Variation within the *Leptodactylus podicipinus-wagneri* Complex of Frogs (Amphibia: Leptodactylidae)

W. RONALD HEYER

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ABSTRACT

Heyer, W. Ronald. Variation within the *Leptodactylus podicipinus-wagneri* Complex of Frogs (Amphibia: Leptodactylidae). *Smithsonian Contributions to Zoology*, number 546, 124 pages, 46 figures, 55 tables, 1994.—Variation was studied in frogs identified as either *Leptodactylus podicipinus* or *L. wagneri* as diagnosed in my previous revision of the *L. melanonotus* species group. Over 6200 adults and juveniles were examined and variation analyses were performed on data from just over 3000 adult and near-adult specimens. The data set consists of a series of three kinds of morphological characters (patterns, structures, measurements), and, when available, advertisement call and habitat data. Intrapopulation variation indicates that variation among the characters studied is extensive within large samples. The intrapopulation variation results are used as a framework to interpret interpopulation and interspecific variation. Study of character variation among sympatric populations typically leads to the following results: (1) when compared side by side, most specimens can be sorted readily into distinct morphotypes representing distinct species; and (2) the variation between sympatric populations is usually distinctive, but not discrete. Advertisement calls in members of this complex appear to contain not only species-coding information, but other information that weakens the utility of calls in assessing species boundaries.

The results of this study are used to delimit species for most of the specimens examined. Available material from most of Venezuela is inadequate to evaluate how many species occur there and which of them are conspecific with geographically adjacent species. Thirteen species are diagnosed as a result of this study, including the description of five new species. The recognition of 13 species is conservative and additional information likely will confirm that some of these species are composite.

The distributions of most taxa within this complex are expected to be modified significantly by either newly collected specimens or data that will redefine currently recognized (composite) species. Only two distributions are considered robust as the result of this study, those of *L. natalensis* and *L. podicipinus*. The provenance of museum specimens collected by Borys Malkin purportedly from Igarapé Belém, Amazonas, Brazil, is called into question.

Unresolved problems are highlighted to encourage and focus further studies to understand the speciation processes and distribution patterns in this complex.

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Contents

Variation within the *Leptodactylus podicipinus-wagneri* Complex of Frogs (Amphibia: Leptodactylidae)

W. Ronald Heyer

Introduction

In 1970, I published the results of a species-level analysis of frogs of the *Leptodactylus melanonotus* species group (Heyer, 1970), which included the taxa that are the topic of this paper. In that paper, six species were recognized: *Leptodactylus dantasi, discodactylus, melanonotus, podicipinus, pustulatus,* and *wagneri. Leptodactylus dantasi,* a very distinct species, is still known from only the holotype. *Leptodactylus discodactylus* has been transferred to the genus *Vanzolinius* (Heyer, 1974). Recently collected material does not change the taxonomic understanding of either *Leptodactylus melanonotus* or *pustulatus.* However, in the just over 20 years since the previous study was undertaken, it has become clear that recognition of only two species, *podicipinus* and *wagneri,* east of the Andes was too conservative.

A current long-term research goal is to present a monographic summary of the systematics and distributions of the frog genus *Leptodactylus.* As preparation for that monograph, I wish to resolve as many species-level problems as practical. The purposes of this paper are to (1) describe the morphological variation within the *Leptodactylus podicipinus-wagneri* complex, (2) reinterpret species limits where appropriate, and (3) identify problem areas and suggest approaches that might provide resolution.

There are two reasons that the results of the present study (involving the same taxa and, in many instances, the same specimens) differ from the conclusions of 20 some years ago.

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Review Chairman: Stanley H. Weitzman, Smithsonian Institution. Reviewers: Janalee P. Caldwell, Oklahoma Museum of Natural History, Norman, Oklahoma, and one anonymous reviewer.

First, the study materials have increased in two critical ways. Now there are some large single-taxa samples from specific localities so that intrapopulation variation can be characterized much more adequately. There also are many more localities from which more than a single taxon of this complex have been collected. In the previous study only two such localities were identified. Study of variation in these sympatric samples allows clarification of species differences and similarities.

Second, and probably more important, my approach differs in the two studies. In the 1970 study, I focussed on trying to identify how many species were involved. My goal was crisply defined species with definitive key characters that would clearly distinguish the taxa. I was looking for simple solutions to patterns of variation; the only variation I was interested in was the kind that could be used to separate species. My philosophical approach was that I had a more or less preconceived idea that I would find well-defined biological species in the sense of the Mayr-Simpson model. Although I can not remember with certainty my methodology of more than 20 years ago, I would not be surprised if my approach influenced the way that I recorded data. If, for example, I thought that a toe tip character seemed to differentiate between taxa A and B and I encountered an intermediate state or a state slightly not fitting B that on the basis of other characters looked like it was B, I likely forced that state to be that "belonging" to B, and I would so record it.

In this study, my focus is on describing the variation encountered. I am as interested in any problems of interpreting the variation encountered as any explanations/interpretations that can be drawn. This time, I am willing to try to "grasp the amoeba" without completely capturing it. Because I tend to draw black and white distinctions in the gray world of collecting data, I made specific attempts to categorize all variation encountered for the characters I studied, rather than

set up a few character states for each character and then record the state that came closest for the individual being studied. I would like to think that this difference in approach is because I have learned something about frog systematics over the last 20 years, including the fact that meaningful patterns of variation may be complex and morphological differences between species may be subtle and/or involve differences of degree that are distinctive rather than discrete.

The duration of the two studies also emphasizes the difference between them. In the first study, I essentially took all the data and examined the specimens a single time over a two-month period. In this study, it took over a year and a half to take the primary set of morphological data, and each specimen has been examined at least twice (with most examined at least a third and fourth time): first when the morphological data were taken and second when samples from local geographic areas were examined. In total, this current study has had a five-year gestation period.

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This study would have not been possible without assembling all the study specimens at one place for an extended period of time. The policies of the following institutions and the patience and understanding of their personnel who loaned specimens to me are deeply appreciated: Academy of Natural Sciences of Philadelphia, John E. Cadle; American Museum of Natural History, Charles W. Myers; The Natural History Museum, London, Barry T. Clarke; California Academy of Sciences, Robert C. Drewes and Jens V. Vindum; Field Museum of Natural History, Hymen Marx, Alan Resetar, and Harold K. Voris; Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Maria Christina Ardila-R. and Pedro M. Ruiz-Carranza; INDERENA, José Vicente Rueda-A.; Instituto Nacional de Pesquisas da Amazônia, Gloria Moreira; Laboratorio de Biogeografia, Universidad de Los Andes, Enrique La Marca; Museu Nacional, Rio de Janeiro, Ulisses Caramaschi; Museu de Zoologia, Universidade de São Paulo, P.E. Vanzolini; Museum of Comparative Zoology, José P. Rosado and Ernest E. Williams; Museum of Natural History, Los Angeles County, Robert L. Bezy, Cynthia Weber, and John W. Wright; Museum of Natural History, University of Kansas, William E. Duellman and John E. Simmons; Museum of Vertebrate Zoology, University of California at Berkeley, David A. Good and David B. Wake; Museum of Zoology, University of Michigan, Ronald A. Nussbaum and Gregory Schneider; Nationaal Natuuristorisch Museum, Marinus S. Hoogmoed; Swedish Museum of Natural History, Sven O. Kullander; Texas Cooperative Wildlife Collection, Texas A&M University, James R. Dixon and Michael E. Retzer; Universidade Estadual de Campinas, Adão J. Cardoso; University of Texas at Arlington, Jonathan A. Campbell and William F. Pyburn.

Adão J. Cardoso and Lily O. Rodriguez allowed me to examine specimens they collected prior to their deposition in collections.

Reginald B. Cocroft kindly made his field data and recordings available to me as well as discussed the taxonomic situation of the forms from Tambopata with me. Because the call-vouchered Tambopata materials were an important key to understanding variation in this complex, Cocrofts' sharing of unpublished data and observations is most appreciated.

Ronald I. Crombie and Addison Wynn undertook specific field work to gather larvae and recordings of members of this complex in the Lesser Antilles, Trinidad, and Tobago for this study. Their field contributions clarified some problems and, equally as important, raised others.

Jennifer Westhoff executed Figure 11.

P.E. Vanzolini proofed the locality data for me, but any errors that remain are mine.

Ronald I. Crombie critically read the entire manuscript. Such an altruistic act is keenly appreciated.

The Museu de Zoologia, Universidade de São Paulo, its Director, P.E. Vanzolini, and the Neotropical Lowlands Research Program, Smithsonian Institution, supported the research leading to this paper. The Smithsonian support came from the Director's Office, National Museum of Natural History, and the International Environmental Sciences Program. This support was necessary and is appreciated.

METHODS AND MATERIALS

At the beginning of this study I had no intention of publishing the results reported herein. I had anticipated that I would be able to sit down with the materials of this complex available at my institution and determine in my own mind how many species were involved and how to tell them apart. Then I would be able to visit other major collections and sort the pertinent materials to get the associated locality data for inclusion in the monographic summary of the genus. However, it immediately became apparent that the patterns of morphological variation were complex and did not allow easy interpretation of species limits. I therefore borrowed as much material as possible to examine for this study (see Appendix 2 for museum symbolic codes used in text).

All specimens of this complex available to me (over 6200) have been examined, and morphological data were taken on all adult and subadult specimens (just over 3000). Based on previous work and initial examination of representative geographic samples of different morphological types, the following qualitative characters initially were chosen to evaluate patterns of variation: (1) degree of distinctiveness of a light posterior lip stripe extending from under the eye, above the angle of the jaw, to the front of the shoulder region; (2) degree of distinctiveness of a light stripe on the posterior face of the thigh; (3) melanophore distribution on the chin, throat, chest, and belly; and (4) degree of expansion of the toe tips. It quickly became apparent that there was variation in degree of

development of dorsolateral folds, and those data were recorded for all individuals except for the first 50–100 specimens examined. Measurements taken at the outset included (1) snout-vent length (SVL), (2) head length, (3) head width, (4) thigh length, (5) shank length, and (6) foot length. About the same time the dorsolateral-fold character was added, I observed what seemed to be variation in tympanum diameter, so those measurements also were recorded, including the specimens that were not initially measured. Measurements were taken as defined in Heyer et al. (1990) with the addition of tympanum diameter, which was measured as the maximum diameter including the annulus.

Data were recorded for adults and subadults in order to determine as precisely as possible minimum adult sizes and to allow examination of possible allometric relationships. For males, the condition of the thumb spines and/or vocal slits were recorded. A specimen was considered adult if the vocal slits were broken through the floor of the mouth and there was a pair of black spines on each thumb. Subadult males showed some development of thumb spines, but the vocal slits had not yet formed. This criterion may be arbitrary, but it can be applied consistently. The situation for females is not as easy. At the beginning of the study until relatively late in the data-recording phase, degree of egg development was used as the basis for distinguishing between adults and subadults. Later a more objective (although perhaps arbitrary) definition was used, i.e., that of oviduct development. A specimen was considered subadult if the oviduct was slender and straight; adult if the oviduct was thickened and convoluted. In only two samples (discussed later) were all specimens re-examined to apply the oviduct development criterion for sexual maturity. Selected individuals were re-examined on a case-by-case basis, as needed.

The best way to refer to the operational taxonomic units (OTUs) used in this study posed a bit of a problem. In some previous studies, I merely numbered the OTUs (OTU 1, OTU 2, etc.), but I now find it extremely difficult in re-reading those studies to associate taxonomic names with those OTUs, even though relatively few OTUs were involved. At the onset of this study, the OTU was the local population sample, of which there were hundreds. Even though somewhat lengthy, three features were used to identify individual OTUs: adult size, a (hopefully) distinctive or characteristic morphological feature, and the specific locality from where the sample was collected. Manuscript reviewers found it difficult to follow OTU name changes in the manuscript and to know to which species each OTU eventually was assigned. As an aid to tracking OTU names, Appendix 1 was prepared. Three adult size categories are defined on the basis of examining the sizes of adults from the 9 localities discussed in the next section: small, most males less than 35 mm, most females less than 45 mm; moderate, most males 35 to 45 mm, most females 45 to 55 mm; large, most males larger than 45 mm, most females larger than 55 mm SVL. For OTUs that are intermediate in the size classification, appropriate combinations of descriptors are used.

Locality data are often of critical importance in variation studies, including this one. These data are provided for the specimens examined (see Appendix 2, including the introductory discussion of how localities were mapped).

Methods of analysis are discussed where appropriate throughout the text. The software package used for all statistical analyses is SAS for personal computers, Version 6 (SAS Institute, Inc.). The *t*-test is used to test the null hypothesis that the means of two are equal. In the case of measurement ratio data, arcsine transformations of the original data were used in the *t*-test calculations. The 0.05 convention is used for significance level. Unaltered measurement data were used for both the multivariate outlier detection analyses and the discriminant function analyses.

Analysis of Single-Taxon Populations

There are 9 samples with at least 20 adult males and/or 20 adult females of a single species from a single locality. These samples are used to determine the degree of intrapopulation variation.

Because the criteria for determining female maturity changed during the study, two populations were re-examined for which egg size had been used initially as the criterion. In the case of the Moderate Size, Light Posterior Belly, Limoncocha, Ecuador OTU, the application of the oviduct development criterion did change the adult size range and the statistics were rerun for that sample (Table 1). In the case of the Small Size, Dark Posterior Belly, Curuçá, Brazil OTU, one female was recategorized as a subadult on the basis of oviduct development, but because the range of values was not affected, the statistics were not recalculated. The difference in the two criteria resulted in few reclassifications of individuals, but the differences were meaningful in particular cases.

TABLE 1.—Comparison of sizes of females of the Medium Size, Light Posterior Belly, Limoncocha, Ecuador OTU using two criteria.

Criteria	N	Minimum	Maximum	Range	Mean	Standard deviation
Egg development	130	41.0	52.8	11.8	48.3	1.90
Oviduct development	126	44.5	52.8	8.3	48.5	1.72

TABLE 2.—Measurement ratios for Small Size, Dark Belly, Porto Velho, Brazil OTU. (N = 113 females, 81 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
Head length/SVL	F	0.304	0.400	0.344	0.015
Head length/SVL	M	0.314	0.378	0.354	0.012
Head width/SVL	F	0.300	0.364	0.326	0.014
Head width/SVL	M	0.304	0.365	0.332	0.012
Tympanum/SVL	F	0.059	0.086	0.068	0.004
Tympanum/SVL	M	0.060	0.082	0.071	0.005
Thigh/SVL	F	0.320	0.452	0.382	0.029
Thigh/SVL	M	0.306	0.447	0.387	0.030
Shank/SVL	F	0.361	0.444	0.403	0.016
Shank/SVL	M	0.379	0.460	0.413	0.015
Foot/SVL	F	0.422	0.551	0.488	0.024
Foot/SVL	M	0.453	0.538	0.503	0.019

INDIVIDUAL OTUS

For morphological features other than measurement data, the data were combined for subadult and adult males and for subadult and adult females. Results are discussed separately for the sexes only if it appeared that there was a difference in features between them. Measurement data are analyzed for each sex, as the adult sizes of males and females differ notably. The order for discussing the OTUs is decreasing sample size.

Small Size, Dark Belly, Porto Velho, Brazil OTU

N = 113 adult and 5 subadult females, 81 adult and 3 subadult males.

Most individuals have some indication of a light posterior lip stripe (32% of the males and 44% of the females were scored as not having any indication of a light lip stripe). Sixteen percent of the males were scored as having distinct lip stripes, whereas only 9% of the females were so scored. Only one male was scored as having a very distinct light lip stripe. Several individuals could not be scored for dorsolateral-fold condition due to state of preservation. Of those scored, about a quarter did not appear to have any dorsolateral folds (although they may have had them in life), and the rest were about evenly divided between having folds extending from the eye to less than halfway to the sacrum and from the eye to at least halfway to the sacrum or to the sacrum itself. Most (87%) individuals have no indication of a light stripe on the posterior face of the thigh. Only three females were scored as having distinct light thigh stripes; the remainder of the 13% of the specimens have indications of light stripes on at least one thigh. Almost all individuals (94%) have distinctive small light spots on the venter, but over half have them restricted to the chin area. Only four individuals (2%) have very distinctive patterns of dark venters with contrasting light spots extending from the chin through the posterior belly. Over two-thirds of the individuals have moderately to extensively dark-mottled or dark- and light-spotted venters. Over three-quarters of the individuals have narrow toe tips, with the rest of the sample having just-swollen or slightly swollen toe tips (just swollen < slightly swollen). Only eight females were noted to have one or two very small white spines on the thumb.

Subadult females range in size from 29.7 to 34.7 mm SVL; the adults range from 31.0 to 47.6 mm SVL, with a 3.7 mm overlap in size between the subadult and adult females, but this value is based on the egg development criterion for determining the adult female condition. The three subadult males range from 29.5 to 29.9 mm SVL; the adult males range from 28.1 to 38.2 mm, with an overlap of only 1.8 mm. The other measurements, expressed as ratios of SVL, are similar between the sexes, but thigh length is the only variable in which the means do not differ statistically (head length/SVL, $t_{(2),190} = -5.232$, $P < 0.001$; head width/SVL, $t_{(2),190} = -2.974$, $P < 0.01$; tympanum/SVL, $t_{(2),192} = -4.406$, $P < 0.001$; shank/SVL, $t_{(2),192} = -4.375$, $P < 0.001$; foot/SVL, $t_{(2),192} = -4.670$, $P < 0.001$) (Table 2)

Moderate Size, Light Posterior Belly, Limoncocha, Ecuador OTU

N = 126 adult and 6 subadult females, 65 adult and 1 subadult males.

Most (about 80%) individuals have some development of a distinct light lip stripe, although it is clearly distinct in relatively few (<10%). Most individuals have indications of dorsolateral folds (about 80%), although preservation artifact could have obscured dorsolateral folds in some or all of the individuals scored as lacking them. Most individuals have moderate-length folds, extending more than half the distance from the posterior eye to the sacrum (54% of males, 73% of females). Only two individuals were scored as having dorsolateral folds extending from the eye to past the sacrum. Development of a light stripe on the posterior surface of the

TABLE 3.—Measurement ratios for Moderate Size, Light Posterior Belly, Limoncocha, Ecuador OTU. (N = 126 females, 65 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
Head length/SVL	F	0.331	0.393	0.357	0.010
Head length/SVL	M	0.346	0.390	0.363	0.009
Head width/SVL	F	0.322	0.364	0.342	0.008
Head width/SVL	M	0.330	0.372	0.351	0.009
Tympanum/SVL	F	0.064	0.078	0.070	0.003
Tympanum/SVL	M	0.067	0.082	0.074	0.003
Thigh/SVL	F	0.384	0.483	0.443	0.016
Thigh/SVL	M	0.380	0.474	0.445	0.017
Shank/SVL	F	0.426	0.495	0.447	0.013
Shank/SVL	M	0.440	0.499	0.469	0.013
Foot/SVL	F	0.466	0.576	0.518	0.019
Foot/SVL	M	0.481	0.559	0.521	0.018

thigh is quite variable. In about a quarter of the individuals, there is no indication of a stripe on either thigh. Most individuals have some indication of a light stripe, at least on one thigh, with about 30% of the sample having a distinct stripe on at least one thigh. Only three individuals have very distinct, dark outlined, light thigh stripes. Only two individuals have distinct light spots on the chin, and eight others have indistinct light chin spotting. The rest of the sample lacks light spots anywhere on the ventral surfaces. Most individuals have heavier ventral mottling from the tip of the chin to no further than midbelly. However, about 25%–30% of the individuals have mottling on the posterior half of the belly as well. In only about 5% of the individuals is the mottling relatively extensive and uniform from the chin to the posterior belly. The ventral mottling is indistinctive in most individuals; less than 2% of the sample was scored as boldly mottled. The toe tips are swollen in virtually the entire sample; only one individual was noted as having almost small toe disks. Just over one-third of the females (characteristically the largest) had one or two very small white spines on each thumb.

Subadult females range in size from 40.6 to 46.0 mm SVL; adults range from 44.5 to 52.8 mm with only 1.5 mm SVL overlap. The single subadult male is 39.6 mm SVL, and adults range from 38.1 to 44.7 mm SVL. Other measurements, expressed as ratios of SVL, are similar between the sexes, although the means differ significantly for head length/SVL ($t_{(2),189} = -3.684$, $P < 0.001$), head width/SVL ($t_{(2),189} = -6.904$, $P < 0.001$), and tympanum/SVL ($t_{(2),189} = -7.796$, $P < 0.001$) (Table 3).

Small Size, Dark Belly, Rurrenabaque, Bolivia OTU

N = 29 adult and 2 subadult females, 31 adult and 1 subadult males.

This was one of the first samples examined. The dorsolateral-fold conditions and tympanum diameter were recorded for relatively few individuals. The latter are omitted from this analysis (but were taken later to include with the "Variation within Taxa/Regions" analyses).

The light posterior lip stripe is distinct in more than two-thirds of the individuals and not distinct in only two. The dorsolateral-fold condition ranges from apparently absent to folds extending from eye to between halfway to the sacrum or to the sacrum. Over half the sample lacks any indication of a light stripe on the posterior surface of the thigh, one individual has a distinct stripe, and the remainder have indistinct stripes. All but one individual have distinctive light spots on the venter, with spots restricted to the chin and throat in over one-third of the sample. Several individuals have distinct dark venters with contrasting small light spots from the chin through the posterior extent of the belly. All individuals have an extensive distribution of melanophores on the venter and narrow toe tips. Two females have small paired white spines on the thumb.

The two subadult females are 29.7 and 34.0 mm SVL; adults range from 34.0 to 42.5 mm SVL. The single subadult male measures 24.5 mm SVL; the adults range from 26.1 to 36.4 mm SVL. The other measurements, expressed as ratios of SVL, are similar between the sexes, although means differ significantly for head length/SVL ($t_{(2),52} = -3.346$, $P < 0.01$), thigh/SVL ($t_{(2),52} = -3.643$, $P < 0.001$), shank/SVL ($t_{(2),52} = -4.425$, $P < 0.001$), and foot/SVL ($t_{(2),52} = -2.642$, $P < 0.01$) (Table 4).

Small/Moderate Size, Dark Belly, Alejandria, Bolivia OTU

N = 41 adult females, 38 adult males.

About one-quarter of the males and one-third of the females have no indication of a light posterior lip stripe. About one-half of the individuals have some indication of a lip stripe, some have distinct lip stripes, and only one individual has a very distinct lip stripe. Only two individuals were recorded as lacking dorsolateral folds. Most (about 85%) have short folds extending from the eye to less than halfway to the sacrum. A few specimens have longer folds extending past halfway to the sacrum to as far as the sacrum. In several individuals the folds

TABLE 4.—Measurement ratios for Small Size, Dark Belly, Rurrenabaque, Bolivia OTU. (N = 29 females, 31 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
Head length/SVL	F	0.333	0.377	0.357	0.014
Head length/SVL	M	0.348	0.410	0.371	0.017
Head width/SVL	F	0.315	0.363	0.338	0.012
Head width/SVL	M	0.314	0.376	0.345	0.016
Thigh/SVL	F	0.342	0.448	0.392	0.024
Thigh/SVL	M	0.359	0.456	0.415	0.024
Shank/SVL	F	0.351	0.436	0.406	0.017
Shank/SVL	M	0.405	0.467	0.423	0.016
Foot/SVL	F	0.433	0.535	0.503	0.024
Foot/SVL	M	0.487	0.559	0.518	0.019

TABLE 5.—Measurement ratios for Small/Moderate Size, Dark Belly, Alejandria, Bolivia OTU. (N = 41 females, 38 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
Head length/SVL	F	0.318	0.363	0.333	0.010
Head length/SVL	M	0.319	0.357	0.335	0.009
Head width/SVL	F	0.295	0.344	0.320	0.009
Head width/SVL	M	0.306	0.348	0.326	0.010
Tympanum/SVL	F	0.065	0.075	0.070	0.003
Tympanum/SVL	M	0.067	0.081	0.072	0.003
Thigh/SVL	F	0.346	0.400	0.373	0.011
Thigh/SVL	M	0.349	0.423	0.386	0.016
Shank/SVL	F	0.361	0.415	0.388	0.014
Shank/SVL	M	0.378	0.425	0.404	0.011
Foot/SVL	F	0.423	0.519	0.466	0.020
Foot/SVL	M	0.427	0.521	0.484	0.018

are dark outlined. No specimens have distinct light stripes on the posterior face of the thigh; a few (about 15%) have indications of or indistinct light stripes on at least one thigh; the rest (about 85%) have mottled thighs without any indication of light stripes. Most individuals (about 80%) have light spots on the venter, restricted to the chin in about half the sample. A few individuals (< 15%) have a distinct pattern of dark venters with distinct light spots extending from the chin through the posterior extent of the belly. All individuals have extensive development of melanophores on the venter. The toe tips are either narrow or barely swollen.

Females range from 39.9 to 47.9 mm SVL; males range from 36.5 to 43.3 mm SVL. The other measurements, expressed as ratios of SVL, are similar between the sexes, but head length/SVL is the only variable for which the means do not differ significantly (head width/SVL, $t_{(2),77} = -2.500$, $P = 0.02$; tympanum/SVL, $t_{(2),77} = -2.951$, $P < 0.01$; thigh/SVL, $t_{(2),65} = -4.140$, $P < 0.001$; shank/SVL, $t_{(2),77} = -5.518$, $P < 0.001$; foot/SVL, $t_{(2),77} = -4.346$, $P < 0.001$) (Table 5).

Small/Moderate Size, Light Thigh Stripe, Buenavista, Bolivia OTU

N = 40 adult females, 23 adult and 1 subadult males.

Almost one-half of the individuals have distinct light posterior lip stripes, almost as many others have at least an indication of a stripe. Very few specimens show either extreme of no indication of a light lip stripe or a very distinct light lip stripe. Almost all individuals have indications of dorsolateral folds, which extend from the eye to at least halfway to the sacrum or to the sacrum, in just over half the specimens. In only three individuals do the dorsolateral folds extend beyond the sacrum. All individuals have at least an indication of a light stripe on the posterior face of the thigh, and the thigh stripe is distinct in most. In just over half the sample the thigh stripes are very distinct and often dark outlined. The majority of individuals (about 3/5) have a ventral pattern of the throat and chin mottled and the entire belly with scattered melanophores (with noticeably more areas on the belly without melanophores

TABLE 6.—Measurement ratios for Small/Moderate Size, Light Thigh Stripe, Buenavista, Bolivia OTU. (N = 40 females, 23 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
Head length/SVL	F	0.335	0.372	0.350	0.010
Head length/SVL	M	0.339	0.374	0.359	0.010
Head width/SVL	F	0.313	0.366	0.331	0.011
Head width/SVL	M	0.326	0.395	0.343	0.015
Tympanum/SVL	F	0.063	0.078	0.072	0.004
Tympanum/SVL	M	0.070	0.083	0.075	0.004
Thigh/SVL	F	0.379	0.499	0.432	0.022
Thigh/SVL	M	0.393	0.475	0.442	0.018
Shank/SVL	F	0.438	0.510	0.471	0.018
Shank/SVL	M	0.431	0.498	0.471	0.017
Foot/SVL	F	0.471	0.595	0.528	0.027
Foot/SVL	M	0.468	0.577	0.527	0.026

than with). A few specimens have distinctive light spots on the throat and/or chin, but they do not extend to the belly. Only two individuals have mottled bellies with more melanophores than without. Most individuals (about 80%) have swollen toe tips; only one was recorded as having narrow toe tips. The rest have either almost small toe disks or, in the case of two specimens, were recorded as having small toe disks.

Females range from 35.1 to 46.9 mm SVL. The single subadult male is 30.5 mm SVL, whereas adult males range from 28.3 to 44.3 mm SVL, thus there is a 2.2 mm overlap in size. The other measurements, expressed as ratios of SVL, are similar for males and females, although the means of head length/SVL ($t_{(2),61} = -3.322$, $P < 0.01$), head width/SVL ($t_{(2),61} = -3.708$, $P < 0.001$), and tympanum/SVL ($t_{(2),61} = -2.756$, $P < 0.01$) differ significantly (Table 6).

Small Size, Light Posterior Lip Stripe, Kartabo, Guyana OTU

N = 9 adult females, 46 adult males.

Just over one-half of the individuals have distinct light posterior lip stripes, most of the others have some indication of a light lip stripe. Only four specimens lack light lip stripes. Few (<10%) individuals lack indications of dorsolateral folds. Most specimens have short dorsolateral folds, extending from the eye to no more than half the distance to the sacrum, although the folds are longer in some individuals, extending as far as the sacrum. The folds are dark outlined in some individuals. About one-half the specimens lack any indication of a light stripe on the posterior face of the thigh, most of the remainder have some indication of light thigh stripes at least on one thigh, and some individuals (<25%) have distinct stripes, at least on one thigh. No individuals have very distinct thigh stripes. The ventral pattern is rather variable, with distinctive light spots on the chin in over half the individuals. The belly ranges from having a few melanophores just in back of the chest region to extensively distributed over the entire belly (and throat and chest, with most specimens intermediate) in either a finely mottled or boldly mottled pattern. The toe-tip condition is the most variable observed, ranging from one individual with narrow toe tips to just about an even distribution of individuals having just-swollen, swollen, just-expanded, expanded, almost small disk, and small disk conditions. In spite of the range of variation of toe-tip development, variation is continuous within the sample.

Females range in size from 36.2 to 42.8 mm SVL; males range from 31.5 to 37.3 mm. The other measurements, expressed as ratios of SVL, are similar for males and females and none differ significantly (Table 7).

Large Size, Boldly Mottled Belly, Santa Cecilia, Ecuador OTU

N = 17 adult and 4 subadult females, 25 adult and 7 subadult males.

Most individuals have an indication of a light posterior lip stripe and about as many specimens have distinct lip stripes as have no indication of lip stripes. No individuals have very distinct light lip stripes. All specimens have long dorsolateral folds, extending past the sacrum in almost all cases (>90%). The dorsolateral folds are dark outlined, at least in part, in over 85% of the individuals. Slightly less than half the individuals have no indication of light stripes on the posterior face of the thigh. In about one-quarter of the sample the stripes are distinct. Some individuals have light spots under the chin. The venter is usually lightly to heavily mottled, although in a few (~7%) specimens the belly mostly lacks melanophores. The venter is boldly mottled in 65% of the males and 81% of the females. The tips of the toes show relatively little variation, ranging from just or slightly swollen to swollen. One female has a single tiny white spine on each thumb.

The subadult females examined range in size from 52.1 to 58.5 mm SVL, with essentially no overlap in size with the adult females examined, which range in size from 58.3 to 76.3 mm SVL. The range in adult female size is considerable, 18.0 mm. The subadult males examined range in size from 37.2 to 53.4

TABLE 7.—Measurement ratios for Small Size, Light Posterior Lip Stripe, Kartabo, Guyana OTU. (N = 9 females, 46 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
Head length/SVL	F	0.344	0.394	0.376	0.019
Head length/SVL	M	0.352	0.414	0.384	0.015
Head width/SVL	F	0.325	0.350	0.337	0.010
Head width/SVL	M	0.318	0.372	0.340	0.014
Tympanum/SVL	F	0.070	0.089	0.078	0.006
Tympanum/SVL	M	0.072	0.094	0.082	0.005
Thigh/SVL	F	0.376	0.480	0.428	0.033
Thigh/SVL	M	0.351	0.525	0.431	0.036
Shank/SVL	F	0.441	0.518	0.475	0.023
Shank/SVL	M	0.432	0.541	0.477	0.027
Foot/SVL	F	0.522	0.567	0.539	0.014
Foot/SVL	M	0.509	0.607	0.553	0.024

TABLE 8.—Measurement ratios for Large Size, Boldly Mottled Belly, Santa Cecilia, Ecuador OTU. (N = 17 females, 25 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
Head length/SVL	F	0.342	0.397	0.364	0.014
Head length/SVL	M	0.356	0.400	0.376	0.009
Head width/SVL	F	0.326	0.368	0.348	0.011
Head width/SVL	M	0.344	0.374	0.356	0.007
Tympanum/SVL	F	0.054	0.076	0.069	0.005
Tympanum/SVL	M	0.069	0.087	0.078	0.005
Thigh/SVL	F	0.392	0.498	0.448	0.029
Thigh/SVL	M	0.401	0.503	0.459	0.026
Shank/SVL	F	0.477	0.546	0.509	0.024
Shank/SVL	M	0.457	0.532	0.506	0.016
Foot/SVL	F	0.482	0.605	0.560	0.028
Foot/SVL	M	0.528	0.598	0.554	0.020

mm SVL, overlapping considerably in size (11.4 mm) with the adult males, which range from 42.0 to 59.6 mm. The range in adult male size, 17.6 mm, is almost as large as the range observed in females. Differences in tympanum size between the sexes is obvious from comparing ratio ranges, means, and standard deviations (Table 8). The means for not only tympanum/SVL differ significantly ($t_{(2),40} = -5.870$, $P < 0.001$), but the means for head length/SVL ($t_{(2),25} = -3.277$, $P < 0.01$) and head width/SVL ($t_{(2),40} = -3.300$, $P < 0.01$) also differ significantly for males and females (Table 8).

Small Size, Dark Belly, Curuçá, Brazil OTU

N = 19 adult and 1 subadult females, 32 adult males.

Over two-thirds of the individuals have distinct posterior light lip stripes, with most of the remainder having some indication of a light stripe. Only one female has no indication of a light stripe. Two males were scored as having very distinct light lip stripes. Some (12%) individuals lack indications of dorsolateral folds. One-half of the sample have moderate folds extending from the eye to between half the distance to the sacrum or to the sacrum. The remainder have short folds not extending past half the distance from the eye to the sacrum. Almost all specimens have mottled posterior faces of the thigh with no indication of a light stripe; only four individuals have indications of a light stripe on at least one thigh. Almost all individuals have light spots on the venter, but they are limited to the chin in about half the sample. Almost one-quarter of the individuals have dark venters with small distinct light spots from the chin through the posterior extent of the belly. All individuals have extensive distribution of melanophores from the chin through the posterior extent of the belly. The toe tips are narrow in about three-quarters of the individuals, just swollen in the rest.

Females range in size from 30.0 to 43.7 mm SVL; males range from 26.4 to 36.4 mm. The other measurements, expressed as ratios of SVL, generally are similar for males and females, but the means differ significantly for head length/SVL

TABLE 9.—Measurement ratios for Small Size, Dark Belly, Curuçá, Brazil OTU. (N = 20 females, 32 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
Head length/SVL	F	0.332	0.373	0.353	0.012
Head length/SVL	M	0.342	0.384	0.362	0.010
Head width/SVL	F	0.316	0.357	0.337	0.011
Head width/SVL	M	0.317	0.354	0.338	0.009
Tympanum/SVL	F	0.067	0.079	0.073	0.004
Tympanum/SVL	M	0.068	0.091	0.076	0.005
Thigh/SVL	F	0.386	0.452	0.422	0.020
Thigh/SVL	M	0.413	0.463	0.438	0.012
Shank/SVL	F	0.383	0.461	0.422	0.022
Shank/SVL	M	0.408	0.456	0.434	0.012
Foot/SVL	F	0.451	0.593	0.511	0.040
Foot/SVL	M	0.467	0.565	0.528	0.022

TABLE 10.—Measurement ratios for Small Size, Light Posterior Lip Stripe, Langaman Kondre, Surinam OTU. (N = 29 females, 8 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
Head length/SVL	F	0.344	0.395	0.369	0.013
Head length/SVL	M	0.356	0.416	0.388	0.020
Head width/SVL	F	0.306	0.345	0.323	0.010
Head width/SVL	M	0.328	0.362	0.337	0.011
Tympanum/SVL	F	0.066	0.082	0.073	0.004
Tympanum/SVL	M	0.076	0.086	0.079	0.004
Thigh/SVL	F	0.374	0.448	0.416	0.018
Thigh/SVL	M	0.388	0.447	0.423	0.020
Shank/SVL	F	0.418	0.478	0.443	0.016
Shank/SVL	M	0.445	0.471	0.457	0.008
Foot/SVL	F	0.496	0.564	0.527	0.019
Foot/SVL	M	0.525	0.566	0.549	0.015

($t_{(2),50} = -2.932$, $P < 0.01$), tympanum/SVL ($t_{(2),50} = -2.567$, $P = 0.01$), thigh/SVL ($t_{(2),28} = -3.323$, $P < 0.01$), and shank/SVL ($t_{(2),26} = -2.347$, $P = 0.03$) (Table 9).

Small Size, Light Posterior Lip Stripe, Langaman Kondre, Surinam OTU

N = 29 adult and 3 subadult females, 8 adult males.

There is at least an indication of a light posterior lip stripe in all specimens examined; the stripe is distinct in 75% of the specimens and very distinct in 10%. All specimens in which the condition of the dorsolateral folds could be determined have either short (all but two individuals, folds no more than half the distance from the eye to sacrum) or moderately long (two individuals, extending no further than sacrum) dorsolateral folds. In over half the individuals, the dorsolateral folds are dark outlined, at least in part. Over two-thirds of the individuals have mottled posterior thigh faces with no indications of light stripes. Only two individuals were recorded as having distinct stripes on both thighs. The rest of the sample has either indications of a light stripe on one or both thighs or a distinct stripe on only one thigh. In over half the sample the chin, throat, chest, and belly have a light to moderate scattering of melanophores. A few individuals (~10%) have dark venters. Most individuals (~85%) have light spots on the chin. Two individuals have boldly mottled venters. The toe tips range from slightly swollen, swollen, to slightly expanded. Twenty percent of the sample has at least broken dark mid-dorsal pin stripes.

The three subadult females recorded have SVLs ranging from 31.0 to 31.9 mm, overlapping only 0.7 mm with the adult females, which range from 31.2 to 39.3 mm SVL. The adult males range from 28.9 to 32.8 mm SVL. The means of all variable ratios except for thigh/SVL differ significantly between the sexes (head length/SVL, $t_{(2),35} = -3.279$, $P < 0.01$; head width/SVL, $t_{(2),35} = -3.378$, $P < 0.01$; tympanum/SVL, $t_{(2),35} = -4.391$, $P < 0.001$; shank/SVL, $t_{(2),35} = -2.317$, $P = 0.03$; foot/SVL, $t_{(2),35} = -3.048$, $P < 0.01$) (Table 10).

Discussion

All of the OTUs analyzed differ from each other at least in degree. At the same time, each of the variables analyzed varies considerably within at least one of the OTUs. In most cases, differences among the OTUs are not discrete or quantitative.

