Variation, Systematics, and Zoogeography of *Eleutherodactylus guentheri* and Closely Related Species (Amphibia: Anura: Leptodactylidae)

W. RONALD HEYER

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ABSTRACT

Heyer, W. Ronald. Variation, Systematics, and Zoogeography of *Eleutherodactylus guentheri* and Closely Related Species (Amphibia: Anura: Leptodactylidae). *Smithsonian Contributions to Zoology*, number 402, 42 pages, 28 figures, 20 tables. 1984.—Intra- and interspecific patterns of variation are examined for species confused with or considered closely related to *Eleutherodactylus guentheri*. A total of six species are recognized in the *E. guentheri* cluster, three of them new. Descriptions are provided for the three new species; diagnoses and definitions are provided for all six. Members of the cluster are collectively associated with the middle and southern extent of the Atlantic Forest Morphoclimatic Domain in Brazil. Morphological differentiation among populations of *E. guentheri* is considerable, but there is no evidence of a strong geographic component to the intraspecific variation. This lack of widespread geographic variation, together with the restricted geographical distributions of the other species of the complex, suggests that differentiation occurred at very localized areas within the collective range of the species complex. The local differentiation pattern indicates that historical factors are critical to understanding present day patterns of differentiation and species distributions.

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Contents

Variation, Systematics, and Zoogeography of *Eleutherodactylus guentheri* and Closely Related Species (Amphibia: Anura: Leptodactylidae)

W. Ronald Heyer

Introduction

This contribution to the understanding of the systematics and zoogeography of the Brazilian Atlantic Forest fauna is a direct outgrowth of previous contributions (Heyer, 1983; Heyer and Maxson, 1983). In previous studies, based on analysis of members of the frog genus *Cycloramphus*, specific zoogeographic and speciation mechanism hypotheses were developed based on species that had very specialized subaerial larvae. The ecological restriction of adult and larval *Cycloramphus* to certain classes of small streams was of central importance in these hypotheses. Consequently, in order to test the generality of the hypotheses developed, I wished to study another group of frogs that occurs within the Atlantic Forests, but which is not restricted in its ecological distribution to streams. Members of the frog genus *Eleutherodactylus* seemed good candidates for such a study. All but one species of *Eleutherodactylus* have direct development, with embryonic and larval stages taking place in encapsulated terrestrial eggs. There are several species of *Eleutherodactylus* that commonly occur in the Atlantic Forests. On initial examination of available names and materials, it appeared that *Eleutherodactylus guentheri* and a few close relatives comprised a well-defined species cluster that was abundantly represented in collections. Consequently, materials of this cluster were borrowed and analyzed.

The purposes of this paper are to (1) report on the intra- and interpopulation variation of *Eleutherodactylus guentheri* and its close relatives, (2) summarize the systematic conclusions that are one result of these analyses, (3) analyze the zoogeographic distribution patterns for this complex, and (4) compare the zoogeographic results with those derived from study of the species of *Cycloramphus*.

DEFINITION OF GROUP

Lynch (1976) recognized four species groups for the 14 species of *Eleutherodactylus* associated with the Atlantic Forests of Brasil. *Eleutherodactylus guentheri* would be a member of the *E. binotatus* group as defined by Lynch (1976), the other members being *E. binotatus*, *gualteri*, *nasutus*, *octavioi*, and *pliciferus*. Of these, *E. binotatus*, *octavioi*, and *pliciferus* either have the first finger much longer than the second, numerous

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dorsolateral folds and/or have small or no digital disks. This combination of features distinguishes *E. binotatus, octavioi,* and *pliciferus* from *E. gualteri, guentheri,* and *nasutus,* the latter three species having been confused with each other in museum collections. Since a homogeneous, clearly identifiable group was wanted for purposes of this study, I borrowed specimens identified as *E. gualteri, guentheri,* and *nasutus,* as well as unidentified *Eleutherodactylus* from the Atlantic Forest region from MNRio and MZUSP (see below for key to these museum abbreviations). As study of these materials progressed, it became obvious that there are several undescribed species of *Eleutherodactylus* from the Atlantic Forest system that do not coincide with Lynch's species groupings. Some of these taxa may well be closely related to *E. gualteri, guentheri,* and *nasutus.* A study adequate to resolve the species group definitions for the Atlantic Forest *Eleutherodactylus* would be, at this point, necessarily a long-term one. I have chosen to limit the cluster of taxa included in this study in such a way that the larger taxonomic problems can be avoided. Thus, the *Eleutherodactylus guentheri* cluster is arbitrarily defined as those taxa that probably would be (or have been) identified as either *E. gualteri, guentheri,* or *nasutus,* based on limited comparative material. Further study of additional taxa may expand the group to include species that are more closely related to the *E. guentheri* cluster as defined here than to any other groups of *Eleutherodactylus.* I believe, however, that the *E. guentheri* cluster as defined here is monophyletic.

MATERIALS

Aside from those from the Museu Nacional, Rio de Janeiro (MNRio) and the Museu de Zoologia da Universidade de São Paulo (MZUSP), some specimens of the *E. guentheri* cluster examined were from the USNM collections of the National Museum of Natural History, Smithsonian Institution. Selected specimens from the W.C.A. Bokermann private collection (WCAB), the Eugenio Izecksohn collection (EI), and the Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (MCN-AN) were also examined. Considered together, these materials include several large series of specimens from single localities and probably also give a good representation of the species' geographic distributions. No effort was made to borrow materials from additional museums as almost all such specimens would represent additions to already large samples in the materials at hand.

METHODS

The following data elements were recorded for each specimen examined.

Sex: Males were determined by presence of vocal slits. Females were determined by large size, egg visibility through the belly wall, or dissection to examine the reproductive organs. For doubtful specimens, dissections were made.

Calcar: Presence or absence of a calcar on the heel was noted. As a calcar is present in all reasonably well preserved members of this cluster, the character is not analyzed further.

Color patterns: Pattern standards were developed on outline drawings for several pattern aspects. When a new pattern was encountered, it was added to the standards. Goin (1950, 1960) has shown that several aspects of the dorsal pattern are inherited independently in some species of *Eleutherodactylus.* Consequently, standards were developed for the following pattern aspects: general dorsal pattern (Figure 1), mid-dorsal pin stripe (Figure 2), broad mid-dorsal stripe (there are but two states—present or absent), dorsolateral stripes (Figure 3), snout pattern (Figure 4), interocular bar (Figure 5), pelvic spots (Figure 6), supratympanic stripe or spot (Figure 7), loreal stripe (Figure 8), upper lip (Figure 9), outer front aspect of the tibia (Figure 10), and posterior surface of the thigh (Figure 11). Only one example of apparent pattern linkage was encountered: in specimens with the extensive light dorsal snout condition (pattern A in Figure 4), the light area included the same area where the light interocular bar occurs. The light interocular bar

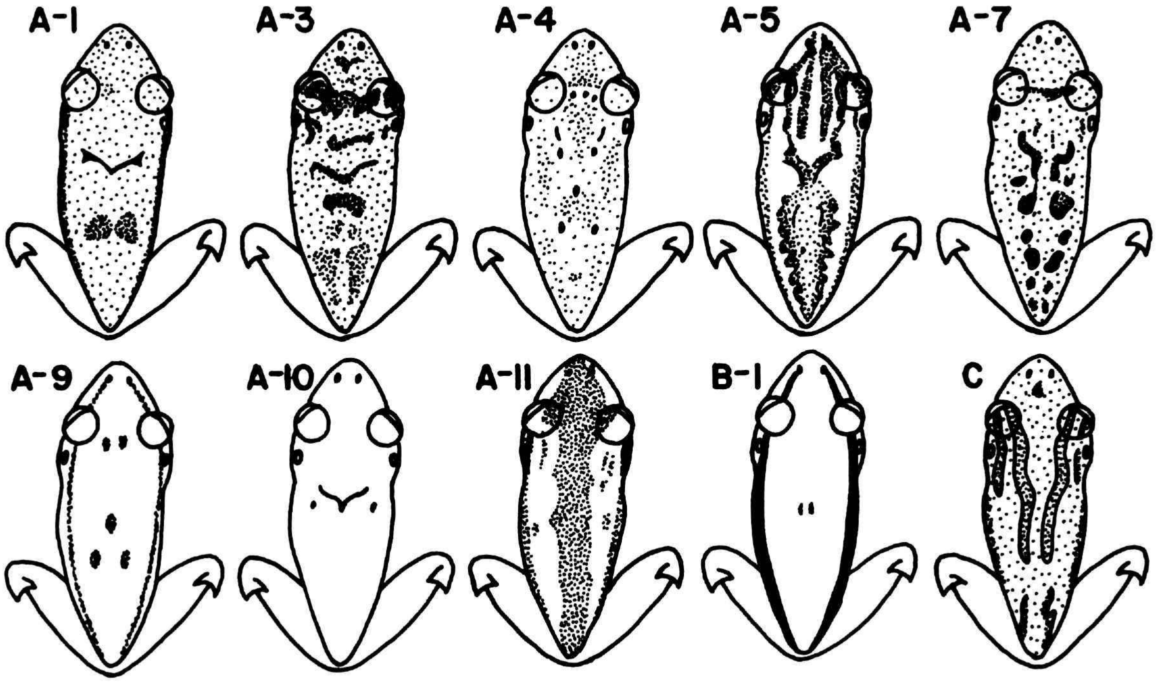


FIGURE 1.—Standards for dorsal patterns. Additional standards not figured are: A-2, uniform with no contrast with lateral color pattern; A-6, not as distinct as A-5; A-8, completely variegated pattern; B-2, like B-1 but lacking dark spots on back.

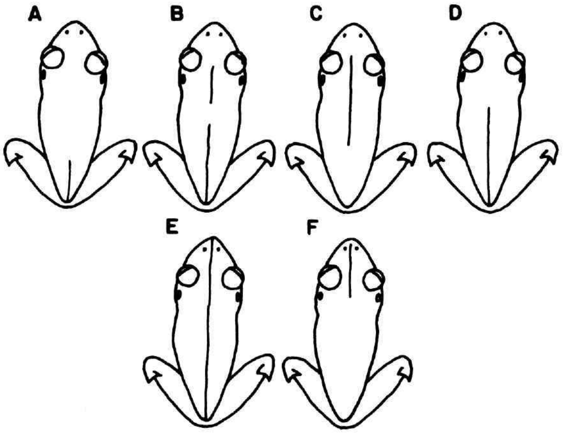


FIGURE 2.—Standards for mid-dorsal pin stripe patterns. The stripe may also be absent.

condition (Figure 5) was arbitrarily assigned to those specimens with the extensive light dorsal snout condition (pattern A in Figure 4).

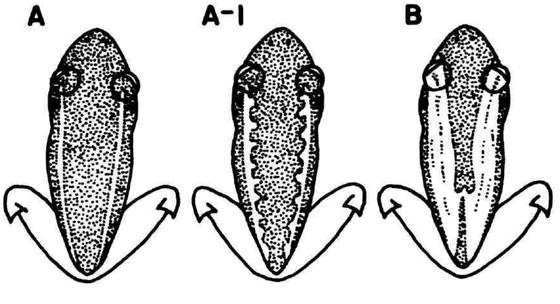


FIGURE 3.—Standards for dorsolateral stripe patterns. The dorsolateral stripe may also be absent.

Measurements: All measurements were taken with dial calipers, recorded to the nearest tenth of a millimeter. Most measurements are repeatable to within 0.5 millimeters. The following measurements were taken: snout-vent length (SVL); head length, from tip of snout to angle of jaw (HL); head width, maximum measurement, at or just in front of angles of jaw (HW); eye–

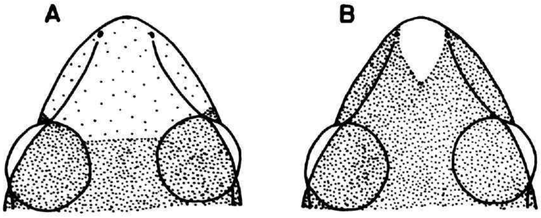


FIGURE 4.—Standards for snout patterns.

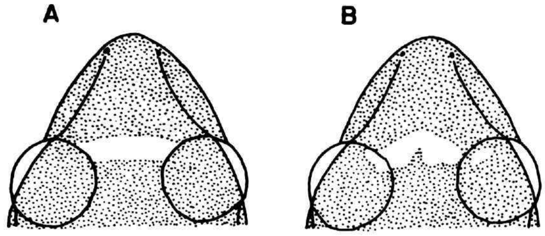


FIGURE 5.—Standards for interocular bar patterns.

nostril distance, from anterior corner of eye to mid-nostril (EN); eye–eye distance, measured between anterior corners of eyes (EE); maximum vertical tympanum diameter, measured from the outside edges of tympanic annulus (TD); femur length, from mid-cloaca to knee when leg held as a Z with femur at right angles to body (femur); tibia length, from knee to heel (tibia); foot length, from proximal end of inner metatarsal tubercle to tip of fourth toe (foot); maximum width of disk on third finger (3FD); and maximum width of disk on fourth toe (4TD).

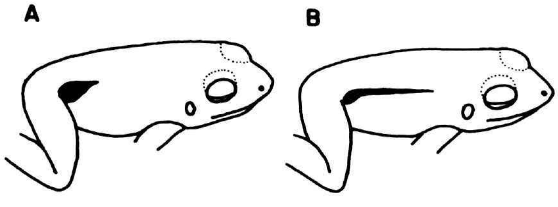


FIGURE 6.—Standards for pelvic spot patterns.

For specimens that were partially faded, only those pattern states were recorded that were clearly visible. For completely faded specimens no pattern states were recorded, but measurement data were recorded. For poorly positioned or preserved specimens where any single measurement could not be recorded, SVL (only) was recorded if possible. Thus, sample sizes are not equal for all characters analyzed.

Analysis of variation was done in three stages. In the first stage, large single-locality samples were analyzed to determine the nature of variation within samples. During the data-taking phase, specimens were sorted into morphospecies, that is, categories thought to represent different species. The second stage of analysis examined the patterns of variation among morphospecies. One morphospecies, *E. guentheri* itself, was represented by several large geographic samples. The third stage of analysis examined variation within the *E. guentheri* morphospecies. Results of all three analyses were used to help define species limits within the *E. guentheri* cluster. The geographic distribution patterns and

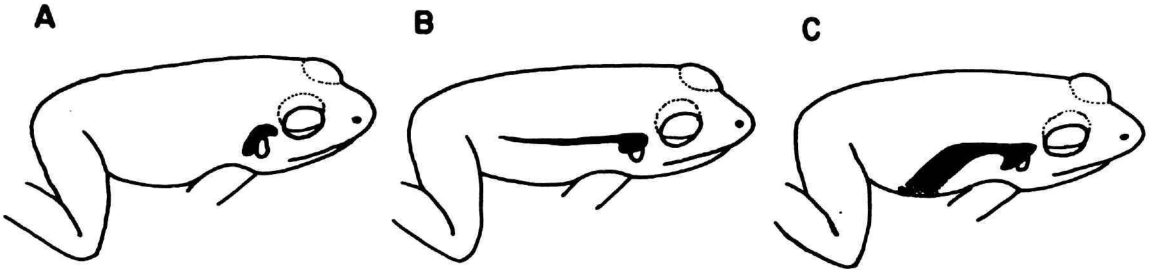


FIGURE 7.—Standards for supratympanic stripe patterns. Each pattern state includes individuals that may demonstrate lighter state expressions than those figured.

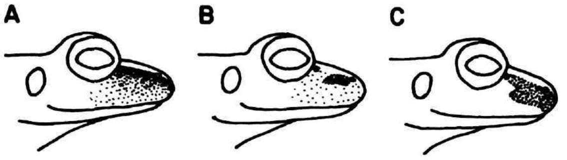
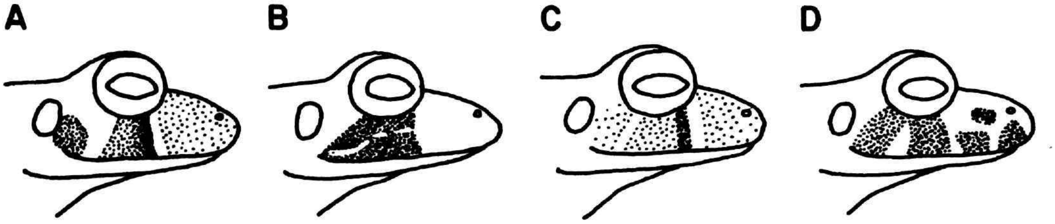


FIGURE 8.—Standards for loreal stripe patterns (left). Uniform state not shown.

FIGURE 9.—Standards for lip patterns (below). Uniform state not shown.



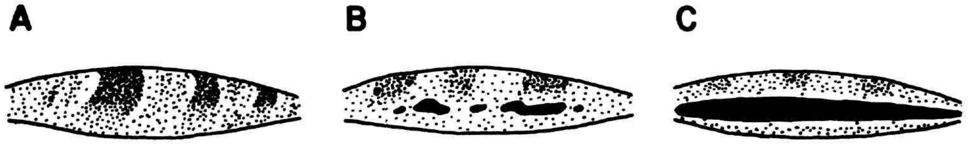


FIGURE 10.—Standards for tibia patterns. Uniform state not shown.

patterns of intraspecific variation were used to develop a zoogeographic hypothesis for the cluster.

