodactylus johnstonei* and *E. martinicensis* are ecological generalists; while both species inhabit pristine island ecosystems, *E. johnstonei* displays a superior ability to colonize dry or disturbed habitats due to its physiology and behavior (Kaiser, 1992; Pough et al., 1977; Stewart, 1977; Chapter 1), while *E. martinicensis* is less competitive though equally able to inhabit drier places (Schwartz, 1967; personal observation). On the Basse-Terre portion of Guadeloupe (Fig. 1), both species are sympatric in various areas with *E. barlagnei* and *E. pinchoni*, which are specialized for semi-aquatic and terrestrial life, respectively. *Eleutherodactylus pinchoni* is a minute frog which preferentially exploits the microhabitat under moss mats and which retreats into shallow burrows when inactive or threatened (Schwartz, 1967; personal observation). The semi-aquatic *E. barlagnei* has webbed feet, a rare trait in *Eleutherodactylus*. This species hides in rock cracks adjacent to or within fast-flowing mountain streams, with males perching on wet boulder faces to attract mates (Schwartz, 1967; personal observation). *Eleutherodactylus euphronides* and *E. shrevei*, the endemic species of Grenada and St. Vincent, respectively, are adapted for a more arboreal life style in montane forest habitats, just as *E. terraebolivaris* on Tobago. However, niche use and partitioning is more difficult to assess on Trinidad and Tobago due to the presence of several frogs belonging to genera other than *Eleutherodactylus*. Nevertheless, *E. urichi*

does reflect the observations made on other islands. It is a minute ground-dwelling species restricted to montane forests in which species of *Hyla* occupy the arboreal niches, *Colostethus* the streams, and where several *Hyla* or *Leptodactylus* are generalists. On Trinidad, no other *Eleutherodactylus* share the habitat of *E. urichi*, while on Tobago *E. terraebolivaris* and a third, as yet undescribed species are sympatric locally (Hardy, 1982; Kaiser et al., 1993a; Chapter 2).

Morphometrics, adaptation, and evolution.—To reduce taxonomic confusion when advanced biochemical investigations are precluded, morphometric studies can assist in determining taxonomic groupings for systematic investigations. Newly developed biochemical technologies have done much to advance our knowledge of the intricate processes of evolutionary change at a molecular level. At the same time, recent computational, algorithmic, and technological advances have made morphometrics a far more powerful tool than it used to be. Multivariate morphometric approaches have been shown to be particularly relevant to studies of morphological divergence and evolution (Atchley et al., 1981, 1982; Baker, 1980; Bookstein et al., 1985; Mensi et al., 1992; Michaux, 1989; Voss, 1988; Voss and Marcus, 1992; Voss et al., 1990), and data from such studies provide a valuable alternative to sometimes contradictory or controversial molecular results. Particularly in investigations where important museum specimens, such as type specimens or single individuals, are unavailable for invasive sampling, modern morphometrics provides a powerful way of integrating state-of-the-art technology with a whole-organism approach to questions of evolution.

In view of their ecological diversity, morphometric data from Eastern Caribbean *Eleutherodactylus* may add to our understanding of the sequence in which adaptation, morphological diversification, and, ultimately, speciation have been hypothesized to occur (Barton, 1988; Diehl and Bush, 1989; Endler, 1989; Grant and Grant, 1989;

Matsuda, 1987; Nevo, 1989). It has been postulated that the potential for evolutionary advancement, as gauged by speciation (*sensu* Willmann, 1988), is increased if localized stressful environments necessitate adaptation, thus creating peripheral isolates and a high potential for premating isolation (Barton, 1988; Diehl and Bush 1989; Endler, 1989; Grant and Grant, 1989; Marchetti, 1993; Nevo, 1989; Parsons, 1988). The Eastern Caribbean is a fluctuating environment, periodically disturbed by abiotic phenomena (e.g., volcanism, sea level changes, hurricanes). Newly arriving organisms must display a certain propensity for rapid adaptation to survive, particularly to changing physiological regimes (Dawson et al., 1977; Hochachka and Somero, 1984). For the Eastern Caribbean *E. johnstonei*, for example, the proposed high physiological potential to adapt rapidly to disturbed environments has already been documented (Pough et al., 1977; Stewart, 1977). Thus, one might hypothesize that localized abiotic disturbances on Eastern Caribbean islands may have given rise to phenotypic variants with higher fitness (= adaptation *sensu* Reeve and Sherman, 1993) in the less than optimal habitats, resulting in ecological diversification among the native *Eleutherodactylus* but as yet only limited morphological change. Among the more famous examples for juxtaposition of divergent functionality and morphological homogeneity are the Galapagos marine iguanas, *Amblyrhynchus cristatus* (see Dawson et al., 1977), and Darwin's finches, genus *Geospiza* (Grant and Grant, 1989). In both cases, a high degree of adaptive divergence exists, while overall external morphology has remained very similar to related taxa.

That frogs of the genus *Eleutherodactylus* are able to adapt particularly well to different environments can be inferred from their rapid chromosomal and biochemical divergence, and from their high degree of single-locality endemism (e.g., Bogart, 1989, 1991; De Weese, 1976; Hedges, 1989; Miyamoto 1983, 1984, 1986; Schmid et al., 1992; see Frost, 1985). Adaptive divergence may then be enhanced

morphologically by character displacement (Losos, 1990; MacArthur and Wilson, 1967; Roughgarden and Pacala, 1989; Schoener, 1988). Thenius (1989) suggested that such an hypothetical sequence may not necessarily imply a cause-and-effect relationship between adaptation and morphological evolution (ecological determinism *sensu* Endler, 1982), a concept considered tautological by some (Dawson et al., 1977; Krimbas, 1984). However, it is useful simply to point out that the limits of an organism's physiological and morphological functionality dictate the environments which it can adapt to and succeed in (Reeve and Sherman, 1993). Given a recognizable degree of adaptive divergence, then, an analysis of body shape and proportions can be used to examine correlations between adaptation and morphological diversification.

Morphometric data may also assist in elucidating biogeographic relationships. The Eastern Caribbean is composed mainly of volcanogenic or raised-reef islands which appeared in a geologically short time-span during the Late Oligocene; thus, it is more difficult to assess the area's biogeography than if known vicariant events had separated or joined geological entities, as elsewhere in the Caribbean (Perfit and Williams, 1989; Savage, 1982; Williams, 1989; see Woods, 1989). Although biogeographic data for mammals (MacFadden, 1980), birds (Lack, 1976), and lizards (Williams, 1969) are available, these organisms are capable of cross-water dispersal, while amphibians are not due to their sensitive permeable skin (Duellman and Trueb, 1986). Attempts at explaining the origin of Eastern Caribbean frogs have so far been limited to the use of distributional data (Lescure, 1979, 1987), and provide little resolution. With the recent discovery of additional species (Kaiser et al., 1993a, b; Chapters 2, 3) it is even uncertain how diverse the frog fauna actually is, let alone where species originated or how they may be related.

In this study, I use a large morphometric data set for multiple purposes. Determination of morphometric groupings allows phenetic inference of systematic relationships, which can in turn be of value in investigating biogeographic hypotheses. Having considered that a sequence of adaptation and morphological diversification is possible, these two concepts should be linked tightly in some quantifiable teleonomic context, i.e. to conclude that adaptation is the underlying concept for the observed variation, morphometry should be reflected in function (Reeve and Sherman, 1993). I thus connect adaptive/functional aspects of species design to the morphometric information in a teleonomic context by comparing a quantitative adaptational character, relative arboreality as expressed by total toepad area, to the most important metric character.

MATERIALS AND METHODS

Specimens of *Eleutherodactylus barlagnei*, *E. euphronides*, *E. johnstonei*, *E. martinicensis*, *E. pinchoni*, *E. shrevei*, *E. terraebolivaris*, and *E. urichi* were collected in the Eastern Caribbean between 1989 and 1992. A total of 876 specimens was brought to the Redpath Museum, McGill University. Sample sizes of highly localized populations (eg., Barbuda, Caracas, Guyana, St. Eustatius; Appendix I) were limited to < 15 specimens in order to minimize disruption of presumably small populations. An additional 126 specimens from museum collections were examined, including the holotypes of *E. barlagnei*, *E. euphronides*, *E. johnstonei*, *E. pinchoni*, *E. shrevei*, and *E. terraebolivaris* (Appendix 1). Twenty length measurements (Table 1) were taken to the nearest 0.1 mm on each frog. The measuring setup consisted of a dissecting microscope outfitted with a camera lucida attachment, and a Numonics 2200 digitizing tablet supported by Jandel Scientific Sigma Scan (version 3.10) software on an IBM

compatible PC. A point light source, visible through the camera lucida setup, was superimposed over the crosshairs of a digitizing mouse. Structures to be measured were placed horizontally under the microscope, and the digitizing mouse was used to enter the extremes of the measurements into the scanning tablet. This technique was found to minimize measurement errors; it also allowed for accurate measurement of both large and small distances under increased magnification (trials at 4.5x and 9x magnification resulted in errors of < 5%).

Toepads were measured for the largest and smallest available specimens of each species, as well as for eight additional specimens chosen randomly. The digitizing setup was used at 18:1 total magnification to draw toepad outlines; Sigma Scan automatically calculated the encircled area based on prior calibration. Total toepad area, considered an assessment of the degree of relative arboreality (Green, 1979; Green and Simon, 1986), was calculated by doubling the sum of measurements for all toepads on the right side of each animal. This variable was corrected for size by scaling to mean snout-vent length for each presumptive group. Data sets were transferred in ASCII format, and Systat software (version 5.2) was used on an Apple Macintosh LC (expanded memory) to perform statistical analyses.

Raw morphometric data were used to calculate basic statistics. Principal components analysis (PCA) was used as an exploratory device to determine the minimum number of informative variables required and to obtain preliminary specimen groupings for further analysis. Log-transformed data were used in a variance-correlation matrix, and sexes were treated separately as well as combined. Only informative variables, those found to be orthogonal in one or more vector plots of the first five principal components, were used in subsequent analyses to reduce calculation time. In order to stabilize the nomenclature for discriminant analyses, the terminology of Hair et al. (1992) was followed. Multiple discriminant function analyses (MDAs)

were then used to test groupings (= categories) of the data used in PCA, standardizing data within each assumed group. Discriminant scores for each individual specimen were saved during MDA runs and plotted. Such plots were used to define a group "morphospace," which here refers to the geometric area inside or immediately surrounding a 50% centroid calculated from the canonical variates for each measured individual. Thus, "South American morphospace" would here be defined to be that space on a plot of South American taxa which lies within and immediately around the 50% centroid of those taxa. This definition is not strict and changes with the addition or removal of specimens.

The Mahalanobis distance (D_M) was calculated and clustered using the UPGMA algorithm (a step-by-step guide to calculating D_M in Systat 5.2 is provided in Appendix 2). This algorithm is the most widely accepted clustering method; it clusters by recalculating the data matrix after each pairing, using only the original matrix data and avoiding clusters due to calculation artifacts. All groupings were resolved equally well, whether sexes were kept separately or combined, thus only results for analyses of sexes combined are reported here.

RESULTS

Vector plots from a PCA run on all twenty measurements for all specimens showed only ten variables were informative for assessing the morphometric variation of Eastern Caribbean *Eleutherodactylus*. Subsequent calculations used only head width (HW), eye diameter (ED), tympanum diameter (TD), tympanum-eye distance (TE), interorbital distance (IOD), snout length (SL), internarial distance (ID), tympanum-naris distance (TN), snout-vent length (SVL), and tibia length (TIB). PCA created two unexpected groups with specimens *a priori* assigned to *E. barlagnei* and *E.*

martinicensis. These groups were treated separately and are hereafter referred to as populations A and B, respectively (Table 2; Appendix 1). Populations of *E. johnstonei* were separated into northern and southern components because the distribution of the species is discontinuous along the island chain (Fig. 1A). Preliminary groupings from PCA also indicated the presence of two species groups; one containing the species endemic to the southern part of the region, on islands up to and including St. Vincent, the other containing all remaining species, including the widely distributed *E. johnstonei* (Fig. 1B). The results from PCA thus led to three MDAs: (1) Data set of all species combined tested against one another, grouped by islands, with populations of *E. johnstonei* and *E. martinicensis* lumped for their entire respective ranges; (2) Data set of all northern species (St. Lucia and islands farther north, including the more widely distributed *E. johnstonei* and *E. martinicensis*) tested against all southern species (south of St. Lucia); (3) Data set of *E. johnstonei* populations north of Dominica tested against those south of Dominica.

All species combined.—General size differences, as expressed by mean SVL, HW, EN, and TIB, respectively (Table 2), suggested that the species can be placed along a size continuum with *Eleutherodactylus pinchoni* (16.8, 6.4, 1.8, 7.4) at the small, and *E. terraebolivaris* (32.5, 13.0, 4.5, 19.8) at the large extreme. Ratios indicative of body proportions (Table 2) showed that TIB measurements were the most important single metric character in contrasting Eastern Caribbean *Eleutherodactylus*. Average values for TIB/SVL were 0.443 for *E. johnstonei*, 0.468 for *E. martinicensis*, 0.461 for *E. barlagnei*, and 0.444 for *E. pinchoni* (Table 2). The same values were significantly higher ($p \leq 0.001$) for *E. euphronides*, *E. shrevei*, *E. terraebolivaris* and *E. urichi* at 0.554, 0.542, 0.598, and 0.503, respectively. On the other hand, values of HW/SVL showed no consistent differences (Table 2).

The MDA of the complete data set showed that both size and shape were important in characterizing Eastern Caribbean *Eleutherodactylus*, and that the loadings for first three discriminant functions (DFs) were sufficient for species assessments. Loadings for DF1 were all positive and for DF3 all negative (Table 3); sign homogeneity identified these as size-determined loadings. The loadings with the greatest discriminating power (ranked in order from greatest to smallest contribution) were TIB, ED, ID, and IOD for DF1, and HW, TE, ED, SL, and ID for DF3 (Table 3). The variables with the greatest discriminating power in DF2, indicative of shape, were TD, EN, TE, and SL (Table 3). Species (= group) assignments based on individual discriminant probabilities (DS) showed that the statistical classification using the calculated discriminant function was 63.9% correct over all 1002 classified specimens (Table 4). Specimens of *E. martinicensis* (34.2%) were the least well classified (Table 4), with all other specimens classified correctly an average of 72.3% of the time. Much of the poor classification for specimens of *E. martinicensis* was due to incorrect grouping (Table 4) with *E. johnstonei* (21.7%) and population B (21.7%). The converse effect was also observed: 14.0% of *E. johnstonei* specimens and 17.2% of specimens from population B were statistically misaligned with *E. martinicensis* (Table 4).

Discriminant score (DS) plots of DS1 against DS2 showed that differences of size (DS1) and shape (DS2) existed between species, but that graphic representation was insufficient to clearly separate taxa (Fig. 2A). Partial overlap of centroids occurred for all species on islands to the north of St. Lucia, indicating a great similarity of morphologies (Fig. 2A). There was partial overlap of the population A centroid with both *Eleutherodactylus barlagnei* and *E. pinchoni* centroids, while there was considerable overlap of all remaining centroids (Fig. 2A). The species occurring to the south of St. Lucia were somewhat better separated, especially on the size axis (Fig.

2A). *Eleutherodactylus euphronides*, *E. shrevei*, and *E. terraebolivaris* were separated from northern species by DS1, while *E. urichi* overlapped *E. martinicensis* and population B centroids (Fig. 2A). Separation of *E. euphronides* and *E. shrevei* from either *E. terraebolivaris* or *E. urichi* was almost complete, but there was complete overlap for the centroids of the former two species (Fig. 2A).

The UPGMA phenogram resulting from clustering of Mahalanobis distances (Fig. 3) showed that species were separated by distances > 1.0 . Populations A and B grouped with *Eleutherodactylus barlagnei* and *E. martinicensis*, respectively. Two larger species clusters were formed, one by *E. euphronides*, *E. shrevei*, and *E. terraebolivaris*, and another including all remaining species (Fig. 3). The small cluster consisting of *E. barlagnei* and Pop. A, and the species *E. terraebolivaris* were the furthest distant from their respective clusters.

Northern vs. southern species.—A MDA of two sets of species, with *Eleutherodactylus terraebolivaris* as a reference, resulted in loadings similar to those for the analysis of all species: DF1 was a size-determined function, whereas DF2 was shape-determined. The greatest discriminating power in DF1, ranked as above, were made again by TIB and ED, followed by ID and IOD (Table 5). The main contributions to shape (DF2) were very different when comparing species sets; the only outstanding contributions were made by SVL and EN (Table 5). Group assignments (Table 6) from individual discriminant probabilities strongly (90.6%) supported the presence of two distinctive species groups: a northern group consisting of *E. barlagnei*, *E. johnstonei*, *E. martinicensis*, *E. pinchoni*, and populations A and B; and a southern group, consisting of *E. euphronides*, *E. shrevei*, and *E. urichi*, more closely aligned with the South American *E. terraebolivaris* than with any northern species. Northern specimens were grouped correctly 93.7% of the time, while southern specimens were

assigned correctly in 87.4% of the cases. A discriminant score plot of DS1 against DS2 (Fig. 2B) showed that species group centroids were clearly separate along the size axis (DS1) and partially along the shape axis (DS2). *Eleutherodactylus terraebolivaris* could be separated along both axes. The phenogram of Mahalanobis distances showed two distinct species groups, with *E. shrevei*, *E. euphronides*, and *E. terraebolivaris* forming a single cluster (Fig. 3). However, *E. urichi* clustered with the northern species.

Eleutherodactylus johnstonei.—In a MDA of northern and southern populations of *E. johnstonei*, using *E. terraebolivaris* as a reference species, loadings for DF1 and DF2 were again indicative of size and shape, respectively (Table 7). In order of importance, TIB, ID, IOD, and ED contributed the most to DF1, while it was ED and SL for DFs2 (Table 7). Group assignments for this analysis (Table 8) were correct in differentiating northern and southern *E. johnstonei* specimens 74.8% of the time. Error with respect to classification of *E. terraebolivaris* was less than 1%. The discriminant score plot (Fig. 2C) showed partial overlap of northern and southern *E. johnstonei* centroids, but some difference along the shape axis (DS2).

Toepad area.—Size-corrected toepad area differed among species, with some displaying relatively larger toepads. Among Eastern Caribbean *Eleutherodactylus*, this variable was proportional to TIB, with species clustering quite tightly ($r^2 = 0.640$) around a line with a slope of 1.87 in a ln-ln plot (Fig. 4). Neither SVL nor total toepad area were found to be significant contributors to TIB in multiple regression analyses of mean values for all species separated or combined ($P > 0.05$), indicating the relative independence of these characters.

DISCUSSION

The clear morphometric separation of northern and southern species groups due to both size and shape (Fig. 2B) indicates the presence of two distinct faunal components in the Eastern Caribbean. The similarity of the three southern species with *Eleutherodactylus terraebolivaris* places them closest to a South American morphospace, while the other species exist in a Lesser Antillean morphospace. This result does not contradict the suggestion of Lescure (1987) that the frogs occurring in this region arrived in two migration waves from South America. It may, however, contradict the view that the species from the southern Lesser Antilles and *E. urichi* belong to the *E. auriculatus* section (Hedges, 1989), the same morphological lineage as most Greater Antillean taxa. Inclusion of additional taxa, from both the Greater Antilles and South America, would be required to further investigate this deviation from previously reported results (e.g., Schwartz, 1967). The most characteristic factors for separation of these two groups are tibia length for size and several head characters for shape (Table 5). Furthermore, the degree of arboreality observed in *E. euphronides*, *E. shrevei*, and *E. terraebolivaris* is elevated with respect to other species (Fig. 4), a reflection of their habit as forest-dwellers.

The results also provide evidence for the hypothesis that Eastern Caribbean *Eleutherodactylus* continue to diverge rapidly. The separation of *E. johnstonei* populations into northern and southern components (Fig. 2C), together with the possibility of two cryptic species in populations A and B (Fig. 2A; Table 4), lends credence to the theory that evolution on these small islands proceeds very rapidly. *Eleutherodactylus johnstonei* is known to have arrived on many islands only recently (Kaiser, 1992; Chapter 1), and the relative homogeneity of populations in both northern and southern areas of the range supports this view. Thus, assuming that introductions

occurred in the past 200-300 years from the southern to the northern islands, along the predominant trade route of that time (Hall, 1982; Mitchell, 1973), the statistical separation of these populations (Fig. 2C; Table 8) shows some rapid divergence has occurred. This divergence may be a result of independent founder effects at initial colonization of each island, or of actual rapid divergence. Divergence is a distinct possibility considering the island of Barbuda. Combination of my data for females from Barbuda with those from Schwartz (1967) shows that these animals have significantly shorter tibiae than found in any other *E. johnstonei*-populations ($TIB/SVL \bar{x} = 0.398$, $n = 16$; $P < 0.05$). Barbuda is the most xeric island in the region and frogs are confined to water cisterns and a few water holes; thus, extreme pressure to adapt may have accelerated morphological divergence since the presumed arrival of frogs after the settlement of the island in 1684. Similarly, populations A and B may have diverged sufficiently in the relatively species-rich central Lesser Antilles (Fig. 1) so as to constitute distinct taxa. The difference with the situation on islands where *E. johnstonei* is the only resident *Eleutherodactylus* is that interspecific competition may be occurring. As with lizards of the genus *Anolis* (Losos, 1990), species inhabiting this region may have, and may still be, experiencing character displacement as a result of the presence of congeners.

As a corollary to rapidity of evolution and the possibility of *in situ* speciation, data from Eastern Caribbean *Eleutherodactylus* also suggest that in these species, behavioral and physiological adaptation precede morphological evolution. Despite the disparate life-styles of these species, there is considerable overlap of Antillean and South American morphospace as exemplified by northern species centroids and those of southern species (Figs. 2A, B; Tables 4, 6). The high degree of ecological specialization expressed by these organisms is thus not clearly reflected in overall morphometric diversity, despite the fact that species can be separated statistically. This

discrepancy between rapid adaptation and morphometric homogeneity may be explained in terms of organismal and environmental interactions, and is attested to by adaptations as wide-ranging as beak specialization for seeds in Darwin's finches (Grant and Grant, 1989), aquatic adaptations of behavior in Galapagos iguanas (Dawson et al., 1977), or structure and function in Mesozoic reptiles (Carroll, 1984). In *Geospiza*, the crucial factor affecting niche occupancy is beak size and shape, whereas in *Amblyrhynchus*, it is the development of a novel foraging behavior. For mosasaurs, plesiosaurs, and advanced ichthyosaurs, specializations for aquatic propulsion were apparently achieved by behaviorally modifying fore- and hindlimb movements, eventually resulting in changes of limb and limb girdle morphology while retaining a constant overall body form (Carroll, 1984). The data from Eastern Caribbean *Eleutherodactylus* show that these frogs are differentiated or becoming differentiated not only in size, shape, or behavior, but in physiology and ecology as well. Such extreme evolutionary flux is likely a major factor in creating large radiations, such as *Bufo*, *Eleutherodactylus*, *Hyla*, and *Rana* among extant anuran genera, as well as several of the larger radiations of paleozoic amphibians or mesozoic reptiles (Carroll, 1988).

Comparative data from digital pad size provide further evidence for the influence of ecology/microhabitat on evolution. Different degrees of adaptation to climbing require appropriate development of toepads, and it has been shown that even within genera, variation in size and structure of toepads can be great (Green and Simon, 1986). Among Eastern Caribbean *Eleutherodactylus*, toepad development reflects disparate life-styles. The species with best developed toepads (*E. euphronides*, *E. martinicensis*, *E. shrevei*, *E. terraebolivaris*) are found at the upper extreme for both tibia and toepad size (Fig. 4) and can be considered more arboreal than the others. *Eleutherodactylus martinicensis* occupies a greater variety of habitats than the other three species, yet based on degree of arboreality, it may be an ecological generalist

which has retained some morphological aspects of a forest species. Functional digital pads are progressively less important for semi-aquatic, generalist, and ground-dwelling life-styles, a prediction reflected exactly by the data (Fig. 4). The close quantitative relationship of these selected morphological and ecological characters shows that the influence of ecology on morphology is significant among these taxa, though these data cannot be used to infer directionality of that influence. Furthermore, I conclude that the disparate life-styles of these frogs have evolved by optimization of fitness through successful phenotypic adaptation in an environmental context, reflecting exactly the recently proposed theory of Reeve and Sherman (1993).

Biogeography and evolution of Eastern Caribbean anurans are not easily resolved due to the difficulties associated with regional geology (Perfit and Williams, 1989), and the instability of habitat on islands that may experience periodic volcanic disturbances or persistent exposure to oceanic weather. For the Lesser Antilles, the hypothesis that frogs arrived by dispersal has never been questioned (Perfit and Williams, 1989; Williams, 1989). Frogs ancestral to the present species may have dispersed from both northern South America and the Greater Antilles (or the "proto-Antilles" *sensu* Savage, 1982) when settlement of the island arc became possible during the mid-Eocene to Miocene (Perfit and Williams, 1989), but neither a timetable nor a possible sequence for colonizations has been presented to date. Just as likely, however, is the scenario of multiple colonizations from South America as proposed by Lescure (1987). The biogeographic scenario for Trinidad and Tobago is much more easily explained. Both islands are part of the continental shelf, and the biotas are depauperate versions of a South American fauna.

The present study provides a systematic and biogeographic assessment for the *Eleutherodactylus* species of the Eastern Caribbean which is incongruent with current subgeneric classification. Only the northern species can be considered members of the

E. auriculatus section, while the others may be linked to one or more of the northern South American groups. This small adaptive radiation also provides an extreme example of how quickly the influence of environment may force adaptation to less than optimal niches, creating distinct ecomorphs with minimal morphometric differentiation.

ACKNOWLEDGMENTS

I am indebted to my indefatigable field assistants C. A. George, H. M. Gray, G. Schäfer, H. H. Schwarten, T. F. Sharbel, D. von Stösser, and A. Werres without whose enthusiastic help and manual dexterity the establishment of a collection of this size would have been impossible. H. M. Reiswig is gratefully acknowledged for patiently supporting my many attempts at digitizing frog lengths and toepad areas on his equipment and for instructing me on the pitfalls of his digitizing software. Long discussions with D. M. Green about anuran morphology and frogs on islands provided sometimes necessary new perspectives. G. Bell, M. W. Caldwell, D. M. Green, L. A. Lowcock, and D. Roff made valuable comments on the manuscript. This research was conducted as part of my doctoral studies, and it was supported by grants from the Hans-Krüger-Stiftung and the Studienstiftung des Deutschen Volkes, Germany, and by an NSERC operating grant to D. M. Green.

LITERATURE CITED

- ATCHLEY, W. R., J. J. RUTLEDGE, AND D. E. COWLEY. 1981. Genetic components of size and shape. II. Multivariate covariance patterns in the rat and mouse skull. *Evolution* 35:1037–1055.
- _____. 1982. A multivariate statistical analysis of direct and correlated response to selection in the rat. *Evolution* 36:677–698.

- BAKER, A. J. 1980. Morphometric differentiation in New Zealand populations of the house sparrow (*Passer domesticus*). *Evolution* 34:638–653.
- BARTON, N. H. 1988. Speciation. Pp. 185–218. *In*: A. A. Myers and P. S. Giller (Eds.). *Analytical Biogeography*. Chapman and Hall, New York.
- BOGART, J. P. 1991. The influence of life history on karyotypic evolution in frogs. Pp. 233–258. *In*: D. M. Green and S. K. Sessions (Eds.). *Amphibian Cytogenetics and Evolution*. Academic Press, New York.
- BOOKSTEIN, F. L., B. CHERNOFF, R. L. ELDER, J. M. HUMPHRIES, G. R. SMITH, AND R. E. STRAUSS. 1985. Morphometrics in evolutionary biology. *Acad. Sci. Philadel. Spec. Publ.* (15):1–277.
- CARROLL, R. L. 1984. The emergence of marine reptiles in the Late Paleozoic and Early Mesozoic. Pp. 41–46. *In*: W.-E. Reif and F. Westphal (Eds.). *Third Symposium on Mesozoic Terrestrial Ecosystems. Short Papers*. Attempto-Verlag, Tübingen, Germany.
- _____. 1988. *Vertebrate Paleontology and Evolution*. W. H. Freeman and Co., New York.
- DAWSON, W. R., G. A. BARTHOLOMEW, AND A. F. BENNETT. 1977. A reappraisal of the aquatic specializations of the Galapagos marine iguana (*Amblyrhynchus cristatus*). *Evolution* 31:891–897.
- DEWEESE, J. E. 1976. The karyotypes of Middle American frogs of the genus *Eleutherodactylus* (Anura: Leptodactylidae): a case study of the significance of the karyologic method. Unpubl. Ph.D. Thesis, Univ. of Southern California, Los Angeles.
- DIEHL, S. R., AND G. L. BUSH. 1989. The role of habitat preference in adaptation and speciation. Pp. 345–365. *In*: D. Otte and J. A. Endler (Eds.). *Speciation and Its Consequences*. Sinauer Associates Inc., Sunderland, Massachusetts.

- DUELLMAN, W. E. 1993. Amphibian species of the world: additions and corrections. Univ. Kansas Mus. Nat. Hist. Spec. Publ. (21):1-372.
- DUELLMAN, W. E. , AND L. TRUEB. 1986. Biology of Amphibians. McGraw-Hill, New York.
- ENDLER, J. A. 1982. Alternative hypotheses in biogeography: introduction and synopsis of the symposium. Amer. Zool. 22:349-354.
- _____. 1989. Conceptual and other problems in speciation. Pp. 625-648. In: D. Otte and J. A. Endler (Eds.). Speciation and Its Consequences. Sinauer Associates Inc., Sunderland, Massachusetts.
- FROST, D. R. (ED.) 1985. Amphibian Species of the World. A Taxonomic and Geographical Reference. Allen Press and the Association of Systematics Collections, Lawrence, Kansas.
- GRANT, P. R., AND B. R. GRANT. 1989. Sympatric speciation and Darwin's finches. Pp. 433-457. In: D. Otte and J. A. Endler (Eds.). Speciation and Its Consequences. Sinauer Associates Inc., Sunderland, Massachusetts.
- GREEN, D. M. 1979. Treefrog toepads: comparative surface morphology using scanning electron microscopy. Can. J. Zool. 57:2033-2046.
- GREEN, D. M., AND M. P. SIMON. 1986. Digital microstructure in ecologically diverse sympatric microhylid frogs, genera *Cophixalus* and *Sphenophryne* (Amphibia: Anura), from Papua New Guinea. Aust. J. Zool. 34:135-145.
- HAIR, J. F., JR., R. E. ANDERSON, R. L. TATHAM, AND W. C. BLACK. 1992. Multivariate Data Analysis. Third Edition. Macmillan Publishing Company, New York.
- HALL, D. 1982. The Caribbean Experience: An Historical Survey 1450-1960. Heinemann Educational Books, London.

- HARDY, J. D., JR. 1982. Biogeography of Tobago, West Indies, with special reference to amphibians and reptiles: a review. *Bull. Maryland Herpetol. Soc.* 18:37-142.
- HEDGES, S. B. 1989. Evolution and biogeography of West Indian frogs of the genus *Eleutherodactylus*: slow-evolving loci and the major groups. Pp. 305-370. *In*: C. A. Woods (Ed.). *Biogeography of the West Indies: Past, Present, and Future*. Sandhill Crane Press, Gainesville, Florida.
- HEDGES, S. B., AND R. THOMAS. 1989. Supplement to West Indian amphibians and reptiles: a check-list. *Milwaukee Publ. Mus. Contr. Biol. Geol.* (77):1-11.
- HOCHACHKA, P. W., AND G. N. SOMERO. 1984. *Biochemical Adaptation*. Princeton University Press, Princeton, New Jersey.
- JOGLAR, R. L. 1989. Phylogenetic relationships of the West Indian frogs of the genus *Eleutherodactylus*: a morphological analysis. Pp. 371-408. *In*: C. A. Woods (Ed.). *Biogeography of the West Indies: Past, Present, and Future*. Sandhill Crane Press, Gainesville, Florida.
- KAISER, H. 1992. The trade-mediated introduction of *Eleutherodactylus martinicensis* (Anura: Leptodactylidae) on St. Barthélemy, French Antilles, and its implications for Lesser Antillean biogeography. *J. Herpetol.* 26:264-273.
- KAISER, H., J. D. HARDY, JR., AND D. M. GREEN. 1993a. The taxonomic status of Caribbean and South American frogs currently ascribed to *Eleutherodactylus urichi* (Anura: Leptodactylidae). *Copeia*. *In press*.
- KAISER, H., L. A. COLOMA, AND H. M. GRAY. 1993b. *Colostethus chalcopis* (Anura: Dendrobatidae), a new species from Martinique, French Antilles. *Herpetologica*. *In press*.
- KRIMBAS, C.B. 1984. On adaptation, neo-Darwinian tautology, and population fitness. *Evol. Biol.* 17:1-57.

- LESCURE, J. 1979. Singularité et fragilité de la faune en vertébrés des Petites Antilles. C. R. Soc. Biogéogr. 482:93-109.
- _____. 1987. Le peuplement en reptiles et amphibiens des Petites Antilles. Bull. Soc. Zool. France 112:327-342.
- LOSOS, J. B. 1990. A phylogenetic analysis of character displacement in Caribbean *Anolis* lizards. Evolution 44:558-569.
- LYNCH, J. D. 1975. A review of the broad-headed *Eleutherodactylus* frogs of South America. Occas. Pap. Mus. Nat. Hist. Univ. Kansas (38):1-46.
- _____. 1979. Leptodactylid frogs of the genus *Eleutherodactylus* from the Andes of Southern Ecuador. Univ. Kansas Mus. Nat. Hist. Misc. Publ. (66):1-62.
- _____. 1980. The *Eleutherodactylus* of the Amazonian slopes of the Ecuadorian Andes (Anura: Leptodactylidae). Univ. Kansas Mus. Nat. Hist. Misc. Publ. (69):1-86.
- _____. 1981. Leptodactylid frogs of the genus *Eleutherodactylus* in the Andes of Northern Ecuador and adjacent Colombia. Univ. Kansas Mus. Nat. Hist. Misc. Publ. (72):1-46.
- LYNCH, J. D. AND C. W. MYERS. 1983. Frogs of the *fitzingeri* group of *Eleutherodactylus* in Eastern Panama and Chocoan South America (Leptodactylidae). Bull. Am. Mus. Nat. Hist. 175:481-572.
- MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Monogr. Pop. Biol. (1):1-203.
- MACFADDEN, B. 1980. Rafting mammals or drifting islands: biogeography of the Greater Antillean insectivores *Nesophontes* and *Solenodon*. J. Biogeogr. 7:11-22.
- MARCHETTI, K. 1993. Dark habitats and bright birds illustrate the role of the environment in species divergence. Nature 362:149-152.

- MATSUDA, R. 1987. *Animal Evolution in Changing Environments*. John Wiley and Sons, New York.
- MENSI, P., A. LATTES, B. MACARIO, C. GIACOMA, AND E. BALLETO. 1992. Taxonomy and evolution of European brown frogs. *Zool. J. Linn. Soc.* 104:293-311.
- MICHAUX, B. 1989. Morphological variation of species through time. *Biol. J. Linn. Soc.* 38:239-255.
- MITCHELL, H. 1973. *Europe in the Caribbean: The Policies of Great Britain, France and the Netherlands Towards Their West Indian Territories*. Cooper Square Publ. Inc., New York.
- MIYAMOTO, M. M. 1983. Frogs of the *Eleutherodactylus rugulosus* group: a cladistic study of allozyme, morphological and karyological data. *Syst. Zool.* 32:109-124.
- _____. 1984. Central American frogs allied to *Eleutherodactylus cruentus*: allozyme and morphological data. *J. Herpetol.* 18:256-263.
- _____. 1986. Phylogenetic relationships and systematics of the *Eleutherodactylus fitzingeri* group (Anura, Leptodactylidae). *Copeia* 1986:503-511.
- NEVO, E. 1989. Modes of speciation: the nature and role of peripheral isolates in the origin of species. Pp. 205-236. *In*: L. V. Giddings, K. Y. Kaneshiro, and W. W. Anderson (Eds.). *Genetics, Speciation, and the Founder Principle*. Oxford University Press.
- PARSONS, P. A. 1988. Adaptation. Pp. 165-184. *In*: A. A. Myers and P. S. Giller (Eds.). *Analytical Biogeography*. Chapman and Hall, New York.
- PERFIT, M. R., AND E. E. WILLIAMS. 1989. Geological constraints and biological retrodictions in the evolution of the Caribbean Sea and its islands. Pp. 47-102.