The light posterior lip stripe and light posterior thigh stripe characters generally are distinct in some populations, indistinct in others, but several have individuals having all states recognized in the analysis. Dorsolateral folds in this complex are not as well developed as in other taxa of *Leptodactylus*, but they are present in most of the individuals analyzed in this section. However, in some individuals, it is impossible to tell whether the dorsolateral fold is absent or is obscured because of preservation method. Nevertheless, the differences between dorsolateral folds in the Large Size, Boldly Mottled Belly, Santa Cecilia, Ecuador OTU and Small Size, Dark Belly, Porto Velho, Brazil OTU are rather obvious when several individuals from both OTUs are compared directly with each other. Ventral patterns are also quite variable within samples, but the ranges of variation differ among the samples and no one sample encompasses the entire range of variation observed for this character. Most of the samples show limited variation in the toe-tip character, but the toe tips in the Small Size, Light Posterior Lip Stripe, Kartabo, Guyana OTU have the full range of conditions observed among all the other samples.

I had hoped at the outset of this analysis to find an association between range of adult sizes with overall size. No such association is obvious, nor is there a relatively uniform single size range for all OTUs (Table 11). The reason for attempting to find an association between size range and overall size was to interpret and predict adult size range in other, smaller samples. For example, if there were a large and small adult male from a given locality, if size ranges could be predicted for each, then one would have at least a clue whether it was likely or not that the two specimens at hand would fall into the size range expected from a single species or would represent two species, based on size considerations.

Relative amounts of variation of measurement data are compared among OTUs to determine whether they are comparable and whether any trends are evident among measurements. Comparison of coefficients of variation among OTUs (Table 12) is used for this purpose. There is a fair range of variation among coefficients of variation, but the coefficients of variation are rather comparable within OTUs in most cases (Table 12). There is no correlation between coefficient of variation of SVL and mean SVL when plotted to determine if there is a correlation of greater variation with larger size (resulting graph is so obvious it is not included). Likewise, except for the three OTUs with smallest sample sizes, which do have the largest coefficients of variation for SVL, there is no correlation between sample size (numbers of individuals within OTUs) and coefficient of variation (Figure 1 is an example using the coefficient of variation for SVL).

TABLE 11.—Size (SVL) statistics for OTUs with sample sizes of 20 or greater.

OTU*	Sex	N	Minimum	Maximum	Range	Mean	Standard deviation
1	F	113	31.0	47.6	16.6	39.1	3.32
2	F	126	44.5	52.8	8.3	48.5	1.72
3	F	29	34.0	42.5	8.5	37.8	2.17
4	F	41	39.9	47.9	8.0	45.1	2.04
5	F	40	35.1	46.9	11.8	41.5	3.39
8	F	20	30.0	43.7	13.7	38.0	3.82
9	F	29	31.2	39.3	8.1	36.0	2.07
1	M	81	28.1	38.2	10.1	34.3	2.12
2	M	65	38.1	44.7	6.6	41.9	1.46
3	M	31	26.1	36.4	10.3	31.8	2.40
4	M	38	36.5	43.3	6.8	39.6	1.56
5	M	23	28.3	44.3	16.0	36.0	3.30
6	M	46	31.5	37.3	5.8	33.9	1.51
7	M	25	42.0	59.6	17.6	50.0	5.56
8	M	32	26.4	36.4	10.0	32.1	2.86

* 1 = Small Size, Dark Belly, Porto Velho, Brazil OTU
2 = Moderate Size, Light Posterior Belly, Limoncocha, Ecuador OTU
3 = Small Size, Dark Belly, Rurrenabaque, Bolivia OTU
4 = Small/Moderate Size, Dark Belly, Alejandria, Bolivia OTU
5 = Small/Moderate Size, Light Posterior Thigh Stripe, Buenavista, Bolivia OTU
6 = Small Size, Light Posterior Lip Stripe, Kartabo, Guyana OTU
7 = Large Size, Boldly Mottled Belly, Santa Cecilia, Ecuador OTU
8 = Small Size, Dark Belly, Curuçá, Brazil OTU
9 = Small Size, Light Posterior Lip Stripe, Langaman Kondre, Surinam OTU

TABLE 12.—Coefficients of variation for variables for OTUs with sample sizes of 20 or greater.

OTU*	Sex	N	SVL	Head length	Head width	Tympanum	Thigh	Shank	Foot
1	F	113	8.50	7.40	7.72	10.19	10.69	7.51	6.58
1	M	81	6.18	6.20	6.10	8.42	9.21	6.31	5.30
2	F	126	3.55	3.88	3.80	5.39	4.45	3.66	4.01
2	M	65	3.49	3.47	3.74	4.84	4.50	3.77	3.80
3	F	29	5.75	5.50	5.02	-†	5.25	4.17	4.39
3	M	31	7.53	6.16	6.32	-†	7.52	6.04	6.41
4	F	41	4.52	3.87	4.32	5.15	4.39	3.77	3.83
4	M	38	3.93	3.35	3.98	4.66	4.98	3.64	3.50
5	F	40	8.17	7.24	7.31	9.38	8.19	7.32	6.66
5	M	23	9.17	7.60	9.53	11.68	8.23	7.55	7.34
6	M	46	4.45	4.40	5.76	5.27	9.13	6.51	5.40
7	M	25	11.11	10.20	11.01	12.89	13.58	10.94	10.36
8	F	20	10.05	8.10	9.57	8.85	8.07	7.19	5.62
8	M	32	8.92	8.43	9.35	9.54	9.39	8.26	8.42
9	F	29	5.74	5.44	5.34	5.76	5.64	4.70	4.56

* 1 = Small Size, Dark Belly, Porto Velho, Brazil OTU
2 = Moderate Size, Light Posterior Belly, Limoncocha, Ecuador OTU
3 = Small Size, Dark Belly, Rurrenabaque, Bolivia OTU
4 = Small/Moderate Size, Dark Belly, Alejandria, Bolivia OTU
5 = Small/Moderate Size, Light Posterior Thigh Stripe, Buenavista, Bolivia OTU
6 = Small Size, Light Posterior Lip Stripe, Kartabo, Guyana OTU
7 = Large Size, Boldly Mottled Belly, Santa Cecilia, Ecuador OTU
8 = Small Size, Dark Belly, Curuçá, Brazil OTU
9 = Small Size, Light Posterior Lip Stripe, Langaman Kondre, Surinam OTU

† Tympanum data not recorded for most individuals of these OTUs.

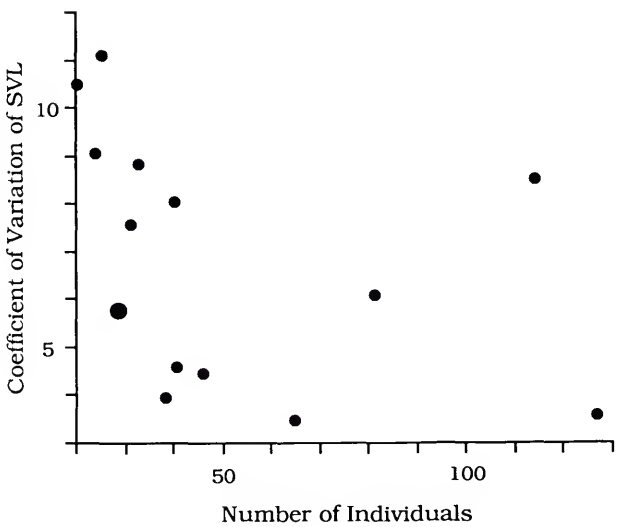

FIGURE 1.—Coefficients of variation for SVL plotted against number of individuals comprising sample sizes for the 9 OTUs analyzed for intraspecific variation. Large dot indicates superposition of two data points.

For the two largest samples, there is a striking difference between the coefficients of variation, with the Small Size, Dark Belly, Porto Velho, Brazil OTU consistently demonstrating almost twice the amount of variation as the Moderate Size, Light Posterior Belly, Limoncocha, Ecuador OTU in the parameters measured. This could relate to the fact that the Moderate Size, Light Posterior Belly, Limoncocha, Ecuador OTU is dominated by specimens that were collected over a two-month period, and the specimens were positioned in a relatively uniform manner as they were preserved. The Small Size, Dark Belly, Porto Velho, Brazil OTU is dominated by specimens also collected over a short period of time, but the specimens were not positioned as they were preserved, and the OTU also includes some well-positioned specimens collected years later.

When the highest and lowest coefficient of variation values are examined within OTUs, some trends are suggested. The SVL has high coefficient of variation values in some OTUs and low values in others. Otherwise, among OTUs, head length, shank length, and foot length have the lowest coefficients of variation; tympanum diameter and thigh length have the highest coefficients of variation. This suggests that head, shank, and foot lengths can be measured more accurately on adult frogs of the *podicipinus-wagneri* complex than can tympanum diameter and thigh length. Differences in position and condition of preservation could account for these results, except for tympanum diameter, which should not be affected by preservation to any significant degree and should be measurable to a relatively accurate level.

Some of the measurement data differences observed among OTUs are difficult to interpret and/or understand. For example, subadults and adults do not overlap in size in some OTUs or barely so, whereas there is considerable overlap in size in other OTUs. Even though the OTUs analyzed are large in numbers of individuals in some cases, the numbers of subadults are small and the differences may be due to sampling error. The degree of statistical differences of means between male and female measurement ratios was surprising. Measurements of preserved frogs are approximate due to the nature of the soft tissues and positioning of the specimen itself. In order to determine whether some of the differences observed could be due to measurement error, the Small Size, Dark Belly, Curuçá, Brazil OTU was remeasured, and the measurements were reanalyzed and compared with the first set of measurements on the same specimens. This OTU was chosen for remeasurement because it had a reasonable (but not overwhelming) number of both males and females and the specimens are well preserved and positioned so that measurements should be repeatable. The coefficients of variation between the two sets of measurements are similar (Table 13). There are differences between the two sets of measurements as reflected in the minimums, maximums, means, and standard deviations (Table 14). The only variable that differs significantly between the original and remeasured data is head width/SVL ratio and it differs for both females($t_{(2),38} = 2.761$) and males ($t_{(2),62} = 2.364$) (Table 15). The only significant difference between *t*-test values when comparing differences between the sexes for the original and remeasured data is for the variable foot/SVL ratio (Table 16; results of *t*-tests are reported above for original data; results for remeasured data are head length/SVL, $t_{(2),50} = -4.042$; tympanum/SVL, $t_{(2),50} = -2.286$; thigh/SVL, $t_{(2),28} = -3.285$; shank/SVL, $t_{(2),27} = -2.545$; foot/SVL, $t_{(2),28} = -2.221$). Certainly some of the differences observed in measurement variables and statistics among the OTUs are due to measurement error. It is impossible to know which results are due to measurement error without doing multiple replicates of measurements for each OTU. Because of this, the approach followed here is to interpret the measurement data conservatively, drawing distinctions and conclusions only from obvious differences (obvious in the sense that the differences are apparent in the data and do not need application of statistical tests to find differences).

TABLE 13.—Coefficients of variation for original and remeasured data for Small Size, Dark Belly, Curuçá, Brazil OTU.

Variable	Females		Males	
	Original	Remeasured	Original	Remeasured
SVL	10.05	9.62	8.92	9.22
Head length	8.10	8.50	8.43	8.43
Head width	9.57	9.68	9.35	8.68
Tympanum	8.85	8.91	9.54	10.19
Thigh	8.07	7.41	9.39	9.66
Shank	7.19	7.27	8.26	8.22
Foot	5.62	6.12	8.42	8.97

The variation within OTUs described does give a basis for understanding intrapopulation and intraspecific variation, but each OTU has to be interpreted individually. There are no generalities that can be applied to all OTUs from the study of the above nine OTUs.

Analysis of Sympatric Species Populations

There are a number of localities where more than one species of the *podicipinus-wagneri* complex occur. Not all of them are discussed in this section. The purpose of this section is to detail enough of these cases where sample sizes of adult specimens are adequate to understand the kinds of variation occurring within and among sympatric species populations. Because relatively extensive and complicated call data are available for all OTUs at Tambopata, Peru, that locality is discussed first. Other localities are discussed more or less according to geographic proximity.

PERU, MADRE DE DIOS, TAMBOPATA OTUS

Reginald Cocroft recorded three call types at Tambopata belonging to two species. He recorded and captured two males

TABLE 14.—Certain statistics for SVL and Foot/SVL ratios (as examples) for original and remeasured data for Small Size, Dark Belly, Curuçá, Brazil OTU.

Variable	Statistic/ Parameter	Females		Males	
		Original	Remeasured	Original	Remeasured
SVL	Minimum	30.0	31.3	26.4	26.4
SVL	Maximum	43.7	43.8	36.4	36.8
SVL	Range	13.7	12.5	10.4	10.4
SVL	Mean	38.0	38.5	32.1	32.5
SVL	Standard deviation	3.82	3.75	2.86	3.00
Foot/SVL	Minimum	0.451	0.434	0.467	0.434
Foot/SVL	Maximum	0.593	0.570	0.565	0.570
Foot/SVL	Mean	0.511	0.503	0.528	0.503
Foot/SVL	Standard deviation	0.040	0.021	0.022	0.036

TABLE 15.—Significance levels for *t*-tests for means of original and remeasured data for Small Size, Dark Belly, Curuçá, Brazil OTU. (N.S. = not significant.)

Variable	Female measurements	Male measurements
SVL	N.S.	N.S.
Head length/SVL	N.S.	N.S.
Head width/SVL	$P < 0.01$	$P = 0.02$
Tympanum/SVL	N.S.	N.S.
Thigh/SVL	N.S.	N.S.
Shank/SVL	N.S.	N.S.
Foot/SVL	N.S.	N.S.

TABLE 16.—Significance levels for *t*-tests for means comparing female and male data for original and remeasured data for Small Size, Dark Belly, Curuçá, Brazil OTU. (N.S. = not significant.)

Variable	Original data	Remeasured data
Head length/SVL	$P < 0.01$	$P < 0.01$
Head width/SVL	N.S.	N.S.
Tympanum/SVL	$P = 0.01$	$P = 0.03$
Thigh/SVL	$P < 0.01$	$P < 0.01$
Shank/SVL	$P = 0.03$	$P = 0.02$
Foot/SVL	N.S.	$P = 0.04$

of each of the call types.

Two individuals of the first species (USNM 307121, 307122) demonstrate a repertoire of call types (Figure 2). One call type is given much more frequently in the field (R. Cocroft, pers. comm.) and is interpreted to be the advertisement call (Figures 2a, 3). This presumed advertisement call is rather complex, consisting of two juxtaposed portions, the first of which has a dominant frequency range of around 1000–1300 Hz with a single harmonic (clearly visible in some analyses, not distinct in others) at about twice that frequency followed by a dominant frequency range of 2000–2500 Hz. Maximum energy varies from call to call between the first and second call components. The second portion of the call is frequency modulated. It appears as though the latter portion of the call represents a switch to the harmonic present in the first part of the call. The initial part of the call in particular is pulsatile. The second part of the call is frequency modulated in a complex fashion and is more obvious than the frequency modulation that occurs in the first portion of the call. The call duration ranges from 0.03 to 0.05 s, given at a rate of about 0.5 per s (Figure 3).

The second species usually gives one of two types of calls, only rarely does a given individual utter both types during any period of observation (R. Cocroft, pers. comm.).

The most frequently given call type recorded for USNM 307123, 307130 (this latter recording has considerable background noise and few calls; most of the call data are based on 307123) is a simple, essentially unpulsed call with a dominant range of about 750–1600 Hz with a single harmonic clearly present at twice the frequency of the dominant. The call is frequency modulated at a slower rate than in the following call type, but the rise time is rapid, nonetheless. The maximum frequency of several calls is 1250 Hz. Call duration is 0.01–0.02 s, given at a rate of 0.3–0.4 calls per s (Figure 4). The function of this call is unclear.

The second call type, presumably the advertisement call, recorded from USNM 307124, 307125, consists of a simple, unpulsed call with a dominant range between about 750–1300 Hz with maximum energy ranging between 1015–1289 Hz. The call is frequency modulated with a very fast rise time. No harmonic structure is evident. Call duration is 0.02 s, given at a rate between 2.3–3.3 per s (Figure 5).

Morphologically, the dorsolateral-fold conditions and toe tips are similar in all six specimens.

USNM 307121, 307122 are 29.3 and 30.8 mm SVL respectively. The posterior lip stripe is distinct in 307122, indistinct in 307121. The posterior faces of the thighs are mottled in both. The belly of 307121 is darker to the eye than 307122, but under the dissecting microscope, the belly is suffused with melanophores in both. The chin is light spotted in 307122.

USNM 307123–307125, 307130 range in size from 36.1 to 42.3 mm SVL. The posterior light lip stripe ranges from very distinct to almost indistinguishable. Light stripes on posterior thigh faces range from distinct to indistinct. The throats are gray or noticeably dark, the chest and anterior bellies are lightly to somewhat extensively mottled, the posterior bellies very lightly mottled or lacking melanophores. USNM 307130 has indistinct light spots on the chin.

USNM 307121, 307122 are distinguishable from the other four by having extensive mottling over the entire belly. These two individuals are smaller than the others, but the ranges in adult size described in the previous section suggest that the sizes of males would at least overlap among the Tambopata OTUs.

In addition to the six call voucher individuals, 98 other specimens of this complex are at hand from Tambopata. All but three specimens of the 98 can be readily associated with one or the other of the two species represented as call vouchers. These three individuals (USNM 247379, 247384, 247409) have intermediate features between the morphologies represented by USNM 307121, 307122 on the one hand and USNM 307123–307125, 307130 on the other. The intermediate morphologies suggest the possibility of limited hybridization at Tambopata.

There is no decisive habitat separation among the OTUs when all available data for Tambopata specimens are examined. USNM 247380, 247381, 247383, 247385, 247386, 247390, 247392, 247395–247399 (morphologically similar to call vouchered specimens USNM 307123–307125, 307130), and USNM 247387, 247388 (morphologically similar to call vouchered specimens USNM 307121, 307122) were all collected from under leaves and logs, or on the ground or leaf

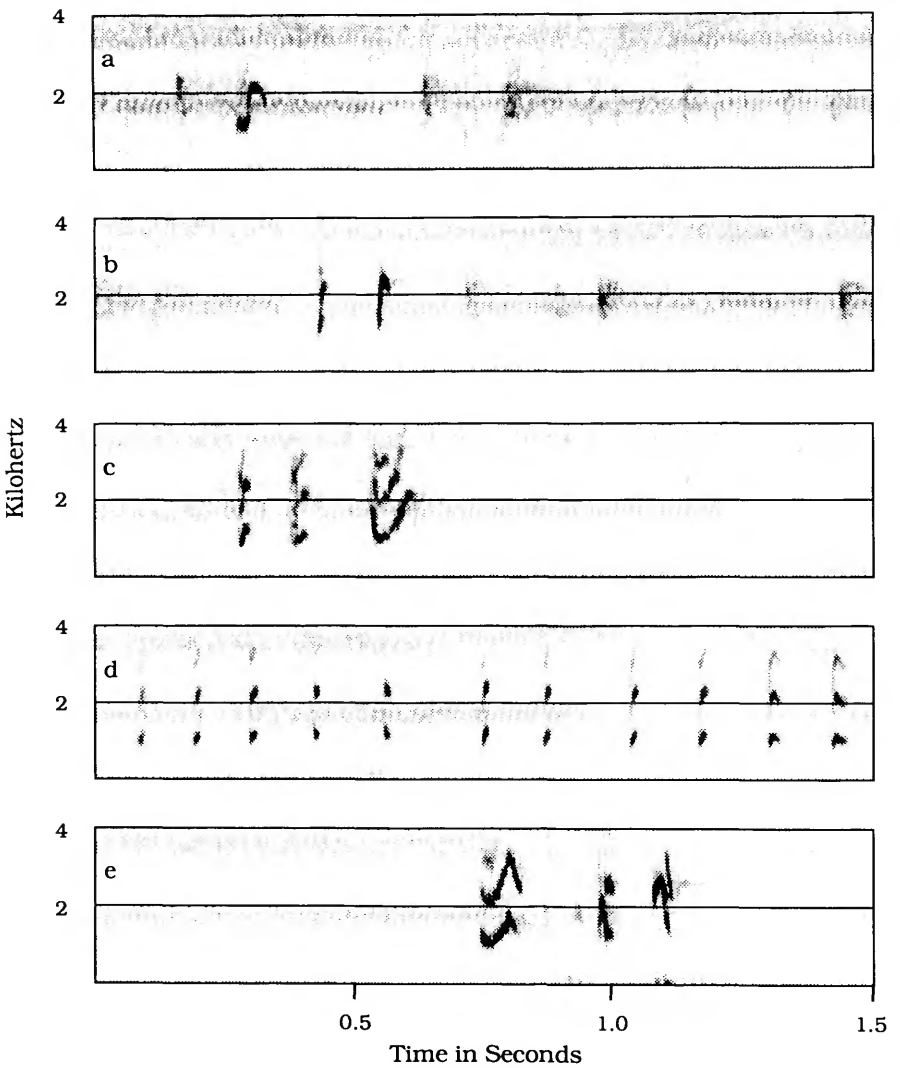

FIGURE 2.—Audiospectrograms of calls of the Small Size, Dark Belly, Tambopata, Peru OTU, USNM Tape 207, cut 19. Recorded from specimen USNM 307122, 12 Jan 1989, 2300 h, 24.9°C air, by Reginald B. Cocroft.

litter at kilometer 0.6 along the Main Trail at Tambopata. The majority of specimens represented by call types USNM 307121, 307122 were collected from or near a swamp forest along the Main Trail, however, so there may be partial habitat separation.

These two species are referred to for analytic purposes as Small Size, Dark Belly, Tambopata, Peru OTU and Moderate Size, Light Posterior Belly, Tambopata, Peru OTU.

PERU, MADRE DE DIOS, CUZCO AMAZONICO OTUS

The same kind of morphological variation discussed for the Tambopata OTUs occurs at Cuzco Amazonico. MVZ 199502, a 31.2 mm SVL male, has a distinctive belly pattern of a dark, anastomosing lattice work over the entire belly, but otherwise it resembles the Small Size, Dark Belly, Tambopata, Peru OTU.

PERU, LORETO, ESTIRÓN, RÍO APIYACU OTUS

This locality (along with Igarapé Belém, Brazil, below) has the most OTUs of those examined. With the exception of one adult female and a couple of small juveniles, all other specimens sort into four distinct OTUs.

The Small/Moderate Size, Toe Disked, Estirón OTU is the most distinctive of the four. Males range in size from 33.1 to 38.0 mm SVL; females range from 34.4 to 44.6 mm SVL. None

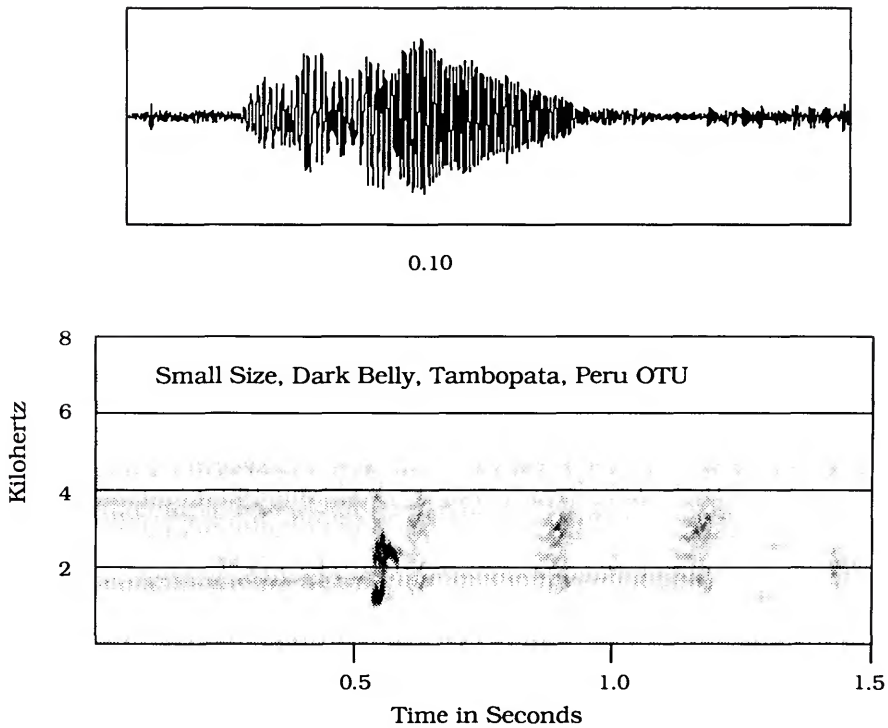

FIGURE 3.—Presumed advertisement call of Small Size, Dark Belly, Tambopata, Peru OTU, USNM Tape 207, cut 19. Recording data same as for Figure 2.

of the specimens have any indications of dorsolateral folds. The bellies are immaculate and the ventral and posterior thigh patterns abut and contrast rather than blend into one another. The tips of the toes are noticeably expanded into small disks. In these features (other than size) members of this OTU differ discretely from the other OTU members from this locality.

The Moderate Size, Light Posterior Belly, Estirón OTU closely resembles the Moderate Size, Light Posterior Belly, Tambopata, Peru, the Moderate Size, Light Posterior Belly, Cuzco Amazonico, Peru, and the Moderate Size, Light Posterior Belly, Limoncocha, Ecuador OTUs, including most specimens having either distinct or indistinct light stripes on the posterior thigh face.

The Small Size, Anastomotic Belly, Estirón OTU is represented by one small juvenile and an adult 33.8 mm SVL male and an adult 41.9 mm SVL female. The posterior thighs of the adults are mottled, there are weakly developed short dorsolateral folds, the toe tips are barely swollen, and the entire belly has an anastomosing dark pattern, with more of the belly lacking rather than having pigment.

The Large Size, Mottled Thigh, Estirón OTU is represented by a few small juveniles and an adult 74.3 mm SVL female. The female lacks a light posterior eye stripe, has a mottled posterior thigh face, has weakly developed, but long dorsolateral folds, swollen toe tips, and a light posterior belly with just a few scattered dark blotches.

The specimens that do not immediately sort into one of these four OTUs are all intermediate between the Small Size, Anastomotic Belly and Large Size, Mottled Thigh, Estirón OTUs. Placement of the intermediate small juveniles is arbitrary. The specimen that is of most interest is an adult 53.0 mm SVL female (MZUSP 24820). The size is intermediate between the two above mentioned OTUs. The belly pattern is nearly that of the Small Size, Anastomotic Belly OTU. The specimen is not well-enough preserved for the dorsolateral-fold condition to be unambiguously interpreted, but the folds appear to resemble those of the Large Size, Mottled Thigh OTU. In the two adult Small Size, Anastomotic Belly OTUs, the metatarsal fold stops short of the outer metatarsal tubercle and the inner toe fold and tarsal fold noticeably overlap either end of the inner metatarsal tubercle. In the adult Large Size, Mottled Thigh OTU specimen, the outer metatarsal fold extends as far as or just past the outer metatarsal tubercle and the inner toe fold and tarsal fold barely overlap either end of the inner metatarsal tubercle. These features in MZUSP 24820 are the same as found in the Large Size, Mottled Thigh OTU. The posterior face of the thigh in MZUSP 24820 has what appears to be an indistinctly developed light stripe, differing in degree

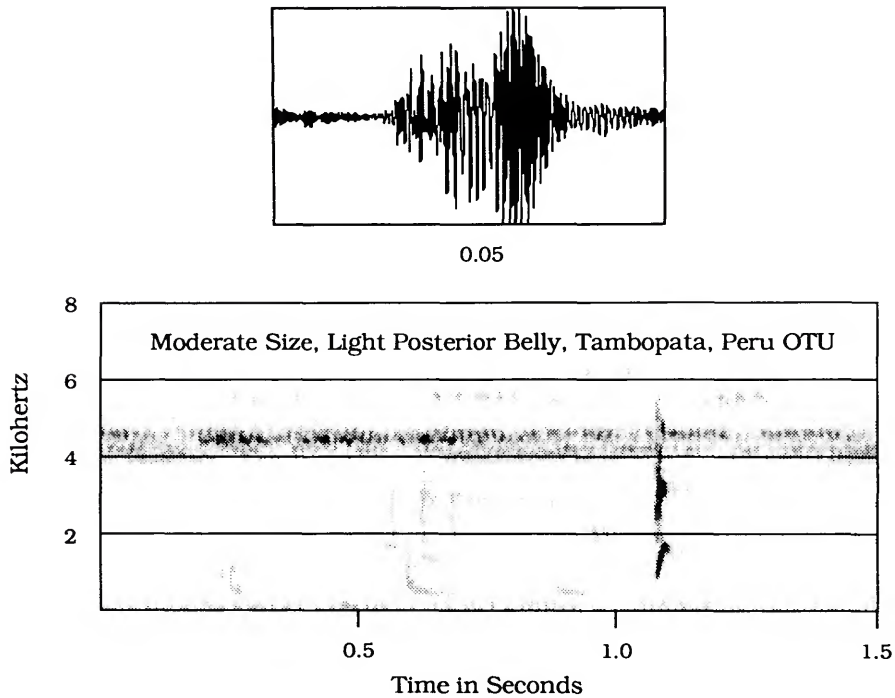

FIGURE 4.—Wave form and audiospectrogram of one call type of Moderate Size, Light Posterior Belly, Tambopata, Peru OTU, USNM Tape 205, cut 23. Recorded from specimen USNM 307123, 5 Jan 1989, 2330 h, 25.1°C air, by Reginald B. Cocroft.

at least from the entirely mottled thighs of the Small Size, Anastomotic Belly and Large Size, Mottled Thigh OTUs. MZUSP 24820 could either represent (1) a fifth OTU, (2) a large individual of the Small Size, Anastomotic Belly OTU, (3) a small individual of the Large Size, Mottled Belly OTU, or (4) a hybrid between the Small Size, Anastomotic Belly and Large Size, Mottled Belly OTUs. Based on overall impression rather than absolutely convincing evidence, I favor the third hypothesis and adopt it as the working hypothesis for purposes of this paper.

PERU, HUANUCO, DIVISORIA OTUS

Although there are few specimens from this locality, two OTUs are represented. The Moderate Size, Light Posterior Belly, OTU is represented by a single 44.3 mm SVL female with mature eggs. The Moderate/Large Size, Mottled Thigh, OTU is represented by two smaller and three larger juveniles, the latter near adult size. The two large subadult males, which do not have vocal slits, are 38.7 and 40.9 mm SVL; the large subadult female, which has a straight, slender oviduct, is 45.8 mm SVL. In addition to the differences in size, the few individuals available for these OTUs differ in degree of belly mottling with the Moderate Size, Light Posterior Belly OTU having moderate mottling on the chest and anterior belly and very light mottling posteriorly. The Moderate/Large Size, Mottled Thigh OTU has extensive dark mottling on the chest and at least the anterior half of the belly, the dark mottle extending at least three-quarters posteriorly on the belly in some individuals. The Moderate Size, Light Posterior Belly OTU has almost distinct light stripes on the posterior face of the thighs, whereas the Moderate/Large Size, Mottled Thigh OTU has no indication of light thigh stripes on any of the individuals.

BOLIVIA, BENI, TUMI CHUCUA OTUS

In addition to Tumi Chucua, there are 11 other localities from Bolivia where two OTUs are known to occur together. In all instances where more than two specimens are involved, the situation is very similar to that discussed for Tumi Chucua, which is presented as an example. The Tumi Chucua specimens are used because, although there are relatively few specimens, adults are available for both OTUs, the specimens are well preserved, and the variation present is representative of that observed from the other 11 localities.

Specimens can be separated rather easily into two groups, but some individuals have rather intermediate characteristics. USNM 280218, a 36.0 mm SVL male, has one extreme type of

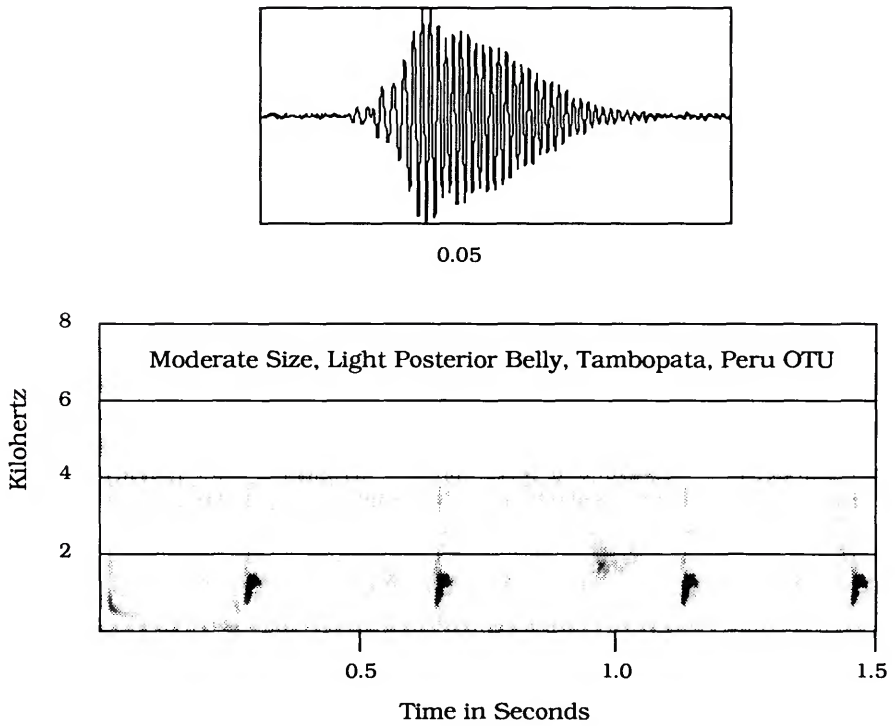

FIGURE 5.—Wave form (of second call) and audiospectrogram of second call type of Moderate Size, Light Posterior Belly, Tambopata, Peru OTU, USNM Tape 207, cut 16. Recorded from specimen USNM 307125 on 11 Jan 1989, 2300 h, 22°C air, by Reginald B. Cocroft.

morphology with short dorsolateral folds, a somewhat distinct light posterior lip stripe, a dark venter with light spots (spots most pronounced on chin and belly), no indication of a light stripe on the posterior face of the thigh, a tarsal fold that is continuous with the inner toe flap, and narrow toe tips. A second extreme type of morphology is found in USNM 280222, a 34.9 mm SVL juvenile female, which has short dorsolateral folds, just a suggestion of a light posterior lip stripe, a chin with ill-defined light spots, a rather uniformly and heavily peppered throat, and a heavily mottled chest (because the melanophores are contracted, the chest is light in appearance to the eye, but under the microscope, the large number of melanophores is evident). In addition, the belly is mostly light with a scattered mottled pattern, the posterior faces of the thighs have a very distinct light stripe, the tarsal fold barely overlaps the inner metatarsal tubercle and is not continuous with the inner toe flap, which also just overlaps with the inner metatarsal tubercle, and the toe tips are very slightly but noticeably expanded. USNM 280217 agrees with 280218 except there are indications of light stripes on the posterior thighs, and the tarsal-fold toe-flap condition is intermediate between the conditions described for 280218 and 280222. USNM 280216 also is similar in most features with 280218 except that the posterior belly has an anastomotic mottled pattern, the tarsal-fold toe-flap condition is the same as in 280216, and the toe tips are just expanded. USNM 280221 has most features in common with 280222 except the chin and throat are dark brown (to the eye), which contrasts with the light belly (with scattered melanophores), and lacks any indication of light spots; the posterior light thigh stripe, if present, is indistinct at best. The variation observed in the Tumi Chucua sample and that observed in samples from the other 11 localities suggests that two OTUs are involved at each site, but with some individuals with intermediate morphologies (limited hybridization?). For purposes of this paper, two OTUs are recognized from Tumi Chucua: the Small Size, Dark Belly, Tumi Chucua, Bolivia OTU and the Moderate Size, Light Posterior Thigh Stripe, Tumi Chucua, Bolivia OTU. Sample sizes are inadequate from nine of the other Bolivian localities from where two OTUs are recognized to determine adult size categories (Carasco, Puerto Almacen, Reyes, Río Blanco and Río Guaporé, Río Grande, Boca del Río Ibarre, Río Mamoré at 13°35′S, Santa Rosa, Trinidad, all in the state of Beni). There are slight size differences at the other two sites. The OTUs from these latter two sites are: Small/Moderate Size, Dark Belly, Alejandria, Bolivia OTU; Moderate Size, Light Posterior Thigh

Stripe, Alejandria, Bolivia OTU; Small Size, Dark Belly, Buenavista, Bolivia OTU; and Small/Moderate Size, Light Posterior Thigh Stripe, Buenavista, Bolivia OTU.

Ecuador, Napo, Santa Cecilia OTUs

The Large Size, Boldly Mottled Belly, Santa Cecilia OTU has been discussed previously and is represented by most of the specimens from Santa Cecilia. The second OTU at Santa Cecilia is the Moderate Size, Light Posterior Belly, Santa Cecilia OTU. The two OTUs are rather similar overall. There are no apparent differences between the OTUs in terms of lip stripes, thigh stripes, or tarsal and metatarsal fold conditions. The OTUs differ in degree with respect to size, dorsolateral folds, and belly patterns. Adult females and males of the Large Size, Boldly Mottled Belly OTU range in size from 60.2 to 74.0 mm SVL and 42.0 to 59.6 mm SVL respectively. The few adult females and males of the Moderate Size, Light Posterior Belly OTU range in size from 47.1 to 51.6 mm SVL and 34.6 to 44.3 mm SVL respectively. The dorsolateral folds in the Large Size, Boldly Mottled Belly OTU are usually long, extending almost the entire length of the body, and are dark outlined laterally, at least in part. None of the Moderate Size, Light Posterior Belly OTU individuals have this particular condition of the dorsolateral folds. Not all individuals of the Large Size, Boldly Mottled Belly OTU have long dorsolateral folds or have the folds dark outlined laterally. Such specimens are indistinguishable from the Moderate Size, Light Posterior Belly OTU specimens in terms of dorsolateral-fold condition. The majority of the Large Size, Boldly Mottled Belly OTU specimens do indeed have distinctive dark and light boldly mottled bellies. None of the Moderate Size, Light Posterior Belly OTU specimens have boldly mottled bellies; however, there are several specimens of both OTUs with bellies that have patterns indistinguishable from each other.

None of the characters that separate the OTUs do so in an absolute fashion; there is some overlap of some individuals of each OTU with individuals of the other OTU with respect to any one of the three characters. However, with the samples at hand, the combination of the three characters allows separation of all adults into one or the other of the two OTUs as well as over 90% of the juveniles, but there are a few juveniles that are not readily sortable. The incomplete separation of the characters between the OTUs and the presence of a very few intermediate juveniles suggests that hybridization may have occurred between the two taxa. However, the two OTUs sort morphologically easier than the specimens at Tambopata, Peru (for example), suggesting that if hybridization has occurred or is occurring at Santa Cecilia, it is limited.