Statistical procedures are used as appropriate and are explained at the time they are used in the text.

For purposes of analysis, the various populations need to be identified. Following is a coded series that was abstracted from the codes developed when taking and formatting the data. Only for the *E. guentheri* morphospecies is more than one sample available from localities represented by at least a total of 25 individuals containing at least five males and five females. This was the minimum population unit arbitrarily chosen to include in the interpopulation analysis within a morphospecies.

Each entry in the coded series contains the code, the number of specimens for which complete measurement data are available, code names, and localities. The values for N given here may not match those given in the tables. The latter values include specimens for which complete data are not available.

PGN, N = 3, "pseudoguentheri," all from near Santa Teresa, Espirito Santo.

PGL, N = 49, "pseudogualteri," all from near Santa Teresa, Espirito Santo.

GLT, N = 91, *E. gualteri*, from two localities in the state of Rio de Janeiro, Teresópolis (N = 82) and Paquequer (N = 9).

RT, N = 18, "red thighs," all from Teresópolis, Rio de Janeiro.

NAS, N = 64, *E. nasutus*, from eight localities in the states of Minas Gerais, Rio de Janeiro, and São Paulo.

GU, N = 949, *E. guentheri*, including the following large, single-locality samples:
- GU RJ1, N = 42, from Teresópolis, Rio de Janeiro
- GU RJ2, N = 40, from Petrópolis, Rio de Janeiro
- GU RJ4, N = 103, from Sumaré and Tijuca, Rio de Janeiro
- GU RJ5, N = 26, from Angra dos Reis, Rio de Janeiro
- GU SP1, N = 112, from Boracéia, São Paulo

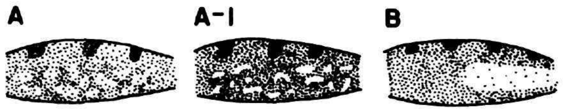


FIGURE 11.—Standards for posterior surface of the thigh pattern. Uniform state not shown.

GU SP2, N = 107, from São Paulo, São Paulo
GU SP3, N = 109, from Cubatão and Paranapiacaba, São Paulo
GU SP4, N = 131, from Serra da Bocaina, São Paulo
GU SP5, N = 33, from Campos do Jordão, São Paulo
GU SC1, N = 29, from Novo Horizonte, Santa Catarina

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Intrapopulation Variation

The purpose of this section is to analyze variation within a geographic population, particularly with respect to (1) differences among juveniles, males, and females, and (2) the extent of variation found within a population from a given locality.

Differences of pattern among juveniles, males, and females are probably due to either selection, ontogenetic change, or sexual dimorphism. It is unlikely that differences due to selection pressures would be detectable in samples of the sizes analyzed here. The 0.05 level is taken to be significant for statistical analysis; this level is appropriate for the size of the samples at hand. Selection coefficients are probably much smaller, however, which means that selection could be important biologically but not be statistically demonstrable. Thus, for all practical purposes, the following analyses examine the presence or absence of ontogenetic pattern change or sexual dimorphism within samples.

As an initial criterion, a search was made for single species samples from single localities with a total sample size of at least 80 individuals containing at least 20 juveniles, 20 females, and 20 males. Four samples met those criteria; two other samples met all but the number of females. One of these latter samples has 19 females, the other 15; of these, only the former is used with the four samples that meet all criteria to analyze intrapopulation variation. The five populations analyzed are: GLT (sample from Teresópolis), GU RJ4, GU SP1, GU SP2, GU SP3.

PATTERN

Goin (1950) has shown that several pattern features are under genetic control of one or two loci in certain *Eleutherodactylus* species. Members of the *E. guentheri* cluster have many of the same pattern polymorphisms studied by Goin (1950). Using Goin's study as a guideline, the pattern data as recorded were examined and categorized into states that are likely to be under direct genetic control. The loreal stripe and lip pattern characters did not have clearly definable, discrete states and are not analyzed in this section. For the dorsal pattern and supratympanic spot pattern, intensities of pattern were combined into single pattern states (see legends of Figures 1 and 7). There are three major dorsal patterns: (1) uniform or mottled/spotted (all A patterns in Figure 1), (2) dorsoconcolor (all B patterns in Figure 1) (3) wavy lines (pattern C in Figure 1). Within the first two major pattern types, several discrete states also occur. Four states of the middorsal pin stripe are recognized for this analysis: absent; short stripe on posterior body (pattern A in Figure 2); short or medium stripe occurring elsewhere than posterior body (patterns B, C, D, and F in Figure 2); full stripe (pattern E in Figure 2). Mid-dorsal stripes and light interocular bars are coded as either present or absent. The other pattern states are analyzed as described above (see page 2).

Occurrence of each pattern state was recorded for juveniles, males, and females. Whenever expedient, chi-square analyses were performed to test whether pattern states differed in occurrence among juveniles, males, and females. For these analyses the expected values are calculated on the assumption that the proportional occurrence of a given state derived from all individuals was the true occurrence for that population (also see Table 1). Dorsal pattern was analyzed in two ways. First, occurrences within the three major pattern types were analyzed; second, within-pattern analyses for the uniform/mottled/spotted pattern were performed where appropriate.

There is no statistical difference in occurrence of pattern states among juveniles, males, and females for dorsal pattern, pin stripe, broad mid-dorsal stripe, dorsolateral stripes, snout pattern, interocular light bar, pelvic spots, or outer tibia pattern (for an example of statistical analysis, see Table 1).

There were statistically significant differences between juveniles and adults in the occurrences of supratympanic spot and posterior thigh patterns (for an example of statistical analysis, see Table 2). Only two populations, GLT and GU SP1, demonstrated a difference among state distributions for the supratympanic spot, whereas all five populations had significantly different state distributions for the posterior thigh patterns. No significant differences between the sexes were found for any state.

TABLE 1.—Analysis of occurrence of tibia pattern states (see Figure 10) among juveniles, males, and females for sample GU RJ4 (O = observed, E = expected values*).

Sample	A		B		C	
	O	E	O	E	O	E
Juveniles	27	20.0	15	19.0	8	11.0
Males	7	9.6	9	9.1	8	5.2
Females	8	12.4	16	11.8	7	6.8
	$\chi^2 = 9.37$, not significant					

* For example, the expected value for A is calculated by dividing 42 (total number of A states) by 105 (total sample size) = percent of occurrence pattern A in entire sample, which is multiplied by 50 (number of juveniles in sample).

TABLE 2.—Analysis of occurrence of posterior thigh pattern states (see Figure 11) among juveniles, males, and females for sample GU SP1 (O = observed, E = expected values).

Sample	Uniform		A	
	O	E	O	E
Juveniles	21	31.7	50	39.2
Males	15	11.6	11	14.4
Females	19	11.6	7	14.4
	$\chi^2 = 16.91, P < .01$			
Juveniles	21	31.7	50	39.2
Adults	34	23.2	18	28.8
	$\chi^2 = 15.67, P < .01$			
Males	15	17.0	11	9.0
Females	19	17.0	7	9.0
	$\chi^2 = 1.34$, not significant			

These results suggest that there is no ontogenetic pattern change for most patterns examined, with the exceptions of the supratympanic spot and the posterior thigh pattern. The posterior thigh pattern differences are clearest: juveniles have a mottled pattern (pattern A in Figure 11) that is either retained or develops into one of the other patterns as they mature. A practical consequence of the pattern analyses is that for most patterns, juvenile, male, and female data can be combined. Male and female data for the supratympanic spot and posterior surface of the thigh pattern can also be combined.

SIZE

Because members of the *E. guentheri* cluster exhibit sexual dimorphism in size (see Table 20),

TABLE 3.—Within population size (SVL) statistics of males and females for five populations.

Sample	Sex	N	$\bar{X}$	Observed min–max (range)	95% confidence limit estimated min–max (range)	Skewness
GLT	♂	36	29.6	23.2–34.1 (10.9)	25.4–33.7 (8.3)	−0.9
GU RJ4	♂	25	25.1	19.9–27.2 (7.3)	21.5–28.6 (7.1)	−1.5
GU SP1	♂	25	24.1	19.3–26.7 (7.4)	20.5–27.7 (7.2)	−0.9
GU SP2	♂	25	24.2	19.2–28.3 (9.1)	18.8–29.6 (10.8)	−0.3
GU SP3	♂	24	23.4	16.4–27.5 (11.1)	17.2–29.5 (12.3)	−0.6
GLT	♀	19	40.2	33.6–45.7 (12.1)	32.5–47.8 (15.3)	−0.7
GU RJ4	♀	29	35.6	32.7–39.0 (6.3)	32.1–39.0 (6.9)	0.1
GU SP1	♀	26	33.9	26.4–40.0 (13.6)	27.6–40.3 (12.7)	−0.5
GU SP2	♀	25	35.2	28.1–43.9 (15.8)	25.2–45.4 (20.2)	0.1
GU SP3	♀	37	38.2	28.7–44.4 (15.7)	29.9–46.5 (16.6)	−0.9

the size data were analyzed separately for the two sexes. The range of adult male size observed in five sample populations (Table 3) varies from 7.3 to 11.1 mm. The corresponding range for adult females is 6.3 to 15.8 mm. A size range of 8 mm can be used conservatively to arrive at either observed or estimated size ranges for males and females (Table 3). With the exception of sample GU RJ4, the size range of females is greater than that of males. The criterion used for distinguishing between juveniles and females (condition of reproductive tract) is not as clear-cut as for distinguishing between juveniles and males (presence or absence of vocal slits). The size range of females might thus include females that are entering their first reproductive cycle, but are not yet sexually mature. Even with the difficulties of establishing when females are first sexually mature, it is likely that the size range of females is greater than that of males. The large size ranges for both males and females, taken together with an overall pattern of left-handed skewness, suggest that more than one annual age class is represented; in other words, the adult life span of some males and females is more than one year.

MEASUREMENT VARIABLE/SIZE RELATIONSHIPS

For each of the five populations in Table 3 the SPSS (Nie et al., 1975) program SCATTERGRAM was run for each variable plotted against SVL for all individuals, and then separately for juveniles, males, and females. The regression lines for the total sample, juveniles, males, and females, were drawn on a single figure for each variable run for each of the five samples, to visually determine whether a linear or a power function best describes the relationship.

All correlations are significant. Most variables demonstrate a simple straight-line correlation with SVL; the regression lines for juveniles, males, and females for each variable are visually indistinguishable for every case where $r^2 > 0.80$. An example of one of the worst deviations from a single straight line shows but moderate deviation (Figure 12). In no case was the r^2 for juveniles, males, or females as groups higher than the r^2 for the combined sample. Size-related variables are thus interpreted to be isometric with absolute body size; allometry does not appear to be a significant factor for any variable. Correlations (for total samples) between HL/SVL, HW/SVL, EN/SVL, EE/SVL, femur/SVL, tibia/SVL, and foot/SVL are very high, with r^2 ranging from 0.96–0.99. Correlations between TD/SVL, 3FD/SVL, and 4TD/SVL are moderately high, with r^2 ranging from 0.86–0.94.

Interpopulation Variation

MORPHOSPECIES

Specimens were sorted by locality, and morphological data were recorded for specimens

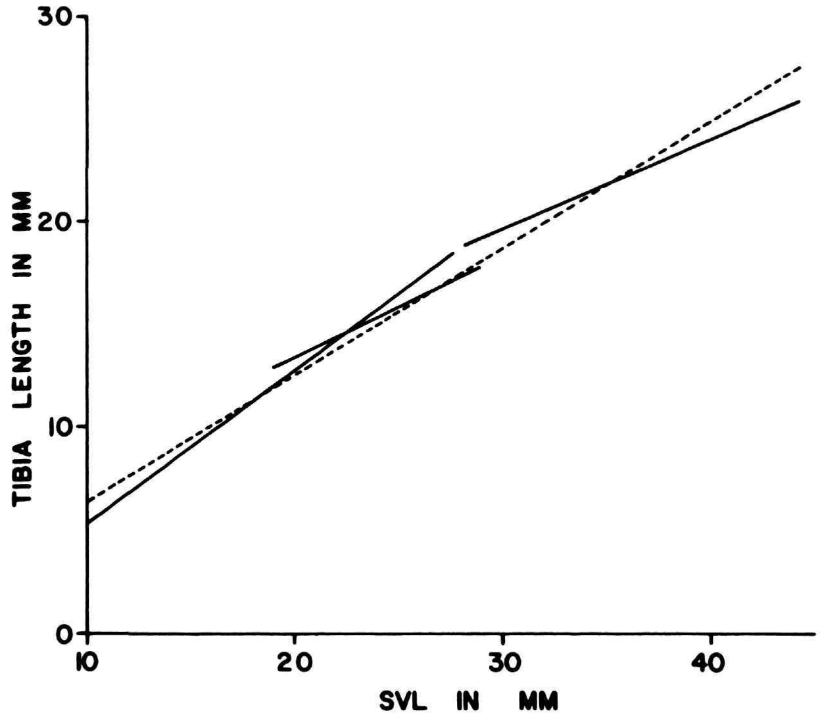

FIGURE 12.—Regression lines for tibia length plotted aginst snout-vent length for population GU SP2. Dashed line is regression line for total sample ($r^2 = 0.96$), solid lines are regression lines for juveniles ($r^2 = 0.96$), males ($r^2 = 0.73$), and females ($r^2 = 0.73$). This example is one that represents the most distinctive regression lines for the 50 figures prepared for the analysis.

from each locality. At two localities, Teresópolis (RJ) and Santa Teresa (ES) four sympatric species were identified. These sympatric taxa, defined on the basis of pattern, size, and shape differences, are treated as morphospecies for purposes of analysis. Two of the morphospecies from Teresópolis and Santa Teresa are very similar and considered to be the same. Thus, between these two localities, six morphospecies are recognized and, for purposes of analysis, identified as GLT, GU, NAS, PGL, PGN, and RT. As data were recorded on specimens from additional localities, almost all additional specimens were readily classified as belonging to one of the six morphospecies. There was a total of 12 adequately preserved specimens that were questionably included in the morphospecies GU. These specimens (EI 716; L 18, 19, 48, 92, 96, 97, 99; MNRio 2425; MZUSP 59666; and USNM 235714) will be discussed after the size and shape analysis. The purpose of this section is to determine the likelihood that the six morphospecies identified during the data-taking phase represent biological species. The results will indicate only the minimum number of species involved in the cluster. Analysis of variation of populations within the species as identified in this section may require recognition of additional species.

Patterns

Pattern states were summarized for each morphospecies. Data were drawn from juveniles and adults for the characters of dorsal pattern (Table 4), pin stripe (Table 5), dorsolateral stripes (Table 7), dorsal snout pattern, interocular bar, pelvic spots, and tibia pattern (Table 8). Data from adults only were used for supratympanic spot,

TABLE 4.—Distribution of dorsal pattern states (in percentages) among the six morphospecies; pattern states as defined in Figure 1 (N = number of individuals for which dorsal pattern data are available; a blank indicates no individuals had the state; a zero indicates that at least one individual with the state was examined, but the rate of occurrence per 100 specimens rounds off to zero).

Morphospecies	N	A-1	A-2	A-3	A-4	A-5	A-6	A-7	A-8	A-9	A-10	A-11	B-1	B-2	C
GLT	96	21	46	5									14		14
GU	954	1	21	0	16	24	12	3	4	0	4	1	5	5	4
NAS	58	3	12	14	5		55		7		2		2		
PGL	49	10	28	10			6		14		2		2	6	20
PGN	3		67				33								
RT	18	6	18		28	39			11						

posterior thigh (Table 9), loreal stripe, and upper lip patterns. Ontogenetic change of patterns was demonstrated for supratympanic spot and posterior thigh patterns on page 5; as the last two characters were not previously analyzed for ontogenetic variation, the conservative approach of using only the adult data was taken.

The results indicate three categories of characters. In the first, the frequencies of character states differ among the morphospecies, but no state is diagnostic. The dorsal snout, interocular bar, pelvic spot, supratympanic spot, loreal stripe, and upper lip patterns fall into this category. The second category is defined by not only a differential frequency of state occurrence among taxa, but some of the states are unique to certain taxa. The specimens having those unique states are thus easily diagnosed from the other taxa. The characters represented by this second category will distinguish only some, not most, individuals within the morphospecies. The characters of this second category are dorsal pattern (Table 4), pin stripe (Table 5), broad mid-dorsal stripe (Table 6), and dorsolateral stripes (Table 7). The third is similar to the second, but its characters, the tibia (Table 8) and posterior thigh (Table 9) patterns, distinguish a larger proportion of specimens. Taken in combination, pattern characteristics will distinguish most, but not all individuals of the six morphospecies.

Measurement Variables

The SPSS stepwise discriminant function program (Nie et al., 1975) was used to analyze morphological variation among the morphospecies. Males and females were analyzed separately, using the minimization of Wilks's λ option; all measurement variables were used in the analysis. The male and female results are reported separately and discussed jointly.

For males, the data for the six morphospecies

TABLE 5.—Distribution of pin stripe states (in percentages) among the six morphospecies; pattern states as defined in Figure 2 (N = number of individuals for which data are available).