- In: C. A. Woods (Ed.). Biogeography of the West Indies: Past, Present, and Future. Sandhill Crane Press, Gainesville, Florida.*
- POUGH, F. H., M. M. STEWART, AND R. G. THOMAS. 1977. Physiological basis of habitat partitioning in Jamaican *Eleutherodactylus*. *Oecologia (Berl.)* 27:285–293.
- REEVE, H. K., AND P. W. SHERMAN. 1993. Adaptation and the goals of evolutionary research. *Quart. Rev. Biol.* 68:1–32.
- ROUGHGARDEN, J., AND S. PACALA. 1989. Taxon cycle among *Anolis* lizard populations: review of evidence. Pp. 403–432. *In: D. Otte and J. A. Endler (Eds.). Speciation and Its Consequences. Sinauer Associates Inc., Sunderland, Massachusetts.*
- SAVAGE, J. M. 1975. Systematics and distribution of the Mexican and Central American stream frogs related to *Eleutherodactylus rugulosus*. *Copeia* 1975:254–306.
- _____. 1982. The enigma of the Central American herpetofauna: dispersals or vicariance? *Ann. Miss. Bot. Garden* 69:464–457.
- _____. 1987. Systematics and distribution of the Mexican and Central American rainfrogs of the *Eleutherodactylus gollmeri* group (Amphibia: Leptodactylidae). *Fieldiana Zool., N. Ser.* (33):1–57.
- SCHMID, M., C. STEINLEIN, AND W. FEICHTINGER. 1992. Chromosome banding in Amphibia. XVII. First demonstration of multiple sex chromomsomes in amphibians: *Eleutherodactylus maussi* (Anura, Leptodactylidae). *Chromosoma* 101:284–292.
- SCHOENER, T. W. 1988. Ecological interactions. Pp. 255–297. *In: A. A. Myers and P. S. Giller (Eds.). Analytical Biogeography. Chapman and Hall, New York.*

- SCHWARTZ, A. 1967. Frogs of the genus *Eleutherodactylus* in the Lesser Antilles. Stud. Fauna Curaçao Carib. Isl. 23:1-62.
- _____. 1969. The Antillean *Eleutherodactylus* of the *auriculatus* group. Stud. Fauna Curaçao Carib. Isl. 30:99-115.
- SCHWARTZ, A., AND R. W. HENDERSON. 1985. A Guide to the Identification of the Amphibians and Reptiles of the West Indies Exclusive of Hispaniola. Milwaukee Public Museum, Milwaukee, Wisconsin.
- _____. 1991. Amphibians and Reptiles of the West Indies: Description, Distribution and Natural History. University of Florida Press, Gainesville, Florida.
- SCHWARTZ, A., AND R. THOMAS. 1975. A check-list of West Indian amphibians and reptiles. Carnegie Mus. Nat. Hist. Spec. Publ. (1):1-216.
- SCHWARTZ, A., 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.
- STEWART, M. M. 1977. The role of introduced species in a Jamaican frog community. Actas IV Simpos. Int. Ecol. Trop. (1):110-146.
- THENIUS, E. 1989. Molekulare und "adaptive" Evolution, Kladistik und Stammesgeschichte. Z. zool. Syst. Evolut.-forsch. 27:94-105.
- VOSS, R. S. 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. Bull. Am. Mus. Nat. Hist. 188:259-493.
- VOSS, R. S., AND L. F. MARCUS. 1992. Morphological evolution in muroid rodents. II. Craniometric factor divergence in seven neotropical genera, with experimental results from *Zygodontomys*. Evolution 46:1918-1934.

- VOSS, R. S., L. F. MARCUS, AND P. ESCALANTE. 1990. Morphological evolution in muroid rodents. I. Conservative patterns of craniometric covariance and their ontogenetic basis in the neotropical genus *Zygodontomys*. *Evolution* 44:1568–1587.
- WILLIAMS, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *Quart. Rev. Biol.* 44:345–389.
- _____. 1989. Old problems and new opportunities in West Indian biogeography. Pp. 1–46. *In*: C. A. Woods (Ed.). *Biogeography of the West Indies: Past, Present, and Future*. Sandhill Crane Press, Gainesville, Florida.
- WILLMANN, R. 1988. Microevolution as the only evolutionary mode. *Eclogae geol. Helv.* 81:895–903.
- WOODS, C. A. (ED.). 1989. *Biogeography of the West Indies: Past, Present, and Future*. Sandhill Crane Press, Gainesville, Florida.

APPENDIX 1

Specimens Examined

All specimens listed under their respective species names (numbers in parentheses) were used in the morphometric study. My own collection is partly listed with DMG (David M. Green field series) numbers, but all specimens will be deposited in the collections of the Canadian Museum of Nature (NMC). Other museum specimens are listed with institutional abbreviations as follows: AMNH (American Museum of Natural History), KU (Museum of Natural History, University of Kansas), MCZ (Museum of Comparative Zoology, Harvard University), UIMNH (Museum of Natural History, University of Illinois), and USNM (United States National Museum of Natural History, Smithsonian Institution). All distances given are road distances.

Eleutherodactylus barlagnei (29).—GUADELOUPE: Basse-Terre—Matouba, alt. 700m, MCZ 35334 (holotype); Chutes du Carbet, along path to lower falls, alt. ca. 700 m, DMG 3636, 3656, 3714, 3738, 3896; Rivière Petit David, 400 m SE les Mamelles, along road D23, alt. ca. 700 m, DMG 3549–52, 3573; Sofaïa, Rivière Salée, end of road D19, alt. ca. 300 m, DMG 3514, 3516–17, 3650, 3745, 3818; 1 km SW Desbonnes, along road D18, alt. ca. 300 m, DMG 3616, 3689, 3715, 3718, 3749, 3815; La Soufrière, 400 m W La Citerne, along road D11, alt. ca. 1200 m, DMG 4038, 4146–47, 4155; Matouba Hot Springs, alt. 1281 m, DMG 4195.

Eleutherodactylus euphronides (84).—GRENADA: Parish of St. Andrew—Grand Etang, AMNH 74536–44, KU 93337–38, 265429–40, MCZ 2976, 43229 (holotype), UIMNH 61641–43; Cable and Wireless station near Mt. St. Catherine, ca. 4 km NW Paraclete, alt ca. 650 m, DMG 4149–50, 4156, 4192, 4199–4202, 4687, 4689, 4701–05, 4742–44. Parish of St. George—8 mi NE St. George's, KU 265442–444, MCZ 2910–30, 2932–35, 2961–62, 51762–64, 51766–67; Mt. Horne Cacao Station, MCZ 31560. Parish of St. David—Les Avocats Waterworks, alt. ca. 400 m, DMG 2844; 1 mi N Vincennes, KU 265441.

Eleutherodactylus johnstonei (523).—ANTIGUA: Parish of St. Mary—End of road in Christian Valley, alt. 35 m, DMG 3221, 3223, 3225–29, 3234. Parish of St. John—Garden of Roslyn's Guest House, sea level, DMG 3141–43, 3146–49, 3152–55, 3157–60. Parish of St. Philip—Gaynor's Mill, sea level, DMG 3217–19. BARBADOS: Parish of St. James—Garden of Bellairs Research Institute, sea level, DMG 2899–2911, 3010–11, 3057–58. Parish of St. Andrew—Turner's Hall Woods, at end of St. Simon road, alt. ca. 50 m, DMG 2913–34. Parish of St. John—Road to

Consett Bay, 1/8 mi. from beach, sea level, DMG 2886–91, 2893–98, 3059. Parish of St. Michael—Bridgetown, Parking lot of Grand Barbados Beach Hotel, sea level, DMG 3004, 3009, 3012, 3015, 3061. BARBUDA: Sunset View Hotel, sea level, DMG 3593, 3624, 3633, 3654, 3667–9, 3695, 3716–17, 3721, 3729. GRENADA: Parish of St. George—St. Ann's Guest House, alt. ca. 60 m, DMG 2792, 2794–2802, 2840–43. Parish of St. Patrick—2.4 km SW Sauteurs, alt. ca. 150 m, DMG 2954–58. Parish of St. David—Bacolet Estate, 450 m beyond Petit Bacaye intersection, alt. ca. 30 m, DMG 2959–67; Les Avocats Waterworks, alt. ca. 400 m, DMG 2756–71, 2845; Parish of St. Andrew—Grand Etang Lake parking lot, alt. ca. 500 m, DMG 2803–05, 2308–13, 2316, 2318, 3013–14, 3016–17, 4154, 4190–91, 4203–04; 1.2 km W Nianganfoix Estate, alt. ca. 300 m, DMG 4063–64, 4160, 4183–84; Cable and Wireless station, ca. 4 km NW Paraclete, alt. ca. 650 m, DMG 4065. GUYANA: Georgetown, courtyard of Park Hotel, sea level, DMG 3864–66, 3885–87, 3899–3901. MONTserrat: Parish of St. Anthony—Richmond Hill, DMG 3161–65, 3167–75, 3177–78.; End of Galways Soufriere road, DMG 3350–52, 3354–55, 3357–59, 3380–88. Parish of St. Peter—Soldier's Ghaut, Fogarty's, DMG 3360–63, 3365–67, 3370–71, 3373–78. NEVIS: St. George Gingerland Parish—Golden Rock Estate, DMG 3122–36, 3139–40. St. James Windward Parish—Nesbitt Plantation, DMG 3180–85, 3187–97. SABA: 1 km N The Gap, DMG 3235, 3239–40, 3249–50, 3252–53; 1 km N Windwardside beyond English Quarter, DMG 3255–61, 3263, 3268–74; Windwardside, beginning of Mt. Scenery steps, DMG 3285–94, 3296–3304. ST. EUSTATIUS: The Quill, DMG 3335, 3337, 3339, 3341–49. ST. KITTS: St. Thomas Middle Island Parish—Romney Manor, 0.8 km N Old Road Town, DMG 3094–3105, 3108, 3110–13. St. Peter Basseterre Parish—Bayford's TV mast, 1 km N Ogee's, DMG 3389–90, 3392–99, 3401–03, 3405–06. St. John Capisterre Parish—St. George's Ghut, 0.5 km S Tabernacle, DMG 3198, 3200, 3202–03, 3205–

11, 3215–16. ST. LUCIA: Sans Soucis, Castries, DMG 2850–68, 3062; 3 km N Gros Islet, DMG 2982–94, 3060; Morne Vent, 600 m W northern Dennery turnoff, DMG 2782–91, 2846–48; 4 km SE Ravine Poisson, DMG 2869–72, 2874–84, 3067. ST-MARTIN: Pic Paradis summit, DMG 3090–93, 3305–07, 3310–18; Terres Basses, DMG 3319–21, 3323–30, 3332–34. ST. VINCENT: Parish of St. George—Kingstown, Kingstown Park Guest House, DMG 2968–81. Parish of St. Andrew—Lowrey, 1.5 km NE Vermont, DMG 2935–53. Charlotte Parish—ca. 4 km W Orange Hill at end of Soufriere jeep track, DMG 2819–22, 2824–37; Mt. William, 800 m W Byera Hill tunnel, DMG 2772–80, 2838–39. VENEZUELA: Caracas, Sebuacán, Altamira, DMG 3867–75.

Eleutherodactylus martinicensis (161).—GUADELOUPE: Basse-Terre—Chutes du Carbet, path to lower falls, alt. ca. 700 m, DMG 3545, 3600, 3628–29, 3639, 3651–52, 3876–77, 3902–03; Rivière Moreau, cr. 7 km SW Douville, alt. ca. 300 m, DMG 3531, 3533–37, 3582, 3638, 3640–41, 3720, 3740; Rivière des Vieux Habitants, Maison du Café, end of D27, alt. ca. 150 m, DMG 3518, 3544, 3666, 3719, 3747; Rivière des Vieux Habitants, Maison du Café, 400 m before end of road D27, alt. ca. 150 m, DMG 3554, 3580, 3635, 3731, 3750, 3819–21; Rivière Petit David, 400 m SE Les Mamelles, along road D23, alt. ca. 700 m, DMG 3736, 3742; Sofaïa, Rivière Salée, end of road D19, alt. ca. 300 m, DMG 3542, 3571, 3584, 3586, 3653, 3693, 3727, 3735; 1 km SW Desbonnes, along road D18, alt. ca. 300 m, DMG 3511, 3540, 3601; no locality, DMG 3623. Grande-Terre—1.7 km S intersection of roads D109 and N5, alt. ca. 75 m, DMG 3512–13, 3553, 3660. LA DÉSIDRADE: 450 m N Beauséjour post office, alt. ca. 100 m, DMG 3497–3500, 3527–30, 3626–27, 3637, 3659, 3741, 3743. MARIE-GALANTE: Les Balisiers gully, 1.5 km S Ste. Croix, alt. 76 m, DMG 3565, 3588, 3603–05, 3607, 3613, 3663, 3676, 3752; Le

Trou à Diable, alt. ca. 100 m, DMG 3524–26, 3625, 3658; Grand-Bourg, sea level, DMG 3569, 3631, 3642–43, 3825. MARTINIQUE: Morne Rouge, 600 m SE Mne. Pelée restaurant, along road D39, DMG 3583, 3634, 3826; Deux Choux, 100 m N intersection of roads N3 and D1, DMG 3684, 3692, 3728, 3823–24; Deux-Terres, intersection of roads D15 and N4, DMG 3557, 3648–49, 3827, 3630, 3644, 3690, 3754; 100 m below top of Mne. Bigot road, DMG 3505, 3602, 3608, 3612, 3645–47, 3661–62, 3696, 3722–24, 3739, 3816–17, 3828–30; Fort-de-France, Vieux Fort Park, DMG 3508–10, 3664–65, 3691, 3748. ST-BARTHÉLEMY: St-Jean, Jean Bart Hotel, DMG 3276, 3278, 3280–84; Anse des Flamandes, DMG 3519; Lorient, Hotel La Normandie, DMG 3566–67, 3847, 3851, 3884, 3888–91, 3897–98. TERRE-DE-HAUT: Terre-de-Haut village, DMG 3521–22, 3546–48, 3555–56, 3609–11.

Eleutherodactylus pinchoni (32).—GUADELOUPE: Basse-Terre—Chutes du Carbet, path to lower falls, alt. ca. 700 m, DMG 3892–95, 3904–07; Rivière Moreau, ca. 7 km SW Douville, alt. ca. 300 m, DMG 3532; Rivière des Vieux Habitants, Maison du Café, end of D27, alt. ca. 150 m, DMG 3594; Rivière Petit David, 400 m SE les Mamelles, along road D23, alt. ca. 700 m, DMG 3597–98; La Soufrière, 400 m before La Citerne along road D11, alt. ca. 1200 m, DMG 4143–44, 4151–52, 4158; Grand-Étang, 500 m beyond Grande Chasse along road D4, alt. ca. 300 m, DMG 4205; 3 km W Grand Café, 600 ft, AMNH 74545–47, MCZ 43231 (holotype), UIMNH 61647–50; 1 km S Prise d'Eau, 650 ft, MCZ 43232, 43237–39; 3 km W Prise d'Eau, 1100 ft, MCZ 43240.

Eleutherodactylus shrevei (42).—ST. VINCENT: Parish of St. Andrew—Lowrt [sic], 1000 ft, KU 265445–54, MCZ 43230 (holotype); Charlotte Parish—ca.

5.5 km W Orange Hill on La Soufrière summit track, alt. ca. 750 m, DMG 4553, 4587, 4592–93, 4604–07, 4681–82, 4695–4700, 4706–08, 4745; Edge of Soufrière crater, alt. ca. 950 m, MCZ 19814–17, 51452–54, 51456, UIMNH 61644–46.

Eleutherodactylus terraebolivaris (38).—COLOMBIA: USNM 144737–38. TOBAGO: 3 mi N Mt. St. George, KU 265455; 1.5–3.5 km ENE Charlotteville, 100 m, AMNH 87408, 87412, 87427–28, 87431; Main Ridge, ca. 7 km N Roxborough, DMG 3850, 4029–33, 4543–46, 4554, 4588, 4590, 4600–01, 4603, 4734. VENEZUELA: Rancho Grande, MCZ 31062 (holotype), USNM 128212–14, 167609–13; Los Canales, USNM 128807–08.

Eleutherodactylus urichi (25).—TOBAGO: Main Ridge, ca. 7 km N Roxborough, DMG 4018, 4542, 4602, 4684; 4 mi NE Pembroke, KU 265456. TRINIDAD: N Arima Valley, DMG 3848–49, 4019–28, 4541, 4555, 4608–10; Arima Ward, Aripo Road, 2 mi N intersection with Eastern Main Road, KU 265458; St. Ann's Ward, Santa Cruz Valley, 7.5 mi N San Juan, KU 265457.

Population A (10).—GUADELOUPE: Basse-Terre—Matoubas, 1 km NE Centre thermal, DMG 4633, 4641, 4644–48, 4675–76; Sofaïa, Rivière Salée, at end of road D19, alt. ca. 300 m, DMG 3515.

Population B (58).—DOMINICA: 2 km NE Vena's Resort, alt. 250 m, DMG 3506–07; Emerald Pool area, alt. ca. 400 m, DMG 3523, 3570, 3587, 3615, 3619–22, 4066, 4598–99, 4683; 500 m SE Layou Park Estate, alt. ca. 325 m, DMG 3655, 3687, 3726, 3737, 3744, 3831–32, 4141–42, 4153; Freshwater Lake area, alt. ca. 800 m, DMG 3501–3504, 3590–92, 4036, 4061–62, 4068, 4140, 4185–87, 4197–98,

4591, 4596–97, 4685–86; Trafalgar Falls area, alt. ca. 330 m, DMG 3543, 3614, 3657, 3685–86, 3688, 3725, 3746, 3751, 3755; Slope of Morne Diablotin along access track, alt. ca. 1000 m, DMG 4037, 4189.

APPENDIX 2

Below is a step-by-step guide to performing a multiple discriminant function analysis of a morphometric data set using Systat 5.2 with a Macintosh computer. This sequence includes the calculation and saving of Mahalanobis distances (D_M^2) between groups, a feature not described in the software manuals. A basic knowledge of Systat 5.2 is assumed. The appendix is formatted in the same style as the manual for Systat 5.2 software.

Step 1.—Sorting the data

- Select **Open...** from the **File** menu and select the data file
- Sort data file by group variable (e.g., **SPECIES**)
- Select **Open...** from the **File** menu and select the sorted file

Step 2.—Creating data means

- Select **By Groups...** from the **Data** menu
- Select the grouping variable (e.g., **SPECIES**). Note: This variable must be sorted.
- Click **OK**
- Select **Stats/Statistics...** from the **Stats** menu
- Check only the **Means** box from the statistics options provided

Step 2 (cont.)

- Select all the variables you wish to analyse. If no selection is made, all numeric variables will be used.
- Click **Save statistic**
- Click **OK**
- Specify the file name
- Click **OK**

Step 3.—Preparing the data matrix

- Open the file containing the means
- Select the whole file and copy it into memory (command-A, command-C)
- Close file
- Open your sorted data file again
- Go to bottom of file and click in the first free cell at bottom left
- Paste the means from memory (command-V)
- Create a new variable **COUNT**
- For each individual in the data file, enter “1” under **COUNT**; for the means at the bottom, enter “0”
- Save file
- Select **Weight...** from **Data** menu
- Select **COUNT**
- Click **OK**

Step 4.—Running the analysis

- Select **Results to >** from the **File** menu and drag pointer to **Printer**
- Select **MGLH/Fully factorial (M)ANOVA...** from the **Stats** menu

- Click on the **Dependent Variable(s)** pop-up box and hold the mouse button down. Choose a variable from the pop-up variable list by sliding the pointer to it and releasing the mouse button. To deselect repeat. Do *not* choose COUNT.
- Click on the **Factor(s)** pop-up box and select the independent variable (eg., SPECIES)
- Click **More**
- Choose **Extended Output**
- Click **OK**
- After results have appeared on the screen answer the printer promptings
- Select **MGLH/Test of effects...** from the **Stats** menu
- Select **SPECIES** from the **Between Subjects** pop-up box
- Click **More**
- Click **Save scores and results**
- If any standardization is required, select an option
- Click **OK**
- Specify the file name

Step 5.—Results and their interpretation

- Open the new file
- The bottom entries (where the means were pasted before) now have values for **FACTOR(1)** etc., as well as a matrix of distances. The squared Mahalanobis distances (D_M^2) are at the bottom of the file occupying the distance columns. They are recognizable by the diagonal row of near-zero values and by the sequential values in the **GROUP** column.
- An understanding of results is most commonly achieved by (1) consulting the loadings for each created discriminant function in the result printout; (2) by

creating a tabulation of GROUP and PREDICT columns; and (3) by plotting at least the first two discriminant scores for each individual, here named FACTOR(1) and FACTOR(2). Systat 5.2 supports a variety of clustering algorithms for the Mahalanobis distances under its **Cluster/Join...** function.

TABLE 1. List and description of twenty measurements taken from 1002 specimens of Eastern Caribbean *Eleutherodactylus*. All measurements were log-transformed before principal components and discriminant function analyses.

	Measurement	Abbreviation	Description
1.	Head width	HW	distance between anterior edges of tympana
2.	Eye diameter	ED	greatest distance from anterior to posterior
3.	Eye-Naris distance	EN	anterior edge of eye to posterior edge of naris
4.	Tympanum diameter	TD	from anterior to posterior extreme
5.	Tympanum-Eye distance	TE	shortest distance from anterior edge of tympanum to posterior edge of eye
6.	Interorbital distance	IOD	shortest distance between eye sockets across the skull
7.	Snout length	SL	tip of snout to intersection with interorbital distance
8.	Internarial distance	IN	measured between medial edges of nares
9.	Tympanum-Naris	TN	anterior edge of tympanum to posterior edge of naris
10.	Snout-Vent length	SVL	tip of snout to posterior margin of vent
11-14.	Finger lengths	F1-F4	—
15.	Hand length	HL	tip of third finger to wrist
16.	Length of longest toe	LT	—
17.	Foot length	FL	tip of longest toe to back of heel
18.	Femur length	FEM	anus to knee
19.	Tibia length	TL	knee to heel
20.	Radioulnar length	RU	wrist to elbow

TABLE 2. Means, standard deviations, and extremes of snout–vent length (SVL), head width (HW), eye–naris distance (EN), tibia length (TIB), and two ratios indicative of body proportions for males (M), females (F), and combined sexes, of Eastern Caribbean *Eleutherodactylus* populations. The total number for a given species or population may include unsexed specimens.

Species	Population	Sex	<i>n</i>	SVL (mm)	HW (mm)	EN (mm)	TIB (mm)	HW/SVL	TIB/SVL
<i>E. barlagnei</i>	Guadeloupe	both	29	22.3±3.4 (16.3–31.5)	8.5±1.0 (6.3–10.3)	2.5±0.4 (1.7–3.4)	10.2±1.2 (8.1–13.0)	0.382±0.022 (0.336–0.451)	0.461±0.039 (0.388–0.526)
		M	6	18.9±1.1 (16.9–19.8)	7.5±0.9 (6.3–8.9)	2.1±0.3 (1.8–2.5)	9.3±0.7 (8.1–10.0)	0.395±0.031 (0.370–0.451)	0.492±0.018 (0.467–0.515)
		F	20	23.6±3.0 (16.3–31.5)	8.9±0.8 (6.9–10.6)	2.6±0.4 (1.9–3.4)	10.6±1.1 (8.5–13.0)	0.378±0.019 (0.336–0.425)	0.452±0.040 (0.388–0.526)
<i>E. euphronides</i>	Grenada	both	84	25.1±4.9 (16.9–39.4)	10.6±2.3 (6.9–17.4)	3.0±0.7 (1.8–5.1)	13.9±2.6 (8.5–21.2)	0.423±0.018 (0.377–0.473)	0.554±0.028 (0.491–0.629)
		M	41	22.7±2.3 (17.7–27.0)	9.5±1.1 (7.2–11.5)	2.7±0.5 (1.8–4.2)	12.6±1.2 (10.1–14.7)	0.419±0.019 (0.377–0.470)	0.557±0.029 (0.493–0.613)
		F	31	28.3±5.0 (19.4–39.4)	12.1±2.4 (8.0–17.4)	3.4±0.8 (1.9–5.1)	15.4±2.7 (10.1–21.2)	0.427±0.014 (0.400–0.454)	0.545±0.025 (0.491–0.594)
<i>E. johnstonei</i>	all populations	both	523	20.5±3.1 (14.6–34.0)	8.0±1.3 (2.8–13.4)	2.2±0.4 (1.3–3.7)	9.0±1.3 (6.2–14.0)	0.389±0.020 (0.157–0.435)	0.443±0.034 (0.311–0.579)

TABLE 2 (cont.)

Species	Population	Sex	<i>n</i>	SVL (mm)	HW (mm)	EN (mm)	TIB (mm)	HW/SVL	TIB/SVL
	N islands	M	110	19.9±2.0 (16.1–26.3)	7.8±0.8 (6.2–10.7)	2.1±0.3 (1.6–3.2)	8.6±0.8 (6.8–11.8)	0.393±0.016 (0.360–0.428)	0.433±0.032 (0.311–0.508)
		F	136	22.0±3.6 (15.6–31.3)	8.7±1.5 (6.5–13.4)	2.3±0.4 (1.4–3.4)	9.7±1.4 (6.8–14.0)	0.398±0.014 (0.360–0.435)	0.446±0.031 (0.355–0.511)
	S islands	M	83	20.4±2.2 (14.6–24.2)	7.7±0.7 (5.7–9.1)	2.2±0.3 (1.3–2.8)	8.7±0.8 (6.9–11.1)	0.378±0.017 (0.344–0.426)	0.429±0.042 (0.350–0.579)
		F	185	20.1±3.2 (14.8–34.0)	7.7±1.3 (2.8–13.4)	2.2±0.4 (1.5–3.7)	9.0±1.3 (6.2–14.0)	0.385±0.023 (0.307–0.433)	0.451±0.030 (0.364–0.521)
	Antigua	M	9	20.6±1.1 (18.3–22.0)	7.9±0.3 (7.6–8.4)	2.1±0.2 (1.8–2.5)	9.0±0.6 (7.8–9.9)	0.384±0.012 (0.372–0.413)	0.436±0.024 (0.404–0.474)
		F	18	22.8±3.9 (16.0–30.7)	9.0±1.5 (6.6–12.4)	2.4±0.4 (1.7–3.1)	10.5±1.7 (8.1–14.0)	0.393±0.011 (0.378–0.414)	0.463±0.023 (0.422–0.508)

TABLE 2 (cont.)

Species	Population	Sex	n	SVL (mm)	HW (mm)	EN (mm)	TIB (mm)	HW/SVL	TIB/SVL
	Barbados	M	7	20.7±1.4 (18.8–22.6)	8.0±0.6 (7.3–9.1)	2.2±0.2 (1.9–2.4)	8.5±0.7 (7.8–9.8)	0.385±0.010 (0.371–0.404)	0.413±0.027 (0.383–0.462)
		F	49	19.4±4.2 (14.8–34.0)	7.5±1.5 (5.8–13.4)	2.2±0.5 (1.5–3.7)	8.7±1.5 (6.6–14.0)	0.390±0.017 (0.358–0.433)	0.455±0.034 (0.373–0.521)
	Barbuda	M	10	21.8±2.7 (16.7–26.3)	8.4±1.2 (6.2–10.7)	2.5±0.4 (1.9–3.2)	9.4±1.1 (7.5–11.8)	0.384±0.021 (0.360–0.428)	0.431±0.032 (0.376–0.476)
		F	1	29.5	10.8	3.3	10.5	0.376	0.355
	Caracas ^a	M	8	22.7±1.0 (20.7–23.8)	8.3±0.5 (7.4–9.1)	2.5±0.2 (2.0–2.8)	9.2±0.8 (8.2–10.2)	0.364±0.010 (0.350–0.383)	0.407±0.026 (0.358–0.437)
		F	1	21.7	7.9	2.3	9.6	0.362	0.442
	Grenada	M	25	20.6±2.6 (14.7–24.2)	7.7±0.8 (5.9–9.1)	2.2±0.2 (1.9–2.5)	9.0±0.9 (6.9–11.1)	0.375±0.019 (0.344–0.426)	0.440±0.050 (0.381–0.579)
		F	45	21.1±2.9 (14.9–27.3)	8.2±1.2 (6.1–11.1)	2.3±0.4 (1.6–3.1)	9.6±1.3 (6.9–12.9)	0.387±0.014 (0.360–0.421)	0.455±0.027 (0.394–0.505)

TABLE 2 (cont.)

Species	Population	Sex	<i>n</i>	SVL (mm)	HW (mm)	EN (mm)	TIB (mm)	HW/SVL	TIB/SVL
	Guyana ^b	M	4	20.1±0.7 (19.2–21.0)	7.8±0.3 (7.5–8.2)	2.2±0.1 (2.0–2.2)	9.3±0.5 (8.6–9.8)	0.387±0.005 (0.381–0.391)	0.462±0.025 (0.433–0.493)
		F	5	22.1±0.9 (20.8–23.2)	8.6±0.3 (8.2–8.9)	2.5±0.3 (2.0–2.8)	10.4±0.3 (10.0–10.7)	0.388±0.014 (0.364–0.399)	0.470±0.018 (0.448–0.495)
	Montserrat	M	13	18.0±1.5 (16.3–20.0)	7.2±0.6 (6.5–8.0)	1.8±0.2 (1.6–2.2)	7.7±0.5 (6.9–8.5)	0.398±0.010 (0.387–0.416)	0.430±0.023 (0.386–0.465)
		F	35	20.9±2.8 (16.2–27.8)	8.3±1.1 (6.9–11.3)	2.2±0.3 (1.7–3.0)	9.2±1.1 (7.1–11.4)	0.398±0.012 (0.374–0.423)	0.441±0.026 (0.390–0.494)
	Nevis	M	21	20.8±1.7 (17.7–25.2)	8.2±0.7 (7.2–10.6)	2.2±0.2 (2.0–2.7)	8.8±0.6 (7.8–10.8)	0.395±0.015 (0.368–0.422)	0.424±0.028 (0.378–0.494)
		F	11	23.5±4.2 (18.4–31.3)	9.4±1.8 (7.6–13.4)	2.5±0.4 (2.2–3.4)	10.5±1.4 (8.9–13.1)	0.402±0.015 (0.378–0.428)	0.452±0.034 (0.400–0.492)
	Saba	M	12	19.8±1.7 (17.4–22.9)	7.5±0.6 (6.4–8.4)	2.0±0.2 (1.7–2.3)	8.5±0.6 (7.7–9.8)	0.379±0.012 (0.360–0.403)	0.433±0.026 (0.396–0.479)
		F	29	20.6±2.9 (17.0–30.1)	8.0±1.1 (6.5–11.6)	2.2±0.4 (1.4–3.3)	9.2±1.0 (7.5–11.8)	0.389±0.011 (0.360–0.407)	0.451±0.032 (0.390–0.511)

TABLE 2 (cont.)

Species	Population	Sex	n	SVL (mm)	HW (mm)	EN (mm)	TIB (mm)	HW/SVL	TIB/SVL
	St. Eustatius	M	9	20.2±1.8 (16.1–21.9)	8.3±0.7 (6.6–8.8)	2.2±0.3 (1.9–2.7)	9.0±0.6 (8.2–9.8)	0.409±0.005 (0.399–0.415)	0.448±0.033 (0.401–0.508)
		F	3	23.5±4.8 (20.4–29.0)	9.4±1.5 (8.2–11.1)	2.6±0.3 (2.4–2.9)	10.8±1.2 (9.9–12.1)	0.400±0.017 (0.381–0.413)	0.463±0.041 (0.416–0.489)
	St. Kitts	M	22	18.6±1.2 (16.5–22.0)	7.3±0.5 (6.6–8.2)	2.0±0.2 (1.7–2.2)	8.2±0.4 (7.3–8.8)	0.393±0.016 (0.369–0.427)	0.440±0.028 (0.359–0.493)
		F	23	21.3±3.6 (15.6–28.8)	8.6±1.4 (6.8–11.7)	2.2±0.4 (1.7–3.3)	9.3±1.3 (6.8–12.5)	0.403±0.013 (0.383–0.435)	0.437±0.032 (0.381–0.486)
	St. Lucia	M	21	19.4±2.0 (15.0–21.9)	7.4±0.7 (5.7–8.5)	2.1±0.3 (1.3–2.7)	8.2±0.7 (7.1–9.6)	0.380±0.020 (0.351–0.415)	0.427±0.042 (0.352–0.499)
		F	41	19.4±2.5 (15.2–25.6)	7.3±1.2 (2.8–10.6)	2.1±0.3 (1.5–3.1)	8.5±1.1 (6.2–11.0)	0.378±0.039 (0.357–0.415)	0.439±0.023 (0.393–0.473)
	St. Martin	M	14	20.3±1.8 (16.6–22.6)	8.1±0.8 (6.6–9.0)	2.2±0.3 (1.6–2.6)	8.6±0.8 (6.8–9.6)	0.400±0.010 (0.384–0.421)	0.426±0.051 (0.311–0.488)
		F	16	24.9±2.9 (20.5–29.7)	10.2±1.3 (8.3–12.5)	2.6±0.4 (2.1–3.4)	10.9±1.1 (8.6–12.9)	0.409±0.012 (0.385–0.432)	0.439±0.036 (0.387–0.511)

TABLE 2 (cont.)

Species	Population	Sex	<i>n</i>	SVL (mm)	HW (mm)	EN (mm)	TIB (mm)	HW/SVL	TIB/SVL
<i>E. martinicensis</i>	St. Vincent	M	18	20.3±1.9 (14.6–22.4)	7.7±0.7 (5.8–8.8)	21.±0.3 (1.3–2.7)	8.6±0.8 (7.1–9.9)	0.378±0.014 (0.353–0.404)	0.426±0.038 (0.350–0.494)
		F	44	20.3±2.6 (14.9–27.9)	7.8±1.1 (5.7–10.9)	2.1±0.3 (1.5–3.0)	9.2±1.1 (7.2–12.2)	0.383±0.015 (0.355–0.425)	0.452±0.032 (0.364–0.501)
	all populations	both	161	23.2±2.6 (17.9–38.8)	9.5±2.6 (6.2±17.9)	2.7±0.7 (2.0–4.8)	10.9±2.8 (6.4–18.2)	0.402±0.026 (0.342–0.461)	0.468±0.040 (0.372–0.563)
	Guadeloupe	M	34	23.7±4.6 (17.7–32.8)	9.6±2.2 (6.4–13.7)	2.8±0.6 (1.7–3.7)	11.2±2.4 (7.2–14.8)	0.402±0.024 (0.360–0.441)	0.470±0.042 (0.377–0.519)
		F	20	26.2±6.7 (17.7–37.6)	10.3±2.9 (6.8–15.4)	3.0±0.9 (1.9–4.8)	12.3±3.4 (8.5–18.2)	0.393±0.022 (0.342–0.433)	0.467±0.027 (0.425–0.515)
	La Désirade	M	6	23.0±1.7 (20.8–25.5)	9.7±0.6 (8.8–10.6)	2.9±0.4 (2.3–3.4)	10.6±0.8 (9.1–11.4)	0.424±0.007 (0.416–0.437)	0.432±0.045 (0.386–0.511)
		F	8	28.8±4.3 (20.9–32.9)	12.5±2.1 (8.5–14.5)	3.3±0.6 (2.7–4.2)	13.6±2.0 (10.5–15.8)	0.433±0.018 (0.407–0.457)	0.474±0.028 (0.436–0.518)

TABLE 2 (cont.)

Species	Population	Sex	<i>n</i>	SVL (mm)	HW (mm)	EN (mm)	TIB (mm)	HW/SVL	TIB/SVL
	Marie-Galante	M	7	21.0±3.8 (17.4–26.5)	8.7±1.6 (7.2–10.7)	2.6±0.4 (2.1–3.5)	10.3±1.3 (9.2–13.0)	0.414±0.020 (0.318–0.451)	0.493±0.035 (0.432–0.535)
		F	8	27.2±7.7 (16.7–38.8)	11.6±3.7 (6.7–17.9)	3.3±1.1 (1.8–4.5)	13.0±3.3 (8.5–17.6)	0.421±0.025 (0.387–0.461)	0.480±0.024 (0.454–0.525)
	Martinique	M	25	21.2±3.0 (17.6–27.6)	8.1±1.5 (6.4–11.6)	2.3±0.5 (1.8–3.4)	9.5±1.7 (7.6–12.9)	0.382±0.021 (0.346–0.432)	0.446±0.030 (0.384–0.505)
		F	13	24.3±3.7 (19.8–32.5)	9.6±1.8 (7.3–13.8)	2.7±0.4 (1.9–3.3)	10.7±2.5 (7.7–15.1)	0.393±0.021 (0.357–0.436)	0.439±0.053 (0.372–0.563)
	St-Barthélemy	M	16	22.6±1.6 (22.6–27.7)	10.1±0.6 (9.1–11.4)	3.0±0.3 (2.4–3.5)	11.1±0.7 (10.0–12.2)	0.410±0.017 (0.372–0.432)	0.449±0.023 (0.410–0.489)
		F	3	25.3±2.1 (24.0–27.7)	10.4±0.7 (9.7–11.0)	3.2±0.0 (3.1–3.2)	12.5±1.7 (11.0–14.4)	0.411±0.017 (0.398–0.430)	0.491±0.034 (0.454–0.519)
	Terre-de-Haut	M	5	19.6±3.6 (13.8–23.1)	8.3±1.6 (5.8–9.7)	2.4±0.4 (1.9–3.0)	10.3±2.2 (6.8–11.9)	0.424±0.013 (0.414–0.449)	0.520±0.027 (0.493–0.553)
		F	3	23.3±4.3 (17.9–26.8)	9.9±1.4 (8.2–11.2)	2.5±0.6 (1.9–3.1)	12.0±2.4 (9.1–14.4)	0.427±0.026 (0.402–0.457)	0.513±0.018 (0.494–0.535)

TABLE 2 (cont.)

Species	Population	Sex	<i>n</i>	SVL (mm)	HW (mm)	EN (mm)	TIB (mm)	HW/SVL	TIB/SVL
<i>E. pinchoni</i>	Guadeloupe	both	32	16.8±1.6 (13.5–21.9)	6.4±0.6 (5.0–8.2)	1.8±0.3 (1.0–2.5)	7.4±0.6 (6.5–9.2)	0.381±0.023 (0.341–0.438)	0.444±0.035 (0.376–0.552)
		M	15	16.7±1.0 (15.3–18.7)	6.5±0.4 (5.8–7.3)	1.9±0.2 (1.6–2.2)	7.3±0.6 (6.5–9.2)	0.392±0.017 (0.370–0.438)	0.438±0.036 (0.405–0.552)
		F	5	18.1±2.6 (15.4–21.9)	6.9±0.8 (6.2–8.2)	2.0±0.4 (1.4–2.5)	7.8±0.8 (6.9–8.9)	0.385±0.029 (0.341–0.421)	0.444±0.042 (0.376–0.475)
<i>E. shrevei</i>	St. Vincent	both	42	26.8±5.8 (19.0–40.1)	11.0±2.7 (7.5–17.5)	3.2±0.8 (1.9–5.3)	14.5±3.1 (10.4–21.7)	0.410±0.019 (0.376–0.454)	0.542±0.026 (0.489–0.595)
		M	16	24.9±4.5 (21.0–38.0)	10.0±1.9 (8.2–15.2)	2.9±0.6 (1.9–4.1)	13.4±2.3 (11.2–19.5)	0.402±0.019 (0.376–0.441)	0.540±0.032 (0.489–0.595)
		F	17	30.0±6.4 (19.0–40.1)	12.6±3.1 (7.6–17.5)	3.6±0.9 (2.3–5.3)	16.2±3.3 (10.4–21.7)	0.417±0.019 (0.376–0.454)	0.543±0.020 (0.494–0.571)
<i>E. terraebolivaris</i>	Tobago and Venezuela ^c		38	32.5±8.1 (20.8–49.3)	13.0±3.3 (8.2–20.3)	4.5±1.2 (2.7–6.9)	19.8±4.8 (13.2–31.1)	0.390±0.015 (0.361–0.424)	0.598±0.037 (0.527–0.673)
<i>E. urichi</i>	all populations	both	25	19.6±1.8 (17.5–25.0)	7.6±0.7 (6.7–9.3)	2.3±0.3 (1.7–2.9)	9.8±1.0 (8.4–12.1)	0.391±0.022 (0.360–0.447)	0.503±0.034 (0.415–0.569)

TABLE 2 (cont.)