Brazil, Acre, Iquiri OTUs

Two OTUs are represented by specimens from Iquiri: a Small Size, Dark Belly OTU and a Moderate Size, Light Belly OTU.

The OTUs are most distinctive in terms of size and belly pattern. There may be slight differences in posterior lip stripe and dorsolateral-fold conditions, but it is difficult to tell due to small sample sizes and because of preservation differences. There is overlap in states of the posterior thigh light stripe condition, with the Small Size, Dark Belly OTU having mostly mottled thighs, but a few individuals with indistinct stripes on one thigh. The same two states occur in the Moderate Size, Light Belly OTU, but in addition, two specimens have a distinct stripe on one thigh. The belly pattern of the Small Size, Dark Belly OTU, although always relatively dark, ranges from heavily mottled to an anastomotic pattern. None of the individuals at hand have the pattern of distinct white spots on a dark belly. The belly of the second OTU ranges from essentially lacking melanophores except just in the area around the chest, to lightly scattered with melanophores. Males of the Small Size, Dark Belly OTU range from 29.4 to 32.7 mm SVL; females range from 36.4 to 37.6 mm SVL. The single available male of the Moderate Size, Light Belly OTU is 40.3 mm SVL; the three females range in size from 46.1 to 51.8 mm SVL.

All available individuals from this locality are readily identifiable as belonging to either one or the other of the two OTUs.

Brazil, Rondônia, Santa Cruz da Serra OTUs

Variation of frogs from this locality is not easy to interpret. There appear to be two types of adults from this locality, which for purposes of discussion will be treated as OTUs. There are three adult males and one adult female of the Small/Moderate Size, Anastomotic Belly OTU and eight subadult and adult males and three adult females of the Moderate Size, Lightly Mottled Belly OTU. There is a slight difference in size in the specimens at hand between the OTUs, but the differences are not great and there is overlap (Figure 6). There is a difference in male tympanum size, that of the Small/Moderate Size, Anastomotic Belly OTU being larger (Figure 6). The belly patterns of the Small/Moderate Size, Anastomotic Belly OTU are rather uniform in being rather heavily pigmented with a dark anastomotic pattern on a light background. Some of the Moderate Size, Lightly Mottled Belly OTU individuals have very light bellies with just a touch of mottling on the chest and anterior belly region (e.g., MZUSP 61577); others have more extensive mottling, but the mottling is stipple-like and the bellies are lighter than they are dark (e.g., USNM 303995). Other individuals (e.g., MZUSP 61570) appear to have an exactly intermediate belly pattern to the kinds described above for the two OTUs. All of the Small/Moderate Size, Anastomotic Belly OTU specimens have mottled posterior thigh surface patterns. There is a complete range from distinct light posterior thigh stripes to mottled thighs among the Moderate Size, Lightly Mottled Belly OTU specimens. All of the Small/Moderate Size, Anastomotic Belly OTU specimens have short or nondistinct dorsolateral folds. Some of the Moderate Size,

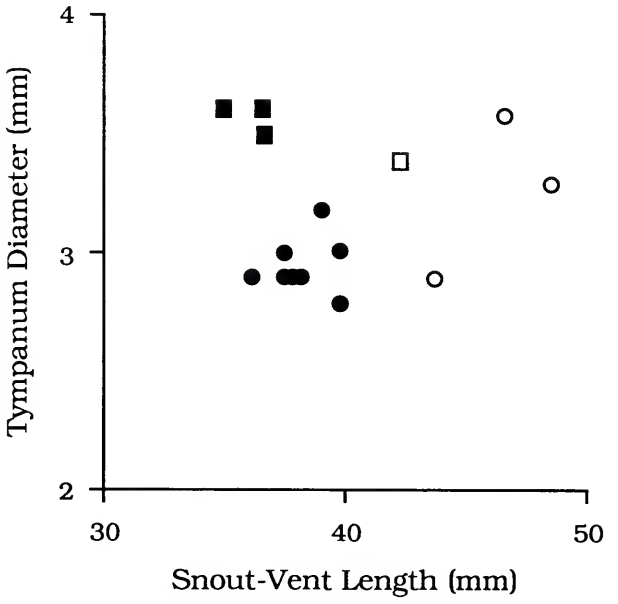

FIGURE 6.—Tympanum diameter plotted against snout-vent length for adults from Santa Cruz da Serra, Rondônia, Brazil. (Dots = males of Moderate Size, Lightly Mottled Belly OTU, circles = females; filled squares = males of Small/Moderate Size, Anastomotic Belly OTU, open squares = females.)

Lightly Mottled Belly OTU individuals have moderate-length dorsolateral folds, other individuals have the same condition as the Small/Moderate Size, Anastomotic Belly OTU individuals. There are no apparent differences between the OTUs in terms of toe-tip development (the just swollen condition is most common in both), development of the posterior lip stripe (distinct to nondistinct in both), or development of small light chin spots (somewhat distinct to indistinct in both).

Not all individuals from this locality are readily placed in one OTU or the other, which suggests that limited hybridization between the two OTUs may be occurring at Santa Cruz da Serra. For present purposes, two OTUs are recognized and as the intermediate specimens at hand appear to have more affinity with the Moderate Size, Lightly Mottled Belly OTU, they are included in it.

Brazil, Amazonas, Boca do Acre OTUs

Only a few specimens are available from Boca do Acre, but all can be readily sorted into two OTUs. A single 50.1 mm SVL female represents the Moderate Size, Lightly Speckled Belly OTU, and four juveniles and one 39.5 mm SVL female represent the Small Size, Moderately Speckled Belly OTU. In addition to the size and belly pattern differences, the Moderate Size, Lightly Speckled Belly OTU specimen has indistinct light stripes on the posterior faces of the thighs. None of the Small Size, Moderately Speckled Belly OTU individuals have any indications of light thigh stripes. Otherwise, the specimens are similar.

Brazil, Amazonas, Borba OTUs

There are two forms of adults from Borba that are discernable when examined side by side (Figure 7), but the differences are subtle and a matter of degree.

The Small Size, Dark Belly OTU has a belly pattern that ranges from small, distinct light spots on a dark background from the chin to the posterior extent of the belly; to a white-spotted chin and extensively mottled throat, chest, and belly; to a white-spotted chin, extensively mottled throat and chest, and moderately mottled belly. The Small Size, Speckled Belly OTU has indications only of light chin spots, the throat is extensively mottled, and the belly is speckled. Most of the toe tips of the Small Size, Dark Belly OTU individuals are narrow, although a couple of individuals have just-swollen tips as in the Small Size, Speckled Belly OTU individuals. The heads of the females are broader in the Small Size, Speckled Belly OTU than in the Small Size, Dark Belly OTU (Figure 7). The tarsal fold appears to be better developed into a flap, particularly near the inner metatarsal tubercle in the Small Size, Speckled Belly OTU. There do not appear to be any differences in posterior eye light stripe conditions, posterior thigh patterns, or dorsolateral-fold conditions. The two adult Small Size, Speckled Belly OTU individuals were collected from the forest on the ground 1/2–1 m from a stream at night. All of the Small Size, Dark Belly OTU individuals and the two juvenile Small Size, Speckled Belly OTU individuals were collected outside the forest near temporary ponds at night. The identification of the small juvenile MZUSP 51248 as the Small Size, Speckled Belly OTU is the only problematical identification of all specimens at hand from Borba.

Brazil, Amazonas, Igarapé Belém, Rio Solimões OTUs

There appear to be four OTUs represented in the available specimens from Igarapé Belém, one OTU being represented by a single individual and another by two specimens.

The Moderate Size, Toe Disked OTU is the most distinctive. The toe tips are expanded into small disks, the bellies lack melanophores, as do the ventral thigh surfaces, and the dark posterior thigh pattern abruptly abuts the light ventral thighs. The posterior and ventral thigh patterns blend into each other in the other OTUs.

There are two adult female Small Size, Dark Belly OTU specimens. The females are 40.0 and 40.6 mm SVL, and the chin, throat, and belly are extensively mottled in both. The toe tips are narrow. The posterior thighs are mottled in one individual and the other has indistinct light stripes.

The only problematical OTU from this locality is a single large male (AMNH 97061) that is either a distinct OTU or the

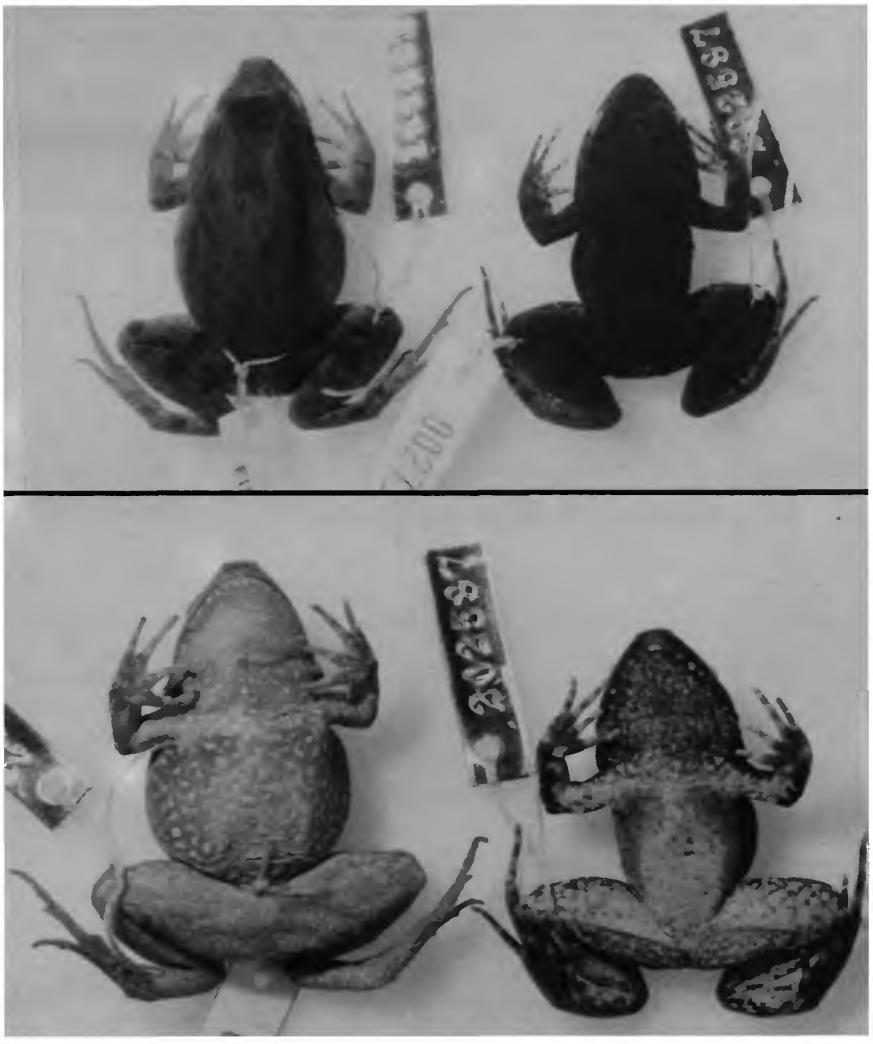

FIGURE 7.—Dorsal and ventral views of Small Size, Dark Belly, Borba, Brazil OTU (USNM 202592, left) and Small Size, Speckled Belly, Borba, Brazil OTU (USNM 202597, right).

same as the Moderate Size, Light Posterior Belly OTU. The Moderate Size, Light Posterior Belly OTU males range from 31.2 to 42.2 mm SVL and the females range from 45.6 to 53.8 mm SVL. In most individuals, the posterior belly lacks melanophores, but in some the posterior belly has scattered melanophores. The posterior thigh patterns range from having distinct light stripes to mottled. The toe tips range from just swollen to noticeably expanded. The problematic specimen is similar to the Moderate Size, Light Posterior Belly OTU specimens in terms of the toe tips (slightly swollen) and posterior thigh pattern (indistinct light stripes), but it differs slightly in degree of belly pattern in that the belly is flecked and intermediate between the Moderate Size, Light Posterior Belly OTU patterns and Small Size, Dark Belly OTU pattern. The most distinctive feature of the specimen is its size, 57.8 mm SVL. The specimen is 26.6 mm larger than the smallest Moderate Size, Light Posterior Belly OTU male, exceeding by about 10 mm the size range found in males where large sample sizes are available (Table 11). Thus, this individual does not fall within the size variation expected for the Moderate Size, Dark Belly OTU. The specimen is not extremely well preserved so that the condition of the thumb spines can not be interpreted with certainty. The spines are somewhat small and white and the tip of one is brown, suggesting that it is a small male rather than the black sheath having been shed from the spines as can happen under certain kinds of preservation. The evidence

suggests that AMNH 97061 should be considered a separate, Large Size, Flecked Belly, OTU.

Brazil, Amazonas, Lago Amanã OTUs

The few adults from this locality are readily sortable into two OTUs. The Moderate Size, Light Belly OTU is represented by two adults, one male and one female. The Small Size, Anastomotic Belly OTU is represented by nine adults, two males and seven females. There are no other discernible differences between the OTUs other than size and belly pattern.

Some of the juveniles from this locality do not agree with the characters found in the adults. The problem is best exemplified by two moderate-size juveniles (MZUSP 59503, 30.0 mm; MZUSP 59511, 30.4 mm). These two individuals have lightly speckled bellies, exactly intermediate between the belly patterns found in the OTUs as represented by the adults from this locality. The posterior thighs of both these juveniles have distinct light stripes, a condition not found in any of the adults from this locality. Only a single adult of each OTU has any indication of light thigh stripes, all other adult thighs are mottled, lacking stripes.

The juveniles as represented by MZUSP 59503, 59511 are not easy to understand. Two possibilities are that they represent a third OTU or represent hybrids between the two OTUs represented by adults. Based on examination of specimens of this complex, I do not think they represent a third OTU, although the distinctive character of the thigh stripes is consistent with this alternative. For the present, I favor the hybrid hypothesis.

Brazil, Pará, Cachoeira do Espelho, Rio Xingu OTUs

Two OTUs are present in the materials at hand from this locality: a Small Size, Anastomotic Belly OTU and a Moderate Size, Light Posterior Thigh Stripe OTU. The Small Size, Anastomotic Belly OTU males range from 30.5 to 33.4 mm SVL; the females range from 32.2 to 37.0 mm SVL. The Moderate Size, Light Posterior Thigh Stripe OTU males range from 35.7 to 42.7 mm SVL; the females range from 38.1 to 48.2 mm SVL. The chin and throat of the Small Size, Anastomotic Belly OTU are dark (heavily suffused with melanophores) and may or may not (most) have scattered light dots. The combined chest and belly pattern ranges from lightly speckled to heavily speckled to anastomotic (majority of specimens). The chin and throat patterns of the Moderate Size, Light Posterior Thigh Stripe OTU are similar to the other OTU, except most are lighter. The chest and belly pattern ranges from just a few scattered melanophores anteriorly to moderately mottled and anastomotic; however, the bellies are noticeably lighter than in the other OTU. Only one posterior thigh of the adults of the Small Size, Anastomotic Belly OTU has an indication of a light stripe; all others are mottled. Only two thighs (of 48 in the total of 24 adults and subadults) of the Moderate Size, Light Posterior Thigh Stripe OTU are mottled; most have distinct light stripes, and there are about as many thighs with very distinct light stripes as indistinct light stripes. There is considerable overlap in posterior lip light stripe conditions between the OTUs, as well as dorsolateral-fold condition and toe-tip expansion.

Most of the juveniles are readily allied with one or the other of the two OTUs; however, several juveniles that in most respects ally with the Moderate Size, Light Posterior Thigh Stripe OTU have heavily mottled bellies (e.g., MZUSP 63359) and approach or are indistinguishable in pattern from the anastomotic pattern (e.g., MZUSP 63367). Yet, in all these juveniles with darker or anastomotic bellies, the posterior thighs have distinct light stripes, and, based on direct comparison, they clearly are allied with the Moderate Size, Light Posterior Thigh Stripe OTU and are so included.

Habitat data are available for most of the specimens examined from this locality. There is no habitat separation between the two OTUs. Most individuals of both OTUs were collected from the forest and several individuals were collected in microsympatry.

Surinam, Marowijne, Loëkreek OTUs

Two adult males are available from this locality. The toe tips are similarly swollen in both individuals. The Moderate Size, Light Belly individual is 41.2 mm SVL, does not have a light posterior lip stripe, but it does have fairly distinct light stripes on the posterior thigh faces, a very short pair of dorsolateral folds just behind the eyes, an intensively finely mottled chin, throat, and anterior chest, with the rest of the chest and belly light, lacking melanophores, and two relatively large black thumb spines on each thumb. The Small Size, Anastomotic Belly individual is 34.9 mm SVL, has a reasonably distinct light posterior lip stripe, dark orange stripes on the posterior faces of the thighs, short dorsolateral folds that extend from behind the eyes to about midway to the sacrum, a darkly suffused chin and throat, a dark anastomotic pattern of melanophore distribution on the chest and belly, and two small black thumb spines on each thumb.

Surinam, Nickerie, Amotopo OTUs

Three females of one OTU and one juvenile of a second OTU from near Amotopo seem to represent a different species pairing than at Loëkreek. The female Small Size, Anastomotic Belly OTU specimens seem to represent the same OTU as the Small Size, Anastomotic Belly, Loëkreek, Surinam OTU. These specimens have indistinct to distinct light posterior lip stripes, mottled posterior thigh faces, dark anastomotically patterned throats, chests, and bellies, and have slightly swollen toe tips. The 27.2 mm SVL juvenile does not appear to be the same as the Moderate Size, Light Belly, Loëkreek, Surinam OTU. This individual (Juvenile, Small Toe Disked OTU) does

not have a light posterior lip stripe, but it does have light stripes on the posterior thigh faces, a moderately heavily mottled chin and throat, the chest and anterior belly moderately mottled in an anastomotic pattern, with the posterior half of the belly lacking melanophores, and toe tips distinctly expanded into small disks.

Surinam, Marowijne, Paloemeu OTUs

Three adult males are available from Paloemeu, apparently representing two OTUs. All three have relatively distinct light posterior thigh stripes and slightly swollen to swollen toe tips. The two males representing the Moderate Size, Light Belly OTU are 37.6 and 41.0 mm SVL, the light posterior lip stripe is either indistinct or absent, the chin is either spotted or mottled, and the belly is lightly mottled. The single male representing the Small Size, Anastomotic Belly OTU is 33.7 mm SVL, has a distinct light posterior lip stripe, the chin is light spotted, and the belly is heavily mottled in an anastomotic pattern. Although two OTUs are clearly distinguishable, the Small Size, Anastomotic Belly OTU appears to share some features that are present separately in two other OTUs discussed previously, for example, the Small Size, Anastomotic Belly, Loëkreek, Surinam OTU and the Small Size, Light Posterior Lip Stripe, Langaman Kondre, Surinam OTU.

Guyana, Kartabo OTUs

The Small Size, Light Posterior Lip Stripe OTU already has been characterized in the previous section, "Individual OTUs," dealing with large samples. There is in addition, one male that is larger (38.6 mm SVL) than any of the Small Size, Light Posterior Lip Stripe OTU males (31.5 to 37.3 mm SVL). This larger male has an indistinct light posterior lip stripe, a distinct light stripe on the posterior thighs, short dorsolateral folds, an almost light spotted chin, a dark throat, heavily mottled anterior belly, very few melanophores on the posterior belly, and expanded toe tips. In all of these characteristics, except size, this individual does not differ from the males of the other OTU. The larger male has two small white spines on each thumb, suggesting that the specimen is a young male, but the vocal slits are broken through. The head shape looks broader and rounder in the larger male when specimens are compared side by side, but the head measurements do not differ. Even though the larger male is very similar to the Small Size, Light Posterior Lip Stripe OTU, I think it represents a second OTU, the Moderate Size, Light Posterior Belly OTU.

Colombia, Amazonas, Leticia OTUs

Two OTUs are represented at Leticia. The Moderate Size, Light Posterior Belly OTU males range from 39.8 to 47.9 mm SVL; the females range from 48.0 to 52.1 mm SVL. The three Small Size, Speckled Belly OTU males range from 33.4 to 34.9 mm SVL, and a subadult female measures 36.6 mm SVL. There is overlap in the posterior lip stripe condition between the two OTUs in that some of the Moderate Size, Light Posterior Belly OTU individuals lack light stripes or have indistinct light stripes as do the Small Size, Speckled Belly OTU individuals. However, some of the Moderate Size, Light Posterior Belly OTU individuals have distinct light stripes, whereas none of the other OTUs have distinct light posterior eye stripes. All the Small Size, Speckled Belly OTU individuals have mottled posterior thigh surface patterns, whereas almost all Moderate Size, Light Posterior Belly OTU specimens have very distinct to at least indistinct light posterior thigh stripes. The chin and throat regions of the Moderate Size, Light Posterior Belly individuals are darkly mottled; some individuals have indications of light chin spots. There is a gradient from darker mottle to much lighter (or no) mottle from the chest to the posterior belly. The chest and belly mottling ranges from speckled to almost anastomotic. The throats of the Small Size, Speckled Belly OTU males are darker than the rest of the venter, but not so for the juveniles or subadult female. The chin and throat may or may not be light spotted. The chest and belly are rather uniformly suffused with melanophores, arranged in a speckled pattern in some. Some Moderate Size, Light Posterior Belly OTU individuals have longitudinal patches of tan ventrolateral glands rather restricted to just either side of the belly. Some Small Size, Speckled Belly individuals have much more extensive red-orange glands that extend much more ventrally toward the middle of the belly and in patches on the limbs.

Only two individuals from Leticia can not be readily sorted into one or the other of the two OTUs. These two juveniles (ICNMNH 18097, 18098) have somewhat intermediate belly patterns, but in most respects they resemble the Moderate Size, Light Posterior Belly OTU and are included within it for purposes of this study.

Colombia, Amazonas, Quebrada Tucuchira OTUs

Quebrada Tucuchira lies about 20 miles northwest of Leticia, but one of the two OTUs from Quebrada Tucuchira differs in at least some details from one of the OTUs from Leticia. Even though the differences may only reflect small sample sizes, it is worth noting the variation encountered.

There are only three adults representing the Moderate Size, Light Posterior Belly OTU; the two males are 40.7 and 41.2 mm SVL and the female is 48.1 mm SVL. Ten adult males of the Small Size, Anastomotic Belly OTU range in size from 32.0 to 35.4 mm SVL; six adult females range from 37.9 to 42.9 mm SVL. There is complete overlap and no notable differences between the OTUs in terms of light posterior lip stripe, dorsolateral folds, or toe-tip expansion. The posterior thighs of the Moderate Size, Light Posterior Belly OTU adults have either distinct or very distinct light stripes. Most of the Small

Size, Anastomotic Belly OTU individuals have mottled thighs with no indication of a light stripe; in a few individuals, indistinct stripes are present on one thigh only. The throats and chins of the Moderate Size, Light Posterior Belly OTU are mottled and in only one adult individual is there any indication of light chin spots. The chest and anterior belly are lightly mottled grading to an almost immaculate posterior belly. Many individuals of the Small Size, Anastomotic Belly OTU have darkly mottled chins and throats with distinct light spots. The chest and belly are rather uniformly patterned, with many individuals having a distinctive anastomotic pattern; the pattern ranges from anastomotic to speckled to indistinctly but uniformly mottled.

There are quite a few metamorphs and juveniles from this locality. A series of metamorphs have quite dark bellies, but seem to associate with the Small Size, Anastomotic Belly OTU. All other juveniles are readily identifiable with one or the other of the two OTUs with only two exceptions (IND-AN 3415, MVZ 172093), which have somewhat intermediate belly patterns and uninformative posterior thigh patterns but seem more allied with the Moderate Size, Light Posterior Belly OTU and are included within it for purposes of this study.

Variation within Taxa/Regions

As documented in the previous section, variation among OTUs from single localities is not straightforward in several instances. Given the complexity of variation documented thus far, variation among all samples also would be expected to be complicated. Due to the number of specimens and localities involved, an attempt to discuss variation of all the material at one time is overwhelming. Based on analyses done thus far, together with examination of the specimens, the following four-step analytic approach was adopted.

1. Any distinct taxa that did not pose any problem of separation from the other taxa and demonstrated relatively little within-taxa variation were identified. Variation in these taxa is discussed and not dealt with in the remaining steps.

2. The remaining taxa were analyzed within core regions to evaluate how many taxa were present and to note any variation within those taxa.

3. Taxa were compared among regions to determine which taxa represented the same species.

4. Specimens were examined from between core areas of analysis to determine whether they represented the same taxa represented in steps 2–3 or represented distinct species.

Distinct Taxa

Two OTUs discussed previously represent a species that is readily distinguished from all other members of the *podicipinus-wagneri* complex. The two previously discussed OTUs that belong to the species involved are the Small/Moderate Size, Toe Disked, Estirón, Peru OTU and the Moderate Size, Toe Disked, Igarapé Belém, Brazil OTU. In addition to these samples, specimens are available from Iquitos, Loreto, Peru; Rio Enuixi, Amazonas, Brazil; 50 km N La Chorrera, Amazonas, Colombia; Puerto Rastrojo, Amazonas, Colombia; near Timbó, Vaupés, Colombia; Wacará, Vaupés, Colombia; near Yapima, Vaupés, Colombia; and Neblina, Amazonas, Venezuela. For ease of discussion, this species will be referred to henceforth as the Toe Disked OTU.

The relatively minor variation within the largest two samples already has been mentioned in the previous section. Most of the variation observed in the other samples falls within that observed within the two largest single locality samples. It is worth noting that in no individual is there any evidence of dorsolateral folds. The toe tips are expanded in all individuals, and in most, the toe tips are expanded into distinct, small disks (there is no expansion of the finger tips). This latter condition of distinct small disks differs in magnitude from all other members of the *podicipinus-wagneri* complex; however, there is overlap with the lesser-expanded disks of the Toe Disked OTU with certain other members of the *podicipinus-wagneri* complex. The dorsal surfaces of the toe disks may or may not have longitudinal grooves or creases.

There is a certain amount of ventral pattern variation in small juveniles in the material at hand. From Estirón, Peru, almost all of the juveniles have the same ventral pattern as the adults, that is, with the chin and throat having a very distinct, bold, mottled pattern including a common pattern of dark mottling containing distinct, relatively large, light spots (in a few small juveniles there is still white pigment in the light spots). The chest and belly are typically immaculate, or the same chin and throat pattern may extend only as far as the anteriormost extent of the belly. The immaculate belly and ventral limb pattern abuts more than blends with the dark dorsal and flank patterns, which contrasts with all other members of the *podicipinus-wagneri* complex. On a few juveniles from Estirón, Peru (e.g., MZUSP 24858), and on most of the juveniles from Igarapé Belém, Brazil (e.g., AMNH 97072–97076), the distinctive chin and throat pattern extends over the entire chest and belly and the undersides of the limbs have a more finely mottled pattern like that seen in most other members of the *podicipinus-wagneri* complex. In a few adults from Colombia, the distinctive throat and chin pattern extends as far as the midbelly; however, most large Colombian specimens have the same ventral pattern as the Toe Disked OTU specimens from Peru and Brazil.

Available samples are not adequate to determine whether there is size variation among geographic samples. The largest sample of specimens is from Estirón, Peru, where the males range in size from 33.1 to 38.0 mm SVL and the females range from 34.4 to 44.6 mm SVL. The Colombian and Venezuelan samples essentially fall within the Peruvian ranges (Colombia: males 29.7–38.7 mm SVL, females 36.8–41.8 mm SVL; Venezuela: single male 37.3 mm SVL). The Brazilian samples differ by being a bit larger (males 38.8–40.4 mm SVL, females 44.1–47.9 mm SVL). It may be that the Estirón, Peru, sample contains mostly small males. Most males in the Estirón sample

have medium-size tan or black thumb spines. Only one of the largest males (AMNH 115721, 36.7 mm SVL) has one large black thumb spine; the other three black thumb spines are medium size. In contrast, most of the Colombian and Venezuelan males have large black thumb spines, but the Brazilian males, which are the largest size, have medium-size black thumb spines.

The two females with mature ova have ova that completely lack melanophores. Some other females with smaller ova seem to have some melanophores either associated with the ovary or the ova, but in other females with smaller ova there is no indication of melanophores.

Brief habitat data are available from only four specimens from Colombia. One individual was calling under water (UTA 8592), two individuals were collected in pockets at the edge of a forest pool (UTA 3726, 3727), and one individual was collected in jungle above a flooded area (UTA 4378).

Core Region Analyses

Seven core regions cover most of the total area in which members of the *podicipinus-wagneri* complex occur. The regions were delineated based on what appeared to be reasonable units in terms of numbers of specimens to examine relative to what taxa occurred within them, morphoclimatic features, and politically defined state or country areas. The latter criterion added a degree of arbitrariness to the areas, but it made for much easier handling of specimens due to the way they were physically organized in bottles and on shelves for the duration of the study.

Region 1—South

Region 1 comprises those areas of Argentina and Paraguay where members of the *podicipinus-wagneri* complex occur.

All specimens from this region appear to represent a single, rather uniform species, designated for purposes of analysis and discussion the Small Size, Dark Belly, Region 1 OTU. There is some variation observed in certain features and very little variation in other features. Of the adult specimens scored from this region, 7% have distinct light lip stripes, 41% have indistinct stripes, and 52% have no indication of light lip stripes. Sixty-five percent of the adults scored from this region have no indication of light stripes on the posterior thighs, 27% have indistinct light thigh stripes, and 8% have distinct light thigh stripes. There is no obvious geographic distribution of light lip or thigh stripes; these conditions appear in low frequency throughout the region. Any variation in dorsolateral-fold condition is confounded by preservation differences. Ventral patterns are rather invariate in this region. Almost all specimens have relatively to very distinct light spots on a dark background from the chin through the posterior extent of the belly. The intensity of the pattern varies to the naked eye depending (apparently) on the degree of expansion or contraction of the melanophores; however, the basic pattern is distinct in all specimens when examined under a dissecting microscope. The greatest variation in belly pattern occurs within a single population sample from Estancia La Golondrina, Presidente Hayes, Paraguay, in which two individuals have distinct light spots on a dark background (UMMZ 66964, 66968), five specimens have relatively distinct light spots on a dark background (UMMZ 166962, 166963, 166965, 166967, 166969), one individual has distinct light spots on a dark chin, throat, and chest, but the belly is relatively boldly mottled dark and light (UMMZ 166910), and one specimen has distinct light spots on a dark chin, whereas its throat and chest are relatively uniformly dark with indistinct light spots and the belly is only moderately, but uniformly, suffused with melanophores that produce an indistinct mottled pattern (UMMZ 166966). These latter two individuals have the most distinctive belly patterns observed in all the individuals examined from this region. The toe tips are essentially uniform in all specimens from this region: the toe tips are narrow, either the same width or barely noticeably swollen and consequently just broader than the toe segment immediately adjacent to the tip.

The measurement data taken indicate that variation among all adults from this region is comparable to that observed within large sample sizes from single localities. For example, the size and ratio ranges and standard deviations for the Region 1 adults (Table 17) are comparable to those of the Small Size, Dark Belly, Porto Velho, Brazil OTU (Tables 2, 11). Outlier detection analyses were run separately on the male and female data to identify any individuals that were obviously distinct from the others based on the measurement data. The results of both analyses are similar in that all specimens pretty much fall within a single cluster when the first principal component is plotted against the second. For the female data, the first two principal components account for 90% of the total variation, for the male data, 86%. For both males and females, there are essentially no outliers along the second principal component axis when the first two principal components are plotted against each other. The two most distinctive females and single most distinctive male in terms of lying outide the main clusters of individuals along the first principal component are FMNH 9271, BMNH 1955.1529, and KU 84734, respectively. FMNH 9271 is the smallest female in this sample (29.3 mm SVL). Re-examination of the individual indicated that it has a straight oviduct, and it was treated as a juvenile female thereafter. Other than size, there is nothing distinctive about the individual. As the first principal component is usually size related, it is likely that this individual was at one end of the plot because of its small size. BMNH 1955.1529 is at the other end of the plot and is one of the larger females (41.8 mm SVL) of the sample (but not the largest). BMNH 1955.1529 is part of a relatively large sample from Primavera, Paraguay. Re-examination of the specimen indicated no distinguishing features between it and the rest of the sample. KU 84734 is the smallest male in the analysis and likely is distinctive in the principal components

TABLE 17.—Minima, maxima, and summary statistics for size and measurement ratios for Small Size, Dark Belly, Region 1 OTU adults. (N = 42 females, 35 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	29.3	43.0	38.0	3.378
SVL	M	28.8	37.9	33.3	2.054
Head length/SVL	F	0.329	0.401	0.360	0.017
Head length/SVL	M	0.337	0.391	0.364	0.012
Head width/SVL	F	0.310	0.357	0.336	0.011
Head width/SVL	M	0.320	0.377	0.343	0.011
Tympanum/SVL	F	0.062	0.082	0.075	0.004
Tympanum/SVL	M	0.064	0.091	0.078	0.006
Thigh/SVL	F	0.352	0.474	0.410	0.028
Thigh/SVL	M	0.367	0.462	0.419	0.022
Shank/SVL	F	0.380	0.443	0.416	0.016
Shank/SVL	M	0.401	0.458	0.429	0.016
Foot/SVL	F	0.447	0.557	0.504	0.026
Foot/SVL	M	0.476	0.560	0.516	0.023

analysis because of its size. The specimen does have vocal slits, but the thumb spines are tan brown, not black, indicating the specimen is a young male. Other than size, there do not appear to be any distinguishing features.

Habitat data are available for 30 specimens from five localities in Paraguay. Fourteen individuals were noted as having been collected from pastures. There is no indication any individuals were collected from forested situations. Most specimens were collected from mud or dirt next to pasture ponds or sluggish streams in pastures. Several specimens were collected from pits of various kinds (clay pit, lime pit, red earth pit) and under boards, presumably in the daytime.

Fifteen advertisement calls from four individuals from El Tirol, Itapua, Paraguay, were analyzed. The call rate varies from 0.7 to 2.7 calls per s. The call duration ranges from 0.026 to 0.036 s (mean 0.029 s). Broadcast frequencies of individual calls range from 1340–2890 Hz to 1580–3240 Hz. The calls are frequency modulated with extremely sharp attacks and frequency upsweeps. The calls are pulsed to pulsatile, with the common situation being a distinct pulse of lower frequency sound immediately followed by a pulse of higher frequency sound, but there may be as many as seven partial pulses in a call. There is no evidence of harmonic structure (Figure 8).

Region 2—East Coast Brazil

The Atlantic Forest Morphoclimatic Domain as defined by Ab'Sáber (1977) extends along coastal Brazil from the State of Rio Grande do Norte through the State of Santa Catarina. Within this area, a single species of the *podicipinus-wagneri* complex occurs from the State of Rio Grande do Norte through the State of Rio de Janeiro. The same taxon is represented by a sample from a brejo in the State of Pernambuco that is surrounded by caatinga vegetation. For purposes of further discussion, the taxon will be referred to as the Small–Moderate Size, Region 2 OTU.

Data were taken on a total of 114 adults and near-adults. The upper lip stripes are distinct in 7%, indistinct in 58%, and 35% have no indication of a light upper lip stripe. Only 6% of the adults have distinct light stripes on the posterior face of the thigh, 20% have indistinct thigh stripes, and the majority (74%) lack any indication of thigh stripes. Short- to moderate-length dorsolateral folds almost always are discernable, about as many extend from the eye to about midway to the sacrum as extend somewhat past the midway point to the sacrum. The folds are often dark outlined, at least in part. The belly pattern is quite variable. The chin (at least) and the throat are dark with distinct small light spots in over half (62%) of the sample; in the remainder, the chins and throats are extensively mottled. The chest and belly regions range from lightly to extensively mottled, but a few individuals (14%) have scattered or no melanophores on the posterior half of the belly. The mottle pattern ranges from speckled to anastomotic to indistinctly densely mottled. No individuals have a pattern of light spots over the entire chin through belly region. The sample from the CEPLAC station, near Itabuna, Bahia, Brazil (MNRJ 4971–4980, 4982–4987, RMNH 23608–23610), is distinctive in that the bellies are generally lighter (but not in all individuals) than in the other geographic samples examined. The toe tips are quite variable, ranging from narrow (12%), just swollen (39%), swollen (26%), slightly expanded (16%), to expanded (7%). No geographic patterns were observed in the variation of these morphological features other than the ventral pattern situation discussed for the CEPLAC sample.

Variation in measurement data is comparable to that seen within large sample sizes from single localities, although the range in snout-vent length in males of 13.4 mm and females of 15.8 mm is at the uppermost end of within-population variation

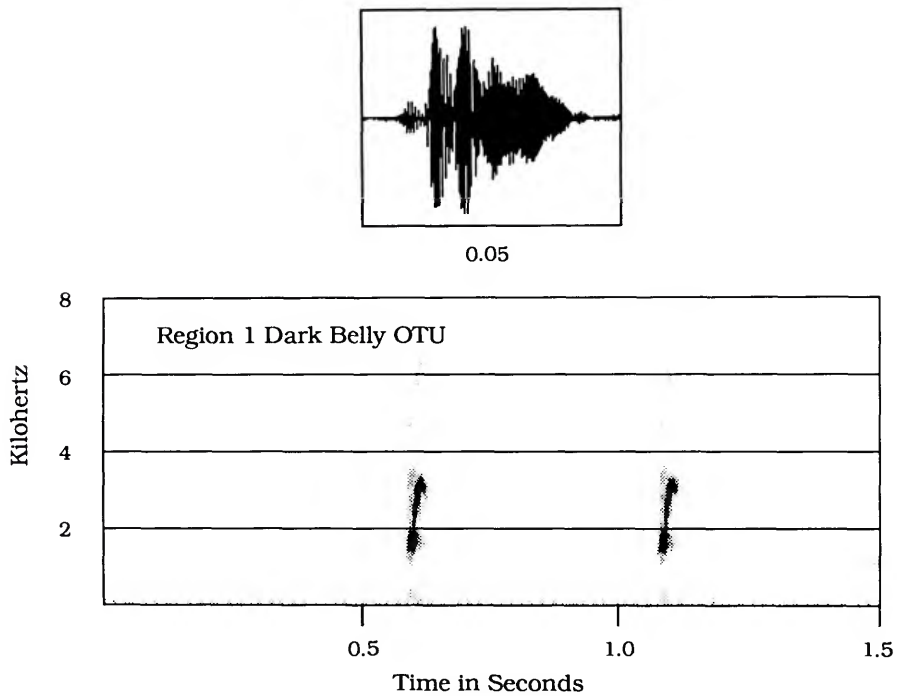

FIGURE 8.—Wave form (of first call) and audiospectrogram of call of Small Size, Dark Belly, Region 1 OTU, USNM Tape 181, cut 16. Recorded from Encarnacion, Itapua, Paraguay, on 8 Jan 1978, by Mercedes S. Foster.