Morphospecies	N	None	A	B	C	D	E	F
GLT	96	44	42	9	5			
GU	936	55	27	2	1	1	12	1
NAS	60	68	27	3				
PGL	49	86	12			2		
PGN	3	100						
RT	18	56	33		11			

TABLE 6.—Distribution of broad mid-dorsal stripe states (in percentages) among the six morphospecies (N = number of individuals for which data are available).

Morphospecies	N	With	Without
GLT	96		100
GU	958	7	93
NAS	60	3	97
PGL	49		100
PGN	3		100
RT	18		100

TABLE 7.—Distribution of dorsolateral stripe pattern states (in percentages) among six morphospecies; pattern states as defined in Figure 3 (N = number of individuals for which dorsolateral stripe pattern data are available).

Morphospecies	N	Without	A	A-1	B
GLT	96	76	23		1
GU	948	94	2	4	
NAS	58	62	38		
PGL	49	92	8		
PGN	3	100			
RT	18	100			

TABLE 8.—Distribution of tibia pattern states (in percentages) among six morphospecies; pattern states as defined in Figure 10 (N = number of individuals for which data are available).

Morphospecies	N	Uniform	A	B	C
GLT	96	20	80		
GU	945		21	38	41
NAS	58		53	33	14
PGL	49	10	90		
PGN	3			33	67
RT	18			56	44

TABLE 9.—Distribution of posterior thigh pattern states (in percentages) among six morphospecies; pattern states as defined in Figure 11 (N = number of individuals for which data are available; a blank indicates no individuals had the state; a zero indicates at least one individual with the state, but the frequency of occurrence rounds off to zero).

Morphospecies	N	Uniform	A	A-1	B
GLT	62	90	10		
GU	485	55	44	1	0
NAS	58		2	98	
PGL	33	18	82		
PGN	3		100		
RT	10				100

were used as the preformed groups for analysis. All variables added significantly to the discrimination of the groups and entered the program in the following order (the Wilks's λ values, in parentheses, indicate the relative contribution of each variable in discriminating among the morphospecies): SVL (0.511), HW (0.313), tibia (0.195), 4TD (0.158), foot (0.133), 3FD (0.114), TD (0.110), femur (0.107), HW (0.104), EN (0.101), EE (0.100).

A posterior classification uses the group (morphospecies) centroid values to determine the probability of each specimen-case belonging to each grouping. The results (Table 10) indicate that generally, the morphospecies are distinct.

The plot of the first two discriminant functions gives a visual picture of the phenetic similarities of the morphospecies groups (Figure 13). The first two axes account for 86% of the total dispersion. The first axis, accounting for 53% of the dispersion, reflects a size component. Head width and foot length have high coefficient values for the second axis, which accounts for 34% of the dispersion. The third axis, which accounts for almost all of the remaining dispersion (12%) has two variables with high coefficient values: tibia length and foot length.

The results indicate three morphological clusters: (1) GLT, (2) NAS, and (3) a cluster including GU, PGL, PGN, and RT, which are not completely discriminated by this analysis. Individual cases for which the posterior classification indicated a higher probability for inclusion in a group other than initially determined by me were examined. Most of these cases involved members of the GU, PGL, PGN, RT cluster, where the probability of belonging to a different group was 50% or less, and the next highest group probability was the one determined by me at the beginning of the analysis. There remain 12 specimens that stand out as distinctive in the analysis (do not fit in well with the groups used for analysis): MNRio 1793 (5 specimens), MZUSP

TABLE 10.—Predicted group membership (in percentages) for males of six morphospecies based on the classification results of the discriminant function analysis (N = number of individuals).

Preformed group	N	GLT	GU	NAS	PGL	PGN	RT
GLT	42	97.6	0	0	2.4	0	0
GU	283	2.5	74.6	2.5	3.9	3.9	12.7
NAS	48	2.1	0	97.9	0	0	0
PGL	22	0	0	0	90.9	9.1	0
PGN	3	0	0	0	0	100	0
RT	3	0	0	0	0	0	100

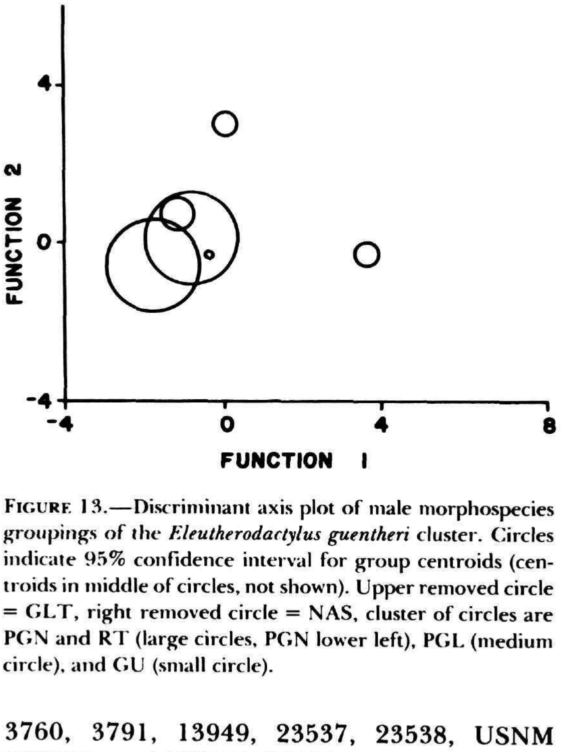

FIGURE 13.—Discriminant axis plot of male morphospecies groupings of the *Eleutherodactylus guentheri* cluster. Circles indicate 95% confidence interval for group centroids (centroids in middle of circles, not shown). Upper removed circle = GLT, right removed circle = NAS, cluster of circles are PGN and RT (large circles, PGN lower left), PGL (medium circle), and GU (small circle).

3760, 3791, 13949, 23537, 23538, USNM 235732, and WCAB 25392. These specimens are discussed further below.

No female PGN were examined, so data for the remaining five morphospecies were used as the preformed groups for analysis. As for the males, all variables added significantly to the analysis. The variables entered the program in the following order (Wilks's λ values in parentheses): foot (0.662), 3FD (0.445), HW (0.368), HL (0.312), 4TD (0.270), SVL (0.235), tibia (0.207), TD (0.188), EE (0.179), femur (0.174), EN (0.171).

The posterior classification results for females (Table 11) indicate the distinctiveness of the morphospecies.

The plot of the first two discriminant axes for females (Figure 14) accounts for 80% of the total dispersion. The first axis, the size related axis, accounts for 49% of the dispersion. Head length has a high coefficient value for the second axis, which accounts for 31% of the dispersion. Head length and tibia length have high coefficient values for the third axis, which accounts for 18% of the dispersion. The first three axes account for almost all (98%) of the dispersion.

The female results also indicate three morphological clusters that are not completely discriminated from one another: (1) GLT, (2) NAS, and (3) GU, PGL, and RT. Distinctive individual cases were examined as for the males. There are seven distinctive female specimens: AL 2318, L 35, MZUSP 86, 171, 173, USNM 96518, 97680. These specimens are discussed further below.

The male and female results are similar in that the same clusterings of morphospecies are represented. The variables that discriminate among morphospecies for both males and females are size, overall head shape (as measured by head length and width), and hind limb proportions. Eye-nostril distance, eye-eye distance, and disk

TABLE 11.—Predicted group membership (in percentages) for females of five morphospecies based on classification results of the discriminant function analysis: no data are available for PGN (N = number of individuals).

Preformed group	N	GLT	GU	NAS	PGL	RT
GLT	20	85.0	15.0	0	0	0
GU	223	2.2	82.1	3.6	1.8	10.3
NAS	14	0	0	100	0	0
PGL	11	0	0	0	100	0
RT	6	0	0	0	0	100

widths do not discriminate well among the morphospecies. The major difference between male and female results is that NAS is characterized differently by factors other than size (compare position of NAS circle in Figures 13 and 14).

Problematical Specimens

Of the 1258 specimens examined, 31 were either difficult to assign to one of the six morphospecies or were distinctive from the assigned morphospecies (specimens cited previously in appropriate sections). The 31 specimens were all individually re-examined to determine whether they required further evaluation. Twenty-six individuals unquestionably conformed to the original designation to morphospecies upon re-examination. Three individuals (L 18, 19, WCAB 25392) appeared to differ in a subtle way from GU (to which they were originally assigned), but on re-examination appear to fall within the general range of variation of GU and are retained in that morphospecies. One individual (MZUSP 86) is so faded that no pattern data can be used to clarify the classification, but the head shape appears to be more like GU than NAS (the morphospecies as classified by the discriminant function analysis), so it is retained as a GU. Finally, one individual, USNM 97680, originally classified as GLT, was classified by the discriminant function analysis as GU; re-examination indicates agreement with the GU morphospecies assignment.

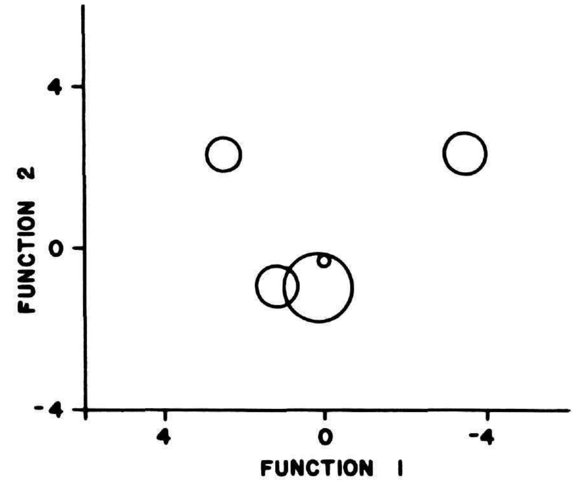

FIGURE 14.—Discriminant axis plot of female morphospecies groupings of the *Eleutherodactylus guentheri* cluster; no data available for morphospecies PGN. Circles indicate 95% confidence level for group centroids (centroids in middle of circles, not shown). GLT is represented by removed circle on upper left, NAS is represented by removed circle on upper right, cluster of circles represent GU (small circle), PGN (medium circle), and RT (large circle).

Life Colors

There are some life color data available for all morphospecies but PGN. The iris is copper colored in GLT; green dorsally, blending into bronze just above the iris and brown laterally and ventrally or, pale yellow dorsally blending to copper laterally and ventrally, or entirely copper in GU; bronze or green dorsally fading into bronze in PGL; (iris color not noted for NAS); and golden bronze above and below and brown in the middle in RT. The posterior surfaces of the thighs lack any flash colors in GU, GLT, NAS, and PGL; the posterior thigh has red flash color in RT. The belly and underside of the limbs are yellow in GU (color not noted for GLT or NAS), yellow or yellow wash tinged with green in PGL and yellow or dirty yellow in RT.

Advertisement Calls

There are only three calls available that have voucher specimens available; one call series each

TABLE 12.—Summarized habitat and ecological data for five morphospecies of the *Eleutherodactylus guentheri* cluster; numbers are individual specimens.

Morphospecies	Time captured	Vegetation			Substrate				
		Forest	Degraded forest	Open	Ground, on leaf or soil	On small plant or tree, 2 m high: Leaf	Stem	Other	Other
GLT	Day	17	3	0	18	1	0	2	0
	Night	27	0	0	14	3	3	3	3
GU	Day	75	40	2	116	0	0	0	1
	Night	10	10	0	4	12	2	1	1
NAS	Day	0	0	1	0	0	0	0	1
	Night	0	1	5	1	1	2	1	1
PGL	Day	15	0	0	15	0	0	0	0
	Night	1	0	0	1	0	0	0	0
RT	Day	15	1	0	15	0	0	0	0
	Night	1	0	0	1	0	0	0	0

TABLE 13.—Occurrence of pattern states among 10 samples of the morphospecies GU (N = numbers of individuals; asterisk indicates a significant difference (<0.05) from an expected occurrence calculated on the basis of the frequency of state occurrence for the entire sample GU).

Sample	N	A-1	A-2	A-3	A-4	A-5	A-6	A-7	A-8	A-9	A-10	A-11	B-1	B-2	C
RJ1	42		1*		2	26*	1	2				7		1	2
RJ2	36		3	1	4	13	2	8	1					3	1
RJ4	102		23		18	28	14	2	11				0*	5	1
RJ5	24		2		2	9	5	2					2	2	
SP1	123		20		14	37	6*	6	4				5	10	21
SP2	112		30		19	17	29*	1	2	1			7	6	
SP3	116	1	26		13	10*	17	3	6		20		10	6	5
SP4	130	2	34		22	23	13	1	4		14		6	11	
SP5	33		11		9	9	3							1	
SC1	29		5		3	7	6	2			2			4	

for GU, GLT, and NAS, each from a different locality. The frequency channel is similar for the three calls, but the temporal aspects of the calls are very distinctive, consistent with species level differentiation (see species accounts for detailed descriptions and figures of calls).

Habitat/Ecology

The data reported here are those I have collected, which offer comparisons, but are incomplete (Table 12). Most individuals of all morphospecies were collected during the day from leaf litter. Those individuals taken at night were often up off the ground on leaves or branches of small plants or on the lower portions of trees. Two trends are suggestive, but not conclusive with the data at hand: (1) GLT, GU, PGL, and RT are forest-associated species, NAS is an open formation associate; and (2) RT may be strictly diurnal. Individuals of GLT, GU, and NAS call at night or dusk (males of PGL not heard by me); only one individual of RT was heard calling, but the individual called during the day.

There are only three localities where more than one morphospecies occur in sympatry in the samples analyzed for this study. At Nova Friburgo, Rio de Janeiro, two morphospecies occur

TABLE 14.—Distribution of pattern state occurrences for ten samples of GU that differ significantly from expected occurrences based on frequency of occurrence for entire sample GU (L indicates observed number of occurrences is significantly less than expected; M indicates observed number of occurrences is significantly more than expected; columns defined in list below).

Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
RJ1	L	M							L			M									M	L	L	M		L	L
RJ2												M															
RJ4				L			L						L											M		L	
RJ5																	M										
SP1			L		L	M		M									M	L	M	M	L	M	L	L			
SP2			M					L	M							M	L			M			M		M	L	M
SP3		L				L				L	M			M			L							M		L	
SP4					L		M	L						L	M				M			M	L	L	L	M	
SP5												L												L		M	
SC1					M	L				L														L			

1 = Figure 1, pattern A-2; 2 = Figure 1; pattern A-5; 3 = Figure 1, pattern A-6; 4 = Figure 1, pattern B-1; 5 = No mid-dorsal pin stripe; 6 = figure 2, pattern A; 7 = Figure 2, pattern E; 8 = Broad mid-dorsal stripe; 9 = Figure 4, pattern A; 10 = Figure 4, pattern B; 11 = No light interocular bar; 12 = Figure 5, pattern A; 13 = Figure 5, pattern B; 14 = No pelvic spot; 15 = Figure 6, pattern B; 16 = Figure 7, pattern A; 17 = Figure 7, pattern C; 18 = No loreal stripe; 19 = Figure 8, pattern B; 20 = Figure 8, pattern C; 21 = Figure 9, pattern A; 22 = figure 9, pattern C; 23 = Figure 9, pattern D; 24 = Figure 10, pattern A; 25 = Figure 10, pattern B; 26 = Figure 10, pattern C; and 27 = Posterior thigh.

(GU and NAS). Four morphospecies occur at Teresópolis, Rio de Janeiro (GU, GLT, NAS, and RT) and at Santa Teresa, Espirito Santo (GU, NAS, PGL, and PGN).

VARIATION WITHIN GU

PGL, PGN, and RT are known at present from single localities. GLT is known only from two localities relatively close to each other. NAS is known from several localities, but there are no series of specimens from single localities with which to analyze intraspecific variation. GU is known from many localities and there are 10 localities from which adequate series of specimens are available to analyze the degree and pattern of inter-population variation. The sample codes and sizes were listed previously.

Patterns

Distributions of pattern states were determined for each of the ten population samples (e.g., Table 13) and the observed occurrences were tested against expected occurrences (based on frequency of distribution for entire sample of GU) with the χ^2 test. The dorsolateral stripe was the only pattern character for which at least one state did not demonstrate a distribution of occurrence significantly different from those expected (Table 14). Dorsal pattern was the only character for which certain state occurrences would be tested inappropriately by χ^2 (expected occurrence of less than five individuals) for which meaningful differences of pattern state occurrence are inferred. These additional states are the occurrence of pattern A-11 (Figure 1) in sample RJ1, the relatively high number of occurrences of pattern C in sample SP1, and the occurrence of pattern A-10 in samples SP3, SP4, and SC1.

Though all patterns examined show variation in occurrence of states among samples, with the occurrence of many states being significantly different among samples, the differences are interpreted to be those of degree, not kind.

Measurement Variables

The stepwise discriminant function statistical procedure (the same used for morphospecies

TABLE 15.—Order of variable entry into the stepwise discriminant function analysis of 10 samples of GU.

