

BULLETIN

of the FLORIDA STATE MUSEUM Biological Sciences

Volume 21

1976

Number 1

VARIATION AND RELATIONSHIPS OF SOME
HISPANIOLAN FROGS (LEPTODACTYLIDAE,
ELEUTHERODACTYLUS) OF THE *RICORDI* GROUP

ALBERT SCHWARTZ



UNIVERSITY OF FLORIDA

GAINESVILLE

Numbers of the BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCIENCES, are published at irregular intervals. Volumes contain about 300 pages and are not necessarily completed in any one calendar year.

CARTER R. GILBERT, *Editor*

RHODA J. RYBAK, *Managing Editor*

Consultant for this issue:

ERNEST E. WILLIAMS

Communications concerning purchase or exchange of the publications and all manuscripts should be addressed to the Managing Editor of the Bulletin, Florida State Museum, Museum Road, University of Florida, Gainesville, Florida 32611.

This public document was promulgated at an annual cost of \$1647.38 or \$1.647 per copy. It makes available to libraries, scholars, and all interested persons the results of researchers in the natural sciences, emphasizing the Circum-Caribbean region.

VARIATION AND RELATIONSHIPS OF SOME HISPANIOLAN FROGS (LEPTODACTYLIDAE, *ELEUTHERODACTYLUS*) OF THE *RICORDI* GROUP

ALBERT SCHWARTZ¹

SYNOPSIS: Five species of Hispaniolan *Eleutherodactylus* of the *ricordi* group are discussed, and variation in these species is given in detail. The relationships of these five species, both among themselves and with other Antillean members of the *ricordi* group, are treated, and a hypothetical sequence of inter- and intra-island trends is given, based upon presence or absence of digital discs and glandular areas. Data on voice, habitat, and distribution of the included species are given.

TABLE OF CONTENTS

INTRODUCTION	2
ACKNOWLEDGMENTS AND MATERIALS	3
SYSTEMATIC DESCRIPTIONS	3
<i>Eleutherodactylus pictissimus</i> COCHRAN 1935: 371	3
<i>Eleutherodactylus pictissimus pictissimus</i> COCHRAN 1935	4
<i>Eleutherodactylus pictissimus apatheatus</i> SCHWARTZ 1965: 102	7
<i>Eleutherodactylus pictissimus eremus</i> SCHWARTZ 1965: 107	9
<i>Eleutherodactylus weinlandi</i> BARBOUR 1914: 246	11
<i>Eleutherodactylus weinlandi weinlandi</i> BARBOUR 1914	11
<i>Eleutherodactylus weinlandi chersonesodes</i> SCHWARTZ 1965: 115	14
<i>Eleutherodactylus weinlandi paralius</i> new subspecies	16
<i>Eleutherodactylus alcoae</i> SCHWARTZ 1971: 26	20
<i>Eleutherodactylus probolaeus</i> SCHWARTZ 1965: 110	23
<i>Eleutherodactylus warreni</i> new species	26
THREE ANOMALOUS SPECIMENS	28
DISCUSSION	30
LITERATURE CITED	41
APPENDIX 1	42
APPENDIX 2	44
APPENDIX 3	46

¹ The author is a Professor in the Department of Biology, Miami-Dade Junior College, Miami, Florida 33167. Manuscript accepted 9 September 1973.

INTRODUCTION

The *Eleutherodactylus ricordi* group has a complex of species on the West Indian islands of Cuba, Hispaniola, Mona, Puerto Rico, and the Virgin Islands that form a compact assemblage of related forms; similarities include general size, dorsal coloration and pattern, and those characters that ally them to each other and are common to all members of the group (Dunn 1926:210, Schwartz 1958:2). The complex of species presently under discussion includes the Cuban species *ricordi* Duméril and Bibron, *thomasi* Schwartz, *bresslerae* Schwartz; the Hispaniolan species *weinlandi* Barbour, *pictissimus* Cochran, *alcoae* Schwartz; as well as *monensis* Meerwarth from Isla Mona, *richmondi* Stejneger from Puerto Rico, and *lentus* Cope from St. Thomas, St. John, and St. Croix, Virgin Islands.

This group of species may be divided into two major subgroups: one has pale dorsa with dark markings (to which all but two of the above species may be assigned); the other is a pair of species (*weinlandi*, *richmondi*) that are richly colored dorsally and lack, or have modified, dorsal dark pattern elements. Shreve and Williams (1963:332-334) discussed the relationships between *pictissimus*, *weinlandi*, *ricordi*, *bresslerae*, and *lentus*, stating quite correctly that these forms show "surprisingly few differences, even in coloration." They cogently suggested that it might be more appropriate to regard some of the members of the complex as subspecies (i.e., *weinlandi* and *lentus*; or *pictissimus*, *weinlandi*, and *lentus*). However, for lack of other than inductive evidence, they elected not to make the corresponding nomenclatural changes. I reviewed the evidence in 1965 and retained the Hispaniolan *pictissimus* and *weinlandi* as distinct species, although their distributions showed some peculiarities—apparently of a mosaic nature—on Hispaniola. In the same paper I named a new subspecies of *weinlandi* (*chersonesodes*) from the Península de Samaná and extreme eastern República Dominicana, and three new subspecies of *pictissimus* (*apantheatus*, *eremus*, *probolaeus*). Of the four subspecies of *E. pictissimus*, all show adjacent distributions or intergradation except *probolaeus*, which is known only from extreme southeastern República Dominicana and is geographically separated from the other subspecies by a distance of about 200 km. At that time (1965) two records of *E. weinlandi* were known from between the ranges of *probolaeus* and the other subspecies of *E. pictissimus*: Cueva de Santa Anna in the city of Santo Domingo (Mertens 1939:30); 12 km NE La Romana, La Romana Province, República Dominicana (Schwartz 1965:119). It seemed apparent that the range of *E. weinlandi* was intermediate to those of two subspecies of *E. pictissimus*, a rather unusual situation.

ACKNOWLEDGMENTS AND MATERIALS

In an effort to clarify the relationships of this complex of taxa on Hispaniola, effort was made between 1968 and 1971 in both Haiti and the República Dominicana to secure additional specimens; this field work was under the sponsorship of National Science Foundation grants G-7977 and B-023603. So much new material has accumulated from these collections that it is appropriate to reassess the status of the named populations and to redefine their distributions. Through the efforts of C. Rhea Warren a series of *Eleutherodactylus* was secured on Ile de la Tortue off the northern Haitian coast; Mr. Warren's visits to that island were greatly facilitated by the cooperation of M. Ramah Théodore, Directeur Général Adjoint de l'Office Nationale du Tourisme et de Propagande. Collections made by Richard Thomas along the northern Haitian littoral and in the vicinity of Mirebalais have clarified some problems but have posed others. In the field I have had the cooperation of Patricia A. Adams, Donald W. Buden, Jeffrey R. Buffett, James R. Dennis, Danny C. Fowler, Ronald F. Klinikowski, David C. Leber, Dennis R. Paulson, James A. Rodgers, Jr., Bruce R. Sheplan, William W. Sommer, James B. Strong, and Richard Thomas. Lewis D. Ober collected an especially interesting *Eleutherodactylus* from Thomonde in central Haiti.

The present paper is based primarily upon material in the Albert Schwartz Field Series (ASFS) collected between 1962 and 1971. For my previous report (1965) on variation in the *weinlandi-pictissimus* complex, I borrowed specimens from the American Museum of Natural History (AMNH), the National Museum of Natural History (USNM), the Museum of Comparative Zoology (MCZ), and the Museum of Zoology, University of Michigan (UMMZ). Holotypes and paratypes were deposited in the Carnegie Museum (CM), the Museum of Natural History, University of Kansas (KU), and the Museum of Natural History, University of Illinois (UIMNH). I have not re-borrowed these specimens, but data from them are included in the lists of specimens examined and in the computations and distributional analyses presented herein. I have borrowed specimens of the Cuban taxa (*bresslerae*, *thomasi*, *ricordi*) from the American Museum; these specimens were collected by me under NSF grants G-3865 and G-6252 between 1957 and 1960. I wish to thank Charles W. Myers and George W. Foley for the loan of these specimens. Not all problems of the relationships of the Antillean taxa to each other may be presently solved, but the large quantity of new Hispaniolan material and new data do manage to clarify these relationships to some extent and to expand our concepts of the Hispaniolan taxa.

I would also like to extend my gratitude to David C. Leber for his artistic rendition of the two new taxa described in this paper.

SYSTEMATIC DESCRIPTIONS

Eleutherodactylus pictissimus COCHRAN 1935: 371

HOLOTYPE AND TYPE LOCALITY: MCZ 19846; Tardieu, Massif de la Hotte, ca 3000 ft (915 m), Département du Sud, Haiti.

DIAGNOSIS.—A species of the Antillean *ricordi* group of *Eleutherodactylus* characterized by the combination of moderate size (snout-vent length: males to 34 mm, females to 43 mm); dorsum brown (rarely) to pale (tan, buffy tan, yellow, pale orange, pale gray, tannish bronze, dull orange-tan, light brown, pale tan, reddish tan), either overlaid with a dense and very dark brown to black reticulum, with a pair of dorsolateral stripes of the dorsal ground color (= not contrastingly colored when compared with the dorsal color), or pattern much reduced to fine stippling with a prominent dark scapular chevron; hind limbs coarsely banded to vaguely stippled with dark brown to black; inguinal and supra-axillary glandular areas present but inconspicuous; expanded digital discs very poorly developed to absent; tympanum

small (\bar{X} =males, 2.2 mm; females, 2.7, 2.5, and 2.4 [see Appendix 1]); and tibia/snout-vent length ($X/100$) moderate (males, 41.3-55.2; females, 42.0-53.3).

DISTRIBUTION.—The Tiburon Peninsula in Haiti east to the Península de Barahona in the República Dominicana. It occurs within this region at high elevations in the Massif de la Hotte (Tardieu) and the Montagne Noire (Furcy) (but is absent from the highlands of the Sierra de Baoruco and the extremely arid Península de Barahona itself); the Cul de Sac-Valle de Neiba Plain (north of the Massif de la Selle and the Sierra de Baoruco) east to the vicinity of Baní in the Llanos de Azua, República Dominicana (Fig. 1). Altitudinal distribution extends from sea level (or below, near Jimaní and Duvergé) to 5800 ft (1769 m) at Furcy in the Montagne Noire, but not higher than 1800 ft (549 m) above Barahona in the Sierra de Baoruco.

Eleutherodactylus pictissimus pictissimus COCHRAN 1935

DIAGNOSIS.—A subspecies of *E. pictissimus* characterized by large size (snout-vent length: males, 34 mm; females, 43 mm); dorsum rarely dark (brown) and usually pale (tan, buffy tan, yellow, pale orange, tannish bronze, yellow-tan, orange-tan, pale gray), heavily and densely covered by dark brown to black spots to form a reticulum in many instances, but leaving a pair of dorsolateral stripes that are unicolor with the dorsal ground color, a dark scapular chevron present but incorporated into the dorsal pattern and not outstanding as a separate dorsal unit; sides grayish and overlaid by the same dark dorsal pattern; hindlimbs prominent and contrastingly banded, reticulate, or mottled with dark pigment, but usually without clearly defined limb bands (if discernible, about three on the thighs and two on the crura); concealed surfaces of femora gray; venter opalescent to whitish; and throat gray.

DISTRIBUTION.—The Tiburon Peninsula in Haiti (from Jérémie and Moron in the north and Les Platons and Les Cayes in the south), east to the southern slopes of the Sierra de Baoruco (above Cabo Rojo); also on Ile-à-Vache, Haiti. Intergrades between *pictissimus* and *apantheatus* occur along the northern coast (and inland to Furcy) of the Tiburon Peninsula between Ça Ira and Dufort on one hand, and Pétionville and Port-au-Prince on the other, and along the extreme southeastern edge of the Sierra de Baoruco near Enriquillo, Juancho, and Caletón, República Dominicana. Altitudinally it ranges from sea level (many localities, including Les Cayes, Aquin, Jérémie, Ça Ira) up to 1700 ft (519 m) in the Sierra de Baoruco northeast of Cabo Rojo, and up to 3000 ft (915 m) both at Tardieu (type locality) and Les Platons in the Massif de la Hotte. Intergrading specimens (*pictissimus* X *apantheatus*) are known at even higher elevations (5800 ft [1709 m]) from Furcy on the Montagne Noire.

REMARKS.—Of the three *E. pictissimus* subspecies, the nominate form is by far the most widely distributed, both geographically and altitudinally, and is also the largest. As pointed out previously (Schwartz 1965), *E. p. pictissimus* is the most darkly patterned of the subspecies and lacks the faded appearance of *apantheatus* and *eremus*. The snout-vent lengths of 119 adults are: 57 males, 23.0-33.9 mm (\bar{X} 26.6); 62 gravid females, 28.5-43.2 mm (\bar{X} 35.7). Additional mensural data are presented in Appendix 1.

Considering the frog's broad distribution and its abundance throughout much of its range, it is truly remarkable that *E. pictissimus* was described so recently and from only one specimen. Although one has the impression that *E. p. pictissimus* is confined to mesic situations, it ob-

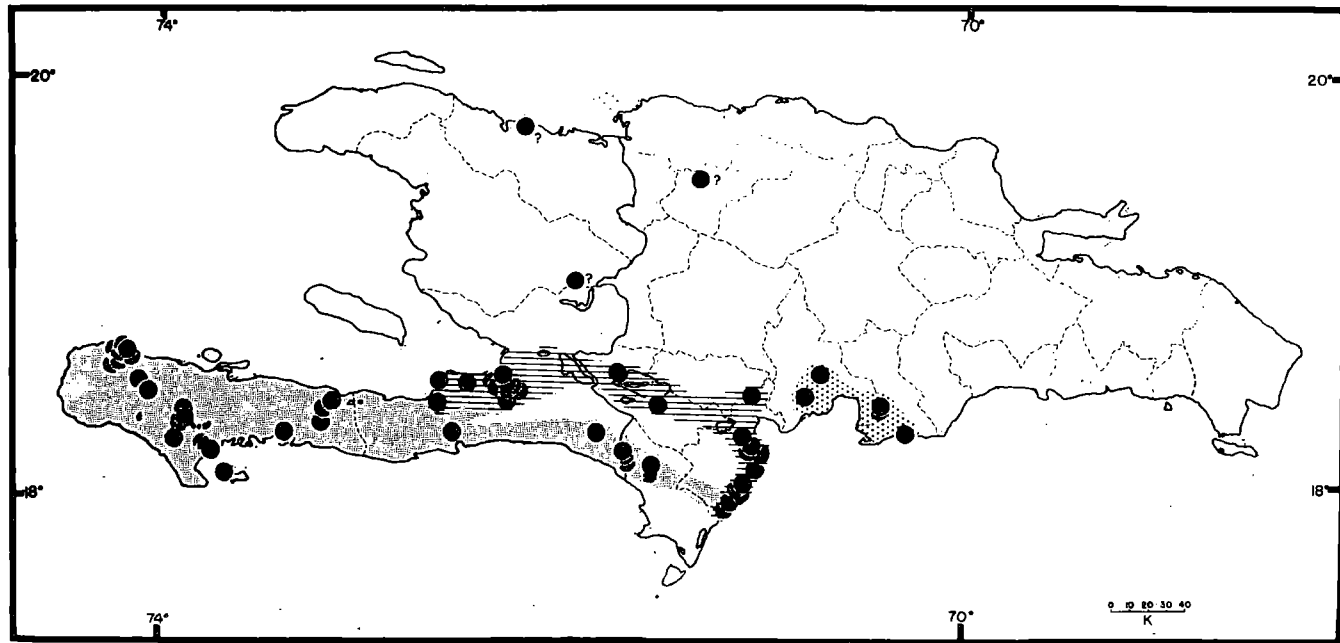


FIGURE 1.—Map of Hispaniola, showing localities and known distributions of three subspecies of *Eleutherodactylus pictissimus* as follows: fine stippling, *E. p. pictissimus*; horizontal lines, *E. p. apanteatus*; coarse stippling, *E. p. eremus*. Overlapping symbols indicate regions of intergradation. The three questioned localities represent individual specimens that are questionably associated with *E. pictissimus*.

viously is also tolerant of much dryer regions and is one of the few Antillean frogs that occurs in areas consistently exposed to salt water. Repeated field data include *E. p. pictissimus* in such local situations as piles of moist Cocos trash (both husks and fronds), rock piles, and under individual rocks. The subspecies is associated with shaded ravines, as at Camp Perrin, but does not shun grassy pastures (L'Eglise, Les Cayes). Twelve were taken in a cave (Grotte de Counou Bois), 150 ft (46 m) inside the entrance, where they were active during the morning hours in an area of small moist stones. Above Cabo Rojo in the Sierra de Baoruco, *E. p. pictissimus* occurs in *Acacia* woods, where it was encountered under rocks in dusty soil during the day and hopping about actively at night both in *Acacia* and semi-mesic deciduous woods (as at L'Eglise).

As I have pointed out (Schwartz 1965:113), *E. pictissimus* has never been heard calling, despite collections made during very favorable weather conditions and at all seasons of the year. Fowler and Sheplan thought they heard a small, whispery call at a locality near La Ciénaga (where *E. p. apantheatatus* is exceptionally abundant), but they were unable to verify their observations. I too have had the impression that a low and indistinct call heard near L'Eglise might have been made by *E. p. pictissimus* but was unable to verify the fact. In all members of the *ricordi* group, the call is irregular and insect-like and easily confused with other nocturnal noises or obscured by them. With no obvious evidence to the contrary, I have assumed that *E. pictissimus* is non-vocal. However, Shreve and Williams (1963:334), quoting field notes from Anthony Curtis on *E. pictissimus* at his house in Port-au-Prince, Haiti, stated, "It made a noise resembling the chirping of a cricket"; these sounds were made by a frog while Curtis was holding it in his hand. Many eleutherodactyls and other anurans make "chuckling" or other distress calls when disturbed, and it is possible that this was the case with Curtis' frog. As yet there is no concrete evidence that *E. pictissimus* vocalizes under natural conditions.