(Table 18). Outlier detection analyses were run separately for males and females. The first two principal component axes account for 92% of the variation in the male analysis and 95% in the female analysis. The results, as summarized in plots of the first two principal components, are similar. The female results demonstrate a more uniform, single cluster with no real outlier points or groups of points, so the male results are discussed in greater detail. For both males and females, there is no pattern of outliers, or separation of groups of individuals, along the second principal component axis (Figure 9 for males, data for females similar). The most distinctive male separated along the first principal component axis is MZUSP 37852, the smallest male analyzed (Figure 9, triangle), which is explained by the fact that the first principal component is usually size related. In fact, the specimens at the other end of the first principal component axis are the largest males in the sample (Figure 9, circles), and, with the exception of a single individual from the State of Rio de Janeiro, all are the males analyzed from the State of Bahia. The female correlation of geography with large size is not as good as for the males, however. All but one of the females analyzed from the State of Bahia are among the largest females, but there are large females also from the states of Paraíba and Pernambuco.

Habitat data are available for seven individuals from three localities in the Ilheus-Itabuna region of Bahia. All seven were collected within cacao plantations. Five specimens were collected from leaf litter near a creek in the plantations in late afternoon or night. One individual was collected from in the water of a creek in a plantation. One specimen was collected in the daytime in a small road puddle.

No advertisement calls are available for this OTU.

There is some variation observed that may have a geographical basis. The samples from the State of Bahia are generally largest in size and have the lightest belly patterns. The nature of this variation appears to be part of a continuum, or alternatively, the variation observed could be due to sampling artifact, as there are no adequate local samples available for this OTU anywhere to assess adequately the degree of intrapopulation variation. Direct comparison of all individuals of the Small–Moderate Size, Region 2 OTU leads to the conclusion that a single OTU is represented. Estimates of genetic relatedness within this OTU should be done to determine whether the Bahia populations are distinctive.

Region 3—Interior Brazil

Region 3 includes the more open habitat formations of Brazil and for purposes of this analysis includes the Distrito Federal, all of the Brazilian states of Mato Grosso, Mato Grosso do Sul, Goiás, Piauí, Tocantins, and the portions of the states of

TABLE 18.—Minima, maxima, and summary statistics for size and measurement ratios for Small-Moderate Size, Region 2 OTU adults. (N = 50 females, 55 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	33.1	48.9	39.9	4.548
SVL	M	28.7	42.1	34.6	2.696
Head length/SVL	F	0.333	0.412	0.372	0.016
Head length/SVL	M	0.350	0.419	0.385	0.013
Head width/SVL	F	0.300	0.385	0.339	0.016
Head width/SVL	M	0.330	0.392	0.355	0.012
Tympanum/SVL	F	0.065	0.087	0.078	0.004
Tympanum/SVL	M	0.074	0.094	0.082	0.005
Thigh/SVL	F	0.381	0.477	0.428	0.023
Thigh/SVL	M	0.393	0.490	0.436	0.021
Shank/SVL	F	0.410	0.511	0.452	0.020
Shank/SVL	M	0.412	0.483	0.455	0.015
Foot/SVL	F	0.463	0.571	0.526	0.025
Foot/SVL	M	0.444	0.578	0.535	0.026

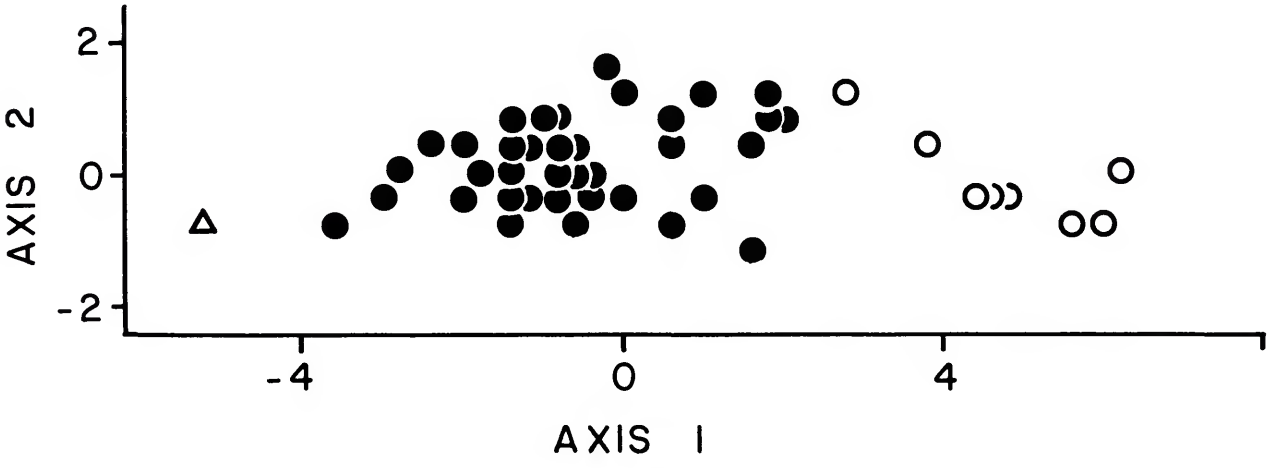

FIGURE 9.—Plot of first against second principal component axes for males of the Small-Moderate Size, Region 2 OTU. (Triangle = smallest male analyzed; circles = largest males analyzed.)

Pernambuco, Bahia, Minas Gerais, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul that are not included in the Atlantic Forest Morphoclimatic Domain.

None of the specimens from this region have been discussed in previous sections of this paper.

This region is drained by several major river systems. With the exception of the samples on hand from the Xingú, Araguaia, and Tocantins drainage systems, all other specimens examined from this region are quite uniform and represent a single OTU (Southern and Eastern Region 3 OTU). The Southern and Eastern Region 3 OTU variation is characterized and then variation within individual locality samples is discussed from the Xingú, Araguaia, and Tocantins drainages.

External morphological data were taken on 218 adults and near-adult individuals of the Southern and Eastern Region 3 OTU. Many individuals (40%) lack light posterior lip stripes, many (41%) have indications of light lip stripes, and some (19%) have distinct light posterior lip stripes. Most individuals (73%) lack any indication of light stripes on the posterior thighs, some (21%) have an indication of a light posterior thigh stripe on at least one thigh, and few individuals (6%) have distinct light stripes on at least one thigh. Virtually all specimens (92%) have moderately short dorsolateral folds extending from the posterior eye to about halfway to the sacrum. There is relatively little variation in belly pattern. All individuals have an extensive profusion of melanophores from

the chin through the belly region (visible under dissecting microscope, if not apparent to naked eye). The majority of individuals (69%) have a pattern of small, distinct light spots on the chin through the belly region; the remaining individuals have variously intermediate patterns where the light spots are more or less well expressed to the extreme pattern found in a few individuals (4%) of a dark mottle from the chin through the belly without any indication of distinct white spots. There is little variation in toe-tip condition with most individuals (71%) having narrow tips and some individuals (29%) having just swollen toe tips. Males (N = 90) range from 25.1 to 38.2 mm SVL; females (N = 120) range from 32.1 to 47.4 mm SVL.

Some samples from localities from the Xingú, Araguaia, and Tocantins drainages are similar to the Southern and Eastern Region 3 OTU characterized above, and others differ primarily in belly pattern. Because of the nature of the variation encountered, each locality sample is discussed with reference to the Southern and Eastern Region 3 OTU.

RIO XINGU SAMPLES.—A sample of 17 adults from Diauarum, Mato Grosso, is the northernmost sample from the Rio Xingú drainage in the State of Mato Grosso (Figure 10, locality 1). The Diauarum specimens do not differ from the Southern and Eastern Region 3 OTU in terms of light posterior lip stripe, light posterior thigh stripe, dorsolateral fold, or toe-tip characteristics. The five males range in size from 35.9 to 38.0 mm SVL, and the 12 females range from 37.2 to 45.1 mm SVL. These sizes fall within the range observed for the Southern and Eastern Region 3 OTU, but the Diauarum specimens are at the upper end of the latter OTU's size range. As such, the Diauarum specimens are somewhat distinctive, but not discretely so. The most striking difference between the Diauarum sample and the Southern and Eastern Region 3 OTU is in terms of belly pattern. None of the Diauarum individuals have distinct light spots on the throat, chest, or belly (about one-third have light spots on the chin). The throat, chests, and bellies are heavily and uniformly mottled, with a couple individuals approaching an anastomotic pattern. Although there were about 10% of the Southern and Eastern Region 3 OTU sample that had similar belly patterns, in all cases where there were at least six individuals from a single locality for the

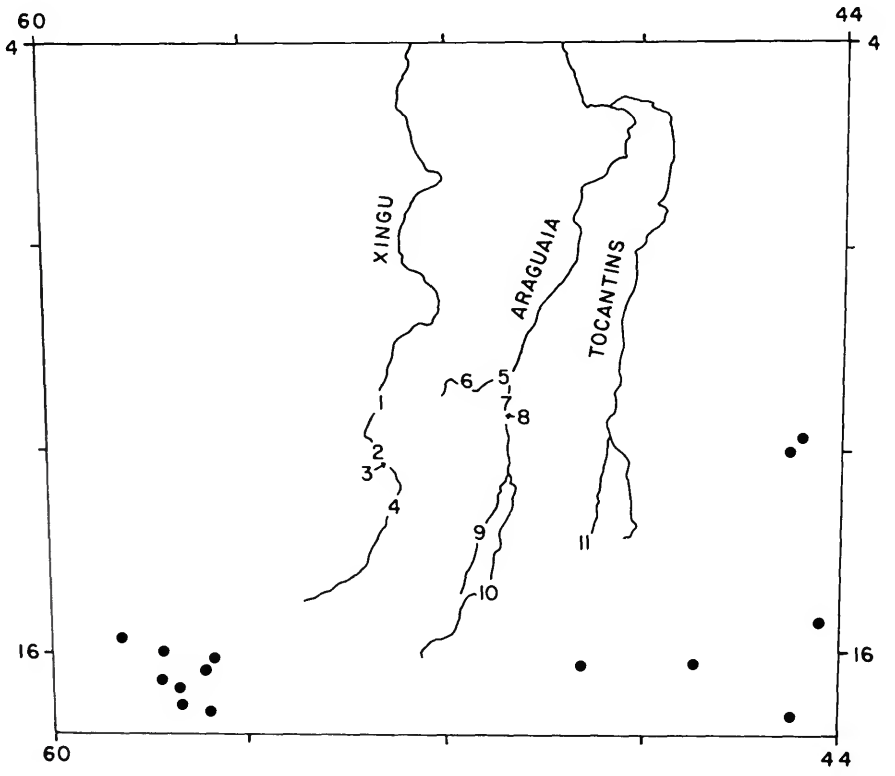

FIGURE 10.—Localities for Region 3 populations discussed in text in detail. (1 = Diauarum, Mato Grosso; 2 = Lagoa Ipavu, Mato Grosso; 3 = Posto Leonardo, Mato Grosso; 4 = Rio Coluene locality, Mato Grosso; 5 = Barra Tapirapés, Mato Grosso; 6 = Aldeia Tapirapés, Mato Grosso; 7 = Mato Verde, Mato Grosso; 8 = Santa Isabel do Morro, Tocantins; 9 = São Domingos, Rio das Mortes, Mato Grosso; 10 = Aruanã, Goiás; 11 = Amaro Leite, Goiás. Dots = nearest southern and eastern Region 3 OTU localities.)

Southern and Eastern Region 3 OTU, at least one individual had a pattern of distinct white spots on the belly.

There is a single male available from Lagoa Ipavu, Mato Grosso, which is the next southern locality along the Rio Xingú drainage in Mato Grosso (Figure 10, locality 2). This individual is very similar to the specimens from Diauarum including having a darkly and extensively mottled venter from chin through the belly without any indication of light spots. It differs from the Diauarum specimens only in size; the male is 38.4 mm SVL, which is 0.2 mm larger than the largest male recorded for the Southern and Eastern Region 3 OTU.

There is a single 16.2 mm SVL juvenile from Posto Leonardo, the next southern locality along the Rio Xingú drainage (Figure 10, locality 3). This individual differs from the Southern and Eastern Region 3 OTU only in terms of ventral pattern. The chin and throat have a pattern approaching light spots on a dark ground, but the pattern is not distinct. The chest and belly have only a few scattered melanophores.

There is a single female from the Rio Coluene, 40 km above the confluence with the Rio Xingú, which is the southernmost locality for which specimens are available along the Rio Xingú drainage (Figure 10, locality 4). The 45.7 mm female matches some specimens from Diauarum in all aspects, including a dark belly with an almost anastomotic pattern.

RIO ARAGUAIA SAMPLES.—Data were recorded for 23 adults and near adult-size individuals from Barra do Tapirapés, Mato Grosso, the northernmost locality sample along the Rio Araguaia in Mato Grosso (Figure 10, locality 5). Specimens from this locality do not differ from the Southern and Eastern Region 3 OTU in terms of posterior lip stripe pattern, thigh pattern, dorsolateral-fold condition, or toe-tip expansion. Of the adult- and near adult-size individuals, many (35%) have distinct light spots on the chin or chin and throat, whereas most (65%) have no light spots on the venter. In the total sample of 63 adults and juveniles available from this locality, the chests and bellies are heavily mottled, with only a very few individuals with patterns of either an almost anastomotic pattern or almost white spotted. In none of the 63 is the belly with distinct white spots. Fourteen adult males range from 29.6 to 39.0 mm SVL, eight females range from 37.3 to 46.2 mm SVL, almost within the size ranges found in the Southern and Eastern Region 3 OTU, but a single 39.0 mm male from Barra do Tapirapés does exceed by 0.8 mm the size observed in the Southern and Eastern Region 3 OTU.

Aldeia dos Tapirapés, Mato Grosso, is further up and off the Rio Tapirapé from Barra do Tapirapés (Figure 10, locality 6). There are 16 specimens at hand from this locality, for which data were taken on 14. The Aldeia do Tapirapés specimens are not distinguishable from the Southern and Eastern Region 3 OTU in terms of lip stripe pattern, thigh pattern, or dorsolateral-fold condition. All of the Aldeia dos Tapirapés individuals have slightly swollen toe tips. None have narrow toe tips, which is a state common in the Southern and Eastern Region 3 OTU. In most individuals, the chins are dark with distinct light spots, a pattern common in the Southern and Eastern Region 3 OTU; however, the chest and belly pattern of the Aldeia dos Tapirapés specimens is quite different from that seen in the Southern and Eastern Region 3 OTU. There is a definite gradient of melanophore distribution, heavy in the chest region and grading to a light posterior belly. In some specimens, there are only a few scattered melanophores on the posterior belly. In most individuals, the melanophores are distributed rather randomly, but in some the melanophore distribution results in a rather boldly patterned mottle. There are no females at hand from Aldeia dos Tapirapés; the 13 adult males range from 31.7 to 38.8 mm SVL, again just exceeding the size range observed in the Southern and Eastern Region 3 OTU.

Mato Verde, Mato Grosso, is the next southern locality along the Araguaia drainage for which specimens are available (Figure 10, locality 7). The sample contains two OTUs. The first OTU comprises 17 adult and juvenile specimens that are virtually identical to those from Barra do Tapirapés. The only differences between the first OTU Mato Verde and Barra do Tapirapés individuals are that fewer of the first OTU Mato Verde specimens have light spots on the chin and there is a single juvenile individual (MZUSP 24024) that has a light chest and belly of rather uniformly scattered melanophores. Otherwise, the description given for the chest and belly pattern for the Barra do Tapirapés specimens matches exactly the variation observed in the Mato Verde specimens. The two adult Mato Verde males range from 28.2 to 34.3 mm SVL, and the four adult females range from 33.3 to 38.3 mm SVL. The second OTU from Mato Verde differs in details of belly pattern and posterior lip stripe from the first OTU from Mato Verde. Twenty of 23 adults of the second OTU from Mato Verde have anastomotic belly patterns. None of the individuals have a pattern approaching distinct light spots on the belly. The light posterior lip stripe, when present, in the second Mato Verde OTU is rather broad and extends from the posterior eye (Figure 11C), contrasting with the narrow light stripe of the first Mato Verde OTU that extends to beneath the eye (Figure 11B). In other aspects, the two OTUs from Mato Verde are quite similar. In the second Mato Verde OTU, the posterior thighs are mottled except in one individual on which an indistinct light stripe occurs on the left thigh (MZUSP 6594). Dorsolateral folds are short or medium length. The toe tips range from narrow to just swollen. Fifteen adult males range from 29.3 to 32.0 mm SVL; eight adult females range from 34.7 to 39.8 mm SVL.

A very small juvenile and an adult female are available from Santa Isabel do Morro, Tocantins, the next southern locality along the Araguaia drainage (Figure 10, locality 8). The 40.3 mm SVL female has a uniformly mottled chin through belly and is indistinguishable from specimens from Barra do Tapirapés.

There is a large sample, mostly juveniles, from São Domingos, Rio das Mortes, Mato Grosso (Figure 10, locality 9), from which data were recorded on 48 adult- and near

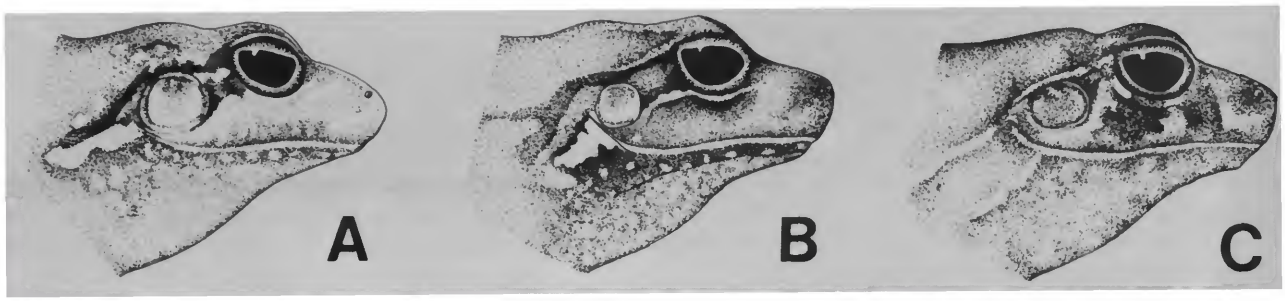

FIGURE 11.—Light posterior lip stripe patterns: A, area under eye light, but stripe not clearly defined ventrally (UMMZ 50201); B, light stripe under eye defined above and below (INPA 1245); C, light stripe extending only to posterior corner of eye (KU 206114).

adult-size specimens. Many individuals (31%) lack any indication of a light stripe on the posterior lip region, most (58%) have some indication of a light lip stripe, and a few (10%) have distinct light lip stripes. Most specimens (62%) have completely mottled posterior thigh patterns, many (27%) have some indication of a light stripe on at least one posterior thigh, and a few (10%) have distinct light stripes on the posterior thighs. All of the specimens have relatively short dorsolateral folds that extend from behind the eye to around the midpoint to the sacrum. There is considerable variation in ventral pattern. About half of the sample has distinct light spots on at least the chin. A few individuals (8%) have the pattern of distinct light spots from the chin through the posterior belly. The single most common pattern (47%) is extensive dark mottle from the chin through the posterior belly. A few specimens (15%) have a rather light, but uniform, scattering of melanophores on the chest and belly. Eight adult males range in size from 30.9 to 33.9 mm SVL, and 30 adult females range from 29.5 to 38.9 mm SVL. The São Domingos sample is quite similar to the Southern and Eastern Region 3 OTU. They both have the same range of variation in belly pattern, but the distinct white-spotted pattern occurs at a much lower frequency in the São Domingos sample. The size range of males from the São Domingos sample falls within the range of Southern and Eastern Region 3 OTU male size, although in the smaller end of the range; some of the São Domingos females are smaller than those recorded for the Southern and Eastern Region 3 OTU.

Five juvenile and one adult female specimens are from Aruanã, Goiás, the southernmost locality from the Araguaia drainage for which specimens are available (Figure 10, locality 10). The few specimens can be matched with individuals from São Domingos, Mato Grosso. All of the chests and bellies are rather evenly and densely mottled, with the female having a pattern approaching light spots. The female measures 32.8 mm SVL.

RIO TOCANTINS SAMPLE.—There are only two specimens available from the Rio Tocantins drainage in the State of Goiás, both from Amaro Leite (Figure 10, locality 11). Both have indistinct light stripes in the posterior lip region. One individual has distinct light stripes on the posterior thighs and the other has one mottled thigh and an indication of a light stripe on the other. The dorsolateral folds are the same condition as found in most specimens from Region 3. One individual has distinct light spots on the chin. Both have densely mottled throats. There is a gradient of melanophore distribution with heavier mottle on the chest and hardly any melanophores on the posterior belly. Both individuals have slightly swollen toe tips. The juvenile male measures 34.0 mm SVL, and the adult male is 41.1 mm SVL.

The first question to deal with is how many species are represented in the specimens from the Xingú, Araguaia, and Tocantins drainages in the states of Mato Grosso, Goiás, and Tocantins.

There are no data on habitats or advertisement calls for any of these specimens.

The variation among populations from the Xingú, Araguaia, and Tocantins drainages in the states of Mato Grosso and Goiás is most pronounced for size and belly pattern. In all other characteristics examined, the specimens from this region are similar among themselves and with specimens of the Southern and Eastern Region 3 OTU.

The belly patterns of individuals from Amaro Leite, Aldeia dos Tapirapés, and the second OTU from Mato Verde are discretely different from the belly patterns of the other specimens from this area. The differences are of the same magnitude seen where two species of this complex co-occur at the same locality (see previous section). The Amaro Leite, Aldeia dos Tapirapés, and second Mato Verde OTU samples are considered to represent the same species. The only difference observed in comparing specimens among these three localities is size. The adult male from Amaro Leite is larger (41.1 mm SVL) than the largest adult male measured from Aldeia dos Tapirapés (38.8 mm SVL) and Mato Verde (32.0 mm SVL). A juvenile male from Aldeia dos Tapirapés measures 29.0 mm and a juvenile male from Amaro Leite is 34.0 mm SVL. The size differences observed between the two

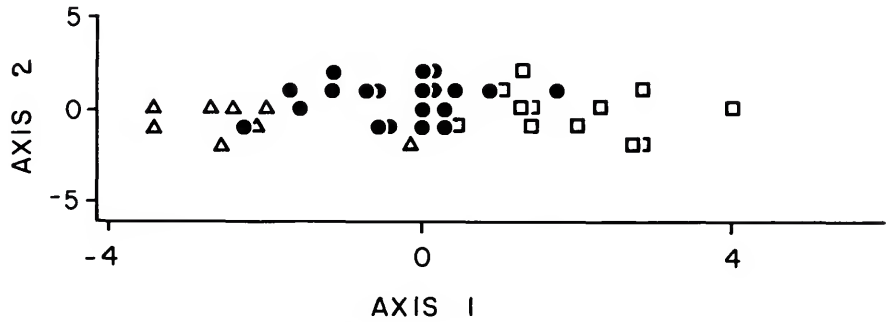

FIGURE 12.—Plot of first canonical variable against second for Region 3 OTUs. (Squares = Light Belly Region 3 OTU; triangles = Northern Region 3 Dark Belly Mato Verde, Santa Isabel do Morro, São Domingos, and Aruanã samples; dots = Region 3 Dark Belly Xingú and Barra do Tapirapés samples. See text for further explanation.)

localities fall within the range of variation found for OTUs with large sample sizes from single localities, but the ranges suggest the Amaro Leite frogs are in fact somewhat larger than those found in the other two samples from Aldeia dos Tapirapés and Mato Verde. For further purposes of discussion, this taxon will be referred to as the Light Belly Region 3 OTU.

The variation in size and belly pattern breaks down in two ways for the remaining samples from the Xingú and Araguaia drainages from Mato Grosso and Goiás. Belly patterns and sizes are similar for all the samples from the Rio Xingú and from Barra do Tapirapés in that no individuals have distinct light spots on the belly and the adults are larger. The pooled samples from Mato Verde, Santa Isabel do Morro, São Domingos, and Aruanã are smaller in size (males 28.2–34.3 mm SVL, females 29.5–40.3 mm SVL) than the Xingú-Barra do Tapirapés pooled samples (males 29.6–39.0 mm SVL, females 37.2–46.2 mm SVL). The São Domingos sample is unique within the Xingú-Araguaia drainage samples in having a few individuals with distinct light spots on the belly. A canonical discrimination analysis between Xingú-Barra do Tapirapés and Mato Verde-Santa Isabel do Morro-São Domingos-Aruanã males indicates some discrimination along the first canonical axis (size related) and the second axis (tympanum highest loading factor, −5.18, next largest variable is head width, 1.10) (Figure 12; Light Belly Region 3 OTU also included in analysis). The size and pattern variation for the Xingú and Araguaia drainage samples exclusive of the Aldeia dos Tapirapés and Mato Verde samples is not discrete and is best interpreted as geographic variation within a species.

The question to resolve now is whether either of the northern Region 3 species represents the same species as the Southern and Eastern Region 3 OTU. In terms of belly pattern, the Light Belly Region 3 OTU differs discretely from Southern and Eastern Region 3 OTU belly patterns. There is overlap of states between the belly patterns of the dark-belly samples from the Xingú and Araguaia drainages, but the relative frequency of occurrence of the distinct light spots on the belly pattern differs markedly. A canonical discriminant analysis of measurement data on males of the three OTUs indicates that virtually all of the discrimination is along the first canonical axis (size related) with virtually no discrimination among OTUs along the second axis. The OTUs can not be completely distinguished from each other on the basis of measurement data, with considerable overlap between the Xingú-Araguaia (minus Aldeia dos Tapirapés and second Mato Verde OTU samples) OTU and the Southern and Eastern Region 3 OTU (Table 19). The level of variation observed appears most consistent with the conclusion that two species occur in Region 3, one the Light Belly Region 3 OTU and a second, referred to hereafter as the Dark Belly Region 3 OTU. The Dark Belly Region 3 OTU, comprised of the Xingú-Araguaia drainage samples (except for the Aldeia dos Tapirapés and second Mato Verde OTU samples) and the Southern and Eastern Region 3 OTU, does exhibit geographic variation.

Morphological features other than measurement data have been described adequately and can be summarized from the previous discussions for the two OTUs recognized as species from Region 3. For further comparisons, the other available data for the two OTUs are summarized.

Outlier detection analyses were run on male and female Dark Belly Region 3 OTU members. For females, the first two principal component axes account for 92% of the total variation and there is essentially but a single cluster of specimens with no outliers on a plot of the first principal component axis against the second. Most of the variation is accounted for by the first principal component (size related), and, in the plot of the first against the second principal component axes, the smallest individuals are in fact on one end and the largest on the other. For males, 90% of the total variation is accounted for by the first two principal components. When the first principal component is plotted against the second, there are three specimens lying outside a single, main cluster, two along the

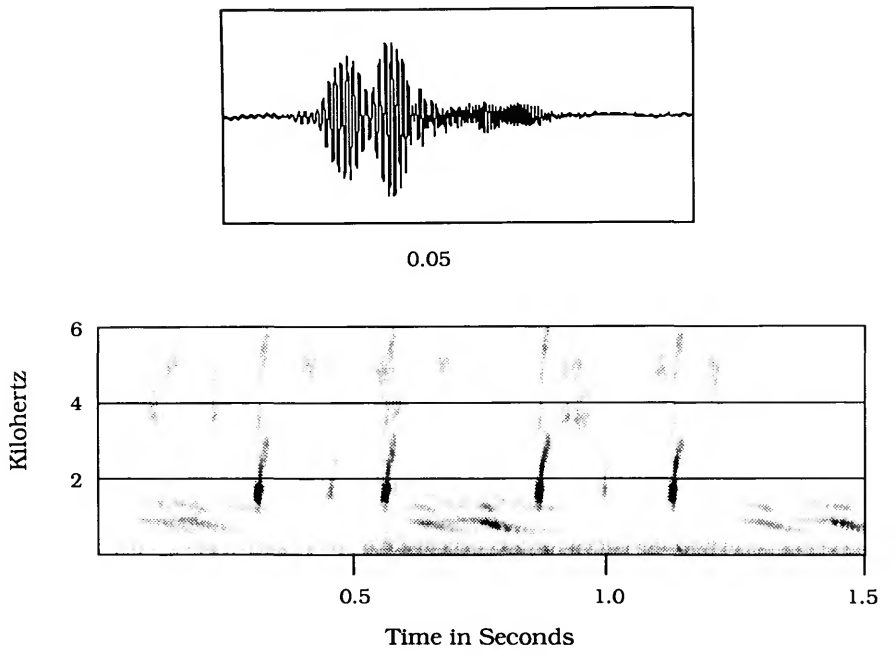

FIGURE 13.—Advertisement call of the Dark Belly Region 3 OTU from Botucatu, Edgardia, São Paulo, Brazil, recorded on 2 February 1970, 2100 h, 21°C air, by Ivan Sazima.

TABLE 19.—Discriminant analysis for males from Region 3. Sample 1 = Xingú-Araguaia drainage samples (except for Aldeia dos Tapirapés) from Mato Grosso, Goiás, and Tocantins; Sample 2 = Amaro Leite-Aldeia dos Tapirapés samples; Sample 3 = Southern and Eastern Region 3 OTU.

Sample	Number of observations (and percent) classified into samples		
	1	2	3
1	18(60%)	2(7%)	10(33%)
2	0(0%)	13(93%)	1(7%)
3	32(36%)	11(12%)	47(52%)

first axis and one along the second. The two outliers along the first principal component axis are the smallest two males in the sample and are part of a sample that includes larger males as well. The outlier male along the second axis is USNM 302833. The highest loading factor on the second axis is tympanum. USNM 302833 does have a small tympanum for its size, does not differ in other respects from the other individuals from the same locality (Estancia Caiman, Mato Grosso do Sul), and the relatively small tympanum is an endpoint of continuous variation.

Adult males of the Dark Belly Region 3 OTU range in size from 25.1 to 39.0 mm. Fourteen subadult males range in size from 23.5 to 30.5 mm SVL. Adult females range in size from 29.5 to 47.4 mm SVL. Eight subadult females range from 27.0 to 32.5 mm SVL. The variation in other measurements for both the Dark Belly Region 3 OTU and the Light Belly Region 3 OTU is of the same magnitude observed for large, single-locality samples (Tables 20, 21).

There is a single recording available for the call of the Dark Belly Region 3 OTU from Botucatu, Edgardia, São Paulo, Brazil. The call rate is 2.7 calls per s, and the call duration ranges between 0.02–0.03 s. The call is pulsatile and frequency modulated, with the initial pulses having the greater intensity with a broadcast frequency of 1500–1800 Hz, rising to just under 3000 Hz at the end of the call. There is evidence of a harmonic at the end of the call in the frequency range 5000–6000 Hz (Figure 13).

Habitat data are available for six individuals from three localities in Mato Grosso, 59 individuals from one locality in Mato Grosso do Sul, and one individual from the State of São Paulo. All specimens were collected at night from open formations (not closed forest vegetation types). Most were collected on roads, most of the rest were collected on the ground or in grass in marshes or next to temporary ponds. Two individuals were collected in the water of a pond.

Region 4—Amazonia

Region 4 corresponds in large part with the lowland Amazon basin. The western limit of Region 4 was determined by

TABLE 20.—Minima, maxima, and summary statistics for size and measurement ratios for Dark Belly Region 3 OTU adults. (N = 177 females, 120 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	29.5	47.4	37.9	3.598
SVL	M	25.1	39.0	33.7	2.707
Head length/SVL	F	0.328	0.396	0.360	0.013
Head length/SVL	M	0.340	0.413	0.372	0.016
Head width/SVL	F	0.308	0.416	0.331	0.013
Head width/SVL	M	0.308	0.386	0.341	0.014
Tympanum/SVL	F	0.062	0.084	0.075	0.004
Tympanum/SVL	M	0.066	0.092	0.079	0.005
Thigh/SVL	F	0.346	0.468	0.402	0.026
Thigh/SVL	M	0.360	0.474	0.419	0.023
Shank/SVL	F	0.380	0.457	0.419	0.017
Shank/SVL	M	0.393	0.477	0.435	0.017
Foot/SVL	F	0.436	0.562	0.508	0.021
Foot/SVL	M	0.487	0.572	0.527	0.019

TABLE 21.—Minima, maxima, and summary statistics for size and measurement ratios for Light Belly Region 3 OTU adults. (N = 8 females, 29 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	34.7	39.8		
SVL	M	29.3	41.1	33.4	3.270
Head length/SVL	F	0.374	0.426		
Head length/SVL	M	0.360	0.437	0.392	0.020
Head width/SVL	F	0.339	0.375		
Head width/SVL	M	0.338	0.394	0.359	0.012
Tympanum/SVL	F	0.080	0.096		
Tympanum/SVL	M	0.078	0.106	0.093	0.008
Thigh/SVL	F	0.388	0.463		
Thigh/SVL	M	0.365	0.483	0.428	0.030
Shank/SVL	F	0.426	0.471		
Shank/SVL	M	0.428	0.475	0.448	0.014
Foot/SVL	F	0.492	0.554		
Foot/SVL	M	0.483	0.584	0.529	0.025

drawing a line on an overlay of the National Geographic map of northwestern South America (scale 1:6,652,800). The line was drawn at the Río Ucayali in Peru where it parallels the Andes in the Peruvian states of Loreto and Ucayali. The line was extended north and south through the Colombian state of Arauca and the Bolivian state of Tarija, respectively. This line separates Region 4 from Region 7. All samples from Colombia, Ecuador, Peru, and Bolivia were separated into these two regions for analytic purposes on the basis of the map overlay line. All localities close to the line were included for analysis in Region 7. Region 4 also includes all materials from the Brazilian states of Acre, Rondônia, Amazonas, and Pará.

All specimens were re-examined from Region 4. About three-quarters of the specimens were readily identifiable as one of four taxa groupings. These groupings include several units that have been discussed already.

Two previously discussed OTUs are the Large Size, Mottled Thigh, Estirón, Peru OTU and the Large Size, Flecked Belly, Igarapé Belém, Brazil OTU. There are only three other comparable large specimens from Region 4, KU 175124, from Río Yasuni, Napo, Ecuador, and AMNH 102991-102992, from Mishana, Loreto, Peru. These samples of large-size frogs have affinities with similar-size frogs from Region 7. These large specimens are included in the Region 7 analysis and are not discussed further with respect to Region 4.

Each of the remaining three Region 4 OTUs (Light Posterior Belly, Anastomotic Belly, and Dark Belly) will be characterized based on the readily identifiable specimens, and those characterizations will be used to discuss the remaining specimens from Region 4 that were not readily identifiable

when re-examined at this stage of analysis.

The Region 4 Light Posterior Belly OTU has only one individual (of 518) that was scored as having a very distinct light posterior lip stripe. Only 7% of the specimens scored have distinct light posterior lip stripes, 57% have indistinct stripes, and 36% have no indication of a posterior lip stripe. About three-quarters (74%) of the sample have at least an indication of a light stripe on the posterior thigh; of these, 4% have very distinct stripes, 34% have distinct stripes, and 36% have indistinct stripes. Most individuals were scored as having short to moderate dorsolateral folds. Only 4% of the sample was scored as having dorsolateral folds that extend almost to the groin. Seven percent of the individuals scored have distinct light spots on the chin. The remainder of the samples have mottled venters. The posterior belly is lacking melanophores or is lightly mottled in 50% of the sample, moderately mottled in 40%, and extensively mottled in 9%. Toe-tip conditions are variable in this OTU, ranging from narrow toe tips (2%) to toe tips with small disks (1%), with most individuals having swollen toe tips (64%). The preceding summary data were gathered separately by regions to determine whether there was any geographic variation in the characters scored. The regions are (1) the State of Pará, Brazil; (2) the State of Amazonas, Brazil; (3) the states of Acre and Rondônia, Brazil; (4) Colombia; (5) Ecuador; (6) Peru; and (7) Bolivia. There are no obvious differences in distribution of states by geography in any of the characters analyzed. There are two characters for which the data are suggestive, but not convincing. The samples from the State of Pará, Brazil, have more specimens with very distinct thigh stripes (25%) and distinct thigh stripes (52%) and fewer specimens with completely mottled thighs (6%) than is true for the OTU as a whole. More specimens from Colombia had very distinct thigh stripes (14%) than the OTU as a whole. The specimens from Ecuador have more individuals with darker bellies than the OTU as a whole (29% with either no melanophores on posterior bellies or lightly mottled posterior bellies, 55% with moderately mottled posterior bellies, and 16% with extensively mottled posterior bellies).

Outlier detection analyses were run on the sexes separately. In the plot of first against second principal component axes for males, there are a few specimens that are not part of a large, rather homogeneous cluster along the first principal component axis. These eight individuals are the smallest in the sample and six of them do not have fully developed thumb spines, indicating that they are young males. Female results are similar, with the addition of one individual being distinct along the second principal component axis. Re-examination of the three most outlying individuals along the first axis indicates that the smallest has straight oviducts, a juvenile by the final criterion used, whereas the other two do have oviducts that are slightly curly. The highest loading variable on the second axis is tympanum diameter. The outlier specimen on the second axis, RMNH 23996, has a 2.3 mm tympanum recorded for a 42.6 mm SVL, which is small. Remeasurement of the tympanum indicates that the original tympanum measurement was in error and should be 2.6 mm.

Readily identified Region 4 Light Posterior Belly OTU males range from 32.8 to 47.9 mm SVL, a range of 15.1 mm, which is comparable to that observed from large, single-site samples. The females range from 35.1 to 53.8 mm SVL, a range of 18.7 mm, which is slightly greater than the range observed in large, single-site samples. There is no obvious geographic variation in female size. The largest females (>50 mm SVL) occur throughout the entire area except for Bolivia. The smallest females (<40 mm SVL) are from Brazil, Pará, Cachoeira do Espelho; Peru, Loreto, Marañon; Peru, Madre de Dios, Tambopata; Bolivia, Beni-Pando, mouth of Río Mapire; and Bolivia, Beni, Santa Rosa. Tambopata, Peru, also has a female over 50 mm SVL. The available samples suggest that the Bolivian and Peruvian females may be smaller, but there are relatively few specimens available from lowland amazonian Bolivia.