Males			Females		
Step	Variable	Wilks's λ	Step	Variable	Wilks's λ
1	Tibia	0.426	1	Head width	0.567
2	Head width	0.281	2	Foot	0.304
3	Finger disk width	0.210	3	Eye-nostril	0.232
4	Eye-nostril	0.170	4	Eye-eye	0.160
5	Head length	0.138	5	Tibia	0.122
6	Femur	0.108	6	Toe disk width	0.096
7	SVL	0.089	7	Head length	0.081
8	Tympanum	0.075	8	SVL	0.067
9	Toe disk width	0.064	9	Tympanum	0.058
10	Eye-eye	0.058	10	Finger disk width	0.054
11	Foot*		11	Femur	0.050

* F level to enter for foot insufficient to add to analysis.

TABLE 16.—Variables with highest loadings on first four canonical discriminant functions for 10 samples of GU. Values in parentheses following functions are percent of variance accounted for.

Males	Coefficient value	Females	Coefficient value
Function 1 (59%)		Function 1 (39%)	
Tibia	1.89	Foot	−1.70
Femur	−1.02	Eye-eye	1.30
		Head length	1.19
		Eye-nostril	−1.11
		Tibia	1.08
		Head width	1.00
Function 2 (14%)		Function 2 (22%)	
Head length	2.17	Tibia	2.34
Femur	−1.05	Eye-nostril	−1.34
		Head length	1.10
Function 3 (10%)		Function 3 (17%)	
Eye-nostril	1.49	Eye-nostril	1.25
		Foot	1.24
		Eye-eye	−1.11
		Tibia	−1.10
Function 4 (8%)		Function 4 (9%)	
SVL	−2.66	Tibia	−1.78
Head width	1.30	Head length	−1.69
		Foot	1.23

analysis) was used to analyze morphological variation among populations. Males and females were analyzed separately; the 10 populations were used as the preformed groups for analysis.

In contrast to the morphospecies analyses, the male and female results for the ten GU samples are quite different. The order in which variables entered the analysis is different (Table 15), as is the amount of variance accounted for by the canonical discriminant functions and the variables with the largest coefficient values for each of the canonical discriminant functions (Table

TABLE 17.—Predicted group membership (in percentages) for males of 10 GU samples based on classification results of the discriminant function analysis (N = number of individuals).

Preformed group	N	RJ1	RJ2	RJ4	RJ5	SP1	SP2	SP3	SP4	SP5	SC1
RJ1	32	81.3	3.1	0	3.1	6.3	3.1	0	0	3.1	0
RJ2	7	0	42.9	0	14.3	28.6	0	0	14.3	0	0
RJ4	25	0	8.0	80.0	0	0	0	8.0	0	0	4.0
RJ5	7	0	0	0	85.7	0	0	0	0	0	14.3
SP1	25	8.0	12.0	0	8.0	48.0	8.0	12.0	0	0	4.0
SP2	25	0	0	0	0	8.0	68.0	16.0	4.0	0	4.0
SP3	24	0	4.2	4.2	0	8.3	8.3	62.5	0	8.3	4.2
SP4	46	10.9	0	0	0	2.2	2.2	0	65.2	15.2	4.3
SP5	7	0	14.3	0	0	0	0	0	14.3	71.4	0
SC1	9	0	0	11.1	0	11.1	0	0	0	0	77.8

TABLE 18.—Predicted group membership (in percentages) for females of 10 GU samples based on the classification results of the discriminant function analysis (N = number of individuals).

Preformed group	N	RJ1	RJ2	RJ4	RJ5	SP1	SP2	SP3	SP4	SP5	SC1
RJ1	6	83.3	0	0	0	16.7	0	0	0	0	0
RJ2	11	0	36.4	36.4	0	0	0	0	0	18.2	9.1
RJ4	29	3.4	10.3	72.4	3.4	3.4	3.4	3.4	0	0	0
RJ5	9	11.1	11.1	0	77.8	0	0	0	0	0	0
SP1	26	3.8	0	0	3.8	76.9	7.7	3.8	0	0	3.8
SP2	24	0	0	4.2	0	12.5	70.8	8.3	4.2	0	0
SP3	38	0	0	5.3	0	10.5	7.9	76.3	0	0	0
SP4	15	0	0	0	0	6.7	13.3	0	60.0	20.0	0
SP5	6	0	0	0	0	0	0	0	16.7	83.3	0
SC1	10	0	0	0	0	10.0	0	10.0	0	0	80.0

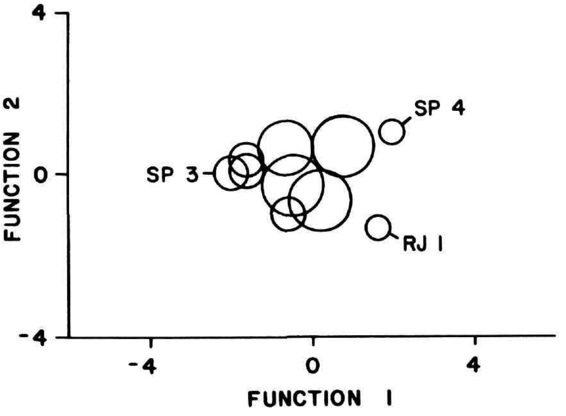

FIGURE 15.—Discriminant axis plot for males of 10 samples of the morphospecies GU. Circles indicate 95% confidence level for group centroids (centroids in middle of circles, not shown). For text reference, SP3, SP4, and RJ1 are individually labeled.

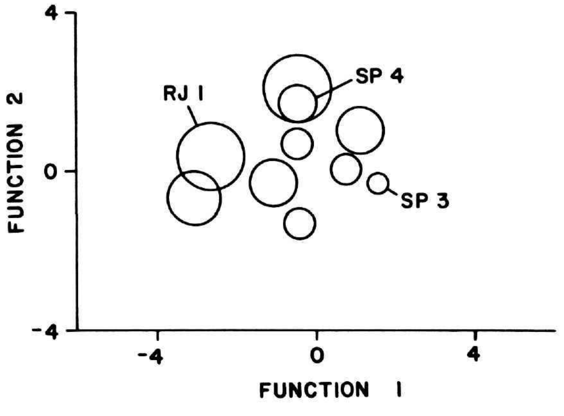

FIGURE 16.—Discriminant axis plot for females of 10 samples of the morphospecies GU. Circles indicate 95% confidence level for group centroids (centroids in middle of circles, not shown). For text reference, RJ1, SP4, and SP3 are individually labeled.

16). Only 68% of the males and 72% of the females were predicted by posterior classification to belong to the same groups in which they were entered in the analysis. For both males and females, the distribution of "incorrectly" predicted individuals was scattered among groups, but there does not appear to be an overall pattern of distribution common to both (compare Tables 17 and 18). The plots of the first two discriminant axes, although showing some similarities, also demonstrate some fundamental differences between the male and female results (Figures 15, 16). For both males and females, the first axis (size related) separates RJ1 and SP3 well. The separation of SP3 and SP4 is better in males than females, however. Also, the two groups best separated on the second axis of the male results, RJ1 and SP4, are poorly distinguished on the second axis in the female results.

The 10-GU-sample results for males and females together contrast with the morphospecies results in 2 major ways. First, the male and female results for the morphospecies analyses were much more similar to each other than the male and female results for the 10 GU samples. Second, almost all of the variance was accounted for by the first three discriminant functions in the morphospecies analyses; a comparable level of variance accountability was not reached until the fifth or seventh functions for the 10 GU sample analyses. These differences, together with the poorer discrimination among the 10 GU samples than the morphospecies analyses are interpreted to mean that the morphological variation among the 10 GU samples differs in kind from the morphological variation among morphospecies and that the variation observed among GU samples is more consistent with intraspecific, rather than interspecific, variation.

TAXONOMIC CONCLUSIONS

Each morphospecies consistently differs from the other morphospecies in one or more features of color pattern, life color, morphology, or advertisement call, with the exception that GU does not consistently differ from either PGL or PGN. The single most diagnostic feature is the tibia pattern; for this character, many, but not all, individuals of GU differ from all PGL individuals in having the B or C state of the tibia pattern. Though not all individuals of GU can be consistently differentiated from all individuals of PGL and PGN, the morphospecies are distinct where the three morphospecies are sympatric, i.e., Santa Teresa, Espirito Santo. At this site, size and pattern differences are distinct, and individuals are readily identifiable by visual inspection as belonging to one of the four cluster members that occur at Santa Teresa. At the other major site of sympatry, Teresópolis, Rio de Janeiro, only three individuals were not readily identifiable. One of these was USNM 97680, originally classified as GLT, but changed to GU after reexamination following the discriminant function analysis. The other two specimens were L 18 and L 19, which appeared to have a head shape more like GLT, but with other features more like GU. These two individuals of the hundreds of specimens examined from Teresópolis are the only possible indications of hybridization among morphospecies. The available evidence is consistent with the conclusion, here accepted, that each morphospecies represents a distinct biological species.

Only one species, GU, was represented adequately to analyze variation among populations. As documented above, variation in details of pattern and morphology occurs among samples, but the variation is considered to differ in degree, not kind, and to represent intraspecific variation.

Nomenclature

Six names have been associated in the literature with members of the *Eleutherodactylus guentheri* cluster. Each name is discussed and associated with the morphospecies as analyzed above, where appropriate.

Hyla grisea Hallowell, 1860, has mistakenly been used in association with members of the *Eleutherodactylus* cluster from Brazil (e.g., Steindachner, 1864:245; Gorham, 1966:75) and some specimens from Brazil are identified as *E. griseus* in collections. Savage (1974) demonstrated that *H. grisea* Hallowell is a synonym of the species currently recognized as *Eleutherodactylus fitzingeri* (O. Schmidt) from Middle America.

Hylodes guentheri Steindachner, 1864 was described on the basis of a single individual listed as from Brazil (no more specific locality data) in the type description. I examined the holotype, Vienna 16515, in September 1982. The specimen is a juvenile, with SVL of 23.0 mm. The dorsal pattern is intermediate between pattern A-4 and an indistinct A-5 (Figure 1). The specimen lacks light mid-dorsal and dorsolateral stripes and does not have a light snout. There is an indication, although not distinctly defined, of a light interocular bar. The holotype has a dark groin spot and the supratympanic pattern is an interrupted dark line (pattern C, Figure 7). There is no dark loreal stripe and the upper lip pattern is indistinct. The outer tibia lacks a dark band (pattern A, Figure 10). The posterior surface of the thigh pattern is difficult to discern, but appears to be uniform. There is a weak heel calcar present, and the dorsum, including the upper eyelids, is scattered with tubercles. The specimen tag bears the information, "Rio dos Macacos 1874. I." Steindachner's report was based on collections assembled by Johann Natterer. The data "1874. I" on the specimen tag must refer to the date the specimen was cataloged. Dr. F. Tiedemann informed me that all catalog information was on the specimen tag: thus there is no information on when the specimen was collected. Bokermann (1966:66) indicated that the type probably came from Rio de Janeiro. Papavero (1971:80–87, map 9), gives a detailed itinerary for Natterer, but does not specifically mention Rio dos Macacos. Although the specific locality within Brazil is uncertain, the association of the holotype is clear. All characteristics listed above, together with direct comparison of samples of the morphospecies with the holotype, are consistent with the holotype of *H. guentheri*, representing the same species as morphospecies GU. This association is that currently used in the herpetological literature.

Hylodes henselii Peters, 1870, was based on a specimen collected by Hensel from near Porto Alegre, Rio Grande do Sul. Lynch (1976:7) indicated that data were inadequate to assign *H. henselii* to one of his groupings of *Eleutherodactylus* and that the type specimen was lost. Hensel (1867) reported that his specimen, on which Peters based *Hylodes henselii*, was found dead on a road and in such a poor condition that he could not determine from the digit tips whether it belonged to either the genus *Cystignathus* (= *Leptodactylus*) or *Hylodes* sensu Peters (= *Eleutherodactylus*). The remainder of his description contains no information that would allow further distinction to be made. Peters, who later examined the specimen, obviously considered the specimen to belong to *Hylodes* (as he described it) rather than *Cystignathus*. Braun and Braun (1980) indicate that only one species of *Eleutherodactylus* is known from the State of Rio Grande do Sul, *E. guentheri*. Thus, if the lost type of *Hylodes henselii* was an *Eleutherodactylus*, then it probably was a synonym of *E. guentheri*. As the available data (only Hensel's description, since Peters added no information in his designation of Hensel's specimen as the type of a new species) will never allow unambiguous association with any frog species from Porto Alegre, an arbitrary decision is appropriate to clarify the nomenclature. I hereby designate as the neotype of *Hylodes henselii* Peters, the specimen from the Vienna Museum 16515. As Vienna 16515 is also the holotype of *Hylodes guentheri* Steindachner, *henselii* is a synonym of *guentheri*.

Elosia divisa Wandolleck, 1907 is a synonym of *H. guentheri* Steindachner, as indicated by Cochran (1955) and Bokermann (1966). The type specimen(s) from the Petrópolis, Rio de Janeiro, were destroyed in World War II, but the excellent figures and description of the type clearly support Bokermann and Cochran's conclusion. As there is no problem of name association, a neotype designation is not required.

Hylodes nasutus A. Lutz, 1925 was first described from Novo Friburgo, Rio de Janeiro. Adolfo Lutz gave a very brief description of the new species. Although not clearly stated, it appears as though A. Lutz based the name on more than one specimen. Cochran (1961:61) listed three cotypes for *H. nasutus* (USNM 96468–96470). She stated that USNM 96470 had been exchanged to the Adolfo Lutz collection. I am only able to locate two of these specimens. USNM 96469, a 32.3 mm SVL male, is somewhat soft and faded, but the diagnostic features of snout shape and inverted parenthesis scapular markings are distinct. The posterior surface of the thigh pattern is difficult to distinguish, but does seem to consist of a bold mottled pattern on the left thigh. All these features associate the cotype with the morphospecies NAS. A second specimen from this series retains the number 96468 in the Adolfo Lutz collection. The specimen is a somewhat firmer, but faded, 34.4 mm SVL male. The specimen has the same characteristics listed above for USNM 96469, but a bold mottled posterior thigh pattern can be visualized only with imagination. I did not locate the specimen Cochran listed as exchanged in the Adolfo Lutz collection. A brief search in the Lutz collection resulted in location of a single specimen, AL 2365, indicated as a cotype of *H. nasutus* on the bottle label. As the specimen was collected in 1932, after the species was described, it cannot be considered part of the type series. Until the Lutz collection is thoroughly searched, there will be confusion as to how many specimens comprise the type series. Until that situation is resolved, I prefer not to designate a lectotype for *Hylodes nasutus.*

Eleutherodactylus gualteri B. Lutz, 1974 represents morphospecies GLT. Although I have not examined the types, the description and figure provided by B. Lutz, including the indication of copper iris color, clearly indicate this conclusion.

There remain three species of the *E. guentheri* cluster that lack names. These are described as new species in the following section.

Species Accounts

The *Eleutherodactylus guentheri* cluster cannot be placed in the context of species groupings due to the number of undescribed taxa that have character combinations that violate the most recent species grouping proposal (Lynch, 1976). The cluster is defined, rather, on the basis of overall similarity of external morphology. Such a characterization has the potential of polyphyly, as the similarities may be due to retention of primitive character states. Nevertheless, based on experience, I believe the members of the *E. guentheri* cluster form a monophyletic unit. The members treated herein may be a subset of a more extensive monophyletic unit, however.

For purposes of species characterizations, it is necessary to diagnose members of the *E. guentheri* cluster from the other *Eleutherodactylus* that occur in the same general geographic region. The *E. guentheri* cluster can be distinguished from most other *Eleutherodactylus* from the general coastal Brazilian area by a combination of a few character states (Table 19). One of the standard characters that has been used to group species of *Eleutherodactylus* has been the relative length of the first and second fingers. Data for this character have not been treated in a table because for the species under study that have approximately equal finger lengths, the actual relationships vary from finger I just shorter than finger II, finger I equal finger II, to finger I just longer than finger II within single-locality populations. There are two described species, *E. binotatus* and *E. pliciferus*, in which the first finger is much longer than the second and is clearly distinct from the situation where the first finger is just longer than the second. There are two described species, *E. hoehnei* and *E. vinhai*, that may be distinguished from members of the *E. guentheri* cluster only on the basis of characteristics not included in Table 19. *Eleutherodactylus hoehnei* has a distinct dark mask extending from the tip of the snout through the eye and tympanum and then curving downward and ending on the side of the body behind the shoulder region. The mask contrasts sharply with the surrounding pattern in contrast to those individuals of the *E. guentheri* cluster that have dark canthal stripes and supratympanic markings. I have not examined specimens of *Eleutherodactylus vinhai.*

TABLE 19.—Diagnostic characteristics for described species of *Eleutherodactylus* from coastal Brazil; character states derived from examination of specimens and literature descriptions.