Despite its broad distribution, *E. p. pictissimus* shows very little geographically correlated variation. Specimens from Ile-à-Vache, for instance, are like those from the adjacent mainland at Les Cayes. Specimens from north and south of the Massif de la Hotte also appear indistinguishable, although a short series from near Jérémie (ASFS V9309-12) has paler pigmentation and is less well marked than other specimens. However, other frogs from the Jérémie area are just as heavily pigmented dorsally as the other *E. p. pictissimus*. There are no obvious pigmental or pattern differences between specimens from the distal Tiburon Peninsula and those from the Sierra de Baoruco. It is interesting to note,

however, that the largest frogs are from the eastern extreme of the range (the Sierra de Baoruco) and are consistently larger than frogs from elsewhere.

SPECIMENS EXAMINED. HAITI. DÉPT. DU SUD: beach area within 1 km of Jérémie (ASFS V21291); 2 km NW Jérémie (ASFS V9309-12); Place Nègre nr. Jérémie (MCZ 33296-98); Mayette (MCZ 37571); Carrefour Sanon nr. Jérémie (MCZ 33818-19; MCZ 37574-85); Fond Rouge Daye nr. Jérémie (not mapped) (MCZ 37565); Bozo nr. Jérémie (not mapped) (MCZ 37566-69); La Source nr. Jérémie (not mapped) (MCZ 37570); Perine nr. Jérémie (not mapped) (MCZ 37572-73); Marfranc (MCZ 37743-49); Moron (USNM 60626); Tardieu, 3000 feet (905 meters) (MCZ 19846); Castillon, 2500 feet (763 meters) (ASFS V24722-25, ASFS V24971); Camp Perrin (ASFS X2526-27, ASFS X2671, ASFS X2683, ASFS X2749-50, ASFS X2813-16, ASFS X3099-106, MCZ 33282-91); 5 mi. (8.0 km) from Camp Perrin (MCZ 36746-47); Grotte de Counou Bois, 1 mi. (1.6 km) SW Camp Perrin (ASFS X3254-65, ASFS X3272-73); Les Platon, 3000 feet (915 meters) (ASFS V20410-13); Les Cayes (ASFS X3712-13, ASFS X3370-71); 1 mi. (1.6 km) NW Les Cayes (ASFS X3822); 4.5 mi. (7.2 km) NW Les Cayes (ASFS X3802-11); Ile-à-Vache, western end (ASFS X3553-55); 0.6 mi. (1.0 km) W Aquin (ASFS V25900-02); Fond des Nègres (MCZ 35194); Mingrette nr. Miragoâne (not mapped) (MCZ 35195); Pemel nr. Miragoâne (not mapped) (MCZ 35196); Butête nr. Miragoâne (not mapped) (MCZ 35197-98); Paillant, 1800 feet (549 meters) (ASFS V26218-20); 4.7 mi. (7.5 km) SW Paillant, 2500 feet (763 meters) (ASFS V26169). DÉPT. DE L'OUEST: ca. 5.5 mi. (8.8 km) NW Jacmel, 600 feet (183 meters) (ASFS V9782-83); Ça Jaqueline nr. Jacmel (not mapped) (MCZ 34500); Thiotte (MCZ 36095-96). REPÚBLICA DOMINICANA. PEDERNALES PROVINCE: 6.0 mi. (9.6 km) N Pedernales, 800 feet (244 meters) (ASFS V30106-07); 13.0 mi. (20.8 km) N Pedernales, 600 feet (183 meters) (ASFS V29735); 26 km N Pedernales (ASFS V21472-73); 20 km N Cabo Rojo, 1400 feet (427 meters) (ASFS V29710-11); 21 km NE Cabo Rojo, L'Eglise, 1500 feet (458 meters) (ASFS V16802, ASFS V30031-37); 21 km NE Cabo Rojo, 1300 feet (397 meters) (ASFS V16795); 22 km NE Cabo Rojo, 1700 feet (519 meters) (ASFS V16753).

Eleutherodactylus pictissimus apantheatus SCHWARTZ 1965:102

HOLOTYPE AND TYPE LOCALITY.—MCZ 43195; 6.5 mi. (10.4 km) NE Jimaní, Independencia Province, República Dominicana.

DIAGNOSIS.—A subspecies of *E. pictissimus* characterized by moderate size (snout-vent length: males to 33 mm, females to 35 mm); dorsum pale (tan, reddish tan, yellow); dorsal markings black to dark brown but much reduced, usually forming a fine vermiculate or reticulate pattern; dark dorsal pattern delimiting a pair of dorsolateral stripes that are concolor with the dorsal ground color; a moderately prominent dark scapular chevron, sides grayish, usually more heavily marked with dark pattern elements than dorsum; hindlimbs marbled or mottled with dark pigment, rarely with any banding indicated; concealed surfaces of femora whitish; venter white to flesh; throat white.

DISTRIBUTION.—The Valle de Neiba in the República Dominicana, from Jimaní east to the vicinity of Barahona, and thence south along the eastern coast of the Península de Barahona as far as Paraíso, and northeast to Fondo Negro. It presumably also occurs in the Haitian Cul de Sac Plain but is not yet known from that area. Intergrades between *apantheatus* and *pictissimus* occur in two areas: in Haiti between Ça Ira-Dufort and Port-au-Prince (and into the Montagne Noire to Furcy), and at the extreme southeastern corner of the Sierra de Baoruco near Enriquillo, Juancho, and Caletón, República Dominicana. Altitudinal distribution ranges from sea level (localities along the eastern coast of the Península de Barahona) or below (in the Valle de Neiba at Jimaní and Duvergé) to 1800 ft (549 m) near Barahona.

REMARKS.—The large amount of additional material of *E. p. apanteatus* confirms the pigment and pattern differences between that subspecies and *E. p. pictissimus* that were noted in the original description of *apanteatus*. The pale dorsal ground color, with the dorsal dark markings reduced but still present, and the moderately conspicuous dark scapular chevron serve to distinguish *E. p. apanteatus* from the nominate subspecies (see Schwartz 1965:figs. 89, 90, for illustrations of these two taxa). In snout-vent length, males are slightly smaller than male *pictissimus* (\bar{X} 24.9 *apanteatus*, 26.6 *pictissimus*; largest male *apanteatus* 33.1, largest male *pictissimus* 33.9), but female *apanteatus* reach a much smaller maximum size (34.7) than do female *pictissimus* (43.2), and the mean female snout-vent length is lower in *apanteatus* (32.0) than it is in *pictissimus* (35.7). Tibia/snout-vent length ($\times 100$) ratios are comparable in both sexes of both subspecies (see Appendix 1 for all mensural data).

Intergrades between the two subspecies occur in two regions. In Haiti there is a broad zone of intergradation between Ça Ira-Dufort in the west, Furcy in the south, and Port-au-Prince in the east. Specimens from this region are extremely variable; some are as poorly patterned dorsally (with a prominent scapular dark chevron) as are *apanteatus*, and others have the heavily patterned dorsa of western *pictissimus*. The second area of intergradation lies along the southeastern edge of the Sierra de Baoruco. In this region *E. pictissimus* is known from a series of coastal localities from near Barahona in the north to Juancho in the south. Fresh specimens from this coastal area indicate that to the south there is a strong tendency for the dorsal patterns to become darker and more definitive, with subsequent obfuscation of the dark scapular chevron, and that specimens from Caletón, for instance, are closer to *E. p. pictissimus* than to *E. p. apanteatus*. There is a gap of some 45 km between the closest records of *pictissimus* and the intergradient localities to the southeast along the southern slopes of the Sierra de Baoruco, but presumably (judging from the small lots of material from Juancho-Caletón-Enriquillo) these southern slopes are inhabited by the nominate subspecies.

Since at least part of the range of *E. p. apanteatus* lies within the hot and dry, and in places below sea level, Valle de Neiba (and presumably in the equally hostile Cul de Sac Plain in Haiti, whence no material is yet available), *apanteatus* is much more confirmedly a local mesophile than is *pictissimus*. In this desert region the holotype (from near Jimaní) was taken under a stack of moist palm fronds, and six specimens from near Cabral were secured under palm slats adjacent to Laguna de Rincón. Two frogs from El Iguito were taken from under

moist *Musa* trash on a banana plantation in an otherwise extremely arid desert. Along the eastern coast of the Península de Barahona, specimens have been secured under palm trash along the beach and under *Cocos* trash in shaded to open *cafetales* (Río Nizaíto; Paraíso). The frog is exceptionally abundant at La Ciénaga, where during the day individuals were caught under rocks in a moist and shaded ravine bed and at night on rocks along the bed of the stream. One individual here was seen 6 inches (15 cm) above the ground in a fern, one of the few instances of climbing noted for the species. One frog was taken on dry earth in *Acacia* woods southwest of Barahona, but at this locality there were adjacent stands of moderately-shady, semi-xeric hardwoods mixed with *Acacia*.

A pair of *E. p. apanteatus* was found in amplexus in a collecting sack; the series of which this pair was a part had been night-collected under extremely rainy conditions. There was a marked size difference between the two sexes, with the male much the smaller, and the position of the male was axillary.

SPECIMENS EXAMINED.—REPÚBLICA DOMINICANA. INDEPENDENCIA PROVINCE: 6.5 mi. (10.4 km) NE Jimaní (MCZ 43195); 6.5 km W Duvergé (ASFS V4417). BARAHONA PROVINCE: El Iquito, 1.6 mi. (2.6 km) NE Fondo Negro (ASFS V30464-65); 4.7 mi. (7.5 km) E Cabral (ASFS X9615-20); El Proprio Esfuerzo, del Monte's finca, 1800 feet (549 meters) (AMNH 44523); 5 km Barahona (ASFS V20589); 4.1 mi. (6.6 km) SW Barahona (ASFS V30406); 3.3 mi. (5.3 km) NE La Ciénaga (KU 79807-10, USNM 150927-30, AMNH 71977-81, UIMNH 55587-90, ASFS V30455, ASFS V30588-615, ASFS V30803); 1.9 mi. (3.0 km) W Paraíso, 600 feet (183 meters) (ASFS V30834); 1 km NE Paraíso, Río Nizaíto (ASFS V16947-51, ASFS V30436-37); 2 km SW Paraíso (CM 38973-78).

Intergrades between *E. p. pictissimus* and *E. p. apanteatus*. REPÚBLICA DOMINICANA. BARAHONA PROVINCE: 0.5 mi. (0.8 km) NE Caletón, 400 feet (122 meters) (ASFS V30742-47); Enriquillo (AMNH 44677-78). HAITI. DÉPT. DE L'OUEST: Ça Ira (MCZ 34489-99); 5 km S Dufort (MCZ 33281); Morne de Cayette (MCZ 33293-94); Diquini (USNM 117187, USNM 140216-17); Port-au-Prince (USNM 117141, USNM 118835, USNM 120968, AMNH 55136); vicinity of Port-au-Prince (AMNH 44009-10); Pétionville (ASFS V20238, ASFS V14965); 1 mi. (1.6 km) NW Pétionville (ASFS V24379); Morne Calvaire, 1 mi. (1.6 km) SW Pétionville, 2300 feet (702 meters) (ASFS X1303); Fort Jacques, 5 km SE Pétionville (airline), north versant, Morne l'Hôpital (ASFS V8309); ca. 7 km (airline) W Pétionville, ca. 2000 feet (610 meters) (ASFS V8480); Furcy (USNM 121018, MCZ 3123, MCZ 31820).

Eleutherodactylus pictissimus eremus SCHWARTZ 1965:107

HOLOTYPE AND TYPE LOCALITY.—MCZ 43196; 9.7 mi (15.5 km) E Azua, Azua Province, República Dominicana.

DIAGNOSIS.—A subspecies of *E. pictissimus* characterized by small size (snout-vent length: males to 28 mm, females to 31 mm); dorsum very pale (yellowish tan or pale tan); dorsal markings much reduced to faint brownish to grayish stippling or filigreeing, but with a prominent dark brown scapular chevron that may be much reduced or fragmented; a pair of faint dorsolateral stripes that are unicolor with the

dorsal color; sides grayish to pinkish, with dark pattern elements much reduced; hind limbs marbled or stippled and rarely with any sort of banding indicated; concealed surfaces pinkish to gray; venter pinkish to dark gray; throat white to grayish.

DISTRIBUTION.—The xeric Llanos de Azua in Azua and Peravia provinces, from sea level to 700 ft (214 m) in the Sierra de Ocoa, República Dominicana.

REMARKS.—At the time of its description *E. p. eremus* was known from only two localities. The new material, from three additional sites, agrees very well with the diagnostic characteristics listed in the original description. The very pale dorsal color, the faint dorsal pattern, and the very prominent dark scapular chevron, which may be faint or fragmented, serve to distinguish *eremus* from both of the western subspecies. In addition, *eremus* is the smallest of the subspecies of *E. pictissimus*. The largest female *eremus* have snout-vent lengths of only 31 mm, in contrast to a maximum of 43 mm for *pictissimus* and 35 mm for *apantheatus*. Snout-vent lengths of males of the three subspecies are: *eremus* 28 mm, *apantheatus* 33 mm, and *pictissimus* 34 mm. The tibia/snout-vent length ($\bar{X} \times 100$) ratio is lower in *eremus* than in any other subspecies (\bar{X} = *eremus* males 47.0 mm, females 44.1 mm; *apantheatus* males 48.9 mm, females 45.4 mm; *pictissimus* males 48.9 mm, females 46.2 mm). All mensural data are presented in Appendix 1.

Because of the arid region occupied by *E. p. eremus*, this subspecies (like *apantheatus*) is found most abundantly in locally mesic situations in the Llanos de Azua and the lower foothills of the adjacent Sierra de Ocoa. At the type locality specimens were taken in huge piles of palm trash within an artificial oasis composed of a coconut grove and large shade trees. The locality north of Cruce de Ocoa is similar but less mesic. The juvenile from south of Baní was taken from under very dry palm fronds on mud at the edge of a mangrove swamp. Once again, the tolerance of *E. pictissimus* to marginal haline situations, as on Ile-à-Vache, is demonstrated.

No intergrades between *eremus* and *apantheatus* are known; the closest known collection localities are 30 km apart (El Iguito; 9.7 mi. E Azua). El Iguito lies on the eastern bank of the Río Yaque del Sur in a locally mesic area, whereas the area between El Iguito and the Azua locality is the hot and extremely dry western portion of the Llanos de Azua. The species probably occurs in the intervening area, but these populations may well be limited to locally, and very restricted, mesic situations within this intermediate region.

SPECIMENS EXAMINED.—REPÚBLICA DOMINICANA. AZUA PROVINCE: 9.7 mi. (15.5 km) E Azua (MCZ 43196, AMNH 71982-86, ASFS X8058-61, ASFS V19359-89); 6 km S Peralta (ASFS V21105). PERAVIA PROVINCE: 16.5 mi. (26.4 km) S San José de Ocoa, 500 feet (153 meters) (USNM 150931-33); 1.9 mi. (3.0 km) N Cruce de Ocoa (ASFS V34095-100); 4.8 mi. (7.7 km) S Baní (ASFS V29439).

Eleutherodactylus weinlandi BARBOUR 1914:246

HOLOTYPE AND TYPE LOCALITY.—MCZ 2050; Puerto Plata, Puerto Plata Province, República Dominicana.

DIAGNOSIS.—A species of the Antillean *ricordi* group of *Eleutherodactylus* characterized by moderate size (snout-vent length: males to 30 mm, females to 40 mm); dorsum heavily to moderately overlaid with chocolate to black marbling or vermiculations on a yellowish, buffy, tan, or dark brown ground color, a pair of brightly colored (orange, golden, rich buffy) dorsolateral stripes; a small, or restricted, to large sacral blotch, contrasting (rust, orange, reddish brown, red, orange-brown, chestnut) with the remainder of the dorsum; hind limbs (including femora and crura) either heavily patterned with crossbars or immaculate, the ground color similar to that of the sacral blotch area; inguinal and supra-axillary glandular areas present, but usually very much obscured by the dark lateral coloration; expanded digital discs very poorly developed to absent; tympanum small (\bar{X} = males 2.1 to 2.4, females 2.4 to 2.9, of three subspecies); tibia/snout-vent length ($X 100$) high (males 41.9-55.7, females 45.1-56.8).

DISTRIBUTION.—Central and eastern Hispaniola. In the República Dominicana from the extreme western portion of the Cordillera Septentrional in Valverde Province, southwestward along the northern and eastern slopes of the Cordillera Central to the vicinity of Santo Domingo, but apparently absent on the eastern tip of the island in much of La Altagracia Province. In Haiti known from the northern coast (Anse à Margot), in the Chaîne de Mathieux and the Montagnes de Trou-d'Eau and their northern affiliates, and in the adjacent Dominican Sierra de Neiba (Fig. 2). Altitudinal distribution from sea level at many localities to 2600 ft (793 m) west of Vallejuelo in the Sierra de Neiba and north of Puesto Grande in the Cordillera Septentrional, and possibly occurring at higher elevations in the latter range (records without precise elevations from Loma Quita Espuela and Monte Isabel de Torres).