Almost no Region 4 Anastomotic Belly OTU specimens have very distinct light posterior lip stripes (1%), some individuals have distinct light posterior lip stripes (11%), several have indications of lip stripes (36%), and about half of the specimens (51%) do not have any indication of light posterior lip stripes. Almost all specimens (94%) have mottled posterior thigh faces, with only a few specimens (6%) having but an indication of a light stripe on the posterior thigh. Dorsolateral folds are not discernible in several (18%) of the specimens; in the remainder, weak dorsolateral folds are short, extending less than halfway to the sacrum from the eyes (62%), or moderate, extending somewhat more than halfway to the sacrum from the eyes (19%). Light spots are distinct at least on the chin in about half the sample (54%). The belly is lightly mottled in a few specimens (7%), moderately mottled in many (31%), and extensively mottled in most (61%). There is no obvious gradient of darker to lighter patterning from anterior to posterior belly. The most common and most distinctive pattern is for the melanophores to be distributed in a bold, anastomotic pattern. In some, the pattern is not as extensive, resulting in speckled bellies. Only one individual was scored as having light spots on the belly. Toe tips range from narrow (15%), just swollen (57%), swollen (13%), to just expanded (15%). The data for the above characters were examined by geographic regions. There is no indication of geographic variation in distribution of states for any of the characters.

Outlier detection analysis of males of the Region 4 Anastomotic Belly OTU results in a reasonably uniform single cluster with most variation along the first principal component axis. Three males are somewhat distinctive at one end of the axis and include the two smallest males in the OTU. Both are probably young in that the thumb spines are not fully developed. The single individual that is somewhat distinctive at the other end of the first axis is the fifth largest male. There is some variation along the second principal component axis with outliers at each end of the axis. The highest loading variable on

the second axis is tympanum diameter, and one outlier at one end of the axis has a somewhat large tympanum and the two outliers at the other end have somewhat small tympani. All four individuals were re-examined and remeasured with no changes in opinion on identification or in measurement. The outlier detection analysis for females of the Region 4 Anastomotic Belly OTU results in a more homogeneous cluster than for males, with outliers only on the first axis. The smallest female is an outlier at one end of the axis. This specimen, KU 205204, had quite a bit of tissue removed for biochemical analyses. The specimen was initially measured as 32.1 mm SVL, but when re-examined, measured 31.4 SVL. Three outliers at the other end of the axis are the largest females in the sample and re-examination indicates no other differences than size.

The size range of readily identifiable Region 4 Anastomotic Belly OTU males is 26.8 to 38.7 mm SVL, a range of 11.9 mm, comparable to size ranges found within large, single OTU samples from single localities. The females range from 31.2 to 51.3 mm SVL, a range of 20.1 mm SVL, which exceeds the range normally found within large single OTU samples from single localities. The three largest females, if excluded, put the size range at 14.8 mm SVL, which is comparable to within single locality OTU variation. The three largest females are from Peru, Loreto, Quebrada Óran (KU 206112); Brazil, Amazonas, Anavilianas (INPA 1218); and Brazil, Pará, UHE Cachoeira Porteira, Rio Trombetas (INPA 469), which does not suggest any geographic component to the distribution of large size in females. However, there are three large subadult females from two localities on the Rio Trombetas, including one of the sites with a large adult female. These three large juvenile females all have straight, narrow oviducts and fall about in the middle of the size range observed in the entire sample of females (USNM 306486, 37.7 mm SVL and USNM 306491, 39.6 mm SVL, both from Brazil, Pará, Reserva Biologica Rio Trombetas; INPA 842, 38.2 mm SVL from Brazil, Pará, UHE Cachoeira Porteira, Rio Trombetas), suggesting that the females in the region of the Rio Trombetas are relatively large within the OTU.

Twenty percent of the Region 4 Dark Belly OTU individuals have distinct light posterior lip stripes (2% have very distinct stripes), 42% have indications of a posterior lip stripe, and 37% have no indication of a posterior lip stripe. Most (89%) have mottled posterior thighs, with only a few (10%) having an indication of a light stripe on the posterior thigh and only rarely (1%) having distinct light thigh stripes. At least weakly developed dorsolateral folds are discernible in most individuals (87%), usually either short, extending less than halfway to the sacrum from the posterior eye (44%), or moderate, extending greater than halfway to the sacrum (42%), and only rarely long, extending to the groin region (1%). The belly, chest, throat, and chin have distinct light spots on a darker ground in 21% of the sample. In most individuals, the belly is extensively profused with melanophores (88%), and the remainder are either moderately to lightly profused with melanophores. In tallying the scoring for toe-tip conditions, all individuals were scored as narrow or just swollen expect for five individuals (of a total of 337 individuals scored). This uniformity of toe-tip scoring is noteworthy, as data were taken over an extensive period of time (years). The five individuals involved initially were scored as having the just-expanded condition. Each of the specimens (AMNH 128419, 128432, 128444, 128446, MZUSP 16696) were re-examined. In all five cases, the toe tips are better classified as just swollen rather than just expanded. Most of the sample (66%) was scored as having narrow toe tips, and the remainder were scored as having just-swollen toe tips. There is only one of the above characters that has any indication of geographic variation in expression, that of light posterior lip stripe development. Most of the specimens (68%) from the states of Amazonas and Pará, Brazil, have distinct light posterior lip stripes (14% have very distinct stripes).

Outlier detection analysis of males of the Region 4 Dark Belly OTU results in a relatively compact single cluster with no real outliers. The two most distinctive individuals along the second principal component axis have relatively short thighs. Both males are from Porto Velho, Rondônia, Brazil (MZUSP 16769, 16852). Most of the data for the large Porto Velho sample was taken at the Museu de Zoologia, and the bulk of the sample was not brought to Washington on loan. The two males in question were in São Paulo at the time of analysis and hence were not available for remeasurement at the time the analysis was performed. The two most distinctive individuals at one end of the first principal component axis are the smallest individuals and presumably are young males as both have white, rather than black, thumb spines. There is a preponderance of males from Alejandria, Beni, Bolivia, that include the most distinctive individuals at the other end of the first principal component axis. The largest male from Alejandria measures 43.3 mm SVL. If the Alejandria males were omitted, the next largest male in the sample is 37.9 mm SVL. There does appear to be some variation in size in males, at least, within this OTU. Outlier detection analysis of the females results in three individuals that are outliers to an otherwise relatively compact cluster. The single outlier (MZUSP 16687) on the second principal component axis, which is most heavily weighted by tympanum diameter, does have a large diameter as recorded. This individual is from Porto Velho and was in the museum in São Paulo at the time of analysis and was not available for remeasurement. The two outliers along one end of the first principal component are RMNH 23838 from near Manacapurú, Amazonas, Brazil, and AMNH 79172 from near Boca Grande, Río Mamoré, Beni, Bolivia. AMNH 79172 is the most distinctive individual on the first axis and is the largest female in the sample, 54.3 mm SVL (the next largest female is 47.9 mm SVL), but on re-examination, it does not differ from other members of this OTU except for size. Re-examination of RMNH 23838 indicates that it is a member of the Region 4, Anastomotic Belly OTU. The belly is extensively mottled, with

TABLE 22.—Discriminant analysis for readily identifiable males and females of three OTUs from Region 4.

Sex and OTU	Number of observations (and percent) classified into samples		
	Anastomotic Belly	Dark Belly	Light Posterior Belly
Males			
Anastomotic Belly	106 (96.6%)	5 (4.5%)	1 (0.9%)
Dark Belly	5 (2.3%)	216 (97.7%)	0 (0%)
Light Posterior Belly	1 (0.6%)	3 (1.7%)	174 (97.8%)
Females			
Anastomotic Belly	79 (92.9%)	5 (5.9%)	1 (1.2%)
Dark Belly	12 (4.6%)	250 (95.4%)	0 (0%)
Light Posterior Belly	9 (2.9%)	1 (0.3%)	299 (96.8%)

a pattern somewhat intermediate between the anastomotic pattern and a pattern with distinct light spots. The toe tips are not well preserved and are either just swollen or just expanded. The posterior lip stripe is faint, but does not extend to under the eye. The head shape is proportioned as in the Region 4 Anastomotic Belly OTU, rather than as in the Region 4 Dark Belly OTU. Thus, for both males and females of the Region 4 Dark Belly OTU, it appears that certain Bolivian populations are larger than populations occurring elsewhere in Amazonia.

Discriminant function analyses were performed separately for males and females. The classification results (Table 22) indicate a good separation of OTUs based on the measurement data with 3% of the 511 males misclassified and 5% of the 656 females misclassified. All but two of the 41 misclassified individuals on the basis of the discriminant analysis were re-examined (two females from Porto Velho, Rondônia, were in São Paulo at the time). The original determination, based on color patterns and toe-tip morphology, was retained for all but three of the 41. One female, MZUSP 59507, from Lago Amanã, Amazonas, Brazil, is equivocal. The specimen originally was identified as a member of the Region 4 Anastomotic Belly OTU, but, based on the discriminant analysis, it has a 94% posterior probability of belonging to the Region 4 Dark Belly OTU. There are unquestioned Region 4 Anastomotic Belly OTU members from the same locality as MZUSP 59507. The head shape of MZUSP 59507 is a bit different when compared with the other specimens from the same locality. The belly pattern is intermediate between the characteristic patterns of the Region 4 Anastomotic and Dark Belly OTUs. Re-examination indicates that the 38.3 mm SVL specimen has a straight, narrow oviduct, and thus it is a juvenile, not an adult female. Identification of this specimen is not certain, but the best overall assessment is that it is a member of the Region 4 Anastomotic Belly OTU. Two males originally were classified as members of the Region 4 Dark Belly OTU, MZUSP 58130 from Paraná Amanã, Amazonas, Brazil, and INPA 473 from UHE Cachoeira Porteira, Rio Trombetas, Pará, Brazil. The two specimens have posterior probabilities of 100% (0.9995) and 96% respectively of belonging to the Region 4 Anastomotic Belly OTU based on the discriminant analysis. MZUSP 58130 has an indeterminate belly pattern, but it does have a relatively large tympanum, slightly dilated toe tips, and a posterior lip stripe that extends to the posterior eye, not under the eye, which all are characteristic of the Region 4 Anastomotic Belly OTU and with which it is hereby classified. INPA 473 has a belly pattern like that of the Region 4 Dark Belly OTU, but it has no indication of a light posterior lip stripe and has somewhat swollen toe tips. Most specimens from the same locality clearly belong to the Region 4 Anastomotic Belly OTU, based on all features. For example, INPA 468 has a light posterior lip stripe to the posterior eye only, the toe tips are expanded, and the belly pattern is distinctly intermediate between INPA 473 and the others in the sample. Comparison of specimens side by side indicates that INPA 473 is part of the same species as the others and not a distinct OTU at Cachoeira Porteira.

Habitat data are available for 469 individuals from 16 localities of the Region 4 Light Posterior Belly OTU, 165 individuals from 15 localities of the Region 4 Anastomotic Belly OTU, and 100 individuals from seven localities of the Region 4 Dark Belly OTU. Twenty-two percent of the individuals with habitat data of the Region 4 Light Posterior Belly OTU were collected from trails, leaf litter, or near ponds, streams, or on river banks in forest habitat. Most of the 78% taken from open formations were collected from pastures at Limoncocha, Napo, Ecuador; other individuals were taken near ponds or puddles, or from stream or river banks in clearings. Ninety-three percent of the Region 4 Anastomotic Belly OTU individuals with habitat data were collected on trails, leaf litter, around ponds, streams, or not near to water in forest habitat. The few (7%) individuals collected from open formations were taken from mud on a floating vegetation mat, near ponds, streams, or rivers in clearings, or on the ground in clearings away from water. All of the Region 4 Dark Belly OTU individuals with habitat data were taken from open formations on the ground, under logs, on or in low vegetation by clearing ponds. A single individual was taken on a stream bank in a clearing. The available data suggest a strong habitat separation

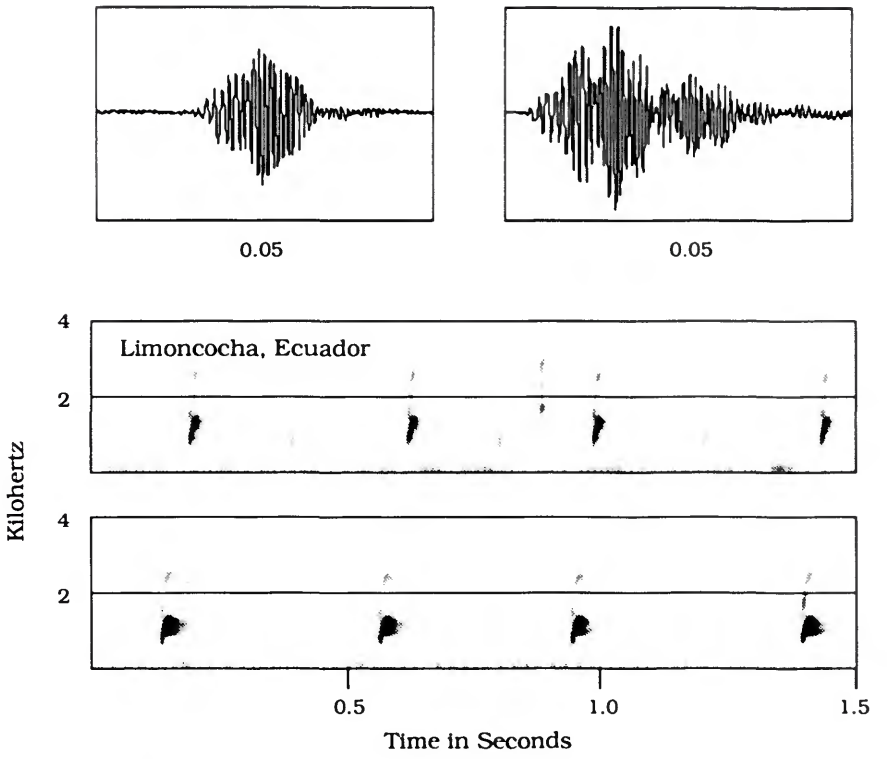

FIGURE 14.—Advertisement calls of Region 4 Light Posterior Belly OTU from Limoncocha, Napo, Ecuador. Wave form on left and upper audiospectrogram from USNM Tape 17, cut 1, recorded in Jun–Jul 1971, 2200 h, 24.6°C air, by W. Ronald Heyer. Wave form on right and lower audiospectrogram from USNM Tape 16, cut 2, recorded 15 Jun 1971, 2000–2200 h, 24.6°C water, by W. Ronald Heyer. Wave forms of first calls on audiospectrograms.

between the Region 4 Anastomotic Belly OTU, being a primarily forest species, and the Region 4 Dark Belly OTU, being entirely an open formation species.

Calls are available for these three Region 4 OTUs. The complex call situation for the Region 4 Light Posterior Belly OTU from Tambopata, Madre de Dios, Peru, was discussed previously (see also Figures 4, 5). In addition, recordings of four unvouchered specimens are available from Limoncocha, Napo, Ecuador, and one vouchered call from Rio Branco, Acre, Brazil. There is some variation among calls from the four Limoncocha individuals that appears to represent continuous variation. Calls range from very short and unpulsed notes (0.02 s duration; Figure 14, left wave form and upper audiospectrogram) to short and partially pulsed notes (0.03–0.04 s duration, 3–5 partial pulses; Figure 14, right wave form and lower audiospectrogram). A very slight harmonic structure may be present, but the quality of the recordings precludes any definite statement. The dominant frequency range is 650–1400 Hz with maximum energy ranging between 1100–1200 Hz. The call is frequency modulated with a very fast rise time. Calls are given at a rate between 1.8–2.4 per s (Figure 14). The calls from Rio Branco are given at a rate of 3.2 per s, with a duration of 0.02–0.03 s. The dominant frequency range is 650–1450 Hz, with maximum energy around 1300 Hz. The call is frequency modulated with a very fast rise time, and there is an indication of harmonic structure (Figure 15). The calls from Limoncocha and Rio Branco are very similar to the call types associated with the Region 4 Light Posterior Belly OTU from Tambopata (Figures 4, 5), indicating that they represent the same species.

The calls of the Region 4 Anastomotic Belly OTU from Tambopata, Madre de Dios, Peru, already have been discussed and figured (Figures 2, 3). There are several other brief recordings available for this OTU. Calls from Cruzeiro do Sul, Acre, Brazil, have been reported on by Cardoso and Vielliard (1990). They indicated that the call they illustrated as fig. 11, 6A is the advertisement call. That recording is from specimen ZUEC 5511, AJC recording 049 cut 4, in which calls are given at a rate of 4.2 per s, call duration 0.05 s, the calls are pulsatile, each call having 3–4 pulses, the dominant frequency range is 700–1200 Hz with maximum intensity at 800 Hz, and

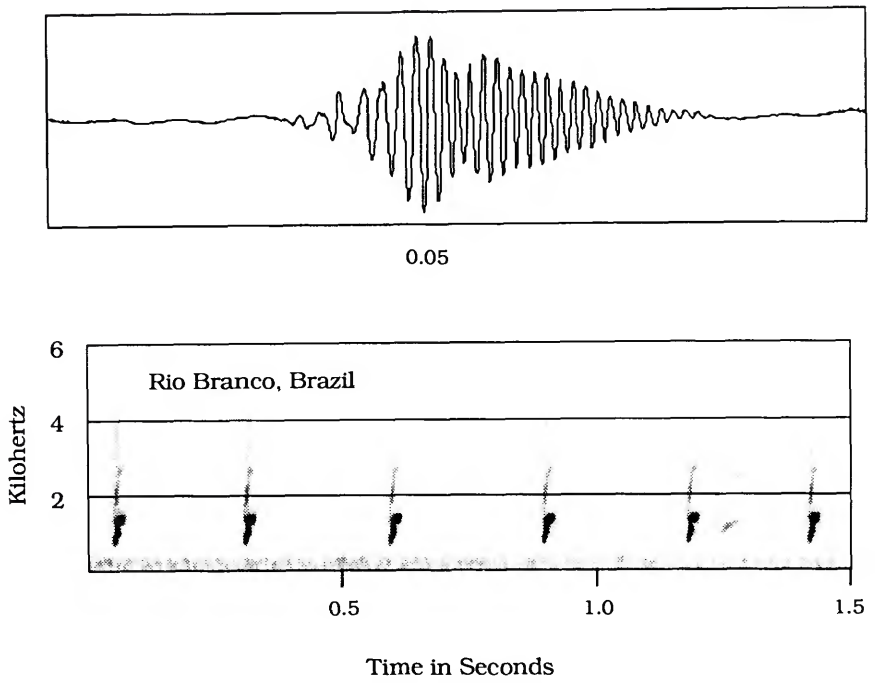

FIGURE 15.—Advertisement calls of Region 4 Light Posterior Belly OTU from Rio Branco, Acre, Brazil, AJC Tape 52, cut 7. Recorded from ZUEC 5639 on 19 Dec 1983, 1915 h, 27°C air, 26°C water, by Adão J. Cardoso. Wave form is of third call shown on audiospectrogram.

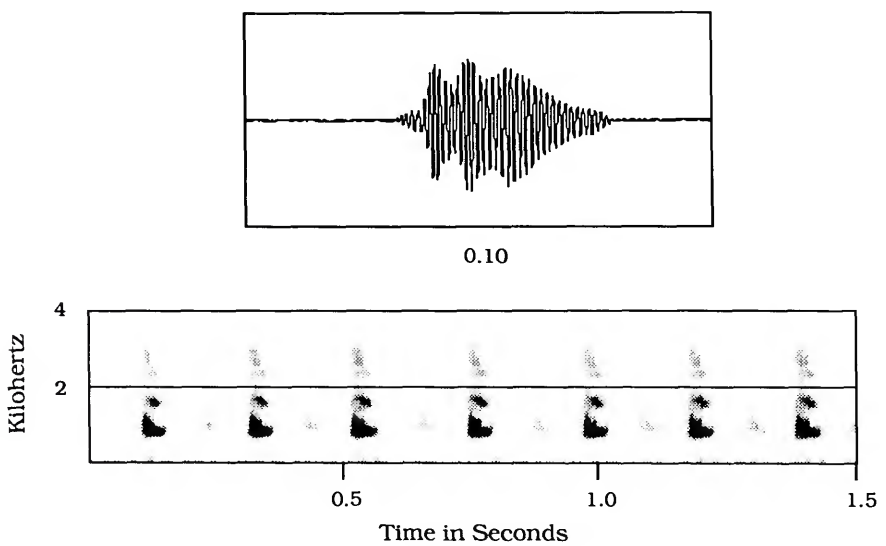

FIGURE 16.—Advertisement call of Region 4 Anastomotic Belly OTU from Cruzeiro do Sul, Acre, Brazil, recording AJC 49, cut 4. Recorded from ZUEC 5511 on 5 Dec 1983, 1950 h, 24°C air and water, by Adão J. Cardoso. Wave form is of first call on audiospectrogram.

harmonic structure is clearly evident (Figure 16). There are, in addition, several different types of calls given by ZUEC 5511 (Figures 17, 18), including what Cardoso and Vielliard (1990) characterized as an aggressive call (fig. 11, 6B; present Figures 17C, 18C). The various calls given by ZUEC 5511 are impressively diverse, with great variation in frequency modulation, sweeping both up and down through a frequency range of 700–2700 Hz, with many of the calls having maximum intensity of the call in the 2100–2300 Hz range. There is also great variation in the distinctiveness of pulses and whether the beginning or end of the individual call has the greatest energy (Figure 18). All calls recorded from specimen ZUEC 4387, also from Cruzeiro do Sul, are almost identical to those represented in Figure 16. The call rate for ZUEC 4387, recorded on 20 April 1981, 2000 h, 26°C air by Adão J. Cardoso, is 2.9 per second, call duration 0.04–0.05 s, each call is pulsatile, with 3–4 weakly to moderately modulated pulses, the dominant frequency range is 700–1200 Hz, with maximum intensity in the 750–800 Hz range, weak harmonics occur after the first pulse only. Seventeen calls recorded from ZUEC 8432, also from Cruzeiro do Sul, show an extreme structure not observed in any of the other calls from Cruzeiro do Sul. The calls are given at a rate of 0.2 per s, the call duration is 0.05–0.07 s, the dominant frequency range is 800–2700 Hz, with extreme upward and

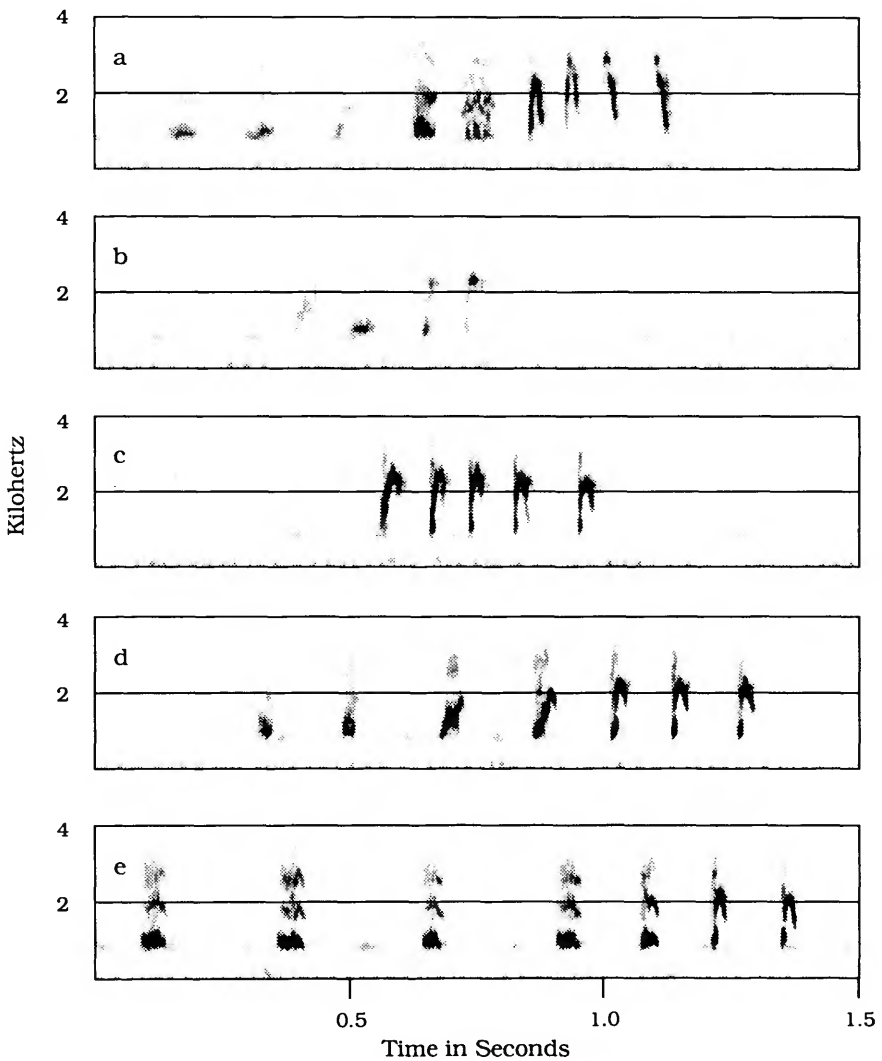

FIGURE 17.—Audiospectrograms of calls of specimen ZUEC 5511 from Cruzeiro do Sul, Acre, Brazil, a member of the Region 4 Anastomotic Belly OTU. See legend for Figure 16 for recording data.

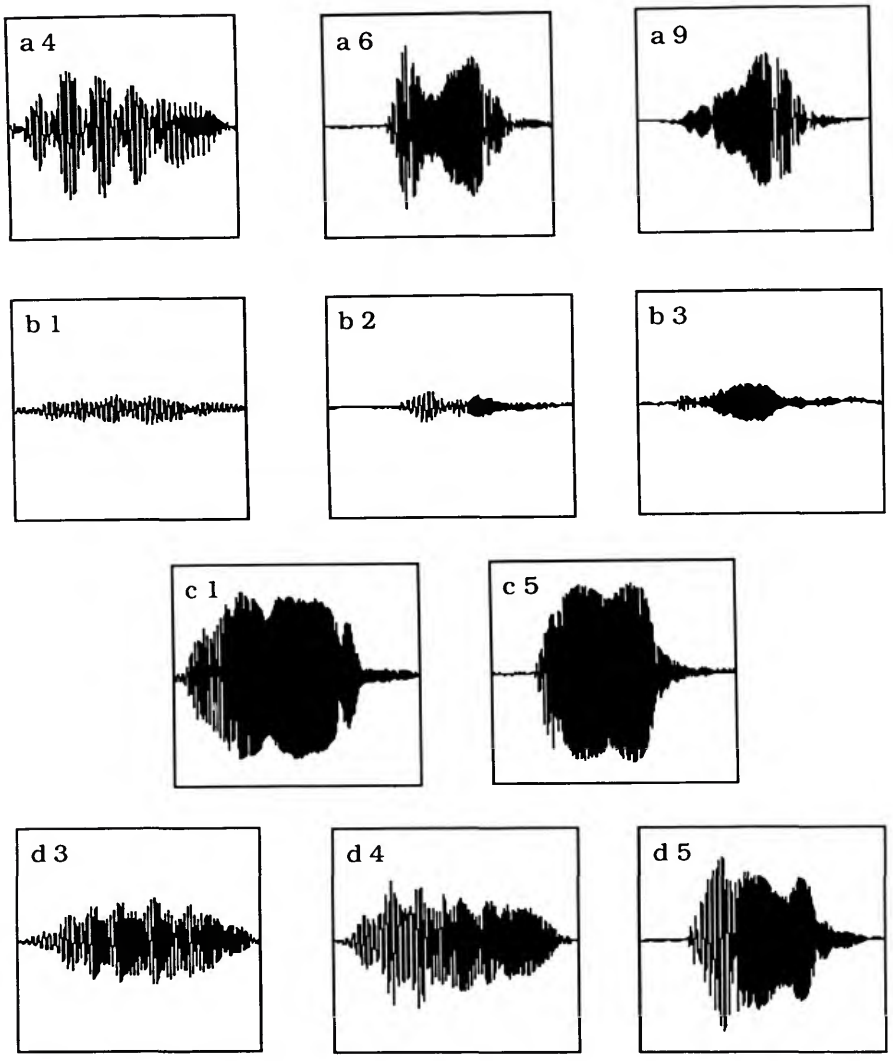

FIGURE 18.—Selected wave forms from audiospectrograms (Figure 17) analyzed from specimen ZUEC 5511 from Cruzeiro do Sul, Acre, Brazil, a member of the Region 4 Anastomotic Belly OTU. All signal lengths = 0.05 s. See legend for Figure 16 for recording data.

downward frequency modulation (Figure 19). Two calls from a single unvouchered specimen from INPA-WWF-SI Reserve 1401 north of Manaus, Amazonas, Brazil, consists of two juxtaposed portions, an initial low frequency portion at about 800–1100 Hz for a duration of about 0.02 s, at the end of which is a harmonic to which the remainder of the call shifts at about 1900–2300 Hz for a duration of about 0.03 s. The second portion of the call is frequency modulated downward. The first portion of the call is pulsatile, the second is not (Figure 20). Three calls from a single unvouchered specimen from IPEAN, Pará, Brazil, are similar in being composed of two juxtaposed portions, the first low frequency, the second higher frequency. The calls differ slightly from those already discussed in having initial frequencies of 800–1400 Hz and final frequencies of 1900–2800 Hz. The total call duration is about 0.04 s. The second part of the call does not have a noticeable downsweep in frequency modulation (Figure 21). The variability of calls given by individuals is impressive. All calls from individuals for which only a single call type was recorded can be matched with one of the call types given by individuals from either the Tambopata or Cruzeiro do Sul specimens or both. However, there is a problem with interpreting what the advertisement call is of this species. The advertisement call of the Tambopata specimens (which seems to be similar to most other recordings

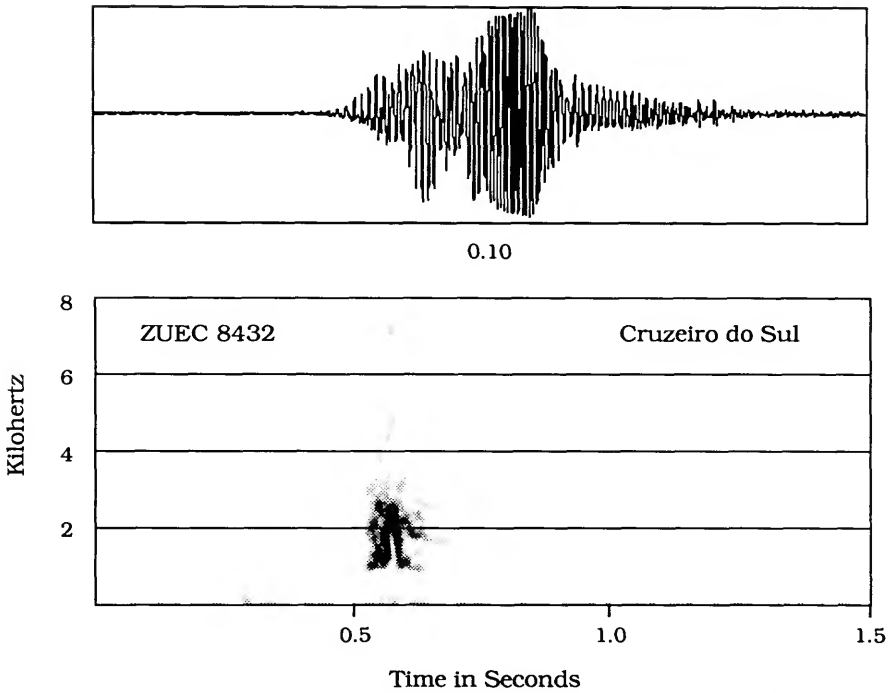

FIGURE 19.—Call of ZUEC 8432, from Cruzeiro do Sul, Acre, Brazil, a member of the Region 4 Anastomotic Belly OTU, recording AJC Tape 90, cut 5. Recorded 29 May 1989, 2130 h, 25°C air, 21°C water, by Adão J. Cardoso.

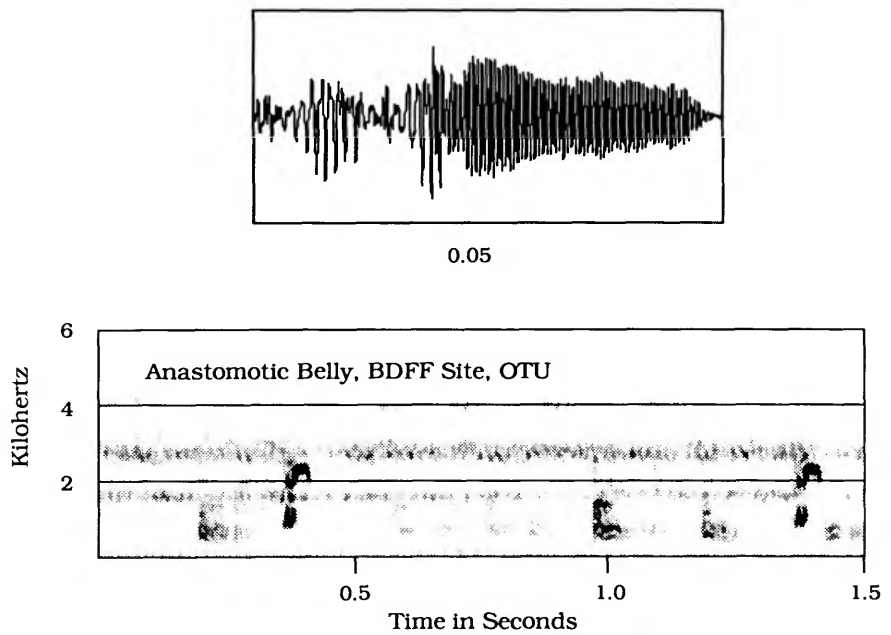

FIGURE 20.—Calls of Region 4 Anastomotic Belly OTU from Biological Dynamics of Forest Fragments research site north of Manaus, Amazonas, Brazil, USNM Tape 163, cut 3. Recorded 9 Apr 1987, 2230 h, by Barbara L. Zimmerman.

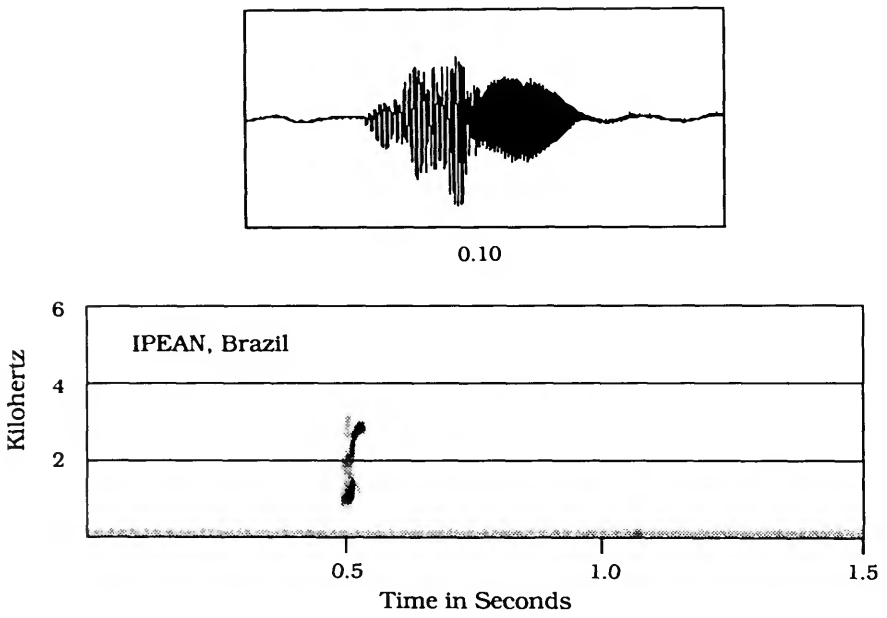

FIGURE 21.—Call of Region 4 Anastomotic Belly OTU from IPEAN, Pará, Brazil, KU Reel 81, tape 1001. Recorded 8 Jul 1970, 2305 h, 29°C air, by Martha L. Crump.

available) resembles the aggressive call of the Cruzeiro do Sul specimens, and nothing like the advertisement call given by the Cruzeiro do Sul specimens has been recorded for the Tambopata specimens. There are at least three explanations that can account for the observed data: (1) what is recognized as a single OTU on morphological grounds actually contains two species differentiated by advertisement calls; (2) the behavioral contexts of the calls have not been characterized adequately so that the use of advertisement and aggressive calls by the different researchers who made the recordings do not have the same meaning; or (3) the designated advertisement call of the Cruzeiro do Sul individuals is given only under certain conditions and has not yet been recorded for Tambopata individuals. Given the calls available, I am struck by the similarities among them, with the exception of the pulsed call given by the Cruzeiro do Sul specimens designated as the advertisement call by Cardoso and Vielliard (1990). For present purposes, I assume either explanation (2) or (3) (or both) is correct and consider all the calls to represent a single OTU.

Two recordings are available for the Region 4 Dark Belly OTU. A recording from Porto Velho, Rondônia, Brazil, has one section where the call rate is 0.5 per s (Figure 22, upper audiospectrogram) and another section where the call rate is 5.8 per s (Figure 22, lower audiospectrogram). Call duration is 0.03 s. Broadcast frequencies range from 1000 to 3000 Hz with maximum energy around 3000 Hz. The calls are frequency modulated with extremely sharp attacks and frequency upsweeps with a short terminal frequency downsweep. The calls are pulsed and have weak harmonics (Figure 22). A recording of an unvouchered individual from Borba, Amazonas, Brazil, has a call given at a rate up to 8.4 per s. Call duration ranges from 0.02 to 0.03 s. Broadcast frequencies range from 1500 to 3500 Hz, with the most intensity around 3000 Hz. The calls are frequency modulated with extremely sharp attacks and frequency upsweeps. The calls are pulsed to pulsatile and have weak harmonics (Figure 23).

The three Region 4 OTUs discussed above clearly represent three species, each with distinctive calls, even though there is considerable variation of calls within OTUs. The characterizations of these taxa are used to discuss the remaining specimens from Region 4.