Name	Belly texture	Tympanum	Largest disk tip shape	Finger disk sizes
E. guentheri cluster	Tuberculate, smooth	Distinct	Triangularly ovate, rounded	I ≅ II < III ≅ IV, I usually just smaller than II
E. bilineatus Bokermann, 1975	Smooth	Distinct	Rounded	All small, about equal
E. binotatus (Spix), 1824	Smooth	Distinct	Rounded	All small or moderate, II < I ≅ III ≅ IV
E. bolbodactylus (A. Lutz), 1925	Smooth	Distinct	Triangularly ovate	I ≅ II ≪ III = IV
E. hoehnei B. Lutz, 1959	Smooth	Distinct	Triangularly ovate	I < II < III ≅ IV
E. juipoca Sazima and Cardoso, 1978	Weakly granular	Distinct	Rounded	All small
E. lactea (Miranda-Ribero), 1923	Smooth	Indistinct	Triangularly ovate	I ≪ II ≅ III ≅ IV
E. nanus (Ahl), 1933	Smooth	Distinct	Pointed	
E. nigriventris (A. Lutz), 1925	Areolate	Hidden	Triangularly ovate	I ≪ II ≪ III ≅ IV
E. octavioi Bokermann, 1965	Smooth	Distinct	Disks essentially absent	
E. parvus (Girard), 1853	Smooth	Hidden	Pointed	All small, I ≅ II < III ≅ IV
E. paulodutrai Bokermann, 1975	Areolate	Distinct	Triangularly ovate	I ≅ II ≪ III ≅ IV
E. pliciferus (Boulenger), 1888	Smooth	Distinct		Small
E. pusillus Bokermann, 1967	Smooth	Hidden	Pointed	All small, I ≅ II < III ≅ IV
E. ramagii (Boulenger), 1888	Areolate	Distinct	Triangularly ovate	I ≅ II ≪ III ≅ IV
E. venancioi B. Lutz, 1959	Areolate	Hidden	Triangularly ovate	I ≪ II ≅ III ≅ IV
E. vinhai Bokermann, 1975	Granular	Distinct	Triangularly ovate	I ≅ II < III ≅ IV

The combination of character states suggests that it may also belong to the *E. guentheri* cluster. The belly texture, originally described as granular, is of major importance. One of the members of the *E. guentheri* cluster has warty belly tubercles, which may or may not be the same condition as for *E. vinhai*. All other members of the *E. guentheri* cluster have smooth bellies. *Eleutherodactylus vinhai* differs from all *E. guentheri* cluster members in having carmine inner and outer tibiae in life.

The diagnostic characters discussed in the preceding paragraph and treated in Table 19 are not repeated in the species accounts; rather only the members of the *E. guentheri* cluster are diagnosed from each other in the accounts.

There are a series of character states shared by all members of the *E. guentheri* cluster, not mentioned above, that help to define the cluster: the upper eyelids are tuberculate, the heel has at least one noticeable tubercle (or calcar), the toes are fringed or free, the tarsus lacks a fold or other decoration, and males have vocal slits and white glandular-appearing nuptial asperities. These characteristics are not repeated in the species accounts.

TABLE 20.—Measurement data for members of the *Eleutherodactylus guentheri* cluster: SVL measurements are means in mm ± standard deviation; other mean values are expressed as ratios ± standard deviation (N = number of individuals for which data were analyzed).

Species	Sex	N	SVL	HL/SVL	HW/SVL	EN/SVL	EE/SVL	TD/SVL	Femur/SVL
E. epipedus	♂	22	20.5±1.8	0.42±.01	0.37±.01	0.12±.01	0.20±.01	0.06±.01	0.53±.02
	♀	11	29.8±2.4	0.42±.01	0.38±.01	0.12±.00	0.19±.01	0.06±.00	0.54±.02
E. erythromerus	♂	3	23.6	0.40	0.36	0.13	0.20	0.07	0.57
	♀	6	30.2	0.41	0.35	0.13	0.18	0.06	0.55
E. gualteri	♂	42	29.2±2.3	0.41±.02	0.37±.01	0.12±.01	0.19±.01	0.06±.01	0.53±.02
	♀	19	40.2±3.7	0.42±.01	0.39±.01	0.13±.01	0.19±.01	0.06±.01	0.55±.02
E. guentheri	♂	282	25.4±2.8	0.41±.01	0.36±.02	0.13±.01	0.20±.01	0.06±.00	0.57±.03
	♀	223	36.2±4.4	0.40±.01	0.36±.02	0.12±.01	0.18±.01	0.06±.01	0.56±.03
E. nasutus	♂	48	32.3±3.5	0.39±.01	0.33±.01	0.12±.01	0.18±.01	0.06±.01	0.53±.02
	♀	14	43.9±4.3	0.39±.01	0.33±.02	0.13±.00	0.17±.01	0.06±.00	0.55±.02
E. oeus	♂	3	17.7	0.41	0.35	0.13	0.20	0.06	0.55
	♀	0							

The morphospecies used in the analyses correlate with the species as follows:

E. epipedus, new species = PGL
E. erythromerus, new species = RT
E. gualteri = GLT
E. guentheri = GU
E. nasutus = NAS
E. oeus, new species = PGN

Measurement data for the cluster members are summarized in Table 20 and not repeated in the species accounts.

Type localities for previously published names are presented in the same format as they were originally given.

***Eleutherodactylus epipedus*, new species**

FIGURE 17

HOLOTYPE.—MZUSP 59633, an adult male from Brazil: Espirito Santo; adjacent to Parque Nova Lombardia, near Santa Teresa. Collected by Ronald I. Crombie, Maria Christina Duchêne, W. Ronald Heyer, and Francisca Carolina do Val on 28 December 1977.

PARATYPES.—Paratopotypes, collected by same collectors from 28 December 1977 to 1 January 1978, MZSUP 59634–59639, USNM 235613–235620; Santa Teresa, AL 1253, 1253a, 1253c, EI 7294–7302, 7304–7316, 7318–7321, 7323, 7326–7327, MNRio 1874, USNM 200446.

FIGURE 17.—Holotype of *Eleutherodactylus epipedus*, new species.

DIAGNOSIS.—The posterior surface of the thigh is uniform or indistinctly mottled in *E. epipedus*, distinguishing it from *E. erythromerus*, which has a light area on the posterior thigh next to the knee (pattern B in Figure 11), and from *E. nasutus*, which has a boldly mottled posterior

Tibia/SVL	Foot/SVL	3FD/SVL	4TD/SVL
0.58±.02	0.55±.02	0.03±.00	0.04±.00
0.58±.03	0.56±.02	0.03±.00	0.04±.00
0.63	0.62	0.04	0.04
0.63	0.58	0.03	0.04
0.59±.02	0.56±.02	0.03±.00	0.04±.00
0.62±.02	0.58±.03	0.04±.00	0.04±.00
0.65±.03	0.62±.03	0.04±.00	0.04±.00
0.64±.04	0.60±.04	0.03±.00	0.04±.00
0.61±.02	0.61±.02	0.03±.00	0.04±.00
0.64±.02	0.64±.03	0.03±.00	0.03±.00
0.62	0.58	0.04	0.04

thigh pattern. No specimens of *E. epipedus* have dark complete or interrupted stripes on the outer surface of the tibia, while many individuals of *E. guentheri* and *E. oeus* have such a pattern (patterns B and C, Figure 10); *E. epipedus* also has a more robust body form than either *guentheri* or *oeus. Eleutherodactylus epipedus* most closely resembles *gualteri*, from which it differs by smaller size (SVL in *E. epipedus* males 16.7–23.5 mm, females 25.6–33.2 mm, in *E. gualteri* males 21.3–34.1 mm, females 33.6–45.7 mm) and in having several dorsal pattern states not found in *gualteri* (patterns A-6, A-8, and A-10 in Figure 1).

DESCRIPTION OF HOLOTYPE.—Snout subelliptical from above, rounded in profile; canthus rostralis indistinct; lorus slightly flared in cross section; tympanum distinct, annulus distinct except for above tympanum; vomerine teeth in two small transverse series, posterior and medial to choanae, separated from each other by about the length of one vomerine tooth series; vocal slit present, vocal sac not noticeably expanded externally; fingers I, II, and IV about equal length, finger III longest; thumb disk small, about same diameter as thumb, disk on finger II slightly larger, disks on fingers III and IV largest, moderate size, ungual flap indented; fingers with lateral ridges; subarticular tubercles moderate, not pointed; large horseshoe-shaped outer metacarpal tubercle narrowly separated from rounded-square shaped inner metacarpal tubercle; inner base of thumb with small white glandular-appearing nuptial asperity; dorsum smooth, upper eyelids tuberculate; supratympanic fold indistinct; no other noticeable body glands or folds; venter smooth; disk of toe I moderate sized, just smaller than disks of toes II, III, and V, disk of toe IV largest, toe disks with indented ungual flaps; toes with lateral ridges not produced into fringes; toe subarticular tubercles moderate, not pointed; rounded outer metatarsal tubercle much smaller than ovate inner metatarsal tubercle; tarsus lacking fold or tubercle; heel with single prominent light tubercle; outer tarsus with a few indistinct light tubercles, sole of foot with one or two distinct light tubercles.

Measurements (in mm): SVL 18.2, HL 8.0, HW 6.9, EN 2.3, EE 3.8, TD 1.1, femur 10.0, tibia 10.9, foot 10.0, 3FD 0.5, 4TD 0.7.

Pattern in preservative indistinctly variegated-mottled tan and brown dorsally; light indistinct interocular spot; faint indications of light tan dorsolateral stripes on posterior half of body; dark indistinct loreal spot; upper lip with three distinct, irregular vertical light stripes; brown band not well differentiated from dorsal color from above tympanum to groin, expanded into dark brown sacral spot posteriorly, band expanded into broad transverse band on side at midbody; groin lacking distinct markings; under surfaces of throat and limb extremities suffused with brown, suffusion of brown lighter on belly and under surfaces of upper arms and thighs; outer tibia with brown transverse bands; posterior surface of thigh barely mottled.

ETYMOLOGY.—From the Greek *epipedos*, on the ground, in allusion to the species most commonly being collected from the forest floor.

ADULT SPECIMEN DEFINITION.—Dorsum mottled or uniform patterns (A-1, A-2, A-3, A-6, A-8, and A-10 in Figure 1), or with dorsoconcolor (patterns B-1 and B-2 in Figure 1), or wavy line morph (pattern C in Figure 1); some individuals with light mid-dorsal pin stripes (patterns A and D in Figure 2); no individuals with broad mid-dorsal stripes; a few individuals with light dorsolateral stripes (pattern A in Figure 3); some individuals with light snouts (patterns A and B in Figure 4); many individuals with light interocular bars (patterns A and B in Figure 5); outer tibia either uniformly dark or transversely banded (pattern A in Figure 10), not dark striped; posterior surface of thigh uniform or indistinctly mottled (pattern A in Figure 11); no flash colors in life, under surfaces yellow or yellow wash tinged with green, iris bronze; males 16.7–23.5 mm SVL, females 25.6–33.2 mm SVL; head broad (Table 20); hind limbs relatively short (Table 20).

ADVERTISEMENT CALL.—Unknown.

DISTRIBUTION.—Known only from near Santa Teresa, Espirito Santo (Figure 18).

ESPIRITO SANTO. Adjacent to Parque Nova Lombardia, near Santa Teresa (MZUSP 59633–59639, USNM 235613–235620); Santa Teresa (AL 1253, 1253a, 1253c, EI 7294–7302, 7304–7316, 7318–7321, 7323, 7326–7327, MNRio 1874, USNM 200446).

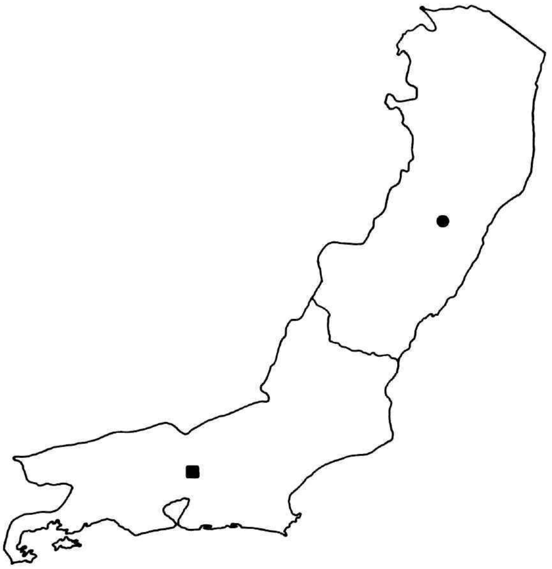

FIGURE 18.—Distribution of *Eleutherodactylus epipedus* (circle) and *E. erythromerus* (square) in the states of Espirito Santo and Rio de Janeiro.

Eleutherodactylus erythromerus, new species

FIGURE 19

HOLOTYPE.—MZUSP 59640, an adult male from Brazil: Rio de Janeiro; near Teresópolis (Alto do Soberbo, 5 km NE junction BR 116 and Teresópolis bypass). Collected by Ronald I. Crombie, Maria Christina Duchêne, and W. Ronald Heyer on 10 December 1977.

PARATYPES.—L 79-80, 140, MZUSP 59641–59647, USNM 208525, 235621–235628, all from near Teresópolis.

DIAGNOSIS.—The light area on the posterior surface of the thigh (red in life) (pattern B in Figure 11) distinguishes *E. erythromerus* from all other species of the *E. guentheri* cluster.

DESCRIPTION OF HOLOTYPE.—Snout subelliptical from above, rounded in profile; canthus rostralis indistinct; lorus slightly concave in cross section; tympanum distinct, annulus distinct ex-

FIGURE 19.—Holotype of *Eleutherodactylus erythromerus*, new species.

cept on top of tympanum; vomerine teeth in two short transverse series posterior and medial to choanae, separated from each other by somewhat less than the length of one vomerine tooth series; vocal slits present, no external indication of a vocal sac; first finger just shorter than second, second about equal to fourth, third longest; thumb disk not much wider than digit, disk of finger II a little bigger, disks of fingers III and IV moderate, larger than disks of finger I and II, disks on fingers III and IV with indented ungual flaps; fingers free; finger subarticular tubercles moderate, not pointed; large heart-shaped outer metacarpal tubercle narrowly separated from large ovoid inner metacarpal tubercle; light glandular-appearing nuptial asperity on inner base of thumb; dorsum almost smooth with a few scattered small tubercles, upper eyelids tuberculate; no supratympanic fold, or other body folds or glands; belly and under forearm with low, white glandular tubercles, ventral thigh surfaces barely granular, rest of ventral surfaces smooth; toe disks on toes I and V moderate, smaller than the disks on toes II, III, and IV, disks with indented ungual flaps; toes free; subarticular tubercles moderate, not pointed; rounded outer metatarsal tubercle smaller than ovoid inner metatarsal tubercle; tarsus lacking fold or tubercle; heel with single prominent light tubercle; posterior tarsus smooth; sole of foot smooth.

Measurements (in mm): SVL 24.2, HL 9.8, HW 8.5, EN 3.1, EE 4.6, TD 1.6, femur 13.3, tibia 14.9, foot 14.6, 3FD 1.0, 4TD 1.1.

Dorsum (in preservative) completely variegated tan and brown, three small dark spots between the eyes; mid-dorsal light pin stripe in sacral region, bifurcating on legs and continuing to mid-posterior thigh; small dark vertical mark below the anterior portion of the eye on the upper lip, a single light, irregular, transverse stripe below middle of eye; irregular dark blotch over and including uppermost tympanum; dark ovoid sacral spot; side of body with indistinct broad brown posteriorly directed transverse mid-body band; soles of feet and outer tarsus surfaces heavily suffused with brown, throat mottled, mostly dark, with indistinct light mid-ventral stripe, belly and under thigh surfaces mottled, mostly light, belly tubercles white; no distinct pattern in groin; outer tibia with dark stripe; posterior surface of thigh suffused with brown, mostly brown proximally, with mostly no pigment distally (as in pattern B, Figure 11).

ETYMOLOGY.—From the Greek *erythro* (red) plus *mēros* (thigh), signalling the distinctive red thighs characteristic of this species in life.

ADULT SPECIMEN DEFINITION.—Dorsal pattern mottled or uniform (patterns A-1, A-2, A-4, A-5, and A-8 in Figure 1), no dorsoconcolor or wavy line morphs known; some individuals with light mid-dorsal pin stripes (patterns A and C in Figure 2); no individuals with broad mid-dorsal stripes known; no light dorsolateral stripes known; a few individuals with light snouts (pattern B in Figure 4); many individuals with light interocular bars (patterns A and B in Figure 5); outer tibia with interrupted or complete dark stripe (patterns B and C in Figure 10); posterior surface of thigh with light area next to knee joint (pattern B in Figure 11); red flash colors in life on posterior thigh, belly yellow, iris golden bronze above and below, brown in middle; SVL in males 22.3–24.4 mm, females 24.3–35.3 mm; head width moderate (Table 20), relatively long hind limbs (Table 20).

ADVERTISEMENT CALL.—Unknown.

DISTRIBUTION.—Known only from the vicinity of Teresópolis, Rio de Janeiro, (Figure 18).

RIO DE JANEIRO. Teresópolis and environs (L 79, 80, 140; MZUSP 59640–59647; USNM 208525, 235621–235628).

Eleutherodactylus gualteri B. Lutz

Eleutherodactylus gualteri B. Lutz, 1974:293, figure 1. [Type locality: "Terezopolis, Granja Comari, Organ Mountains, Brazil." Holotype: MNRio 4096, an adult female (not examined).]