Eleutherodactylus weinlandi weinlandi BARBOUR 1914

DIAGNOSIS.—A subspecies of *E. weinlandi* characterized by small size (snout-vent length: males to 27 mm, females to 36 mm); dorsum tan, creamy yellow, yellow, or gray, heavily overlain with a very dark brown to black reticulum so that the ground color often is apparent only as a fine vermiculation between the extensively dark dorsal pattern; a pair of brightly colored (buffy, golden, yellow, orange, deep yellow, orange, or orange-red) dorsolateral stripes that contrast sharply with the general dorsal pattern join a small and restricted brightly colored (rust, orange-brown, rusty brown, pale orange-tan, reddish, bright orange, orange, or orange-red) sacral area; hind limbs brightly colored, the hue similar to that of the sacral area and heavily banded or stippled (especially on the crura) with dark brown to black; concealed surfaces of femora whitish to flesh, heavily mottled or irregularly banded with brown or black; venter opalescent whitish to gray; ratio of tibia/snout-vent length ($X 100$) high (males 41.9-55.1, females 45.1-54.3).

DISTRIBUTION.—Northern Haiti (Anse à Margot); the Chaîne de Mathieux and the Montagnes du Trou-d'Eau and their northern affiliates in southern Haiti, and the adjacent Sierra de Neiba in the República Dominicana; central República Dominicana from Valverde and Espaillat provinces in the north, south along the northern and eastern slopes of the Cordillera Central in Santiago and La Vega provinces, central San Cristóbal Province to within 17 km of Santo Domingo in the Distrito Nacional. Altitudinal distribution extends from sea level along the northern Dominican and Haitian coasts to maximum elevations of 2000 ft (610 m) in the Cordillera Central (west of Jarabacoa) and 2600 ft (793 m) in the Cordillera Septentrional (north of Puesto Grande) and in the Sierra de Neiba (west of Vallejuelo).

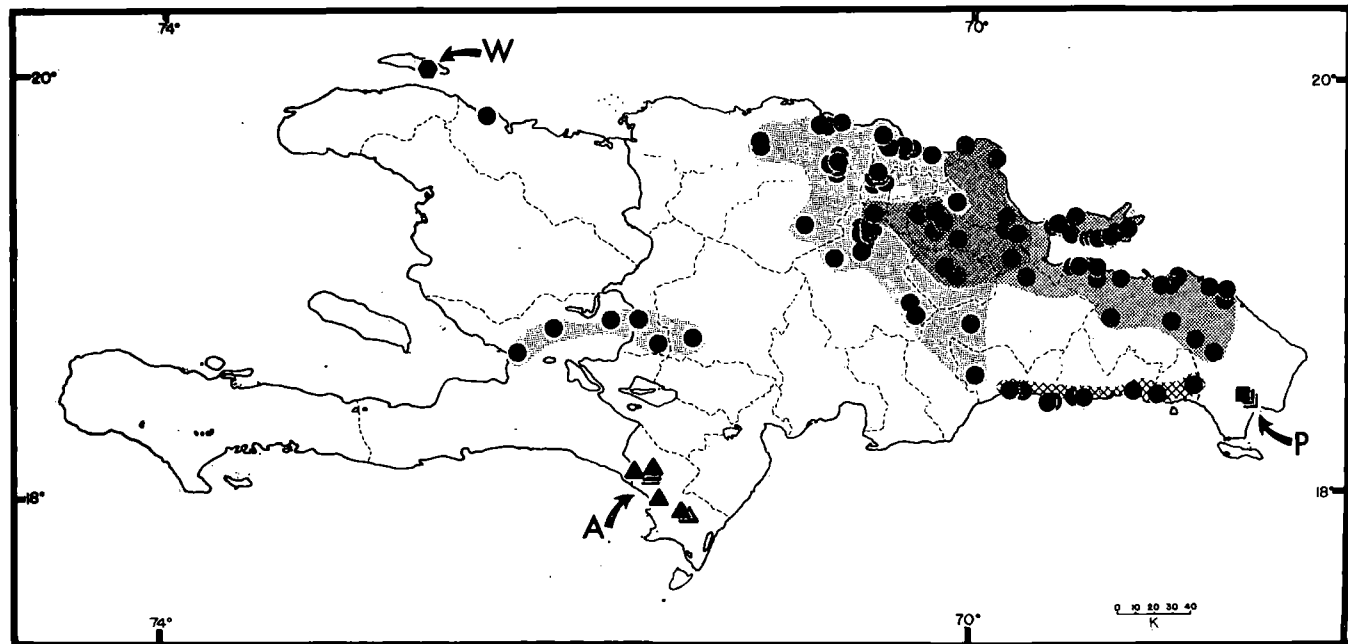


FIGURE 2.—Map of Hispaniola, showing localities and known distributions of four species of *Eleutherodactylus* as follows: hexagon, *E. warreni*; triangles, *E. alcoae*; squares, *E. probolaeus*; circles, *E. weinlandi*. Subspecies of *E. weinlandi* indicated by shading: fine stippling, *E. w. weinlandi*; coarse stippling, *E. w. chersonesodes*; crosshatching, *E. w. paralius*; overlapping symbols indicate area of intergradation between *weinlandi* and *chersonesodes*.

REMARKS.—Throughout its broad geographic range, *E. w. weinlandi* shows very little chromatic, pattern, or size variation. The pattern and coloration described above apply to most specimens. There is some variation in size of the sacral blotch, which is usually very small and restricted but is somewhat larger in a few specimens. The regular banding or stippling on the crura is a common feature of the series (see Schwartz 1965: fig. 93).

E. w. weinlandi occupies mesic situations, from the lowlands to elevations of 2600 ft (793 m) in the mountains. In the lowlands, the species is most commonly encountered, like *E. pictissimus*, in Cocos trash piles, under logs and rocks, and in piles of cacao husks. Because much of the area occupied by *E. w. weinlandi* has dark soils and the habitats are well shaded and dark, the coloration of the frogs is remarkably cryptic. At night the species is active on the ground, and we have never taken specimens on shrubs or above the surface, except on small rocks. Occasional individuals have been taken in small earthen cavities in ravine banks, and one frog was taken from a large pile of old and rotten logs in a purely edificarian situation at an abandoned sugar mill (Hojas Anchas).

E. weinlandi can vocalize, but we heard it calling on only one occasion, north of Puesto Grande; the call was a double insect-like chirp or buzz that is typical of *ricordi* group members.

E. w. weinlandi intergrades with *E. w. chersonesodes* over a compact area in northeastern República Dominicana (see details and specimens examined beyond). What is puzzling about *E. weinlandi* is the extreme disjunction of the western populations. The Anse à Margot locality (from which a series was taken in moist piles of palm-tree shavings in a *Theobroma* grove) is separated by 150 km from the nearest localities to the east (Cordillera Septentrional north of Cruce de Guayacanes). At least some of the intervening area (the xeric Valle de Cibao in Monte Cristi Province) is totally unsuitable for such a mesophile as *E. weinlandi*. However, within the Cibao, there are locally suitable areas (for instance, near the Laguna de Salodillo on the Dominico-Haitian border) that appear adequate for the species, but where it does apparently not occur. Even more puzzling is the apparent disjunct distribution of the population in the Chaîne des Mathieux-Montagne du Trou-d'Eau-Sierra de Neiba, no records being available for a distance of some 80 km (nearest approximations Vallejuelo and Jarabacoa). Much of this intervening area is mesic or semi-mesic, although it includes the xeric Llanos de Azua (which, it may be recalled, are occupied by *E. pictissimus*). One logical area of continuity between the eastern and western segments of *E. w. weinlandi* in this region is the southern mesic slopes

of the Cordillera Central (north of the Valle de San Juan), but we have not yet found the species in that region. The distributional picture in the area of the disjunctions is further complicated by the presence of three frogs from localities circumscribed by the three regions occupied by *E. w. weinlandi*. Details of this situation will be discussed beyond.

SPECIMENS EXAMINED. —HAITI. DÉPT. DU NORD: ca. 2 km inland from Anse à Margot (ASFS V10282-302). DÉPT. DE L'OUEST: 9.1 mi. (14.6 km) SE Mirebalais (ASFS V26541); 8.0 mi. (12.8 km) E Lascahobas (ASFS V26600-01); 12 mi. (19.2 km) N Port-au-Prince (MCZ 24289). REPÚBLICA DOMINICANA. VALVERDE PROV.: 8 km N Cruce de Guayacanes, 1400 ft (427 m) (ASFS V1237); 5.9 mi. (9.4 km) N Cruce de Guayacanes, 1400 ft (427 m) (ASFS V32272-74). PUERTO PLATA PROV.: Puerto Plata (MCZ 2050, MCZ 23526); Monte Isabel de Torres (MCZ 22466); 25 km S Puerto Plata (USNM 107596, MCZ 23548-50); 1 km N pass between Santiago and Puerto Plata, 2000 ft (610 m) (ASFS V1868-69); 1 km N La Cumbre, 2000 ft (610 m) (ASFS V18100); Hojas Anchas, 9.0 mi. (14.4 km) NE Altamira, ca. 800 ft (244 m) (ASFS V32184); 8 km E Imbert, 1100 ft (336 m) (ASFS V1690); 11 km SE Sosúa (ASFS V1718-19). ESPAILLAT PROV.: 4 km SE Sabaneta de Yásica (ASFS V1699-701); 6 km SE Sabaneta de Yásica (ASFS V1697); 9 km W Sabaneta de Yásica (ASFS V1713); 2 km SW José Contreras, 2000 ft (610 m) (ASFS V1886); 2 km N Puesto Grande, 1400-2200 ft (427-671 m) (ASFS V18055, ASFS V33572); 3.5 mi. (5.6 km) N Puesto Grande, 2600 ft (793 m) (ASFS V33522); 10 km N Puesto Grande, 1900 ft (580 m) (ASFS V18300-02); 10 mi. (16.0 km) N San Victor, 1400 ft (427 m) (ASFS V34029); 3.2 mi. (5.1 km) SE Gaspar Hernández (ASFS V33732-33); 3.0 mi. (4.8 km) NW Gaspar Hernández (ASFS V33768). SANTIAGO PROV.: La Cumbre, 2000 ft (610 m) (ASFS V18033); 1 km S La Cumbre (ASFS V18209); 4 km S La Cumbre (ASFS V18074-83, ASFS V18143-47); 0.5 mi. (0.8 km) SE Pedro García, 1500 ft (458 m) (ASFS V32211-17); 3.4 mi. (5.4 km) SE Los Montones, Río Bao, 1600 ft (488 m) (ASFS V33811, ASFS V33944). LA VEGA PROV.: 3 km NW La Vega (ASFS V1782); ca. 5 km N La Vega (ASFS V4174-76); 4 km N La Vega (ASFS V4177); ca. 3 km N La Vega (ASFS V4263-64); 1.5 mi. (2.4 km) N La Vega (ASFS V14087); Bayacanes (ASFS V16155-56); 13 km SW La Vega (ASFS V1734); 17 km NE Jarabacoa (ASFS V1931-32); 8 km W Jarabacoa, 2000 ft (610 m) (ASFS V18388); 1.2 mi. (1.9 km) SE Bonao, 700 ft (214 m) (ASFS X8128); 75 km N Santo Domingo, road to Santiago (=near Piedra Blanca) (AMNH 44018, AMNH 44021). DUARTE PROV.: Loma Quita Espuela (MCZ 23525). SAN CRISTÓBAL PROV.: 2 km W Esperalvilla (ASFS V14394). DISTRITO NACIONAL: 17 km NW Santo Domingo (ASFS V3145-46). LA ESTRELETA PROV.: 5 km S Elias Piña, 2200 ft (671 m) (ASFS V415); 6.7 mi. (10.7 km) E Hondo Valle, 2500 ft (763 m) (ASFS V31409, ASFS V31425-26). SAN JUAN PROV.: 7 km W Vallejuelo, 2600 ft (793 m) (ASFS V392).

Eleutherodactylus weinlandi chersonesodes SCHWARTZ 1965:115

HOLOTYPE AND TYPE LOCALITY.—MCZ 43203; 8 km W Samaná, Samaná Province, República Dominicana.

DIAGNOSIS.—A subspecies of *E. weinlandi* characterized by small size (snout-vent length: males to 28 mm, females to 35 mm); dorsum almost completely overlain with a dark brown reticulum with faint indications of a pale tan ground color; a pair of contrasting, but not particularly brightly colored (yellow-buff, yellow, dull yellow, buffy) dorsolateral stripes that join a large, richly colored (rich orange-brown, rich reddish brown, reddish brown, or dark orange-brown) sacral area; hind

limbs as richly colored as sacral area, without markings on the crura but with a dark brown reticulum on a pinkish-white background on the concealed surfaces of the femora, and with a band of the sacral color extending along the anterior face of the femora; venter and throat gray to dark pearl gray; ratio of tibia/snout-vent length ($\times 100$) high (males 47.4-55.7, females 45.4-56.8).

DISTRIBUTION.—Eastern Hispaniola, including the Península de Samaná and the eastern República Dominicana from northeastern San Cristóbal Province south-eastward to central La Altagracia Province. Intergradation with *E. w. weinlandi* in Duarte, María Trinidad Sánchez, Sánchez Ramírez, and La Vega provinces.

REMARKS.—The large number of specimens presently available of *E. w. chersonesodes* confirm the diagnostic characters of the subspecies. Juvenile individuals may have the crura with some vague stippling or marbling, which is regularly absent in the long series of adults from both the Península de Samaná and eastern República Dominicana. This pattern easily distinguishes *chersonesodes* from *weinlandi*. In addition, the dorsum of *chersonesodes* is more solidly dark brown (see Schwartz 1965:figs. 93 and 94), with only faint remnants of a paler ground color; the sacral blotch area is much more extensive in *chersonesodes* than in *weinlandi*; and the basic colors involved in the sacral blotch area in *chersonesodes* are darker and richer than those in *weinlandi*. The two subspecies are approximately of the same size (and there are now long series of *chersonesodes* available), and the tibia/snout-vent length ratios are quite comparable. The darker gray ventral color of *chersonesodes* is distinctive when compared with the pale ventral color of *weinlandi*.

E. w. chersonesodes is extremely abundant on the Península de Samaná, where it occurs both in the lowlands near the coast (where one specimen was secured from a small and decayed pile of *Cocos* trash within 10 ft [3.1 m] of the mangrove border) and in the Sierra de Samaná, where natives found many more specimens than we preserved. In the eastern non-Samaná, areas of the República Dominicana, *chersonesodes* occupies mesic regions and occurs in coastal *Cocos* groves (as at Playa El Coco and Playa de Guaco) and in *cacaotales* and *cafetales* associated with the lowlands of the Cordillera Oriental. The altitudinal distribution of *chersonesodes* is from sea level to 1000 ft (305 m) between Sánchez and Las Terrenas in the Sierra de Samaná and near Gonzalo in the *haitises* region. Although there are presently no records from the Cordillera Oriental (which reaches a maximum elevation of 2296 ft [700 m] in its eastern section), I have no doubt that the species occurs there, and also that the hiatus shown on the map (Fig. 2) is artificial.

Intergradation between *weinlandi* and *chersonesodes* occurs in a compact region embracing four provinces. In this lowland and very mesic region, specimens show precisely those characteristics which are intermediate between the two subspecies—vague banding or marbling on the hind limbs, medium size of the sacral blotch, and intermediate extent

of the dark dorsal pigmentation, as well as less rich and more bright coloration of the sacral area.

SPECIMENS EXAMINED.—REPÚBLICA DOMINICANA. SAMANÁ PROVINCE: 3.3 mi. (5.3 km) NE Sánchez, 1000 ft (305 m) (ASFS V34126); 7.6 mi. (12.2 km) NE Sánchez, 1000 ft (305 m) (ASFS V34288-96, ASFS V34352-83, ASFS V34839-81); 14 km E Sánchez (ASFS V2010); 22 km E Sánchez (ASFS V14120); 5 km E Las Terrenas (ASFS V21848-51); Samaná (USNM 74983-92, AMNH 34201-02); west of Samaná (AMNH 34519); Samaná and Laguna (USNM 65106-08); 6 km W Samaná (ASFS V1868-71); 8 km W Samaná (MCZ 43203, ASFS V1989-93); Laguna (AMNH 34495-96); Rojo Cabo (USNM 34261); Las Flechas (not mapped) (AMNH 34177-80); Río San Juan (USNM 74625, USNM 74629-40, UMMZ 92212-13); Península de Samaná (USNM 66980). EL SEBO PROV.: Caño Hondo (AMNH 3297-301); Cueva de Caño Hondo (ASFS X9278-83); Boca del Infierno (USNM 74960-61); Sabana de la Mar (AMNH 34199, AMNH 44133); 3.5 mi. (5.6 km) S Sabana de la Mar (ASFS X7971-74); Las Cañitas (USNM 65709, ASFS V35321); 10.5 km N Hato Mayor (ASFS V35328, ASFS V35301-02, ASFS V35306-07); 1.4 mi. (2.2 km) E Miches (ASFS X9341); 1.1 mi. (1.8 km) W Miches (ASFS V28786-92); 2.6 mi. (4.2 km) NE La Vacama (ASFS V28986-91); 20.2 mi. (32.3 km) NW, 3.4 mi. (5.4 km) N La Vacama, Playa de Guaco (ASFS V29327-76, ASFS V29415-16); 7 km W El Cuy (ASFS V17584-85). LA ALTAGRACIA PROV.: 24.8 mi. (39.7 km) ESE Miches (ASFS X7893); Playa El Coco, 46 km N Higüey (ASFS V17499-505); 3.2 mi. (5.1 km) W Higüey (ASFS X751-57); 4.7 km NW La Enea (ASFS V948). SAN CRISTÓBAL PROV.: 5.0 mi. (8.0 km) NE Gonzalo, 1000 feet (305 meters) (ASFS V29539).