A single male of the Region 4 Anastomotic Belly OTU from Cachoeira do Espelho, Rio Xingú, Pará, Brazil, is distinctive within a series from the same locality. The individual (MZUSP 69065) is probably a young male as the thumb spines are small, white, and tan-tipped. The belly pattern is uniformly darkly mottled and closely approaches a pattern of distinct light spots on a dark ground. The belly pattern is more similar to the Region 4 Dark Belly OTU belly pattern than to the characteristic Region 4 Anastomotic Belly OTU pattern. The light posterior lip stripe stops at the posterior angle of the eye and does not extend under the eye, as is typical of the Region 4 Anastomotic Belly OTU. The toe-tip condition is slightly swollen, which is a common condition to both the Anastomotic Belly and Dark Belly OTUs in Region 4. The tympanum

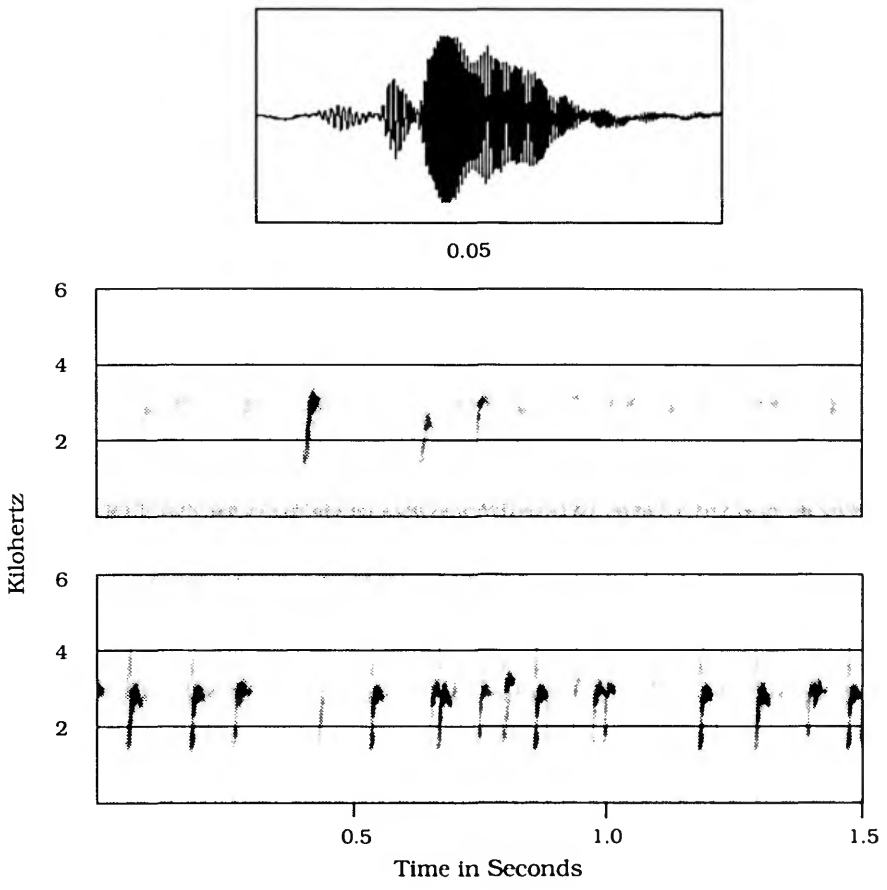

FIGURE 22.—Advertisement calls of Region 4 Dark Belly OTU from Porto Velho, Rondônia, Brazil, recording AJC Tape 42, cut 3. Recorded from specimen ZUEC 5381, 23 Feb 1983, 0700 h, 23°C air and water, by Adão J. Cardoso. Wave form is of first, loudest call on upper audiospectrogram.

diameter of readily identified Region 4 Anastomotic Belly OTU males ranges from 8% to 11% SVL, and for Region 4 Dark Belly OTU males it ranges from 6% to 9% SVL. The tympanum diameter of MZUSP 69065 is 10% SVL. MZUSP 69065 is considered to be a member of the Region 4 Anastomotic Belly OTU even though the belly pattern is unusual.

A small series of specimens from the relatively close-by localities of Boca do Figueredo, Rio Nhamundá, Pará, Brazil (MZUSP 24983, 24985–24988), Fazenda Paciencia, Rio Nhamundá, Pará, Brazil (MCZ 90833, MZUSP 44311), Lago Ururiá, near Oriximiná, Rio Trombetas, Pará, Brazil (MZUSP 24993–24995, 32313–32317), and Oriximiná, Pará, Brazil (MNRJ 4898–4902), all represent the same taxon. This series matches the Region 4 Dark Belly OTU in terms of toe-tip expansion (most narrow, a few just swollen), posterior lip stripe (extending to under the mid-eye in several), and overall appearance. In most specimens the belly is rather lightly pigmented, and in one (MNRJ 4902) there are only a couple of melanophores distinguishable on the chest. The specimens from Lago Ururiá show a complete gradation from a light belly (MZUSP 24905) to a dark belly that is almost light spotted (MZUSP 24994). Because there is a complete continuum from light to dark bellies in the Lago Ururiá series, all specimens from the four localities are included in the Region 4 Dark Belly OTU.

There is considerable variation in belly pattern within the sample from Humaitá, Amazonas, Brazil (MNRJ 4924–4928, 4930–4970). Other than belly pattern, the sample is typical of the Region 4 Dark Belly OTU in having narrow or just-swollen toe tips, males with moderate-size tympani, and, in those individuals with light posterior lip stripes, the stripes extending to under the middle of the eye. The belly patterns range from dark with distinct light spots (MNRJ 4959) to darkly and indistinctly mottled (MNRJ 4939) to anastomotic (MNRJ 4937) to lightly, but rather uniformly, speckled (MNRJ 4961),

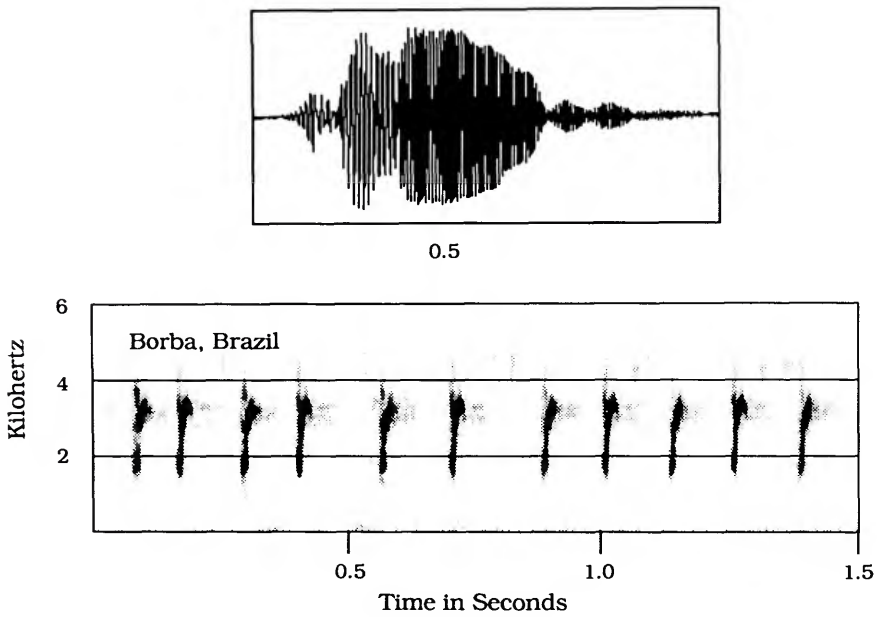

FIGURE 23.—Advertisement call of Region 4 Dark Belly OTU from Borba, Amazonas, Brazil, USNM Tape 22, cut 4. Recorded Nov 1975, 2110 h, by W. Ronald Heyer. Wave form is of first call on audiospectrogram.

with every gradation in between. Examination of the sample leads to the conclusion that it represents a single OTU with a variable belly pattern and is the same as the Region 4 Dark Belly OTU.

A single 14.2 mm individual from São João, near Tapurucuara, Amazonas, Brazil (MZUSP 37508), is tentatively identified as belonging to the Region 4 Anastomotic Belly OTU. The specimen also is similar to the Region 4 Dark Belly OTU. The belly is darkly mottled and is consistent with patterns found in both of the OTUs mentioned. The specimen does not have any indication of a light posterior lip stripe. The toe tips are very slightly expanded. Until additional material becomes available from this locality, the locality should not be used as a record for either the Anastomotic Belly or Dark Belly OTU from Region 4.

Two individuals are at hand from Restauração, Amazonas, Brazil. MZUSP 51335 was collected at night from a second growth/clearing mixture on the ground next to a pond. The specimen is a 29.4 mm juvenile with an anastomotic belly pattern, a faint light lip stripe on one side that does not extend to under the middle of the eye, and slightly swollen toe tips. The specimen clearly is associated with the Region 4 Anastomotic Belly OTU. The other specimen, USNM 202553, is not as clearly assignable to an OTU. The specimen is a 36.0 mm male. Rather than a discrete light lip stripe, there is an entire light band from the loreal region passing under the eye and through the commissural gland past the angle of the jaw. The chin has distinct light spots, the throat is extensively mottled, and the belly has a rather random but uniform scattering of melanophores over its entirety. The toe tips are narrow. The specimen was collected at night from open formation vegetation on the ground two meters from a stream. USNM 202553 represents either the Anastomotic Belly or Dark Belly OTU from Region 4. Comparison of USNM 202553 with MZUSP 51335 indicates they do not represent the same OTU. USNM 202553 is considered to be a member of the Region 4 Dark Belly OTU with a somewhat unusual belly pattern.

MZUSP 53757 from Lago Marinheiro, Amazonas, Brazil, is a 33.4 mm SVL female. The specimen is a member of the Region 4 Dark Belly OTU, with indications of a light posterior lip stripe extending to under the eye. The belly pattern is not typical, however, in being lightly mottled overall, but with a somewhat denser mottle anteriorly on the belly.

Specimens from Ilha da Marchantaria, entrada Lago dos Reis, Amazonas, Brazil, represent three OTUs, two of them are represented by juveniles with the materials at hand. The three adults (INPA 772, 778, 779) all represent the Region 4 Dark Belly OTU. Each of the specimens has indications of a light posterior lip stripe extending under the eye. The belly is distinctly light spotted in INPA 772, mottled in INPA 778, but with scattered melanophores in INPA 779. Four juveniles ranging from 14.9 to 23.4 mm SVL (INPA 771, 774, 775, 777) belong to the Region 4 Anastomotic Belly OTU. Each of these individuals has distinct light lip stripes that extend only from

the posterior corner of the eye and have somewhat dark bellies, ranging from rather uniformly suffused with melanophores to a pattern approaching an anastomotic one. The other two juveniles are 13.4 mm and 29.4 mm SVL (INPA 773, 775) and represent the Region 4 Light Posterior Belly OTU. Both have very light bellies with almost no melanophores posteriorly, and one (INPA 773) has distinct light stripes on the posterior thighs.

Three juveniles from Igarapé Belém, Amazonas, Brazil, were not readily identified during the first examination of the Region 4 specimens. These specimens (MZUSP 24902, 24910, 24931), upon re-examination, are clearly Region 4 Anastomotic Belly OTU members and represent the only individuals of this OTU from this locality where several other OTUs have been discussed previously.

A sample of seven Region 4 Light Posterior Belly OTU specimens from Príncipe da Beira, Rondônia, Brazil, is somewhat unusual in that most of the individuals have rather heavily speckled or blotched bellies, approaching the condition typical of the Region 4 Anastomotic Belly OTU pattern. All seven have rather well-developed light stripes on the posterior thighs, however, which is characteristic of the Region 4 Light Posterior Belly OTU.

Three individuals of the Region 4 Dark Belly OTU from São Carlos, Rondônia, Brazil, show extreme variation in belly pattern from dark with almost distinct light spots (MZUSP 51465) to a scattering of melanophores (USNM 202545). All three individuals have narrow toe tips and have faint indications of a light posterior lip stripe extending to under the eye.

ICNMNH 18093, a female from Araracuara, Amazonas, Colombia, is quite similar to the Region 4 Light Posterior Belly OTU, but it has a quite heavily mottled belly and the faintly indicated dorsolateral folds appear to extend the full length of the body. There is but the one specimen from the locality; for present purposes, it is considered as a Region 4 Light Posterior Belly OTU member.

The samples of the Region 4 Light Posterior Belly OTU from the State of Vaupés, Colombia, include several individuals with rather heavily mottled bellies, very similar to the belly pattern found in the Region 4 Anastomotic Belly OTU. Both OTUs are represented from the junction of the Río Ariari and Río Guaviare. The single representative of the Anastomotic Belly OTU is a 36.3 mm SVL female (UTA 8047), and the belly pattern is very similar to that of the 52.9 mm SVL female Light Posterior Belly OTU (UTA 3718). Yet, when the specimens are compared side by side, slight differences in belly pattern can be discerned.

Most of the specimens from the Beni Biosphere Reserve, Beni, Bolivia, are juveniles. In most of the Region 4 Light Posterior Belly OTU individuals, the bellies are moderately to extensively mottled. Light stripes on the posterior thighs are distinct in almost all of the Light Posterior Belly OTU specimens from this locality.

All but one individual of the specimens at hand from Ivon, Beni, Bolivia, are readily placed with either the Region 4 Anastomotic Belly OTU or the Region 4 Dark Belly OTU. The exception, BMNH 1967.2086, a male, has a ventral pattern found in examples of both OTUs. The toe tips are narrow, also characteristic of both OTUs. In the other specimens, the posterior lip stripes are clear enough to determine whether they extend under the eye or not. In BMNH 1967.2086, the posterior lip stripe is indeterminate such that it could be interpreted variously. Comparison of the specimens side by side suggests that the individual most resembles the Region 4 Dark Belly OTU and it is included therein, although with reservation.

Re-examination of a small series from Tumi Chucua, Beni, Bolivia, indicates that all three Region 4 OTUs are represented and that all available specimens are clearly assignable.

Several specimens were neither readily sorted initially nor discussed above. These (including quite a few juveniles) turned out to be placed readily into one or the other of the three Region 4 OTUs as characterized in the initial portion of this section.

Size and proportion statistics indicate that the addition of the few more adult specimens to each of the OTUs did not change the size ranges (Tables 23–25).

The specimens added after the first characterization of the OTUs provide no new advertisement call data. Habitat data are added for only one more individual; the additional data do not change the previous habitat characterizations for the three OTUs.

The Region 4 Anastomotic Belly, Dark Belly, and Light Posterior Belly OTUs represent well-defined species for which variation within OTUs is within reasonable limits with two exceptions. There is greater size variation within OTUs than found within populations; the degree of female size variation in the Region 4 Anastomotic Belly and Dark Belly OTUs (Tables 23, 24) is particularly large. The second exception is that the variation in calls purported to be the main advertisement calls for the Region 4 Anastomotic Belly OTU would seem to represent two different species; however, the morphological data indicate but a single species for this OTU. Until further call data become available to resolve the problem, the morphological data conclusions are adopted and a single species is recognized for this OTU.

Region 5—Guiana Shield

Region 5 includes French Guiana, Surinam, Guyana, all of Venezuela except for the State of Amazonas, and the Brazilian states of Amapá (no specimens at hand from Amapá) and Roraima.

Re-examination of all specimens from this area resulted in the following. Most specimens from French Guiana, Surinam, and Guyana were readily sorted into three OTUs: an Anastomotic Belly Region 5 OTU, a Small Size Guianas OTU, and a Moderate Size, Light Posterior Belly, Guianas OTU. Most of the specimens from Venezuela and Roraima, Brazil,

TABLE 23.—Minima, maxima, and summary statistics for size and measurement ratios for Region 4 Anastomotic Belly OTU adults. (N = 85 females, 117 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	31.2	51.3	38.9	4.044
SVL	M	26.8	38.7	32.9	2.633
Head length/SVL	F	0.351	0.421	0.388	0.015
Head length/SVL	M	0.361	0.445	0.398	0.017
Head width/SVL	F	0.322	0.379	0.355	0.011
Head width/SVL	M	0.332	0.400	0.365	0.014
Tympanum/SVL	F	0.067	0.097	0.081	0.006
Tympanum/SVL	M	0.077	0.111	0.095	0.008
Thigh/SVL	F	0.365	0.506	0.431	0.025
Thigh/SVL	M	0.358	0.486	0.436	0.026
Shank/SVL	F	0.403	0.495	0.445	0.017
Shank/SVL	M	0.411	0.489	0.450	0.018
Foot/SVL	F	0.488	0.597	0.534	0.021
Foot/SVL	M	0.481	0.582	0.535	0.022

TABLE 24.—Minima, maxima, and summary statistics for size and measurement ratios for Region 4 Dark Belly OTU adults. (N = 275 females, 230 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	30.0	54.3	39.7	3.983
SVL	M	26.2	43.3	34.5	3.336
Head length/SVL	F	0.304	0.400	0.347	0.016
Head length/SVL	M	0.314	0.388	0.356	0.015
Head width/SVL	F	0.295	0.393	0.327	0.013
Head width/SVL	M	0.290	0.365	0.332	0.012
Tympanum/SVL	F	0.056	0.087	0.071	0.005
Tympanum/SVL	M	0.060	0.091	0.074	0.005
Thigh/SVL	F	0.320	0.454	0.387	0.027
Thigh/SVL	M	0.306	0.463	0.400	0.029
Shank/SVL	F	0.359	0.462	0.403	0.019
Shank/SVL	M	0.360	0.466	0.416	0.018
Foot/SVL	F	0.400	0.593	0.489	0.028
Foot/SVL	M	0.427	0.572	0.508	0.025

could not be sorted readily into the OTUs from the Guianas nor could they be sorted into discrete OTUs within the geographic area covered. Within Venezuela, there are clusters of specimens from three small geographic areas that appear to represent distinct OTUs, but the relationships among the three and with the Guiana OTUs are unclear at the outset. The three recognizable OTUs are (1) the Aragua OTU from the states of Aragua, Distrito Federal, Falcon, and Miranda, (2) the Small Size Bolívar OTU from the State of Bolívar, and (3) the Medium Size Bolívar OTU from the State of Bolívar.

Each of the Region 5 OTUs as recognized above are characterized and then used as a basis for comparison among each other and with the Region 5 specimens not readily placed into these OTUs. As there are but a few recordings available for these OTUs, discussion of the advertisement call of Region 5 OTUs is deferred until later in the analysis.

The posterior lip stripe of the Small Size Guianas OTU is very distinct in few (3%) individuals, distinct in half the specimens, indistinct in many (42%), and not discernible in only a few (5%) specimens. The stripe pattern is quite variable. The predominant pattern, and the characteristic pattern, is for the light stripe to be clearly and distinctly bordered above from the posterior portion of the eye, below the tympanum, and to the jaw commissure region, whereas the lower border of the stripe is ill-defined, more or less blending into the head pattern, and the anterior extent of the stripe extends forward in an indeterminate fashion toward the middle of the eye region (Figure 11A). The next most common pattern is for the stripe to be bordered by darker pattern above and below and extend forward only to the posterior corner of the eye. A rarer pattern

TABLE 25.—Minima, maxima, and summary statistics for size and measurement ratios for Region 4 Light Posterior Belly OTU adults. (N = 314 females, 181 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	35.1	53.8	46.8	3.409
SVL	M	32.8	47.9	40.7	2.572
Head length/SVL	F	0.322	0.410	0.359	0.013
Head length/SVL	M	0.340	0.412	0.366	0.012
Head width/SVL	F	0.304	0.381	0.340	0.012
Head width/SVL	M	0.312	0.376	0.348	0.011
Tympanum/SVL	F	0.058	0.085	0.071	0.004
Tympanum/SVL	M	0.058	0.086	0.075	0.005
Thigh/SVL	F	0.340	0.486	0.434	0.024
Thigh/SVL	M	0.347	0.486	0.436	0.026
Shank/SVL	F	0.415	0.516	0.468	0.018
Shank/SVL	M	0.424	0.511	0.472	0.016
Foot/SVL	F	0.465	0.614	0.526	0.024
Foot/SVL	M	0.472	0.625	0.532	0.024

is that the stripe is very white and very narrow from the jaw commisure gland to under the eye region. No individuals have very distinct stripes on the posterior face of the thighs, many have distinct (18%) or indistinct (23%) stripes, and most (60%) have no indication of light thigh stripes. A few specimens (5%) have no indications of dorsolateral folds (preservation artifact?), most (85%) have at least indications of short dorsolateral folds extending from the eye to less than half the distance from the eye to the sacrum, and some (10%) specimens have moderate folds, extending more than half the distance from the eye to the sacrum. Most individuals (79%) have light-spotted chins. The belly pattern is quite variable, including mottling or speckling, and there may or may not be an anterior-posterior gradient in pattern intensity. Most specimens (62%) have lightly patterned bellies, many (31%) have moderately patterned bellies, and a few (8%) have extensively patterned bellies. Toe tips are variable, ranging from just swollen (14%), swollen (35%), just expanded (26%), expanded (14%), to having small disks (10%). In males with black thumb spines, only one (2%) has small/medium-size spines, almost all (95%) have medium-size spines, and 2 individuals (3%) have medium/large-size spines.

Outlier detection analyses of measurement data were run separately for males and females of the Small Size Guianas OTU. The plot of the first against the second principal components for males (accounting for 85% of the variation) indicates that there is but minor differentiation along the first axis. The two most distinctive individuals along the first axis include the smallest and the third smallest males in the sample. The smallest and most distinct male is part of a small series (RMNH 23683–23690) and re-examination indicates no change of taxonomic opinion on my part. The second most distinctive male (MZUSP 24001) is part of the previously discussed series from Langaman Kondre, Surinam. The two most distinctive males at the other end of the first principal component axis include the largest male in the sample; both specimens are part of the previously discussed series from Kartabo, Guyana. There is greater differentiation along the first principal component axis for females than for males, but there is relatively little variation along the second axis (Figure 24). The variation accounted for by the first two axes is 89% of the total. The most distinctive individuals identified by the analysis include the largest females. The largest and most distinctive female along the first axis, CAS 146925 (Figure 24, solid square), does not differ from the others except for size. The next three most distinctive females (Figure 24, circle = AMNH 11687, triangle = AMNH 11688, open square = AMNH 70883) are part of a large series from Kartabo, Guyana, discussed previously.

Males of the Small Size Guianas OTU range from 27.8 to 37.3 mm SVL; females range from 31.2 to 44.9 mm SVL. There is one noteworthy apsect of size observed among the females analyzed. A series of 10 juvenile females ranges in size from 30.3 to 38.9 mm SVL. Excluding the four largest juvenile females, the range of the remaining six is 30.3 to 32.7 mm SVL, which is not unusual. The four largest juvenile females come from two localities. Three, including the largest, UMMZ 50198, are from Dunoon, Guyana. That individual, and UMMZ 50188, a 36.1 mm SVL individual, have nematodes in the body cavity suggesting that the parasite load is preventing the females from storing enough energy to initiate reproduction, but not growth. The third large juvenile female from Dunoon, UMMZ 50187, a 34.9 mm SVL specimen, does not appear to have nematodes in the body cavity. Other females from Dunoon are mature at a smaller SVL than these large juvenile specimens. The fourth specimen, RMNH 23902 from Widagron, Surinam, at 35.3 mm SVL, does not appear to have nematodes in the body cavity.

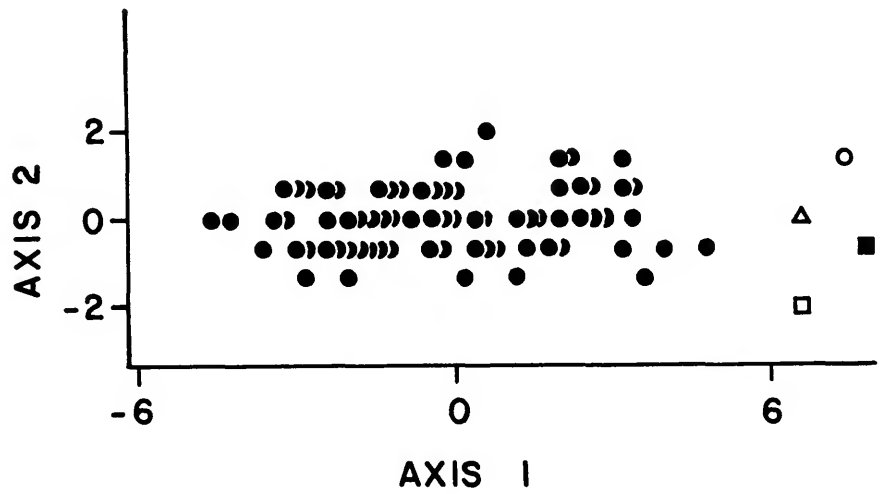

FIGURE 24.—Principal component analysis, plot of first principal component axis against second, for Small Size Guianas OTU females. See text for further explanation.

Habitat data are available for 48 individuals from 20 localities. Just over half (56%) of the individuals were collected from open habitats including roads and farms. Many specimens (29%) were collected from within rainforest and a few (14%) were taken from forest/open intermediate habitats including swamp forest and savannah forest.

Few (12%) Anastomotic Belly Region 5 OTU individuals have distinct posterior lip stripes, even fewer (4%) have very distinct stripes, many (44%) have an indication of a light stripe, and many (40%) have no indication of a light posterior lip stripe. The posterior lip stripe, when present, typically is more or less dark bordered and extends from the posterior corner of the eye. A few (6%) specimens have distinct light stripes on the posterior face of the thigh, a few (8%) have indications of light stripes, but most (86%) do not have any indication of light stripes. Almost all (94%) of the specimens have indications of short dorsolateral folds extending to no more than half the distance from the eye to the sacrum, a few (6%) have indications of moderate dorsolateral folds extending from the eye to no further than the sacrum. The chin is light spotted in most (75%) specimens. The belly is moderately (32%) to heavily (68%) pigmented, with the distribution of pigment uniformly spread over the belly. The belly pattern ranges from mottled to (usually and characteristically) boldly mottled in an anastomotic pattern. Toe tips range from narrow (16%) to just swollen (61%) to swollen (16%) to just expanded (7%). None of the specimens were scored as having expanded toe tips or having small toe disks. For males with black thumb spines, almost all (95%) have medium-size spines, a few (4%) have small-size spines.

Outlier detection analysis results for males indicate that a plot of the first two axes (which account for 92% of the variation) shows a single rather uniform cluster, with no obvious outlier individuals. For females, there again is only separation along the first principal component axis (accounting for 92% of the variation, the first two axes accounting for 95%). Re-examination, using the oviduct criterion, of two specimens at one end of the first axis indicates that they are juvenile females. The two outliers at the other end of the axis are the largest females, the largest of which is from a locality with a female that lies in the middle of the first axis.

Males range in size from 30.0 to 37.1 mm SVL; females range from 33.1 to 45.0 mm SVL.

Habitat data are available on 34 specimens from 16 localities. All specimens were collected from forests, most of them along creek banks in, on, and among leaves, stones, or tree trunks. A few individuals were collected from the sides of forest puddles.

Only nine Moderate Size, Light Posterior Belly, Guianas OTU individuals were readily assigned to this OTU. The posterior light lip stripe is distinct in one individual, indistinct in six, and absent in two. The light stripe on the posterior thigh is variable; two individuals have very distinct thigh stripes, three have distinct, two have indistinct stripes, and two individuals have no indication of a light stripe on the thighs. All nine have indications of short dorsolateral folds. The chin is spotted in five individuals. The belly is lightly mottled in four, moderately mottled in four, and extensively mottled in one, with the pigment being more extensive anteriorly. Toe tips are swollen in seven individuals, expanded on two. All five males with black thumb spines have medium-size spines.

Six males range from 38.4 to 44.0 mm SVL; three females

range from 41.9 to 48.8 mm SVL.

Habitat data are available for seven specimens from two localities. Two were taken in high forest along a creek either on the bank or in leaves. Three were taken by a pool at the edge of high forest. Two were taken under leaves by pools in a palm forest.

Twenty-three Aragua OTU individuals are available for analysis for this OTU. Posterior light lip stripes range from distinct (9%) to indistinct (68%) to no indication of a lip stripe (23%). The lip stripes, when present, extend from the posterior corner of the eye and are as well defined above as below. The light stripe on the posterior face of the thighs ranges from very distinct (13%) to distinct (56%) to indistinct (22%) to without any indication of a stripe (9%). In some (18%) individuals, no dorsolateral folds are discernible; most have indications of short folds (77%), with one individual (4%) having moderate folds. Light chin spots occur on 35% of the sample. The belly is lightly pigmented (20%), moderately pigmented (75%), or extensively pigmented (5%). Toe tips range from just swollen (13%), swollen (48%), just expanded (17%), to expanded (22%). In the eleven males with black thumb spines, five have medium-size spines and six have medium/large-size spines.

Twelve males range from 33.9 to 42.2 mm SVL; 11 females range from 39.2 to 49.1 mm SVL.

No habitat data are available.

Ten Small Size Bolívar OTU individuals are available for analysis for this OTU. One has a distinct light posterior lip stripe, five have indistinct stripes, and four have no indications of stripes. All stripes extend from the posterior corner of the eye and are as distinct above as below. The light stripes on the posterior faces of the thighs range from distinct (3), indistinct (5), to no indication of a light stripe (2). In half the sample, no dorsolateral folds are discernible (preservation artifact?). In the rest, the folds are either short (4) or medium (1) in length. Light chin spots occur in two of the individuals. The belly is lightly pigmented in eight specimens, moderately pigmented in one, and extensively pigmented in one. In the three males with black thumb spines, two have medium-size spines and one has medium/large-size spines.

Four males range from 31.9 to 40.6 mm SVL; two females range from 34.9 to 38.8 mm SVL.

Habitat data are available for seven individuals from four localities. One was taken from a dry stream bed in the forest, one was taken at the edge of forest, and five were collected from open habitats of clearings or savannahs.

Twenty-eight Medium Size Bolívar OTU specimens are available for analysis of this OTU. The posterior light lip stripes range from distinct (11%), indistinct (39%), to no indication of a stripe (50%). Lip stripes, when present, extend from the posterior corner of the eye and are as distinctly bordered above as below. The light thigh stripes on the posterior faces of the thighs range from distinct (23%) to indistinct (43%) to without any indication of a stripe (34%). Dorsolateral folds are either medium length, extending more than half the distance from the eye to the sacrum to as far as the sacrum (68%), or long, extending from the eye to the sacrum or beyond (32%). The chin is light spotted in some (14%) individuals. The belly is lightly mottled (14%), moderately mottled (61%), or extensively mottled (25%). The toe tips range from just swollen (46%) to swollen (36%) to just expanded (18%). In the 19 males with black thumb spines, twelve have medium-size spines, six have medium/large-size spines, and one has large spines.

Nineteen males range from 40.5 to 46.4 mm SVL; nine females range from 42.1 to 56.9 mm SVL.

Habitat data are only available for two individuals from two localities. One was collected from a low forest at the edge of a pool. One was collected by a small marsh along a road in high forest.

The six OTUs differ from each other at least qualitatively, but it is difficult to tell whether some of the differences are due to sampling artifact. In order to evaluate the measurement differences among OTUs, discriminant function analyses were performed on males and females separately. The results of the discriminant function analyses are discussed together with the morphological features other than measurements.

Examination of the generalized squared distances among the OTUs and posterior classification results of the discriminant function analyses (Tables 26, 27) indicates that the Anastomotic Belly Region 5 OTU is quite distinct based on measurement data from the other OTUs. All specimens initially identified by me as Anastomotic Belly Region 5 OTU members but posteriorly classified as either Small Bolívar OTU, Medium Size, Light Posterior Belly, Guianas OTU, or Small Size Guianas OTU as well as those initially identified by me as Small Size Guianas OTU members but posteriorly classified as Anastomotic Belly Region 5 OTU individuals were re-examined. Based on the morphological features discussed in detail previously, all but two individuals are considered to belong to the same OTU to which I originally identified them. RMNH 23852 from Kaw, French Guiana, initially was identified as a Small Size Guianas OTU member. The specimen has a somewhat faint, but distinct, anastomotic pattern that has an uniform intensity over the entire belly; the specimen does in fact belong to the Anastomotic Belly Region 5 OTU. The second specimen is AMNH 25233, a male from Kartabo, Guyana, from which a fairly large series of specimens was identified as all belonging to the Small Size Guianas OTU. Several of the specimens in this series are poorly preserved. AMNH 25233 does in fact have an extremely faint anastomotic pattern on the belly seemingly of equal intensity throughout. All specimens in this series were re-examined. In most, there is no question that the Small Size Guianas OTU designation is correct. However, there is considerable variation in belly pattern in this sample, ranging from almost no melanophores to speckled to mottled and a few individuals approach an anastomotic belly pattern. Those that do, such as AMNH 70897, have an anastomotic pattern on the anterior half of the

TABLE 26.—Generalized squared distances between OTUs. The full names of abbreviated OTUs are: Anastomotic Belly Region 5 OTU; Small Size Guianas OTU; Moderate Size, Light Posterior Belly, Guianas OTU.

Sex and OTU	Anastomotic Belly	Aragua	Medium Bolívar	Small Bolívar	Small Guianas	Moderate Guianas
Females						
Anastomotic Belly	0	14.2	36.0	6.5	10.0	15.0
Aragua		0	18.2	11.2	18.5	2.6
Medium Bolívar			0	39.4	46.3	18.3
Small Bolívar				0	2.7	17.1
Small Guianas					0	24.0
Moderate Guianas						0
Males						
Anastomotic Belly	0	22.4	33.8	19.0	11.9	28.1
Aragua		0	16.3	2.6	11.4	5.4
Medium Bolívar			0	20.8	34.6	13.4
Small Bolívar				0	5.2	7.4
Small Guianas					0	17.6
Moderate Guianas						0

TABLE 27.—Discriminant analysis for readily identifiable males and females of six OTUs from Region 5. Values are the number of observations classified into OTUs. The full names of abbreviated OTUs are: Anastomotic Belly Region 5 OTU; Small Size Guianas OTU; Moderate Size, Light Posterior Belly, Guianas OTU.

Sex and OTU	Anastomotic Belly	Aragua	Medium Bolívar	Small Bolívar	Small Guianas	Moderate Guianas
Females						
Anastomotic Belly	11	0	0	4	0	1
Aragua	0	5	0	2	0	4
Medium Bolívar	0	1	7	0	0	1
Small Bolívar	0	0	0	0	2	0
Small Guianas	5	2	0	11	95	1
Moderate Guianas	0	3	0	0	0	0
Males						
Anastomotic Belly	32	0	0	0	4	0
Aragua	0	6	0	4	1	1
Medium Bolívar	0	1	15	0	0	3
Small Bolívar	0	2	0	0	1	1
Small Guianas	2	1	0	13	66	1
Moderate Guianas	0	1	0	0	0	5

belly that breaks down posteriorly. There are, in addition to AMNH 25233, four other individuals from this locality that also are considered to belong to the Anastomotic Belly Region 5 OTU. Three of them are juveniles, two not very well preserved (AMNH 39630, 39633), one reasonably well preserved (AMNH 39697). All three juveniles have the distinctive and characteristic anastomotic pattern on the belly. A problematical specimen is the poorly preserved female, AMNH 39631. The specimen has been gutted and the posterior belly skin is missing. The anterior belly skin has an anastomotic pattern, however, and direct comparison with similar-size females from the same locality indicates that it more likely represents the Anastomotic Belly Region 5 OTU than the Small Size Guianas OTU. With these adjustments, the morphological data are robust in considering the Anastomotic Belly Region 5 OTU a species distinct from the other OTUs analyzed for Region 5.

The Medium Size Bolívar OTU also is quite distinct based on the generalized squared distances of the discriminant function analysis using measurement data (Table 26), with a consequence that there are few misclassifications from the posterior classification procedure (Table 27). This measurement-based distinctiveness is supported by other features. The other Region 5 OTUs have predominantly short dorsolateral folds and some have moderate dorsolateral folds. Most Medium Size Bolívar OTU specimens have medium dorso-

lateral folds and several have long folds. Medium/large black thumb spines are more frequent in occurrence in this OTU than in most of the others, and the Medium Size Bolívar OTU is the only Region 5 OTU for which large black thumb spines were recorded. The Medium Size Bolívar OTU is distinctive in relation to the other Region 5 OTUs.

For the remaining OTUs, the situation is not as clear. The discriminant function analysis (Tables 26, 27) does indicate that the OTUs from the same geographic regions are quite distinct from each other. Specifically, the Small Size Guianas OTU is distinct from the Moderate Size, Light Posterior Belly, Guianas OTU (the two specimens, AMNH 11687, 13518 from Kartabo, Guyana, originally identified as belonging to the Small Size Guianas OTU but classified posteriorly as having a greater likelihood of belonging to the Moderate Size, Light Posterior Belly, Guianas OTU, have no features to suggest that the identification should be changed from that made originally), and the Medium Size Bolívar OTU is distinct from the Small Size Bolívar OTU. Examination of the discriminant function analysis (Tables 26, 27) indicates that the Aragua OTU and Moderate Size, Light Posterior Belly, Guianas OTU are similar, the cluster of Aragua OTU—Small Size Bolívar OTU—Small Size Guianas OTU are similar, and that the Aragua OTU, Small Size Bolívar OTU, and Moderate Size, Light Posterior Belly, Guianas OTU are not robust in that many to all individuals are not correctly classified posteriorly. These OTUs are discussed further below in conjunction with Region 5 specimens that were not sorted initially into OTUs.

There are only a few specimens from the Guianas that were not sorted initially into the three OTUs recognized from French Guiana, Surinam, and Guyana. Of two specimens from Kaw, French Guiana, one (RMNH 23852) already has been discussed. RMNH 23852, a female, originally was identified as a Small Size Guianas OTU member but was changed to the Anastomotic Belly Region 5 OTU. The second specimen, MCZ 99132, a male, has a very similar belly pattern to RMNH 23852; however, MCZ 99132 has a distinct, narrow light posterior eye stripe that extends to under the middle of the eye region. This condition was never observed in the Anastomotic Belly Region 5 OTU specimens and is present only rarely, but exclusively, in the Small Size Guianas OTU among OTUs analyzed from the Guianas. Comparison of the two specimens side by side suggests that they represent distinct species. MCZ 99132 is considered to be a member of the Small Size Guianas OTU. Three juveniles from near Mana, French Guiana (TCWC 65569–65571), have character states that could belong to either the Anastomotic Belly Region 5 or Small Size Guianas OTUs. All three appear to represent the same taxon. Based on interpretation of indistinct light posterior lip stripes in two of the specimens, they are considered to represent the Small Size Guianas OTU, but this locality record should be confirmed with additional material. Two OTUs clearly are represented by specimens from Kaiserberg Airstrip, Nickerie, Surinam: the Anastomotic Belly Region 5 OTU and the Small Size Guianas OTU. One adult female Anastomotic Belly Region 5 OTU member (RMNH 23643) is distinctive in terms of having light stripes on the posterior thighs (a condition only rarely encountered in the other Anastomotic Belly Region 5 OTU specimens), and the belly pattern, although clearly anastomotic, has a more noticeable anterior-posterior intensity gradient than other members of this OTU. The degree of distinctiveness of RMNH 23643 is most consistent with its inclusion as a member of the Anastomotic Belly Region 5 OTU and is not indicative of a third species from this locality. Two males from Paloemeu, Surinam (RMNH 24013, 24014), and one male from Loëkreek Camp, Surinam (RMNH 23898), are similar to the Medium Size, Light Posterior Belly, Guianas OTU in all features (including belly pattern and size) except for the condition of the male thumb spines. In these three individuals, the spines are medium/large, not medium as scored for the Medium Size, Light Posterior Belly, Guianas OTU. Re-examination of specimens indicates that the spine condition represents part of a continuum; the three males are included in the Medium Size, Light Posterior Belly, Guianas OTU.