DIAGNOSIS.—The posterior surface of the thigh is uniform or indistinctly mottled in *E. gualteri*, distinguishing *gualteri* from *erythrome-*

rus, which has a light area on the posterior thigh next to the knee (pattern B in Figure 11), and from *nasutus*, which has a boldly mottled posterior thigh pattern. No *gualteri* have dark complete or interrupted stripes on the outer surface of the tibia, while many individuals of *guentheri* and *oeus* have such a pattern (patterns B and C in Figure 10); *gualteri* also has a more robust body form than either *guentheri* or *oeus*. *Eleutherodactylus gualteri* most closely resembles *E. epipedus*, from which it differs by larger size (SVL in *gualteri* males 21.3–34.1 mm, females 33.6–45.7 mm, *epipedus* males 16.7–23.5 mm, females 25.6–33.2 mm), and in lacking several dorsal pattern states found in *epipedus* (patterns A-6, A-8, and A-10 in Figure 1).

ADULT SPECIMEN DEFINITION.—Dorsal pattern uniform or mottled (patterns A-1, A-2, and A-3 Figure 1), some individuals with dorsoconcolor (pattern B-1 in Figure 1) or wavy line morphs (pattern C in Figure 1); many individuals with light mid-dorsal pin stripes (patterns A, B, and C in Figure 2); no individuals with broad mid-dorsal stripes; several individuals with light dorsolateral stripes; some individuals with light snouts (patterns A and B in Figure 4); several individuals with light interocular bars (patterns A and B in Figure 5); outer tibia either uniformly dark or transversely banded (pattern A in Figure 10), not dark striped; posterior surface of thigh uniform or indistinctly mottled (pattern A in Figure 11); no flash colors in life, posterior thigh gray or very slightly red, iris copper; SVL measurement, males 21.3–34.1 mm, females 33.6–45.7 mm; head broad (Table 20); hind limb relatively short (Table 20).

ADVERTISEMENT CALL.—Call duration 1.5–1.9 s; calls given sporadically; calls beginning quietly, ending loudly; 4–9 notes per call, given at a rate of 3–4 notes per second; note duration short, about 0.01 s; dominant (= fundamental) frequency between about 2100–2700 Hz; notes with harmonic structure (N = 3, Figure 20).

DISTRIBUTION.—Known only from a limited portion of the State of Rio de Janeiro (Figure 21).

RIO DE JANEIRO. Paquequer (L 27–35); Teresópolis and vicinity (EI 2537, 2538, 6136–6139, L 1–5, 13–15, 49–54, 72, 109, 110, 116, 119, 154, 155, 157, 164, MNRio 1835, 2072[2],

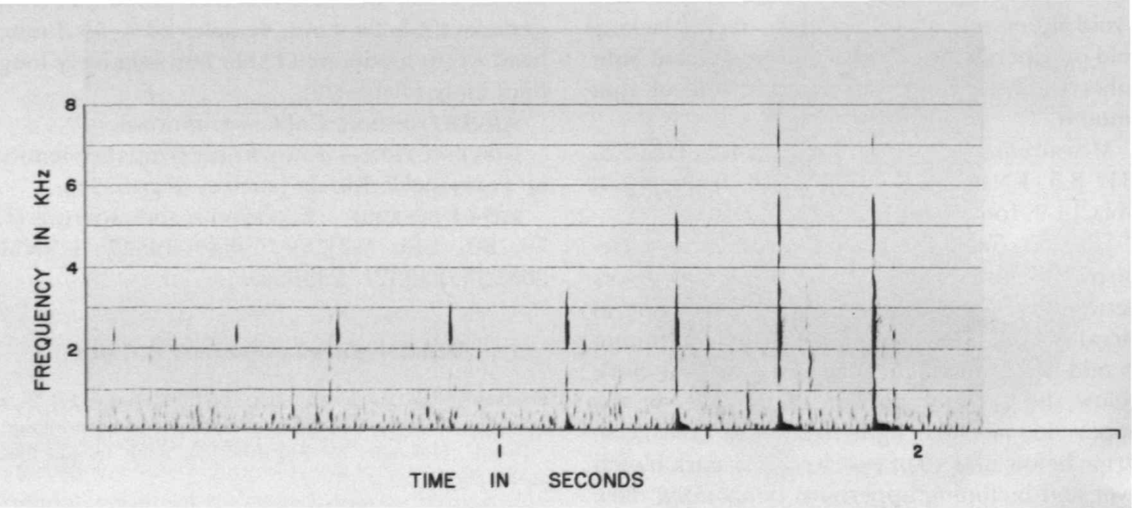

FIGURE 20.—Audiospectrogram of advertisement call of *Eleutherodactylus gualteri*. Recorded from near Teresópolis, Rio de Janeiro, Brasil, about 20:00 hours, on 14 December 1977, air temperature 15–16°C, specimen USNM 208530.

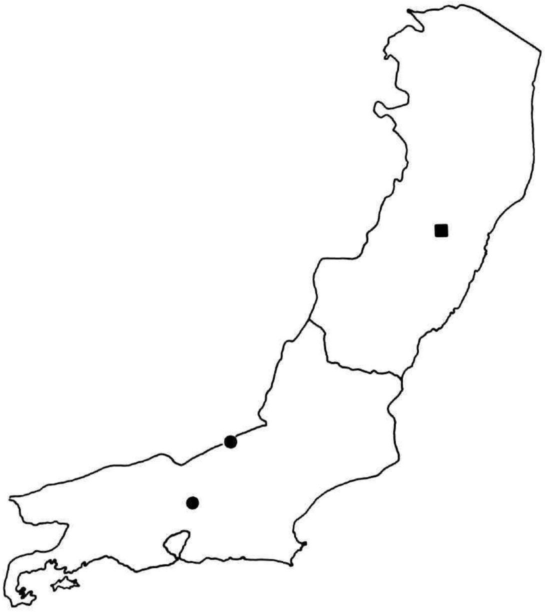

FIGURE 21.—Distribution of *Eleutherodactylus gualteri* (circles) and *E. oeus* (square) in the states of Espirito Santo and Rio de Janiero.

2167, 2688, MZUSP 53216–53239, 53332–53333, 53387, USNM 96452–96454, 208506–208524, 208526–208530).

Eleutherodactylus guentheri (Steindachner)

Hylodes guentheri Steindachner, 1864:246, pl. 17: figs. 1, 1a. [Type locality: "Brasil, Rio dos Macacos." Holotype: Vienna 16515, juvenile.]

Hylodes henselii Peters, 1870:648. [Holotype lost; neotype established herein, p. 00: Vienna 16515, juvenile.

Elosia divisa Wandolleck, 1907:4, table 1, figs. 7, 7a. [Type locality: "Petrópolis, Brasil." Holotype: Presumably destroyed, formerly in Königlichen Zoologischen Anthropologisch-Ethnographischen Museums zu Dresden.]

DIAGNOSIS.—Almost all individuals of *E. guentheri* have uniform or indistinctly mottled posterior surface of the thigh patterns. *E. erythromerus* have light areas on the posterior thighs next to the knee joint (pattern B in Figure 11) and *E. nasutus* have boldly mottled thigh patterns. The posterior thigh is red in life in *E. erythromerus*; there is no thigh flash color in life in *E. guentheri*. The head is broader in *E. guentheri* than in *E. nasutus* (Table 20). Many individual *E. guentheri* have an interrupted or complete dark stripe on the outer tibia (patterns B and C in Figure 10); no *E. epipedus* or *gualteri* have a dark outer tibial stripe. The body is more gracile in *E. guentheri*, more robust in *E. epipedus* and *gualteri*. *Eleutherodactylus guentheri* most closely resembles *E. oeus*. At the site of sympatry, *guentheri* differs most notably from *E. oeus* in size (SVL in male *E. guentheri* 28.0–30.5 mm, in male *oeus* 17.1–18.8 mm at Santa Teresa).

ADULT SPECIMEN DEFINITION.—Dorsal pattern uniform or mottled (patterns A-1–A-11 in Figure 1), or with dorsoconcolor (patterns B-1 and B-2 in Figure 1) or wavy line morph (pattern C in Figure 1); most individuals with light mid-dorsal pin stripes (patterns A–F in Figure 2); some individuals with a broad, light mid-dorsal stripe; a few individuals with light dorsolateral stripes; many individuals with light snouts (patterns A and B in Figure 4); many individuals with light interocular bars (patterns A and B in Figure 5); most individuals (80%) with an interrupted or complete dark stripe on the outer tibia (patterns B and C in Figure 10); posterior surface of the thigh pattern uniform or indistinctly mottled, very rarely boldly mottled or with a light area next to the knee region; no flash colors in life, dorsum brown or rich red brown, dorsal spots, if present, white or green, throat white, belly and under legs yellow, iris green dorsally, blending into bronze just above the pupil, then blending into brown, or pale yellow above blending to copper or entire iris copper; SVL measurement, males 16.4–32.3 mm, females 26.4–49.5 mm; moderate head width (Table 20); hind limbs relatively long (Table 20).

ADVERTISEMENT CALL.—Call duration 1.10–1.75 s; calls given sporadically; calls beginning quietly, ending loudly; 19–28 notes per call, given at a rate of 16–17 notes per second; note duration short, about 0.01 s; dominant (apparently, in this case, the same as the fundamental) frequency between 1900–2900 Hz; notes with weak harmonic structure (N = 3, Figure 22).

DISTRIBUTION.—Southeastern Brazil from the States of Espirito Santo to Rio Grande do Sul (Figure 23).

ESPIRITO SANTO. Santa Teresa (EI 7322, 7324–7325).

MINAS GERAIS. Mariana (MZUSP 912).

PARANA. Banhado (USNM 123896, 125507); Rio Cubatão, Baia de Guaratuba (MZUSP 15788, 23565); São João da Graciosa, 9–16 km W (MZUSP 59668–59669, USNM 235721, 235722); Serra de Araraquara (MNRio 1781[5], 1793[26], USNM 149451–149454); Volta Grande (USNM 125506).

RIO DE JANEIRO. Angra dos Reis (Al 786–798, 819, 819a, 1472–1478, 2752, USNM 70583–70586, 96505–96518); Coronel Cardoso, Mun. Valença (EI 2540–2541); Correias (MNRio 2036); Guapi, Alcindo Guanabara (AL 3011–3016); Ilha Grande (MNRio 2200); Itatiaia (EI 914, L 76–78, MZUSP 7756–7758); Itatiaia, Maromba (L 70, MZUSP 4115, 4116, 4118, 4123, 4126, 13634); Leopoldina (MNRio 2014); Nova Friburgo (AL 2708–2711, 2713–2714, MZUSP 282); Palmeiras (AL 485); Parati (MNRio 2021[3], 2464[8]); Petrópolis (AL 1695, 2804–2813, 4154, EI 716–717, 1306, 2542–2543, L 81–105, USNM 97646–97647); Rio de Janeiro (MZUSP 20856–20858, 20898, USNM 96383–96385); Sernambetiba, Recreio dos Bandeirantes (AL 2728–2731); Serra da Estrella (L 45, USNM 97232–97233); Serra de Macaé (MZUSP 171, 173, 517, 528, 531, 535); Serra do Peral (MNRio 2306); Serra Mambucaba (MNRio 2211, 2310); Sumaré (USNM 70587); Teresópolis (EI 2535–2536, L 20, 46–48, 71, 106–108, 111–115, 117–118, 120–127, 133, 148–153, 160–163, MNRio 2425, MZUSP 384, 392, 398, USNM 97680, 97724–97725, 235629); Tijuca (L 68–69, MNRio 1843, USNM 12999, 13300–13301, 96276–96283, 96285–

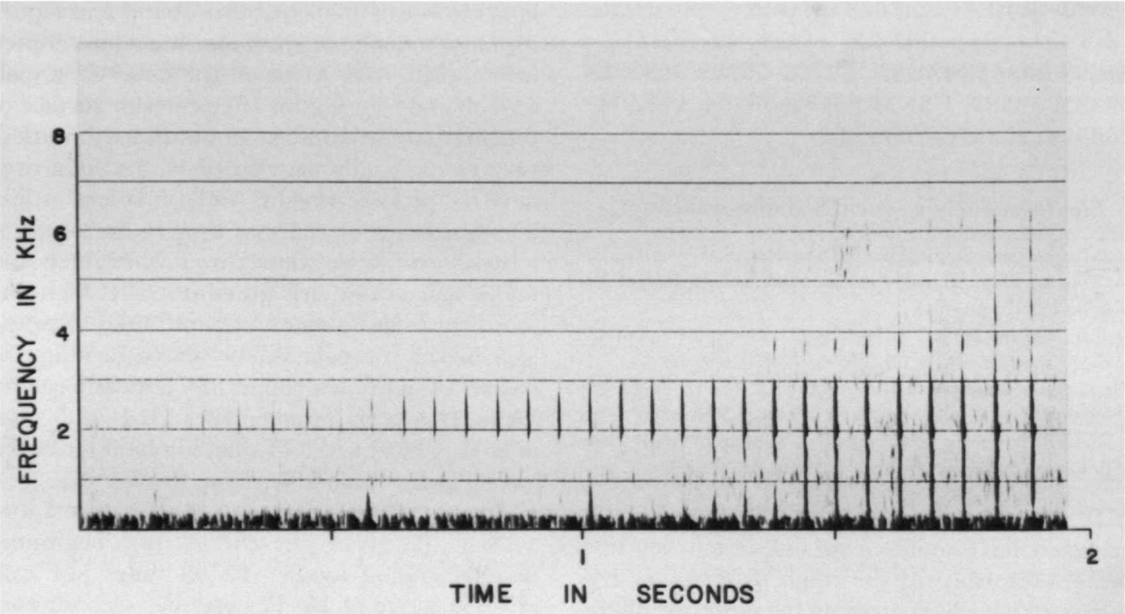

FIGURE 22.—Audiospectrogram of advertisement call of *Eleutherodactylus guentheri*. Recorded from Pirabeiraba, Santa Catarina, Brazil, at 2030 hours, on 10 December 1978, specimen USNM 235727.

FIGURE 23.—Distribution of *Eleutherodactylus guentheri* in the states of Espirito Santo, Minas Gerais, Rio de Janiero, São Paulo, Parana, Santa Catarina, and Rio Grande do Sul. Dashed lines indicate 20° and 32° latitude lines through the states of Minas Gerais and Rio Grande do Sul.

96296, 97404–97414, WCAB 25362–25434); Tinguá (MNRio 1487, 2281[5], 2285[3], 2974[5], MZUSP 486).

RIO GRANDE DO SUL. Cambará do Sul (MCN-AN 9955), Canela-Caracol (MCN-AN 8356), São Francisco de Paula (MCN-AN 7586, 7588, 7599–7601, 8024–8025).

SANTA CATARINA. Blumenau (MZUSP 1054); Campo Alegre, 3 km W (MZUSP 59670, Ibirama (MZUSP 512, 1836–1838); Novo Horizonte (MZUSP 35059–35087); Pirabeiraba (MZUSP 59671–59682, USNM 235723–235733); Queçaba (USNM 137696–137705); Rio Novo, Humboldt (= Corupá) (USNM 132380); Sta. Luzia (AL 2961[2]); São Bento do Sul (AL 1864–1868, L 143–144, USNM 97173).