Species	Population	Sex	n	SVL (mm)	HW (mm)	EN (mm)	TIB (mm)	HW/SVL	TIB/SVL
Population A ^d	Tobago	M	3	19.3±1.9 (17.8–22.6)	7.4±0.8 (6.7–8.7)	2.2±0.4 (1.7–2.6)	10.4±1.1 (8.9–12.0)	0.382±0.008 (0.373–0.394)	0.539±0.028 (0.500–0.569)
		F	1	25.0	9.3	2.8	12.1	0.370	0.486
	Trinidad	M	17	19.1±0.8 (17.5–20.7)	7.5±0.4 (7.0–8.4)	2.3±0.2 (1.9–2.7)	9.4±0.6 (8.4–10.5)	0.394±0.024 (0.360–0.447)	0.493±0.030 (0.415–0.535)
		F	1	23.1	9.1	2.9	11.8	0.394	0.511
	Guadeloupe	both	10	20.0±3.7 (14.4–28.9)	7.6±1.5 (5.8–11.4)	2.0±0.4 (1.6–3.2)	8.8±2.0 (6.7–14.2)	0.379±0.013 (0.357–0.403)	0.441±0.029 (0.404–0.491)
		M	5	18.3±2.5 (14.4–21.2)	6.9±0.8 (5.8–7.9)	1.9±0.2 (1.6–2.1)	8.1±0.9 (6.7–9.0)	0.380±0.014 (0.364–0.403)	0.443±0.021 (0.410–0.465)
		F	5	21.6±4.2 (18.5–28.9)	8.2±1.9 (6.6–11.4)	2.1±0.6 (1.8–3.2)	9.6±2.6 (8.0–14.2)	0.377±0.014 (0.357–0.394)	0.440±0.038 (0.404–0.491)

TABLE 2 (cont.)

Species	Population	Sex	<i>n</i>	SVL (mm)	HW (mm)	EN (mm)	TIB (mm)	HW/SVL	TIB/SVL
Population B ^d	Dominica	both	58	27.1±9.0 (10.6–49.7)	11.4±4.0 (4.4–21.8)	3.2±1.2 (1.2–6.5)	12.8±4.0 (5.3–22.1)	0.418±0.018 (0.383–0.464)	0.477±0.030 (0.415–0.555)
		M	25	21.8±2.4 (16.1–26.4)	9.0±0.9 (7.5–10.9)	2.6±0.3 (1.9–3.4)	10.5±1.2 (7.8–13.3)	0.415±0.022 (0.383–0.464)	0.482±0.030 (0.438–0.555)
		F	31	32.1±9.6 (15.9–49.7)	13.6±4.3 (6.8–21.8)	3.8±1.3 (1.6–6.5)	15.1±4.1 (7.9–22.1)	0.422±0.015 (0.392–0.457)	0.474±0.030 (0.415–0.552)

^aThese specimens are representative of those introduced into the city of Caracas around 1958 (Hardy and Harris, 1979). A second population of *E. johnstonei* was established in Cumaná with specimens brought from Caracas in December 1967 (Hardy and Harris, 1979).

^b*E. johnstonei* is still restricted to the city of Georgetown and its immediate environs. Its distribution within the city seems patchy, despite the fact that it has been a resident since before 1923 (Hardy and Harris, 1979).

^cMost of the specimens of this species are unsexed museum specimens (see Appendix 1) and could thus not be differentiated further.

^dThe taxonomic status of these populations is at present undetermined. A current investigation still in progress (Kaiser, unpubl.) suggests that the taxonomic separation of Population A from *E. barlagnei* and Population B from *E. martinicensis* may be warranted.

TABLE 3. Discriminant loadings from a multiple discriminant function analysis of ten length measurements of Eastern Caribbean *Eleutherodactylus*. Characters with the relatively greatest discriminating power for each discriminant function (DF) are marked with asterisks (*). Cutoff values were arbitrarily assigned at 0.400 (DF1), + or - 0.100 (DF2), and -400 (DF3). Abbreviations of measurements are listed in Table 1.

	DF 1	DF 2	DF 3
log HW	0.342	0.020	-0.544*
log ED	0.485*	0.062	-0.441*
log EN	0.273	-0.296*	-0.340
log TD	0.261	0.385*	-0.230
log TE	0.253	0.204*	-0.486*
log IOD	0.451*	-0.019	-0.324
log SL	0.388	0.185*	-0.419*
log ID	0.481*	0.077	-0.418*
log SVL	0.305	0.008	-0.354
log TIB	0.560*	-0.013	-0.344

TABLE 4. Group assignments for 1002 specimens of *Eleutherodactylus* from the Eastern Caribbean from a multiple discriminant function analysis (MDA) of 10 metric characters. Rows are MDA predictions, columns are actual population groupings (ie., of 161 MART specimens, 55 are correctly classified by the MDA, while 35 are incorrectly classified statistically as JHN). Differences between MDA groupings tested significant at $P \leq 0.001$ (Pearson chi-square). Species codes are *E. martinicensis* (MART), *E. johnstonei* (JHN), *E. barlagnei* (BAR), *E. euphronides* (EUP), *E. shrevei* (SHR), *E. urichi* (URI), *E. pinchoni* (PIN), *E. terraebolivaris* (TER). The two unnamed populations may represent as yet undescribed species. Population A occurs on Guadeloupe, population B on Dominica. Percent classification success > 10% is given in parentheses.

	MART	JHN	BAR	EUP	SHR	URI	PIN	TER	Pop. A	Pop. B	Total
MART	55 (34.2)	35 (21.7)	9	4	5	8	6	0	4	35 (21.7)	161
JHN	73 (14.0)	359 (68.6)	10	0	2	6	41	0	26	6	523
BAR	1	1	22 (75.9)	0	0	1	0	0	4 (13.8)	0	29
EUP	3	0	0	56 (66.7)	19 (22.6)	2	0	3	0	1	84
SHR	1	0	0	6 (14.3)	31 (73.8)	1	0	3	0	0	42
URI	1	1	1	0	1	18 (72.0)	2	1	0	0	25
PIN	1	2	1	0	0	0	25 (78.1)	0	3	0	32
TER	0	0	0	2	2	1	0	33 (86.8)	0	0	38
Pop. A	0	0	2	0	0	0	1	0	7 (70.0)	0	10
Pop. B	10 (17.2)	2	2	1	1	3	4	0	1	34 (58.6)	58
Total	145	400	47	69	61	40	79	40	45	76	1002 (63.9)

TABLE 5. Discriminant loadings from a multiple discriminant function analysis of ten length measurements of northern and southern Eastern Caribbean *Eleutherodactylus*. Characters with the relatively greatest discriminating power for each discriminant function (DF) are marked with asterisks (*). Cutoff values were arbitrarily assigned at 0.400 (DF1) and 0.200 (DF2). Abbreviations of measurements are listed in Table 1.

	DF 1	DF 2
log HW	0.281	0.079
log ED	0.432*	-0.082
log EN	0.259	0.237*
log TD	0.220	-0.037
log TE	0.185	0.137
log IOD	0.416*	0.173
log SL	0.319	0.128
log ID	0.417*	-0.106
log SVL	0.268	0.267*
log TIB	0.507*	0.159

TABLE 6. Group assignments for 1002 specimens of northern and southern Eastern Caribbean *Eleutherodactylus* from a multiple discriminant function analysis (MDA) of 10 metric characters. Rows are MDA predictions, columns are actual population groupings (ie., of 813 N specimens, 762 are correctly classified by the MDA, while 50 are incorrectly classified statistically as S). Differences between groupings tested significant at $P \leq 0.001$ (Pearson chi-square). Species codes are northern species (N), southern species (S), *E. terraebolivaris* (TER). Percent classification success is given in parentheses.

	N	S	TER	Total
N	762 (93.7)	50	1	813
S	9	132 (87.4)	10	151
TER	0	5	33 (86.8)	38
Total	771	187	44	1002 (90.6)

TABLE 7. Discriminant loadings from a multiple discriminant function analysis of ten length measurements of northern and southern populations of *Eleutherodactylus johnstonei*. Characters with the relatively greatest discriminating power for each discriminant function (DF) are marked with asterisks (*). Cutoff values were arbitrarily assigned at 0.400 (DF1) and 0.500 (DF2). Abbreviations of measurements are listed in Table 1.

	DF 1	DF 2
log HW	0.360	0.408
log ED	0.490*	0.542*
log EN	0.317	0.317
log TD	0.239	-0.008
log TE	0.262	0.338
log IOD	0.530*	0.311
log SL	0.423*	0.527*
log ID	0.557*	0.209
log SVL	0.369	0.267
log TIB	0.642*	0.236

TABLE 8. Group assignments for 561 specimens of northern and southern populations of *Eleutherodactylus johnstonei* from the Eastern Caribbean from a multiple discriminant function analysis (MDA) of 10 metric characters. Rows are MDA predictions, columns are actual population groupings (ie., of 254 jN specimens, 191 are correctly classified by the MDA, while 62 are incorrectly classified statistically as jS). Differences between groupings tested significant at $P \leq 0.001$ (Pearson chi-square). Species codes are northern *E. johnstonei* (jN), southern *E. johnstonei* (jS), *E. terraebolivaris* (TER). Percent classification success is given in parentheses.

	jN	jS	TER	Total
jN	191 (75.2)	62 (24.4)	1	254
jS	69 (25.7)	199 (74.3)	0	268
TER	2	0	37 (94.9)	39
Total	262	261	38	561

FIGURE 1. Distribution of Eastern Caribbean *Eleutherodactylus*. (A) Distribution of *E. johnstonei*. (B) Distribution of the remaining species. Dark areas on Trinidad approximately delineate the fragmented range of *E. urichi* on that island. Populations with questionable taxonomic status (see Table 2) are marked with question marks (?) in open circles. Introduced populations of *E. johnstonei* and *E. martinicensis* (see Kaiser, 1992) are marked with asterisks (*) if introduction is assumed to have occurred since 1975 or with a dot (•) if introduction occurred prior to 1975.

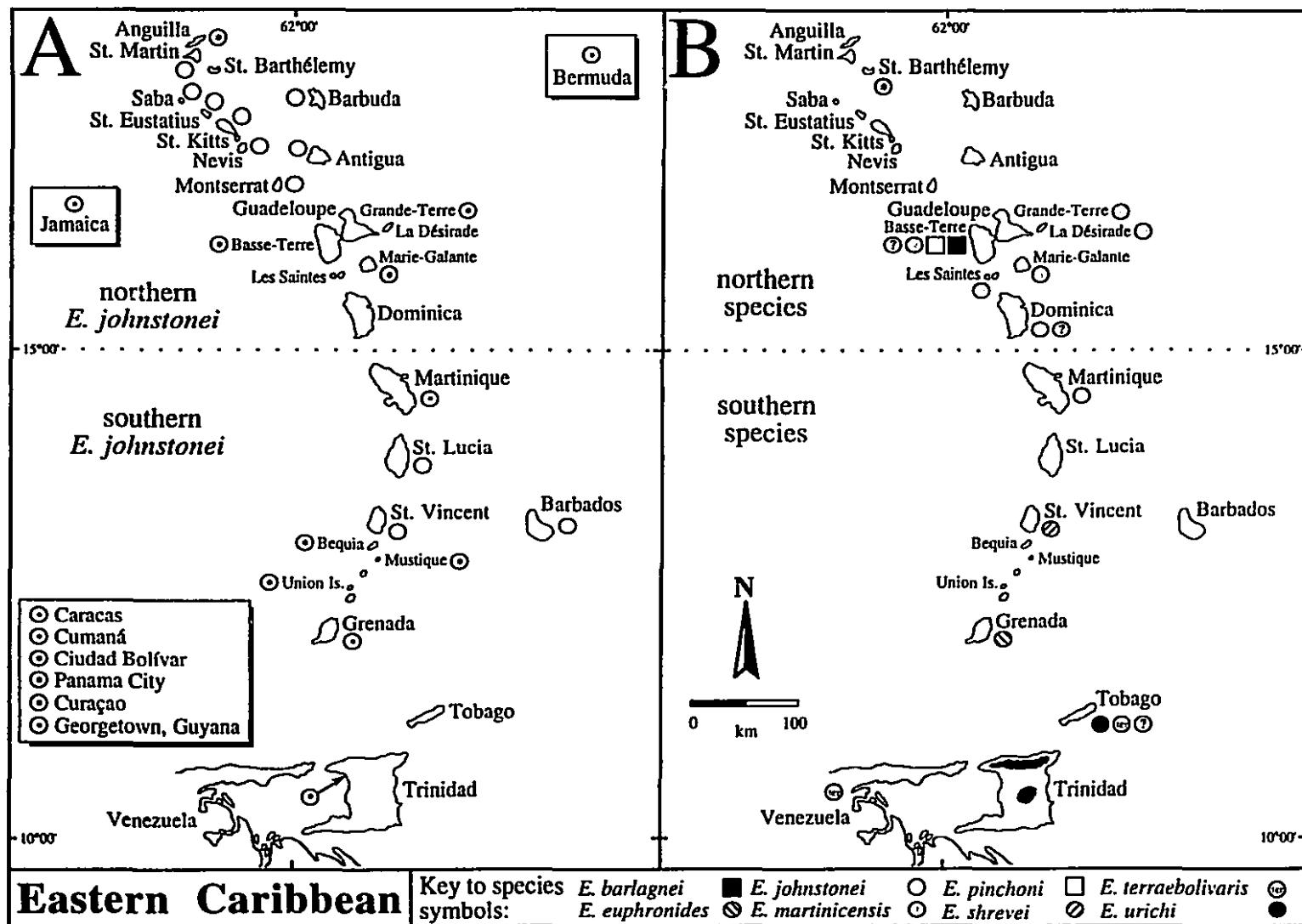


FIGURE 2. Discriminant score (DS) plots for results of multiple discriminant function analyses of 1002 Eastern Caribbean *Eleutherodactylus*. (A) Analysis by individual taxon. Centroids of the southern species group are denoted by thick lines. (B) Northern (N) versus southern (S) species groups, by species group. (C) Northern (jhnN) versus southern (jhnS) populations of *E. johnstonei*. Species are coded as “bar” (*E. barlagnei*), “eup” (*E. euphronides*), “jhn” (*E. johnstonei*), “mart” (*E. martinicensis*), “pin” (*E. pinchoni*), “shr” (*E. shrevei*), “ter” (*E. terraebolivaris*), and “uri” (*E. urichi*). Two populations of uncertain taxonomic status are shown as “Pop. A” (Guadeloupe) and “Pop. B” (Dominica).

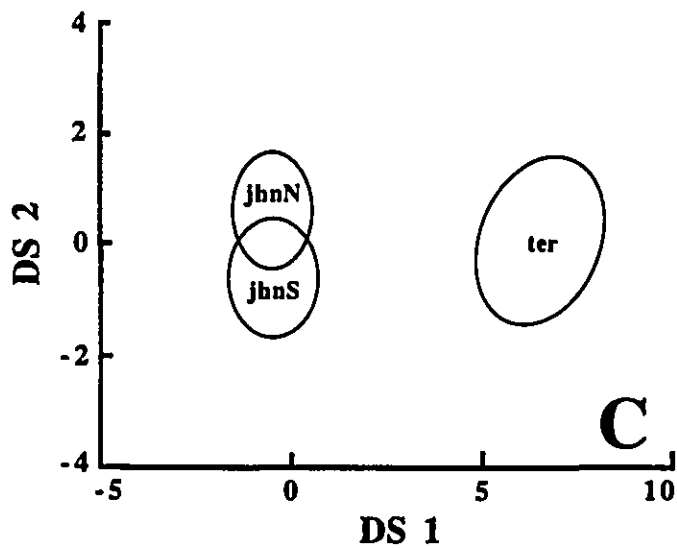
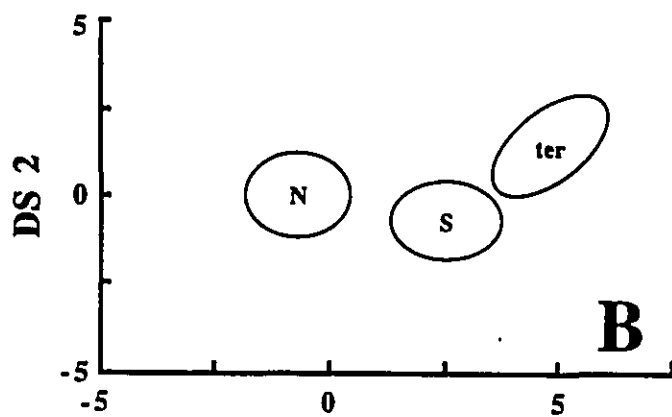
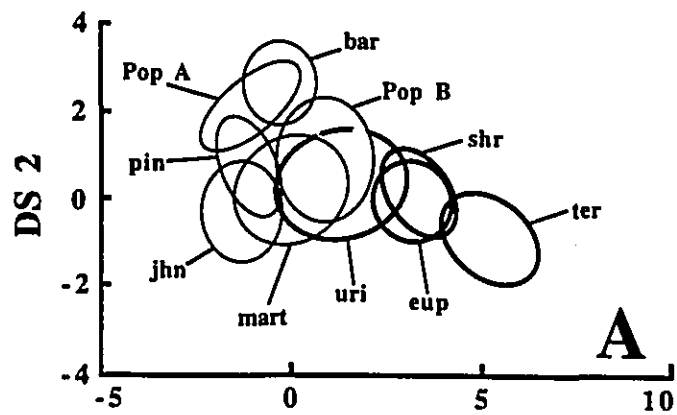


FIGURE 3. UPGMA phenogram of Mahalanobis distances (D_M) between Eastern Caribbean *Eleutherodactylus*. Abbreviations used for taxa are as in Fig. 2.

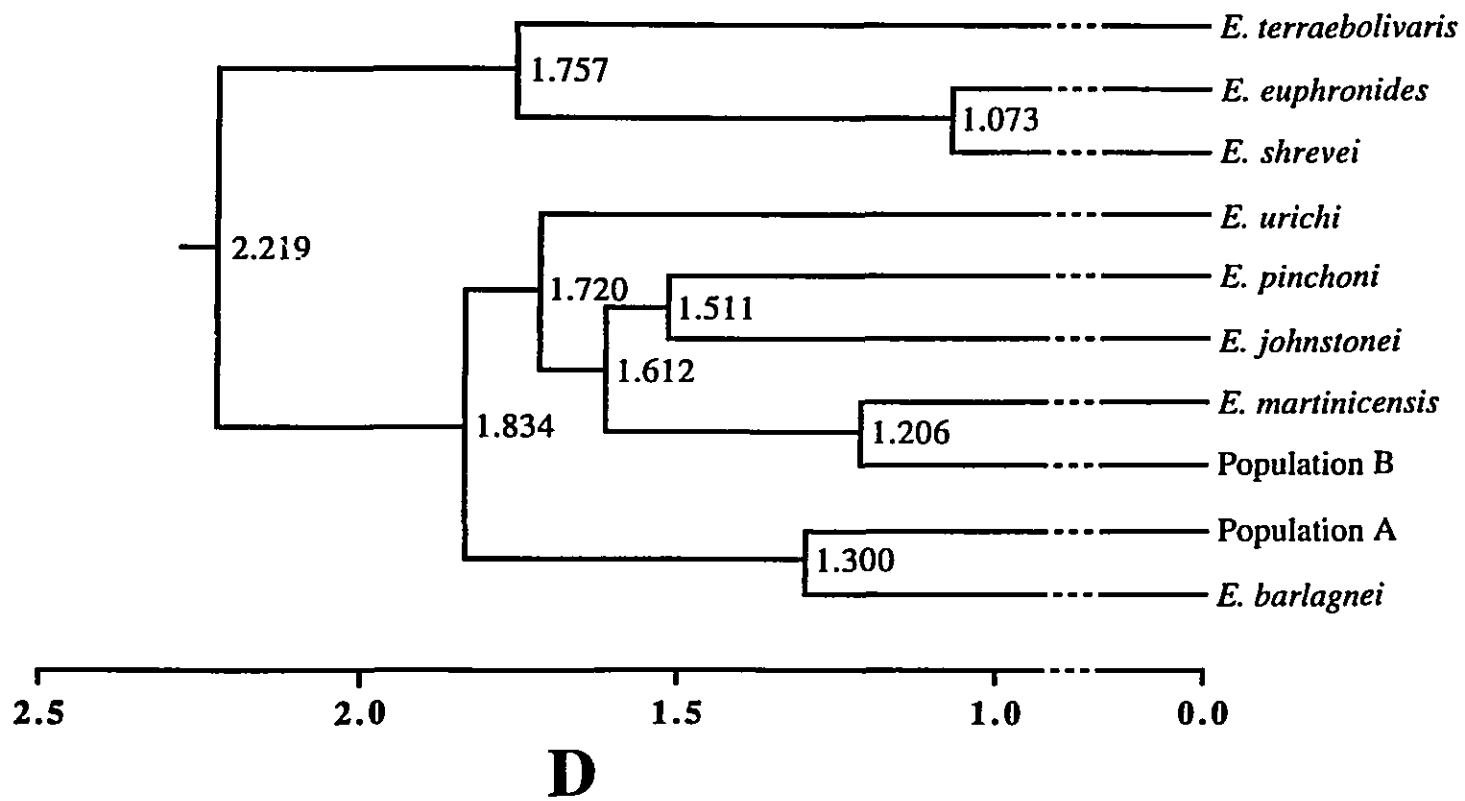
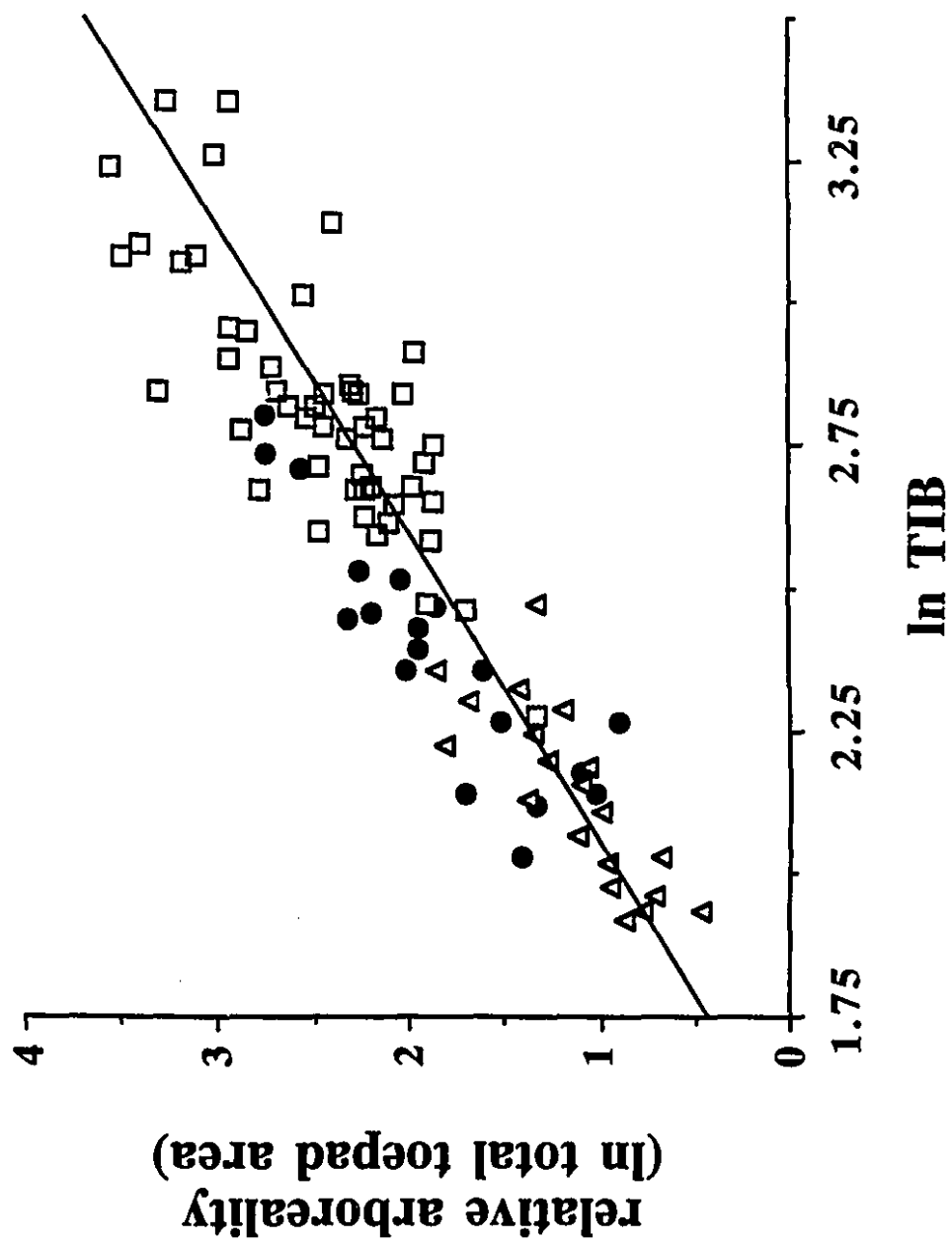


FIGURE 4. Degree of arboreality of Eastern Caribbean *Eleutherodactylus* as indicated by a plot of \ln tibia length against \ln total toepad area. Total toepad area was size-corrected using snout-vent length. The regression line has a slope of 1.87 ($r^2 = 0.640$). Miniaturized, terrestrial species (*E. pinchoni*, *E. urichi*) are denoted by triangles, the ecological generalist *E. johnstonei* by closed circles, and the arboreal species (*E. euphronides*, *E. martinicensis*, *E. shrevei*, *E. terraebolivaris*) by squares.



6

**Systematics and Biogeography of Eastern Caribbean
Eleutherodactylus (Anura: Leptodactylidae) with the Description of a
New Species from Dominica**

To be published as: Kaiser, H., and D. M. Green. Systematics and biogeography of Eastern Caribbean *Eleutherodactylus* (Anura: Leptodactylidae) with the description of a new species from Dominica.

PREAMBLE CHAPTER 6

Two hypotheses developed from the morphometric analysis. Firstly, the suggestion that the populations of uncertain taxonomic status on Dominica, referred to as "population B" in Chapter 5, might be a distinct species needed to be tested. Secondly, the morphometric data indicated that two distinct groups of *Eleutherodactylus* inhabit the Eastern Caribbean. Although I consider the morphometric information taxonomically useful, there are no comparative studies of *Eleutherodactylus* to verify the taxonomic inference from morphometric data. Since any purely statistical inference certainly benefits from evidence from other data sources, I conducted an investigation of 142 internal and external morphological characters to test the two-group hypothesis, and to see whether the taxonomic status of population B could be resolved.

ABSTRACT

Populations of *Eleutherodactylus* on the island of Dominica, West Indies, differ from other Lesser Antillean members of the genus by their vocalizations, morphology, sexual size dimorphism, and allozymes. These populations thus comprise a new endemic species, closely related to *E. johnstonei* and *E. martinicensis*. The new species is most abundant in montane forest habitats at elevations of more than 500 m. Females commonly attain snout-vent lengths of more than 35 mm, making them the largest Lesser Antillean *Eleutherodactylus*. Frogs are brown during the day, but change color to a dark orange when active by night. This new species is the ninth Eastern Caribbean *Eleutherodactylus*, and the fifth single-island endemic. A phylogenetic analysis of external and internal morphological characteristics shows that these species are members of two distinct clades, one of South American origin, the other of Greater Antillean ancestry. It is suggested that the present distribution of these species resulted from the dispersal of elements of the larger herpetofaunas from the Greater Antilles and South America, and that rapid divergence is continuing. The phylogenetic analysis also shows that morphological characters of *Eleutherodactylus* species can be highly homoplastic. Thus, hypotheses of phylogenetic relationships may be unreliable unless the morphological data can be supported with phylogeny estimates independently derived from other data sources.

INTRODUCTION

The neotropical frog genus *Eleutherodactylus* is the largest vertebrate genus with over 500 species (Duellman, 1993). Although some of its members have very distinctive external features (e.g., Lynch, 1975, 1980), it is very difficult to differentiate most species of *Eleutherodactylus*. Intraspecific variability is high yet the many species are variants of a conservative morphotype: a small brownish frog. Several phylogenetic analyses of species group relationships within *Eleutherodactylus* have been conducted over the years with varying degrees of success (e.g., Hedges, 1989; Joglar, 1989; Miyamoto, 1983, 1984, 1986). Invariably, the addition of biochemical data sets improved the resolution of systematic relationships.

At least eight species of *Eleutherodactylus* inhabit the Eastern Caribbean (Table 1), a region comprising the Lesser Antilles, Trinidad, and Tobago (Fig. 1). Most of these species are single-island endemics whose origin and systematic relationships are largely unexplored. The detailed synopsis of these taxa by Schwartz (1967) provides little data to support sister group relationships or wider ranging affinities for these taxa. Their inclusion in the Greater Antillean *E. auriculatus* section (Hedges, 1989; "*auriculatus* group" of Schwartz, 1969) is supported by six characteristics: (1) external submandibular vocal sac in males; (2) "patch-like" vomerine teeth; (3) areolate venter; (4) highly vocal; (5) calling sites above ground; and (6) prominent digital disks. However, the phylogenetic significance of these characters is still uncertain (Hedges, 1989). Hedges (1989) also defined a *martinicensis* series based on allozyme data (but lacking morphological synapomorphies) and postulated that Lesser Antillean *Eleutherodactylus*, inclusive of *E. urichi*, were members of a monophyletic *martinicensis* group within the *martinicensis* series.

A detailed survey of Eastern Caribbean taxa was conducted to test the hypothesis of monophyly for Lesser Antillean taxa, and to determine whether there was any influx into the Lesser Antilles from South America, as suggested by Lescure (1983, 1987). The survey led to the realization that populations at higher elevations on the island of Dominica were distinct from *E. martinicensis* at the level of species. This discovery now allows a more comprehensive analysis of phylogenetic relationships between Eastern Caribbean *Eleutherodactylus*.

MATERIALS AND METHODS

Frogs were collected in the Eastern Caribbean over a 3-yr period (1990–92). Sampling on Dominica was carried out at six localities (Appendix 1) during January 1990 and during the month of August in 1990–92. A conscious effort was made to survey as many topographically dissimilar localities as feasible within the time available. For biochemical comparisons, 211 specimens of *Eleutherodactylus johnstonei*, *E. martinicensis*, and of the Dominica populations were captured (Appendix 2) and taken to the lab in Montréal. All procedures with animals, including captive care, conformed to guidelines established by the Canadian Council on Animal Care (1980–84) and were approved by the Animal Care Committee of McGill University. Institutional abbreviations follow Leviton et al. (1985). Specimens with NMC or KU designations and DMG numbers are being deposited in those institution; receipt of numbers is pending. Tissue samples (liver, heart, kidney, muscle, spleen) were homogenized and centrifuged, and the supernatant was stored separately from the original tissues at -80°C. Horizontal starch gel electrophoresis was carried out to obtain allozyme data (Table 2), following the recommendations made by Murphy et al. (1990).

Length measurements for morphometric comparisons were taken from 720 specimens (Table 3) to the nearest 0.1 mm using a dissecting microscope with camera lucida and digitizer attachments (Numonics 2200 digitizing tablet) and supported by Jandel Scientific Sigma Scan (version 3.10) software on an IBM personal computer. Statistical analyses were performed using Systat 5.2 software on a Macintosh LC computer. Sound recordings were made on Dominica (August 1990), Guadeloupe (January, June, and August 1990), Martinique (January and August 1990), and Montserrat (August 1990), using a SONY professional walkman WM-D3. Audiospectrograms were created with a Kay Elemetrics Corp. digital sonagraph 7800. Terminology for vocalizations follows Duellman and Trueb (1986), and all means reported are for $n = 10$ calls.

The format of the species diagnosis follows Lynch (1979), with the addition of the condition of the *M. depressor mandibulae* (see Lynch, 1993). Descriptions of snout shape, structure of vocal sac, and tongue shape follow the definitions given by Duellman (1970). Terminology for finger disks follows Savage (1987). Measurements included are ranges, means \pm standard deviation, and sample sizes for both females and males.

Several morphological characters were scored from live or freshly preserved animals, or from photographs of living specimens. Specimens of potential outgroups were obtained from several North American herpetological collections (Appendix 1). Several specimens of each species under investigation were cleared and double-stained in consultation with the protocols of Dingerkus and Uhler (1976), Hanken and Wassersug (1981), Hardaway and Williams (1975), and Wassersug (1976).

Characters were identified *a priori* using the character lists in the dissertations of Ford (1989) and Joglar (1986), adding several novel characters (Appendix 3). Character states were determined during a preliminary survey of specimens; they were

adjusted as appropriate during scoring. Not all of the described character states (Ford, 1989; Joglar, 1986) may be present in the species considered here; they are included in the character descriptions to permit comparisons and to facilitate subsequent inclusion of other taxa into this data set. Some characters are notoriously difficult to assess when relying exclusively on preserved specimens, even taking into account descriptions from the literature. Total character variability may not be reflected by the individuals examined (e.g., tuberculation, patterning, coloration). Thus, two analyses were carried out, one using the complete data matrix, the other excluding characters for which there was any scoring uncertainty (Appendix 3). The phylogenetic analysis was accomplished using PAUP 3.1.1 (Swofford, 1993) with option requests for outgroup rooting (ingroup monophyletic with respect to outgroup), both ACCTRAN and DELTRAN optimization, and unordered characters. Since the data matrix was too large for branch-and-bound or exhaustive searches, replicated heuristic searches (100 repetitions) were conducted using closest stepwise addition, uncollapsed zero-length branches, the steepest descent option, and tree bisection-reconnection branch swapping with swapping carried out on minimal and non-minimal trees. Both strict and majority-rule consensus cladograms were constructed and displayed as phylogenetic trees and phylograms. Exploratory manual branch swapping was carried out on the most parsimonious topologies using MacClade 3.01 (Maddison and Maddison, 1992), admitting only combinations that did not increase the number of steps in the tree(s) found by parsimony analysis.

As with any phylogenetic analysis, choice of correct outgroup(s) and appropriate characters was of paramount importance. The primary concern with the Eastern Caribbean *Eleutherodactylus* is the taxonomic uncertainty caused by their geographic position between the *Eleutherodactylus*-rich faunas of the Greater Antilles and South America. As a consequence, an outgroup analysis may be confounded either

by the introduction of paraphyly if the chosen outgroup is really part of the ingroup, or by omission of certain key taxa from the ingroup. While the second problem defies solution at this time due to the unresolved relationships between South American *Eleutherodactylus*, the first problem can be alleviated by considering the biochemical evidence presented in Chapter 7, using the relationships postulated therein as a working hypothesis. Thus, southern Eastern Caribbean taxa are used here as outgroups in the analysis of relationships of Puerto Rican and northern Eastern Caribbean taxa. One species, *E. fitzingeri*, was added to the outgroup because of its proposed close affinity with *E. terraebolivaris* (Rivero, 1961).

TAXONOMY

In the following section I describe a new species of *Eleutherodactylus* from forested habitats at higher elevations on Dominica, West Indies. A striking feature of these populations is the occurrence of females whose body size is over twice that of males. For these distinctive populations I propose the name

Eleutherodactylus amplinympha sp. nov.

Dominica Whistling Frog

Figs. 2–3

Holotype.—Canadian Museum of Nature (NMC [DMG 5019]), an adult female from near Freshwater Lake, Dominica, West Indies (ca. 61°20' W, 15°20' N; altitude ca. 800 m). The specimen is one of a series collected on 26 August 1992 by T. F. Sharbel and H. Kaiser.

Paratypes.—Two female topotypes (KU [DMG 4197], NMC [DMG 4198]), collected on 7 August 1990 by G. Schäfer, D. von Stösser, A. Werres, and H. Kaiser. Two male topotypes (KU [DMG 4185], NMC [DMG 4186]) and a female topotype (KU [DMG 4187]), collected on 21 August 1990 by H. M. Gray and H. Kaiser. One male topotype (KU [DMG 4733]) and two female topotypes (KU [DMG 4591], NMC [DMG 4686]), collected on 7 August 1991 by H. M. Gray and H. Kaiser. Two males (KU [DMG 4730], NMC [DMG 4732]) and two females (NMC [DMG 4598–99]) from near Emerald Pool, alt. ca. 400 m, collected on 6 August 1991 by H. M. Gray and H. Kaiser. One male (NMC [DMG 3737]) from 500 m SE Layou Park Estate, alt. ca. 325 m, collected on 13 January 1990 by H. H. Schwarten and H. Kaiser. Two females (NMC [DMG 4141, 4153]) from the previous locality, collected on 8 August 1990 by G. Schäfer, D. von Stösser, A. Werres, and H. Kaiser. One male (NMC [DMG 3543]) from the Trafalgar Falls area, alt. ca. 330 m, collected on 14 January 1990 by H. H. Schwarten and H. Kaiser. One female (NMC [DMG 4189]) from the slopes of Morne Diablotin, alt. ca. 1000 m, collected along trail on 22 August 1990 by H. M. Gray and H. Kaiser.