There are specimens from clusters of localities and from a few scattered localities from Venezuela and the State of Roraima, Brazil. These materials are not entirely adequate to understand the variation encountered, in all likelihood because the variation in frogs correlates in some way with the extensive habitat diversity occurring in Venezuela and Roraima. The previous sortings into OTUs, although useful as a first step, were not particularly instructive in evaluating the specimens not sorted into OTUs during the initial analysis. All localities were plotted and all specimens were re-examined taking both morphology and geography into account. Generally, in the specimens at hand, there are samples from low elevations that represent at least two species and series of samples associated with three higher elevation regions.

Specimens from Delta Amacuro, the lowland locality of Caripito, Monagas, Venezuela, and the lowland localities of near Bohordal and near Guaraunos, Sucre, Venezuela, represent the same species as the Small Size Guianas OTU, although only two specimens from Monagas and Sucre have the posterior lip stripe character being well-outlined above and poorly defined below but extending to under the middle of the eye (Figure 11A). There is only one specimen from the upland regions found in the Venezuelan states of Anzoátegui, Monagas, and Sucre. The specimen is a poorly preserved 47.8 mm female from Caripe, Monagas, 1150 m. It is noticeably larger than the series of 10 females at hand from the nearby lowland (100 m) locality of Caripito, Monagas, which range from 32.0 to 42.5 mm SVL. With only a single specimen from this upland region, it is impossible to determine whether it represents an altitudinal cline in size of the nearby lowland species or a distinct species from the adjacent lowland form. A series of specimens from El Manteco, Bolívar, and environs (including elevations of 300–350 m) and two specimens from the northeastern Bolívar locality of near El Palmar also

represent the same species as the Small Size Guianas OTU, the only difference being that none of these Bolívar specimens have the well-defined upper edge of the light posterior eye stripe with the lower edge ill defined but extending to under the middle of the eye. The El Manteco region and El Palmar specimens include all but one locality sample included in the Small Bolívar OTU discussed above.

A series of specimens collected along the road between El Dorado and Santa Elena de Uairen, Bolívar, Venezuela, include all the specimens included in the Medium Size Bolívar OTU discussed above as well as two specimens from Cabanayen that were included in the Small Size Bolívar OTU. All specimens from between 1200–1400 m along this road represent the same taxon. Two specimens (MVZ 176010, 176011) from the elevation of 700 ft (215 m) just north of a locality at 1250 m along the same road are problematic. Based on appearance, the two are very similar to the Small Size Guianas OTU; however, the 38.0 mm SVL male and the 47.3 mm SVL female are larger than any other Small Size Guianas OTU specimens, and they fit in at the low size range of the Medium Size Bolívar OTU. For the moment, these two specimens are not assigned to an OTU. A series of juveniles, most not well preserved, from Arabopó, Bolívar, 1200–1300 m, and Paulo, Mt. Roraima, Bolívar, 5100 ft (~1550 m), are somewhat questionable as to identity, but they are provisionally included in the Medium Size Bolívar OTU. Three specimens from Pacaraima, BV-8, Roraima, Brazil, on the Brazil-Venezuela border, just south of Santa Elena de Uairen, represent two species. INPA 1304, a 35.4 mm SVL male, and INPA 1302, a 38.8 mm SVL female, have light-speckled bellies and are members of the Small Size Guianas OTU. INPA 1303, a 44.9 mm SVL female, has a heavily mottled, almost anastomotic, patterned belly. INPA 1303 matches well with Medium Size Bolívar OTU specimens and is included in that OTU.

All other specimens at hand from the State of Roraima are the same as either the Anastomotic Belly Region 5 OTU or the Small Size Guianas OTU. Both OTUs occur sympatrically at the localities of Colonia Apiaú and Ilha de Maracá.

Specimens from several localities on or adjacent to the Venezuelan Andes in the states of Tachira, Mérida, Barinas, Trujillo, Falcón, Aragua, Miranda, Guarico, and Distrito Federal appear to represent a single taxon. This taxon includes all the individuals of the Aragua OTU discussed above. Most of the specimens have been collected from higher elevations (850–1900 m), but specimens from lowland localities adjacent to the mountains appear to be the same (except for specimens discussed in the following paragraph). Within this OTU, specimens from two localities are distinctive or questionable. Five specimens from near Bocono, Trujillo, Venezuela, 1575 m (KU 132815–132820) are distinctive in that none of the specimens have light stripes on the posterior thighs as occurs frequently in the other samples, and the three adult males and one adult female are a bit larger than the other specimens (Bocono males 44.3–48.5 mm SVL, largest male from other localities 42.2 mm SVL; Bocono female 51.6 mm SVL, largest female from other localities 50.3 mm SVL). A single juvenile from the foothill locality of Quebrada de Las Palmas, Barinas, Venezuela (MNRJ 4891), is somewhat questionable, but it appears to represent the same taxon as the Venezuelan Andes taxon. Adults are needed from this locality to confirm the identification.

A few specimens from mostly lowland localities around Lake Maracaibo differ from the Venezuela Andes OTU, most notably in size. The Lake Maracaibo specimens are small (female 39.0 mm SVL, males 29.4–34.1 mm SVL), in the same size range as the Small Size Guianas OTU. With only a few adult individuals, no clearcut decisions can be made at this point regarding their allocation. Further discussion of these Lake Maracaibo specimens is deferred until these specimens are considered with geographically close specimens from Colombia.

There remain a handful of specimens from scattered lowland localities in the greater Orinoco drainage in the states of Guarico, Apure, and westernmost Bolívar that are quite geographically distant from the previously discussed lowland forms from eastern Bolívar, Monagas, and Delta Amacuro. These specimens are small size, the four adult females range from 29.5 to 38.9 mm SVL, and the two adult males range from 30.4 to 32.0 mm SVL. All specimens have just-swollen or swollen toe tips; in all other characteristics they match at least some individuals of the Small Size Guianas OTU. These specimens are tentatively included in the Small Size Guianas OTU for purposes of this paper.

To summarize at this point, with few exceptions, Region 5 specimens are assigned to five OTUs: an Anastomotic Belly Region 5 OTU; a Small Size Guianas OTU; a Moderate Size, Light Posterior Belly, Guianas OTU; a Medium Size Bolívar OTU; and a Venezuela Andes OTU.

Discriminant function analyses using measurement data were run separately for males and females for the five Region 5 OTUs exclusive of the Lake Maracaibo specimens and the three other adults for which no OTU allocation is appropriate. Examination of the generalized squared distance values (Table 28) indicates that, based on measurements, the Venezuela Andes, Medium Size Bolívar, and Moderate Size, Light Posterior Belly, Guianas OTUs are quite similar to each other. The classification results (Table 29) indicate that there is only moderate success in properly classifying the Venezuela Andes, Medium Size Bolívar, and Moderate Size, Light Posterior Belly, Guianas OTUs and that the latter OTU has the poorest classification based on measurement data.

Examination of the data and specimens for the cases where there was a higher probability of belonging to an OTU different from the original identification indicates two items worth noting. First, re-examination of CAS 146925 from French Guiana, between Cayenne and Tonate, which was originally identified as a Small Size Guianas OTU member, is actually a member of the Anastomotic Belly Region 5 OTU as suggested

TABLE 28.—Generalized squared distances among OTUs for Region 5. Full names of abbreviated OTUs are: Anastomotic Belly Region 5 OTU; Small Size Guianas OTU; Moderate Size, Light Posterior Belly, Guianas OTU.

Sex and OTU	Anastomotic Belly	Medium Bolívar	Small Guianas	Venezuela Andes	Moderate Guianas
Females					
Anastomotic Belly	0	26.3	9.6	14.8	12.0
Medium Bolívar		0	34.1	13.2	12.6
Small Guianas			0	16.8	19.8
Venezuela Andes				0	4.2
Moderate Guianas					0
Males					
Anastomotic Belly	0	23.9	10.3	23.6	20.6
Medium Bolívar		0	22.7	9.7	6.5
Small Guianas			0	10.6	16.2
Venezuela Andes				0	5.1
Moderate Guianas					0

TABLE 29.—Discriminant analysis for Region 5 OTUs. Values are the number of observations classified into OTUs. Full names of abbreviated OTUs are: Anastomotic Belly Region 5 OTU; Small Size Guianas OTU; Moderate Size, Light Posterior Belly, Guianas OTU.

Sex and OTU	Anastomotic Belly	Medium Bolívar	Small Guianas	Venezuela Andes	Moderate Guianas
Females					
Anastomotic Belly	16	0	3	0	2
Medium Bolívar	0	8	0	1	1
Small Guianas	6	0	135	2	2
Venezuela Andes	2	0	1	15	5
Moderate Guianas	1	0	0	2	0
Males					
Anastomotic Belly	37	0	4	0	0
Medium Bolívar	1	16	0	3	2
Small Guianas	1	0	87	5	0
Venezuela Andes	0	3	3	11	3
Moderate Guianas	0	2	0	2	5

by the discriminant analysis. The belly pattern is very close to an anastomotic pattern. There are two other specimens from this locality, CAS 146926, 146927. Re-examination of all three specimens indicates that they do represent two OTUs, the other two specimens being members of the Small Size Guianas OTU. The second observation is that all of the Venezuela Andes OTU specimens that were classified as members of other OTUs are from the northern cluster of localities in the Venezuelan states of Aragua, Falcón, Guarico, Miranda, and the Distrito Federal.

There are no additional habitat data to those discussed previously for the additional specimens added after the first analysis for Region 5 specimens.

Five calls (four of them vouchered) are available from Region 5. These five calls appear to represent four species. An unvouchered call from Rancho Grande, Aragua, Venezuela, is not used as it is not clear which of two distinct calls (or both?) on the recording is *Leptodactylus*.

The first call type was recorded from MZUSP 62430 from Ilha de Maracá, Roraima, Brazil, a member of the Anastomotic Belly Region 5 OTU. Calls are given at a rate of 1.3 per s. Each call is composed of two abutting notes. The duration of entire calls ranges from 0.03 to 0.04 s. The first note is composed of 2 to (usually) 4 distinct pulses at a frequency range of 900–1600 Hz. The first note is intensity modulated, the first pulse with noticeably less energy than the following pulses. The first note is frequency modulated, rising rapidly from the lowest to highest frequency of the note. The second note is either very weakly pulsatile or not pulsed at all with a frequency range of 1800–2700 Hz. The second note is intensity modulated with a sharp attack to maximum intensity and with a regular lessening of intensity to the end of the note. The second note is frequency modulated, typically rising from the lowest frequency to the highest frequency about midnote, then falling in frequency. The second note has more intensity than

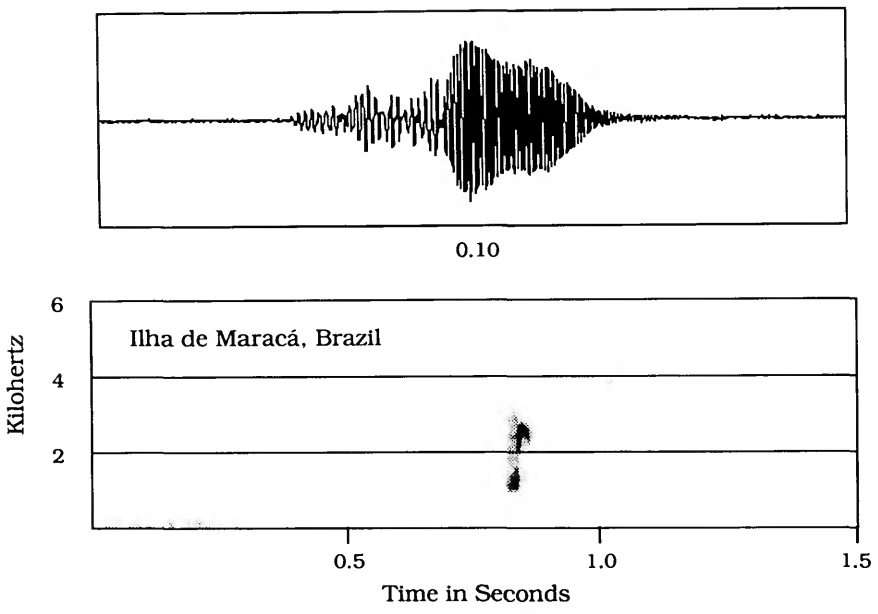

FIGURE 25.—Call of MZUSP 62430, a member of the Anastomotic Belly Region 5 OTU, USNM Tape 213, cut 10. Recorded from Ilha de Maracá, Roraima, Brazil, Sep–Oct 1985, 2350 h, 23.5°C air, by Celso M. de Carvalho.

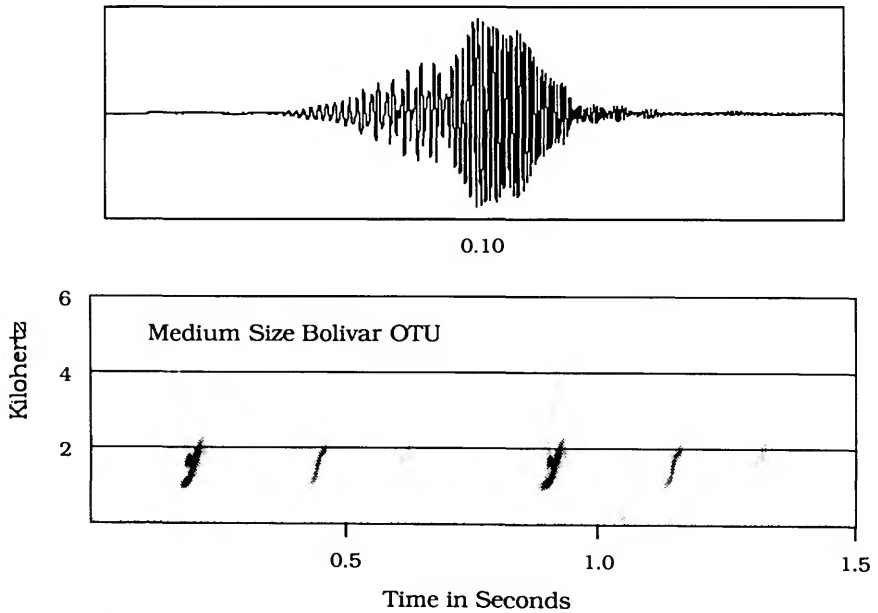

FIGURE 26.—Call of AJCardoso 346, a member of the Medium Bolívar OTU, AJC Tape 107, cut 9. Recorded from near the Monumento al Soldado Pionero, Gran Sabana, Bolívar, Venezuela, 19 Jun 1990, 1900 h, 20°C air, 25°C water, by Adão J. Cardoso. The wave form is of the first call on the audiospectrogram.

the first note (Figure 25).

The second call type was recorded from AJCardoso 346 from near the Monumento al Soldado Pionero, Gran Sabana, Bolívar, Venezuela, a member of the Medium Size Bolívar OTU. The call rate is 1.2 per s. Call duration ranges from 0.04 to 0.06 s. The calls are frequency modulated, sweeping upward, beginning between 900–1000 Hz and ending between 2200–2300 Hz. The call is intensity modulated, loudest in midcall between the frequencies 1400–1800 Hz (Figure 26).

The remaining three calls appear to represent the same species, the Small Size Guianas OTU. One vouchered call is that of USNM 302409 from Igarapé Cocal, Roraima, Brazil. Calls are given at a rate of 0.8 per s. Each call is composed of two abutting notes. The duration of the entire call ranges from 0.03 to 0.04 s. The first note is composed of a single pulse at a frequency range of 1500–1900 Hz. The second note is pulsatile, with 2–5 (usually 4) partial pulses with a frequency range of 2300–3200 Hz. The second note is weakly intensity modulated, the strength of the signal diminishing after a sharp initial increase of intensity. The second note is frequency modulated, starting at the lower frequency and rising to the highest frequency at the end of the note; there is no evidence of a fall in frequency in the latter half of the note. The second note has more intensity than the first (Figure 27). An unvouchered call from BV-8, Roraima, Brazil, is very similar to the second note of the vouchered call described for the Small Size Guianas OTU, specimen USNM 302409. In none of the calls analyzed (6), is there any evidence of a lower frequency initial note (Figure 28). A call from AJCardoso 225–227 from Mantecal, Apure, Venezuela, is similar to the call from Igarapé Cocal in having an initial low frequency note followed by a pulsatile higher frequency note. The call rate is 2.7 per s, the call duration is 0.04–0.05 s. The only obvious difference between this call and that from Igarapé Cocal is that the Mantecal recording has a higher broadcast frequency, with an initial peak between 1800–2200 Hz and a second between 2800–3500 Hz (Figure 29).

The available call data demonstrate that the Region 5 Anastomotic Belly OTU and Medium Size Bolívar OTU each have calls very distinct from the other available recordings. Additional recordings for the Venezuela Andes OTU are needed for characterization of the call and to determine how distinctive the call is from the Small Size Guianas OTU. The three recordings available for the Small Size Guianas OTU are similar enough to consider them as representing variation

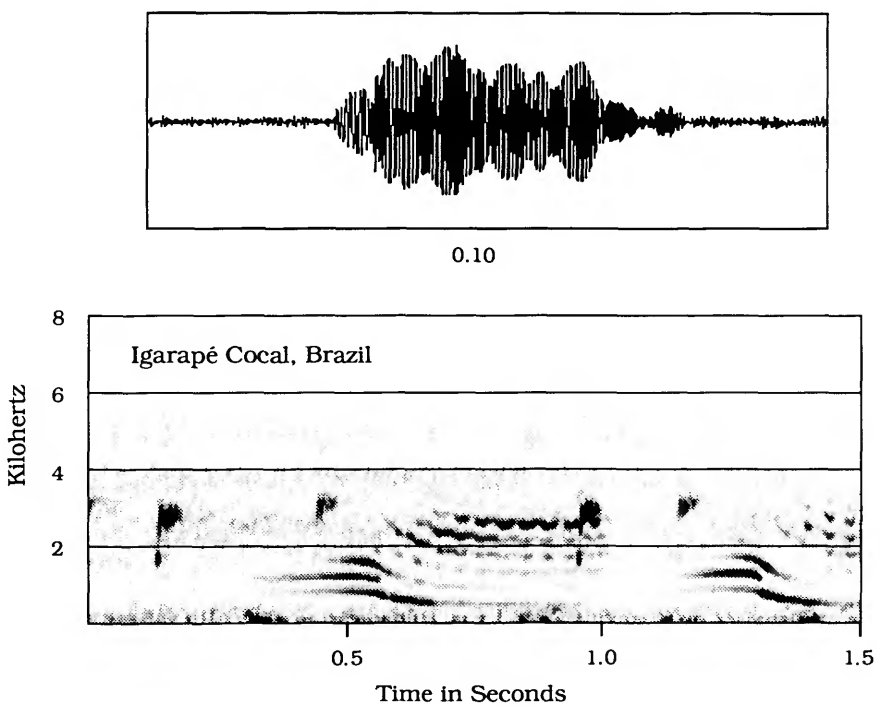

FIGURE 27.—Call of USNM 302409, a member of the Small Size Guianas OTU from Igarapé Cocal, Roraima, Brazil, USNM Tape 209, cut 1. Recorded 22 May 1989, 1945 h, by W. Ronald Heyer.

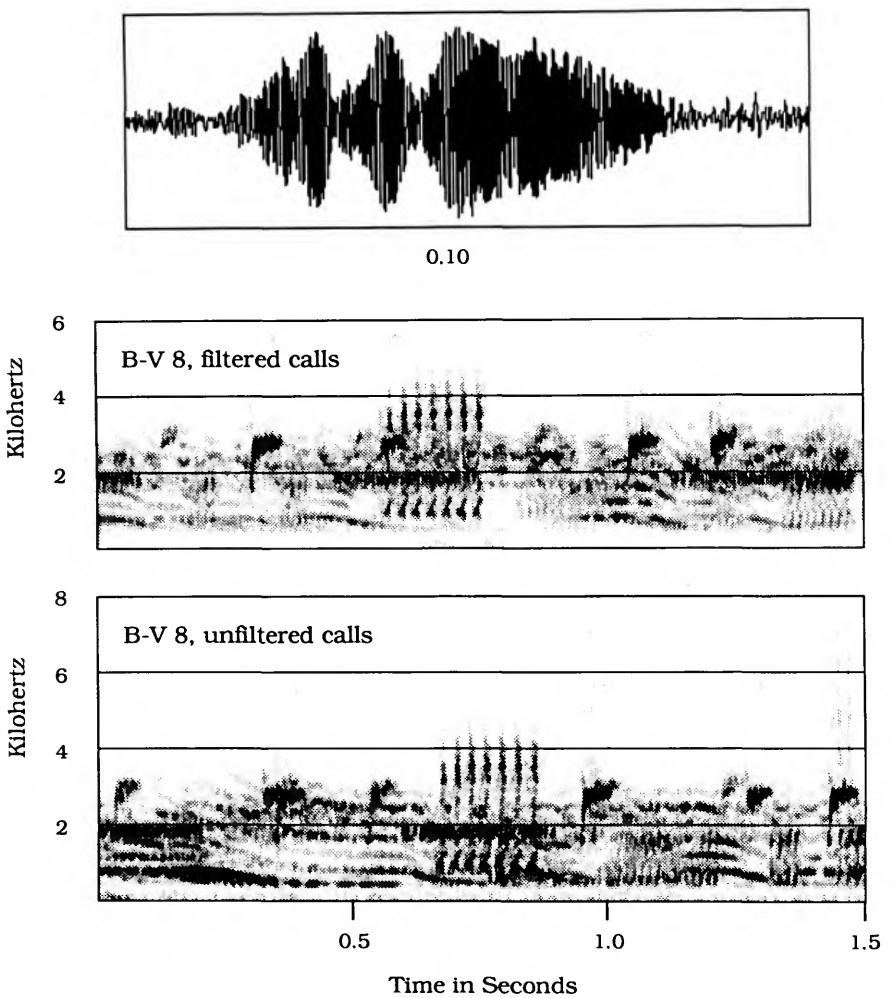

FIGURE 28.—Unvouchered call from B-V 8, Roraima, Brazil, presumably of the Small Size Guianas OTU, USNM Tape 209, cut 4. Recorded 23 May 1989, 2000 h, by W. Ronald Heyer. Upper audiospectrogram with frequencies below 1000 Hz filtered in order to produce wave form of first call on audiospectrogram. Lower audiospectrogram of unfiltered (and different) calls.

within a species.

The call and morphological data combined are adequate to determine that the following OTUs from Region 5 each represent distinct species: Small Size Guianas OTU; Anastomotic Belly Region 5 OTU; and Medium Size Bolívar OTU. The data suggest that the Venezuela Andes OTU represents a single species (although this may be too conservative a conclusion) that is distinct from the Medium Size, Light Posterior Belly, Guianas OTU. The data for the Lake Maracaibo OTU are equivocal, as is the situation for the three adults from Venezuela not assigned to an OTU.

Summary statistics for the five Region 5 OTUs are presented in Tables 30–34.

Region 6—Trinidad, Tobago, Lesser Antilles

Samples are available from the continental islands of Trinidad and Tobago and the oceanic Lesser Antillean islands of Grenada, Bequia, and St. Vincent. None of these samples have been discussed or analyzed in previous sections.

Only on Trinidad are two taxa represented. In the Small–Moderate Size OTU the males range from 30.5 to 39.8 mm SVL, and the females range from 39.7 to 49.0 mm SVL. The posterior lip stripes are sometimes (27%) distinct, usually indistinct (54%), and sometimes not discernible (19%). When present, the stripes extend only to the posterior corner of the eye and are often narrow. The posterior thigh stripes are rarely very

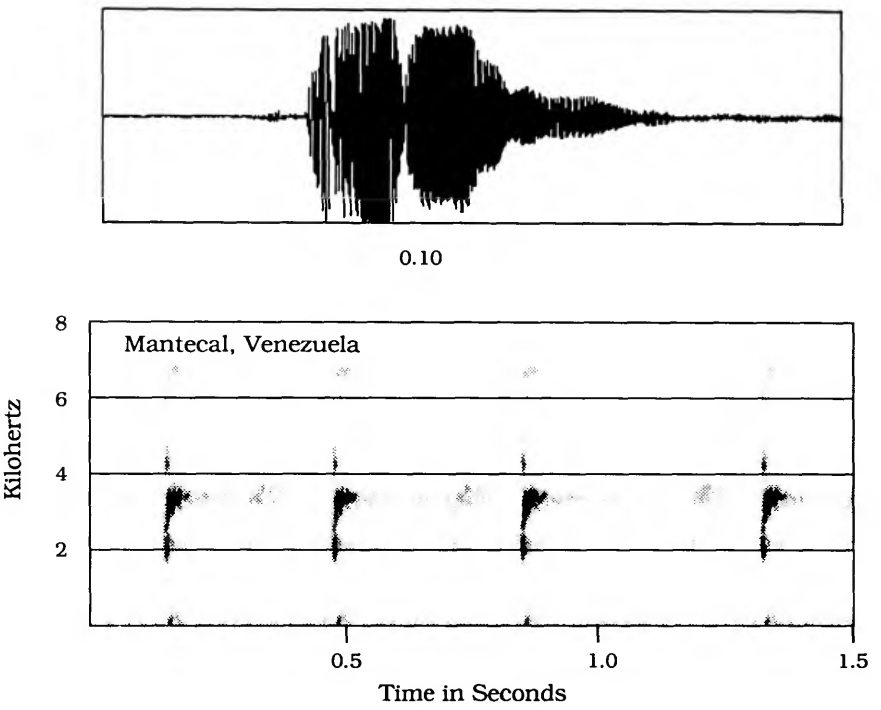

FIGURE 29.—Call of AJCardoso 225-227, from Mantecal, Apure, Venezuela, a Small Size Guianas OTU member, AJC Tape 105, cut 5. Recorded 8 Jun 1990, 1100 h, 19°C air, 21°C water, by Adão J. Cardoso. Wave form is of third call shown in audiospectrogram.

TABLE 30.—Minima, maxima, and summary statistics for size and measurement ratios for Anastomotic Belly Region 5 OTU adults. (N = 22 females, 41 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	33.1	45.0	40.0	3.129
SVL	M	30.0	37.1	33.1	1.904
Head length/SVL	F	0.355	0.414	0.385	0.014
Head length/SVL	M	0.375	0.430	0.403	0.013
Head width/SVL	F	0.325	0.357	0.345	0.009
Head width/SVL	M	0.335	0.386	0.361	0.012
Tympanum/SVL	F	0.070	0.087	0.079	0.005
Tympanum/SVL	M	0.080	0.104	0.095	0.007
Thigh/SVL	F	0.383	0.474	0.429	0.023
Thigh/SVL	M	0.381	0.469	0.430	0.020
Shank/SVL	F	0.415	0.489	0.447	0.019
Shank/SVL	M	0.415	0.471	0.450	0.016
Foot/SVL	F	0.485	0.564	0.532	0.018
Foot/SVL	M	0.480	0.564	0.534	0.020

distinct (3%), often distinct (40%), indistinct (25%), or not discernible (32%). Dorsolateral folds are usually short (84%) and sometimes moderately long (16%). Toe tips range from just swollen (3%), swollen (30%), just expanded (8%), expanded (32%), to having small disks (27%). Some (11%) individuals have light spots on the chin, the rest lack light chin spots. The belly is more heavily pigmented anteriorly, the total belly ranging from lightly mottled (58%), moderately mottled

TABLE 31.—Minima, maxima, and summary statistics for size and measurement ratios for Region 5 Small Size Guianas OTU adults. (N = 144 females, 93 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	29.5	42.8	36.9	2.559
SVL	M	27.8	37.3	33.3	1.895
Head length/SVL	F	0.322	0.400	0.368	0.014
Head length/SVL	M	0.344	0.416	0.380	0.016
Head width/SVL	F	0.295	0.370	0.324	0.015
Head width/SVL	M	0.304	0.378	0.340	0.015
Tympanum/SVL	F	0.061	0.089	0.074	0.005
Tympanum/SVL	M	0.069	0.094	0.081	0.005
Thigh/SVL	F	0.358	0.482	0.421	0.026
Thigh/SVL	M	0.351	0.526	0.430	0.030
Shank/SVL	F	0.415	0.522	0.459	0.024
Shank/SVL	M	0.415	0.541	0.471	0.025
Foot/SVL	F	0.476	0.603	0.535	0.024
Foot/SVL	M	0.500	0.607	0.551	0.023

TABLE 32.—Minima, maxima, and summary statistics for size and measurement ratios for Region 5 Medium Size, Light Posterior Belly, Guianas OTU adults. (N = 3 females, 9 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	41.9	48.8		
SVL	M	37.6	44.0	40.0	1.959
Head length/SVL	F	0.348	0.401		
Head length/SVL	M	0.376	0.412	0.389	0.011
Head width/SVL	F	0.334	0.365		
Head width/SVL	M	0.347	0.394	0.364	0.015
Tympanum/SVL	F	0.074	0.079		
Tympanum/SVL	M	0.078	0.092	0.084	0.005
Thigh/SVL	F	0.387	0.475		
Thigh/SVL	M	0.431	0.476	0.447	0.018
Shank/SVL	F	0.466	0.499		
Shank/SVL	M	0.471	0.513	0.489	0.014
Foot/SVL	F	0.513	0.535		
Foot/SVL	M	0.526	0.580	0.548	0.018

(36%), to rarely extensively mottled (6%).

There is but a single 33.3 SVL male of the Small Size Trinidad OTU at hand. The specimen has a slightly less than distinct posterior eye stripe, but the stripe is broad, well defined above and poorly below, and extends to under the middle of the eye. The posterior surface of the thigh is mottled. The dorsolateral folds are short. The toe tips are swollen. The chin has light spots and the belly is moderately speckled.

The populations on the other islands are most similar to the Small-Moderate Size Trinidad OTU. Sample sizes from these other islands are relatively small, such that it is difficult to determine whether the relatively minor differences observed are due to sampling artifact or population differentiation. Tobago males range from 34.8 to 42.9 mm SVL, and females range from 41.4 to 48.7 mm SVL. Grenada males range from 36.2 to 41.3 mm SVL, with females ranging from 41.0 to 47.8 mm SVL. Four Bequia males range from 34.8 to 37.1 mm SVL; the single female at hand is 42.9 mm SVL. St. Vincent males range from 33.9 to 39.0 mm, and females range from 40.7 to 51.5 mm SVL. One adult or subadult individual each from Tobago and St. Vincent have very distinct light posterior eye stripes. The conditions for posterior thigh stripes, dorsolateral folds, and toe tips are similar to the Small-Moderate Size Trinidad OTU. None of the Tobago, Grenada, Bequia, or St. Vincent samples have light chin spots. On Tobago, most individuals have lightly mottled bellies (86%), and only some have moderately mottled bellies (14%). On Grenada, Bequia, and St. Vincent, all individuals have lightly mottled bellies, with light mottle only in the anterior belly region.

Samples are (barely) adequate to perform a discriminant

TABLE 33.—Minima, maxima, and summary statistics for size and measurement ratios for Region 5 Medium Bolívar OTU adults. (N = 10 females, 22 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	42.1	56.9	51.0	4.825
SVL	M	35.0	46.4	43.0	2.662
Head length/SVL	F	0.344	0.390	0.370	0.015
Head length/SVL	M	0.348	0.396	0.376	0.012
Head width/SVL	F	0.327	0.359	0.343	0.011
Head width/SVL	M	0.321	0.378	0.354	0.013
Tympanum/SVL	F	0.070	0.084	0.079	0.004
Tympanum/SVL	M	0.079	0.095	0.088	0.004
Thigh/SVL	F	0.430	0.489	0.463	0.017
Thigh/SVL	M	0.409	0.486	0.453	0.021
Shank/SVL	F	0.443	0.522	0.490	0.024
Shank/SVL	M	0.452	0.516	0.478	0.016
Foot/SVL	F	0.486	0.614	0.562	0.039
Foot/SVL	M	0.514	0.600	0.549	0.024

TABLE 34.—Minima, maxima, and summary statistics for size and measurement ratios for Region 5 Venezuela Andes OTU adults. (N = 23 females, 20 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	39.2	51.6	45.7	3.483
SVL	M	33.4	48.5	38.8	3.748
Head length/SVL	F	0.324	0.390	0.354	0.018
Head length/SVL	M	0.338	0.386	0.364	0.013
Head width/SVL	F	0.310	0.375	0.344	0.014
Head width/SVL	M	0.336	0.367	0.350	0.009
Tympanum/SVL	F	0.063	0.086	0.073	0.006
Tympanum/SVL	M	0.069	0.090	0.080	0.006
Thigh/SVL	F	0.393	0.492	0.439	0.021
Thigh/SVL	M	0.396	0.468	0.432	0.020
Shank/SVL	F	0.420	0.533	0.471	0.026
Shank/SVL	M	0.451	0.513	0.481	0.016
Foot/SVL	F	0.492	0.602	0.531	0.030
Foot/SVL	M	0.498	0.594	0.543	0.028

function analysis for males of the Small-Moderate Size Trinidad, Tobago, Grenada, Bequia, and St. Vincent OTUs. Generalized squared distances among OTUs are generally small values, with the most similar OTUs based on measurement data being the cluster of Grenada-Bequia-St. Vincent (Table 35). The generally small squared distance values likely account for the several cases of mistaken posterior classifications (Table 36).

Ronald I. Crombie (field notes, pers. comm.) recorded a series of color notes on specimens from Trinidad (USNM 314627, 314628, 314645, 314646, 314671, 314672), Grenada (USNM 314785, 314786), and St. Vincent (USNM 314718, 314726). The following coloration is common among the geographic samples: iris brass or dull brass with (or without) a black reticulum and a dark median streak; basic dorsal color ranging from pale tan with gray green markings, or reddish tan with olive markings, or medium brown with pinkish tan scapular area, to gray brown with darker gray markings; interocular spot ranging from olive to black, sometimes the anterior edge bright yellowish tan; the snout either the same color as the back or lighter tan; perianal warts either not differentially marked or distinct tan color; groin ranging from no distinct coloration to rich ivory or lemon yellow wash; throat pale gray with white stippling to heavy purplish gray mottling, with or without enamel white spots along mandible; chest whitish, white with broad, pale gray mottling, or with sparse purplish gray mottling; belly white or ivory, sometimes yellowish laterally and toward groin; posterior thigh with dull yellow and black reticulum to yellow-orange and black marbling with or without an irregular black stripe bordered

TABLE 35.—Generalized squared distances among OTUs for Region 6 Small-Moderate Size OTU males.

OTU	Trinidad	Tobago	Grenada	Bequia	St. Vincent
Trinidad	0	4.5	4.4	5.0	4.1
Tobago		0	4.9	11.0	8.5
Grenada			0	3.3	1.7
Bequia				0	1.7
St. Vincent					0

TABLE 36.—Discriminant analysis for Region 6 Small-Moderate Size OTU males. Values are the number of observations classified into OTUs.

OTU	Trinidad	Tobago	Grenada	Bequia	St. Vincent
Trinidad	13	3	4	2	0
Tobago	4	17	1	1	1
Grenada	1	1	6	2	2
Bequia	1	0	0	2	1
St. Vincent	1	1	3	2	2

above by a light stripe. The following differences were noted among the geographic samples: the posterior lip stripe was copper on the specimens from Trinidad and St. Vincent, pinkish tan on the Grenada specimen with a stripe; the body warts on the Trinidad specimens are not distinctively colored, the dorsal and lateral warts and tubercles in the Grenada and St. Vincent individuals ranged from pale tan outlined in black to brick red; the under limbs in the Trinidad and St. Vincent individuals were translucent yellow and translucent pink or pinkish in the Grenada specimens.

Habitat data are available for 130 individuals from Trinidad, Tobago, Grenada, and St. Vincent. All were taken from open habitats along airstrips, roadside ditches, near small streams, or next to pasture pools at night.

Calls are available for one Small Size Trinidad OTU individual, two Small-Moderate Size Trinidad OTU individuals, and one Small-Moderate Size Tobago OTU individual, and choruses from Grenada and St. Vincent.

The call of the Small Size Trinidad OTU is given at a rate of 3.8 per s. Call duration is 0.03 s. Each call consists of one partially pulsed note containing 4–5 partial pulses. The call is frequency modulated with the initial pulse having peak intensity around 1500 Hz and the remainder of the call with maximum energy range of 1800–2000 Hz (Figure 30).

The call of an individual Small-Moderate Size Trinidad OTU from C.I.B.C. pond is given at a rate of 1.6 per s. Call duration ranges from 0.05 to 0.06 s. Each call consists of two notes, an initial single-pulsed note, followed by a note with 2–5 partial pulses. The call is frequency modulated with the initial note and first pulse of the second note having a maximum intensity around 1600 Hz and the rest of the second note with maximum intensity ranging from 3100 to 3250 Hz (Figure 31, upper audiospectrogram).

The call of an individual Small-Moderate Size Trinidad OTU from Brasso Seco is given at a rate of 1.9 per s. Call duration is 0.04–0.05 s. Each call consists of two notes, an initial single pulsed note followed by a note of 5–6 partial pulses. The call is frequency modulated with the first note and first pulse of the second note having a maximum intensity from 1300 to 2100 Hz and the rest of the second note with maximum intensity ranging from 2700 to 3500 Hz (Figure 31, middle audiospectrogram).

The call of the Small-Moderate Size Tobago OTU individual is given at a rate of 1.8 per s. Call duration ranges from 0.04 to 0.05 s. Each call consists of one or two notes (if two notes, the first is weak in intensity). The first note, when present, consists of a single pulse. The long note consists of 4 partial pulses. The call is frequency modulated with the initial note and first pulse of the longer or second note having a maximum intensity of 1300–1800 Hz, followed by maximum intensities of 2300–3200 Hz (Figure 31, lower audiospectrogram).

Calls of the Grenada individuals are given at a rate of about 1.3 per s. Call duration is 0.03–0.04 s. There is a weak or indistinguishable initial note followed by a partially pulsed longer note. The call is frequency modulated with the initial energy around 1800–1900 Hz followed by the dominant broadcast frequency in the 2900–3400 Hz range (Figure 32).