E. w. weinlandi X *E. w. chersonesodes*. REPÚBLICA DOMINICANA. DUARTE PROV.: 6 km NE San Francisco de Macorís (ASFS V2947); ca. 4 km NE Pontón, Río Cuaba (ASFS V3001); 6.4 mi. (10.2 km) SE Tenares, 700 ft (214 m) (ASFS V33555); 7.5 mi. (12.0 km) NW Cruce de Pimentel (ASFS V33481-84); 9 km NW Pimentel (ASFS V1820-22); 3 km NE Villa Riva (ASFS V1827-32). MARÍA TRINIDAD SÁNCHEZ PROV.: 3.3 km S Cabrera (ASFS V4253); 2.1 mi. (3.4 km) NE Río San Juan (ASFS V33698-702); 2 km S El Factor (ASFS V1853-59); 4 km N Azucey (ASFS V16081-83); 1.0 mi. (1.6 km) S Caño Hondo (ASFS V34135-39). SÁNCHEZ RAMÍREZ PROV.: 4.4 km E Cotuí (ASFS V627-29); 1 km SE La Mata (ASFS V18439, ASFS V18574-78, ASFS V33671). LA VEGA PROV.: 8 km S Moca (ASFS V4332).

Eleutherodactylus weinlandi paralius new subspecies

FIGURE 3

HOLOTYPE.—USNM 194004, an adult female, from 14 km SE, 1 km N Boca Chica, San Pedro de Macorís Province, República Dominicana, one of a series taken by James R. Dennis, James A. Rodgers, Jr., and Albert Schwartz on 12 August 1969. Original number ASFS V19390.

PARATYPES.—AMNH 87216-49, CM 54132-35, MCZ 84637-40, USNM 194005-08, same data as holotype; ASFS X9321, 12 km NE La Romana, La Romana Province, República Dominicana, R. Thomas, 19 July 1963; ASFS V35081, 12 km NE La Romana, La Romana Province, República Dominicana, D.C. Fowler, 22 November 1971; ASFS V28596-97, 7 km S Aeropuerto Internacional de las Américas, Punta Caucedo, Distrito Nacional, República Dominicana, D. C. Fowler, 1 July 1971; MCZ 84641, 11 km S Aeropuerto Internacional de las Américas, Punta Caucedo, Distrito Nacional, República Dominicana, D. C. Fowler, 7 July 1971; ASFS V29511-14, 11 km E Boca Chica, Distrito Nacional, República Dominicana, D. C. Fowler, A. Schwartz, 6 August 1971; ASFS V22445, Santo Domingo, La Feria, Distrito Nacional, República Dominicana, A. Schwartz, 19 December 1970; ASFS V2465,



FIGURE 3.—Dorsal views of (left) *Eleutherodactylus w. paralius* (holotype, USNM 194004) and (right) *E. warreni* (holotype, CM 54138).

ASFS V2467, 5.1 mi. (8.2 km) E Santo Domingo (from Río Ozama), Distrito Nacional, República Dominicana, D. C. Leber, 19 June 1964; CM 54136-37, USNM 194009-11, 1.8 mi. (2.9 km) S Boca del Soco, San Pedro de Macoris Province, República Dominicana, D. C. Fowler, native collectors, 16 July 1971; AMNH 87250-51, MCZ 84642-44, 15.5 mi. (24.8 km) E San Pedro de Macoris, Río Cuyamaya, La Romana Province, República Dominicana, D. C. Fowler, A. Schwartz, 12 July 1971.

DISTRIBUTION.—The southern Dominican coast, from Santo Domingo in the west, east to La Romana Province. Intergradation with *E. w. weinlandi* and *E. w. chersonesodes* unknown, but see discussion beyond.

DIAGNOSIS.—A subspecies of *E. weinlandi* characterized by large size (snout-vent length: males to 30 mm, females to 41 mm); dorsum yellow, pale yellow-tan, or pale buffy; dorsolateral stripes unicolor with dorsal ground color (occasionally slightly more yellow to golden); dorsal dark pattern brown, usually very restricted and diffuse, with only a dark scapular chevron clearly defined in many specimens; sacral area pale rusty, brick red, rich orange, rust, or bright orange, restricted by paler ground color anteriorly; hind limbs pale rusty, pale orange, dull reddish brown, rust, bright orange, or tan; crura unmarked, with darker or with some vague darker gray marbling or suffusions, occasionally with clear dark transverse bars; concealed surfaces whitish, tan, or gray, with dark brown marbling; venter white to pale gray; ratio of tibia/snout-vent length ($\times 100$) low (males 44.1-50.5, females 44.8-50.6).

DESCRIPTION OF HOLOTYPE.—An adult female with the following measurements (in mm): snout-vent length 40.4, head length 14.8, head width 14.5, longitudinal diameter of tympanum 3.2, longitudinal diameter of eye 5.0, distance from naris to anterior corner of eye 4.5, femur 17.5, tibia 18.3, fourth toe 16.0, tibia/snout-vent length ($\times 100$) 45.3. Head slightly longer than distance from snout to posterior border of tympanum; snout truncate, with nares prominent at anterior ends of canthus rostralis; diameter of eye longer than distance from naris to anterior corner of eye; interorbital space 5.0, equal to diameter of eye; diameter of tympanum much less than diameter of eye; distance from tympanum to eye equal to one-third diameter of tympanum. Digital discs present, small, largest on digits 3 and 4, that of digit 3 the largest and equal to about one-quarter size of tympanum. Fingers long, unwebbed, 3-4-2-1 in order of decreasing length; subarticular tubercles well developed, prominent, pale gray. Toes relatively long, all with slight basal webbing, 4-3-5-2-1 in order of decreasing length; subarticular tubercles large, prominent, gray. Heels do not touch when femora are held at right angles to body axis. Dorsum smooth, with two non-glandular warts between the angle of the jaw, tympanum, and forelimb insertion; throat and venter smooth, belly disc feebly developed.

Dorsal surfaces of all limbs smooth; posterior faces of thighs with low, pavement-like granules. Inguinal and supra-axillary glands absent. Tongue large, very slightly nicked, free behind, its greatest width equal to about one-half that of floor of mouth. Prevomerine teeth in two long arched series, extending from outside the choanae and adpressed against them, the two series separated from each other medially by a distance equal to about one-quarter the diameter of a choana.

COLORATION OF HOLOTYPE.—Dorsal ground color yellow, with a dark brown dorsal pattern composed of an irregular dark interocular bar and a moderately prominent scapular chevron, the area between these two figures marbled irregularly with dark brown; a pair of dorsolateral stripes, which are concolor with the dorsal ground color; sides and mid-back irregularly marbled with dark brown, with a restricted pale rusty sacral blotch area; upper surfaces of hind limbs pale rusty, with the concealed surfaces marbled heavily with dark brown, the crura and pedes virtually immaculate; forelimbs yellow with some vague grayish markings; ventral ground color white with fine brownish stippling on throat.

VARIATION.—Eleven males have the following measurements (in mm) (extremes and means): snout-vent length 22.0-29.5 (25.6); head length 8.7-11.7 (9.9); head width 8.4-11.1 (9.7); tympanum 2.2-2.7 (2.4); eye 3.0-4.0 (3.4); naris to eye 2.4-3.6 (2.9); femur 9.3-13.3 (11.1); tibia 10.6-14.6 (12.0); fourth toe 8.9-12.7 (9.6); tibia/snout-vent length ($\times 100$) 44.1-50.0 (46.7). Thirteen gravid and adult females measure: snout-vent length 29.3-40.4 (35.4); head length 10.9-14.8 (12.2); head width 10.9-14.9 (13.2); tympanum 2.4-3.3 (2.9); eye 3.9-5.0 (4.5); naris to eye 3.1-4.7 (4.1); femur 12.2-18.0 (15.7); tibia 13.2-19.3 (16.5); fourth toe 11.8-16.9 (14.5); tibia/snout-vent length ($\times 100$) 44.8-50.6 (46.7).

E. w. paralius is somewhat variable in dorsal pattern. Some specimens (AMNH 87248-49) are almost as heavily patterned dorsally as *E. w. weinlandi*. The heavy dorsal markings of ASFS X9321 from 12 km NE La Romana have been previously noted (Schwartz 1965:119). Taken as a group, however, both adults and juveniles agree quite well with the pattern description of the holotype. There is no evidence that specimens from the two range extremes (Santo Domingo; 12 km NE La Romana) are any closer to the respective subspecies, which they approximate geographically (*weinlandi* in the west, *chersonesodes* in the east), than are specimens from the more central portion of the range of *paralius*. Consequently, there are no known intergrades between *paralius* and either *weinlandi* or *chersonesodes*.

The dorsal pattern typically consists of a much reduced dark brown reticulum (that is usually apparent only on the dorsum) bounded by a fairly well-defined interocular dark bar, and a dark scapular chevron, and another at about the middle of the back. Pale dorsolateral stripes are present but usually are similar to the pale (yellow, pale yellow-tan, pale buffy) dorsal ground color. The sacral area is faintly colored with pale rusty, brick red, rust, rich or bright orange; the same colors occur on the hind limbs, the crura of which are immaculate or with some vague grayish or brownish marbling or stippling. The concealed surfaces of the femora are whitish, tan, or gray, and extensive dark brown markings are present. The venter is white to pale gray, as is the throat, and the venter has, in addition, some fine dark brown stippling in most adults.

The supra-axillary and inguinal glandular areas' distinctness is variable in occurrence, but both areas are readily discernible in less heavily pigmented individuals.

COMPARISONS.—*E. w. paralius* differs from both *E. w. weinlandi* and *E. w. chersonesodes* in having a greatly reduced dorsal pattern and larger size (see Appendix 1). The hues involved in the sacral area and hind limbs of *paralius* are less bright than in either of the other two subspecies, and the tibia/snout-vent ratio is much less in both sexes of *paralius* than in both sexes of either *weinlandi* or *chersonesodes*. Detailed comparisons are unnecessary; the three subspecies are ex-

ceptionally distinct in numerous details of size, pattern, and coloration. The differences are so striking that when I collected the first series from the type locality, I was uncertain that these frogs were correctly assigned to *E. weinlandi*.

REMARKS.—*E. w. paralius*, as its name implies, occurs along the southern coast of the República Dominicana, a region that is moderately mesic, with residual stands of semi-mesic woods often situated on limestone platforms or substrate. The type locality is such a place, having a rich but open lowland forest on a *diente de perro* base. The woods south of the Aeropuerto Internacional on Cabo Caucedo are somewhat more luxuriant and lie on a raised limestone platform surrounded by sand and rock beach. The specimens from La Romana were found in a deep, rocky, well-forested, mesic ravine that cuts through otherwise cultivated sugar cane fields—an altogether specialized situation. One frog was taken from under an old, deep trash pile behind the exposed beach on Cabo Caucedo, and the specimens from the Río Cumayasa were taken at night from paths in a grassy riverside pasture and on rocks adjacent to a gravel road. The Boca del Soco frogs were secured in Cocos trash piles at the edge of a coastal palm grove, and the single specimen from Santo Domingo was taken from beneath a large rock in a moist, dead grass pile near the ocean. Mertens (1939:30) reported a specimen from Cueva de Santa Anna, which lies within the city of Santo Domingo; he described the sacral area and hind limbs as “lebhaft ziegelrot,” in agreement with the rust color typical of *paralius*. The specimens from east of Santo Domingo were secured at night in a mesic limestone-cliff forest.

The voice of *E. w. paralius* has been described as “a series of irregular bubbly ‘bleeps’ or ‘ticks’” (type locality), and a “low intensity ‘peep’” (east of Santo Domingo). The males call erratically and are easily disturbed, even under very favorable moisture conditions. The calling sites include a cave (east of Santo Domingo), large rocks, and herbs and shrubs (up to 3 ft [0.9 m] above the ground) at the type locality. The favored shrub for calling here is *Zamia*. At the Río Cumayasa a male was secured as it called from exposed rocks adjacent to a gravel road through semi-mesic *Acacia* woods. Another male was found calling on a low shrub, 6 in (15 cm) above the ground in limestone woods 11 km E Boca Chica.

The association of *E. w. paralius* with limestone areas on this southern coast is probably not fortuitous. Such porous limestone outcroppings and platforms offer advantageous diurnal retreats for the frogs and also support (even today) relatively luxuriant wooded growth for nocturnal protection and activities. However, it is also obvious that *E. w. paralius* can persist in situations close to and associated with human

activities, if there are trash and vegetational heaps that offer moist diurnal havens.

The absence of acknowledged intergrades between *paralius* and either *weinlandi* or *chersonesodes* is puzzling, because *paralius* presumably comes in contact with these subspecies at the western and eastern extremes of its range, respectively. Although only a short distance separates the closest *paralius* and *weinlandi* localities (Santo Domingo and 17 km NW Santo Domingo), the two taxa remain quite distinct in these areas. The same holds true at the eastern extreme of the range, where the localities for *paralius* and *chersonesodes* (12 km NE La Romana and 4.7 km NW La Enea, respectively) are separated by about 25 airline km. In neither case is there an obvious geographic barrier that might explain the separation of, and lack of intergradation between, the subspecies.

The map (Fig. 2) shows a large hiatus in the range of *E. weinlandi*. The subspecies *paralius* occurs in the south, *weinlandi* in the west, and *chersonesodes* in the north and east. I do not think this hiatus actually exists. The area is quite mesic, and there are extensive riverine gallery forests that must support *E. weinlandi*. The relationships of the three subspecies within this region will be most interesting to ascertain.

Eleutherodactylus alcoae SCHWARTZ 1971:26

HOLOTYPE AND TYPE LOCALITY.—CM 45889; 22 km NE Cabo Rojo, 1500 ft (458 m), Pedernales Prov., República Dominicana.

DIAGNOSIS.—A species of the Antillean *ricordi* group of *Eleutherodactylus* characterized by the combination of moderate size (snout-vent length: males to 38 mm, females to 45 mm); dorsum yellow or flesh-colored to tan or pale tan to yellow-green with various dark dorsal markings, the most stable of which are a dark (gray to almost black) interocular bar and a dark scapular chevron; remainder of dorsum mottled, marbled, or irregularly marked with dark brown pigment; dorsolateral stripes absent; hind limbs stippled or marbled with dark (never crossbanded), concealed surfaces brown to purplish, occasionally suffused with orange, and without a dark reticulum or vermiculations; venter white; throat heavily to moderately stippled with brown; throat ground color, underside of all limbs and brachia bright yellow in some specimens; inguinal and supra-axillary glandular areas present; digital discs expanded and well developed, that of digit 3 equal to about one-third to one-half size of tympanum; tympanum large (\bar{X} = males 3.1, females 3.4), and tibia/snout-vent length ($X/100$) low (males 41.8-51.6, females 43.6-47.5).

DISTRIBUTION.—The República Dominicana, south of the Massif de la Selle-Sierra de Baoruco, from the Río Pedernales east to 32 km SE Pedernales, on the Península de Barahona; may also be expected in extreme southeastern Haiti (Fig. 2).¹ Altitudinal distribution from sea level to 2000 ft (610 m) in the Sierra de Baoruco.

¹ Since this manuscript was completed, specimens of *E. alcoae* (ASFS V39545, ASFS V39976-84) were collected at the village of Los Patos, Barahona Province, República Dominicana, immediately adjacent to the ocean on the east coast of the Península de Barahona. The habitat is a steep and cave-riddled hillside with dense hardwood forest cover, a much more mesic situation than any other where *E. alcoae* has been collected. One frog was taken during the day on the

REMARKS.—*E. alcoae* was described on the basis of five frogs from two general regions: a cave in the very arid lowlands of the Península de Barahona and rather mesic deciduous-*Acacia* forests at elevations between 1500 and 2000 ft (458 and 610 m) on the Sierra de Baoruco above Cabo Rojo. We made a special search for additional *E. alcoae* in 1971, and there are now 52 specimens of the species from eight localities in this region. The westernmost specimens are from 6.0 mi (9.6 km) N Pedernales, along the Dominico-Haitian border, and the easternmost are from 7 km N, 20.0 km SE Cabo Rojo (= 32 km SE Pedernales). The species extends into the Sierra de Baoruco along the road from Cabo Rojo to Aceitillar to an elevation of 2000 ft (610 m) but appears to be rather uncommon at such a high elevation. In some areas *E. alcoae* is precisely syntopic with *E. p. pictissimus*; and although the two species are not easily recognized at night in the field by flashlight, they are nevertheless quite distinct in many ways. Both reach about the same size (it may be recalled that it is the Sierra de Baoruco *E. p. pictissimus* that are the largest specimens of that subspecies), but the tympanum of *alcoae* is larger in both sexes (*alcoae*: males 2.6-3.7, females 4.2-5.6; *p. pictissimus*: males 1.8-2.8, females 2.2-3.9). Other mean differences are also apparent for most measurements (see Appendix 1), but the tibia length means for females of both species are very comparable. *E. alcoae* may also be readily differentiated from *E. pictissimus* by its well-developed digital discs.

I have noted previously that *E. pictissimus* is apparently mute. *E. alcoae*, on the other hand, is vocal, and loud choruses of the species were encountered on several occasions in one of the most rigorous situations for an anuran in the Antilles. On 14 August 1971 we visited an arid limestone area with a flora of cacti and *Acacia* that lies 32 km SE Pedernales. Many males were heard vocalizing (the call a single "cheep"), despite no previous rain in this desert area. There was a brief 10 minute rain that greatly increased the number of calls, but we were unable to secure or even locate any males actively calling. We revisited this same locality on 22 August 1971, and once again, despite no rains on that day (but heavy rains occurred during the late evening of 21 August), we heard many calling male *alcoae*. Their vocalizations were a single, or occasionally double, "cheep," and we were successful in locating and collecting calling males from shrubs, bushes, and a tree crotch

floor of a cave, and the remainder were secured at night while the males were calling a single (occasionally two-note) chirp from vines and shrubs up to 6 ft (1.8 m) above the ground and from rock crevices near the cave entrance. Many more were heard than were collected. Thirty-two eggs were deposited over-night in the plastic bag in which both males and females were housed; whether this represents the clutch of more than one female is unknown. In color and pattern, the Los Patos series does not differ strikingly from specimens from low elevations on the Península de Barahona; the venters are white and the throats are finely stippled with gray. The Los Patos locality is not shown on the distribution map in the present paper.

up to 4 ft (1.2 m) above the ground. None was found calling from the ground, rocks, or the pocketed limestone substrate. Even more remarkably, two frogs were secured in amplexus, completely exposed on bare limestone. The upper frog was grasping the lower frog anterior to the forelimbs, and both were walking slowly with the hind limbs straight and in almost tetanic contraction. Amplexing pairs of any Antillean *Eleutherodactylus* are extremely difficult to locate, and rarely has amplexus been seen in any Antillean species (only *E. cundalli* and *E. nubicola* in Jamaica and *E. patriciae* in Hispaniola as far as I am aware). However, the peculiar stance and gait of this pair suggested that open and exposed areas may not be the customary site of amplexus; when the two individuals were dissected in the laboratory, it was found that they were both males. This is the first instance of which I am aware of homosexual amplexus being observed in *Eleutherodactylus*, although it is a common occurrence in many (primarily water-breeding) anurans.