Diagnosis.—A forest-dwelling member of the *E. auriculatus* section with the following diagnostic features: (1) Skin on dorsum coarsely shagreened with decreasing number of larger tubercles from anterior to posterior; a fine middorsal ridge extending from back of head to venter; dorsolateral folds absent; venter coarsely areolate between pectoral and pelvic areas; groin region coarsely areolate; (2) tympanum round, distinct, about one-third size of the orbit; supratympanic fold present; (3) snout trapezoid in dorsal view, rounded in profile; eye–naris distance greater than length of eye; canthus rostralis sharply angled, canthal ridge straight, with dark line; (4) interorbital distance 1.5–2 times width of upper eyelid; supraocular tubercles

present; cranial crests absent; (5) dentigerous processes of vomers triangular and slightly oblique, each with a single row of teeth; choanae ovoid; (6) males with external vocal slits and weakly bilobate subgular vocal sac; nuptial pads absent; (7) size of fingers (I = II) < IV < III, III about 1.5 times longer than I; finger disks II–IV about 1.5 times wider than digits, disk I only slightly wider; subarticular tubercles round and raised; two palmar tubercles, medial one elliptical, lateral one conical; thenar tubercle elliptical, covering base of finger I laterally; numerous supernumerary palmar tubercles; (8) fingers with weak lateral fringes; (9) several tubercles on forearm and elbow; several raised postorbital tubercles, particularly in the area from angle of jaw to axil; (10) several small heel and knee tubercles; inner tarsal fold absent; (11) two metatarsal tubercles, inner large and elliptical, outer one third size of inner and conical; numerous supernumerary plantar tubercles; (12) toe disks oval, about equal in size, slightly wider than digits; lateral fringes weak; webbing absent; (13) dorsum dark brown, sometimes with a middorsal hairline or one to two ill-defined dark chevrons; venter cream with variable numbers of dark brown stellate melanophores; concealed surfaces of hind limbs cream to light orange in life; labial area brown, with or without light mottling; solid dark, boomerang-shaped supratympanic stripe extending from corner of eye to arm; upper iris color dark bronze in life; (14) SVL of females 15.9–49.7 mm ($\bar{x} = 32.1 \pm 9.6$, $n = 30$), of males 16.1–26.4 mm ($\bar{x} = 21.8 \pm 2.4$, $n = 21$); (15) **dfsq*** at condition of *M. depressor mandibulae*.

Eleutherodactylus amplinympha is readily distinguished from other Lesser Antillean *Eleutherodactylus* by its vocalizations (see below; Fig. 4). The most striking morphological feature of *E. amplinympha* is the large size of adult females, with mature females on average 1.5 times the size of mature (vocalizing) males. In life, there is a distinctive diurnal color change, from dark brown when resting to orange brown when active at night. Adults of *E. pinchoni* can generally be differentiated from *E.*

amplinympha by size alone, reaching a maximum SVL of only about 22 mm. In addition, this species has a characteristic dark postsacral region which is not differentially colored in *E. amplinympha*. *Eleutherodactylus barlagnei* is one of few *Eleutherodactylus* with foot webbing. Specimens characteristically are almost black in coloration, with large numbers of prominent dorsal tubercles. The southern Lesser Antillean species *E. euphronides* and *E. shrevei* can be distinguished from *E. amplinympha* by the bright coloration of the hidden portions of the thigh, which are colored orange in *E. euphronides* and red in *E. shrevei*, and by their relatively longer tibiae (55.4 and 54.2% of SVL for *E. euphronides* and *E. shrevei*, respectively, compared with 47.7% for *E. amplinympha*).

The most similar species to *Eleutherodactylus amplinympha* are *E. johnstonei* and *E. martinicensis*. These two species have traditionally been confused with one another (Frost, 1985) and although separating either from *E. amplinympha* can be accomplished by traditional morphological or statistical means, it is most easily done using diagnostic allozyme loci. There are thirteen diagnostic loci (Table 4) that allow differentiation of *E. amplinympha* from both *E. johnstonei* and *E. martinicensis*. There are three fixed allelic differences (GAPDH, GPI, LDH-1) between *E. martinicensis*, *E. johnstonei*, and *E. amplinympha*. Three other loci (GCDH, MDH-1, PEP[LGG]) approach fixation at different alleles when comparing *E. amplinympha* with *E. martinicensis*, whereas two additional loci (MPI-1, PEP[LA]) are nearly fixed different vis-à-vis *E. johnstonei* (Table 4). This clearly suggests that the three tested groups represent independent evolutionary lineages.

Basic statistics (Table 3), of the type employed by Schwartz (1967), show subtle, yet statistically significant differences ($P < 0.005$) between the species, but none of these differences is striking and would not assist in identification when only a few specimens are available. Morphological differences are evident in features such as

dorsal tuberculation (much smoother in *E. johnstonei* and *E. martinicensis*), snout shape (snout rounded in dorsal view in both *E. johnstonei* and *E. martinicensis*), finger lengths (in *E. johnstonei* and *E. martinicensis* fingers are all of different lengths), toe lengths (in *E. amplinympha* toe V reaches the penultimate subarticular tubercle of toe IV), or hand tuberculation (only one palmar tubercle in *E. johnstonei*, differences in size of thenar and palmar tubercles in *E. martinicensis*). These are very detailed characteristics and may not be reliable in older or poorly preserved specimens given the shrinkage of fluid-preserved specimens (Simmons, 1991). However, color of the testicular peritoneum seems to be a nearly constant difference; 90% of male *E. amplinympha* have a black or darkly reticulated testicular peritoneum, whereas those of *E. johnstonei*- and *E. martinicensis*-males are white. Dorsal pattern variation of *E. johnstonei* is much greater than in either *E. amplinympha* or *E. martinicensis*, including one or two clearly outlined dark chevrons, middorsal stripes, dorsolateral stripes, and combinations of these. In the latter species, dorsal patterns are absent or ill-defined and limited to middorsal stripes and one faint dark chevron.

Eleutherodactylus amplinympha possesses three autapomorphic osteological characters that reliably distinguish it from *E. johnstonei* and *E. martinicensis*. The anterior end of the cultriform process of the parasphenoid is pointed, whereas it is rounded in the other species. The metacarpal length formula (Ford, 1989) of *E. johnstonei* and *E. martinicensis* is 3-2-1-4, but it is 3-2-4-1 in *E. amplinympha*. Neither *E. johnstonei* nor *E. martinicensis* have a lateral extension of the proximal prehallical element.

Description.—Thirty adult females, twenty-one males. Head wider than body, longer than wide; head width 39.2–45.1% ($\bar{x} = 42.2 \pm 1.5$) of SVL in females, 38.3–46.4% ($\bar{x} = 41.6 \pm 2.1$) in males; marginally rounded snout, trapezoid in shape in

dorsal view, rounded in lateral profile; terminal mouth; lower lip bearing a small but well defined papilla; eye-naris distance 63.1–122.0% ($\bar{x} = 90.6 \pm 13.0$) of eye length in females, 64.6–110.3% ($\bar{x} = 85.3 \pm 13.2$) in males; eyes large, prominent; upper eyelid with tubercles; interorbital distance about 24.2–37.9% ($\bar{x} = 30.7 \pm 3.1$) of head width in females, 24.8–35.9% ($\bar{x} = 29.8 \pm 2.7$) in males. Top of head flat; cranial crests absent; canthus rostralis straight, sharply angled; loreal region slightly concave in anterior half, with several tubercles; lips not flared; internarial area not depressed; nares round, protruding slightly laterally. Supratympanic fold distinct, describing a posteroventral, boomerang-shaped curve from posterior corner of orbit, barely obscuring dorsal part of tympanic annulus; tympanum round, medium-sized, in females 24.0–50.6% ($\bar{x} = 36.8 \pm 6.3$) of eye length, 16.5–51.6% ($\bar{x} = 37.4 \pm 7.2$) in males; separated from eye by a distance about equal to or slightly less than tympanum diameter. Choanae ovoid, widely separated, unobscured by palatal shelf of maxillary arch when viewed from above; dentigerous processes of vomers prominent, triangular, aligned in a posteriorly elevated transverse row with a slightly posteriorly angled aspect and each bearing a single row of teeth, posteromedially inclined, but with lateral third of processes sometimes extending more laterally than medial margin of choanae; dentigerous processes separated by distance greater than width of individual process. Tongue oval, longer than wide, shallowly notched posteriorly, free behind for about one half of its length; vocal slits elongate, extending from midlateral base of tongue towards angle of jaw; vocal sac bilobate, subgular, external.

Skin on dorsum coarsely shagreened with narrow middorsal ridge extending from back of occiput to groin; flanks areolate; several raised tubercles below supratympanic fold posterior to tympanum; several low tubercles on forearm; several small tubercles on each knee and heel, but not on tarsus; ventral posterior surface of

thighs coarsely areolate. Anal opening unmodified, directed posteriorly at upper level of thighs.

Forearms moderately robust; fingers long, slender, bearing subtruncate disks with broadly elliptical pads, relative disk sizes $I < II < (III = IV)$; relative lengths of fingers $I = II < IV < III$; number of subarticular tubercles 1-2-2-2 for fingers I-IV, respectively, subarticular tubercles round and raised; numerous supernumerary palmar tubercles; two palmar tubercles, medial one elliptical, lateral one conical; thenar tubercle elliptical, covering base of finger I laterally; nuptial pads absent. Hindlimbs moderately robust, long; heels broadly overlapping when hindlimbs flexed at right angles to body axis; tibia length in females 41.5–55.3% ($\bar{x} = 47.4 \pm 3.0$) of SVL, 43.8–55.5% ($\bar{x} = 48.2 \pm 2.9$) in males. Inner tarsal fold absent; two metatarsal tubercles, inner large and elliptical, outer 1/3 size of inner and conical; toes long, slender, bearing oval disks about the size of disks on fingers III and IV; with narrow lateral fringes, without any webbing; relative length of toes $I < II < V < III < IV$; number of subarticular tubercles 1-1-2-3-2 for toes I-V, respectively, subarticular tubercles round and conical; numerous supernumerary plantar tubercles (Fig. 3).

Color in preservative (n = 53).—Dorsum of head and body uniformly dark brown; 27.1% of specimens without any dorsal pattern, 16.9% with middorsal hairline, 10.2 % with middorsal stripe, 23.7% with one ill-defined dark middorsal chevron, 11.9% with a light dorsolateral area; with narrow dark interorbital bar, 8.5% having a cream interocular bar offsetting the former; dark canthal stripe; lower edge of supratympanic stripe dark brown; flanks dark brown, rarely lighter than middorsal area (two individuals). Dorsal surfaces of limbs dark brown, with or without 1–2 darker brown crossbars, sometimes offset by lighter borders (percentages in parentheses for occurrence of 1 and 2 crossbars, respectively) on forearms (91.5, 3.4), thighs (64.4,

5.1), shanks (91.5, 5.1, diagonal), and/or tarsi (74.6, 1.7); anterior surface of thighs tan and mottled, posterior surfaces tan. Venter cream to tan with some mottling caused by differential distribution of dark brown, stellate melanophores; ventral surface of palm and finger disks white, disk covers brown with the exception of conspicuously darkly pigmented disk cover on finger IV; toe disks white ventrally, disk covers darkly pigmented; plantar surfaces dark brown, sometimes offset by a medial cream hairline.

Color in life.—Dorsum dark brown by day, taking on a distinctly orange hue during night activity; venter cream to tan with some degree of mottling; hidden surfaces of thighs cream to faint orange; upper iris color bronze.

Measurements (in mm).—Values given are for the holotype, followed by ranges with means in parentheses for thirty females and twenty-one males, respectively. SVL 37.8, 15.9–49.7 (32.1 ± 9.6), 16.1–26.4 (21.8 ± 2.4); tibia length 19.3, 7.9–22.1 (15.1 ± 4.1), 7.8–13.3 (10.5 ± 1.2); foot length 27.7, 10.6–33.6 (21.5 ± 6.3), 10.6–18.5 (14.5 ± 1.6); head width 11.8, 6.8–21.8 (13.6 ± 4.3), 7.5–10.9 (9.0 ± 0.9); interorbital distance 5.1, 2.2–7.6 (4.2 ± 1.4), 1.9–3.2 (2.7 ± 0.3); eye–naris distance 4.9, 1.6–6.5 (3.8 ± 1.3), 1.9–3.4 (2.6 ± 0.3); eye diameter 5.1, 2.4–6.3 (4.2 ± 1.1), 2.4–3.7 (3.1 ± 0.4); tympanum diameter 1.8, 0.7–2.3 (1.5 ± 0.5), 0.6–1.6 (1.1 ± 0.2).

Distribution and Ecology.—The species is found only on the island of Dominica, West Indies. It is uncertain at this time whether the population is continuous or fragmented, because there has been some development of broad agricultural strips paralleling either side of the main roads traversing the island. Frogs were most abundant in the area of Morne Macaque in Morne Trois Pitons National Park. Despite

the establishment of the park, the area around Freshwater Lake has suffered recently from construction of a hydroelectric development. Tarred wooden pipes have been constructed along a 10–15 m wide deforested and leveled corridor alongside the mountain; chemically treated wood and metal debris has been discarded into the surrounding forest. However, the government of Dominica is conscious of its natural resources and has established precedents (e.g., hunting seasons for the edible frog *Leptodactylus fallax*, restraint in construction of tourist facilities in favor of locally controlled ecotourism) in the Lesser Antilles for responsible use and management of its unique biota.

Eleutherodactylus amplinympha is most abundant near the transition zone from montane rainforest to elfin woodland (Nicolson, 1991). This habitat is characterized by relatively great temperature variation between day and night (from as high as 25°C to as low as 17°C), high annual rainfall, and nearly ubiquitous fog. During all visits to the Freshwater Lake area, I encountered either rain or fog, with high gusting winds at night often preventing effective recording of vocalizations. The montane rain forest vegetation at this elevation consists of few trees (height < 20 m), shrub thickets, palm brakes, and ferns (Davis et al., 1986; Nicolson, 1991). The low thicket-like forest, frequently covered by epiphyllous hepatics or bearing moist moss mats (Nicolson, 1991) is an ideal refugium for anurans and nearly impenetrable to humans.

A single terrestrial egg mass was found in January 1990 in a rock crevice near Freshwater Lake. It contained thirteen firm opaque eggs (estimated maximum diameter 7 mm) with an outer gelatinous layer in a three-dimensional clump and was attended by a male frog. The total size of the egg clump was about twice that of the attending frog. Eggs were positioned on a small mat of ground moss. After collection, no changes in egg morphology occurred, and dissection of several eggs showed no recognizable development (D. S. Townsend, pers. comm.). Seven females (range of SVL 25.0–

46.5 mm, \bar{x} = 37.6 mm) caught during a reproductive episode, as determined by the presence of large and yolky (= ripe) ovarian eggs, contained on average 29.3 eggs, with averages of 14.7 and 14.6 eggs in the right (n = 7) and left (n = 5) ovaries, respectively. The females whose left ovaries were not counted had few or no eggs on the left side, one carrying thirty-two ripe eggs in her right ovary, four in the left, and the other, smaller female carrying thirteen in the right, none in the left ovary. Such an imbalance suggests that these females produced one clutch, but retained one ovary's egg content to lay a second clutch later during the same reproductive episode. The smallest female with ripe eggs (NMC[DMG 4187], SVL = 25.0 mm) had only four ripe eggs in each ovary, while progressively larger females were found to carry greater numbers of ripe eggs; this may be indicative of a more general correlation between female size and clutch size. Average size (length) of testes was 2.6 mm (n = 9). Seven specimens have black testes (NMC[DMG 3502–03, 3543, 3620, 3737, 3755, 4172]) and two specimens (NMC[DMG 3506, 5029]) have testes with a dark reticulating pattern; no specimen had white testes.

Vocalizations.—The primary call of *Eleutherodactylus amplinympha* (Fig. 4B) is a triphasic compound call consisting of two notes and a click. The first note is produced at a constant dominant frequency of 1750 Hz, with a spectral bandwidth ranging from 200 Hz at the beginning of the note to 350 Hz at its end. This note comprises about one third of the total length of the call (\bar{x} = 135 ms). The second note directly connects to the first after a frequency jump to 2600 Hz. After a rise time of 160 ms, which is the total length of the second note or two-fifths of total call length, the frequency reaches 3300 Hz, with a maximum spectral bandwidth of 480 Hz. The click follows after a 100 ms gap in the call and is only 30 ms long; its dominant frequency is 3100 Hz. The spectral bandwidth of the click decreases rapidly from 1050 Hz to 350

Hz. The total length of a typical call is 450 ms. Calls of *E. martinicensis* (Fig. 4A) and *E. johnstonei* (Fig. 4C) are biphasic and of considerable similarity to those of *E. amplinympha* and to each other. However, specific differences are sufficient to recognize the individuality of each call.

Frogs were never heard to produce a series of complete calls, including clicks, in immediate and rapid succession. Males were observed to initiate calling bouts with several single "whistle-click" calls spaced apart several seconds. They then switched to continuous "whistle-whistle-..." calling (at a rate of greater than one per second) for several seconds until ending the bout with a "whistle-click" call. In *Eleutherodactylus amplinympha*, "ramping patterns" were never observed. These are series of chorusing events usually initiated by a single individual which is joined by more and more males, leading to rapid chorusing. Ultimately, though, there is abrupt cessation of calling activity until the next bout of ramping is initiated (Drewry and Rand, 1983). Ramping is common in *E. martinicensis* (pers. obs.).

The vocalizations of *Eleutherodactylus amplinympha* have components homologous to those described for *E. coqui* by Narins and Capranica (1976, 1978). In *E. coqui*, the initial note is a territorial, male-specific signal, whereas the second note is issued to broadcast courtship readiness. The attached click may serve as an agonistic signal, as observed in physical encounters of *E. urichi* (Wells, 1981). Frogs were also observed to issue series of shorter clicks with great spectral bandwidths (> 1200 Hz) after much reduced and weak primary calls. Such a series usually consisted of five clicks in a row at slightly increasing dominant frequencies (2900–3500 Hz). These were heard most frequently at dusk when males are presumed to establish their calling position for that night, and may serve as an agonistic or territorial signal to other males.

Etymology.—The specific name *amplinympa* is a composite noun used in apposition. It is derived from the Latin *amplus* (large) and the Latin *nympha* (nymph, a female forest and mountain spirit). We choose this name in reflection of the relatively large size of females of the species, and the fact that these scarcely seen yet frequently heard frogs live in the mountains on Dominica.

ANALYSIS OF PHYLOGENETIC RELATIONSHIPS

The phylogenetic analysis of the data matrix for Eastern Caribbean *Eleutherodactylus* from external and internal morphology, including all characters, produced two most parsimonious trees of length 310 steps with a consistency index (CI) of 0.471 (Fig. 5A). Neither tree contradicted the hypothesis of diphyly for Eastern Caribbean taxa. Only two sister group relationships were apparent, one for *Eleutherodactylus amplinympa* and *E. martinicensis*, the other for *E. terraebolivaris* and *E. fitzingeri*. All other taxa in both trees were placed in a nested fashion, with either *E. johnstonei* or *E. antillensis* originating at the node giving rise to *E. amplinympa* and *E. martinicensis*, and with *E. coqui*, *E. barlagnei*, and *E. pinchoni* originating at subsequent nodes closer to the base of the tree. The southern taxa are similarly nested, with *E. shrevei*, *E. euphronides* and *E. urichi* originating at nodes progressively closer to the base of the tree. Of the 142 characters used in the analysis, seventeen were constant (12.0 %), but only five were uninformative (3.5 %). Given the two most parsimonious topologies, only 26 characters (18.3 %) showed no indication of homoplasy, whereas 41 characters (28.9 %) carried homoplasy values > 0.500; 26 of these were osteological characters.

The analysis excluding the more questionable characters (Appendix 3) resulted in seven most parsimonious trees (length 243 steps, CI = 0.477; Fig. 5B). The only

differences in topology from the previous analysis were the formation of a sister-group relationship for *E. euphronides* and *E. shrevei*, and the switching of nodes for *E. barlagnei* and *E. pinchoni*. Imposing the topology from an electrophoretic analysis (Chapter 7) using MacClade 3.01 results in a tree of length 316 steps with a CI = 0.46 (Fig. 6). Although this topology results in a slightly lower CI, homoplasy is eliminated completely for three important non-morphological characters: vocalizations, egg tooth, and chromosome number.

DISCUSSION

General systematics.—Analysis of morphological data lends further support to the hypothesis that Eastern Caribbean taxa do not form a monophyletic assemblage. Although the data sets from morphology and allozymes (Chapter 7) differ in their ability to resolve relationships within a given tree, as indicated by lower CI-values in the morphological analysis, there is congruence in the main conclusion: northern Eastern Caribbean *Eleutherodactylus* are members of a Greater Antillean assemblage, whereas southern Eastern Caribbean species have South American affinities. However, indications from morphological data suggest that northern Eastern Caribbean species may not form a monophyletic group, as strongly indicated by allozyme data (Chapter 7), but that the present species diversity may be the result of multiple colonizations.

Northern Eastern Caribbean species.—Taking the conclusions from the morphological data to the extremes, there may have been as many as four independent colonization events in the northern Eastern Caribbean, for *E. barlagnei*, *E. johnstonei*, *E. pinchoni*, and for the common ancestor of *E. amplinympha* and *E. martinicensis*.

However, there are certain facts that strongly contradict such a scenario of multiple introductions. Although frogs of the genus *Eleutherodactylus* are known for their karyological variability (e.g., DeWeese, 1976; Bogart, 1970, 1981) and their potential for rapid chromosomal change (e.g., Bogart, 1991), the independent derivation of a $2n = 28$ chromosome complement from $2n = 24$ or 26 has in all likelihood not occurred four times in the Eastern Caribbean. The chromosomes of the Eastern Caribbean *E. johnstonei* ($2n = 28$), for example, are very dissimilar to those of Greater Antillean species with karyotypes of $2n = 24$, 26 , or 28 (Bogart, 1981, 1991; Bogart and Hedges, unpubl.), but similar to those of other northern Eastern Caribbean species ($2n = 28$; unpubl.). This suggests a unique derivation of northern Eastern Caribbean chromosome complements. Furthermore, the occurrence of *E. barlagnei* and *E. pinchoni* in macrosympatry but microallopatry on Guadeloupe may not necessarily be suggestive of their sequential arrival but of habitat partitioning or niche differentiation after *in situ* speciation. This suggestion is borne out by the calls of these frogs: whereas *E. pinchoni* has a high pitched uniphaseic call which pierces the moss mats from under which it calls, *E. barlagnei* has a series of loud clicks added to a uniphaseic call that enables it to be heard above the din of rushing water. In the same vein, great similarities in vocalizations as well as identity of chromosome number support the triad of *E. amplinympha*, *E. johnstonei*, and *E. martinicensis* over the topology that places *E. antillensis* as the sister taxon to *E. amplinympha* and *E. martinicensis*.

The great morphological and biochemical similarity of *Eleutherodactylus amplinympha*, *E. johnstonei*, and *E. martinicensis* is further evidence of a close phylogenetic relationship. Communality of several external morphological characteristics place *E. amplinympha* and *E. martinicensis* into a sister-group relationship, with *E. johnstonei* as the sister taxon to that clade. Biochemical data also suggest a closer relationship for *E. amplinympha* and *E. martinicensis* than for either

with *E. johnstonei* (Chapter 7). It has been suggested that *E. martinicensis* may have been imported to Dominica from Martinique and/or Guadeloupe by refugees during the turmoil of the French Revolution (Lescure, 1983). However, none of the specimens examined from Dominica are referable to that species. Thus, two biogeographical scenarios seem possible that establish *E. amplinympha* on Dominica, either one conforming to current ideas about speciation (see Giddings et al., 1989; Otte and Endler, 1989). In one scenario, possible multiple colonization events by an ancestral species, most likely from the Greater Antilles (Schwartz, 1969; Hedges, 1989), succeeded in establishing island populations of *Eleutherodactylus* in the Lesser Antilles. These island populations subsequently speciated, resulting in the observed species radiation, and thus the evolution of several single-island endemic species. The second scenario begins with single or multiple introductions of *E. martinicensis* onto Dominica, either by natural dispersal or through the agency of early Amerindian or more recent French settlers. The established peripheral isolate(s) on Dominica may have been exposed to differential selection pressures, ultimately creating recognizable divergence. It is possible that additional research on Dominica may reveal pockets of introduced or remnant *E. martinicensis*, and given the ease with which these frogs are transported (Kaiser, 1992), additional introductions are likely.

As it is, the two species are concentrated in slightly different habitats. Whereas *E. amplinympha* is most common at higher elevations, *E. martinicensis* is encountered most frequently in the lowlands. The species are sympatric for a vertical altitudinal segment of about 100 m along the road to Freshwater Lake, and near Emerald Pool (pers. obs.). The collections of Dominican specimens made by A. Schwartz (KU, uncatalogued) are mainly from lowland populations. However, Schwartz remarked (A. Schwartz field notes 19 February 1962, remarks during collection of Albert Schwartz Field Series [ASFS] 18947–69; 19 February 1962, ASFS 19040–106; 7 March 1962,

ASFS 19116–29) that he considered two species present, one large and one small, with the calls of the smaller identical to those of *E. martinicensis* (22 March 1961, ASFS 11377–98). He also commented on the orange coloration of some frogs (23 March 1961, ASFS 11406–30). My inspection of the ASFS specimens listed above was inconclusive as to the identities of the frogs, and Schwartz did not detail which of the collected series were differently colored in life or which vocalized differently. Small *E. amplinympha* would be difficult to identify, especially considering the effects of specimen shrinkage in fluid preservatives (Simmons, 1991). The exact ranges of *E. amplinympha* and *E. martinicensis* on Dominica are as yet undetermined.

The great morphological similarities between *Eleutherodactylus johnstonei* and *E. martinicensis* have long caused taxonomic confusion. Although the two species can be easily distinguished in life, it becomes nearly impossible to separate long-preserved museum specimens. Similarly, *E. amplinympha* is easily distinguished from either of these species in life, yet the smaller specimens examined are difficult to match to one species or the other after only two years in preservative. However, since both frozen tissues and chromosomal preparations were retained for most specimens, unequivocal assignment to species by biochemical or cytogenetic means can provide a reliable alternative to morphological identification.

Southern Eastern Caribbean species.—Phylogenetic relationships of southern Eastern Caribbean *Eleutherodactylus* are not as easily resolved given the present data set. However, the inclusion of *E. fitzingeri* in the analysis gives some indication of relationships with South American taxa. All topologies (Figs. 5, 6s) support the hypothesis of close relationship between *E. terraebolivaris* and *E. fitzingeri* (fide Rivero, 1961; Lynch 1976). The phylogenetic position of *E. euphronides* and *E. shrevei* allies these species more closely with the *E. terraebolivaris*-*E. fitzingeri* clade

than with *E. urichi* in two topologies (Figs. 5B, 6). Sister-group relationships of *E. urichi* cannot be determined unless additional South American taxa are included in the analysis.

Character evolution.—The morphological analysis of Eastern Caribbean *Eleutherodactylus* provides an example of the high degree of homoplasy found in this genus. Just as in the only other comprehensive cladistic analysis of morphology for West Indian *Eleutherodactylus* (Joglar, 1986, 1989), many of the studied characters were too variable to be informative. In fact, Joglar (1986) excluded 24 of 52 characters which had CIs lower than 0.200 and did not even report the CI of his analysis before exclusion of these characters; after exclusion the CI was 0.417. Regarding these values, the present analysis compares favorably (41 characters of 142 with CIs < 0.500; CI = 0.471). In addition, Joglar (1986) reduced the number of taxa to ten by excluding "apomorphic species," improving the CI to 0.691. This analysis does not require a reductionist approach since, in part, homoplasy problems can be alleviated or explained by consulting allozyme data (Chapter 7).

Among the characters used in this analysis, three distinct qualities can be identified. Osteological characters have often been considered to be the most reliable for phylogenetic analyses, in part because relationships based on such characters can in some instances be verified by material from the fossil record. For *Eleutherodactylus*, there is very little such material, and the scarce fossils known from the West Indies are fragmentary (e.g., Auffenberg, 1958; Lynch, 1966; Pregill et al., 1988; Steadman et al., 1984); the only complete fossil *Eleutherodactylus* is embedded in amber (Poinar and Cannatella, 1987) and is of limited comparative value due to its uniqueness. Thus, no evolutionary trends have been identified that could assist with determining the direction of osteological modifications over evolutionary time. However, there are

some structures where little variation has been described for anurans or where variation is constrained (Duellman and Trueb, 1986; Ford, 1989); these may be more useful in elucidating relationships than those for which there is a high degree of variability. The phylogram (Fig. 6) is largely based on such characters. At the other extreme are those characters which display such a high degree of variability between species (or even sometimes within species) that they do not allow any unequivocal phylogenetic inference. These are by and large characters of external morphology (e.g., tuberculation, coloration, gross shape). Lastly, there are a few characters, such as chromosome number, vocalization, and aspects of development, whose relative stability in phylogenetic usage has been valuable in a variety of other anuran families, although their success may be variable depending on the level of classification.

Although there may be some degree of homoplasy even in the more conservative characters, I consider the following to be good indicators of an Antillean subgroup, likely synonymous with the proposed *Eleutherodactylus martinicensis* group (Hedges, 1989): (1) posterior extent of maxillary teeth to beyond maxilla-quadratojugal articulation; (2) medial ramus of pterygoid narrow medially; (3) **dfsq*** at condition of *M. depressor mandibulae*; (4) palatine and vomer overlap; (5) lateral sides of hyoid plate concave; (6) alary process of hyoid plate present; (7) dorsal crest of ilium reaches sacral region; (8) two tarsal sesamoid elements present; (9) tympana round; (10) weak supratympanic fold; (11) finger II > I; (12) toe disks of about the same size. These observations are consistent with data for the same characters from 14 additional Antillean species (unpubl. data).

CONCLUSIONS

This study confirms that Eastern Caribbean *Eleutherodactylus* do not form a monophyletic group. However, resolution of sister-taxon relationships is less well substantiated despite, or because of, the large number of characters. Unless our knowledge of the evolutionary history of morphological characteristics among *Eleutherodactylus* can be improved, for instance by developmental studies, their indiscriminate use in isolation may prevent the discovery of meaningful hypotheses of relationships due to homoplasy. The alternative is to use an analysis of a second data type, such as biochemical data, as a working hypothesis, and to conduct a careful *a posteriori* inspection and interpretation of all characters. This is a luxury not yet available to those studying vertebrate fossils.

Problems with diagnostic features are all too common among the polytypic *Eleutherodactylus*. Even species descriptions of these frogs have traditionally been based entirely on external morphological characters, even to the exclusion of vocalizations. Considering the difficulties encountered in this study with elucidating phylogenetic relationships based on morphology, a minimal, single-data-set-approach may make accurate taxonomic decisions too tenuous to be of practical value. It is symptomatic in that respect to have several new *Eleutherodactylus* described each year, while others are synonymized. As combinations of morphological and biochemical data are beginning to influence the classification of *Eleutherodactylus* more and more (e.g., Hedges, 1989; Miyamoto, 1983, 1984, 1986), taxonomic decisions will become better documented and probably more durable. In the case of the 512 currently recognized species of *Eleutherodactylus* (Duellman, 1993), ongoing revisions of subgeneric and species group classification (e.g., Hedges, 1989; Lynch, 1986, 1989,

1993) are certain to benefit from the increased usage of a full, multidisciplinary systematics toolbox.

ACKNOWLEDGMENTS

I am grateful to C. A. George, H. M. Gray, G. Schäfer, H. H. Schwarten, T. F. Sharbel, D. von Stösser, and A. Werres for field assistance. The patience and guidance of H. M. Reiswig, who endured hours of frog measuring on his equipment, is gratefully acknowledged. Thanks to R. E. Lemon for permitting me to use his sound analysis setup, and to D. J. Mountjoy for providing hints at how to make it work for frog voices. D. S. Townsend dissected the eggs of *E. amplinympha*. Special thanks to J. P. Bogart and S. B. Hedges for sharing some insights from their unpublished work. This study benefitted greatly from discussions with A. Baéz, M. W. Caldwell, R. L. Carroll, C. M. Dwyer, L. S. Ford, D. M. Green, T. F. Sharbel, J. E. Simmons, and L. Trueb. I thank F. R. Cook, W. E. Duellman, L. S. Ford, R. M. Rankin, and J. E. Simmons for authorizing and preparing specimen loans. The manuscript was improved during its development by comments from W. E. Duellman and C. M. Dwyer. Its final version was critically read by M. W. Caldwell and D. M. Green. Most of the work on specimens was conducted at the Museum of Natural History, The University of Kansas, and my thanks go to staff and students for their support. This research was funded in part by grants and scholarships from the Hans-Krüger-Stiftung and the Studienstiftung des Deutschen Volkes, West-Germany, and by NSERC Canada operating grants to D. M. Green.

LITERATURE CITED

- AUFFENBERG, W. 1958. A small fossil herpetofauna from Barbuda, Leeward Islands, with the description of a new species of *Hyla*. Quart. J. Fla. Acad. Sci. 21:248-254.
- BARBOUR, T. 1914. A contribution to the zoögeography of the West Indies, with especial reference to amphibians and reptiles. Mem. Mus. Comp. Zool. 44:209-359.
- BARNHART, C. L., AND R. K. BARNHART. 1983. The World Book Dictionary. World Book, Inc., Chicago.
- BOETTGER, O. 1894. *Eleutherodactylus urichi* sp. nov. P. 88. In: R. R. Mole and F. W. Urich. A preliminary list of reptiles and batrachians of the island of Trinidad. J. Trinidad Field Nat. Club 2:87-89.
- BOGART, J. P. 1970. Systematic problems in the amphibian family Leptodactylidae (Anura) as indicated by karyotypic analysis. Cytogenetics 9:369-383.
- _____. 1981. Chromosome studies in *Sminthillus* from Cuba and *Eleutherodactylus* from Cuba and Puerto Rico (Anura: Leptodactylidae). Life Sci. Contr. Royal Ont. Mus. (129):1-22.
- _____. 1991. The influence of life history on karyotypic evolution in frogs. Pp. 233-258. In: D. M. Green and S. K. Sessions (Eds.). Amphibian Cytogenetics and Evolution. Academic Press, New York.
- CANADIAN COUNCIL ON ANIMAL CARE. 1980-84. Guide to the Use and Care of Experimental Animals. 2 Vols. CCAC, Ottawa.
- CLAYTON, J. W., AND D. N. TRETIAK. 1972. Amine citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Bd. Canada 29:1169-1172.

- DAVIS, S. D., S. J. M. DROOP, P. GREGERSON, L. HENSON, C. J. LEON, J. LAMLEIN VILLA-LOBOS, H. SYNGE, AND J. ZANTOVSKA. 1986. Plants in Danger. What do we know? IUCN, Cambridge, United Kingdom.
- DEWEESE, J. E. 1976. The karyotype of Middle American frogs of the genus *Eleutherodactylus* (Anura: Leptodactylidae): a case study of the significance of the karyologic method. Ph.D. Thesis. Univ. of Southern California, Los Angeles.
- DINGERKUS, G., AND L. D. UHLER. 1976. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technol.* 52:229-232.
- DREWRY, G. E., AND A. S. RAND. 1983. Characteristics of an acoustic community: Puerto Rican frogs of the genus *Eleutherodactylus*. *Copeia* 1983:941-953.
- DUELLMAN, W. E. 1970. Hylid frogs of Middle America. *Monogr. Mus. Nat. Hist. Univ. Kansas* (1):1-753.
- _____. 1993. Amphibian species of the world: additions and corrections. *Univ. Kansas Mus. Nat. Hist. Spec. Publ.* (21):1-372.
- _____, AND L. TRUEB. 1986. *Biology of the Amphibia*. McGraw-Hill, New York.
- DUMÉRIL, A.M.C. AND G. BIBRON. 1841. *Érptologie Générale*. Roret, Paris.
- FORD, L. S. 1989. The phylogenetic position of poison-dart frogs (Dendrobatidae): reassessment of the neobatrachian phylogeny with commentary on complex character systems. Ph.D. Thesis. Univ. of Kansas, Lawrence
- FROST, D. R. 1985. *Amphibian Species of the World. A Taxonomic and Geographical Reference*. Allen Press, Inc., and The Association of Systematics Collections, Lawrence, Kansas.

- GIDDINGS, L. V., K. Y. KANESHIRO, AND W. W. ANDERSON (EDS.). 1989. Genetics, Speciation, and the Founder Principle. Oxford University Press, New York.
- HANKEN, J., AND R. J. WASSERSUG. 1981. The visible skeleton. A new double-stain technique reveals the nature of the "hard" tissues. *Functional Photogr.* 16:22-26, 44.
- HARDAWAY, T. E., AND K. L. WILLIAMS. 1975. A procedure for double staining cartilage and bone. *Brit. J. Herpetol.* 5:473-474.
- HARDY, J. D., JR. 1982. Biogeography of Tobago, West Indies, with special reference to amphibians and reptiles: a review. *Bull. Maryland Herpetol. Soc.* 18:37-142.
- _____. 1984. Frogs, egg teeth, and evolution: preliminary comments on egg teeth in the genus *Eleutherodactylus*. *Bull. Maryland Herpetol. Soc.* 20:1-11.
- _____. 1985. Frog mountain: preliminary comments on the genus *Eleutherodactylus* on the island of Guadeloupe, West Indies. *Bull. Maryland Herpetol. Soc.* 21:27-33.
- HARDY, J. D., JR., AND H. S. HARRIS. 1979. Occurrence of the West Indian frog, *Eleutherodactylus johnstonei*, in South America and on the island of Curaçao. *Bull. Maryland Herpetol. Soc.* 15:124-133.
- HEDGES, S. B. 1989. Evolution and biogeography of West Indian frogs of the genus *Eleutherodactylus*: slow-evolving loci and the major groups. Pp. 305-370. In: C. A. Woods (Ed.). *Biogeography of the West Indies: Past, Present, and Future*. Sandhill Crane Press, Gainesville, Florida.
- JOGLAR, R. L. 1986. Phylogenetic relationships of the West Indian frogs of the genus *Eleutherodactylus*. Ph.D. Thesis. Univ. of Kansas, Lawrence.