SÃO PAULO. Boracéia (MZUSP 23698–23703, 23705–23744, 23749–23754, 37806, USNM 235630–235698); Campo Grande da Serra (MZUSP 98, 106); Campos do Jordão (EI 809, MZUSP 86, 1293, 2749–2751, WCAB 34354–34372, 37726–37730, 45350–45354);

Capivari (MZUSP 60, 1816); Caraguatatuba (MZUSP 23962); Casa Grande (MZUSP 37326); Cidade Azul (MZUSP 14942–14945, 14948, 14950–14954, 14957–14958); Cidade Jardim (AL 2658, 2670, 2672); Cubatão (AL 384–387, 389, 390[10], 715–717, 1290–1300, 1301[3], 1302–1308, 1309[2], 3351–3356, 4061–4069, MZUSP 10020, 10179–10180, 10310–10317, 10371, USNM 96805, 97819–97822, 97823 [5], 97824, 97856–97857, 123899, 196318, WCAB 45771–45773); Eugenio Lefevre (MZUSP 11329, 53181–53186, 59648–59650, USNM 235717–235719); Fazenda do Veado, Serra da Bocaina (MZUSP 59651–59667, USNM 235699–235716); Ilha de São Sebastião (MZUSP 8811, 8991–8993, 9971, 23543, USNM 235720); Itanhaem (MZUSP 1839, 1841, 1843–1844, 1848); Itapercerica da Serra (MZUSP 23433); Paranapiacaba (L 44, MNRio 3867[5], MZUSP 319, 409–410, 412, 418, 421, 472, 1093, 1437, 1823, 1826, 1828–1830, 1832–1833, 8843–8848, 9016–9020, 9022, 9632–9633, 10598–10601, 10624–10626, 10651–10652, 10780–10782, 10944, 10992, 11015, 11268–11272, 13939, 13941–13945, 13947–13949, 13951, 13955–13956, 13958, WCAB 12223–12224); Piassaguera (MZUSP 342, 10702); Piedade (MZUSP 2280–2281, 23309); Piquete (MZUSP 51, 1297); São Paulo (MZUSP 579, 910, 1062, 1849, 2660–2662, 2666, 2674–2675, 2677–2680, 2734, 2973, 3309, 3311–3314, 3316, 3450, 3452, 3456–3457, 3459, 3462, 3465–3467, 3469, 3471–3472, 3474, 3476–3478, 3483, 3533, 3748–3751, 3753–3782, 3784–3785, 3788–3791, 3794–3795, 3797, 3799–3805, 3807–3808, 9323–9324, 9596, 9606–9607, 10569–10576, 23307–23308, 23537–23538, 23545–23547, USNM 129160–129162); Serra da Bocaina (AL 2079–2083, MNRio 2680, MZUSP 1073–1074, 1851–1854, 1856–1857, 23462–23463, 53060–53074, 53076–53095, USNM 102310–102311, WCAB 31116–31139); Serra da Bocaina, Bonito (AL 910–915, 2318–2323, L 6–9, 142, USNM

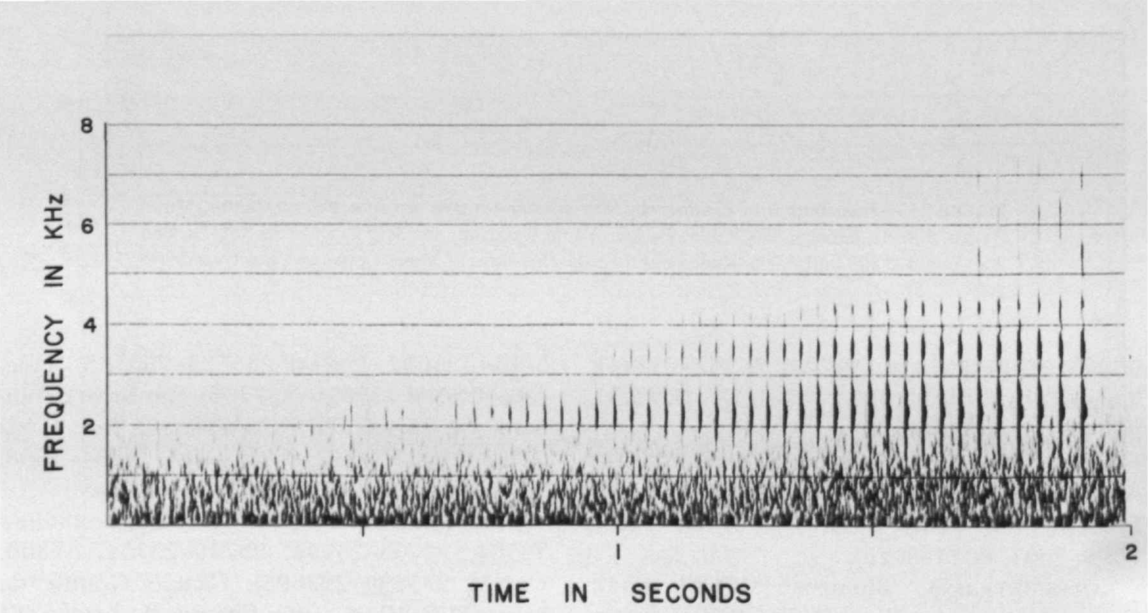

FIGURE 24.—Audiospectrogram of advertisement call of *Eleutherodactylus nasutus*. Recorded from Parque Nacional do Caparaó, Minas Gerais, Brasil at 19:45 hours, on 3 December 1980, specimen USNM 229857.

96724–96727); Serra da Bocaina, Corrego do Pinheiro (L 42–43); Serra da Bocaina, Garrafas (MNRio 2120); Serra da Bocaina, Mambucaba (L 156); Serra da Bocaina, descida da Ponte Alta (L 141); Serra da Bocaina, Posto de Biologia, Mun. Bananal (EI 1179–1181, 1229); Serra da Cantareira (L 16–19).

Eleutherodactylus nasutus (A. Lutz)

Hylodes nasutus A. Lutz, 1925:213. [Type locality: "Novo Friburgo, Brasil." Purported cotypes: USNM 96468–96470.]

DIAGNOSIS.—*Eleutherodactylus nasutus* has a boldly mottled posterior surface of the thigh pattern, distinguishing *nasutus* from *erythromerus*, which has a light area near the knee (pattern B in Figure 11) and from *epipedus*, *gualteri*, *oeus*, and most *guentheri*, which have uniform or indistinctly mottled posterior thigh patterns. *Eleutherodactylus nasutus* also has a narrower head than *guentheri*.

ADULT SPECIMEN DEFINITION.—Dorsal pattern uniform or mottled (patterns A-1, A-2, A-3, A-4, A-6, A-8, and A-10 in Figure 1), or rarely with the dorsoconcolor (pattern B-1 in Figure 1) morph, never with the wavy line morph; many individuals with light mid-dorsal pin stripes (patterns A, B, and E in Figure 2); specimens rarely with broad light mid-dorsal stripes; many individuals with light dorsolateral stripes (pattern A in Figure 3); few individuals with a light snout (patterns A and B in Figure 4); some individuals with light interocular bars; many individuals with interrupted or continuous black stripes on the outer tibia (patterns B and C in Figure 10); posterior surface of the thigh boldly mottled; no flash colors in life; SVL measurement, males 24.7–41.5 mm, females 36.1–53.9 mm; head narrow (Table 20); hind limbs relatively long (Table 20).

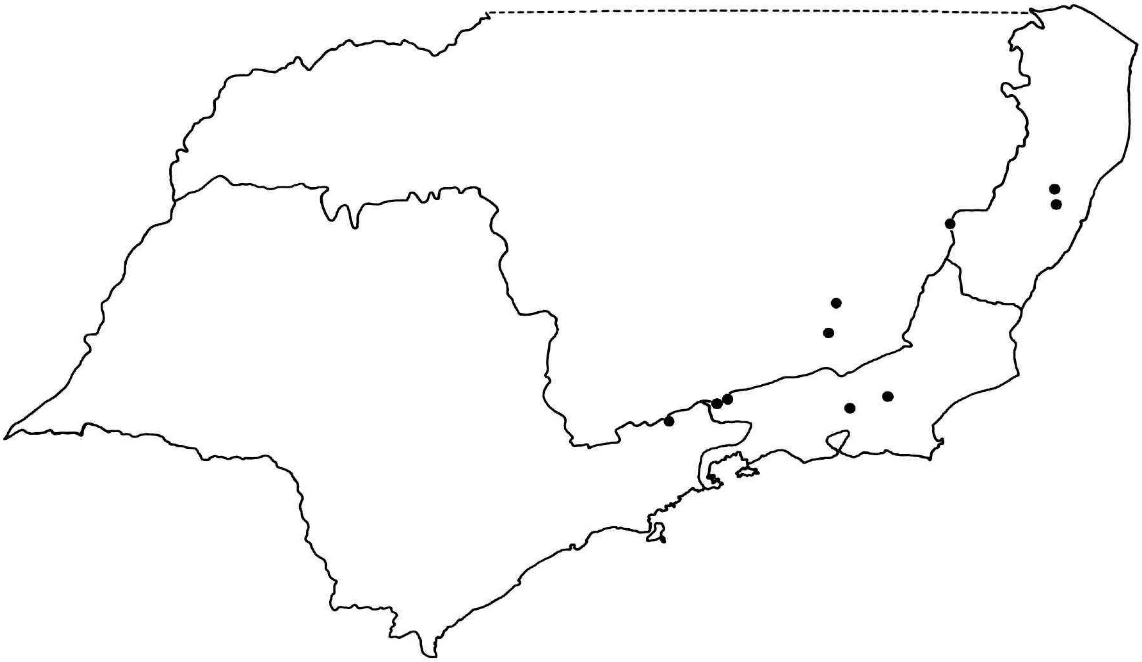

FIGURE 25.—Distribution of *Eleutherodactylus nasutus* in the states of Espirito Santo, Minas Gerais, Rio de Janiero, and São Paulo. Dashed line indicates 18° latitude line across state of Minas Gerais.

ADVERTISEMENT CALL.—Call duration 1.15–1.50 s; calls given sporadically; calls beginning quietly, ending loudly; 34–43 notes per call, given at a rate of 28–29 notes per second; note duration short, about 0.01 s; dominant (apparently the first harmonic) frequency between about 2100–2600 Hz; notes with harmonic structure (N = 4, Figure 24).

Distribution.—Eastern and Southeastern Brazil from the states of Espirito Santo to São Paulo (Figure 25).

ESPIRITO SANTO. Chaves (MZUSP 2342); Santa Teresa (EI 7303, 7317).

MINAS GERAIS. Agua Limpa, near Juiz de Fora (L 55–67, 146); Parque Nacional do Caparaó (MZUSP 57946–57948, USNM 229856, 229857); Pomba (L 10–12).

RIO DE JANEIRO. Itatiaia (MZUSP 10823, 10824); Mauá (L 36–40); Nova Friburgo (AL 2686–2689, 2707, 2712, 3558–3560, 96468, MZUSP 289, USNM 96465, 97762); Teresópolis (L 21–26, 41, 73–75, 128–132, 134–138, 145, 147, MZUSP 59683, USNM 235734).

SÃO PAULO. Piquete (MZUSP 50, 263, 649, 1296, 1858).

Eleutherodactylus oeus, new species

FIGURE 26

HOLOTYPE.—MNRio 1244, an adult male from Brazil: Espirito Santo; Santa Teresa. Collected by Augusto Ruschi in December 1942.

PARATOPOTYPES.—MZUSP 59684, USNM 235612.

DIAGNOSIS.—*Eleutherodactylus oeus* has indistinctly mottled posterior thigh surface patterns, *E. erythromerus* has light areas on the posterior faces of the thighs next to the knee joint (pattern B in Figure 11) and *E. nasutus* has boldly mottled thigh patterns. The outer face of the tibia of *E. oeus* has a dark stripe (patterns B and C in Figure 10); such dark stripes are absent in *E. epipedus* and *gualteri*. The head is also narrower in *E. oeus* than in *epipedus* and *gualteri* (Table 20). *Eleutherodactylus oeus* most closely resembles *E. guentheri*. At the site of sympatry, *oeus* differs most notably from *guentheri* in size (SVL measurements, male *E. oeus* 17.1–18.8 mm, male *E. guentheri* 28.0–30.5 mm at Santa Teresa).

FIGURE 26.—Holotype of *Eleutherodactylus oeus*, new species

DESCRIPTION OF HOLOTYPE.—Snout subelliptical from above, rounded in profile; canthus rostralis indistinct, lorus very slightly flared in cross section; upper tympanic annulus hidden, tympanum and annulus distinct below; vomerine teeth in short transverse series posterior and medial to choanae, vomerine tooth series separated from each other by not quite the length of a single vomerine tooth row; vocal slit present, external vocal sac barely indicated by a slight fold of skin; finger I just longer than finger II, I about equal to IV, fingers I, II, IV shorter than III; disk on finger I not much wider than digit diameter, disk width of other digits moderate, II narrower than IV narrower than III, larger disks with indented ungual flaps; fingers free; finger subarticular tubercles moderate, not pointed; outer broadly horseshoe-shaped metacarpal tubercle narrowly separated from inner ovoid metacarpal tubercle; inner base of thumb with whitish, glandular-appearing nuptial asperity; dorsal texture finely granular, upper eyelids warty-tuberculate; weak indication of dorsolateral folds behind eyes to just past shoulder region, no indication of supratympanic fold, no body glands; venter smooth, outer portion of ventral femur surface areolate; toe disks moderate, disk on toe IV largest, disks with indented ungual flaps; toe with weak lateral ridges; toe subarticular tubercles moderate; rounded outer metatarsal tubercle much smaller than ovoid inner metatarsal tubercle; tarsus lacking fold or tubercle; single pronounced heel tubercle; outer tarsus smooth; sole of foot smooth with one or two feebly developed light tubercles.

Measurements (in mm): SVL 17.1, HL 7.4, HW 6.0, EN 2.3, EE 3.6, TD 1.1, femur 10.0, tibia 11.1, foot 10.4, 3FD 0.7, 4TD 0.8.

Dorsal pattern in preservative indistinctly mottled cream, tan, and brown, irregular light cream interorbital bar and irregular light mid-dorsal blotch in scapular region, break in darker tan dorsal color to lighter cream lateral color in area of dorsolateral stripes, but no stripes indicated; tip of snout and front of eye with short dark brown stripes, upper lip with three irregular light vertical stripes, middle stripe just in front of eye broadest and most distinct, dark bordered behind; upper limbs irregularly barred; dark rectangular blotch including upper tympanum continuous with somewhat lighter dark stripe flaring into broad oblique lateral band at mid-body, dark sacral spot with short anterior projection; belly and middle portions of ventral limb surfaces light with a scattering of brown pigment, throat boldly mottled brown and light; outer tibia surface with distinct dark stripe; posterior surface of thigh indistinctly mottled, mostly brown, with light pin stripe on lower portion of thigh from below anus to mid-thigh.

ETYMOLOGY.—From the Greek *oios* (unique, peculiar), in allusion to the fact that many taxa have been described as new from Santa Teresa, seemingly without distributions other than at Santa Teresa. This taxon is further peculiar in that of the many frog specimens collected from the Santa Teresa area, there are only three individuals of *E. oeus* known, all collected in 1942.

ADULT SPECIMEN DEFINITION.—Dorsum uniform or mottled (patterns A-2 and A-6 in Figure 1); no mid-dorsal pin stripes; no broad light mid-dorsal stripes; no light dorsolateral stripes; one individual with a light snout (pattern A in Figure 4); light interocular stripes present; interrupted or continuous dark stripes on outer tibia (patterns B and C in Figure 10); posterior surface of the thigh indistinctly mottled; life colors unknown; males 17.1–18.8 mm SVL; head width moderate (Table 20); hind limb length moderate (Table 20).

ADVERTISEMENT CALL.—Unknown.

DISTRIBUTION.—Known only from the type-locality (Figure 21).

ESPIRITO SANTO. Santa Teresa (MNRio 1244, MZUSP 59684, USNM 235612).

Zoogeography

Zoogeographic understanding requires two kinds of data: distribution and relationship. I am unable, with the data as analyzed in this paper, to produce a satisfactory hypothesis of relationships among the members of the *E. guentheri* cluster. Attempts to cladistically analyze the various pattern characters were frustrated in that there were but a handful of characters for which polarities could be determined and the derived states had a mosaic distribution among the species. Nevertheless, some general zoogeographic features are evident from the species distributions of the cluster members.

Somewhat surprisingly, the combined distribution of all species in the cluster correlates well with the middle and southern Atlantic Forest Morphoclimatic Domain (as defined by Ab'Sáber, 1977) (Figure 27). Whereas the cluster was chosen for study because the members occurred throughout the Atlantic Forests, more southerly records (Braun and Braun, 1980) were known. I also assumed that the cluster members, specifically *E. guentheri*, would extend at least

FIGURE 27.—Composite distributions for members of the *Eleutherodactylus guentheri* cluster. Bold line indicates approximate limits of the Atlantic Forest Morphoclimatic Domain. Dashed lines are state boundaries.

into the Atlantic Forest of Bahia and in various adjacent buffer zones or morphoclimatic domains. This assumption was made because other members of the genus *Eleutherodactylus*, which also have a direct development mode of reproduction, occur in the areas mentioned. However, the known distributions of the *E. guentheri* cluster members are rather restricted within the Atlantic Forest Morphoclimatic Domain.

Available data indicate that the presently known distributions are a good approximation of the actual northern distributional limits. When present, such species as *E. epipedus*, *gualteri*, *guentheri*, and *nasutus* are likely to be collected. At most places, cluster members are relatively common and although cluster members may be reproductively active at night, they are often encountered on the leaf litter during the day. Thus, negative data (specimens not collected from given localities) have more meaning for this cluster of frogs than for many other frog groups. The frog fauna from Linhares, Espirito Santo, has been reasonably sampled. This locality, on the north side of the Rio Doce, lies about 80–90 km north of Santa Teresa. No members of the *E. guentheri* cluster were in the MNRio collections, where collections from Linhares are deposited. The next northern locality that has been well sampled is around Ilhéus, Bahia. Bokermann (1975) reported on the *Eleutherodactylus* from the area. He did not collect any member of the *E. guentheri* cluster as defined in this paper. Bokermann (1975) described a new species, *E. vinhai*, from Ilhéus, indicating that it was a member of the *E. guentheri* group. The species has a granular belly, which might ally it with *E. erythromerus*. If *E. vinhai* does turn out to be a member of the *E. guentheri* cluster, it would be the most northerly member known of the *E. guentheri* cluster. All other *Eleutherodactylus* known from the northern Atlantic Forests belong to species groups that are quite distinctive from *E. guentheri* and its close relatives. Thus, although definition of the northern limit of the *E. guentheri* cluster awaits determination of whether *E. vinhai* is a cluster member, it seems safe to conclude that the species defined in this paper have their northern limit south of the Rio Doce.