A second instance of male vocalization occurred on 21 August 1971 in the vicinity of L'Eglise at an elevation of 1500 ft (458 m) in the Sierra de Baoruco. Here males were calling from exposed rocks, cavities in rocks, an exposed root 3 in (8 cm) above the ground, and the stems and leaves of shrubs. Finally, males were heard calling and collected 6.0 mi (9.6 km) N Pedernales at an elevation of 800 ft (244 m). The frogs were calling from saplings (3 ft [0.9 m] above the ground), vine tangles (3 ft), and on *diente de perro* limestone outcroppings on the ground in a more or less shaded and semi-mesic cut-over *Acacia* hillside adjacent to an open field. Many other males were heard calling on the east side of the road at this locality, in *Acacia* weeds with a *Bryophyllum* understory.

The locality records suggest that *E. alcoae*'s distribution is primarily lowland, and it is associated in these lowland regions with eroded limestone. In every instance, our specimens were taken on or near pocketed and eroded limestone, regardless of the surrounding vegetational associations (varying from harsh open desert to semi-mesic *Acacia*-deciduous woods). The species may be extremely abundant and easily secured, once one knows the calling sites and habitat requirements. The Península de Barahona is sandy along its eastern and western shores, but a rugged and raised limestone ridge courses down the center of the peninsula. This ridge supports an extensive forest, and our collecting localities southeast of Pedernales lie on or immediately adjacent to this ridge, which reaches a maximum elevation of 322 m in Cerro Caballo south of the Pedernales-Oviedo road. We never collected *alcoae* at Oviedo, in the now cultivated savannas in the east, nor at Pedernales in the very arid and sandy regions in the west. Once one begins to ascend

the Massif de la Selle above Pedernales, however, the limestone outcroppings begin and *E. alcoae* occurs.

E. alcoae is exceptionally variable in dorsal pattern and to some extent in coloration. The dorsal ground color is pale (yellow, flesh, pale tan, tan, or yellow-green), with dark gray to brown markings. These markings may be more or less uniform in distribution (ASFS V30093), or they may be more coarse and show a prominent dark interocular bar and scapular chevron (ASFS V30044). All variations between these two extremes occur; in one extreme instance the dorsum appeared uniformly and faintly stippled, without an interocular bar or chevron (ASFS V30065). The concealed surfaces are brown, but occasional specimens have an orange wash or suffusion on these surfaces. The most striking differences in color in *E. alcoae* are those associated with elevation. Lowland (up to 600 ft [183 m] elevation) frogs are pale and much less brightly colored than those from upland areas (1500 ft [458 m] and above). In the latter specimens, the throat, brachia, and undersides of the hind limbs are bright yellow, whereas in lowland specimens the throat is white, stippled or blotched with brown, and the brachia and limbs lack any bright pigment. It has not yet been determined whether these differences result from deme formation in a frog with specialized habitat requirements or from differentiation at the subspecific level in *E. alcoae* populations. The fact that the known range of *E. alcoae* is at present so circumscribed argues against the latter interpretation. Once specimens are available from southeastern Haiti (where *E. alcoae* undoubtedly occurs, since we have specimens from very near the Río Pedernales, which here forms the international boundary), a more definite interpretation can be made of these pigmental differences between lowland and highland specimens.

SPECIMENS EXAMINED.—REPÚBLICA DOMINICANA. PEDERNALES PROVINCE: 6.0 mi (9.6 km) N Pedernales, 800 ft (244 m) (ASFS V30091-105); 24 km NE Cabo Rojo, 2000 ft (610 m) (ASFS V16678); 22 km NE Cabo Rojo, 1500 ft (458 m) (CM 45889); 21 km NE Cabo Rojo, 1500 ft (458 m) (USNM 166959); 21 km N Cabo Rojo, L'Eglise, 1500 ft (458 m) (ASFS V30038-46); 8 km N, 2 km E Cabo Rojo (ASFS V21544, MCZ 43255); 7 km N, 2.4 km SE Cabo Rojo, 200 ft (61 m) (ASFS V29708-09); 7 km N, 17.6 km SE Cabo Rojo (ASFS V30075-78); 7 km N, 20.0 km SE Cabo Rojo, 600 ft (183 m) (ASFS V29763-65, ASFS V30059-72).

Eleutherodactylus probolaeus SCHWARTZ 1965:110

HOLOTYPE AND TYPE LOCALITY.—MCZ 43197; 0.5 mi (0.8 km) NW Boca de Yuma, La Altagracia Province, República Dominicana.

DIAGNOSIS.—A species of the Antillean *ricordi* group of *Eleutherodactylus* characterized by the combination of moderate size (snout-vent length: males to 30 mm, females unknown); dorsum tan, pale tan, or yellow-tan, having mottled dark brown

to black pattern with three prominent dark areas (an eroded or truncate inter-orbital triangle with its apex pointed posteriorly, a broad scapular chevron, and an irregular rectangular or subquadrate mid-back blotch); dorsolateral stripes pale, same color as dorsal ground color; hind limbs marbled dark brown, the pattern of which may consist of two or three vague crossbars on the crura; concealed surfaces of femora black or dark brown, paler (gray) medially and showing some remnants of the pale dorsal ground color; venter opalescent; throat and underside of limbs gray; inguinal and supra-axillary glands present; expanded digital discs well developed, that of digit 3 equal to about one-quarter size of tympanum; tympanum small (2.3-3.0 in males); and tibia/snout-vent length ($\times 100$) low (47.0-51.7 in males).

DISTRIBUTION.—Known only from the vicinity of the type locality, La Altagracia Province, República Dominicana (Fig. 2).

REMARKS.—*E. probolaeus* was described (as a subspecies of *E. pictissimus*) from three male specimens collected in 1963. Despite repeated visits to the type locality and the fact that the frog appears to be common there, only six additional specimens (all males) have been found. Many males have been heard calling (a trilling "brrrt" call, followed at times by a series of "bzeut's"), but the dense woods and the fact that the frogs call primarily from areas of dense understory makes it extremely difficult to collect specimens. The two new localities are both almost adjacent to the type locality.

The area where *E. probolaeus* occurs is remarkably specialized. All specimens have been taken from the flat top of a limestone ridge that parallels the coast behind the village of Boca de Yuma. The forest is semi-mesic, with many high trees, lianas, epiphytes, often a dense understory consisting of *Bryophyllum* and *Zamia*, as well as other small herbs and shrubs. The old road between Higüey and Boca de Yuma ascended this ridge and then descended on the southern face, so that the crossing was accomplished in 2.5 km, much of which was steep. A new road has been completed between these two settlements. It reaches Boca de Yuma from the west, ascends, and then passes along the ridge top for several kilometers. In 1971 we did not find *E. probolaeus* along this new stretch of road, which passes through virtually undisturbed forest similar to that at and near the type locality, just a few kilometers to the east. The frogs were not heard calling in this region, although on the same night many were heard calling at the type locality. Likewise, in the slightly more xeric, but far from arid, deciduous woods near the coast between Punta Cana and Juanillo, we did not hear or encounter *E. probolaeus*, although this area also appears at least grossly suitable. I can offer no explanation for the apparently very circumscribed distribution of *E. probolaeus*. It appears to be a recent arrival from elsewhere, but the species seems not to be closely allied to *E. pictissimus* (see below), and certainly not to *E. weinlandi*. *E. probolaeus* may

demonstrate a relict distribution in this southeastern area, but even this suggestion suffers from the very small area it is known to occupy.

I described *E. probolaeus* as a subspecies of *E. pictissimus*, even though there is a hiatus of some 185 km to the east of the closest known *E. pictissimus* station (south of Bani). We now know that the intervening area is in large part occupied by *E. weinlandi paralius*, a species with which *E. probolaeus* cannot logically be associated. Although the patterns of *pictissimus* and *probolaeus* are somewhat similar (dark dorsal markings on pale dorsal ground and dorsolateral stripes that are colored similarly to the back), the pattern details are quite different (Schwartz 1965:fig. 92). The digital discs in *probolaeus* are larger than those of *pictissimus*, and *probolaeus* is vocal whereas *pictissimus* appears to be mute. Although *probolaeus* is a stockier frog, this difference is not apparent when comparing the tibia/snout-vent length ratios in males of the two species (Appendix 1). Everything considered, it seems likely that *probolaeus* is an eastern Hispaniolan endemic whose history has not been closely allied to that of *pictissimus* (see discussion below).

Calling male *E. probolaeus* have been taken from a shrub limb and a *Bryophyllum* leaf, both 2 ft (0.6 m) above the ground. *Bryophyllum* and *Zamia* both are common calling sites for males, and the frogs have been taken between 1 and 6 ft (0.3 and 1.8 m) on these plants. A single male was collected on a pile of dead and leafless slash adjacent to a path through the forest at a height of 4 ft (1.2 m) above the ground. Interestingly, many males were heard calling on nights following hot and dry days, whereas on nights after rainy and overcast days the number of calling males was decreased.

In an effort to locate a related (to *E. probolaeus*), non-Hispaniolan species of the *Eleutherodactylus ricordi* group, I have examined a series of 26 *E. monensis* Meerwarth, taken by Richard Thomas in 1965 at Anclaje Sardinero, on Isla Mona. This inlet lies some 70 km to the east of the extreme southeastern tip of Hispaniola, and thus it would seem reasonable from a geographic standpoint that *E. probolaeus* might be related to *E. monensis*. The two species are similar, but no more so than either is to other species within the complex. Examination of eight male *E. monensis* shows that the Mona species appears not to reach so large a size as *probolaeus* (26.4 versus 29.8 mm) and has lower means in all head and limb segments measurements (Appendix 1). The tibia/snout-vent length ratio also is slightly lower in *monensis* than in *probolaeus*. Thomas's field notes on *E. monensis* indicate that the dorsum is light brown to tan (somewhat paler on the sides) with chocolate brown dorsal markings the most constant of which are an interocular bar and

a scapular chevron. The venter is brown to pinkish-gray, and the concealed surfaces are tan, heavily marbled with brown and occasionally suffused with reddish brown. The discs are large, as in *probolaeus*, the voice was reported by Thomas to be a "short, whispering trill of 2 or 3 notes, repeated several times." Diurnal retreats include rock and palm trash piles as well as isolated rocks, and at night the frogs were seen on the ground in a *Cocos* grove. One frog was taken while on a leaf about 1 ft (0.3 m) above the ground in this same grove, but the species is primarily terrestrial. Although *E. monensis* and *E. probolaeus* resemble each other in several ways, they are distinct and are probably no more closely related to each other than either is to, say, *E. pictissimus* or *E. alcoae*.

Since Puerto Rico lacks a spotted member of the *ricordi* complex, it seems much more likely that *E. monensis* has been derived from Hispaniola than from the richly-colored and unmarked Puerto Rican *E. richmondi*. Schmidt (1926:153-154) allied *monensis* with an unnamed Hispaniolan species (thus following Stejneger 1904:564) and also placed it in a sequence of *weinlandi-monensis-richmondi-lentus* as a series of vicarious species. Although Schmidt's sequence may not be correct, still the relationships of these four species (and many others in the Greater Antilles) are unequivocal.

SPECIMENS EXAMINED.—REPÚBLICA DOMINICANA. LA ALTAGRACIA PROV.: 0.5 mi (0.8 km) NE Boca de Yuma (MCZ 43197-98, ASFS V964); 1 mi (1.6 km) NW Boca de Yuma (ASFS V28948-49, ASFS V29050); 2 km NW Boca de Yuma (ASFS V17610-12).

Eleutherodactylus warreni new species

FIGURE 3

HOLOTYPE.—CM 54138, a gravid female, from vicinity of Palmiste, Ile de la Tortue, Haiti, one of a series obtained by native collectors for C. Rhea Warren between 15 and 27 August 1970. Original number ASFS V20253.

PARATYPES.—ASFS V20254-57, ASFS V20263-64, CM 54139, MCZ 84645-46, USNM 194013-14, same data as holotype; USNM 194012, same locality as holotype, native for C. R. Warren, 26 January 1968.

DIAGNOSIS.—A species of the Antillean *Eleutherodactylus ricordi* group characterized by the combination of moderate size (snout-vent length: males to 26 mm, females to 33 mm); dorsum yellow-brown to medium brown with black dorsal markings consisting primarily of the remnants of an interocular bar and a scapular chevron and some scattered dark markings on the back and (more heavily) sides, adjacent to a pair of dorsolateral stripes that are colored similar to the dorsal ground color; hind limbs concolor with dorsum and with concealed surfaces marbled purplish-brown; crura with some vague grayish-brown crossbar remnants; venter white; some dark brown stippling on throat; digital discs moderately expanded, that of digit 3 equal to or slightly less than one-quarter size of tympanum; supra-axillary and inguinal glandular areas apparently absent; tympanum small (\bar{X} = males 2.4, females 2.6); and tibia/snout-vent length ($X/100$) high (males 51.0-51.4, females 47.6-50.2).

DISTRIBUTION.—Known only from Ile de la Tortue off the northern Haitian coast (Fig. 2).

DESCRIPTION OF HOLOTYPE.—A gravid female with following measurements (in mm): snout-vent length 33.3, head length 12.1, head width 12.4, longitudinal diameter of tympanum 2.6, longitudinal diameter of eye 4.2, distance from naris to anterior corner of eye 3.4, femur 15.0, tibia 16.0, fourth toe 13.5, tibia/snout-vent length (X 100) 48.0. Head width slightly greater than distance from snout to posterior border of tympanum; snout truncate with nares conspicuous at anterior ends of canthus rostralis; diameter of eye longer than distance from naris to anterior corner of eye; interorbital space 3.5, less than diameter of eye; diameter of tympanum much less than diameter of eye, distance from tympanum to eye equal to about one-third diameter of tympanum. Fingers long, unwebbed, 3-4-2-1 in order of decreasing length; subarticular tubercles well developed, prominent, white. Toes relatively long, slightly webbed at their bases, 4-3-5-2-1 in order of decreasing length; subarticular tubercles large, prominent, white. Heels overlap when femora are held at right angles to body axis. Dorsum smooth to slightly wrinkled, snout minutely tuberculate, upper eyelids tuberculate, one large non-glandular wart between the angle of the jaw, tympanum, and forelimb insertion; throat and venter smooth, belly disc feebly developed. Dorsal surfaces of all limbs smooth to finely rugose; posterior faces of thighs with low, small, pavement-like granules. Inguinal and supra-axillary glandular areas absent. Tongue large, only very slightly nicked, free behind, its greatest width equal to about one-half that of floor of mouth. Prevomerine teeth in two long arched series (extending from just outside the lateral margins of the choanae and separated from the choanae by a distance equal to about one-eighth of a choana) that are separated medially by a distance equal to about three-quarters the diameter of a choana.

COLORATION OF HOLOTYPE.—Dorsum medium brown, overlaid with irregular black markings, the most prominent being a narrow and much dissected interocular bar and the remnants of a scapular chevron, as well as a few scattered dark blotches and spots. Dorsal zone separated from more heavily dark-blotched sides by an indistinct pair of dorsolateral stripes that are not colored differently from the dorsal ground color. A black supratympanic crescent which sends a dark bar to the center of the tympanum. Sides heavily blotched with black, particularly above the forelimb insertion and behind the tympanum. Lores totally black, thus no dark loreal stripes. Fore- and hindlimbs concolor with dorsum; forelimbs with irregular dark and medium brown stippling and marbling; hind limbs with vague crural mottling, the concealed femoral surfaces with a purplish-brown area, more or less solid but with intrusions and spotting of the dorsal medium brown ground. Pes irregularly mottled with dark brown. Venter white, throat and undersides of fore- and hindlimbs darkly stippled with brown. Iris metallic bronze, suffused with reddish below.

VARIATION.—Three male *E. warreni* have the following measurements (in mm) (extremes and means): snout-vent length 24.7-25.5 (25.2); head length 9.5-10.4 (9.9); head width 9.7-10.2 (10.0); tympanum 2.2-2.7 (2.4); eye 3.0-4.1 (3.6); naris to eye 2.8-3.0 (2.9); femur 12.0-12.5 (12.3); tibia 12.7-13.1 (12.9); fourth toe 10.5-11.8 (11.3); tibia/snout-vent length (X 100) 51.0-51.4 (51.3). Nine gravid and adult females measure: snout-vent length 30.0-33.3 (31.5); head length 11.2-12.1 (11.6); head width 11.6-12.4 (12.0); tympanum 2.5-2.7 (2.6); eye 3.7-4.5 (4.2); naris to eye 3.2-3.7 (3.5); femur 13.2-15.0 (14.1); tibia 14.7-16.0 (15.2); fourth toe 12.6-13.7 (13.1); tibia/snout-vent length (X 100) 47.6-50.2 (48.5). The series of paratypes includes one subadult specimen (USNM 194012) with a snout-vent length of 19.8 mm.