- _____. 1989. Phylogenetic relationships of the West Indian frogs of the genus *Eleutherodactylus*: a morphological analysis. Pp. 371-408. In: C.A. Woods (Ed.). Biogeography of the West Indies: Past, Present, and Future. Sandhill Crane Press, Gainesville, Florida.
- JOHNSON, T. H. 1988. Biodiversity and conservation in the Caribbean: profiles of selected islands. Int. Council Bird Preserv. Monogr. (1):1-144.
- KAISER, H. 1992. The trade-mediated introduction of *Eleutherodactylus martinicensis* (Anura: Leptodactylidae) on St. Barthélemy, French Antilles, and its implications for Lesser Antillean biogeography. J. Herpetol. 26:264-273.
- KAISER, H., J. D. HARDY, JR., AND D. M. GREEN. 1993. The taxonomic status of Caribbean and South American frogs currently ascribed to *Eleutherodactylus urichi* (Anura: Leptodactylidae). Copeia. In press.
- KURAMOTO, M. 1990. A list of chromosome numbers of anuran amphibians. Bull. Fukuoka Univ. Educ. 39:83-127.
- LESCURE, J. 1983. Introductions passives et actives des reptiles et d'amphibiens dans les Antilles et les Guyanes. C. R. Soc. Biogéogr. 59:59-70.
- _____. 1987. Le peuplement en reptiles et amphibiens des Petites Antilles. Bull. Soc. Zool. France 112:327-342.
- LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802-832.
- LYNCH, J. D. 1965. A new species of *Eleutherodactylus* from Guadeloupe, West Indies. Breviora (220):1-7.
- _____. 1966. The status of the tree frog, *Hyla barbudensis* Auffenberg, from Barbuda, British West Indies. Copeia 1966:524-530.

- _____. 1975. A review of the broad-headed eleutherodactyline frogs of South America (Leptodactylidae). *Occas. Pap. Mus. Nat. Hist. Univ. Kansas* (38):1-46.
- _____. 1976. The species groups of the South American frogs of the genus *Eleutherodactylus* (Leptodactylidae). *Occas. Pap. Univ. Kansas Mus. Nat. Hist.* (61):1-24.
- _____. 1979. The frogs of the genus *Eleutherodactylus* in the Andes of southern Ecuador. *Misc. Publ. Mus. Nat. Hist. Univ. Kansas* (66):1-62.
- _____. 1980. Two new species of earless frogs allied to *Eleutherodactylus surdus* (Leptodactylidae) from the Pacific slopes of the Ecuadorian Andes. *Proc. Biol. Soc. Wash.* 93:327-338.
- _____. 1986. The definition of the Middle American clade of *Eleutherodactylus* based on jaw musculature (Amphibia: Leptodactylidae). *Herpetologica* 42:248-258.
- _____. 1989. Intrageneric relationships of mainland *Eleutherodactylus* (Leptodactylidae). I. A review of the frogs assigned to the *Eleutherodactylus discoidalis* species group. *Milwaukee Publ. Mus. Contr. Biol. Geol.* (79):1-25.
- _____. 1993. The value of the *M. depressor mandibulae* in phylogenetic hypotheses for *Eleutherodactylus* and its allies (Amphibia: Leptodactylidae). *Herpetologica* 49:32-41.
- _____, and C. W. Myers. 1983. Frogs of the *fitzingeri* group of *Eleutherodactylus* in Eastern Panama and Chocoan South America (Leptodactylidae). *Bull. Am. Mus. Nat. Hist.* 175:481-572.

- MADDISON, W. P., AND D. R. MADDISON. 1992. MacClade: Analysis of Phylogeny and Character Evolution. Version 3.01. Sinauer Associates, Sunderland, Massachusetts.
- MIYAMOTO, M. M. 1983. Frogs of the *Eleutherodactylus rugulosus* group: a cladistic study of allozyme, morphological and karyological data. *Syst. Zool.* 32:109–124.
- _____. 1984. Central American frogs allied to *Eleutherodactylus cruentus*: allozyme and morphological data. *J. Herpetol.* 18:256–263.
- _____. 1986. Phylogenetic relationships and systematics of the *Eleutherodactylus fitzingeri* group (Anura, Leptodactylidae). *Copeia* 1986:503–511.
- MIYAMOTO, M. M., AND M. R. TENNANT. 1984. Phylogenetic relationships of the lower Central American rain frog *Eleutherodactylus melanostictus*. *Copeia* 1984:765–768.
- MURPHY, R. W., J. W. SITES, D. G. BUTH, AND C. H. HAUFLE. 1990. Proteins I: isozyme electrophoresis. Pp. 45–126. *In*: D. M. Hillis and C. Moritz (eds.). *Molecular Systematics*. Sinauer Associates, Sunderland, Massachusetts.
- NARINS, P. M., AND R. R. CAPRANICA. 1976. Sexual differences in the auditory system of the treefrog *Eleutherodactylus coqui*. *Science* 192:378–380.
- _____. 1978. Communicative significance of the two-note call of the treefrog *Eleutherodactylus coqui*. *J. Comp. Physiol. Part A* 127:1–9.
- NICOLSON, D. H. 1991. Flora of Dominica, part 2: Dicotyledoneae. *Smithson. Contr. Bot.* (77):1–274.
- NOMENCLATURE COMMITTEE OF THE INTERNATIONAL UNION OF BIOCHEMISTRY. 1984. *Enzyme Nomenclature 1984*. Academic Press, New York.

- NUSSBAUM, R. A. 1982. Heterotopic bones in the hindlimbs of frogs of the families Pipidae, Ranidae and Sooglossidae. *Herpetologica* 38:312-320.
- OTTE, D., AND J. A. ENDLER (EDS.). 1989. Speciation and Its Consequences. Sinauer Associates Inc., Sunderland, Massachusetts.
- PETERS, J. A. 1964. Dictionary of Herpetology. Hafner Publ. Co., New York.
- POINAR, G. O., AND D. C. CANNATELLA. 1987. An Upper Eocene frog from the Dominican Republic and its implication for Caribbean biogeography. *Science* 237:1215-1216.
- PREGILL, G.K., D.W. STEADMAN, S.L. OLSON, AND F.V. GRADY. 1988. Late Holocene fossil vertebrates from Burma Quarry, Antigua, Lesser Antilles. *Smithson. Contr. Zool.* (463):1-27.
- RIVERO, J. A. 1961. Salientia of Venezuela. *Bull. Mus. Comp. Zool.* 126:1-207.
- SAVAGE, J. M. 1975. Systematic and distribution of the Mexican and Central American stream frogs related to *Eleutherodactylus rugulosus*. *Copeia* 1975:254-306.
- _____. 1987. Systematics and distribution of the Mexican and Central American rainfrogs of the *Eleutherodactylus gollmeri* group (Amphibia: Leptodactylidae). *Fieldiana Zool., N. Ser.* 33:1-57.
- SCHWARTZ, A. 1967. Frogs of the genus *Eleutherodactylus* in the Lesser Antilles. *Stud. Fauna Curaçao Carib. Isl.* 24:1-62.
- _____. 1969. The Antillean *Eleutherodactylus* of the *auriculatus* group. *Stud. Fauna Curaçao Carib. Isl.* 30:99-115.
- _____, and R. THOMAS. 1975. A check-list of West Indian amphibians and reptiles. *Carnegie Mus. Nat. Hist. Spec. Publ.* 1:1-216.

- _____, 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.
- _____, and R.W. HENDERSON. 1985. *A Guide to the Identification of the Amphibians and Reptiles of the West Indies Exclusive of Hispaniola*. Milwaukee Public Museum, Milwaukee, Wisconsin.
- _____. 1991. *Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History*. University of Florida Press, Gainesville, Florida.
- SIMMONS, J. E. 1991. Conservation problems of fluid-preserved collections. Pp. 69-89. *In*: P. S. Cato and C. Jones (Eds.). *Natural History Museums: Directions for Growth*. Texas Tech University Press, Lubbock.
- STEADMAN, D.W., G.K. PREGILL, AND S.L. OLSON. 1984. Fossil vertebrates from Antigua, Lesser Antilles: evidence for Late Holocene human-caused extinctions in the West Indies. *Proc. Natl. Acad. Sci. USA* 81:4448-4451.
- SWOFFORD, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.1. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.
- TRUEB, L. 1993. Patterns of cranial diversity. Pp. 255-343. *In*: J. Hanken and B. K. Hall (Eds.). *The Skull*. Vol. 2. *Patterns of Structural and Systematic Diversity*. University of Chicago Press, Chicago.
- TRUEB, L., AND R. CLOUTIER. 1991. A phylogenetic investigation of the inter- and intrarelationships of the Lissamphibia (Amphibia: Temnospondyli). Pp. 223-313. *In*: H.-P. Schultze and L. Trueb (Eds.). *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*. Cornell Univ. Press, Ithaca, New York.

- WASSERSUG, R. J. 1976. A procedure for differential staining of cartilage and bone in whole formalin-fixed vertebrates. *Stain Technol.* 51(2):131-134.
- WELLS, K. D. 1981. Territorial behavior of the frog *Eleutherodactylus urichi* in Trinidad. *Copeia* 1981:726-728.

APPENDIX 1

Specimens examined

The following cleared and double-stained specimens of *Eleutherodactylus* were examined to determine osteological character states. Ten alcohol-preserved specimens of each species were examined to determine character states of external morphology. Unless otherwise noted, these are housed in the herpetological collection at KU. Specimens were picked randomly from a series; numbers were not recorded. Specimens marked with an asterisk (*) are alcoholic specimens from North American collections or from my own (with David M. Green [DMG] field tags).

Eleutherodactylus alticola.—JAMAICA: Portland Parish, Blue Mt. Peak, AMNH 55648, 55649-50*.

Eleutherodactylus amplinympha.—DOMINICA: Emerald Pool area, alt. ca. 400 m, DMG 3619-22*, 4598-99*; 500 m SE Layou Park Estate, alt. ca. 325 m, DMG 3726, 3831-32*, 4141-42*; Freshwater Lake area, alt. ca. 800 m, DMG 3590-92*, 4591*, 4596-97*; Slope of Morne Diablotin along access track, alt. ca. 1000 m, DMG 4037*, 4189*.

Eleutherodactylus antillensis.—VIRGIN ISLANDS: St. Thomas, AMNH A52646. Tortola, AMNH A 77502*. St. John, Catherineberg, alt. 640', AMNH A 109414*; 0.5 mi N, 0.2 mi E Lameshur, KU 45589. PUERTO RICO: Bayamon, AMNH A 10228*; Aibonito, AMNH A 10118*.

Eleutherodactylus auriculatus.—CUBA: Isla de Pinos, just W Nueva Gerona, E base Sierra de las Casas, AMNH A 63278*; Isla de Pinos, 11 mi. NE Siguanea, AMNH A 63279*; Oriente, Gran Piedra, La Esperancita, 3 kms SE, 16 km NE Sevilla, 1065 m, AMNH A 64343–45*, KU 203372, 203373–75*.

Eleutherodactylus barlagnei.—GUADELOUPE: Basse-Terre—Matouba, alt. 700m, MCZ 35334 (holotype)*; Chutes du Carbet, along path to lower falls, alt. ca. 700 m, DMG 3738*, 3896*; Sofaïa, Rivière Salée, end of road D19, alt. ca. 300 m, DMG 3650, 3745, 3818; La Soufrière, 400 m W La Citerne, along road D11, alt. ca. 1200 m, DMG 4038*, 4146–47*, 4155*, 4675; Matouba Hot Springs, alt. 1281 m, DMG 4195*.

Eleutherodactylus cochranae.—VIRGIN ISLANDS: St. Thomas, AMNH A 77499*, 77500, 77501*; St. John, Catherineberg, alt. 640', A 109417*; St. John, Bordeaux Mtn. Rd., AMNH A 109418*.

Eleutherodactylus coqui.—PUERTO RICO: 3–5 mi. S El Verde, AMNH 71998*, 71999, 72000, 72010–11*.

Eleutherodactylus eileenae.—CUBA: 2.9 km S Topes de Collantes, KU 203389, 203392.

Eleutherodactylus euphronides.—GRENADA: Parish of St. Andrew—Grand Etang, AMNH 74536–44, KU 93337–38, 265429–40, MCZ 2976, 43229 (holotype), UIMNH 61641–43; Cable and Wireless station near Mt. St. Catherine, ca. 4 km NW Paraclete, alt ca. 650 m, DMG 4149, 4199–4202*, 4701–05*, 4742–44*.

Eleutherodactylus fitzingeri.—PANAMÁ: Panamá Province—Tapia, Río Tapia, AMNH A 40680, 40681–82*; nr. Altos de Pacora, E Cerro Jefe, 700–800 m, KU 107149–49. COSTA RICA: Limon, nr. Tortuguera Village, AMNH A 81466*. San José, La Sisica, 15 km SW Isidro del General, alt. 865 m, AMNH A 86489*.

Eleutherodactylus johnstonei.—BARBUDA: Sunset View Hotel, sea level, DMG 3633, 3667–69*. GRENADA: Parish of St. George—St. Ann's Guest House, alt. ca. 60 m, DMG 2794–2802*, 2840–43*. MONTSERRAT: Parish of St. Anthony—End of Galways Soufriere road, DMG 3380–88*. ST. KITTS: St. Thomas Middle Island Parish—Romney Manor, 0.8 km N Old Road Town, DMG 3094–3105*. ST. LUCIA: Sans Soucis, Castries, DMG 2850–68. ST. VINCENT: Parish of St. George—Kingstown, Kingstown Park Guest House, DMG 2968–81.

Eleutherodactylus karlschmidtii.—PUERTO RICO: El Yunque, La Mina, 1550', KU 79212.

Eleutherodactylus klinikowskii.—CUBA: Pinar del Rio, Cueva de Santo Tomas, 10 km N Cabezas, KU 203403–04.

Eleutherodactylus leprus.—GUATEMALA: El Peténs, ca. 15 km NW Chinaja, alt. ca. 120 m, KU 55963.

Eleutherodactylus longipes.—MEXICO: Tamaulipas, Cueva de Infiernillo, KU 182345.

Eleutherodactylus martinicensis.—DOMINICA: Emerald Pool area, alt. ca. 400 m, DMG 4066*, 4683*; 500 m SE Layou Park Estate, alt. ca. 325 m, DMG 3744*; Freshwater Lake area, alt. ca. 800 m, DMG 4685*; Trafalgar Falls area, alt. ca. 330 m, DMG 3725*. GUADELOUPE: Basse-Terre—Chutes du Carbet, path to lower falls, alt. ca. 700 m, DMG 3651–52*, 3876–77*, 3902–03*. Grande-Terre—1.7 km S intersection of roads D109 and N5, alt. ca. 75 m, DMG 3512–13*, 3553*, 3660*. LA DÉSIDERADE: 450 m N Beauséjour post office, alt. ca. 100 m, DMG 3527–30*, 3626–27*. MARIE-GALANTE: Les Balisiers gully, 1.5 km S Ste. Croix, alt. 76 m, DMG 3603–05*; Le Trou à Diable, alt. ca. 100 m, DMG 3524–26*. MARTINIQUE: Morne Rouge, 600 m SE Mne. Pelée restaurant, along road D39, DMG 3634, 3826*; Deux Choux, 100 m N intersection of roads N3 and D1, DMG 3823–24*; Deux-Terres, intersection of roads D15 and N4, DMG 3648–49*, 3827*; 100 m below top of Mne. Bigot road, DMG 3645–47*, 3661–62*, 3828–30*.

Eleutherodactylus pinchoni.—GUADELOUPE: Basse-Terre—Chutes du Carbet, path to lower falls, alt. ca. 700 m, DMG 3892–95*, 3904–07*; La Soufrière, 400 m before La Citerne along road D11, alt. ca. 1200 m, DMG 4143–44*, 4151; 3 km W Grand Café, 600 ft, AMNH 74545–47*, MCZ 43231 (holotype)*, UIMNH 61647–50*.

Eleutherodactylus planirostris.—BAHAMAS: Great Abaco Island, Marsh Harbour, AMNH A 57619, A 57622–23*. CUBA: Las Villas, Soledad, AMNH A 61509–10*.

Eleutherodactylus richmondi.—PUERTO RICO: El Yunque peak, AMNH A 10230–31*, 10233.

Eleutherodactylus shrevei.—ST. VINCENT: Parish of St. Andrew—Lowrt [sic], 1000 ft, KU 265445–54, MCZ 43230 (holotype); Charlotte Parish—ca. 5.5 km W Orange Hill on La Soufrière summit track, alt. ca. 750 m, DMG 4604–07*, 4695–4700*, 4707, 4745*; Edge of Soufrière crater, alt. ca. 950 m, MCZ 19814–17*, UIMNH 61644–46*.

Eleutherodactylus terraebolivaris.—COLOMBIA: USNM 144737–38*. TOBAGO: 3 mi N Mt. St. George, KU 265455*; Main Ridge, ca. 7 km N Roxborough, DMG 3850, 4029–33*, 4543–46*, 4600–01*. VENEZUELA: Rancho Grande, MCZ 31062 (holotype)*, USNM 128212–14*, 167609–13*; Los Canales, USNM 128807–08*.

Eleutherodactylus unistrigatus.—COLOMBIA: Nariño—nr. end of Laguna de la Cocha, alt. 2850 m, AMNH A 86774; 7 km NE Guachual, alt. 3000 m, AMNH A 86779*. ECUADOR: Quito, Lago Cotoral, AMNH A 20442*, 20444–45*. Putamayo, Colon, alt. 2220 m, KU 168624.

Eleutherodactylus urichi.—TOBAGO: Main Ridge, ca. 7 km N Roxborough, DMG 4018*, 4542*, 4602*, 4684*; 4 mi NE Pembroke, KU 265456*. TRINIDAD:

N Arima Valley, DMG 4019–25*, 4026, 4027–28*, 4608–10*; Arima Ward, Aripo Road, 2 mi N intersection with Eastern Main Road, KU 265458*; St. Ann's Ward, Santa Cruz Valley, 7.5 mi N San Juan, KU 265457*.

Eleutherodactylus varleyi.—CUBA: Oriente—Gran Piedra, La Esperancita, 3 km SE and 16 km NE Sevilla, 1065 m, KU 203435; 3 km E Gran Piedra, KU 203438.

APPENDIX 2

Localities sampled for allozymes

Eleutherodactylus amplinympha.—DOMINICA: Emerald Pool area, alt. ca. 400 m ($n = 10$); 500 m SE Layou Park Estate, alt. ca. 325 m ($n = 8$); Freshwater Lake area, alt. ca. 800 m ($n = 15$); Trafalgar Falls area, alt. ca. 330 m ($n = 4$); Slope of Morne Diablotin along access track, alt. ca. 1000 m ($n = 1$).

Eleutherodactylus johnstonei.—ANTIGUA: Parish of St. Mary—End of road in Christian Valley, alt. 35 m ($n = 2$); Parish of St. Philip—Gaynor's Mill, sea level ($n = 3$). BARBADOS: Parish of St. James—Garden of Bellairs Research Institute, sea level ($n = 4$); Parish of St. Andrew—Turner's Hall Woods, at end of St. Simon road, alt. ca. 50 m ($n = 3$); Parish of St. John—Road to Consett Bay, 1/8 mi. from beach, sea level ($n = 1$); Parish of St. Michael—Bridgetown, parking lot of Grand Barbados Beach Hotel, sea level ($n = 3$). BARBUDA: Sunset View Hotel, sea level ($n = 4$). GRENADA: Parish of St. Patrick—2.4 km SW Sauteurs, alt. ca. 150 m ($n = 5$); Parish of St. David—Les Avocats waterworks, alt. ca. 400 m ($n = 1$); Parish of St. Andrew—Grand Etang Lake parking lot, alt. ca. 500 m ($n = 5$). GUYANA:

Georgetown, courtyard of Park Hotel, sea level ($n = 2$). MONTSERRAT: Parish of St. Anthony—End of Galways Soufriere road ($n = 19$); Parish of St. Peter—Soldier's Ghaut, Fogarty's ($n = 1$). NEVIS: St. George Gingerland Parish—Golden Rock Estate ($n = 2$); St. James Windward Parish—Nesbitt Plantation ($n = 2$). SABA: 1 km N The Gap ($n = 3$); 1 km N Windwardside beyond English Quarter ($n = 3$); Windwardside, beginning of Mt. Scenery steps ($n = 2$). ST. EUSTATIUS: The Quill ($n = 15$). ST. KITTS: St. Thomas Middle Island Parish—Romney Manor, 0.8 km N Old Road Town, ($n = 2$); St. Peter Basseterre Parish—Bayford's TV mast, 1 km N Ogee's ($n = 2$); St. John Capisterre Parish—St. George's Ghut, 0.5 km S Tabernacle ($n = 2$). ST. LUCIA: Sans Soucis, Castries ($n = 1$); 3 km N Gros Islet ($n = 1$). ST-MARTIN: Pic Paradis summit ($n = 6$); Terres Basses ($n = 6$). ST. VINCENT: Parish of St. George—Kingstown, Kingstown Park Guest House ($n = 2$); Parish of St. Andrew—Lowrey, 1.5 km NE Vermont ($n = 2$). VENEZUELA: Caracas, Sebuacán, Altamira ($n = 2$).

Eleutherodactylus martinicensis.—DOMINICA: Emerald Pool area, alt. ca. 400 m ($n = 2$); 500 m SE Layou Park Estate, alt. ca. 325 m ($n = 1$); Freshwater Lake area, alt. ca. 800 m ($n = 1$); Trafalgar Falls area, alt. ca. 330 m ($n = 1$). GUADELOUPE: Basse-Terre—Chutes du Carbet, path to lower falls, alt. ca. 700 m ($n = 4$); Rivière Moreau, ca. 7 km SW Douville, alt. ca. 300 m ($n = 2$); Rivière des Vieux Habitants, Maison du Café, 400 m before end of road D27, alt. ca. 150 m ($n = 2$); Rivière Petit David, 400 m SE Les Mamelles, along road D23, alt. ca. 700 m ($n = 1$); Sofaïa, Rivière Salée, end of road D19, alt. ca. 300 m ($n = 2$). Grande-Terre—1.7 km S intersection of roads D109 and N5, alt. ca. 75 m ($n = 2$). LA DÉSIDRADE: 450 m N Beauséjour post office, alt. ca. 100 m ($n = 5$). MARIE-GALANTE: Les Balisiers gully, 1.5 km S Ste. Croix, alt. 76 m ($n = 2$); Le Trou à Diable, alt. ca. 100

m ($n = 2$). MARTINIQUE: Morne Rouge, 600 m SE Mne. Pelée restaurant, along road D39 ($n = 1$); Deux Choux, 100 m N intersection of roads N3 and D1 ($n = 3$); Deux-Terres, intersection of roads D15 and N4 ($n = 1$); 100 m below top of Mne. Bigot road ($n = 6$); Fort-de-France, Vieux Fort Park ($n = 4$). ST-BARTHÉLEMY: St-Jean, Jean Bart Hotel ($n = 9$); Lorient, Hotel La Normandie ($n = 5$). TERRE-DE-HAUT: Terre-de-Haut village ($n = 2$).

APPENDIX 3

List of characters and character states

The following list contains the characters used in the phylogenetic study. Characters in each subsection are listed in anterior–posterior order and explanations are given only where clarification is required. Many of the characters used here are identical to those used by Joglar (1986) and/or Ford (1989) to facilitate comparisons, and detailed explanations of these characters (e.g., historical use, homology, variability) can be found there. Modification of characters used by these authors was required to deal with the specific taxa under investigation. Characters (C) used strictly as by Ford (1989) are identified by a C^F-designation (e.g., C^F1 is Ford's character 1), while those of Joglar (1986) have a C^J-designation. Characters that I modified from the original meaning or usage by these authors include the label "m" (e.g., mC^F3). Paired structures are treated in the singular unless both elements are compared or used in establishing the character. Character uncertainties, e.g. where variability could not be ascertained or where preservation may have altered a character, are identified by the superscripted letters V and P, respectively.

INTERNAL MORPHOLOGY

I. HEAD

A. DERMAL ROOFING BONES

1. Nasals, relative size (mC^J22).—In some *Eleutherodactylus*, the nasals are small, whereas in others they cover most of the anterior region of the skull roof. There are two discrete states visible without quantifying the character further than relative cover. 0 = nasals covering most or all of preorbital area; 1 = nasals covering less than half of preorbital area.
- 2^V. Nasals, medial contact (mC^F1, mC^J23).— 0 = extensive contact, more than half length of nasals; 1 = little contact, less than half the length of nasals; 2 = no contact.
3. Nasals, degree of contact with frontoparietals (mC^J24).—In some taxa, the nasals nearly overlap the frontoparietals when examined in dorsal view, whereas in others there is a wide separation between these bones. 0 = nasals overlapping frontoparietals or abutting them; 1 = bones widely separated.
4. Frontoparietals, shape (mC^F3).— 0 = rectangular; 1 = anterior of frontoparietals wider than posterior; 2 = posterior of frontoparietals wider than anterior.
5. Frontoparietal, anterolateral ala.—In some taxa, there is a lateral extension to the anterior portion of each frontoparietal. This

extension is not considered in determining the state of C4. 0 = absent; 1 = present.

- 6^v. Frontoparietal, fusion with elements of occiput (C^J25).— 0 = not fused; 1 = suture clearly evident; 2 = fused, no suture visible.

B. NEUROCRANIUM

7. Sphenethmoid, degree of ossification (mC^F7).— 0 = sphenethmoid divided middorsally and midventrally; 1 = sphenethmoid complete ventrally, divided middorsally; 2 = sphenethmoid complete both dorsally and ventrally; 3 = complete dorsally but divided midventrally.
8. Sphenethmoid, ossification of septum nasi.—In some species the sphenethmoid, whether complete or not, extends anteriorly beyond the level of the nasals when examined in dorsal view. 0 = septum nasi ossified anteriorly underneath nasals; 1 = septum nasi ossified only up to level of nasals.
9. Sphenethmoid, distance to optic foramen (mC^F8).— 0 = distance greater than anterior-posterior diameter of foramen; 1 = distance less than or equal to anterior-posterior diameter of foramen.

C. MAXILLARY ARCADE

10. Premaxilla, orientation of alary process (C^F12).— 0 = perpendicular to horizontal plane of skull as seen in lateral view; 1 = anteriorly inclined; 2 = posteriorly inclined.

11. Premaxilla, size of lateral process of the pars palatina (CF13, mCJ31).—This process is always present in the species studied, but to varying degrees. In some taxa, the process is shallow or thin, whereas in others it is wide and robust. 0 = process shallow or thin; 1 = process wide and robust.
12. Premaxilla, orientation of lateral process of the pars palatina (CJ32).—0 = process oriented posterolaterally; 1 = process oriented posteromedially.
13. Maxilla, depth of pars facialis (mCF15).—This character serves two functions in assessing features of the nasals as well as the maxilla. These features are individually difficult to compare or quantify. The pars facialis is expanded dorsally in all taxa studied, but to different degrees. All taxa have a preorbital process of the maxilla, and a maxillary process of the nasal. This character assesses how far the lateral shelf (pars maxillaris) of the nasal curves ventrally and how much of the area is uncovered. 0 = pars facialis of maxilla and pars maxillaris of nasal widely separated; 1 = pars facialis of maxilla and pars maxillaris of nasal almost touching, touching, or overlapping.
14. Maxilla, anterior “flange” of pars palatina (CF17).—0 = absent; 1 = present.
15. Maxilla, depth of pars palatina (CF18, mCJ34).—0 = pars palatina shallower than deepest portion of premaxillary pars palatina; 1 =

pars palatina as deep as or deeper than deepest portion of premaxillary pars palatina.

16. Maxilla, posterior extent of maxillary teeth.—Numbers of maxillary teeth vary within and between species, so that a dentition character based on numbers is inappropriate. However, the maxillary tooth row terminates either posteriorly to the anterior part of the maxillary-quadratojugal articulation, or it terminates anteriorly to it. 0 = maxillary teeth do not extend to quadratojugal articulation; 1 = maxillary teeth extend beyond quadratojugal articulation.
17. Maxilla-quadratojugal overlap (mCF22).—In the studied taxa there always was some overlap between maxilla and quadratojugal. A variable feature was the degree of overlap and the resulting free portion of the quadratojugal. 0 = free portion of quadratojugal less than half diameter of anterior-posterior diameter of subtemporal fenestra; 1 = free portion of quadratojugal equal to or greater than half diameter of anterior-posterior diameter of subtemporal fenestra.
18. Quadratojugal, dorsal enlargement (CF23).— 0 = dorsal enlargement of quadratojugal less than pars facialis of maxilla; 1 = dorsal enlargement of quadratojugal greater than or equal to pars facialis of maxilla.

D. SUSPENSORIUM

- 19^v. Pterygoid, anterior ramus (CF31).— 0 = anterior ramus of pterygoid straight; 1 = anterior ramus of pterygoid bowed laterally.

20. Pterygoid, medial ramus.—In some taxa, the medial ramus of the pterygoid narrows medially and is acuminate. In others, the end is expanded or of the same size as the origin of the ramus. 0 = end expanded or of the same size as origin of ramus; 1 = end of ramus not expanded, or acuminate.
21. Pterygoid, relation of anterior ramus to orbit (mCF32).—In none of the specimens examined does the anterior ramus of the pterygoid reach the planum antorbitale. However, there are two distinct groups of species, some in which the free portion of the anterior ramus extends far forward beyond the middle of the orbit, and others where that portion is shorter. 0 = free portion of anterior ramus of pterygoid reaches beyond middle of orbit; 1 = free portion of anterior ramus of pterygoid terminates at or before middle of orbit.
22. Pterygoid, overlap with parasphenoid (mCF43).— 0 = pterygoid in contact with lateral alae of parasphenoid; 1 = pterygoid not in contact with lateral alae of parasphenoid.
23. Squamosal, orientation in relation to skull roof (CF24).— 0 = zygomatic/otic rami crossbar tilted anteroventrally; 1 = zygomatic/otic rami crossbar parallel skull roof.
- 24^v. Squamosal, lateral profile of ventral ramus (CF25).— 0 = ventral ramus straight; 1 = ventral ramus curved.
25. Squamosal, otic ramus (mCF28, mCJ30).— 0 = otic ramus absent; 1 = otic ramus robust; 2 = otic ramus slender.

26. Squamosal, elongation of zygomatic ramus (mC^F30, mC^J28).— 0 = zygomatic ramus longer than otic ramus; 1 = zygomatic ramus shorter than or equal to otic ramus.
27. Squamosal, structure of zygomatic ramus in lateral view (mC^J29).— 0 = zygomatic ramus slender and pointed; 1 = zygomatic ramus robust and expanded.
28. *M. depressor mandibulae*, condition.—This character was studied in detail by Lynch (1993), who questioned its systematic value for the genus *Eleutherodactylus* and its subgenera. It is included here because Lynch (1993) studied only four West Indian taxa of the subgenus *Eleutherodactylus*, one from the subgenus *Euhyas*, and one from the subgenus *Syrrhophus*, all of which have the dfsq*at condition.— 0 = dfsq; 1 = dfsq*at.

E. PALATE

29. Choana, size relative to dentigerous process of vomer.—The dentigerous process (= prevomer of some authors) sits postero-ventrally on the vomer. It is composed of a raised stalk or platform which bears a flattened plate of varying shapes and, sometimes, teeth. It may cover part or all of the posteromedial region of the vomer. This structure has also been termed “vomerine odontophore,” but that term is preoccupied by a feature of the molluscan radula (Barnhardt and Barnhardt, 1983). The measurement used for comparison is the lateral width of both dentigerous process and choana. In taxa where dentigerous processes are secondarily lost,

C34 and C36–40 are scored as “?”. 0 = choana larger than dentigerous process; 1 = choana same size as dentigerous process; 2 = choanae smaller than dentigerous process; 3 = dentigerous process lost secondarily.

- 30^V. Choana, shape.—Choanal dimensions are determined in part by presence and absence of pre- and postchoanal processes of the vomer; however, individual characteristics of these processes are difficult to assess, and the shape of the choana provides a relationship between them. 0 = round; 1 = oval; 2 = triangular.
31. Vomer, anterior process (C^F37).— 0 = anterior process absent; 1 = anterior process present.
32. Vomer, prechoanal process (C^F39).— 0 = prechoanal process absent; 1 = prechoanal process present.
33. Vomer, postchoanal process.—All taxa under investigation have the postchoanal process. The relative robustness of this process can be used to distinguish two discrete groups. 0 = postchoanal process slender; 1 = postchoanal process robust.
34. Vomers, medial separation.— 0 = less wide than greatest width of dentigerous processes; 1 = as wide or wider than greatest width of dentigerous processes.
35. Vomer, width at level of anterior margin of postchoanal process.— This characteristic is one way to assess the relative size (width) of the vomer. I prefer using this character to the more general character

"size of vomer" (as in C^J37) because it is compared with the size of the premaxilla, a structure reasonably uniform in size among studied taxa. 0 = width less wide than greatest lateral width of premaxilla; 1 = width as wide as or wider than greatest lateral width of premaxilla.

36. Vomer, dentigerous process (mC^F43, mC^J38–40).— 0 = dentigerous process absent; 1 = dentigerous process positioned medial to choana; 2 = dentigerous process extending laterally to or beyond medial margin of choana.
37. Vomer, shape of dentigerous process in ventral view (mC^J39+40).— 0 = triangular; 1 = arched or weakly arched; 2 = round; 3 = oval; 4 = shallowly hemispherical.
38. Vomer, orientation of dentigerous processes in ventral view.— Where no specific orientation is evident, as may be the case for rounded dentigerous processes, a "3" is scored. 0 = horizontal; 1 = anterolaterally to posteromedially inclined; 2 = anteromedially to posterolaterally inclined; 3 = no orientation.
39. Vomer, distribution of vomerine teeth on dentigerous processes.— The taxa under investigation usually have several large teeth, and often several minor toothlike projections. Considering prominent vomerine teeth only, some taxa have a row of single teeth positioned evenly at the posterior margin of the dentigerous process (see C42), whereas others have additional teeth in a second, more irregular

- row. Several taxa also have a few clumped teeth. 0 = one row of single teeth; 1 = more than a row of single teeth; 2 = teeth clumped.
40. Vomerine teeth, configuration of teeth (mCF44).— 0 = teeth follow posterior margin of dentigerous process; 1 = teeth reach posterior margin of dentigerous process but angle away anteriorly from margin; 2 = teeth clumped in posteromedial corner of dentigerous process.
41. Palatine-vomer relation.—In all taxa examined, a palatine bone is present. This bone has also been called “neopalatine” (Trueb, 1993) because the palatine is absent in Jurassic anurans (e.g., *Vieraella*). However, the use of “neopalatine” is based on Trueb and Cloutier’s (1991) analysis of amphibian relationships and a parsimony argument. Given that the influence of development (e.g., delayed ossification) on taxa known only as fossils is uncertain, I choose the least controversial nomenclature here (akin to the continued usage of the term “patella” in birds, mammals, and reptiles; R. L. Carroll, pers. comm.). A degree of overlap between palatine and the posterior margin of the vomer can be observed in some species, with the vomer overlaying the palatine when examined in ventral view. 0 = palatine and vomer separated; 1 = vomer overlaps palatine at least partially.
42. Palatine, curvature.—The palatine can be straight or curved depending on its relation to the orbit. 0 = palatine straight; 1 = palatine bent around anterior edge of orbit.

43. Palatine, shape of medial terminus.—In some species, the palatine is more prominent than in others, and its width at the medial terminus varies accordingly. 0 = pointed and narrow; 1 = not pointed, as wide as or wider than lateral portion.
44. Parasphenoid, shape of termini of lateral alae (mCF47).— 0 = pointed; 1 = rounded or dilated and rounded; 2 = sharply angled.
45. Parasphenoid, anterior end of cultriform process.—The cultriform process of some taxa is well rounded, whereas it may be distinctly sharp and pointed, or truncate, in others. 0 = round; 1 = pointed; 2 = truncate.
- 46^V. Parasphenoid, lateral borders of cultriform process (mCF45).— 0 = straight; 1 = convex.
47. Parasphenoid, length of cultriform process (mCF46).— 0 = cultriform process ends before or just extends to level of palatine; 1 = cultriform process extends beyond level of palatine.

F. MANDIBLE

- 48^V. Mentomeckelian bones, shape in dorsal view (mCF51+52).— 0 = straight; 1 = spindle-shaped.
- 49^V. Angulosplenic, posterior extension (CF53).— 0 = angulosplenic terminating at jaw articulation; 1 = angulosplenic extending beyond jaw articulation.

G. HYOLARYNGEAL APPARATUS

50. Hyoid plate, shape.—Several taxa have straight lateral edges parallel to one another, whereas many have edges which are laterally concave. 0 = lateral edges concave; 1 = lateral edges parallel.
51. Hyoid plate, alary (anterolateral) process of hyoid plate (CF58, CJ44).— 0 = absent; 1 = present.
52. Hyoid plate, hyolaryngeal sinus (CF57).—In some taxa, the broad invagination which invades the hyoid plate (the hyolaryngeal sinus) extends to or beyond the level of the alary process of the hyoid plate (deep); in others it never reaches that depth (shallow). This character is coded as “?” when the alary process is absent. 0 = deep; 1 = shallow.
53. Hyoid plate, mineralization.—The term “mineralization” is used here preferentially since I have no evidence for which type of mineralization is occurring. While in most taxa under investigation there is no evidence of mineralization of hyoid elements, several mineralize quite distinctively. For example, *Eleutherodactylus shrevei* has the posterior half of the hyoid plate mineralized, extending from the center of the plate to the posterior end, medial to the posterolateral processes of the hyoid plate (= posteromedial). Conversely, *E. klinikowskii* has a narrow mineralized strip at each lateral edge of the hyoid plate, extending from the area midway between the anterolateral and posterolateral processes of the hyoid plate (= lateral). 0 = none; 1 = lateral; 2 = posteromedial.

54. Larynx (C^F64 included).—Simple: small larynx (<< half of hyoid plate size); cricoid ring thin or incomplete with a thin esophageal process; flaps of arytenoid cartilage poorly developed without any processes. Complex: large larynx (> half of hyoid plate size); widened cricoid ring with one esophageal processes; flaps of arytenoid cartilage wide, expansive, with one or two processes. 0 = simple; 1 = complex.

II. BODY

A. AXIAL SKELETON

55. Vertebra II (axis), degree of expansion of lateral ends of transverse processes (mC^F68).— 0 = lateral greater than medial width; 1 = lateral equal to medial width.
56. Vertebra III, orientation of transverse processes (C^F69).— 0 = lateral; 1 = posterolateral; 2 = anterolateral.
57. Vertebrae III–IV, lengths of transverse processes (C^F70).— 0 = V3 longest; 1 = processes of same length; 2 = Vertebra IV longest.
58. Vertebrae V–VIII, length of transverse processes (mC^F71).— 0 = subequal to width of sacral diapophyses; 1 = greater than width of sacral diapophyses.
59. Vertebra VIII, orientation of transverse processes (mC^F74).— 0 = lateral; 1 = anterolateral.