The locality records outside of the Atlantic Forest Morphoclimatic Domain in the States of Minas Gerais, São Paulo, and the southermost two records in Rio Grande do Sul (Figure 27) occur in a mesic forest vegetation, identified as deciduous mesophytic subtropical forests of east and south Brazil by Hueck and Seibert (1972, vegetation type number 29 on the map). *Eleutherodactylus guentheri* cluster members do not occur throughout this vegetation type, but appear to have quite restricted distributions within it. The same general mesophytic subtropical forest vegetation occurs in the Misiones region of Argentina where the late Avelino Barrio, in particular, made efforts to collect the herpetofauna. Cei (1980), in his summary of the amphibians of Argentina, indicates that no *Eleutherodactylus* is known from Misiones. The localities within the mesophytic subtropical forests where *E. guentheri* cluster members have been collected may represent local edaphic conditions where the forest conditions approximate those found in the Atlantic Forests.

The locality outside of the Atlantic Forest Domain in the State of Paraná (Figure 27) is Volta Grande. I do not have personal experience with this locality, but it appears to be well within the Araucaria Domain (as defined by Ab'Sáber, 1977). The northern record in Rio Grande do Sul, Cambará do Sul, is definitely in the Araucaria Domain. Again, the presence of *E. guentheri* cluster members appears to be restricted, not widespread, within the Araucaria Domain. Pedro Canisio Braun has been working on the distributions of frogs in the State of Rio Grande do Sul for many years. The record from Cambará do Sul is the only one reported from the Araucaria Domain in Rio Grande do Sul (Braun and Braun, 1980).

A key to understanding the distributional limits of *Eleutherodactylus guentheri* and *nasutus* will lie in understanding why these two species only occur in a few restricted localities, and not throughout the mesophytic subtropical vegetation and the Araucaria Domain of Brazil.

As presently understood, the distribution range of *E. guentheri* almost includes the distribution ranges of all other species in this cluster. *Eleutherodactylus nasutus* has a broader distribution than previously known, but the southern limit of distribution is enigmatic in that there is no a priori reason, based on ecological considerations, for the species not to occur further to the south. This is also true for the extremely restricted distributions of the remaining four species of the cluster. Without a detailed, probable hypothesis of relationships among the species, it is pointless to speculate on the mode of speciation and geographic consequences involved.

The rather amazing sympatric occurrence of four members of the same species cluster at Teresópolis and Santa Teresa reflects a general pattern of *Eleutherodactylus* diversity in the Atlantic Forests. Although very few data points are available, they describe a pattern of reduced diversity at the northern and southern extremes with the highest diversity occurring from the Organ Mountains to the area including Santa Teresa. The available data, from north to south, are as follows: two species are known from the State of Pernambuco; Bokermann (1975) reported a total of five species from Ilhéus, Bahia; nine species occur at Teresópolis; six species at Boracéia; and only one species gets into the State of Rio Grande do Sul (Braun and Braun, 1980), just beyond the southernmost extent of the Atlantic Forest Domain. The diversity gradient correlates with temperature; rainfall patterns differ throughout the Atlantic Forests, but in a complex, not clinal, fashion. The *Eleutherodactylus* diversity gradient suggests that there is relatively little eco-physiological stress on *Eleutherodactylus* at the center of diversity and greater stress at the northern and southern extremes of the Atlantic Forests. Understanding the ecophysiology of the Atlantic Forest *Eleutherodactylus* may provide greater understanding of the distribution patterns and patterns of point diversity than explanations invoking competition.

A major reason in choosing the *E. guentheri* cluster to analyze was that it appeared from the outset that it would be possible to analyze patterns of differentiation within *E. guentheri* itself and to see if the variation correlated with geography. Two kinds of data are available: pattern characteristics and morphology.

The pattern characteristics were analyzed as follows. The data from Table 14 were combined with data for two states that differed, but due to sample sizes, not statistically significantly (dorsal patterns A-11, and C in Figure 1). The total number of significantly differentiated states was noted for each population and, on a geographic plot, the significant states that were shared between populations were indicated by drawing lines connecting the populations (Figure 28). These data thus provide an index of relative differentiation among populations and an index of possible relatedness through sharing of derived states (assuming significantly differentiated states are derived) among populations.

The morphological data used were from the discriminant function analysis, specifically the posterior classification results (Tables 17, 18). The methodology used is best explained by example. The individuals of population RJ1 that were posteriorly classified as SP1 individuals are more similar to the SP1 centroid, thus most SP1 individuals, than they are to the RJ1 centroid, thus most RJ1 individuals, in the features (measurements) analyzed. These "missed" classifications are used as an indication of morphological similarity between these two populations and the greater the incidence of "missed" classifications, the more similar the populations are assumed to be to each other. These data were figured geographically (separately for males and females) by connecting those populations in which "missed" classifications occurred (Figure 28). This index of morphological similarity, based on "missed" classifications, could be the result of two different causes: either a sharing of derived morphological states or a retention of the ancestral morphology. If geographic variation is evident among populations, either cause of morphological similarity should demonstrate a pattern of geographic variation.

If differentiation of populations correlated completely with geographic variation, the following two general patterns would be predicted. First, for both the pattern state and morphological data, the strongest connections among populations should be with the geographically closest populations, resulting in localized spider web patterns with few, if any, connections among distant populations. Second, because of the differences in kind of the pattern state and morphological data, differences of detail would not be

FIGURE 28.—Differentiation among population samples of *Eleutherodactylus guentheri.* Upper left shows geographic distribution of the 10 samples used for analysis: 1 = Teresópolis (RJ1), 2 = Petrópolis (RJ2), 3 = Sumaré and Tijuca (RJ4), 4 = Angra dos Reis (RJ5), 5 = Serra da Bocaina (SP4), 6 = Campos do Jordão (SP9), 7 = Boracéia (SP1), 8 = Cubatão and Paranapiacaba (SP3), 9 = São Paulo (SP2), 10 = Novo Horizonte (SC1). Dots in diagrams correspond to numbered locations. First diagram offshore shows differentiation of pattern states. Large circles indicate strongly differentiated populations, small circles indicate weakly differentiated populations. Dashed narrow line indicates sharing of one significantly differentiated pattern state, solid narrow line indicates sharing of two states, solid wide line indicates sharing of three states. Lower pair of figures show morphological similarities of males (upper) and females (lower), based on discriminant function analyses of posterior classification of individuals. Dashed narrow lines indicate a few individuals (one individual or less than 10%) of one sample identified as the connected sample, but the reciprocal not true. Solid narrow lines indicate a few individuals reciprocally identified as belonging to the connected samples. Dashed wide lines indicate several (10% or more) individuals identified as the connected sample, but reciprocal not true. Solid wide lines indicate several individuals reciprocally identified as belonging to the connected samples. See page 36 for further clarification.

surprising when comparing overall patterns; however, there should be concordance between the male and female morphological data set as illustrated.

Visual inspection of these data sets as analyzed and illustrated (Figure 28) indicates that the patterns of variation do not, in fact, have a series of web-like connections. Rather, there are several long-distance connections among populations resulting in patterns with a lot of noise. Some signals are discernable within the generally noisy framework, nonetheless.

The pattern state data indicate that considerable population differentiation has occurred, ranging from 1 (populations 2, 4, Figure 28) to 13 significantly differentiated states (population 7, Figure 28) per population (note that in Figure 28, the basic dichotomy of weakly differentiated [small circles, 1–5 differentiated states] or strongly differentiated [large circles, 9–13 differentiated states] populations is shown). The distribution of differientiated states is not dependent on sample sizes available for analysis. For example, sample 1 (Figure 28) from Teresópolis with a moderate sample size is well differentiated, and sample 3 (Figure 28) from Rio de Janeiro with a large sample size is weakly differentiated.

Two kinds of comparisons argue against a geographic component of differentiation. The first is that the largest number of shared significantly differentiated pattern states occurs between the populations from Serra da Bocaina and Boracéia (Figure 28, samples 5 and 7). On geographic grounds, the Boracéia population would be expected to share the greatest number of pattern states with the Paranapiacaba-Cubatão sample (Figure 28, samples 7 and 8), which in fact share no differentiated pattern states (also see p. 15). The second kind of comparison involves examining pairs of populations, which based on geography, should be most similar to each other. These are Teresópolis and Petrópolis in the Organ Mountains of Rio de Janeiro (Figure 28, samples 1 and 2) and Boracéia and Cubatão-Paranapiacaba in the same block of the Serra do Mar of the State of São Paulo (Figure 28, samples 7 and 8). For these comparisons, there is no indication from any of the data sets that these population pairs are most similar to each other.

The arguments against geographic variation accounting for the observed differentiation among populations analyzed do not preclude a component of geographic variation in fact occurring among populations of *E. guentheri*. The morphological data arguably suggest a component of geographic variation among the State of São Paulo samples (Figures 28, samples 5–9). The data themselves have certain liabilities that may limit their usefulness in describing geographic variation patterns. The pattern-state data were taken on samples that had been pooled over a 60-year period in some cases. Certainly there should be year-to-year variation in frequency of occurrence of pattern states that may add noise to the analysis. Also, for example, the morphological differences observed may be in response to similar adaptations of size to similar local climates, resulting in similar body forms in lowland populations at southern latitudes and higher elevation populations at northern latitudes. These morphological adaptations would have to be factored out in an analysis of geographic variation. The available data lead to the following hypothesis, which is accepted for purposes of this paper: differentiation is evident among populations of *E. guentheri*, but no geographic pattern is evident in the differentiation. The *E. guentheri* complex would be an ideal candidate for electrophoretic analysis, which would provide much more direct evidence on the degree and nature of intra- and inter-species variation and relationships.

Comparison With the *Cycloramphus* Model

The speciation and zoogeographic model proposed for the stream associated species of *Cycloramphus* (Heyer and Maxson, 1983) consists of the following elements. Each species has a restricted, localized distribution; collectively, the species distributions correlate with areas of sharp topographic relief within the middle and southern extent of the Atlantic Forest Domain where small mountain brooks occur; the allopatric model of speciation best accounts for the patterns of relationships and distributions as described by Heyer and Maxson (1983:367):

> The outstanding feature of the allopatric model of speciation for *Cycloramphus* is the small sizes of geographic areas of isolation and speciation. The scale is local areas of high relief. . . . Each local area had a unique history in terms of geological formation (when and how they were formed), hydrology, extent of Atlantic Forest cover during cooler and more arid times, and colonization, adaptations, and extinctions of *Cycloramphus* populations. No single zoogeographical pattern is apparent. Local patterns of distribution and relationships predominate. This very local effect results from some aspect in the life history of riparian *Cycloramphus* that confines occurrence to a very narrow and precisely defined microhabitat. The larval phase of the life cycle is the assumed limiting aspect, because the larvae are adapted to the wet surface covered rock splash zone of small brooks. Occurrence is, thus, limited to mountain brooks within areas of high relief and occurrence is discontinuous between areas of high relief.

The specialized larval ecology in stream-associated *Cycloramphus* was a dominant factor in the development of the *Cycloramphus* model. Thus, the interplay of ecology and history was considered crucial to understanding the zoogeography of stream associated *Cycloramphus*. Using the model, several predictions were made, two of which involved possible tests with members of the genus *Eleutherodactylus* (Heyer and Maxson, 1983:370):

> This narrow specialization [splash zone tadpole], combined with a long evolutionary history in an unstable area (geologically and climatically), suggests that *Cycloramphus* exhibits an extreme example of speciation in very local areas. We predict that this same pattern would only be repeated in other groups which have life history features that limit their distributions to very patchily distributed habitats. Some other stream associated insect groups might be expected to show a pattern very similar to that seen in *Cycloramphus*. The areas of isolation and differentiation should be at a somewhat larger scale for fishes and frogs that have larvae that live in the waters of the streams. Thus, for groups that have occurred in the Atlantic Forest Domain throughout the Cenozoic, such as *Hylodes*, the total distributional range should be greater, individual species ranges should be larger, and there should be fewer species per comparable geographic region than for *Cycloramphus*. . . . For stream frogs (with aquatic larvae) that have relatively short histories in the Atlantic Forest Domain, individual species ranges should be large and intraspecific variation should occur due to Pleistocene isolation of population units. . . . At another level, frogs with life histories not tied to patchily distributed habitats within the Atlantic Forest Domain, such as *Eleutherodactylus*, should have broader distributions both locally and geographically than either *Cycloramphus* or *Hylodes*. Further, there should be fewer species within the Atlantic Forest Domain per major lineage than for either *Cycloramphus* or *Hylodes*.

The *Cycloramphus* model predictions are not entirely borne out by the *Eleutherodactylus* data. A comment is appropriate at this point comparing the nature of the *Cycloramphus* and *Eleutherodactylus guentheri* cluster data bases. Both data bases have the same reliability of taxonomic assessment and precision of distributional understanding. The data bases differ in two ways. The *Cycloramphus* data set included genetic estimates of relationships; the relationships among *E. guentheri* cluster members remain unknown. The combination of relationship and distribution data for *Cycloramphus* allowed a rather inclusive and detailed zoogeographic model to be constructed. This model, as seen above, allowed predictions regarding other Atlantic Forest associated groups. Whereas there are not enough data for the *E. guentheri* cluster to propose a model comparable to that developed from the *Cycloramphus* data, there are elements of the *Eleutherodactylus* data that can be used to test the *Cycloramphus* based model. The second way the data sets differ is that data were not adequate to analyze intraspecific variation for any *Cycloramphus* species in the manner done for *E. guentheri*.

The *Cycloramphus* model predicted that *Eleutherodactylus* species would have: (1) broader local distributions, (2) broader geographic distributions, and (3) fewer species per major lineage than for *Cycloramphus*. These predictions are discussed in turn.

1) *Eleutherodactylus* do have broader local distributions than stream associated *Cycloramphus*. *Eleutherodactylus guentheri* occurs throughout the

forest floor, including stream-side locations, while *C. semipalmatus* is only found next to streams at Boracéia, for example.

2) Only *E. guentheri* and *nasutus* have broader geographic ranges than stream-associated *Cycloramphus*. The distributions of *E. epipedus, erythromerus, gualteri,* and *oeus* are similar to those of stream associated *Cycloramphus*. These latter distributions violate the predictions for *Eleutherodactylus* drawn from the *Cycloramphus* model.

3) The major lineages of Atlantic Forest *Eleutherodactylus* are not understood at present and the following may require revision if the *E. guentheri* cluster turns out to be a component of a larger lineage. There are 16 species of stream associated *Cycloramphus*, which appear to form a major lineage (Heyer, 1983; Heyer and Maxson, 1983). This figure of 16 is considerably greater than the six species comprising the *E. guentheri* cluster. For the present, this *Cycloramphus* model prediction is assumed to be validated by the *Eleutherodactylus* data.

The pattern of intraspecific differentiation and variation within *E. guentheri* is consistent with the very local centers of differentiation proposed for the *Cycloramphus* model. These *E. guentheri* data are therefore consistent with the hypothesis that during the Pleistocene, the Atlantic Forest vegetation was extremely fragmented and differentiation of *E. guentheri* occurred very locally, rather than within more extensive forest refugia. Present knowledge of Pleistocene forest refugia locations along coastal Brasil is not adequate to test this hypothesis.

The comparison of the *Cycloramphus* and *Eleutherodactylus* data indicates that there is some concordance between the *Cycloramphus* model predictions and confirmation with *Eleutherodactylus* data, but that there are enough differences to require re-assessment of the *Cycloramphus* model. The *Cycloramphus* model gave somewhat equal weight to the factors of ecology and history in understanding the zoogeography of the Atlantic Forest fauna. Rather than the *Eleutherodactylus* data showing a markedly different pattern than stream-associated *Cycloramphus*, as predicted from the model, several *Eleutherodactylus* species have geographic distribution patterns just like those of stream-associated *Cycloramphus*. Also, the pattern of differentiation within *E. guentheri* is consistent with a very local level of differentiation, like that seen at the species level in *Cycloramphus*. The ecologies of stream-associated *Cycloramphus* and *Eleutherodactylus* are very different. Both *Cycloramphus* and *Eleutherodactylus* have shared histories within the Atlantic Forest Domain, however. Thus, the restricted species distribution patterns common to *Cycloramphus* and *Eleutherodactylus* are likely due to common historical factors. Thus, the *Cycloramphus* model needs revision to the extent that in certain cases, historical factors leading to restricted distributions seemingly override ecological factors.

The combined *Cycloramphus* and *Eleutherodactylus* zoogeographical data indicate that the interplay of history and ecology is paramount to our understanding of the Atlantic Forest biotic distributions. Ecology is critical to the understanding of local distributions. Ecology is a component, but may not be as important as history, in understanding species ranges. At this point, I believe the challenge to understanding fully the zoogeography of the Atlantic Forest biota lies with knowing, in detail, the historical factors associated with population fragmentations and dispersals.

The *Eleutherodactylus* data suggest one additional insight into Atlantic Forest faunal zoogeography. *Eleutherodactylus nasutus* is an open formation associated species, with its close relatives being closed forest associates. The ecology of *E. nasutus* suggests that it could occur throughout open formations whether associated with the Atlantic Forest Domain or the buffer mesophytic subtropical forest. That *E. nasutus* shows as much fidelity to the Atlantic Forest Domain as it does indicates that there is a faunal element that is ecologically adapted to open formations, but zoogeographically restricted to the Atlantic Forest Domain.

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