As noted in the diagnosis, the dorsal ground color varies between yellow-brown and medium brown, with dorsal black markings. The black markings consist principally of a narrow interocular bar, or its remnants, and a scapular chevron, or its remnants. One individual (ASFS V20264) shows the low extreme of dorsal dark

pigmentation, since it lacks an interocular bar and the scapular chevron is restricted to a pair of small discrete spots; the dorsum otherwise has no pattern. The dorsolateral stripes are more or less evident in all specimens, but they are not contrastingly colored in comparison with the dorsal ground color. The area between the stripes is variously marbled, blotched, or stippled with dark pigment, but never so much that the scapular chevron is obscured. The sides below the dorsolateral stripes are usually more heavily pigmented with dark blotches than the dorsum itself, with a supratympanic crescent and a large dark area above the forelimb insertion commonly present. The venter is white with fine and uniform dark brown stippling on the throat and the undersides of the limbs. The iris in all specimens is as described for the holotype. No specimen shows supra-axillary or inguinal glandular areas; these may be truly absent, but in many species they are obscured by dark lateral pigmentation, which may be the case in *E. warreni*.

COMPARISONS.—*E. warreni* differs from *E. weinlandi* by lacking a heavy dorsal dark pattern, although *E. w. paralius* resembles *E. warreni* in the general absence of a dorsal pattern. The two species are easily distinguished in life by the brighter colors in the sacral blotch area and on the hind limbs in *weinlandi*. In addition, *warreni* has expanded digital discs, which are feebly developed or absent in *weinlandi*. This same character will also separate *E. warreni* from *E. pictissimus*. *E. warreni* differs from both *E. alcoae* and *E. probolaeus* in having small (versus expanded) digital discs, a much smaller tympanum than *alcoae*, and a much different pattern than *probolaeus*. *E. warreni* is much smaller in size than *alcoae*, as is also apparently true of *probolaeus* (female *probolaeus* are unknown).

Remarkably, *E. warreni* is closest in coloration and pattern to *E. monensis*. The latter species has slightly larger digital discs than *E. warreni* and also has a supra-axillary glandular area, which is absent in *warreni*. *E. monensis* reaches a larger size (males to 26.4, females to 37.5) than *E. warreni* (males to 25.5, females to 33.3), and the tibia/snout-vent length means are higher in *warreni* (males 51.3, females 48.5) than in *monensis* (males 47.9, females 44.5). Although the two species are quite close in many respects, I regard them as separate species rather than subspecies, primarily because of the wide separation (460 km) between the two islets upon which they occur. The problem of their relationships, as well as that of *warreni* to other Hispaniolan members of the complex (*weinlandi*, *pictissimus*), is compounded by the specimens noted below.

E. warreni is named in honor of C. Rhea Warren, whose collecting activities on Ile de la Tortue have been responsible for our greatly increased knowledge of the herpetofauna of that island. Only our other *Eleutherodactylus* (*E. inoptatus* Barbour) is known to occur on Tortue; however, that species is very large and thus there is little possibility of confusing the two.

THREE ANOMALOUS SPECIMENS

There remain for discussion three extremely puzzling specimens. Each is a subadult female from a separate locality, so that a series of specimens is unavailable for analyses.

1) The first of these specimens (ASFS V1258) is from 19 km SE Martín García, 600 ft (183 m), Santiago Rodríguez Province, República Dominicana (see Fig. 1 for localities of anomalous specimens). I had earlier (Schwartz, 1965:113-114) considered this specimen to be *E. pictissimus* from a locality far removed from the balance of the range of the species and separated from southern *E. pictissimus* by an intervening population of *E. w. weinlandi*. I see no reason at this time to change my assignment. The specimen in life was pale, with a prominent

scapular chevron and prominent dorsolateral stripes that were not concolored to the tan dorsal ground color. In most respects the frog resembles *E. p. apantheatatus*, but its locality is far removed from the known range of that subspecies and separated from it by the intervening high Cordillera Central. We made a special effort in 1971 to collect both at the locality where the frog was taken (along a deeply entrenched stream with gallery forest in an otherwise xeric area) and an area along the Río Guarabo, which is nearby and close to Los Quemados. The Guarabo is a large river with extensive rich gallery forest traversing desert scrub. At neither locality did we find even one more frog of this type, despite optimal habitat and weather conditions. The fact is inescapable that there is a population of *E. pictissimus* in the northern República Dominicana (I reject the hypothesis that this single froglet is a fortuitous introduction), but only further intensive and extensive collecting in that region may reveal its taxonomic status.

2) The second frog (ASFS V22430) is from Thomonde, 400 ft (122 m), Dépt. de l'Artibonite, Haiti, collected by Lewis D. Ober in a crab hole beneath very high grass at the edge of a small stream which flows into the Rivière Thomonde. The locality lies some 25 km northwest of a known locality for *E. w. weinlandi* (8.0 mi. E Lascahobas). The dorsum is pale tan, and there is a black dorsal pattern (of the general *E. weinlandi* type), with bold dorsolateral stripes, that are still lighter (rather than brighter) than the dorsal ground color. The concealed surfaces are violet, overlaid with a black reticulum; the crura are marbled with grayish to brownish. There is no bright sacral area (as is typical of *weinlandi*, and the hindlimbs are not brightly colored (also as in *weinlandi*). It may well be that the Thomondé specimen is merely a peculiarly patterned *E. weinlandi*, but it differs in so many features from typical *E. weinlandi* that I am reluctant to make this assumption. The two localities are separated by the Rivière de l'Artibonite, and it is possible that this large river separates two distinctive subspecies of *E. weinlandi* in this region. Without further specimens from north of the river, no further comments are possible.

3) The third specimen (ASFS V10223) is from Cap-Haïtien, Dépt. du Nord, Haiti, collected by Richard Thomas from a pile of rocks on a more or less mesic hillside. The dorsal ground color is tan, and the dorsolateral stripes are prominent and an even paler tan (just as in the Thomonde specimen). The ground color of the sides and femora is gray and that of the crura tan. There is no brightly colored sacral blotch area. The dorsum is heavily marked with black vermiculations, and the scapular chevron is obvious, despite the densely patterned dorsum. In many ways, this specimen strongly resembles the Martín García

specimen, the locality of which is about 100 km away. The Cap-Haïtien locality is 90 km from Thomonde, the third locality for anomalous specimens.

An especially puzzling aspect of the Cap-Haïtien specimen is that it lies between Anse à Margot and Cruce de Guayacanès, both of which are known localities for *E. w. weinlandi*. If the Cap-Haïtien specimen is anything other than *E. w. weinlandi* (and it does not agree with my concepts of that taxon), the implication is that *E. pictissimus*, or some other *ricordi* group species, occurs along this northern coastal area. None of these specimens bear any resemblance to *E. warreni*; this makes the situation even more complicated, since the species whose range on the mainland comes closest to Ile de la Tortue is *E. weinlandi* (Anse à Margot). This northern Haitian littoral is so poorly known, especially as far as its anuran fauna is concerned, that only by more detailed collecting will we be able to understand the relationships of the frogs in this northwestern area.

DISCUSSION

The five species (*pictissimus*, *weinlandi*, *alcoae*, *probolaeus*, *warreni*) discussed in this paper form a complex of species within the *ricordi* group of Antillean *Eleutherodactylus*. Although these species seem more closely related to each other than to any other Hispaniolan species, they nevertheless show a degree of variation in both pigmental and structural characters that suggests they represent part of an even larger complex of species in the West Indies. The fact that Mertens (1939:30) used the combination *Eleutherodactylus lentus weinlandi*, thereby combining *E. weinlandi* with the Virgin Islands *E. lentus*, suggests a close phylogenetic relationship of *weinlandi* to the more eastern species. Shreve and Williams (1963:333) also noted that the relationships of *pictissimus* and *weinlandi* to the Cuban forms (*ricordi* and *bresslerae*) were difficult to evaluate, as was evident especially from their statement that *bresslerae* "looks strikingly like *weinlandi*." They suggested that *pictissimus* and *weinlandi* might well be conspecific, since the only differences between them involved details of color and pattern. Study of recently collected material of these two taxa has done nothing to change the original picture, and there is still a very real possibility that *pictissimus* and *weinlandi* might best be regarded as subspecies. This association becomes even more likely with the removal of *E. probolaeus* from *E. pictissimus*.

I have seen no evidence of intergradation in color or color pattern between *pictissimus* and *weinlandi*, which would serve as an argument against a subspecific relationship. On the other hand, that their geo-

graphic ranges do not overlap could be viewed as a counter-argument. I have the impression that *E. pictissimus* generally is far more tolerant of xeric conditions than *E. weinlandi*. *E. pictissimus* occurs in the extremely hot and dry Valle de Neiba, probably in the equally hot, dry, and contiguous Haitian Cul de Sac Plain, and in the Llanos de Azua. In these xeric regions, *pictissimus* avoids the general desert areas, an attribute that is necessary for the successful occurrence of any anuran in such hostile habitats. *E. weinlandi*, on the other hand, is partial to very mesic situations, and (except for the situation noted below) I know of no records of this species outside of moist-to-wet forest or pseudoforest (coffee and cacao groves, Cocos groves, etc.). The exception is the area along the southern Dominican coast that is inhabited by *E. w. paralius*. This region is less moist than those usually occupied by *E. weinlandi*; on the other hand, this coastal area is still well forested, with much of it being underlain by pocked limestone, a situation that favors occupation by terrestrial frogs like *E. weinlandi*. If the habitat preferences and tolerances of the two species form a continuum, from very xeric to very mesic, then *E. pictissimus* occupies the lower end of this spectrum and *E. weinlandi* the upper, with some overlap of tolerances of both species toward the central portion of the continuum. None of these data implies *de facto* separation of *weinlandi* and *pictissimus* at the species level, but they do suggest that these two taxa are adapted for quite different sorts of habitats.

Disregarding for the moment the peculiar northern mosaic of localities for *E. pictissimus* and *E. weinlandi* in Haiti and the República Dominicana, the two species approach each other without dilution of characteristics in two general areas. *E. weinlandi* is the frog of the Montagnes du Trou-d'Eau and its associated ranges in Haiti and the Sierra de Neiba in the República Dominicana. These ranges form the northern edge of the Cul de Sac-Valle de Neiba plain, at least the latter of which is occupied by *E. pictissimus*. The nearest approximations of these two species in this region is 12 mi N Port-au-Prince (*weinlandi*) and Port-au-Prince (*pictissimus*), and at 6.5 km W Duvergé (*pictissimus*) and 6.7 mi E Hondo Valle (*weinlandi*), an airline distance of 37 km. Between the last two localities lies the high range of the Sierra de Neiba, which reaches an elevation of 7416 ft (2261 m).

The second area of geographic approximation of the two species lies between Peravia Province and the Distrito Nacional. *E. pictissimus* occurs 4.8 mi S Baní, and *E. weinlandi* is known from 17 km NW Santo Domingo; the intervening distance is 47 km airline. It should be recalled that in both this and the previously detailed approximation, the subspecies involved are *E. w. weinlandi* and either *E. pictissimus apan-*

theatus or *E. p. eremus*. The nominate subspecies of *E. weinlandi* is dark and colorful, and contrasts sharply with the pale and vaguely patterned subspecies of *E. pictissimus*. The region about Baní is ecologically a transitional region between the xeric Llanos de Azua to the west and the more mesic southern portion of the República Dominicana. The area represents the eastern range limits for some species (*Ameiva lineolata* Duméril and Bibron, *Leiocephalus semilineatus* Dunn, and *Sphaerodactylus brevirostratus* Shreve), and in other cases is the area of intergradation for several subspecies (western xerophilic *Ameiva chrysolaema boekeri* Mertens and eastern mesophilic *A. ch. procax* Schwartz and Klinikowski; western *Diploglossus stenurus weinlandi* Cope and eastern *D. s. rugosus* Cope; western *Anolis distichus ravitergum* Schwartz and eastern *A. d. ignigularis* Mertens). Transitional areas such as this may also serve to separate species or subspecies in other cases. The intervening region between the known records of *weinlandi* and *pictissimus* (primarily southern San Cristóbal Province) comprises mesic lowlands and uplands, and appears to be much more suitable for *E. weinlandi* than *E. pictissimus*. Collecting in this intervening area still has yielded no specimens of either taxon.

The above discussion deliberately ignores the problem inherent in the three widely-spaced localities in northern Haiti and the northern República Dominicana of what I interpret as *E. pictissimus* (or at least a species more closely allied to *E. pictissimus* than to *E. weinlandi*). Since these northern localities of *pictissimus* are rather effectively separated from the parent population of *pictissimus* by the intervening occurrence of *E. weinlandi* in the Montagnes du Trou-d'Eau and Sierra de Neiba, there seems to be no reasonable way to associate them geographically with southern *E. pictissimus*. These northern frogs may have reached their respective areas via the xeric Valle de San Juan, which extends northwestward from the Llanos de Azua (occupied by *E. p. eremus*) to the Dominico-Haitian border at Bánica-Pedro Santana on the Rivière de l'Artibonite, and thence (in Haiti) onto the Plateau Central (specifically the Plateau de Hinche). The Thomonde locality for *E. pictissimus* lies within the Plateau Central. The proposed history of *E. pictissimus* in this area suffers from the fact that, despite extensive collecting in the Valle de San Juan, we have never found either *E. pictissimus* or *E. weinlandi*; the Plateau Central in Haiti is one of the least known regions of that country, and negative evidence for occurrence there of *E. pictissimus* cannot be taken as fact.

The two other northern localities of *E. pictissimus* are less easily explained. There seems today to be no pathway for the species to have reached Cap-Haïtien in Haiti and the Martín García region in the

northern República Dominicana. The situation is made even more complex by the fact that both these places lie between two known localities for *E. weinlandi*—Anse à Margot and north of Cruce de Guayacanes. It is possible that the Cap-Haïtien and Martín García localities were invaded from the south along the deeply entrenched valley of the Rivière de l'Artibonite, and thence into the watershed of the Río Massacre, from which the frog may have spread both to the east and west, there occupying xeric areas that were unsuitable for the already established *E. weinlandi*. This is pure conjecture—there are no specimens of either species from this presumed area of invasion, and indeed the species may no longer occur there. Certainly the border area from south of Villa Anacaona to Monte Cristi seems much more suitable ecologically for *E. pictissimus* than *E. weinlandi*, but we have never taken either species of this pair in several months' collecting in this region.

Mertens (1939) first proposed that the Hispaniolan fauna might be catalogued into two old faunas that were localized on the two islands (north and south), which have subsequently been fused to form the present island of Hispaniola along the Cul de Sac-Valle de Neiba plain. This basic tenet has been amplified by Williams, Thomas, and myself, and there is little doubt that the present low-lying (and in places below sea level) plain separates two rather different herpetofaunas. There has been some faunal interchange since the closure of the paleostrait (and probably before it) resulting from chance trans-strait dispersal by some tolerant species. Invading species have had varying success once they reached the other island. I have no doubt that *E. pictissimus* is a south island species, since it occurs throughout that region, except at higher elevations in the Sierra de Baoruco and from sea level to an elevation of 5800 ft (1769 m) at Furcy. *E. pictissimus* invaded the north island, where it gave rise to a distinctive subspecies (*eremus*), whose range extends as far east (Bani) as the limits of suitable xeric habitat permit. Apparently *E. pictissimus* also invaded much of the northern areas of Haiti and the República Dominicana, but perhaps with less success; the records are too few and scattered to generalize.

E. weinlandi, on the other hand, is completely a north island species, occupying mesic regions primarily in the eastern part of Hispaniola. With few exceptions, the range of *E. weinlandi* is fairly compact. The Anse à Margot record is one exception. The major exception, however, involves the population in the Montagnes du Trou-d'Eau and the Sierra de Neiba, an area that is some 80 km disjunct from the next closest *E. weinlandi* locality (Vallejuelo and Jarabacoa). As I previously pointed out, the logical area for continuity between the Sierra de Neiba and more eastern populations of *E. weinlandi* is not across the Cordillera Central

between Jarabacoa and Vallejuelo, but rather along the southern slopes of the Cordillera Central between La Cumbre and San Juan. Unfortunately, these regions are poorly known herpetologically. As far as the isolated Anse à Margot record in northern Haiti is concerned, I suspect that *E. weinlandi* will be found to occur along the northern flanks of the Cordillera Central (where it is already known from the Río Bao near Los Montones), and thence into the Massif du Nord in northern Haiti. The distribution of *E. weinlandi* in this region may no longer be continuous, but this seems a likely avenue for invasion from the east of the northern Haitian littoral.

In order to place *E. weinlandi* and *E. pictissimus* in their proper perspective within the *ricordi* complex in the Greater Antilles, the morphological characters (presence of supra-axillary and inguinal glands, presence of postfemoral glands, presence of throat glands, development of digital discs) of these two species and the other with which they are associated have been summarized in Appendix 3. Measurements for all taxa included in this study are given in Appendix 1 (for the Hispaniolan and Mona taxa) and Appendix 2 (for the non-Hispaniolan taxa). In addition, the following species are known to be vocal: *weinlandi*, *alcoae*, *probolaeus*, *richmondi*, and *monensis*. The other species are presumably mute, although *pictissimus* and *thomasi* have been assumed to make sounds. I have had no field experience with *warreni*, but Mr. Warren reported no vocal activities on the part of this frog. *E. bresslerae* has been collected only once (under very favorable moisture conditions) but was not heard calling; *E. ricordi* has been collected often but has never been heard vocalizing. My experience with *E. lentus* is limited to St. Thomas, which at the time of my visit was very dry. Grant (1937:505) did not mention calling *lentus* on St. Croix, nor did Richard Thomas and David C. Leber who collected the species there.