- 60. Sacral diapophyses, dilation (mCF75).— 0 = dilated, slightly wider than medial end; 1 = not dilated, cylindrical or round.
- 61. Coccyx, anterior process on dorsal coccygeal ridge (mCF79).— 0 = expanded anteriorly; 1 = not expanded.

B. PECTORAL GIRDLE

- 62^v. Pectoral girdle, degree of mineralization.—In some taxa, cartilaginous elements of the pectoral girdle contain some degree of mineralization, while there is very little in others. 0 = most elements with mineralization; 1 = little mineralization.
- 63. Omosternum, condition (CF90).— 0 = cartilaginous or partially mineralized; 1 = with ossified, bifurcate style; 2 = with ossified nonbifurcate style.
- 64. Clavicle, shape (mCF84).— 0 = arched; 1 = not arched.
- 65. Clavicle, structure.—The degree of robustness of the clavicle is indicative of the degree of support the clavicle has to provide in strengthening the pectoral girdle. Whereas some taxa have relatively broad clavicles, others have thin ones. 0 = broadened laterally; 1 = thin throughout.
- 66. Coracoid, size (CF80).— 0 = lateral end of coracoid wider than medial end; 1 = medial and lateral end of coracoid equal in width; 2 = medial end of coracoid wider than lateral end width.

67. Coracoid, pectoral fenestra (CF82).— 0 = bordered medially by epicoracoid cartilage and coracoid; 1 = bordered medially by coracoid only.
68. Scapula, pars acromialis (CF97).— 0 = not expanded; 1 = expanded.
69. Sternum (CJ45).— 0 = bifurcated posteriorly; 1 = elongated rectangular; 2 = pendulum-shaped; 3 = anchor-shaped.

C. PELVIC GIRDLE

70. Ilium, dorsal crest.—The dorsal crest of the ilium reaches the sacral region in some specimens, whereas it terminates well before the sacrum in others. 0 = reaches area of articulation with sacrum; 1 = does not reach area of articulation with sacrum.

D. FORELIMBS

71. Terminal phalanges, shape (mCF117, mCJ44).—The assessment of the shape of the terminal phalange considers the end of Finger III only, in order to minimize problems which may be caused by variation within the same hand. There are taxa with straight distal transverse processes (T-shaped), with distally bifurcated (Y-shaped), and with rounded or knoblike ("simple") termini. 0 = T-shaped; 1 = Y-shaped; 2 = simple.
72. Prepollex, number of prepollical elements (CF112).— 0 = one element; 1 = two elements; 2 = three elements.

73. Prepollex, degree of ossification.—Aside from variation in number of prepollical elements, there are also varying degrees of ossification. 0 = prepollical elements cartilaginous; 1 = some proximal ossification of prepollical elements; 2 = complete ossification of prepollex.
74. Preaxial centrale, size in relation to postaxial centrale (CF106).— 0 = equal size; 1 = preaxial half the size of postaxial; 2 = preaxial one-third size of postaxial.
75. Distal Carpale II, fusion (CF110).— 0 = Distal Carpale II present as individual bone; 1 = Distal Carpale II fused.
76. Digital sesamoid elements (CF 113).— 0 = absent; 1 = present.
77. Metacarpals, length formula (CF114).—There is considerable variation in the relative lengths of metacarpal elements in the taxa studied. Elements are listed in decreasing size, with integers assigned to metacarpals from innermost to outermost digit. This character is less variable, but nevertheless of interest, in the metatarsals (C86). 0 = 3-2-4-1; 1 = 1-3-2-4; 2 = 3-1-2-4; 3 = 3-1-4-2; 4 = 3-2-1-4; 5 = 3-4-2-1.
78. Radioulnar-carpal joint, sesamoid elements.—Nussbaum (1982) investigated the presence or absence of sesamoid bones in the hind limbs. I have found variation in both fore- and hind limbs in the studied taxa, thus extending Nussbaum's definition to include both the manus and pes. 0 = absent; 1 = present.

79. Carpal sesamoid elements.— 0 = none; 1 = one; 2 = two.

E. HINDLIMB

80. Terminal phalanges, shape (C^J47).—Assessment as for C71 above.
0 = T-shaped; 1 = Y-shaped; 2 = simple.
81. Prehallux, number of prehallical elements (C^F122).— 0 = one element; 1 = two elements, no expansion of elements; 2 = two elements, with the proximal element expanded laterally.
82. Prehallux, degree of ossification.—Assessment as for C73 above.
0 = cartilaginous; 1 = proximal ossification; 2 = complete ossification.
83. Distal Tarsale II, fusion (C^F119).— 0 = Distal Tarsale II present as individual bone; 1 = Distal Tarsale II fused.
84. Tibiofibular-tarsal joint, sesamoid elements.—see comment under C78. 0 = absent; 1 = present.
85. Tarsal sesamoid elements.—see comment under C78. 0 = none; 1 = one; 2 = two; 3 = three.
86. Metatarsals, length formula (C^F124).—see comment under C77. 0 = 4-3-5-2-1; 1 = 4-5-3-2-1.

EXTERNAL MORPHOLOGY

I. HEAD

87. Snout, shape in dorsal view.— 0 = truncate (= trapezoid); 1 = rounded; 2 = acuminate.
88. Snout, shape in lateral view.—This assessment follows the examples and terms provided by Duellman (1970). 0 = truncate; 1 = round; 2 = sloping; 3 = acuminate; 4 = protruding.
89. Mouth, aspect.— 0 = terminal; 1 = subterminal.
90. Canthus rostralis, shape in dorsal view.— 0 = straight; 1 = concave; 2 = convex.
91. Canthus rostralis, distinctiveness.— 0 = sharp; 1 = rounded.
92. Loreal region, shape in frontal view.—Assessment of this character approximately follows the examples in Rivero (1961; Figs. 1w, y-z), taken just anterior to the orbit. 0 = straight; 1 = slightly angled ($90^\circ < x < 110^\circ$); 2 = oblique ($> 110^\circ$).
93. Tympanum, distinctiveness (mC^J1).— 0 = distinct; 1 = indistinct.
94. Tympanum, shape.— 0 = round; 1 = oval.
95. Supratympanic fold.— 0 = pronounced; 1 = weak; 2 = absent.
96. Cranial crests (C^J4).— 0 = absent; 1 = present.
97. Vocal slits (C^J5).— 0 = absent; 1 = present.

- 98. Vocal sacs.— 0 = absent; 1 = present.
- 99. Tongue, shape.— 0 = oval; 1 = rounded; 2 = triangular.
- 100. Tongue, shape of unattached tip.— 0 = round; 1 = notched.

II. BODY

- 101. Foot webbing.— 0 = absent; 1 = remnant; 2 = fully webbed.
- 102. Fingers I and II, relative lengths (mC^J6).— 0 = I > II; 1 = I = II; 2 = II > I.
- 103. Finger Disks III and IV, shape (mC^J7).— 0 = absent; 1 = round; 2 = oval to elliptical.
- 104. Finger Disks, size.— 0 = disks II, III and IV of same size; 1 = III and IV larger than I and II but less than twice their size; 2 = III and IV over twice as large as I and II.
- 105. Finger Disk I, size.— 0 = much wider than digit; 1 = barely wider than digit or reduced.
- 106. Toe Disks, size.— 0 = disks III and IV larger than inner disks; 1 = disks of about the same size.
- 107. Toe Disk V, size.— 0 = much wider than digit; 1 = barely wider or reduced.
- 108. Toe III, relative length.— 0 = III does not reach penultimate subarticular tubercle of IV; 1 = III reaches penultimate subarticular tubercle of IV.

109. Toe V, length.— 0 = V does not extend to distal subarticular tubercle of IV; 1 = V extends to distal subarticular tubercle of IV.
- 110^V. Toes IV and V, degree of fusion.— 0 = proximal subarticular tubercle of V on free part of digit or right at interdigital juncture; 1 = IV and V connected up to or beyond proximal subarticular tubercle of V.
111. Nuptial pads (C^J10).— 0 = absent; 1 = present.
- 112^V. Skin, consistency on dorsum (mC^J20).—Consistency of skin surface is a rather puzzling character. A great variety of descriptive terms have been used in the literature, and their use has been inconsistent. To make this a more reliable character, I assessed the skin areas between the back of the head and the sacral region on the dorsum, and between the pectoral and pelvic girdles on the venter. I consulted Peters (1964) in defining terms, with one exception: In disagreement with Peters (1964), I consider the term “tubercle” not in connection with non-glandular skin bumps (i.e., those of the hands and feet), but also in the context of any small raised prominence of glandular nature on the dorsal skin. It is thereby equivalent to the term “areola, -ae” for the venter. For the purposes of this study, I describe texture according to the following definitions: “smooth”—no visible tubercles, bumps, prominences, or glands on skin surface; “shagreen”—with varying numbers of tubercles, bumps, or prominences, spread over the entire surface,

referring to dorsal skin only; "areolate"—with varying numbers of areolae, referring to ventral skin and regions of the inner groin only. In achieving a more detailed assessment of skin texture, it is usually necessary to use one or more qualifiers in addition to the texture term. I allow the following qualifiers: "fine"—with many small tubercles/areolae; "weak"—with a mixture of few small and larger tubercles/areolae; "strong"—with a mixture of many small and larger tubercles/areolae; "coarse"—with many larger tubercles/areolae; "sparse"—with few large tubercles. 0 = smooth; 1 = finely shagreened; 2 = weakly shagreened; 3 = strongly shagreened; 4 = coarsely shagreened; 5 = sparsely shagreened.

113^V. Skin, consistency on venter (mC^J19).—Definitions are used as described in C112. 0 = smooth; 1 = finely areolate; 2 = weakly areolate; 3 = strongly areolate; 4 = coarsely areolate; 5 = sparsely areolate.

114. Dorsolateral folds or glandular ridges (mC^J18).— 0 = absent; 1 = present.

III. TUBERCULATION

115. Supraocular tubercles (C^J2).— 0 = absent; 1 = present.

116. Interorbital tubercles.— 0 = absent; 1 = present.

117. Post-tympanic tubercles.— 0 = absent; 1 = present.

118. Palmar tubercles.— 0 = single, round or oval; 1 = bifid; 2 = two separate tubercles.
119. Supernumerary palmar tubercles (C^J11).— 0 = absent; 1 = present.
- 120^P. Subarticular tubercles on hands, height (C^J9).—As defined by Savage (1987). 0 = low; 1 = raised.
- 121^V. Subarticular tubercles on hands, shape (C^J8).—As defined by Savage (1987). 0 = oval; 1 = round.
122. Inner thenar tubercle.— 0 = absent; 1 = present.
- 123^P. Hand, tubercles on lateral border.— 0 = absent; 1 = present.
- 124^P. Antebrachial tubercles.— 0 = absent; 1 = present.
- 125^P. Ulnar tubercles.— 0 = absent; 1 = present.
- 126^P. Elbow tubercles.— 0 = absent; 1 = present.
- 127^P. Knee tubercles.— 0 = absent; 1 = present.
- 128^P. Heel tubercles.—As defined by Savage (1987). 0 = absent; 1 = present.
129. Inner metatarsal tubercle.— 0 = round; 1 = oval.
130. Outer metatarsal tubercle.— 0 = round; 1 = elongate.
- 131^P. Supernumerary plantar tubercles (C^J16).— 0 = absent; 1 = present.

132^P. Subarticular tubercles on feet, height (C^J15).—As defined by Savage (1987). 0 = low; 1 = raised.

133^V. Subarticular tubercles on feet, shape (C^J14).—As defined by Savage (1987). 0 = oval; 1 = round.

IV. PATTERN

134^V. Dark eye mask.—As defined by Savage (1987). 0 = absent; 1 = present.

135. Supratympanic stripe.—0 = absent; 1 = present.

136^P. Throat pigmentation.—As defined by Lynch and Myers (1983) and Savage (1975). 0 = unpigmented or lightly mottled; 1 = mottled; 2 = uniformly darkened.

137^P. Pigmentation of dorsum.—As defined by Savage (1975). 0 = uniform or only very lightly mottled; 1 = dark mottling on a light background.

138^P. Pigmentation on posterior surface of thigh.—Modified from Lynch and Myers (1983) and Savage (1975). 0 = same as dorsal coloration; 1 = reticulated or spotted; 2 = uniformly pigmented, darker than dorsum; 3 = uniformly pigmented, lighter than dorsum.

139^P. Groin, pigmentation.—Modified from Savage (1975). 0 = uniform; 1 = spotted; 2 = mottled.

OTHER CHARACTERS

140. Vocalization (Fig. 4).—Call information for species I did not record myself were obtained from the literature; even phonetic call descriptions are useful to distinguish between phases and for presence and absence of clicks (= chirps of some authors). Calls with a rapid rise in frequency are considered unphasic if uninterrupted. Most of the species under study use some form of clicking in what have been considered antagonistic or territorial encounters (Narins and Capranica, 1976, 1978; Wells, 1981). Thus, clicks could be considered plesiomorphic by the principle of commonality. However, only very few species vocalize using both uni- or biphasic call components as well as clicks in their most frequently issued call (e.g., *Eleutherodactylus amplinympha*, *E. barlagnei*). The call of *E. shrevei* consists mainly of clicks, but occasional uniphaseic calls are given. In such a case, the most frequently heard type of vocalization is scored. 0 = clicks only; 1 = uniphaseic; 2 = biphasic; 3 = uni- or biphasic with clicks.
141. Egg tooth, shape.—Taken from Hardy (1984). 0 = non-bifurcate; 1 = bifurcate.
142. Chromosome number (2n).—Taken from Kuramoto (1990) or DeWeese (1976), unless determined by myself. 0 = 18; 1 = 22; 2 = 26; 3 = 28; 4 = 30; 5 = 32.

APPENDIX 4. Data matrix for 142 morphological characters of Caribbean *Eleutherodactylus*.

	5	1 0	1 5	2 0	2 5	3 0	3 5	4 0	4 5	5 0	5 5	6 0	6 5	7 0
amplinympa	00120	12010	11000	10011	11011	00121	10001	10000	11101	01100	10011	10020	11001	111?0
antillensis	00121	12011	00010	10001	01011	00121	01101	11100	11000	01100	10001	00100	10001	21101
barlagnei	00020	10110	10010	00011	10001	00100	01000	10122	00021	11010	100?1	00021	10001	01110
coqui	00121	11010	10011	10011	01001	00?20	11101	21100	00122	11110	10011	00101	10001	11101
euphronides	01120	13110	10010	00000	01012	00000	11011	10000	01111	10101	0?200	00100	11001	011?0
fitzingeri	00020	12012	01000	00000	00012	10012	11100	10000	00121	11111	10011	00101	10000	11100
johnstonei	00121	12010	11010	10011	11012	00110	11101	10100	10120	10110	10011	00000	10001	11101
martinicensis	01120	10011	11000	10011	11012	00121	11101	10000	11020	11110	10011	01100	10001	01100
pinchoni	00120	12012	10010	00011	01012	00110	11111	14100	00110	11110	10001	00111	11001	01111
shrevei	00121	12010	10010	00010	00011	00021	11001	10000	01121	11001	0?201	00100	10001	01100
terraebolivaris	02121	10011	11011	00010	00001	00101	11011	10102	00011	11101	0?011	00000	10010	111?0
urichi	01121	12012	10100	00011	01012	00102	11010	10122	01110	10111	0?011	00110	11001	011?0

APPENDIX 4. (cont.)

						1	1	1	1	1	1	1	1	1
	7	8	8	9	9	0	0	1	1	2	2	3	3	4
	5	0	5	0	5	0	5	0	5	0	5	0	5	0
amplinympa	10121	10111	20112	10001	01001	01101	02200	10110	01411	01111	10101	01110	10001	10003 ?3
antillensis	10121	14001	11111	10101	01001	01111	02210	10110	01301	01011	11101	10110	11101	00112 12
barlagnei	00221	04000	11102	12411	01011	01111	12221	10111	03401	01200	10111	11110	10101	10303 13
coqui	10121	04001	10112	10002	12001	01110	02220	00111	02401	01211	10101	11110	11101	00302 12
euphronides	00021	04000	20111	10100	01010	01101	01220	00111	01401	01111	10111	10110	11101	00300 ?5
fitzingeri	01221	02000	21113	00311	00010	0??11	20210	11100	00001	01101	11000	00110	01011	001?? 01
johnstonei	10221	04101	12112	10100	11001	01101	01200	10110	03401	01001	11101	10110	01001	00002 13
martinicensis	11121	04001	12112	11100	01001	01111	02200	10001	02401	01110	01101	10110	10001	00002 03
pinchoni	10021	04001	10112	11100	11011	01100	02101	10101	01401	01210	10011	01110	11101	00001 13
shrevei	00221	04000	22111	11100	11010	01101	01220	00101	01401	01111	10101	11110	11101	00300 ?5
terraebolivaris	00021	02000	20111	10100	01010	0??11	00220	00001	01401	01101	00001	11110	01011	00301 05
urichi	00221	00000	12111	11101	11101	01101	02211	00011	01401	01201	10101	01110	11101	00300 05

TABLE 1. Species of *Eleutherodactylus* in the Eastern Caribbean. All species have been considered members of the *E. auriculatus* section, *martinicensis* group, *martinicensis* series (Hedges, 1989; Schwartz, 1969).

Species	Distribution	References
<i>E. barlagnei</i> Lynch, 1965	Basse-Terre, Guadeloupe	Hardy, 1985; Schwartz, 1967
<i>E. euphronides</i> (Schwartz, 1967)	Grenada	Kaiser et al., 1993; Chapter 2
<i>E. johnstonei</i> Barbour, 1914	Bermuda, Curaçao, Jamaica, most Lesser Antilles, Panamá, Venezuela	Hardy and Harris, 1979; Kaiser, 1992; Chapter 1
<i>E. martinicensis</i> (Duméril and Bibron, 1841)	Dominica, Guadeloupe archipelago, Martinique, St-Barthélemy	Kaiser, 1992; Chapter 1
<i>E. pinchoni</i> Schwartz, 1967	Basse-Terre, Guadeloupe	Hardy, 1985
<i>E. shrevei</i> (Schwartz, 1967)	St. Vincent	Kaiser et al., 1993; Chapter 2
<i>E. terraebolivaris</i> Rivero, 1961	Tobago, northern South America	Hardy, 1982
<i>E. urichi</i> (Boettger, 1894)	Tobago, Trinidad	Hardy, 1982; Kaiser et al., 1993; Chapter 2

TABLE 2. Allozyme loci diagnostic for *Eleutherodactylus amplinympha*, *E. johnstonei*, and *E. martinicensis*, and electrophoretic conditions employed in their resolution.

Protein ^a	Enzyme Commission		Electrophoretic conditions ^c
	Locus ^a	Number ^b	
1. Dipeptidase (leucalanine)	PEP(LA)	3.4.13.11	1
2. Glyceraldehyde-3-phosphate Dehydrogenase	GAPDH	1.2.1.12	2
3. Glucose Dehydrogenase	GCDH	1.1.1.118	1
4. Glucose-6-phosphate isomerase	GPI	5.3.1.9	2
5. Isocitrate Dehydrogenase (2 loci)	IDH	1.1.1.42	1
6. L-Lactate Dehydrogenase (2 loci)	LDH	1.1.1.27	2
7. Malate Dehydrogenase (2 loci)	MDH	1.1.1.37	1
8. Mannose-6-phosphate Isomerase (2 loci)	MPI	5.3.1.8	1
9. Peptidase-B (L-leucylglycylglycine)	PEP (LGG)	3.4.11.4	1
10. Phosphogluconate Dehydrogenase	PGDH	1.1.1.44	1

^aNomenclature Committee of the International Union of Biochemistry (1984), modified according to Murphy et al. (1990).

^bNomenclature Committee of the International Union of Biochemistry (1984).

^c(1) Tris-citrate pH 8.0, 130 V, 4 h; (2) Amine citrate pH 6.1 (Clayton and Tretiak 1972), 75 mA, 4 h.

TABLE 3. Ranges and means (± 1 SD) of selected metric characters for three species of Lesser Antillean *Eleutherodactylus*. Differences between values in each column are statistically significant in pairwise independent samples t-tests at $P < 0.005$. The asterisk (*) indicates the only variable which showed no significance.

Species	<i>n</i>	SVL	HW	ED	EN	TD	IOD
<i>E. johnstonei</i>	523	14.5–34.0 20.5±3.1	4.8–13.4 8.0±1.3	1.0–4.2 2.6±0.4	1.3–3.7 2.2±0.4	0.4–1.8 1.0±0.2	1.2–4.0 2.3±0.5
<i>E. martinicensis</i>	144	17.9–38.8 23.2±5.5	6.2–17.9 9.4±2.5	1.7–5.3 3.1±0.8	2.0–4.8 2.7±0.7	0.6–2.0 1.1±0.3	1.4–5.9 2.8±0.9
<i>E. amplinympha</i>	53	15.9–49.7 27.1±9.0	6.8–21.8 11.4±4.0	1.8–6.3 3.6±1.0	1.2–6.5 3.2±1.2	0.4–2.3 1.3±0.4	1.6–7.6 3.5±1.3

Species	<i>n</i>	FEM	TIB	FOOT	HW/SVL	TIB/SVL*
<i>E. johnstonei</i>	523	5.7–12.7 8.2±1.2	6.2–14.0 9.0±1.3	7.7–20.4 12.5±1.8	0.234–0.435 0.389±0.020	0.311–0.579 0.443±0.034
<i>E. martinicensis</i>	144	3.5–18.2 9.6±2.5	3.4–18.2 10.9±2.7	4.6–26.1 14.8±3.9	0.342–0.461 0.402±0.026	0.372–0.563 0.469±0.040
<i>E. amplinympha</i>	53	4.9–21.0 11.4±3.6	7.8–22.1 12.8±3.9	7.0–33.6 18.1±6.0	0.383–0.464 0.418±0.018	0.415–0.555 0.477±0.030

TABLE 4. Allele frequencies at thirteen polymorphic allozyme loci of three species of Eastern Caribbean *Eleutherodactylus*. Loci are abbreviated as in Table 2. Alleles are designated based on anodal migration, i.e. allele *a* migrated the greatest distance towards the anode. Numbers in parentheses are total specimen numbers; not every locus was resolvable for every individual.

Locus	allele	<i>E. johnstonei</i> (110)	<i>E. martinicensis</i> (56)	<i>E. amplinympha</i> n. sp. (38)
GAPDH	<i>a</i>	0.136	0.750	—
	<i>b</i>	0.864	—	—
	<i>c</i>	—	0.250	1.000
GCDH	<i>a</i>	0.875	0.100	1.000
	<i>b</i>	0.125	0.900	—
GPI	<i>a</i>	0.026	—	—
	<i>b</i>	0.974	1.000	—
	<i>c</i>	—	—	1.000
IDH-1	<i>a</i>	—	0.174	—
	<i>b</i>	1.000	0.250	0.459
	<i>c</i>	—	0.576	0.541
LDH-1	<i>a</i>	—	0.073	1.000
	<i>b</i>	0.333	—	—
	<i>c</i>	0.560	—	—
	<i>d</i>	0.107	0.720	—
	<i>e</i>	—	0.280	—
LDH-2	<i>a</i>	0.064	0.125	—
	<i>b</i>	0.921	0.875	0.987
	<i>c</i>	0.015	—	0.013

TABLE 4. (cont.)

Locus	allele	<i>E. johnstonei</i>	<i>E. martinicensis</i>	<i>E. amplinympha</i> n. sp.
MDH-1	<i>a</i>	—	0.717	0.158
	<i>b</i>	1.000	0.283	0.842
MDH-2	<i>a</i>	1.000	1.000	0.632
	<i>b</i>	—	—	0.368
MPI-1	<i>a</i>	1.000	0.586	0.087
	<i>b</i>	—	0.414	0.913
MPI-2	<i>a</i>	—	0.174	0.583
	<i>b</i>	1.000	0.826	0.417
PEP (LA)	<i>a</i>	0.963	0.053	—
	<i>b</i>	0.037	0.894	0.250
	<i>c</i>	—	0.053	0.750
PEP (LGG)	<i>a</i>	—	—	0.100
	<i>b</i>	0.776	1.000	0.900
	<i>c</i>	0.224	—	—
PGDH	<i>a</i>	1.000	0.800	0.447
	<i>b</i>	—	0.200	0.553

FIGURE 1. Distribution of *Eleutherodactylus* in the Lesser Antilles. The distribution of *E. johnstonei* includes all shaded islands.

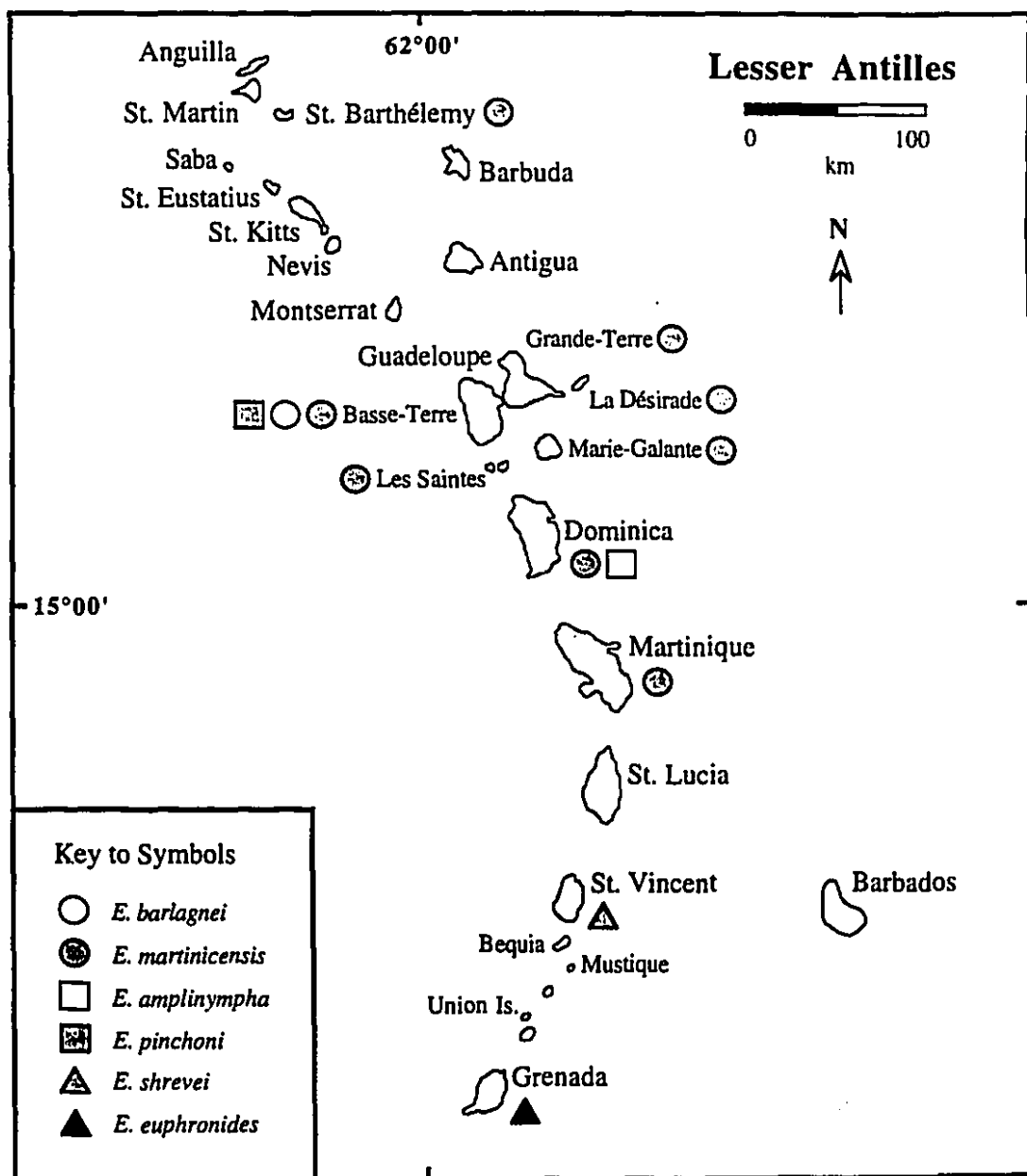


FIGURE 2. Female holotype of *Eleutherodactylus amplinympha* sp. nov., NMC [DMG 5019], 37.8 mm SVL.



FIGURE 3. Right hand and foot of *Eleutherodactylus amplinympha* sp. nov., NMC [DMG 5019]. Line = 5 mm.

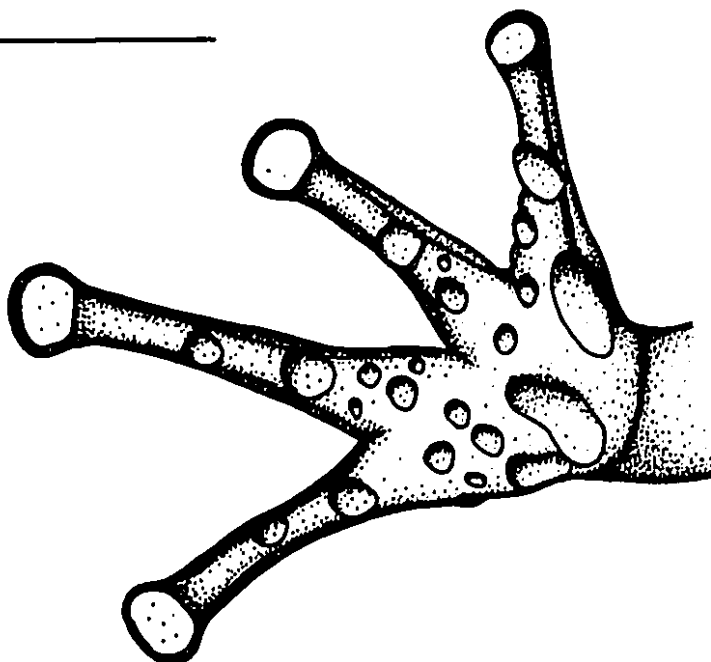
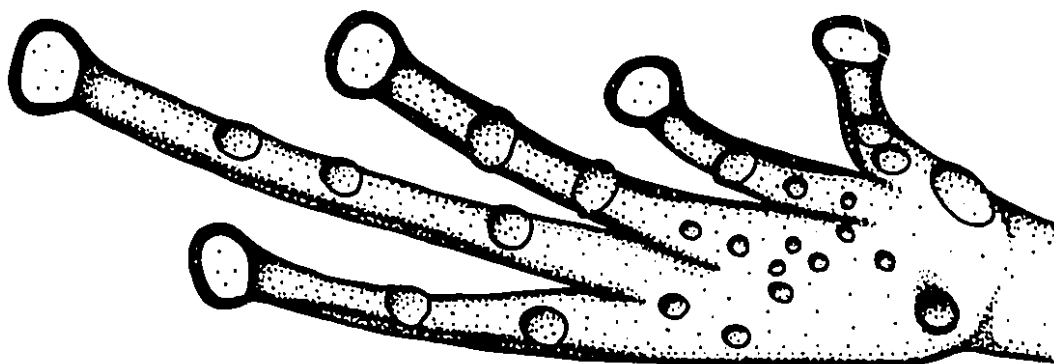
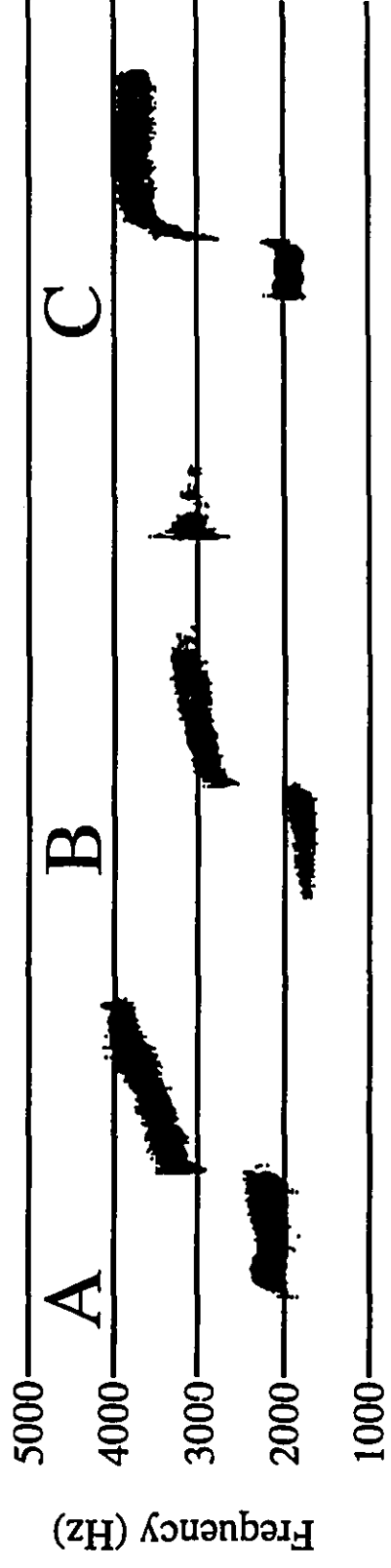


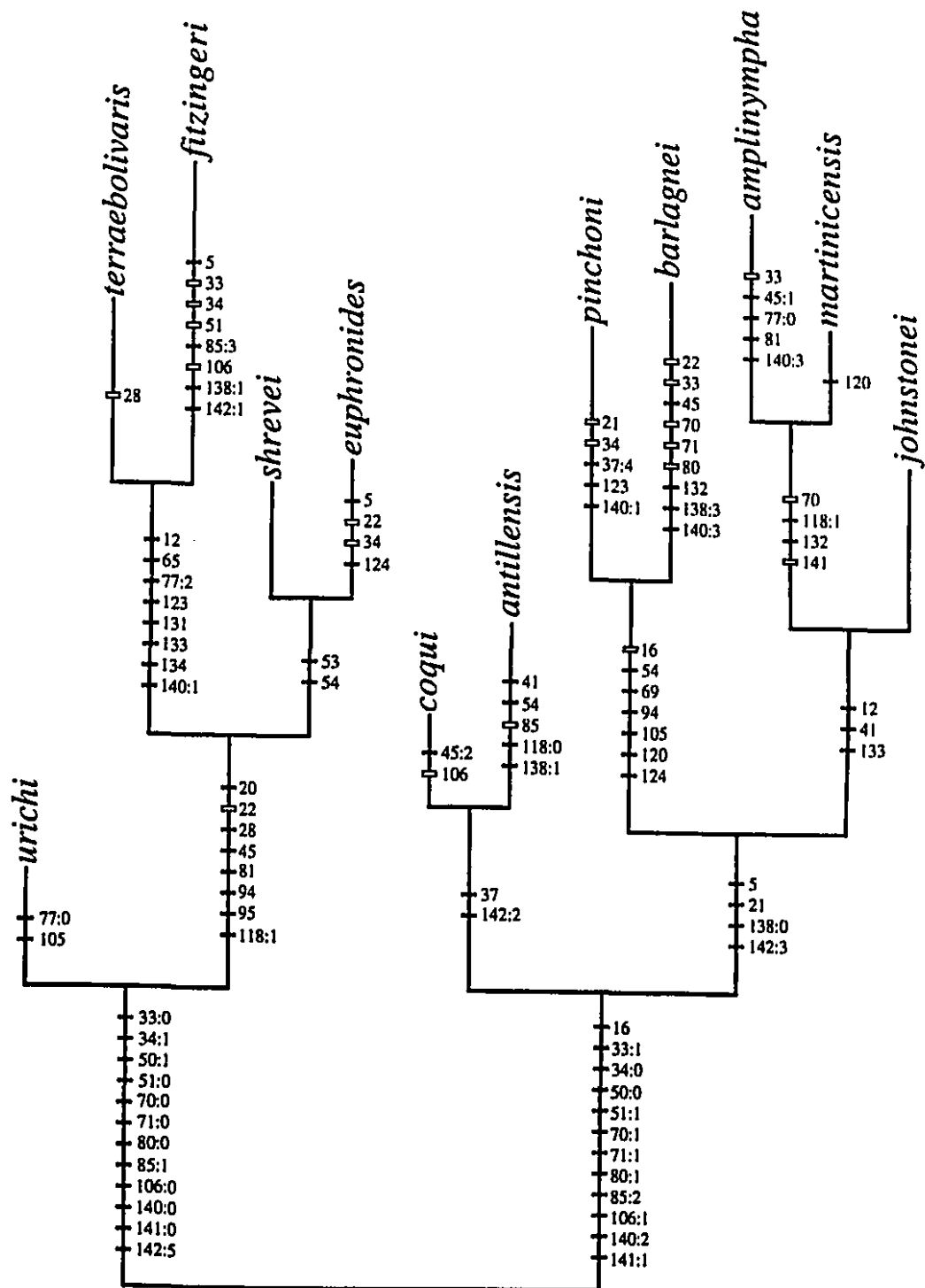
FIGURE 4. Advertisement calls of (A) *Eleutherodactylus martinicensis*, (B) *E. amplinympha* sp. nov., and (C) *E. johnstonei*. Scale bar = 0.2 s.



I

FIGURE 5. Phylogenetic trees from analyses of morphological characters of West Indian *Eleutherodactylus*. (A) Strict consensus tree from an analysis of 142 characters (310 steps, CI = 0.471). (B) Majority-rule consensus tree from an analysis excluding 28 problematic characters (Appendix 3; 243 steps, CI = 0.477). Shaded areas highlight the only topological differences between the two trees.

FIGURE 6. Phylogram from a cladistic analysis of West Indian *Eleutherodactylus* (316 steps, CI = 0.460). Branch lengths are proportional to the number of character state changes along each branch; not all changes have been mapped onto the tree. Black bars are apomorphies for species higher in the tree, open bars indicate reversals. Character states are indicated after a colon.



**Systematics and Biogeography of Eastern Caribbean Frogs of the Genus
Eleutherodactylus (Anura: Leptodactylidae): Evidence from Allozymes**

To be published as: Kaiser, H., T. F. Sharbel, and D. M. Green. Systematics and biogeography of Eastern Caribbean frogs of the genus *Eleutherodactylus* (Anura: Leptodactylidae): evidence from allozymes.