Examination of Appendix 3 shows that of the included 11 species, the Puerto Rican *E. richmondi* is most distinctive. Although the species lacks supra-axillary, inguinal, or postfemoral glandular areas, males are unique in having a large single (or somewhat divided) glandular area on the throat. *E. richmondi* also differs from other members of this group in having basically a brightly-colored (rich brown, reddish tan, bright chestnut) dorsum, often set off laterally by a pair of fine golden to yellow or cream dorsolateral stripes that separate the dark brown sides (see Schmidt 1928 fig. 20, for an excellent delineation of this species). Like *E. weinlandi*, *E. richmondi* has a reddish or rusty sacral area, but unlike *weinlandi*, *richmondi* has an unmarked (versus patterned) dorsum. *E. richmondi* is vocal and lacks well developed digital discs. In addition, the species is a mesophile and almost exclusively

terrestrial, although I have taken calling males from low shrubs (1 ft [0.3 m]) and other individuals on grass and leaves of herbs 6 in (15 cm) above the ground. By taking the above characteristics into consideration, I cannot consider *E. richmondi* a central member of the frog group under discussion; rather it seems to be a peripheral member of this compact group of frogs that is in some ways specialized when compared with other members of the complex.

The remaining members of the group fall into two major categories: (1) those with well developed digital discs, and (2) those with the discs poorly developed or absent. In this complex I consider presence of well developed discs primitive and their absence specialized, as appears to be true of the entire genus, in fact, since discs are regularly well developed in the Antillean members of the *auriculatus* group (see Schwartz 1969). This primary dichotomy separates those species with well developed discs (*ricordi*, *thomasi*, *alcoae*, *probolaeus*, *bresslerae*, *monensis*) from those with the discs poorly developed or absent (*lentus*, *weinlandi*, *pictissimus*, *warreni*).

Tracing the postulated history of each of these lines further (see Fig. 4 for a graphic representation of these relationships), I regard the presence of three glandular areas (supra-axillary, inguinal, postfemoral) as primitive, and loss of any of these as specialized. Of the disced members, only *ricordi* occasionally shows postfemoral glands, whereas all other members lack them. A third dichotomy in this sequence is the absence or presence of supra-axillary and inguinal glands. *E. bresslerae* lacks these glandular areas, and *monensis* has them reduced. Supra-axillary and inguinal glands are present in *probolaeus*, *alcoae*, and *thomasi* (occasionally absent in *thomasi*).

In the non-disced sequence, only *lentus* has all three glandular areas present, and thus its relationships to the non-disced species are comparable to those of *ricordi* to the disced species. The postfemoral glands have been lost in all other non-disced species. *E. warreni* has lost both supra-axillary and inguinal glandular areas, but *pictissimus* and *weinlandi* have retained these two areas. Thus, within the disced and non-disced series, there is a progressive loss of glandular areas.

Examining these two lines of divergence within the group in the light of geography, we find the following. The primitive members of each line (*lentus*, *ricordi*) occur either on islets that are far removed from the balance of the group (*lentus* on St. Thomas, St. John, and St. Croix in the Virgin Islands, east of Puerto Rico), or they have a restricted and primarily upland distribution (*ricordi* only in the uplands of the Sierra Maestra, Sierra de la Gran Piedra, and the Cuchillas de Toa in Oriente Province in eastern Cuba) (Fig. 5). Of the non-disced species,

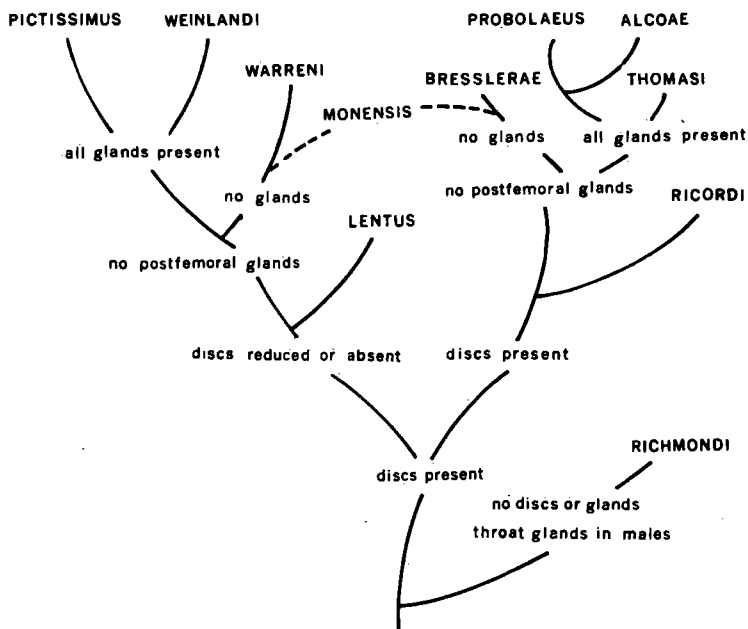


FIGURE 4.—Dendrogram showing suggested relationships of 11 species of Antillean *Eleutherodactylus*, as discussed in text. The dashed lines to *monensis* indicate the problematical relationships of that species, which is closer to the line with discs reduced or absent than to that with discs present. The relationship to *warreni* seems more logical than that to *bresslerae*.

all except *lentus* are from Hispaniola (including *warreni* on Tortue). The fact that *warreni* occurs on a Hispaniolan satellite and lacks glandular areas suggests this species has had a long independent history from gland-bearing *pictissimus* and *weinlandi* on the mainland. There is no serious problem with this distributional picture except for the remote position of primitive *lentus*. This series' proposed history would be more satisfying were there a certain member of the complex on Puerto Rico, which lies between the Virgin Islands and Hispaniola. It is possible that *richmondi* is that member, but it appears too highly specialized to be derived or derivable from *lentus*. That the Virgin Islands have had a history both allied to, but different from, that of Puerto Rico is unquestioned, and these islets have many species of amphibians and reptiles in common with Puerto Rico. On the other hand, they have several species that are restricted to and very distinct from the Puerto Rican herpetofauna, including *Amphisbaena fenestrata* Cope, *Sphaerodactylus parthenopion* Thomas, and (if we include the islets just east of Puerto Rico with the Virgin Islands) *Anolis roosevelti* Grant. Thus we need not expect complete similarity between the Virgin Island and

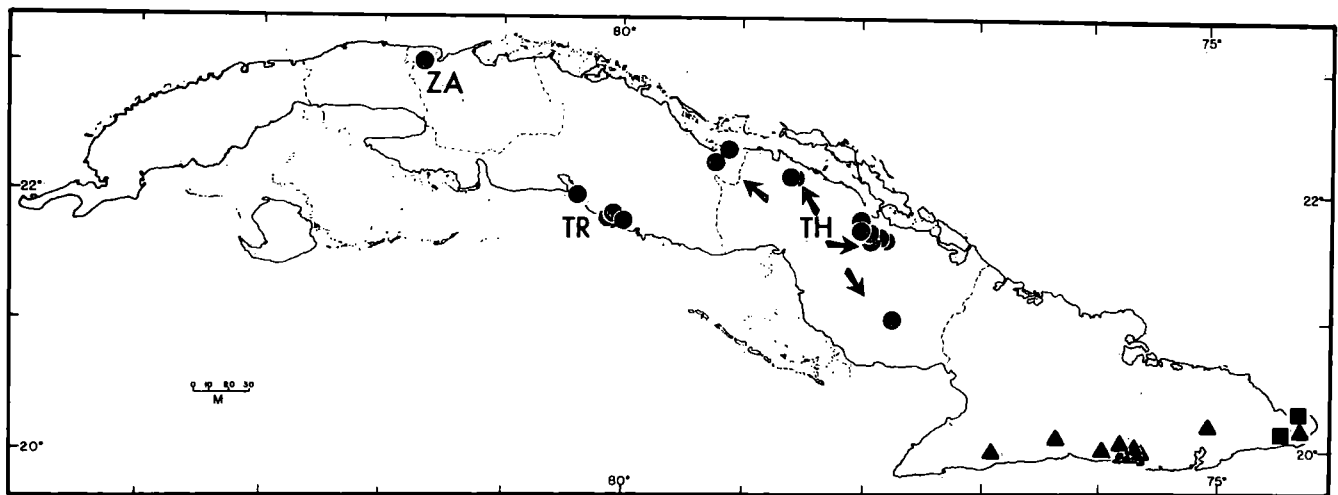


FIGURE 5.—Map of Cuba, showing localities for three species of *Eleutherodactylus* as follows: triangles, *E. ricordi*; squares *E. bresslerae*; circles, *E. thomasi*. Subspecies of *E. thomasi* are indicated by TH (*E. t. thomasi*); TR (*E. t. trinidadensis*); and ZA (*E. t. zayasi*). Frogs from the westernmost four localities of *E. t. thomasi* show intergrading tendencies between that subspecies and *E. t. trinidadensis*.

Puerto Rican herpetofaunas. It seems probable that *lentus* is a primitive relict species that has persisted on three of the many Virgin Islands, but whose close Puerto Rican relatives have since disappeared. Presence of some member of this complex on Puerto Rico would also enhance the probability that the Hispaniolan members of the group were derived from Puerto Rico; although I feel certain that this was the case, the intermediate Puerto Rican member of the group apparently no longer exists.

A proposed history of this frog group's disced members is somewhat more difficult and puzzling. Assuming that *ricordi* is the most primitive of the disced species, there is no problem in accounting for the presence of two disced species (*bresslerae*, *thomasi*) on Cuba. Of these two species, *thomasi* is more widely distributed, occurring from Matanzas Province in the west to Camagüey Province in the east (Fig. 5). The Matanzas population (*E. t. zayasi*) is apparently disjunct, and *E. t. trinidadensis* in the Sierra de Trinidad in southern Las Villas Province also appears to be a geographic isolate. Only in the Sierra de Cubitas, the Sierra de Najasa (*E. t. thomasi*) and the mountains near the Las Villas-Camagüey border does there appear to be any continuity among the known records from *E. thomasi*. Interestingly, I regard the material from the Las Villas-Camagüey line (Cueva de Caguanes, Yaguajay) and from Loma de Cunagua, near Morón in northwestern Camagüey Province, as intermediate between *thomasi* and *trinidadensis*, although closer to the former in both characters and geography. Thus the distribution of *E. thomasi* seems to be discontinuous. This may be due partly to lack of suitable habitat in some of the intervening regions (*thomasi* is associated with forested limestone areas) and partly to retraction of distribution coincident with changing ecology.

E. bresslerae has a very limited distribution in extreme eastern Cuba; the species is known from two stations in the Cuchillas de Toa (Fig. 5), the complex montane mass that occupies much of the eastern interior of Cuba. Although there are only two records of *ricordi* from these same mountains, it is probable that *bresslerae* and *ricordi* are sympatric throughout much of this area. In general, *ricordi* elsewhere is an upland species, whereas *bresslerae* is known from at least one coastal (but well forested) locality.

The two Hispaniolan disced members (*alcoae* and *probolaeus*) may be interpreted as peripherally derived from the Cuban species, and, in fact, *probolaeus* resembles *bresslerae* in dorsal pattern details. The restricted distributions of *alcoae* and *probolaeus* suggest that as species they are either quite recently derived or have distributions increasingly restricted. The latter seems much more likely. This implies there was an

early invasion of disced frogs from Cuba that became adapted to life in limited areas which were unoccupied by already resident species. This almost certainly is the situation with *alcoae*, which inhabits the rigorous Península de Barahona. The problem of *probolaeus* is somewhat different, because it seems not to occur in large areas of eastern Hispaniola that appear suitable and unoccupied by any member of this complex. Both *alcoae* and *probolaeus* are associated with limestone areas.

E. monensis poses the only serious problem with my proposed sequence of disced forms. As I previously pointed out, this species cannot logically be derived from any extant Puerto Rican species (*richmondi*) and is much more plausibly associated with a species from Hispaniola. Since *monensis* has the glandular areas reduced, it seems most likely to be in the line of evolution that led to *bresslerae*. However, these two species are quite dissimilar (see Schwartz 1960:fig. 6 for *bresslerae*, Schmidt 1928:fig. 21 for *monensis*), and I find it very difficult to associate them. Of all the involved species, *monensis* most closely resembles *warreni* in general aspect. Although discs are present in *monensis*, they are reduced and only slightly larger than those of *warreni*. Perhaps the logical explanation is that *monensis* and *warreni* represent insular remnant populations of an otherwise extinct primitive disced species.

Whatever the history of such peculiar species as *E. monensis* and *E. warreni*, it seems evident that Hispaniola has been invaded twice by members of this complex of frogs. One invasion of non-disced members came from the east and resulted in *weinlandi* on the old Hispaniolan north island and *pictissimus* on the south island. The second invasion was from Cuba in the west, where all members of this group have enlarged digital discs. The second invasion resulted in two species (*alcoae*, *probolaeus*), one each on the north and south islands, and both presently have very limited distributions.

Members of this complex are all moderate- to large-sized frogs of the *ricordi* group. Within the complex, the largest males vary in snout-vent lengths (rounded off to the nearest mm) between *alcoae* (38) and *monensis* and *warreni* (26). Between these two extremes are *ricordi* (35), *pictissimus* (34), *thomasi* (32), *weinlandi*, *probolaeus*, and *bresslerae* (30), and *lentus* (28). Female size extremes vary from *bresslerae* (46) to *warreni* (33), with *alcoae* (45), *pictissimus* and *thomasi* (43), *ricordi* and *weinlandi* (40), *monensis* (38), and *lentus* (37) being of intermediate size.

The most striking sexual differences in maximum snout-vent length (in mm) are shown by *bresslerae* (16) and *monensis* (12), and the least sexual dimorphism in *warreni* (7) and *ricordi* (5). Generally, the

non-disced members shows less sexual dimorphism (between 7 and 10) than do the disced members (8 to 16). In the latter group *E. ricordi* is exceptional, because the largest members of each sex differ by only 5 mm. These data suggest that sexual dimorphism is greater in the (primitive) disced members of the complex (with the exception of *ricordi*), and less pronounced in the more specialized discless members. It is interesting that the problematical *monensis* has a sexual dimorphic difference of 12 mm, greater than that of any discless member species and within the range of the species with discs.

Comparison of the two groups' dorsal coloration and pattern shows the following. In those species with discs, dorsolateral stripes are absent in *ricordi*, *alcoae*, and *monensis* and present, but unicolor with the dorsal ground color, in *bresslerae*, *probolaeus*, and *thomasi*. In *thomasi* stripes are variable in the nominate subspecies and *E. t. trinidadensis*, but occur in all *E. t. zayasi*. In the non-disced members, dorsolateral stripes are absent in *warreni*, present and unicolor with the dorsum in *pictissimus* and *lentus*, and present but brightly colored in *weinlandi*. Thus, dorsolateral stripes are absent in the advanced forms (*bresslerae*, *probolaeus*, *alcoae*, *thomasi*) and the two presumably primitive species (*ricordi*, *monensis*) among the disced group, are present in all non-disced species except *warreni* (including the basal *lentus*), and are brightly colored as well as present in *weinlandi*.

As pointed out in the introduction, this entire frog assemblage has one of two dorsal colors and patterns. One group has generally pale dorsa, more or less heavily overlaid with a dark pattern that includes a scapular chevron and an interocular bar (although these elements may be greatly obscured by additional dark dorsal patterning). To this group belong (among the species without discs) *warreni*, *pictissimus*, and *lentus*, as well as all members of the group possessing discs. *E. lentus* tends to have brighter (yellow to golden or orange tan) dorsa than other members of the species without discs and thus tends toward *weinlandi* in dorsal color and pattern. Of this latter group, *bresslerae* tends to be brighter dorsally, especially posteriorly. The second style of dorsal coloration is shown by *weinlandi*, which has a bright dorsal ground color that may be heavily overlaid with dark brown to black, as in the subspecies *chersonesodes*. The clear and bright sacral blotch of *weinlandi* shows some resemblance to the brighter dorsal colors in *bresslerae*.

In the above summary, I have attempted to indicate the relationships between this complex of 10 Greater Antillean species of the *Eleutherodactylus ricordi* group. They form a compact and obviously closely related complex of species within that group of *Eleutherodactylus* that

is represented by the most species in the West Indies. I have had the advantage of seeing all but two of these species (*warreni*, *monensis*) in the field, and I have handled living *warreni*. Such familiarity with *Eleutherodactylus* in the field is essential in understanding their relationships, because only by knowledge of the colorations, habits, voice, and patterns of these frogs in life can one gain even partial insight into their relationships.

LITERATURE CITED

- Barbour, T. 1914. A contribution to the zoogeography of the West Indies, with especial reference to amphibians and reptiles. Mem. Mus. Comp. Zool., 44(2): 209-359, 1 pl.
- Cochran, D. M. 1935. New reptiles and amphibians collected in Haiti by P. J. Darlington. Proc. Boston Soc. Nat. Hist., 40(6):367-376.
- Dunn, E. R. 1926. Additional frogs from Cuba. Occ. Pap. Boston Soc. Nat. Hist., 5:209-215.
- Grant, C. 1937. Herpetological notes with new species from the American and British Virgin Islands, 1936. Agri. Univ. Puerto Rico, 21(4):503-522, 4 pls.
- Mertens, R. 1939. Herpetologische Ergebnisse einer Reise nach der Insel Hispaniola, Westindien. Abh. senckenberg. naturf. Ges., 449:1-84, 10 pls.
- Schmidt, K. P. 1926. The amphibians and reptiles of Mona Island, West Indies. Field Mus. Nat. Hist., Zool. Ser., 12(12):149-163, 6 figs.
- . 1928. Scientific survey of Porto Rico and the Virgin Islands. New York Acad. Sci., 10(1):1-160, 52 figs., 4 pls.
- Schwartz, A. 1958. Four new frogs on the genus *Eleutherodactylus* (Leptodactylidae) from Cuba. Amer. Mus. Novitates, 1873:1-20, 4 figs.
- . 1960. Nine new Cuban frogs of the genus *Eleutherodactylus*. Reading Public Mus. Art Gallery (Sci. Publ.), 11:1-50, 6 figs.
- . 1965. Geographic variation in two species of Hispaniolan *Eleutherodactylus*, with notes on Cuban members of the *ricordi* group. Stud. Fauna Curaçao and Caribbean Is., 22(86):98-123, 7 figs.
- . 1969. The Antillean *Eleutherodactylus* of the *auriculatus* group. Stud. Fauna Curaçao and Caribbean Is., 30(114):99-115.
- . 1971. A new species of *Eleutherodactylus* (Amphibia, Leptodactylidae) from Hispaniola. Ann. Carnegie Mus., 43(2):25-31, 1 fig.
- Shreve, B., and E. E. Williams. 1963. The herpetology of the Port-au-Prince region and Gonave Island, Haiti. Part II. The frogs. Bull. Mus. Comp. Zool., 129(5):302-342, 5 pls.
- Stejneger, L. 1904. The herpetology of Porto Rico. Report U. S. Natl. Mus., 1902, pp. 549-724, 197 figs.

APPENDIX 1.—NINE MEASUREMENTS (MEANS AND EXTREMES) OF SIX SPECIES OF
Eleutherodactylus FROM HISPANIOLA AND ISLA MONA.

Taxon	Sex	N ¹	Snouth-vent length	Head length	Head width	Tympanum
<i>p. pictissimus</i>	M ²	57	26.6 (23.0-33.9)	9.9 (8.7-12.5)	9.6 (8.2-11.6)	2.2 (1.8- 2.8)
	F ³	62	35.7 (28.5-43.2)	13.0 (10.8-16.1)	12.9 (10.9-16.0)	2.7 (2.2- 3.9)
<i>p. apanteatus</i>	M	25	24.9 (21.6-33.1)	9.6 (8.3-12.5)	9.8 (8.4-13.2)	2.2 (1.9- 2.8)
	F	6	32.0 (29.7-34.7)	11.7 (10.6-12.6)	12.0 (11.2-13.0)	2.5 (2.3- 2.8)
<i>p. eremus</i>	M	12	25.0 (22.7-27.7)	9.5 (8.5-10.7)	9.7 (8.7-11.1)	2.2 (1.9- 2.5)
	F	4	31.0 (30.6-31.3)	10.8 (10.3-11.4)	11.3 (10.9-11.8)	2.4 (2.0- 2.6)
<i>w. paralius</i>	M	11	25.6 (22.0-29.5)	9.9 (8.7-11.7)	9.7 (8.4-11.1)	2.4 (2.2- 2.7)
	F	13	35.4 (29.3-40.4)	12.2 (10.9-14.8)	13.2 (10.9-14.9)	2.9 (2.4- 3.3)
<i>w. chersonesodes</i>	M	16	23.8 (20.8-27.6)	9.1 (7.7-11.0)	8.9 (7.4-11.0)	2.1 (1.8- 2.5)
	F	111	29.8 (24.8-34.9)	10.9 (9.4-13.8)	10.7 (9.3-13.7)	2.4 (1.9- 3.1)
<i>w. weinlandi</i>	M	18	21.7 (20.0-27.4)	9.3 (7.7-10.4)	9.1 (7.1-11.0)	2.1 (1.7- 2.5)
	F	36	32.6 (27.2-35.8)	11.5 (9.1-13.2)	11.5 (9.0-13.2)	2.4 (1.8- 2.8)
<i>warreni</i>	M	3	25.2 (24.7-25.5)	9.9 (9.5-10.4)	10.0 (9.7-10.2)	2.4 (2.2- 2.7)
	F	9	31.5 (30.0-33.3)	11.6 (11.2-12.1)	12.0 (11.6-12.4)	2.6 (2.5- 2.7)
<i>alcoae</i>	M	44	33.1 (26.2-37.5)	12.5 (10.1-14.2)	12.8 (10.9-14.2)	3.1 (2.6- 3.7)
	F	8	38.6 (33.5-44.5)	14.9 (13.7-16.6)	15.0 (13.6-17.0)	3.4 (3.0- 4.1)
<i>probolaeus</i>	M	9	27.9 (25.8-29.8)	11.2 (10.3-12.7)	11.3 (10.5-12.0)	2.6 (2.3- 3.0)
<i>monensis</i>	M	8	23.4 (20.4-26.4)	9.5 (8.2-10.8)	9.8 (8.5-11.1)	2.3 (2.0- 2.7)
	F	15	33.1 (28.0-37.5)	13.1 (10.3-15.2)	13.9 (11.5-16.1)	3.0 (2.7- 3.6)

¹ N=number of individuals.

² Measurements are of largest males.

³ Measurements are of gravid, adult females.

APPENDIX 1.—(CONTINUED)

Eye	Naris-eye	Femur	Tibia	Fourth toe	Tibia/SV length (X 100)
3.4	3.0	11.2	12.8	11.2	48.9
(2.9- 4.0)	(2.4- 4.1)	(9.7-14.5)	(10.8-15.6)	(9.2-14.4)	(41.3-53.2)
4.3	4.1	15.5	17.3	15.5	46.2
(3.4- 5.8)	(3.0- 4.8)	(12.2-19.8)	(13.5-21.6)	(12.2-19.2)	(42.0-53.3)
3.4	3.1	11.3	12.2	10.9	48.9
(2.8- 4.4)	(2.5- 4.3)	(9.7-16.2)	(9.7-16.2)	(9.2-14.8)	(45.4-55.2)
4.0	3.7	14.0	14.5	13.3	45.4
(3.6- 4.2)	(3.2- 3.9)	(13.0-15.2)	(13.1-16.0)	(12.2-14.6)	(43.7-48.2)
3.4	3.0	10.0	11.9	11.6	47.0
(2.8- 3.7)	(2.4- 3.8)	(9.7-12.5)	(10.6-14.1)	(9.8-12.8)	(42.6-51.6)
3.9	3.6	13.0	13.7	12.3	44.1
(3.5- 4.4)	(3.5- 3.7)	(12.5-13.4)	(12.9-14.6)	(11.9-12.7)	(42.0-46.6)
3.4	2.9	11.1	12.0	9.6	46.7
(3.0- 4.0)	(2.4- 3.6)	(9.3-13.3)	(10.6-14.6)	(8.9-12.7)	(44.1-50.5)
4.5	4.1	15.7	16.5	14.5	46.7
(3.9- 5.0)	(3.1- 4.7)	(12.2-18.0)	(12.2-18.0)	(11.8-16.9)	(44.8-50.6)
3.4	2.5	11.2	12.3	10.9	51.5
(2.4- 4.1)	(2.2- 3.1)	(9.2-14.3)	(10.1-15.1)	(8.6-14.7)	(47.4-55.7)
4.1	3.1	13.9	15.2	13.4	50.6
(2.7- 5.1)	(2.5- 4.2)	(11.6-18.0)	(13.0-18.3)	(10.9-15.8)	(45.4-56.8)
3.3	2.7	10.6	12.1	10.8	52.8
(2.6- 3.8)	(2.2- 3.4)	(8.8-13.6)	(9.6-15.1)	(8.7-12.7)	(41.9-55.1)
4.0	3.5	14.4	15.8	14.0	50.0
(3.2- 4.8)	(2.6- 4.2)	(11.3-16.2)	(12.5-17.8)	(11.2-15.9)	(45.1-54.3)
3.6	2.9	12.3	12.9	11.3	51.3
(3.0- 4.1)	(2.8- 3.0)	(12.0-12.5)	(12.7-13.1)	(10.5-11.8)	(51.0-51.4)
4.2	3.5	14.1	15.2	13.1	48.5
(3.7- 4.5)	(3.2- 3.7)	(13.2-15.0)	(14.7-16.0)	(12.6-13.7)	(47.6-50.2)
4.2	4.0	14.5	15.5	12.3	47.9
(3.5- 4.9)	(3.0- 4.9)	(12.4-16.8)	(12.7-17.8)	(10.5-14.4)	(41.8-51.6)
4.8	4.9	16.7	17.8	14.1	46.1
(4.2- 5.6)	(4.4- 5.5)	(15.2-18.9)	(15.9-19.4)	(12.7-15.2)	(43.6-47.5)
4.2	3.7	12.6	13.8	11.7	49.5
(3.9- 4.5)	(3.4- 4.2)	(11.3-13.7)	(12.8-15.2)	(10.7-12.9)	(47.0-51.7)
3.4	2.7	10.4	11.2	10.2	47.9
(3.1- 3.8)	(2.3- 3.1)	(9.0-11.3)	(10.1-12.0)	(9.3-10.8)	(44.3-50.0)
4.5	4.1	13.8	14.7	13.6	44.5
(4.1- 5.0)	(3.3- 5.0)	(12.2-14.6)	(12.8-16.1)	(11.5-15.9)	(41.4-49.2)

APPENDIX 2.—NINE MEASUREMENTS (MEANS AND EXTREMES) OF FIVE *Eleuthero-*
dactylus SPECIES FROM THE VIRGIN ISLANDS, PUERTO RICO, AND CUBA.

Taxon	Sex	N ¹	Snout-vent. length	Head length	Head width	Tympanum
<i>lentus</i>	M ²	16	24.9 (21.8-27.9)	9.5 (8.4-10.8)	9.2 (7.4-10.7)	2.2 (1.9- 2.5)
	F ³	10	33.6 (31.2-38.3)	12.1 (11.2-13.9)	12.4 (11.4-13.7)	2.7 (2.4- 3.1)
	M	25	27.7 (26.4-29.0)	10.7 (10.3-11.5)	10.4 (9.9-11.0)	1.9 (1.5- 2.1)
<i>richmondi</i>	F	17	39.6 (36.2-41.7)	15.1 (13.2-16.1)	15.2 (14.0-16.2)	2.7 (2.1- 3.1)
	M	7	25.3 (21.9-30.4)	10.3 (9.0-12.0)	9.9 (8.3-11.6)	2.3 (2.0- 2.8)
<i>bresslerae</i>	F	1	45.8	17.6	17.2	3.5
	M	23	26.6 (19.6-34.6)	10.5 (7.8-13.6)	10.3 (7.5-13.4)	2.3 (1.6- 2.8)
	F	28	33.3 (25.4-40.0)	13.1 (9.5-19.6)	12.7 (9.0-15.0)	2.7 (1.8- 3.2)
<i>t. zayasi</i>	M	28	29.0 (26.9-31.8)	11.4 (10.3-12.6)	11.2 (9.9-11.9)	2.6 (2.2- 3.3)
	F	15	38.8 (37.5-40.9)	14.6 (14.1-15.0)	13.9 (13.2-14.7)	2.8 (2.6- 3.2)
	M	24	27.8 (24.8-31.1)	10.9 (9.8-12.0)	10.6 (9.5-11.9)	2.8 (2.3- 3.3)
<i>t. trinidadensis</i>	F	18	34.0 (31.5-39.5)	13.6 (11.8-15.0)	13.4 (11.5-14.6)	3.0 (2.7- 3.2)
	M	10	25.3 (24.5-26.3)	10.3 (9.8-10.8)	9.9 (9.2-10.4)	2.3 (2.1- 2.4)
	F	23	38.9 (31.9-43.4)	14.7 (12.3-16.5)	14.8 (12.4-16.7)	2.9 (2.5- 3.3)

¹ N=number of individuals.² Measurements are of largest males.³ Measurements are of gravid, adult females.

APPENDIX 2.—(CONTINUED)

Eye	Naris-eye	Femur	Tibia	Fourth toe	Tibia/SV length (X 100)
3.5	2.7	11.1	11.9	10.9	47.8
(2.8- 4.3)	(2.2- 3.1)	(9.6-12.2)	(10.3-13.3)	(9.7-12.0)	(44.7-51.6)
4.4	3.7	14.7	15.5	14.2	46.2
(3.5- 4.9)	(3.2- 4.4)	(12.7-16.6)	(14.3-17.8)	(12.8-17.0)	(42.4-49.3)
4.3	2.8	12.3	13.0	12.7	47.0
(3.9- 5.0)	(2.4- 3.1)	(11.3-13.2)	(12.4-13.5)	(11.7-13.6)	(44.4-49.5)
5.5	4.3	17.8	18.9	18.0	47.8
(4.9- 6.0)	(3.6- 5.5)	(16.6-20.0)	(17.6-21.8)	(16.6-20.2)	(44.6-51.4)
3.8	3.3	11.4	11.8	10.5	46.7
(3.0- 4.0)	(2.6- 4.1)	(9.7-13.1)	(10.3-14.4)	(8.7-11.9)	(44.7-47.6)
6.0	6.1	20.4	21.3	18.1	46.5
3.8	3.4	12.3	13.3	12.3	50.2
(2.8- 5.0)	(2.2- 4.6)	(9.0-16.1)	(9.1-18.7)	(9.1-18.7)	(44.4-54.0)
4.6	4.2	15.4	16.7	15.2	49.6
(3.6- 6.0)	(3.1- 5.1)	(11.6-19.0)	(12.2-20.0)	(12.1-18.5)	(45.1-53.6)
3.9	3.7	13.3	14.3	12.1	49.2
(3.2- 4.4)	(3.0- 4.6)	(11.7-14.3)	(13.3-15.5)	(11.3-13.1)	(46.5-52.1)
4.9	4.9	17.2	18.4	15.8	47.5
(4.5- 5.7)	(4.4- 5.2)	(16.1-18.4)	(17.2-19.3)	(14.0-17.2)	(44.7-49.3)
3.7	3.4	13.0	13.1	11.7	47.3
(3.3- 4.6)	(2.7- 3.8)	(10.7-13.3)	(11.8-14.1)	(10.2-12.5)	(43.4-50.2)
4.7	4.4	15.5	16.3	14.3	45.3
(4.1- 5.2)	(3.5- 5.0)	(13.4-16.9)	(14.5-17.3)	(12.3-15.5)	(43.0-48.0)
3.7	3.4	12.2	12.4	11.0	51.1
(3.0- 4.1)	(3.0- 3.8)	(11.5-13.0)	(11.5-13.2)	(9.6-11.7)	(48.4-53.6)
5.1	5.1	17.8	17.0	15.9	48.9
(4.3- 6.0)	(4.0- 6.1)	(14.9-20.3)	(16.5-22.2)	(13.5-18.0)	(45.8-52.7)

APPENDIX 3.—TEN SPECIES OF *RELATED Eleutherodactylus* SHOWING OCCURRENCE OF STRUCTURAL FEATURES (GLANDULAR AREAS AND DIGITAL DISCS) AND PRESENCE OF VOCAL ACTIVITY.

Species	Supra-axillary and inguinal glands	Postfemoral glands	Throat glands	Digital discs	Voice ¹
<i>pictissimus</i>	+	—	—	Poorly developed	?
<i>weinlandi</i>	+	—	—	Poorly developed	Vocal
<i>alcoae</i>	+	—	—	Well developed	Vocal
<i>probolaeus</i>	+	—	—	Well developed	Vocal
<i>lentus</i>	+	+	—	Poorly developed	?
<i>richmondi</i>	—	—	+	Poorly developed	Vocal
<i>bresslerae</i>	—	—	(males) —	Well developed	?
<i>ricordi</i>	+	+	—	Well developed	?
	(inguinal only, and rarely)	(rarely)			
<i>thomasi</i>	+	—	—	Well developed	?
<i>monensis</i>	+	—	—	Well developed	Vocal
	(supra-axillary only, and rarely)				
<i>warreni</i>	—	—	—	Moderately developed	?

¹ "?" in this column suggests species may be mute (see text for comments).

Contributions to the BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCIENCES SERIES, may be in any field of biology. Manuscripts dealing with natural history of systematic problems involving the southeastern United States or the New World tropics are solicited especially. Manuscripts should be of medium length—circa 35 to 200 pages (10,500-16,000 words). Examination for suitability is made by an Editorial Board.

The BULLETIN is distributed worldwide through institutional subscriptions and exchanges. It is considered the responsibility of the author to distribute his paper to all interested individuals. To aid in this the author(s) receives(s) 50 copies free, and he may purchase additional separates at cost if ordered when page proof is returned. The author is also responsible for any charges incurred for alterations made by him on galley or page proofs. The Museum will send an invoice to the author for this amount upon completion of publication.

PREPARATION OF MANUSCRIPT

Contributors should consult recent numbers of the BULLETIN for preferred style and format. Highly recommended as a guide is the CBE Style Manual, 3rd Edition, 1972 (Washington, D.C., Amer. Inst. Biol. Sci.).

MSS must be submitted in duplicate (please no onionskin) and satisfy the following minimal requirements: They should be typewritten, double-spaced (*especially* tables, figure captions, and "Literature Cited"), on one side of numbered sheets of standard (8-1/2x11 in.) bond paper, with at least one-inch margins all around. Tables (which should be unruled) and figure legends should be typed on separate sheets. All illustrations are referred to as figures. They must comply with the following standards: Photographs should be sharp, with good contrast, and printed on glossy paper. Drawings should be made with dense black waterproof ink on quality paper or illustration board. All illustrations should have a cover sheet. All lettering will be medium weight, sans-serif type (e.g. Futura Medium, News Gothic) in cutout, dry transfer or lettering guide letters. Make allowance so that after reduction no lowercase letter will be less than 1 mm high (2 mm is preferred) nor any capital letter greater than 5 mm high. The maximum size for illustrations is 8-5/8x14 in. (twice typepage size); illustrations should not be less than typepage width (4-5/16 in.). Designate the top of each illustration and identify on the back with soft pencil by author's name, MS title, and figure number.

Manuscripts and all editorial matters should be addressed to:

Managing Editor of the BULLETIN
Florida State Museum
Museum Road
University of Florida
Gainesville FL 32611