PREAMBLE CHAPTER 7

Given the difficulties in dealing with frogs of the genus *Eleutherodactylus* at the level of morphology, and given the clearer resolution of problems when allozyme data were added to an investigation (e.g., Chapters 1, 2, 6), a comprehensive analysis for all Eastern Caribbean *Eleutherodactylus* was the obvious conclusion to this study. This would not only provide additional evidence, but these data might provide even more conclusive in questions of biogeography.

ABSTRACT

Eastern Caribbean frogs, genus *Eleutherodactylus* assort into two distinct lineages. Species from northern islands (*E. amplinympha*, *E. barlagnei*, *E. johnstonei*, *E. martinicensis*, *E. pinchoni*) are a monophyletic group of Greater Antillean origin, whereas species from the southern islands (*E. euphronides*, *E. shrevei*, *E. urichi*) have South American affinities. Phenetic and cladistic analyses support sister-group relationships for *E. barlagnei* and *E. pinchoni*, and for *E. euphronides* and *E. shrevei*. *Eleutherodactylus amplinympha*, *E. martinicensis*, and *E. johnstonei* are each other's closest relatives, but further resolution within this clade is confounded by their great biochemical similarity. The dual origin of Eastern Caribbean *Eleutherodactylus* is due to "jump" dispersal, at least once from the Greater Antilles, and once from northern South America. The dispersal from South America was most plausibly made possible by the historic presence of a land bridge between Trinidad, Tobago, and the Paria Peninsula of northern South America, and by the annual rainy season discharge of the Orinoco River into the Caribbean Sea.

INTRODUCTION

The Eastern Caribbean is the distinctive biogeographical province composed of the Lesser Antillean island arc plus Trinidad and Tobago, two continental shelf islands (Fig. 1). The geological history of these islands is disparate: some islands are of volcanic origin, others were formed on a coralline base, and Trinidad and Tobago separated vicariantly from continental South America. Consequently, the geology and biogeography of the region as a whole is complex and has been the cause of some controversy (Liebherr, 1991; Perfit and Williams, 1989; Rosen, 1975; Roughgarden et

al., 1987; Savage, 1982; Williams, 1989). However, its great biogeographic importance as a potential conduit between the species-rich faunal assemblages of South America and the Greater Antilles is undisputed (e.g., Williams, 1989).

The Lesser Antillean island arc can be considered a series of "stepping stones" (MacArthur and Wilson, 1967; Williams, 1989) which may facilitate the dispersal of organisms between South America and the Greater Antilles. Although the biogeographic exchange between the South American or Greater Antillean faunas and the Eastern Caribbean has been the subject of a variety of studies concerning a variety of organisms, including junipers, butterflies, spiders, and bats (see papers in Woods, 1989), evidence from organisms with poor cross-water dispersal abilities is lacking. Thus an analysis of relationships between endemic anurans would be an important piece in the puzzle of how the Caribbean island fauna has achieved its present diversity.

The Caribbean-wide distribution of the genus *Eleutherodactylus* provides a unique opportunity to investigate the possibility of single or multiple origins for Eastern Caribbean anurans. At last count, 512 species were considered members of this genus (Duellman, 1993), making it the largest vertebrate genus. The relatively conservative *Eleutherodactylus*-morphotype (a small brownish frog) exhibits high karyological and biochemical variability (e.g., Bogart, 1991; Hedges, 1989a, b; Miyamoto, 1982, 1983, 1984, 1986; Smith et al., 1981). As a result of such conservatism on the one hand and diversity on the other, questions of phylogenetic relationships and origin for specific groups of these frogs have frequently been confounded.

The nine *Eleutherodactylus* in the Eastern Caribbean (Schwartz, 1967; Kaiser et al., 1993; Chapters 2, 6) form a small assemblage consisting largely of single-island endemics (Fig. 1). Systematic and biogeographic relationships of these taxa

have only been studied partially (e.g., Schwartz, 1967, 1969), and a complete evaluation has not been attempted using either morphological or biochemical means. Two competing hypotheses of relationships have emerged. Whereas Schwartz (1967) considered all Lesser Antillean *Eleutherodactylus* and the Trinidadian *E. urichi* members of the Greater Antilles-based *E. auriculatus* group based on external morphology, Lescure (1987) suggested a South American origin for all Eastern Caribbean *Eleutherodactylus*. Neither the species-group level phylogeny based largely on osteological characters presented by Joglar (1989) nor the study using six "slow-evolving" allozyme loci of West Indian taxa by Hedges (1989b) succeeded in resolving the relationships for the Eastern Caribbean species. However, this was mainly due to the exclusion of the key taxon *E. urichi* and because the Eastern Caribbean was only of peripheral interest to these authors.

In this study, I investigate the phylogenetic relationships of Eastern Caribbean *Eleutherodactylus* species using allozyme data. These data provide further evidence to test the hypothesis that the Eastern Caribbean is a mixed faunal assemblage, composed of South American and Greater Antillean elements, and that this dual dispersal scenario applies even to poor cross-water dispersers such as frogs.

MATERIALS AND METHODS

Specimens of *Eleutherodactylus* were obtained during multiple visits to the Eastern Caribbean (Appendix) and carried alive to the Redpath Museum, Montréal. Sample sizes of highly localized populations (e.g., Barbuda, Caracas, Guyana, St. Eustatius) were limited to fewer than 15 specimens in order to minimize disruption of presumably small populations. All procedures with animals, including captive care,

conformed to guidelines established by the Canadian Council on Animal Care (1980–84) and were approved by the Animal Care Committee of McGill University.

Animals were over-anaesthetized using a 1% solution of “MS-222” (3-Aminobenzoic Acid Ethyl Ester). Liver, kidney, heart, spleen, leg and abdominal muscle were removed and placed in 1.5 ml microfuge tubes. Specimens smaller than 20 mm were skinned and used in their entirety, with the exception of the small species *E. pinchoni* and *E. urichi*. Tissues were homogenized and centrifuged for 5 min at 15,000 rpm. The supernatant was pipetted off and frozen separately from the remaining tissue at -80°C. This was done to minimize loss of enzyme activity in original tissue samples due to repeated freezing and thawing before gel loading.

Horizontal starch gel electrophoresis (see Murphy et al., 1990) was used to resolve the allelic composition of 22 presumptive allozyme loci (Table 1) using standard lab setup and techniques. Gels and stains were adjusted to provide optimal resolution for *Eleutherodactylus* using protocols derived from Harris and Hopkinson (1972), Murphy et al. (1990), Pasteur et al. (1988), and Richardson et al. (1986). Loci and alleles were numbered from anode to cathode, designating the locus closest to the anode as locus-1, and the most anodal allele as allele a at each locus.

Allele frequencies (Table 2) were input into the computer program of Green (1979, 1984) to calculate Nei's (1978) genetic distances (D), adjusted for small sample sizes. The KITSCH program of J. Felsenstein's computer package PHYLIP was employed to create a Fitch-Margoliash tree (Fitch and Margoliash, 1967). Not all loci could be resolved for all individuals; genetic distance calculations were therefore made using the minimum sample size of each taxon for which all loci could be scored. A UPGMA phenogram (Sneath and Sokal, 1973) was constructed using Nei's D . These phenetic algorithms were useful in creating a working hypothesis of relationships and to identify functional outgroup taxa for cladistic analysis.

For phylogenetic purposes, coding of the data set generally followed the recommendations of Murphy (1993) in treating the locus as the character. All characters were treated as independent, with allelic arrays constituting character states. The data were assessed conservatively by scoring additions and using ordered states whenever possible. This was done to avoid potential problems with secondary types of evaluation (Murphy, 1993) such as non-redundant linear coding or character weighting. Character states were treated both as ordered (according to the suggestions of Green and Borkin [in press]) and unordered. Rare alleles (frequency < 0.050) were eliminated from the analysis.

Data for the phylogenetic analysis were coded using the preliminary results of the phenetic analysis as a working hypothesis. Thus, the appropriate outgroup to the Greater Antillean and northern Eastern Caribbean taxa was a southern Eastern Caribbean "supertaxon," a single operational taxonomic unit (OTU) created by combining the allelic information of *E. euphronides*, *E. shrevei*, *E. terraebolivaris* and *E. urichi*. Conversely, a single OTU composed of Greater Antillean taxa and northern Eastern Caribbean taxa was used to find relationships among the four southern Eastern Caribbean taxa. Phylogenetic analysis of the two resulting data matrices was accomplished using PAUP 3.1.1 (Swofford, 1993) with outgroup rooting and DELTRAN optimization. Choice of optimization is based on the assumption that parallelisms are more likely than reversals among biochemical characters. Since reading from electrophoretic gels allows only a minimal assessment of allelic variability in the first place, the evolution of a near-identical character state is more likely and more parsimonious than the exact reversal to an ancestral condition. This is especially true in the particular case of the highly polytypic genus *Eleutherodactylus*. Characters were coded as unordered or ordered depending on the availability of a consistent transformation series. Green and Borkin (1993)

recommended consideration of charge differences and the likelihood of charge changes when scoring alleles; thus, a single charge change (allele a to allele b) can be considered more likely than a double charge change (allele a to allele c). Although there is no empirical evidence to verify this assumption, it serves as a useful theory on which to base character ordering. Invariably, a second search was conducted using all characters as unordered; all searches were exhaustive. For each analysis, strict and majority rule consensus trees as well as phylograms were constructed to visualize topologies and relative branch lengths. Majority-rule consensus was also calculated for trees with lengths greater than the most parsimonious one(s) to investigate the stability of a given most parsimonious topology. Exploratory branch swapping after determination of the most parsimonious tree(s) was done using MacClade 3.01 (Maddison and Maddison, 1993). Both ordered and unordered data matrices were bootstrapped (1000 repetitions) to create a majority rule tree to test the robustness of the phylogeny with the heuristic algorithm of PAUP set to (1) closest stepwise addition; (2) zero-length branches not collapsed; and (3) steepest descent enabled.

RESULTS

Of the 22 loci resolved (Table 2), only GTDH was found to be monomorphic. For the polymorphic loci, a total of 100 alleles was found, with an average of 4.4 alleles per locus. Among genotypes present within each species, a heterozygote deficiency was noted, with total absence of heterozygous genotypes at 7 loci (AAT-2, CK-1, FUMH, G3PDH, IDDH, PEP[LA], PEP[LGG]). Only the heterozygosity value of the *Eleutherodactylus johnstonei* population on St. Eustatius (0.733, $n = 15$) at AAT-1 deviated non-significantly from equilibrium. Average heterozygosity

ranged from 0.060–0.260 in taxa with sample sizes > 1 ($\bar{x} = 0.135$, $n = 10$). Nei's D between the most distantly related groups was calculated to be > 0.902 .

Phenetic analysis.—The clusters in UPGMA and Fitch-Margoliash trees (Fig. 2) were identical, with the exception of the placement of *E. urichi*. In both cases, species from the Eastern Caribbean formed into northern and southern species groups. Among northern species, *E. barlagnei* and *E. pinchoni* formed one cluster, while *E. johnstonei*, *E. martinicensis*, and *E. amplinympha* formed a second. The southern group consisted of the closely related species *E. euphronides* and *E. shrevei*, with *E. terraebolivaris* outside of that group. In the UPGMA tree (Fig. 2A), *E. urichi* placed outside the cluster containing these three species, whereas it clustered outside all other species in the Fitch-Margoliash tree (Fig. 2B). The three Puerto Rican species were consistently grouped together, with *E. coqui* and *E. portoricensis* more similar. As a group, these species were more closely placed to the northern Eastern Caribbean species than to the southern ones. The Hispaniolan *E. probolaeus* was closest to the northern Eastern Caribbean group.

Cladistic analysis.—The analysis of Greater Antillean and northern Eastern Caribbean *Eleutherodactylus* using the southern Eastern Caribbean taxa as the outgroup, permitted ordering of seventeen characters (Table 3), with three constant characters. The analysis of ordered characters produced ten most parsimonious trees of length 49 steps with a consistency index (CI) of 0.653. A majority-rule consensus tree (Fig. 3A) shows that northern Eastern Caribbean *Eleutherodactylus* formed a monophyletic group that was supported in all trees. Puerto Rican, Hispaniolan, and northern Eastern Caribbean species formed an unresolved trichotomy. Within the ingroup, two clades were evident, one clade containing the sister taxa *E. barlagnei*

and *E. pinchoni*, the other the sister taxa *E. amplinympha* and *E. martinicensis* grouped with *E. johnstonei* (Fig. 3A). The topology of this tree was stable in the consensus of 110 trees with tree lengths up to one step greater than that of the most parsimonious tree. Values from bootstrapping (Fig. 3A) confirmed the monophyly of northern Eastern Caribbean taxa (74%), with sister group relationships supported as well.

The analysis using unordered characters also produced 10 most parsimonious trees (length 46 steps, CI = 0.696). The majority-rule consensus tree (Fig. 3B) supported the topology for the northern Eastern Caribbean species indicated in the analysis using ordered characters. Here, Puerto Rican taxa were more closely related to the northern Eastern Caribbean taxa than the Hispaniolan *E. probolaeus*. Within each of the two major clades, polytomies existed, one for the three Puerto Rican taxa, the other for *E. barlagnei*, *E. pinchoni* and the remaining northern Eastern Caribbean species. The triad of *E. amplinympha*, *E. johnstonei*, and *E. martinicensis* was again supported. The topology for northern Eastern Caribbean species was stable in consensus of 1696 trees with tree lengths up to three steps greater than that of the most parsimonious tree. As before, bootstrapping supported this arrangement (Fig. 3B).

Using the opposite outgroup arrangement, with northern Eastern Caribbean and Greater Antillean taxa forming the outgroup, ten characters could be ordered (Table 3), and ten characters were constant. The analysis of ordered characters produced a single most parsimonious and fully resolved tree with length 24 steps and CI = 0.833 (Fig. 3C). The arrangement supported a sister taxon relationship of *E. euphronides* and *E. shrevei*, with *E. urichi* as the sister taxon to that clade, and with *E. terraebolivaris* a sister taxon to the three other species. However, this topology was not robust either when taking into account consensus for trees with lengths greater

than that of the most parsimonious tree, or with results from bootstrapping (yielding a completely unresolved tree).

Reanalysis of this data matrix using unordered character states produced two most parsimonious trees (length 21 steps, CI = 0.952). The consensus tree (Fig. 3D) supports a close relationship of *E. euphronides*, *E. shrevei*, and *E. terraebolivaris*, although sister group relationships are unresolved. This trichotomy is also supported by values from the bootstrap analysis (Fig. 3D). *Eleutherodactylus urichi* is placed as the sister taxon to the other three species.

DISCUSSION

Systematics.—Phenetic and phylogenetic results show that Eastern Caribbean *Eleutherodactylus* do not form a monophyletic group, contrary to previous indications (Schwartz, 1967, 1969). Northern Eastern Caribbean species form a monophyletic group most closely related to Greater Antillean species (Fig. 2), while southern Eastern Caribbean species have a closer affinity to species in northern South America. The analyses are highly informative with respect to sister group relationships. Among northern species, sister group relationships are suggested for *E. barlagnei* and *E. pinchoni*, and for *E. amplinympha* and *E. martinicensis* (Figs. 3A, B). Both *E. barlagnei* and *E. pinchoni* are endemic to the Basse-Terre portion of Guadeloupe, where they are restricted to montane habitats.

The species triad of *E. amplinympha*, *E. johnstonei*, and *E. martinicensis* has historically been cause for misidentification and confusion. Fully grown females of each species are easily distinguished by size and coloration alone (Chapter 6). However, distinction between younger animals of both sexes, especially after preservation, is difficult. Although allozymes allow differentiation of these taxa more

readily than morphology, phenetic and cladistic analyses yield different topologies. The UPGMA tree (Fig. 2A), for example, groups *E. amplinympha* with *E. johnstonei*, whereas the cladistic analysis (e.g., Fig. 3A) groups *E. amplinympha* with *E. martinicensis*. It is difficult to say how much of differentiation or alignment can be attributed to convergence or ancestor-descendent relationships.

Among the southern species, the sister group relationship of *Eleutherodactylus euphronides* and *E. shrevei* is always supported, and their close relationship to *E. terraebolivaris* and *E. urichi* is evident. Although the placement of *E. urichi* is inconclusive in both phenetic and cladistic approaches, it is generally placed more closely to the southern species than the northern species. *Eleutherodactylus euphronides* and *E. shrevei* are not necessarily most closely related to *E. urichi*, of which they had previously been considered subspecies (Kaiser et al., in press b).

Although the support for the relationships of northern Eastern Caribbean species is strong, the exact affinities of the southern Eastern Caribbean taxa cannot be determined based on the present data. Although there is little doubt that *E. euphronides* and *E. shrevei* are sister taxa, the relationships of these taxa to *E. urichi* or *E. terraebolivaris* are not completely resolvable because ingroup taxa may be missing from the analysis. Until recently, *E. terraebolivaris* had consistently been placed in the Central and South American *E. fitzingeri* group (*sensu* Lynch, 1976, 1979) based on external morphology, despite its affinities with taxa close to *E. conspicillatus* (Rivero, 1961; Lynch, pers. comm.). My data indicate an affinity of *E. terraebolivaris* with *E. euphronides* and *E. shrevei*, but cannot support inclusion of the southern Eastern Caribbean species in any particular species group at this time. Given the complex relationships of South American members of this genus, it may be a long time until a complete list of taxa for a comprehensive study can be assembled.

Biogeography.—The hypotheses of relationships presented here allow for an assessment of the biogeographical history of anurans in the Eastern Caribbean region. Two clades, of South American and Greater Antillean origin, meet in the southern Lesser Antilles, making *Eleutherodactylus* the only truly circum-Caribbean frog genus. Given the relationships determined from allozyme data and the current knowledge of the morphology of the taxa involved, dispersal is the only biogeographic scenario that can satisfactorily explain the composition of the Eastern Caribbean *Eleutherodactylus*-fauna. For many of the larger Caribbean islands, instances of dispersal have been documented, yet there is continuing controversy over exactly which species dispersed to which island, and from where. The situation can further be complicated by the effects of human-mitigated introductions (Kaiser, 1992; Chapter 1). One of the problems with assessing the effect of dispersal on faunal distributions is that there is not necessarily a preferred direction for transfer of animals or plants by random, natural or unnatural phenomena; it is usually impossible to determine if the resulting faunal shifts were due to single or multiple dispersals, and whether dispersal is ongoing at the time of an investigation. I here infer from my data a dispersal mechanism for the Eastern Caribbean taxa that is conservative and parsimonious, assuming minimal animal movement and single successful colonizations. These assumptions are to some extent falsified *a priori* because multiple introductions have occurred involving at least *E. martinicensis* and *E. johnstonei*, the latter a species of great adaptive potential (Pough et al., 1977) which has established healthy populations in some quite inhospitable environments (Kaiser, 1992; Chapter 1). However, since none of the other Eastern Caribbean species seems ecologically, physiologically, or behaviorally capable of such drastic adjustments, the assumptions retain their validity.

As the volcanic arc formed at the eastern edge of the Caribbean Plate during the Oligocene (Perfit and Williams, 1989), the "proto-Antilles" (sensu Savage, 1982) were still shifting position, sea levels were not constant, and volcanic activity was high. At some point, frogs ancestral to the present northern Eastern Caribbean taxa must have dispersed to the newly formed Lesser Antilles, either by direct "jump" dispersal (Myers and Giller, 1988:158), a mechanism that seems particularly appropriate for frogs, or via a series of "stepping stones" (MacArthur and Wilson, 1967; Williams, 1989). These types of cross-water dispersals (Darlington, 1957; Simpson, 1956; Williams, 1969) have occurred in recent times as well. For example, Barbour (1917) reported that pumice rafts in the Virgin Islands were used in the dispersal of small vertebrates. Subsequent dispersals to other islands, along with the shifts in environmental conditions and differential selective pressures likely led to the frog diversity observed today.

In the southern Eastern Caribbean, Trinidad and Tobago were at some point an integral part of the South American mainland, and there is geological continuity from the Paria Peninsula of Venezuela to Tobago (Hardy, 1982). Thus, Trinidad's anuran fauna is mainly composed of species shared with the South American mainland, *E. urichi* being one of few exceptions. *Eleutherodactylus terraebolivaris* is now absent from Trinidad, but present both in Tobago and Venezuela, while *E. urichi* exists on both Trinidad and Tobago. Although dispersal cannot be excluded as a means of establishing residence for either of these species, the historical presence of a land bridge to the South American mainland also allows a vicariant origin for their present distribution. The southern Lesser Antillean *E. euphronides* and *E. shrevei* are most likely descendants of an ancestor which arrived in the southern Lesser Antilles from South America via rafting dispersal. The coastlines of Trinidad and Tobago annually get inundated with outflow from one of South America's great rivers, the

Orinoco (Gade, 1961). The Atlantic currents curve around the northeastern part of South America and into the Caribbean Sea, picking up some of the Orinoco outflow. In addition, prevailing winds in this area blow southeast to northwest, along the coast of the Guianas towards the Caribbean Sea. The combined effect of current and wind may occasionally reach the southern Lesser Antilles. Rafting on part of the Orinoco flotsam may provide an especially good opportunity for survival, considering that animals are not transported alone, but a good portion of their biota may travel with them, a "microvicariant event" (Perfit and Williams, 1989).

The data from the preceding analysis clearly support the hypothesis that faunal interchange from South America and the Greater Antilles to the Eastern Caribbean has occurred for frogs of the genus *Eleutherodactylus*, and it can be inferred from other sources that this interchange is ongoing. This assessment compares favorably with hypotheses developed for some organisms that disperse with relative ease (e.g., bats, butterflies, spiders; see papers in Woods, 1989), but more significantly with recent information available for the freshwater fish fauna (Burgess and Franz, 1989). There is thus a consensus between the data for frogs and freshwater fish which indicates that dispersal is an important mechanism for colonization of Eastern Caribbean islands by organisms that are poor cross-water dispersers. From a zoological viewpoint, the Eastern Caribbean is host to a mosaic biota, characterized by elements from South America, the Greater Antilles, and by a high degree of endemism.

ACKNOWLEDGMENTS

This study would have been impossible without the competent field assistance of C. A. George, H. M. Gray, G. Schäfer, H. H. Schwarten, T. F. Sharbel, D. von Stösser, and A. Werres. S. B. Hedges generously provided samples of Puerto Rican taxa. Thanks to J. P. Bogart for safely transporting the frozen tissues to Montréal. I benefitted from discussions with D. M. Green, L. A. Lowcock and T. F. Sharbel throughout the preparation of this study. This study was supported by grants from the Studienstiftung des Deutschen Volkes and the Hans-Krüger-Stiftung, Germany, and by an NSERC Canada operating grant to D. M. Green.

LITERATURE CITED

- BARBOUR, T. 1917. Notes on the herpetology of the Virgin Islands. *Proc. Biol. Soc. Wash.* 30:97–104.
- BOGART, J. P. 1991. The influence of life history on karyotypic evolution in frogs. Pp. 233–258. *In*: D. M. Green and S. K. Sessions (Eds.). *Amphibian Cytogenetics and Evolution*. Academic Press, New York.
- BURGESS, G. H., AND R. FRANZ. 1989. Zoogeography of the Antillean freshwater fish fauna. Pp. 263–304. *In*: C. A. Woods (Ed.). *Biogeography of the West Indies: Past, Present, and Future*. Sandhill Crane Press, Gainesville, Florida.
- CANADIAN COUNCIL ON ANIMAL CARE. 1980–84. *Guide to the Use and Care of Experimental Animals*. 2 Vols. CCAC, Ottawa.
- CLAYTON, J. W., AND D. N. TRETIK. 1972. Amine citrate buffers for pH control in starch gel electrophoresis. *J. Fish. Res. Board Canada* 29:1169–1172.

- DARLINGTON, P. J. 1957. Zoogeography: The Geographical Distribution of Animals. John Wiley and Sons, New York.
- DUELLMAN, W. E. 1993. Amphibian species of the world: additions and corrections. Univ. Kansas Mus. Nat. Hist. Spec. Publ. (21):1-372.
- FITCH, W. M., AND E. MARGOLIASH. 1967. The construction of phylogenetic trees. Science 155:279-284.
- GADE, H. G. 1961. On some oceanographic observations in the southeastern Caribbean Sea and the adjacent Atlantic Ocean with special reference to the influence of the Orinoco River. Bol. Inst. Oceanogr. Univ. Oriente (Venez.) 1:287-342.
- GREEN, D. M. 1979. A BASIC computer program for calculating indices of genetic distance and similarity. J. Hered. 70:429-430.
- _____. 1984. Calculation of indices of genetic distance and similarity: unbiased estimation corrected for sample size in BASIC computer program. J. Hered. 75:415.
- GREEN, D. M., AND L. J. BORKIN. 1993. Evolutionary relationships of Eastern Palearctic brown frogs, genus *Rana*: paraphyly of the 24-chromosome species group and the significance of chromosome number change. Zool. J. Linn. Soc. *In press*.
- HARRIS, H., AND D. A. HOPKINSON. 1972. Handbook of Enzyme Electrophoresis in Human Genetics. North-Holland Publ., Amsterdam.
- HEDGES, S. B. 1989a. An island radiation: allozyme evolution in Jamaican frogs of the genus *Eleutherodactylus* (Leptodactylidae). Carib. J. Sci. 25:123-147.
- _____. 1989b. Evolution and biogeography of West Indian frogs of the genus *Eleutherodactylus*: slow-evolving loci and the major groups. Pp. 305-370.

- In: C. A. Woods (Ed.). Biogeography of the West Indies: Past, Present, and Future. Sandhill Crane Press, Gainesville, Florida.*
- JOGLAR, R. L. 1989. Phylogenetic relationships of the West Indian frogs of the genus *Eleutherodactylus*: a morphological analysis. Pp. 371–408. *In: C. A. Woods (Ed.). Biogeography of the West Indies: Past, Present, and Future. Sandhill Crane Press, Gainesville, Florida.*
- KAISER, H. 1992. The trade-mediated introduction of *Eleutherodactylus martinicensis* (Anura: Leptodactylidae) on St. Barthélemy, French Antilles, and its implications for Lesser Antillean biogeography. *J. Herpetol.* 26:264–273.
- KAISER, H., J. D. HARDY, JR., AND D. M. GREEN. 1993. The taxonomic status of Caribbean and South American frogs currently ascribed to *Eleutherodactylus urichi* (Anura: Leptodactylidae). *Copeia. In press.*
- KENNY, J. S. 1980. Some recent animal colonizations. *Living World (J. Trinidad Field Nat. Club)* 1979-80:27.
- LESCURE, J. 1987. Le peuplement en reptiles et amphibiens des Petites Antilles. *Bull. Soc. Zool. France* 112:327–342.
- LIEBHERR, J. K. 1991. Biogeographic patterns of Antillean insects: the emerging picture of Antillean geohistory and faunal diversification. Pp. 409–411. *In: E. C. Dudley (Ed.). The Unity of Evolutionary Biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology. Discoroides Press, Portland, Oregon.*
- LYNCH, J. D. 1976. The species groups of the South American frogs of the genus *Eleutherodactylus* (Leptodactylidae). *Occas. Pap. Univ. Kansas Mus. Nat. Hist.* (61):1–24.

- _____. 1979. The amphibians of the lowland tropical forests. Pp. 189–215.
In: W. E. Duellman (Ed.). The South American Herpetofauna: Its Origin,
Evolution, and Dispersal. Mus. Nat. Hist. Univ. Kansas Monogr. (7).
- MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography.
Monogr. Pop. Biol. (1):1–203.
- MADDISON, W. P., AND D. R. MADDISON. 1992. MacClade: Analysis of Phylogeny
and Character Evolution. Version 3.01. Sinauer Associates, Sunderland,
Massachusetts.
- MIYAMOTO, M. M. 1982. Cladistic studies of Costa Rican frogs, genus
Eleutherodactylus: phylogenetic relationships based on multiple character
sets. Ph. D. Thesis, Univ. Southern California, Los Angeles.
- _____. 1983. Frogs of the *Eleutherodactylus rugulosus* group: a cladistic
study of allozyme, morphological and karyological data. Syst. Zool. 32:109–
124.
- _____. 1984. Central American frogs allied to *Eleutherodactylus cruentus*:
allozyme and morphological data. J. Herpetol. 18:256–263.
- _____. 1986. Phylogenetic relationships and systematics of the
Eleutherodactylus fitzingeri group (Anura, Leptodactylidae). Copeia
1986:503–511.
- MIYAMOTO, M. M., AND M. R. TENNANT. 1984. Phylogenetic relationships of the
lower Central American rain frog *Eleutherodactylus melanosticus*. Copeia
1984:765–768.
- MURPHY, R. W. 1993. The phylogenetic analysis of allozyme data: invalidity of
coding alleles by presence/absence and recommended procedures. Biochem.
Syst. Ecol. 21:25–38.

- MURPHY, R. W., J. W. SITES, D. G. BUTH, AND C. H. HAUFLE. 1990. Proteins I: isozyme electrophoresis. Pp. 45–126. *In*: D. M. Hillis and C. Moritz (Eds.). Molecular Systematics. Sinauer Associates, Sunderland, Massachusetts.
- MYERS, A. A., AND P. S. GILLER. Biological processes in biogeography. Introduction. Pp. 149–163. *In*: A. A. Myers and P. S. Giller (Eds.). Analytical Biogeography. Chapman and Hall, New York.
- NEI, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89:583–590.
- NOMENCLATURE COMMITTEE OF THE INTERNATIONAL UNION OF BIOCHEMISTRY. 1984. Enzyme Nomenclature 1984. Academic Press, New York.
- PASTEUR, N., G. PASTEUR, F. BONHOMME, J. CATALAN, AND J. BRITTON-DAVIDIAN. 1988. Practical Isozyme Genetics. Ellis Horwood Ltd., Chichester, U. K.
- PERFIT, M. R., AND E. E. WILLIAMS. 1989. Geological constraints and biological retrodictions in the evolution of the Caribbean Sea and its islands. Pp. 47–102. *In*: C. A. Woods (Ed.). Biogeography of the West Indies: Past, Present, and Future. Sandhill Crane Press, Gainesville, Florida.
- POUGH, F. H., M. M. STEWART, AND R. G. THOMAS. 1977. Physiological basis of habitat partitioning in Jamaican *Eleutherodactylus*. *Oecologia (Berl.)* 27:285–293.
- RICHARDSON, B. J., P. R. BAVERSTOCK, AND M. ADAMS. 1986. Allozyme Electrophoresis: A Handbook for Animal Systematics and Population Studies. Academic Press, San Diego, California.
- RIVERO, J. A. 1961. Salientia of Venezuela. *Bull. Mus. Comp. Zool.* 126:1–207.
- ROSEN, D. E. 1975 (1976). A vicariance model of Caribbean biogeography. *Syst. Zool.* 24:431–464.

- ROUGHGARDEN, J. S. D. GAINES, AND S. W. PACALA. 1987. Supply side ecology: the role of physical transport processes. Pp. 491–518. *In*: J. H. R. Gee and P. S. Giller (Eds.). *Organization of Communities Past and Present*. Blackwell Scientific Publishers, Boston.
- SAVAGE, J. M. 1982. The enigma of the Central American herpetofauna: dispersals or vicariance? *Ann. Miss. Bot. Garden* 69:464–457.
- SCHWARTZ, A. 1967. Frogs of the genus *Eleutherodactylus* in the Lesser Antilles. *Stud. Fauna Curaçao Carib. Isl.* 23: 1–62.
- _____. 1969. The Antillean *Eleutherodactylus* of the *auriculatus* group. *Stud. Fauna Curaçao Carib. Isl.* 30:99–115.
- SCHWARTZ, A., AND R. W. HENDERSON. 1991. *Amphibians and Reptiles of the West Indies: Description, Distribution and Natural History*. University of Florida Press, Gainesville, Florida.
- SIMPSON, G. G. 1956. Zoogeography of West Indian land mammals. *Am. Mus. Novitates* (1759):1–28.
- SMITH, M. H., D. O. STRANEY, AND G. E. DREWRY. 1981. Biochemical similarities among Puerto Rican *Eleutherodactylus*. *Copeia* 1981:463–466.
- SNEATH, P. H. A., AND R. R. SOKAL. 1973. *Numerical Taxonomy*. W. H. Freeman, San Francisco.
- SWOFFORD, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.1. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.
- WILLIAMS, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *Quart. Rev. Biol.* 44:345–389.

- _____. 1989. Old problems and new opportunities in West Indian biogeography. Pp. 1–46. *In*: C. A. Woods (Ed.). Biogeography of the West Indies: Past, Present, and Future. Sandhill Crane Press, Gainesville, Florida.
- WOODS, C. A. (ED.). 1989. Biogeography of the West Indies: Past, Present, and Future. Sandhill Crane Press, Gainesville, Florida.

APPENDIX

Specimens examined

All specimens listed under their respective species names (number in parentheses) were used in the electrophoretic study. All distances given are road distances.

Eleutherodactylus amplinympha (39).—DOMINICA: Emerald Pool area, alt. ca. 400 m, DMG 3570, 3587, 3615, 3621–22, 4598–99; 500 m SE Layou Park Estate, alt. ca. 325 m, DMG 3655, 3687, 3726, 3831–32, 4141, 4153; Freshwater Lake area, alt. ca. 800 m, DMG 3577, 3590–92, 4061–62, 4140, 4185–87, 4197–98, 4596–97, 4686; Trafalgar Falls area, alt. ca. 330 m, DMG 3614, 3657, 3688, 3746; Slope of Morne Diablotin along access track, alt. ca. 1000 m, DMG 4172, 4188–89.

Eleutherodactylus barlagnei (11).—GUADELOUPE: Basse-Terre—Chutes du Carbet, along path to lower falls, alt. ca. 700 m, DMG 4728; Rivière Petit David, 400 m SE les Mamelles, along road D23, alt. ca. 700 m, DMG 3576–77; Sofaïa, Rivière Salée, end of road D19, alt. ca. 300 m, DMG 3650; 1 km SW Desbonnes, along road D18, alt. ca. 300 m, DMG 3749, 3815; La Soufrière, 400 m W La Citerne, along road D11, alt. ca. 1200 m, DMG 4155; Matouba Hot Springs, alt. 1281 m, DMG 4195; Matouba, 1 km NE Centre Thermal, DMG 4595, 4673, 4729.

Eleutherodactylus euphronides (9).—GRENADA: Parish of St. Andrew—Cable and Wireless station near Mt. St. Catherine, ca. 4 km NW Paraclete, alt ca. 650 m, DMG 4150, 4200–02, 4688, 4704–05.

Eleutherodactylus johnstonei (110).—ANTIGUA: Parish of St. Mary—End of road in Christian Valley, alt. 35 m, DMG 3221, 3229–30, 3233. Parish of St. Philip—Gaynor's Mill, sea level, DMG 3217–20. BARBADOS: Parish of St. James—Garden of Bellairs Research Institute, sea level, DMG 2899, 2908, 3010, 3057. Parish of St. Andrew—Turner's Hall Woods, 0.6 km S St. Simon's, alt. ca. 50 m, DMG 2913, 2922, 2931. Parish of St. John—0.2 km W Consett Bay, sea level, DMG 2897. Parish of St. Michael—Bridgetown, Parking lot of Grand Barbados Beach Hotel, sea level, DMG 3004, 3009, 3015. BARBUDA: Codrington, yard of Nedd's Supermarket, sea level, DMG 3275; Sunset View Hotel, sea level, DMG 3593, 3624, 3667. GRENADA: Parish of St. Patrick—2.4 km SW Sauteurs, alt. ca. 150 m, DMG 2954–58. Parish of St. David—Les Avocats Waterworks, alt. ca. 400 m, DMG 2761. Parish of St. Andrew—Grand Etang Lake parking lot, alt. ca. 500 m, DMG 2803, 2814, 4191, 4203; 1.2 km W Nianganfoix Estate, alt. ca. 300 m, DMG 4063–64, 4160, 4183–84. GUYANA: Georgetown, courtyard of Park Hotel, sea level, DMG 3900–01. MONTSERRAT: Parish of St. Anthony—End of Galways Soufriere road, DMG 3350–59, 3380–88. Parish of St. Peter—Fogarty's, Soldier's Ghaut, DMG 3360. NEVIS: St. George Gingerland Parish—Golden Rock Estate, DMG 3126, 3131. St. James Windward Parish—Nesbitt Plantation, DMG 3190, 3194. SABA: 1 km N The Gap, DMG 3235, 3240, 3253; 1 km N Windwardside beyond English Quarter, DMG 3255–56, 3260–61; Windwardside, beginning of Mt. Scenery steps, DMG 3298, 3303. ST. EUSTATIUS: The Quill, DMG 3335–49. ST.

KITTS: St. Thomas Middle Island Parish—Romney Manor, 0.8 km N Old Road Town, DMG 3096, 3109. St. Peter Basseterre Parish—Bayford's TV mast, 1 km N Ogee's, DMG 3392, 3396. St. John Capisterre Parish—St. George's Ghut, 0.5 km S Tabernacle, DMG 3211, 3215. ST. LUCIA: Sans Soucis, Castries, DMG 2850; 3 km N Gros Islet (Le Sport Hotel), DMG 2988, 3060; ST-MARTIN: Pic Paradis summit, DMG 3090, 3093, 3305, 3312–13, 3317; Terres Basses, DMG 3319, 3322, 3324, 3326, 3332, 3334. ST. VINCENT: Parish of St. George—Kingstown, Kingstown Park Guest House, DMG 2974, 2976. Parish of St. Andrew—Lowrey, 1.5 km NE Vermont, DMG 2949, 2951. VENEZUELA: Caracas, Sebucán, Altamira, DMG 3870, 3873.

Eleutherodactylus martinicensis (63).—DOMINICA: Emerald Pool area, alt. ca. 400 m, DMG 4066, 4683; 500 m SE Layou Park Estate, alt. ca. 325 m, DMG 3744; Freshwater Lake area, alt. ca. 800 m, DMG 4685; Trafalgar Falls area, alt. ca. 330 m, DMG 3725. GUADELOUPE: Basse-Terre—Chutes du Carbet, path to lower falls, alt. ca. 700 m, DMG 3628–29, 3876, 3903; Rivière Moreau, ca. 7 km SW Douville, alt. ca. 300 m, DMG 3641, 3740; Rivière des Vieux Habitants, 1 km N Maison du Café, alt. ca. 150 m, DMG 3580, 3821; Rivière Petit David, 400 m SE Les Mamelles, along road D23, alt. ca. 700 m, DMG 3736; Sofaïa, Rivière Salée, end of road D19, alt. ca. 300 m, DMG 3586, 3693; Matouba, 1 km NE Centre Thermal, DMG 4594. Grande-Terre—1.7 km S Espérances, alt. ca. 75 m, DMG 3553, 3660. LA DÉSIDERADE: 450 m N Beauséjour post office, alt. ca. 100 m, DMG 3626–27, 3659, 3741, 3743. MARIE-GALANTE: Les Balisiers gully, 1.5 km S Ste. Croix, alt. 76 m, DMG 3605, 3607; Le Trou à Diable, alt. ca. 100 m, DMG 3625, 3658. MARTINIQUE: Morne Rouge, 600 m SE Montagne Pelée restaurant, along road D39, DMG 3634; Deux Choux, 100 m N intersection of roads N3 and D1, DMG

3692, 3728, 3823; Deux-Terres, intersection of roads D15 and N4, DMG 3690; 100 m below top of Montagne Bigot road, DMG 3602, 3612, 3647, 3662, 3739, 3828; Fort-de-France, Vieux Fort Park, DMG 3508, 3510, 3691, 3748. ST-BARTHÉLEMY: St-Jean, Jean Bart Hotel, DMG 3276–78, 3278, 3280–84; Anse aux Flamandes, DMG 3558–60; Lorient, Hotel La Normandie, DMG 3566–67, 3889–91. TERRE-DE-HAUT: Terre-de-Haut village, DMG 3555–56.

Eleutherodactylus pinchoni (23).—GUADELOUPE: Basse-Terre—Chutes du Carbet, path to lower falls, alt. ca. 700 m, DMG 3892–95, 3904–06; Rivière Petit David, 400 m SE les Mamelles, along road D23, alt. ca. 700 m, DMG 3597–98; La Soufrière, 400 m before La Citerne along road D11, alt. ca. 1200 m, DMG 4143, 4152, 4158, 4547, 4549, 4584, 4946–47, 5015, 5017–18; Grand-Étang, 500 m beyond Grande Chasse along road D4, alt. ca. 300 m, DMG 4205; Matouba, 1 km NE Centre Thermal, DMG 4634.

Eleutherodactylus shrevei (10).—ST. VINCENT: Charlotte Parish—ca. 5.5 km W Orange Hill on Soufrière volcano summit track, alt. ca. 750 m, DMG 4592–93, 4604, 4606–07, 4681, 4695–96, 4699, 4700.

Eleutherodactylus terraebolivaris (6).—TOBAGO: Main Ridge, ca. 7 km N Roxborough, DMG 4543, 4548, 4588, 4600–01, 4603.

Eleutherodactylus urichi (6).—TOBAGO: Main Ridge, ca. 7 km N Roxborough, DMG 4602. TRINIDAD: N Arima Valley, DMG 4019, 4541, 4608–10.

TABLE 1. Protein loci and electrophoretic conditions.

Protein ^a	Enzyme Commission		Electrophoretic conditions ^c
	Locus ^a	Number ^b	
1. Aspartate Aminotransferase (2 loci)	AAT	2.6.1.1	2
2. Creatine Kinase (2 loci)	CK	2.7.3.2	2
3. Dipeptidase (leucylalanine)	PEP (LA)	3.4.13.11	1
4. Fumarate Hydratase	FUMH	4.2.1.2	2
5. Glucose Dehydrogenase	GCDH	1.1.1.118	1
6. Glucose-6-phosphates Isomerase	GPI	5.3.1.9	2
7. Glutamate Dehydrogenase	GTDH	1.4.2.1	1
8. Glyceraldehyde-3-phosphate Dehydrogenase	GAPDH	1.2.1.12	2
9. Glycerol-3-phosphate Dehydrogenase	G3PDH	1.1.1.8	2
10. L-Iditol Dehydrogenase	IDDH	1.1.1.14	1
11. Isocitrate Dehydrogenase (2 loci)	IDH	1.1.1.42	1
12. L-Lactate Dehydrogenase (2 loci)	LDH	1.1.1.27	2
13. Malate Dehydrogenase (2 loci)	MDH	1.1.1.37	1
14. Mannose-6-phosphate Isomerase (2 loci)	MPI	5.3.1.8	1
15. Peptidase-B (L-leucylglycylglycine)	PEP (LGG)	3.4.11.4	1
16. Phosphogluconate Dehydrogenase	PGDH	1.1.1.44	1

^aNomenclature Committee of the International Union of Biochemistry (1984), modified according to Murphy et al. (1990).

^bNomenclature Committee of the International Union of Biochemistry (1984).

^c(1) Tris-citrate pH 8.0, 80 mA, 6 h; (2) Amine citrate pH 6.1 (Clayton and Tretiak, 1972), 65 mA, 6 h.

TABLE 2. Allozyme frequencies of selected West Indian *Eleutherodactylus* at 21 polymorphic loci. One locus (GTDH) was monomorphic. Sample sizes for each locus are given in italics. Abbreviations are ant (*E. antillensis*), coq (*E. coqui*), por (*E. portoricensis*), prob (*E. probolaeus*), ampl (*E. amplinympha*), bar (*E. barlagnei*), jhn (*E. johnstonei*), mart (*E. martinicensis*), pin (*E. pinchoni*), eup (*E. euphronides*), shr (*E. shrevei*), ter (*E. terraebolivaris*), uri (*E. urichi*).

Locus	Allele	Species ^a												
		Greater Antilles				northern Eastern Caribbean					southern Eastern Caribbean			
		ant	coq	por	prob	ampl	bar	jhn	mart	pin	eup	shr	ter	uri
AAT-1	a	—	—	—	1.000	—	—	—	—	—	—	—	—	—
	b	—	—	—	—	—	—	0.006	—	—	—	0.450	—	—
	c	—	—	1.000	—	—	—	—	—	—	1.000	0.550	1.000	0.916
	d	1.000	1.000	—	—	0.026	—	0.820	0.173	0.200	—	—	—	0.083
	e	—	—	—	—	0.974	1.000	0.174	0.827	0.800	—	—	—	—
	<i>n</i>	<i>1</i>	<i>4</i>	<i>1</i>	<i>1</i>	<i>39</i>	<i>9</i>	<i>89</i>	<i>49</i>	<i>15</i>	<i>10</i>	<i>10</i>	<i>6</i>	<i>6</i>
AAT-2	a	—	—	—	—	—	—	—	—	—	0.100	—	—	—
	b	1.000	—	—	—	—	—	—	—	—	—	—	—	—
	c	—	1.000	1.000	—	—	—	—	—	—	0.900	1.000	—	—
	d	—	—	—	—	—	—	—	—	—	—	—	—	1.000
	e	—	—	—	1.000	1.000	1.000	1.000	1.000	1.000	—	—	1.000	—
	<i>n</i>	<i>1</i>	<i>4</i>	<i>1</i>	<i>1</i>	<i>38</i>	<i>9</i>	<i>49</i>	<i>43</i>	<i>13</i>	<i>10</i>	<i>10</i>	<i>6</i>	<i>6</i>

Table 2 (cont.)

		ant	coq	por	prob	ampi	bar	jhn	mart	pin	eup	shr	ter	uri
CK-1	a	—	—	—	1.000	—	—	—	—	—	0.100	—	—	—
	b	—	—	—	—	—	—	—	—	—	—	1.000	—	—
	c	—	—	—	—	—	—	—	—	—	0.900	—	—	—
	d	—	—	—	—	—	—	—	—	—	—	—	1.000	1.000
	e	—	1.000	1.000	—	1.000	—	1.000	1.000	1.000	—	—	—	—
	f	1.000	—	—	—	—	1.000	—	—	—	—	—	—	—
	n	1	1	1	1	4	5	25	15	7	10	10	4	5
CK-2	a	—	—	—	—	—	—	—	—	—	0.050	—	—	—
	b	—	—	—	—	—	—	—	—	—	0.050	—	—	—
	c	—	—	—	—	—	—	—	—	—	0.100	—	—	—
	d	—	—	—	—	—	—	—	—	—	0.800	1.000	—	—
	e	—	—	—	—	—	—	—	—	—	—	—	1.000	1.000
	f	—	—	—	1.000	1.000	1.000	1.000	1.000	1.000	—	—	—	—
	g	—	1.000	1.000	—	—	—	—	—	—	—	—	—	—
	h	1.000	—	—	—	—	—	—	—	—	—	—	—	—
	n	1	1	1	1	4	5	3	5	7	10	10	4	5

Table 2 (cont.)

		ant	coq	por	prob	ampl	bar	jhn	mart	pin	eup	shr	ter	uri
FUMH	a	—	—	—	1.000	—	—	—	—	—	—	—	—	—
	b	1.000	1.000	—	—	1.000	1.000	1.000	1.000	1.000	—	—	—	—
	c	—	—	1.000	—	—	—	—	—	—	1.000	1.000	1.000	—
	d	—	—	—	—	—	—	—	—	—	—	—	—	1.000
	n	1	3	1	1	22	8	19	19	13	7	6	6	6
G3PDH	a	—	—	1.000	—	—	—	—	—	—	1.000	1.000	1.000	1.000
	b	1.000	1.000	—	—	—	—	—	—	—	—	—	—	—
	c	—	—	—	1.000	1.000	1.000	1.000	1.000	1.000	—	—	—	—
	n	1	3	1	1	39	8	20	25	13	7	10	6	6
GAPDH	a	—	—	—	—	—	—	0.136	0.750	—	—	—	—	1.000
	b	—	—	—	—	—	1.000	0.864	—	1.000	—	—	0.875	—
	c	1.000	1.000	1.000	1.000	1.000	—	—	0.250	—	1.000	1.000	0.125	—
	n	1	2	1	1	37	8	22	20	7	10	10	4	6
GCDH	a	1.000	—	—	1.000	1.000	0.250	0.875	0.100	0.769	0.167	—	—	1.000
	b	—	1.000	—	—	—	—	—	—	0.077	—	—	1.000	—
	c	—	—	—	—	—	0.750	0.125	0.900	0.154	0.833	1.000	—	—
	n	1	2		1	6	8	16	5	13	6	6	5	3

Table 2 (cont.)

		ant	coq	por	prob	ampl	bar	jhn	mart	pin	eup	shr	ter	uri
GPI	a	–	–	–	–	–	–	–	–	–	–	–	1.000	–
	b	–	–	–	–	–	–	0.026	–	–	–	–	–	1.000
	c	–	–	–	–	–	–	–	–	–	1.000	0.786	–	–
	d	1.000	1.000	–	1.000	–	–	0.974	1.000	–	–	–	–	–
	e	–	–	–	–	–	0.450	–	–	0.846	–	0.214	–	–
	f	–	–	1.000	–	1.000	–	–	–	–	–	–	–	–
	g	–	–	–	–	–	0.550	–	–	0.154	–	–	–	–
	n	1	3	1	1	43	8	19	25	13	7	7	4	6
IDDH	a	1.000	1.000	–	–	–	–	–	0.250	1.000	1.000	1.000	1.000	–
	b	–	–	–	1.000	0.500	–	0.722	0.500	–	–	–	–	1.000
	c	–	–	1.000	–	0.500	1.000	0.278	0.250	–	–	–	–	–
	n	1	2	1	1	2	2	18	4	1	2	3	2	2
IDH-1	a	–	1.000	1.000	1.000	–	–	–	0.174	–	–	–	–	–
	b	1.000	–	–	–	0.459	1.000	1.000	0.250	0.977	–	0.100	1.000	–
	c	–	–	–	–	0.541	–	–	0.576	0.023	0.250	0.550	–	–
	d	–	–	–	–	–	–	–	–	–	0.750	0.350	–	–
	e	–	–	–	–	–	–	–	–	–	–	–	–	1.000
	n	1	4	1	1	37	9	60	46	22	10	10	4	6

Table 2 (cont.)

		ant	coq	por	prob	ampl	bar	jhn	mart	pin	eup	shr	ter	uri
IDH-2	a	—	—	—	1.000	—	—	—	—	—	—	—	—	—
	b	1.000	1.000	1.000	—	0.310	1.000	0.370	0.238	1.000	1.000	1.000	1.000	—
	c	—	—	—	—	0.690	—	0.630	0.762	—	—	—	—	1.000
	n	1	4	1	1	21	9	73	42	22	10	10	6	6
LDH-1	a	—	—	—	—	—	—	—	—	—	—	—	—	0.333
	b	1.000	—	—	—	—	—	—	—	—	—	—	—	—
	c	—	1.000	1.000	1.000	1.000	—	—	0.073	—	—	—	—	—
	d	—	—	—	—	—	—	0.333	—	—	1.000	—	—	0.667
	e	—	—	—	—	—	—	0.560	—	0.071	—	—	—	—
	f	—	—	—	—	—	1.000	0.107	0.683	0.929	—	—	—	—
	g	—	—	—	—	—	—	—	—	—	—	1.000	—	—
	h	—	—	—	—	—	—	—	0.244	—	—	—	—	—
	i	—	—	—	—	—	—	—	—	—	—	—	1.000	—
	n	1	4	1	1	39	10	42	41	14	10	10	6	6
LDH-2	a	—	—	—	—	—	—	0.064	0.125	—	—	—	—	—
	b	1.000	1.000	1.000	1.000	0.987	1.000	0.921	0.875	1.000	1.000	1.000	1.000	1.000
	c	—	—	—	—	0.013	—	0.015	—	—	—	—	—	—
	n	1	4	1	1	39	11	101	56	19	10	10	6	6

Table 2 (cont.)

		ant	coq	por	prob	ampl	bar	jhn	mart	pin	eup	shr	ter	uri
MDH-1	a	—	—	—	—	0.158	—	—	0.717	—	0.200	0.100	—	—
	b	1.000	0.500	—	—	0.842	1.000	1.000	0.283	0.462	0.500	—	—	1.000
	c	—	—	—	1.000	—	—	—	—	0.538	—	—	0.600	—
	d	—	0.500	1.000	—	—	—	—	—	—	0.300	—	—	—
	e	—	—	—	—	—	—	—	—	—	—	0.900	0.400	—
	n	1	4	1	1	38	8	66	46	13	10	10	5	6
MDH-2	a	—	—	—	1.000	—	—	—	—	—	—	—	—	—
	b	—	—	—	—	0.632	0.600	1.000	1.000	0.583	1.000	0.900	—	—
	c	1.000	1.000	—	—	—	0.400	—	—	0.417	—	0.100	—	1.000
	d	—	—	—	—	0.368	—	—	—	—	—	—	1.000	—
	n	1	1	—	1	38	5	60	45	6	10	10	6	6
MPI-1	a	—	0.667	1.000	—	—	—	—	—	—	1.000	0.556	—	—
	b	—	0.333	—	—	—	—	—	—	—	—	0.444	—	1.000
	c	1.000	—	—	—	0.087	—	1.000	0.586	1.000	—	—	—	—
	d	—	—	—	1.000	0.913	1.000	—	0.414	—	—	—	1.000	—
	n	1	3	1	1	23	4	39	29	5	8	9	6	6

Table 2 (cont.)

		ant	coq	por	prob	ampl	bar	jhn	mart	pin	eup	shr	ter	uri
MPI-2	a	—	0.333	1.000	1.000	—	—	—	—	—	—	0.071	0.400	—
	b	1.000	0.333	—	—	—	1.000	—	—	0.200	1.000	0.786	—	1.000
	c	—	0.333	—	—	0.583	—	—	0.174	0.800	—	—	0.600	—
	d	—	—	—	—	0.417	—	1.000	0.826	—	—	—	—	—
	e	—	—	—	—	—	—	—	—	—	—	0.143	—	—
	n	1	3	1	1	24	4	39	23	5	6	7	5	5
PEP (LA)	a	1.000	—	1.000	—	—	—	—	—	—	—	—	—	—
	b	—	1.000	—	1.000	—	—	0.963	0.053	—	1.000	—	—	—
	c	—	—	—	—	0.250	1.000	0.037	0.894	1.000	—	1.000	—	—
	d	—	—	—	—	0.750	—	—	0.053	—	—	—	1.000	1.000
	n	1	2	1	1	8	8	54	19	11	2	3	2	2
PEP(LGG)	a	1.000	—	1.000	—	—	—	—	—	—	—	—	—	—
	b	—	—	—	—	0.100	—	—	—	—	—	—	1.000	—
	c	—	0.500	—	1.000	0.900	—	0.776	1.000	0.071	1.000	1.000	—	1.000
	d	—	0.500	—	—	—	1.000	0.224	—	0.929	—	—	—	—
	n	1	2	1	1	10	8	58	18	14	10	10	2	2

Table 2 (cont.)

		ant	coq	por	prob	ampl	bar	jhn	mart	pin	eup	shr	ter	uri
PGDH	a	–	0.250	–	1.000	–	0.063	–	–	–	–	–	–	–
	b	1.000	0.250	1.000	–	0.447	0.937	1.000	0.800	1.000	–	–	–	–
	c	–	0.250	–	–	0.553	–	–	0.200	–	–	–	–	1.000
	d	–	–	–	–	–	–	–	–	–	1.000	1.000	1.000	–
	e	–	0.250	–	–	–	–	–	–	–	–	–	–	–
	n	1	4	1	1	38	8	62	35	13	7	10	6	6

TABLE 3. Data matrices and character types for two cladistic analysis of allozyme data from Eastern Caribbean and Greater Antillean *Eleutherodactylus*. Analysis I was scored using the allelic arrays of four southern Eastern Caribbean taxa as the outgroup. Nine Greater Antillean and northern Eastern Caribbean taxa were scored combined as the outgroup for analysis II. Letters are used to indicate character types as follows: ordered (O), unordered (U), uninformative (*). Abbreviations for loci correspond to those listed in Table 1. Character numbers are assigned to loci in the same order as in Table 2.

Character	12345	1 67890	11111 12345	11112 67890	2 1
Character Type (Analysis I)	OOOOO	O**OO	OOUOO	*OOOO	O
Outgroup	10000	00020	00101	00001	0
<i>E. amplinympha</i>	20111	20001	10310	01101	1
<i>E. antillensis</i>	11231	10010	00001	01010	1
<i>E. barlagnei</i>	20211	20031	00221	00000	1
<i>E. coqui</i>	10121	10010	10322	00000	2
<i>E. johnstonei</i>	20111	20011	00221	01101	1
<i>E. martinicensis</i>	20111	20011	10420	01101	1
<i>E. pinchoni</i>	20111	20030	00221	01000	1
<i>E. portoricensis</i>	10120	00001	10302	00010	1
<i>E. probolaeus</i>	00012	20010	11311	00000	1
Character Type (Analysis II)	OOOOO	***O*	O*U*O	**O**	O
Outgroup	01200	00010	00000	00000	0
<i>E. euphronides</i>	02330	00000	10000	00000	1
<i>E. shrevei</i>	11120	00000	10000	10011	1
<i>E. terraebolivaris</i>	01010	00020	00000	10002	1
<i>E. urichi</i>	00011	00000	20000	00003	0

FIGURE 1. Distribution of *Eleutherodactylus* species in the Eastern Caribbean. *Eleutherodactylus johnstonei* exists on all islands with gray shading and in several urban areas in Venezuela. On Trinidad, the species is limited to a small, highly localized population in the harbour area (Kenny, 1980). Explanation of symbols is provided in the key.

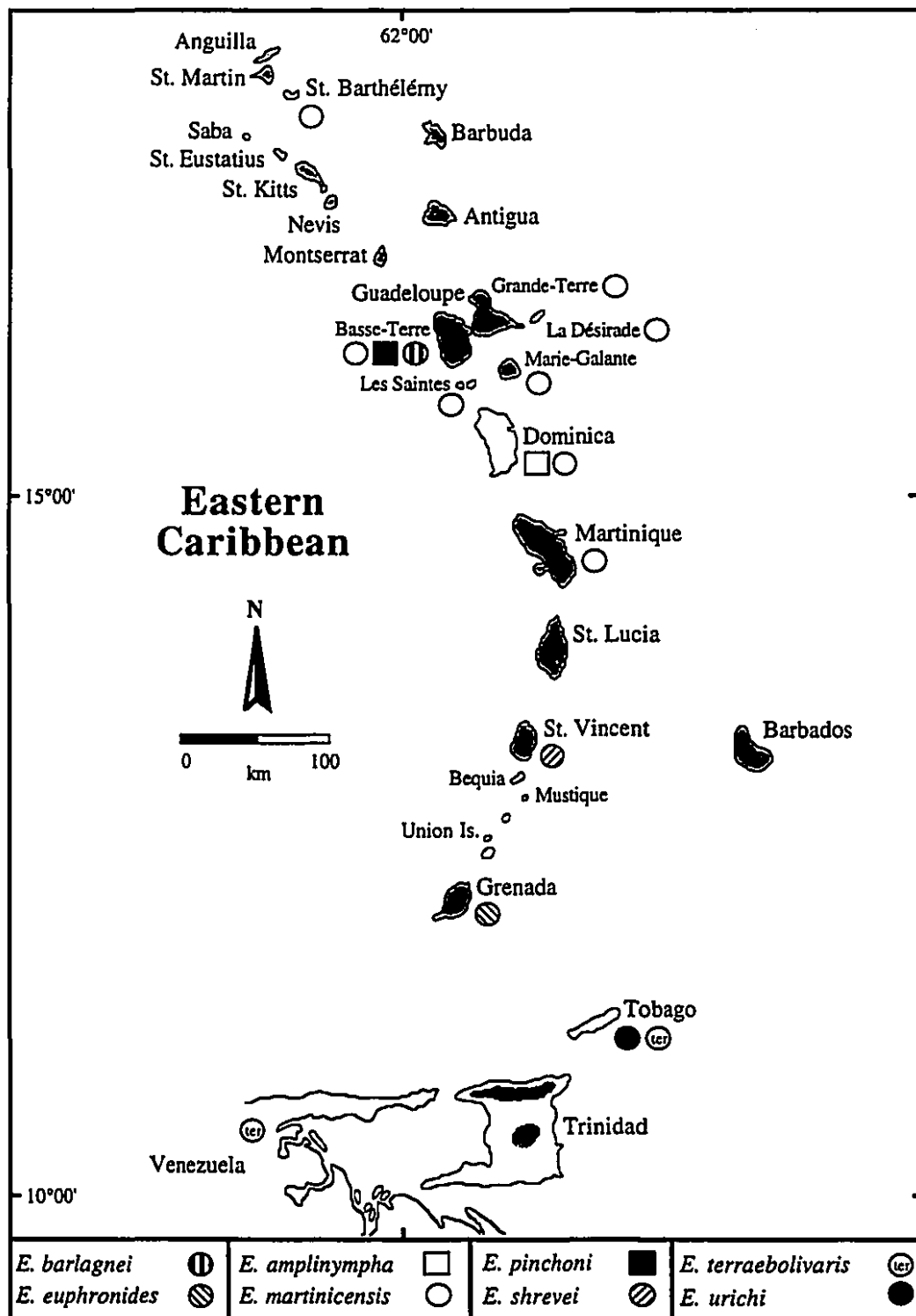


FIGURE 2. Phenograms constructed from two genetic distance indices for Eastern Caribbean and Greater Antillean *Eleutherodactylus*. (A) UPGMA phenogram for Nei's (1978) genetic distance. (B) Fitch-Margoliash tree. Both phenograms split Eastern Caribbean *Eleutherodactylus* into two very distinct groups, with variable placement of *E. urichi*, suggesting multiple origins for these species. Abbreviations of group designations are PR (Puerto Rico), nEC (northern Eastern Caribbean), DR (Dominican Republic), and sEC (southern Eastern Caribbean).

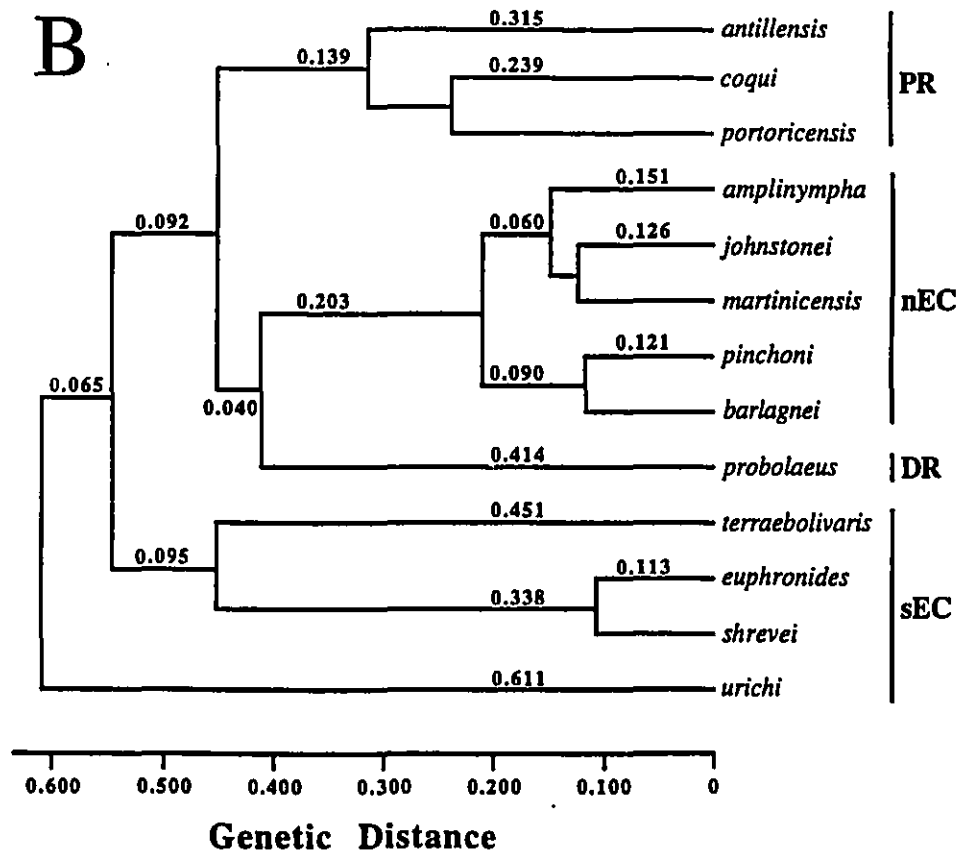
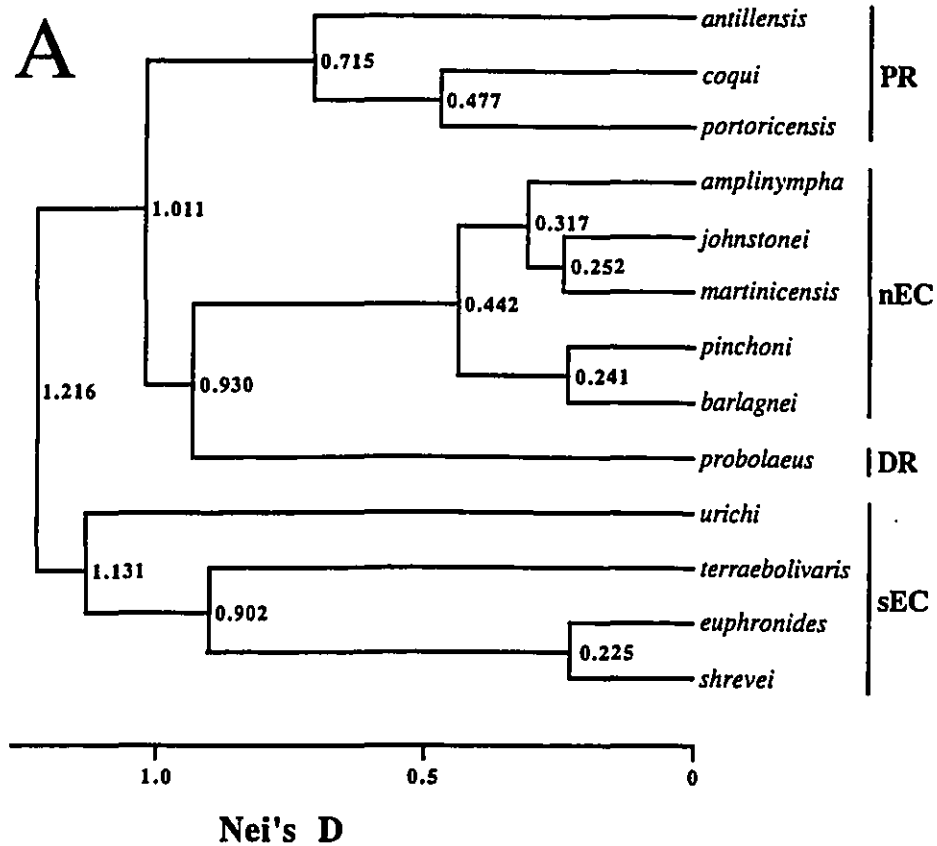
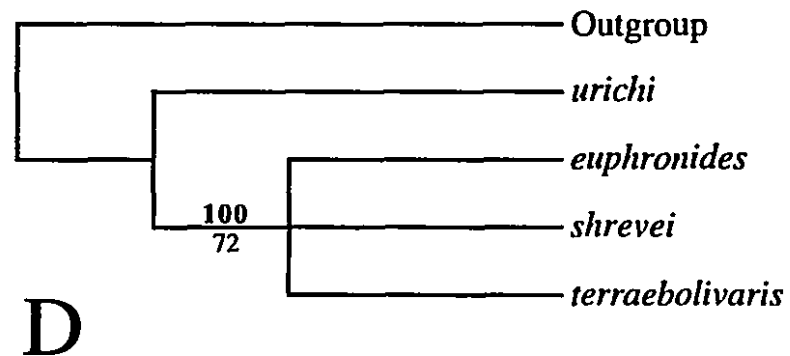
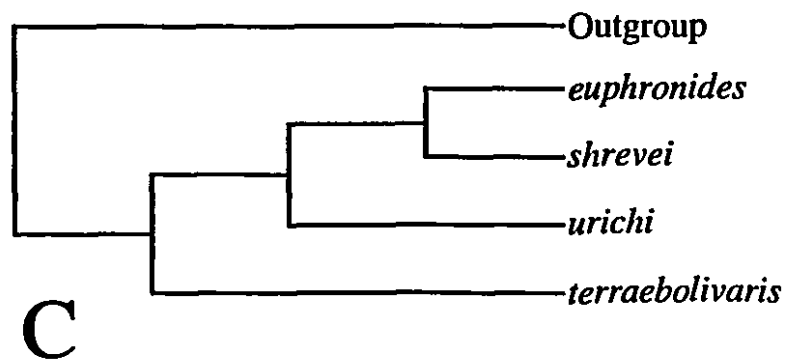
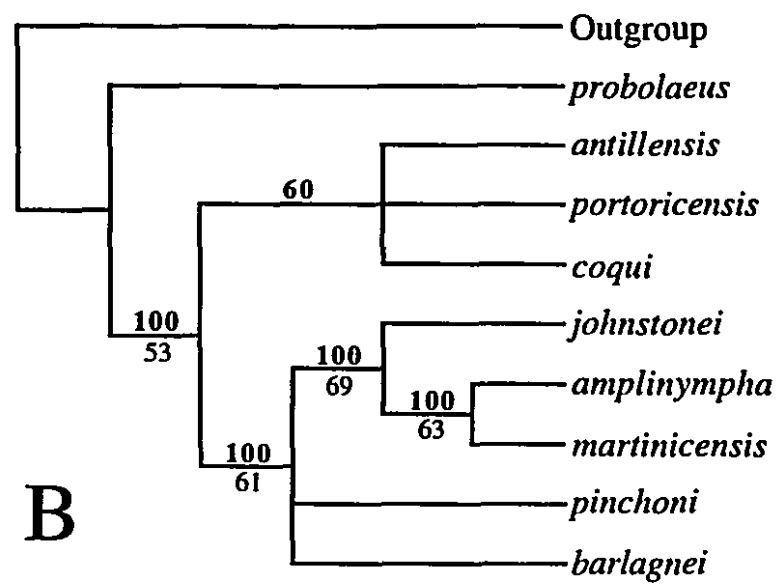
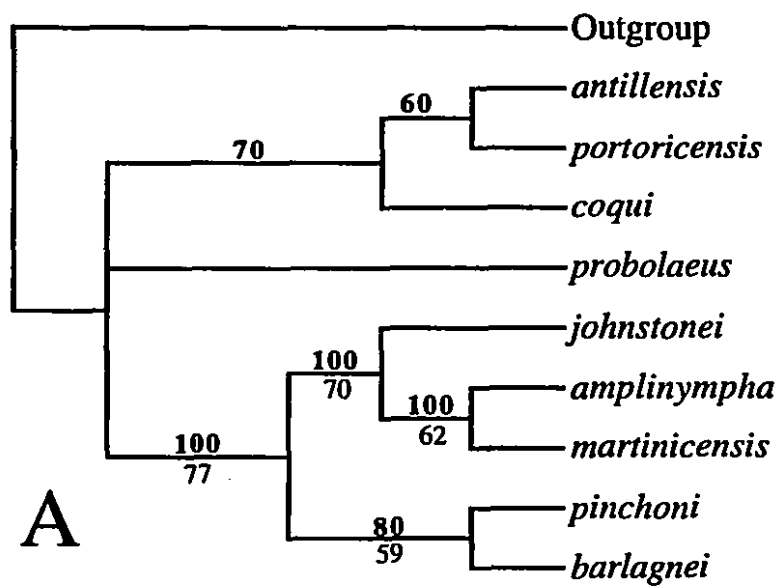


FIGURE 3. Cladograms from a phylogenetic analysis of allozyme data for Eastern Caribbean *Eleutherodactylus*. Numbers in boldface are values for majority-rule consensus, plain numbers are values from bootstrapping (1000 repetitions). (A) Majority-rule consensus tree of fifteen most parsimonious trees (length 49 steps, CI = 0.653) from a parsimony analysis of characters ordered using the suggestions of Green and Borkin (in press). (B) Majority-rule consensus tree of eleven most parsimonious trees (length 46 steps, CI = 0.696) from a parsimony analysis of unordered characters. As functional outgroup for (A) and (B) we used the allelic arrays of the southern Eastern Caribbean species *E. euphronides*, *E. shrevei*, *E. terraebolivaris*, and *E. urichi*. (C) Single most parsimonious tree (length 24 steps, CI = 0.833) from a parsimony analysis of ordered characters (as above). (D) Majority-rule consensus tree of the two most parsimonious trees (length 21 steps, CI = 0.952) from a parsimony analysis of unordered characters. The functional outgroup for (C) and (D) was a northern Eastern Caribbean and Greater Antillean "supertaxon," using the accumulated allelic arrays of *E. amplinympha*, *E. antillensis*, *E. barlagnei*, *E. coqui*, *E. johnstonei*, *E. martinicensis*, *E. pinchoni*, *E. portoricensis*, and *E. probolaeus*.



Summary

SUMMARY

This study is the first comprehensive synopsis of the taxonomy, systematics, and biogeography of Eastern Caribbean frogs that uses an interdisciplinary array of techniques. Three character sets were used to study the taxonomic and systematic position of specimens collected on all Eastern Caribbean islands: discrete characters from an investigation of external and internal morphology, twenty metric variables, and allele frequencies at 22 presumptive allozyme loci.

The assessment of α -level taxonomy for *Eleutherodactylus urichi* showed that populations on Grenada and St. Vincent are distinct at the level of species. They are redescribed as the species *E. euphronides* and *E. shrevei*, respectively. Multivariate morphometrics provided conclusive evidence that records for *E. urichi* from the South American mainland are due to misidentification with *E. johnstonei* or with other, potentially unnamed species.

The dendrobatid *Colostethus chalcopis* is described from Martinique. This small frog is unusual among *Colostethus* by the absence of distinctive dorsolateral stripes and by its atypical tadpole. The tadpole is one of only three endotrophic larvae in the genus *Colostethus*, yet it has fully developed mouthparts. This species is the only member of the family Dendrobatidae endemic to an oceanic island. *Eleutherodactylus amplinympha* is described from Dominica; it is nearly cryptic with *E. martinicensis*. Based on vocalizations, allozyme differences, and sexual size dimorphism, this species is the sister-taxon of *E. martinicensis*.

The morphometric analysis of twenty metric characteristics for Eastern Caribbean *Eleutherodactylus* shows that these species have a relatively conservative phenotype despite their ecological disparity. I suggest that evolutionary divergence of a given morphology may lag when extreme environmental pressures require rapid adaptation to prevent extinction. This hypothesis is supported by the highly correlated

relationship of arboreality, an indirect measure of ecotype, with tibia length, a morphological component.

Analysis of all three data sets supports the hypothesis that Eastern Caribbean frogs have two different origins. For some genera, such as *Colostethus* and *Leptodactylus*, South America is easily identified as the ancestral biota by the distribution of congeners. For species of the genus *Eleutherodactylus*, the only truly circum-Caribbean frog genus, a decision of origin is much more difficult to make. However, the analysis provides unequivocal evidence from internal and external morphology for the hypothesis that four Eastern Caribbean *Eleutherodactylus* (*E. euphronides*, *E. shrevei*, *E. terraebolivaris*, *E. urichi*) are of South American stock, whereas the others (*E. amplinympha*, *E. barlagnei*, *E. johnstonei*, *E. martinicensis*, *E. pinchoni*) are of Greater Antillean stock. Among these taxa, phylogenetic analyses indicate that *E. euphronides* and *E. shrevei*, *E. barlagnei* and *E. pinchoni*, and *E. amplinympha* and *E. martinicensis* are sister taxa.

Whereas most of the anurans in the Eastern Caribbean are single-island endemics, two species of *Eleutherodactylus* have particularly extensive distributions. *Eleutherodactylus martinicensis* exists on all islands in the central part of the island arc, as well as on St-Barthélemy. Since there were no frogs on St-Barthélemy before the French began development of a tourist industry, I suggest that frogs were introduced with material transports. An extrapolation of this type of human-mitigated introduction leads to the realization that *E. johnstonei* and *E. martinicensis* are distributed exactly along the boundaries of the historic British and French trade empires, respectively. Given the continuing advance of small *E. johnstonei*-populations to far-distant cities and islands, I suggest that accidental human introductions should be considered valid dispersal mechanisms for small vertebrates and should not be excluded as a factor in assessing the biogeography of anurans in the Eastern Caribbean.