Calls of the St. Vincent individuals are given at an approximate rate of 1.1 per s. Call duration ranges from 0.03 to 0.05 s. There is usually a weak initial note followed by a longer, partially pulsed note. The call is frequency modulated with

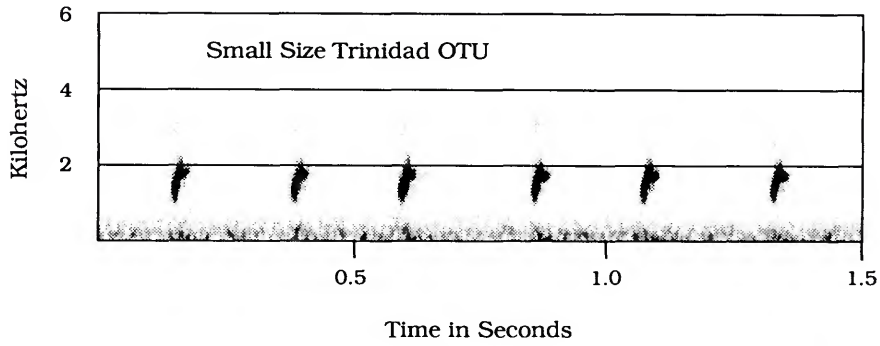

FIGURE 30.—Call of Small Size Trinidad OTU, from Icacos, Trinidad, recorded by J.R. Downie.

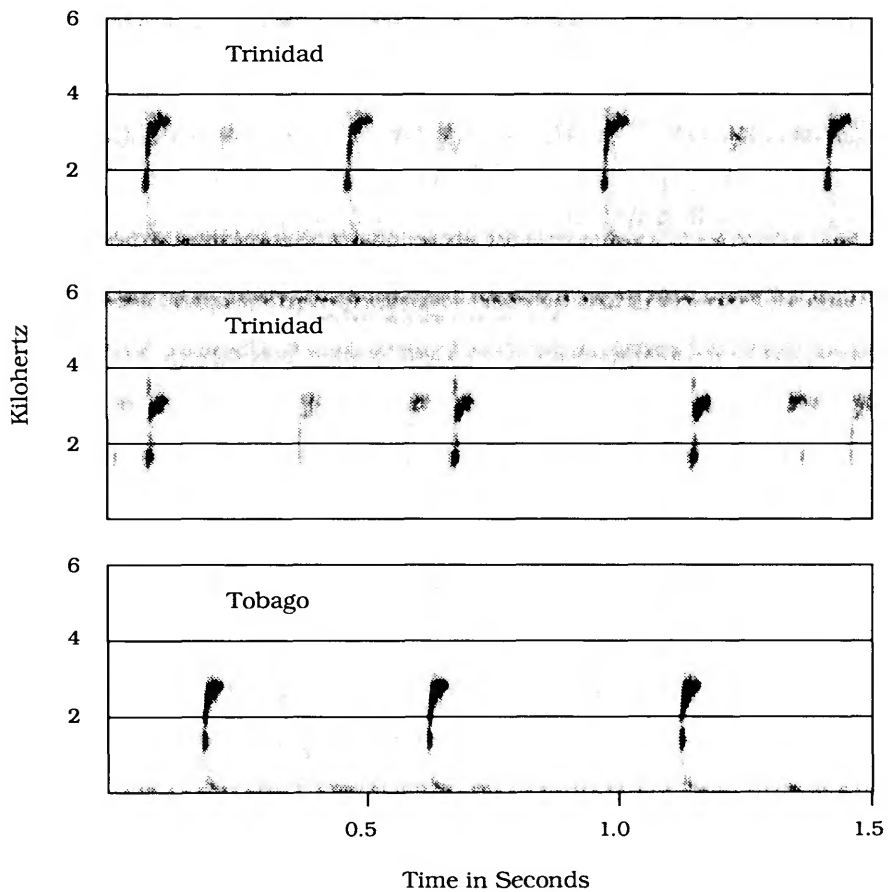

FIGURE 31.—Calls of Small-Moderate Size Trinidad and Tobago OTUs. Upper audiospectrogram recording from C.I.B.C. pond, Trinidad, recorded Jun 1983 by J.R. Downie. Middle audiospectrogram recording from Brasso Seco, Trinidad, USNM Tape 220, cut 3, recorded from USNM 306105, 8 Jul 1989, 1945–2015 h, 22.8°C air, by Addison Wynn. Lower audiospectrogram recording from Tobago, no further data, recorded by Jerry David Hardy, his tape number 32.

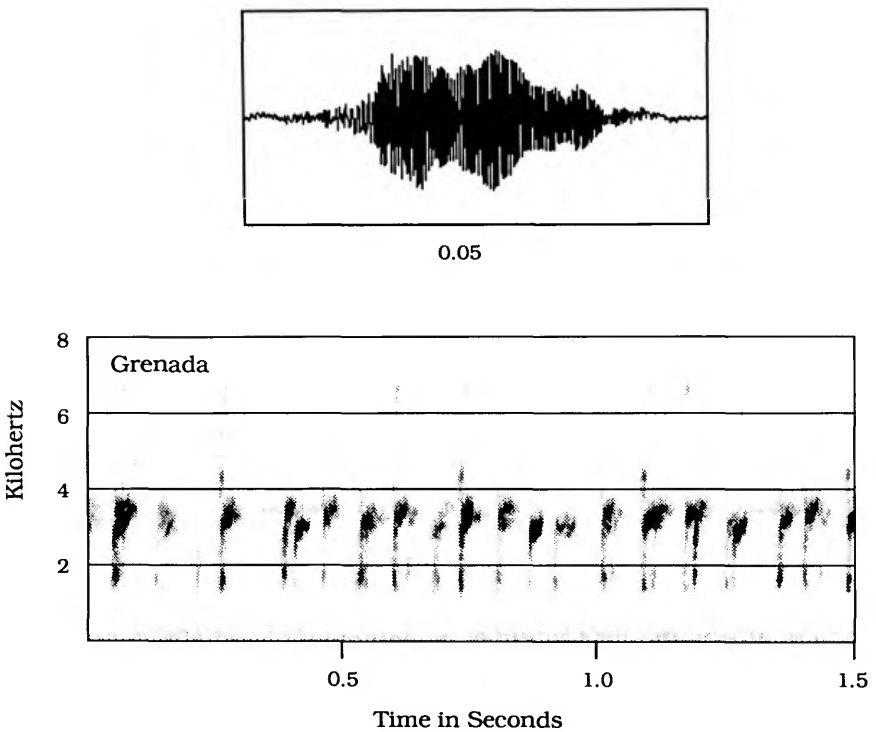

FIGURE 32.—Calls from chorus at Grenada, St. George Parish, USNM Tape 246, cut 11. Audiospectrogram of portion of chorus recorded 24 Aug 1991, 2030 h, 27°C, by Ronald I. Crombie.

initial energy around 1800–1900 Hz followed by the dominant broadcast frequency (which may continue to rise through the note) in the 2900–3300 Hz range (Figure 33).

There appears to be very modest differentiation among island populations based on morphology, calls, and life colors that would best be considered intraspecific in nature. Therefore, the Small–Moderate Size Trinidad OTU, the Small–Moderate Size Tobago OTU and OTUs from Grenada, Bequia, and St. Vincent represent the same species, referred to from hereon as the Small–Moderate Size Island OTU.

Summary statistics for the Small–Moderate Size Island OTU from Region 6 are presented in Table 37.

Region 7—Andean Slopes

Re-examination of specimens from this region that extends from Colombia through Bolivia (see discussion for Region 4 for geographical definition of the extent of Region 7) indicates that some specimens resemble three of the OTUs that occur in Region 4, and almost all of the rest of the specimens can be allocated to geographically coherent OTUs, but it is not immediately obvious whether these latter OTUs are all distinct from each other or whether some represent the same species. Analysis of OTUs from this region is best approached as a four step process. First, the three OTUs that resemble Region 4 OTUs are characterized. Second, a series of OTUs from southern Colombia through Bolivia are characterized and evaluated among themselves to best evaluate how many species are represented. Third, the few specimens from southern Colombia through Bolivia not allocated to an OTU in the previous steps are discussed. Fourth, a series of OTUs from the midnorthern Andean slopes and inter-Andean valleys of Colombia are characterized and evaluated to determine how many species are represented and whether one or more of them are the same species from further south in Region 7. No tape recordings are available for analysis for any specimens from Region 7.

The three OTUs from Region 7 that resemble Region 4 OTUs are the Region 7 Dark Belly OTU, the Region 7 Anastomotic Belly OTU, and the Region 7 Light Posterior Belly OTU. Certain populations belonging to these three OTUs already have been discussed (see also Appendix 1). Two populations were discussed previously in the section on analysis of sympatric OTUs. The Moderate Size, Light Posterior Belly, Divisoria, Peru OTU is sympatric with an OTU discussed in the third part of this analysis. The Moderate Size

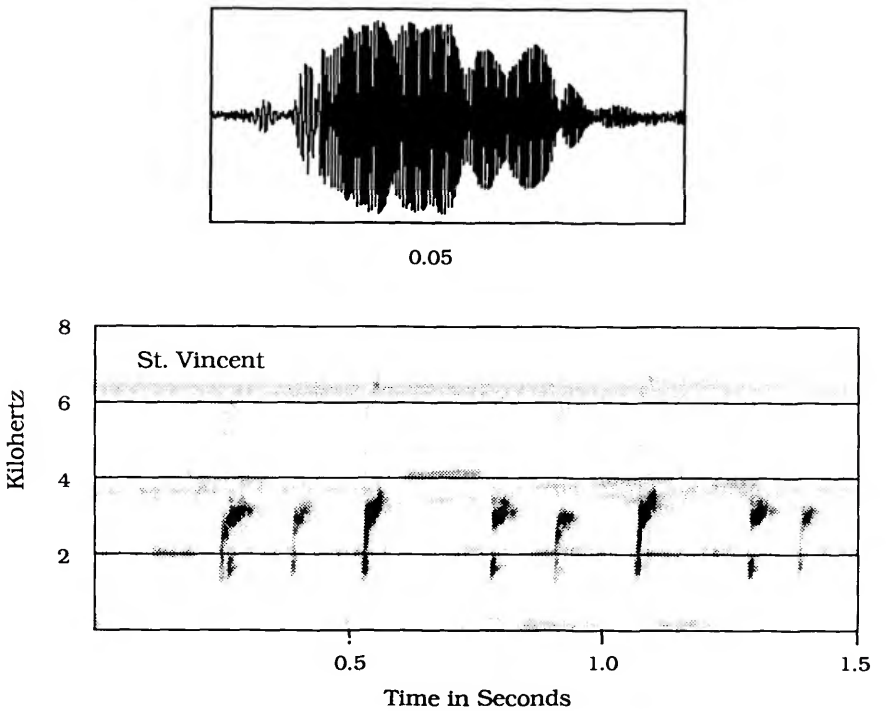

FIGURE 33.—Calls from chorus at St. Vincent, St. George Parish, near Arno's Vale, USNM Tape 246, cut 10. Recorded 13 Aug 1991, 1900–2150 h, by Ronald I. Crombie.

TABLE 37.—Minima, maxima, and summary statistics for size and measurement ratios for Region 6 Small-Moderate Size Island OTU adults. (N = 36 females, 71 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	38.1	51.5	44.3	2.873
SVL	M	30.5	42.9	37.8	2.574
Head length/SVL	F	0.346	0.386	0.363	0.013
Head length/SVL	M	0.338	0.407	0.373	0.016
Head width/SVL	F	0.315	0.364	0.341	0.012
Head width/SVL	M	0.321	0.386	0.354	0.012
Tympanum/SVL	F	0.068	0.086	0.077	0.005
Tympanum/SVL	M	0.072	0.093	0.080	0.004
Thigh/SVL	F	0.404	0.491	0.439	0.021
Thigh/SVL	M	0.411	0.519	0.448	0.021
Shank/SVL	F	0.439	0.499	0.471	0.017
Shank/SVL	M	0.450	0.526	0.484	0.014
Foot/SVL	F	0.484	0.577	0.527	0.022
Foot/SVL	M	0.496	0.587	0.542	0.019

Light Posterior Belly, Santa Cecilia, Ecuador OTU is sympatric with an OTU discussed in the next section of this analysis. In addition, the following combinations occur in sympatry in Region 7. The Region 7 Anastomotic Belly OTU and Region 7 Light Posterior Belly OTU are known to occur sympatrically at Peru, Madre de Dios, Cocha Cashu; Peru, Ucayali, Colonia Callaría, Río Callaría; Peru, Ucayali, Río Suhayo; and Peru, Ucayali, Yarinacocha (but see reidentification of the Yarinacocha Light Posterior Belly specimens in the second section). The Region 7 Dark Belly OTU and Region 7 Light Posterior

Belly OTU are known to occur in sympatry at Bolivia, Beni, near Reyes, and Bolivia, Santa Cruz, Buenavista. The Region 7 Light Posterior Belly OTU is known to occur in sympatry with an OTU discussed in the third section of this analysis. The Region 7 Anastomotic Belly OTU is known to occur in sympatry in Colombia with an OTU discussed in the fourth section of this analysis.

Region 7 Dark Belly OTU specimens rarely (3%) have very distinct posterior light lip stripes, most (58%) have distinct stripes, several (30%) have indistinct stripes, and few (9%) have no indication of a light posterior lip stripe. The light posterior lip stripes characteristically extend from underneath the middle of the eye. The posterior surfaces of the thighs rarely (3%) have distinct light stripes, often (32%) have indistinct light stripes, and usually (66%) are mottled with no indication of light stripes. In most of the sample, the dorsolateral-fold condition is difficult to discern because of preservation problems. However, there appears to be a continuum from no folds (artifact of preservation?) through short, medium, and long folds. All individuals have light spots on a dark background at least on the chin and in many (43%) of the individuals, distinct light spots occur from the chin and extend throughout the throat, chest, and belly. The toe tips are narrow (98%) or just swollen (2%). Adult males have medium-size or medium/small-size black thumb spines. Two females (36.9, 40.3 mm SVL) have two tiny white thumb spines.

Outlier detection analyses were run for male and female Region 7 Dark Belly OTU individuals separately. In both analyses, there is a single cluster of points with a single outlier individual on the first principal component axis. The outlying male, USNM 280737, is an adult by the definition used as it has vocal slits, but the thumb spines are very small and the individual is clearly a young male. USNM 280737 does not differ from other individuals from Rurrenabaque, Beni, Bolivia, except in size. Re-examination of UMMZ 74354 from Buenavista, Santa Cruz, Bolivia, indicates that it is actually a juvenile female as it has straight oviducts.

Region 7 Dark Belly OTU males range from 24.5 to 36.4 mm SVL; the females range from 34.0 to 42.5 mm SVL.

Data are available for ten adult and near adult Region 7 Anastomotic Belly OTU individuals. The light posterior lip stripe condition ranges from distinct, indistinct, to absent. When present, the light stripes extend only to the posterior corner of the eye and do not extend under the middle of the eye. All posterior thighs are mottled with no indication of a light stripe. Dorsolateral folds are short to moderate in length. The chins and throats are white spotted or mottled; the chests and bellies are moderately to extensively mottled. Two individuals have almost light-spotted bellies and one individual has the anastomotic pattern. Toe tips range from narrow, just swollen, to just expanded. Black thumb spines are small to medium in size. The males range from 26.6 to 32.5 mm SVL; the females range from 36.5 to 40.8 mm SVL.

Region 7 Light Posterior Belly OTU posterior light lip stripe expression encompasses the total range of variation observed, but the very distinct condition rarely occurs (2%). The distinct, indistinct, and no evidence of lip stripe conditions occur in about the same frequencies. When light posterior lip stripes are present, they extend only from the posterior corner of the eye, not from underneath the middle of the eye. Posterior light thigh stripes often are very distinct (30%), distinct (38%), or somewhat distinct (20%); no indication of a light stripe is found in some (12%). Dorsolateral folds range from rarely absent (preservation artifact?) (5%), often short (25%), usually moderate (60%), to sometimes long (9%). Most individuals (85%) lack any indication of distinct light spots on the chin or throat. The bellies are sometimes lightly mottled (19%), usually moderately mottled (72%), or occasionally extensively mottled (9%). There is an intensity gradient in belly pattern being more intense next to the chest. Toe-tip conditions cover the entire range of variation observed in this complex, although the extreme states of narrow tips and small disks are rare (2% each) and most individuals (70%) have the swollen toe tip state. Black thumb spines in males range in size from small to medium, with one male having large spines. Three females (48.8, 51.6, 52.6 mm SVL) have either one or two very small white thumb spines.

Outlier detection analyses were run separately for Region 7 Light Posterior Belly OTU males and females. The female results when the first and second principal component axes are plotted indicate a single cluster of points. The smallest female in the analysis (UMMZ 64101) was rechecked for adult status; it is an adult with curly oviducts. The results for males indicate a single cluster of points with a single outlier on the first principal component axis. The outlier, UMMZ 66618, is the smallest male in the analysis, but it is an adult as indicated by the presence of vocal slits. The specimen does not differ in any other way than size from other males at the same locality of Buenavista, Santa Cruz, Bolivia. The size range of males is 28.3–44.3 mm SVL and that for females is 34.8–56.2 mm SVL.

Habitat data are available for only a few specimens of the Region 7 Anastomotic Belly OTU and the Region 7 Light Posterior Belly OTU. Six of seven individuals from two localities of the Region 7 Anastomotic Belly OTU were collected from either primary or old growth secondary forest by pools; the seventh individual was collected from a clearing. Four of 11 specimens from three localities of the Region 7 Light Posterior Belly OTU were collected by pools in old growth secondary or primary forests; the other seven were taken from open habitat situations in clearings, along a stream, or on a trail.

Along the amazonian Andean slopes from southern Colombia to mid-Bolivia there are series of populations that appear to be entirely or essentially restricted to the slopes. There are five groupings that include most of the specimens from this region that are geographically separated from each other. The five, in North-South order are the Region 7 Large Size Mid-Andes

OTU, Region 7 Moderate Size Central Peru OTU, Region 7 Large Size Central Peru OTU, Region 7 Moderate/Large Size South-Central Peru OTU, and Region 7 Moderate Size Bolivia OTU. As indicated, none of these five occur sympatrically among themselves (or with any of the specimens from intermediate areas that do not match these five OTUs and are omitted from this part of the analysis). The Large Size, Boldly Mottled Belly, Santa Cecilia, Ecuador OTU, analyzed previously as both a large sample, single taxon population and as a sympatric occurrence with the Region 7 Light Posterior Belly OTU, belongs to the Region 7 Large Size Mid-Andes OTU. During the examination that led to recognition of these five groupings as OTUs, it was not immediately apparent whether the two large-size OTUs represented one or two species or whether the other three OTUs represented one, two, or three species. The approach used was to characterize each of the five, then evaluate how many species they represented.

The Region 7 Large Size Mid-Andes OTU ranges from southern Colombia to northern Peru. The large size specimens from Region 4 deferred to this section for analysis all belong to the Region 7 Large Size Mid-Andes OTU. Light posterior lip stripe conditions range from distinct (27%) to some indication of a light stripe (54%) to no indication of a light stripe (19%). When stripes are present they extend only to the posterior corner of the eye. The posterior thighs rarely (1%) have very distinct light stripes and often have distinct (32%), indistinct (28%), or no indication (39%) of light stripes. No dorsolateral folds were rarely (2%) scored (preservation artifact?). Most individuals (75%) have long dorsolateral folds, extending from the eyes to past the sacrum. Some have moderate-length folds (21%) and hardly any (1%) were scored as having short folds. Distinct or moderately distinct light spots on a dark background are limited to the chin region in several (27%) specimens. The bellies are boldly mottled in a majority (57%) of the specimens. The extent of the melanophores on the belly ranges from light (3%) to moderate (49%) to extensive (48%). Particularly for the lightly to moderately pigmented bellies, there is a gradient with the more extensive distribution of melanophores anteriorly. Toe tips are rarely narrow (2%) or just expanded (1%), often just swollen (43%), and usually swollen (54%). The black thumb spines in males are mostly medium size (68%), but they do range from small (1%), medium-small (5%), medium-large (18%), to large (8%).

Outlier detection analyses were run separately for males and females for the Region 7 Large Size Mid-Andes OTU. For males, the first two principal component axes account for 93% of the variation and the plot results indicate a single cluster of points. For females, the first two principal component axes also account for 93% of the variation. On the plot of the first two principal component axes, there are a few individuals that lie outside a single cluster of points (Figure 34). On the first axis, KU 175124 lies at one end (Figure 34, solid inverted triangle) and is the largest female in the sample, but it does not differ except in size from others from the same locality. At the other end of the first axis, USNM 196791 is the smallest female (46.6 mm SVL) in the sample (Figure 34, open triangle farthest on left). Rechecking the specimen indicates that it is a juvenile female with straight oviducts. Rechecking the next few smallest females indicates that USNM 196793, a 51.2 mm SVL specimen, and USNM 196822, a 53.1 mm SVL specimen, are juvenile females with straight oviducts (Figure 34, other two open triangles), but USNM 283834, a 52.3 mm SVL specimen is an adult with just curly oviducts. Two individuals are outliers on one end of the second principal component and one

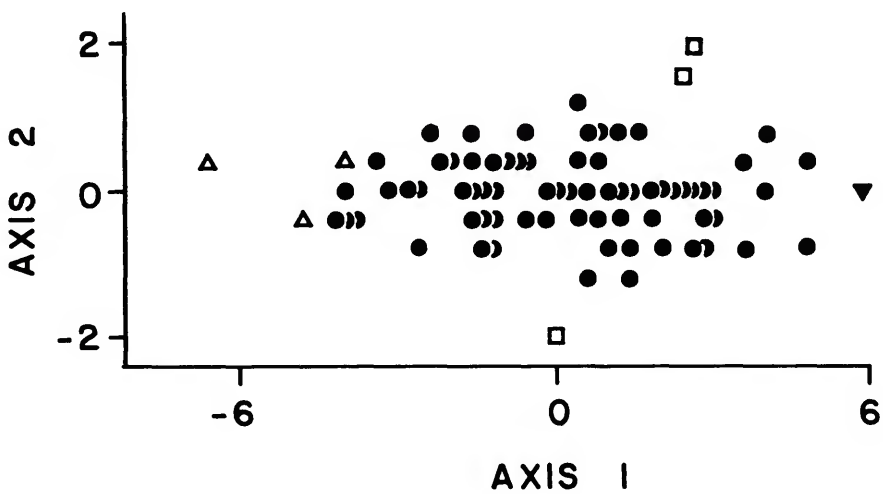

FIGURE 34.—Plot of first against second principal components axes for females of the Region 7 Large Size Mid-Andes OTU. Triangles and squares are outlying individuals discussed in text.

individual is an outlier at the other end of the axis (Figure 34, squares). The character with the highest loading value on the second axis is tympanum diameter (0.87, the next largest value for a variable is –0.32). RMNH 23977 and KU 152264 have the largest tympani measured for the sample (5.8 and 5.6 mm respectively; Figure 34, top two squares). Both specimens were remeasured and the tympani are large, but the second set of measurements are a bit smaller (5.6 and 5.3 mm, respectively). UMMZ 129284 has a small tympanum for its size (3.5 mm, 65.0 mm SVL; Figure 34, lower square). Re-examination of the specimen indicates that the right tympanum (which was the one measured as 3.5 mm) is damaged; the undamaged left tympanum measures 4.9 mm.

There is considerably more size variation in this OTU than observed in other OTUs analyzed up to this point. Juvenile females range from 44.0 to 66.9 mm SVL in size, adult females 52.3 to 81.7 mm, juvenile males 37.2 to 53.4 mm, and adult males 39.1 to 60.7 mm. As there is considerable range in altitude of localities where this OTU has been collected from, males and females from Ecuador were plotted by size and altitude. There is no obvious correlation of size with altitude, and the Santa Cecilia samples encompass most of the size range observed for the entire OTU. As an example of the distribution of size versus altitude, a sample of 11 adult males from an altitude of 900 m from Sucua, Morona-Santiago, range from 44.9 to 53.9 mm SVL, whereas a sample of four adult males from an altitude of 914 m from Mendez, Morona-Santiago, range from 40.2 to 44.6 mm SVL. The only point that can be drawn is that of the samples from Ecuador (and for which altitudes are known through primary sources), the very largest males and females occur below 500 m.

Habitat data are available only for the Region 7 Large Size Mid-Andes OTU of the five OTUs being analyzed at this step. Fugler and Walls (1979:154) summarized habitat data on specimens from the Río Upano valley of Ecuador by noting that "the greater number of the series was obtained at night. Individuals were discovered in debris-strewn cleared fields, marshy areas, and undisturbed forest." In addition, data are available for 36 specimens from 10 localities. Most of the specimens came from open habitats such as along roads and in pastures or meadows. Several were collected on riverbanks. It is unclear whether some, such as those collected from swamps and under logs or rocks, were collected from primary forest or not.

The Region 7 Moderate Size Central Peru OTU occurs in the Departments of San Martín and Huanuco. The light posterior lip stripe is rarely (6%) distinct, usually indistinct (50%), or with no indication of a light stripe (44%). When light stripes are indicated, they usually extend only to the posterior corner of the eye, although in a few specimens from Aucayacu and Tingo Maria, Huanuco, the stripes extend to under the eye. Posterior thighs usually are mottled (86%), but some have distinct (6%) or indistinct (8%) light stripes. Dorsolateral folds range from absent (artifact of preservation?) to moderate length. There are no light spots on a dark ground on the venters. The bellies range in intensity of mottling from light (50%), moderate (39%), to extensive (11%). There is an anterior-posterior gradient of mottling on the belly, heaviest anteriorly. Toe tips range from narrow to expanded, with most (53%) being just expanded. Male black thumb spines are all large in size. Females range in size from 39.4 to 49.6 mm SVL; males range from 34.7 to 42.5 mm SVL.

The Region 7 Large Size Central Peru OTU occurs in the departments of Huanuco and Pasco; there is but a sample of seven individuals available. The light lip stripe condition ranges from indistinct (extending only from corner of eye) in two specimens to no indication of a stripe in five specimens. The posterior thigh pattern has an indistinct stripe on one thigh of one individual. The rest of the thighs are mottled. Dorsolateral folds are (apparently) absent in three individuals, short in two, and moderate in length in two individuals. The chin and throat of one individual is light spotted; the rest have entirely mottled ventral patterns. The bellies are lightly (5 individuals) or moderately (2) mottled, with more extensive distribution of melanophores anteriorly. The three males all have large black thumb spines. The three males range in size from 60.3 to 61.4 mm SVL; the four females range from 52.4 to 66.6 mm SVL.

The Region 7 Moderate/Large Size South-Central Peru OTU occurs in the departments of Pasco, Junín, and Ayacucho and is represented by 14 adult- or near adult-size individuals. Light posterior lip stripe conditions range from distinct (4 specimens), indistinct (4), to no indication of a stripe (6). When stripes are indicated, they usually extend only to the posterior corner of the eye, although in a series of juveniles from near Oxapampa, Pasco, the stripes clearly extend to under the mideye area. There is the barest indication of light stripes on the posterior thighs in one individual; the thighs are mottled in the others. Dorsolateral-fold conditions range from (apparently) absent, short, to moderate length. The chins are light spotted in eight specimens. The bellies are lightly (11 specimens) or moderately mottled (3), with more melanophores anteriorly. The toe tips range from narrow to swollen except for a single individual from the Department of Pasco (USNM 306766), which has almost small disks. The six males with black thumb spines all have large-size spines. Males range from 38.2 to 51.3 mm SVL in size; females range from 40.0 to 55.0 mm SVL.

The Region 7 Moderate Size Bolivia OTU occurs in the Department of La Paz; 29 adults and near adults are at hand for this OTU. The light posterior lip stripe is indistinct (52% and extending only to the posterior corner of the eye) or not indicated (48%). Most of the posterior thighs are mottled (84%), but some (16%) have indistinct light stripes. Dorsolateral folds are either (apparently) absent (8%), moderate (83%), or long (8%). One individual has a light-spotted throat; the venters are completely mottled in the others. Belly mottling ranges from light (76%), moderate (17%), to extensive (7%), with more melanophores anteriorly. Toe tips are narrow (14%), just swollen (7%), or swollen (79%). One male has medium/

large black thumb spines, and six males have large black spines. Males range in size from 39.7 to 47.3 mm SVL; females range from 44.8 to 53.0 mm SVL.

A discriminant analysis was performed on males and females separately for the five OTUs analyzed in this section as well as the three OTUs characterized in the previous section. The reasons for including all eight OTUs in the analysis are three fold: (1) they occur in the same general geographic area; (2) inclusion of the three OTUs from the previous section could add a perspective to understanding the results by comparing results within the cluster of three and five OTUs and combinations between the three and five; and (3) it would facilitate the analysis of the morphological similarities and distinctivenesses among all eight OTUs.

Several conclusions can be drawn from the results (summarized in part in Tables 37, 38). First, males are more distinguishable based on measurement data than females among the eight OTUs. For example, the total error rate in the posterior classification procedure was 18% for males and 39% for females. Second, the two large-size OTUs are morphologically distinctive based on measurement data (Table 38). Third, for both male and female data, the least discrimination among OTUs occurs between the Moderate/Large Size South-Central Peru and Moderate Size Bolivia OTUs and between the Light Posterior Belly and Moderate Size Central Peru OTUs. Fourth, for the female data in particular, there is very poor discrimination between the Dark Belly and Anastomotic Belly OTUs.

All specimen records where the posterior probability was greater for belonging to an OTU different than originally assigned were examined, and, where appropriate, specimens were re-examined. As a result, the identifications of two specimens are changed. RMNH 23872, 23873 from Yarinacocha, Ucayali, Peru, originally were classified as belonging to the Region 7 Light Posterior Belly OTU. The discriminant analysis assigned both specimens a higher probability of belonging to the Region 7 Moderate Size Central Peru OTU, with which I concur after re-examination and comparison of the specimens. The Region 7 Anastomotic Belly OTU also occurs at this locality. Most of the misclassified male and female Region 7 Large Size Mid-Andean OTU specimens are the smallest individuals.

In order to determine how many species are represented by the eight Region 7 OTUs analyzed to this point, the data and analyses presented thus far indicate that decisions need to be drawn for the following OTU comparisons: (1) Large Size Mid-Andean OTU and Large Size Central Peru OTU; (2) Moderate Size Central Peru OTU with Light Posterior Belly OTU; and (3) Moderate Size Central Peru OTU with Moderate/Large Size South-Central Peru OTU and with Moderate Size Bolivia OTU. Each of these comparisons is discussed in turn.

The Region 7 Large Size Mid-Andean OTU differs from the Region 7 Large Size Central Peru OTU in several pattern and morphological features including expression of light posterior lip stripe, thigh pattern, dorsolateral folds, and belly pattern (see previous characterization statements), as well as distinc-

TABLE 38.—Generalized squared distances between OTUs from Region 7, mid-Colombia through Bolivia.

Sex and OTU	Large Mid-Andes	Moderate Central Peru	Large Central Peru	Mod./Large South-Central Peru	Moderate Bolivia	Light Posterior Belly	Anastomotic Belly	Dark Belly
Females								
Large Mid-Andes	0	43.8	16.9	30.2	19.4	34.1	66.6	74.9
Moderate Central Peru		0	29.3	8.1	8.0	1.6	7.2	5.8
Large Central Peru			0	9.8	11.0	26.1	48.6	49.4
Mod./Large South-Central Peru				0	3.7	7.9	18.8	18.8
Moderate Bolivia					0	5.6	24.1	24.9
Light Posterior Belly						0	10.8	10.6
Anastomotic Belly							0	2.4
Dark Belly								0
Males								
Large Mid-Andes	0	33.1	25.1	13.5	7.7	24.8	66.3	63.1
Moderate Central Peru		0	59.0	11.7	17.1	4.3	12.7	7.3
Large Central Peru			0	27.0	33.2	63.7	99.9	97.7
Mod./Large South-Central Peru				0	4.1	14.0	33.0	35.2
Moderate Bolivia					0	14.1	42.6	44.0
Light Posterior Belly						0	20.3	11.2
Anastomotic Belly							0	11.2
Dark Belly								0

tive measurement data of size and shape as analyzed by discriminant analyses. Although there is no one character state that separates these OTUs 100% of the time, the magnitude of the differences observed is the same as seen where OTUs occur in sympatry. The evidence is most consistent with the conclusion that these two OTUs represent distinct species.

The Region 7 Moderate Size Central Peru OTU individuals are very similar in size and shape with individuals of the Region 7 Light Posterior Belly OTU (as indicated by discriminant analysis of measurement data, Tables 38, 39). The two OTUs also are similar in terms of expression of light posterior lip stripes, belly patterns, dorsolateral folds, and toe tips. The two OTUs differ in degree of expression of light posterior thigh stripes and size of male thumb spines (see previous characterization statements). When compared side by side, members of the two OTUs are distinctive from each other. Based on the morphological evidence, the two OTUs are considered to represent two distinct species. This conclusion should be tested with advertisement call data or genetic estimates of relatedness data.

The Moderate Size Central Peru, Moderate/Large Size South-Central Peru, and Moderate Size Bolivia Region 7 OTUs are quite similar to each other. They do not differ in expression of posterior lip stripes, posterior thigh stripes, dorsolateral folds, or size of male thumb spines. There apparently is some differentiation in that the toe tips are often just expanded in the Moderate Size Central Peru OTU individuals, which state was not scored for either of the other two OTUs. The ventral patterns are mostly similar, but some minor differences in light chin and throat spotting are found in the samples at hand. The sizes of the three OTUs broadly overlap. The discriminant analysis of measurement data indicated rather good separation between the Moderate Size Central Peru OTU and the other two OTUs (Tables 38, 39). An examination of the variable coefficient vectors of the three OTUs indicates that tympanum diameter is the most important variable in discriminating these three for both males and females (female results in Table 40, with Large Size Mid-Andes OTU results for comparison). The discrimination among these three OTUs appears to be based on head shape differences (Table 40). Comparison of specimens side by side emphasizes the similarities among them. Faced with the lack of continuous geographic samples and advertisement call data, the available data are most consistent with recognition of a single species embracing all three OTUs with some intraspecific geographic variation as noted. For further analytic purposes, this species is referred to as the Moderate Size Andes OTU.

Specimens from five localities that were not included in the previous analysis were re-examined. Two specimens from Ixiamas, La Paz, Bolivia (UMMZ 74816), are small, completely faded juveniles. They are assigned to the Moderate Size Andes OTU, but any species assignment must be tentative until additional specimens are examined from the same locality. The specimens from the other localities are all considered to be members of the Moderate Size Andes OTU. With these additional identifications, a discriminant analysis was rerun on males and females on the Region 7 OTUs, using the Moderate Size Andes OTU rather than the three component parts as

TABLE 39.—Discriminant analysis for eight OTUs from Colombia through Bolivia from Region 7. The values are the number of observations classified into OTUs.

Sex and OTU	Large Mid-Andes	Moderate Central Peru	Large Central Peru	Mod./Large South-Central Peru	Moderate Bolivia	Light Posterior Belly	Anastomotic Belly	Dark Belly
Females								
Large Mid-Andes	75	0	3	0	3	0	0	0
Moderate Central Peru	0	13	0	1	1	5	1	2
Large Central Peru	0	0	2	1	1	0	0	0
Mod./Large South-Central Peru	0	1	1	2	1	1	0	0
Moderate Bolivia	0	0	0	3	8	1	0	0
Light Posterior Belly	0	12	0	3	4	55	0	1
Anastomotic Belly	0	0	0	0	0	0	1	2
Dark Belly	0	1	0	0	0	0	5	32
Males								
Large Mid-Andes	96	0	1	2	9	2	0	0
Moderate Central Peru	0	9	0	1	0	1	0	2
Large Central Peru	0	0	3	0	0	0	0	0
Mod./Large South-Central Peru	0	0	1	5	0	1	0	0
Moderate Bolivia	1	0	0	2	5	0	0	0
Light Posterior Belly	0	7	0	0	0	37	0	0
Anastomotic Belly	0	0	0	0	0	0	4	1
Dark Belly	0	0	0	0	0	0	0	34

TABLE 40.—Discriminant function variable values for females of four Region 7 OTUs. OTU A = Moderate Size Central Peru OTU; OTU B = Moderate/Large Size South Central Peru OTU; OTU C = Moderate Size Bolivia OTU; OTU D = Large Size Mid-Andes OTU.

Variable	OTU A	OTU B	OTU C	OTU D
Constant	−50.6	−67.3	−70.4	−117.1
SVL	0.7	−0.2	−0.1	−0.4
Head Length	0.3	−2.8	−1.2	0.2
Head Width	−1.0	3.0	−0.5	−0.5
Tympanum Diameter	10.5	15.4	14.5	6.9
Thigh Length	0.7	1.1	0.5	0.1
Shank Length	−3.1	−2.8	−1.1	1.4
Foot Length	4.2	4.8	4.9	5.1

analyzed previously. The additional specimens from Peru, Huanuco, Divisioria, and Huanuco, 30 km NNE Tingo Maria were classified posteriorly as belonging to the Moderate Size Andes OTU. The Moderate Size Andes OTU specimens from Divisioria already have been noted as occurring in sympatry with Region 7 Light Posterior Belly OTU specimens. A male (MCZ 75024) from Peru, Ucayali, Iparia was classified posteriorly as having a higher probability of belonging to the Large Size Mid-Andes OTU, whereas a female (MCZ 75021) from the same locality was included in the Moderate Size Andes OTU. The male is large for the Moderate Size Andes OTU, but no change in identification of the specimens is called for after rechecking the specimens. Iparia is also a locality of sympatric occurrence of two OTUs, the Moderate Size Andes and Light Posterior Belly Region 7 OTUs, as noted previously. A female from Ganzo Azul, Huanuco, Peru (FMNH 45144), was classified posteriorly as belonging to the Large Size Central Peru OTU. It is the largest female in the Moderate Size Andes OTU, but morphologically is a member of the latter OTU rather than the former when specimens are compared directly. One additional specimen that stands out in the discriminant analysis, based on using the Moderate Size Andes OTU, is USNM 306766, a male from near Oxapampa, Pasco, Peru, which was classified posteriorly as having a 99% probability of belonging to the Large Size Central Peru OTU. Re-examination of this specimen, along with juveniles from the same locality does not lead to a firm conclusion as to which OTU the specimens represent, thus raising the possibility that the Large Size Central Peru OTU does not represent a species distinct from the Moderate Size Andes OTU. Additional data, particularly advertisement call and genetic relatedness data would be invaluable in resolving the situation.

The five OTUs from the central and northern portion of Colombia from Region 7 now are characterized. These OTUs represent allopatric groups that occur in different drainage systems.

Colombian Andes Amazonian Drainage OTU members rarely (1%) have very distinct light posterior lip stripes, sometimes (15%) have distinct stripes, usually (45%) have indistinct stripes, but often (38%) have no indication of a stripe. In most (73%) of the individuals with discernible stripes, the stripes extend only from the posterior corner of the eye; however, in some (17%), there is an extension of the stripe from just under and posterior to the middle of the eye. The posterior thigh light stripe is rarely (5%) very distinct, commonly distinct (41%) or indistinct (43%), but sometimes (12%) the thigh is completely mottled with no indication of a stripe. Dorsolateral folds range from (apparently) absent (11%), short (12%), moderate (57%), to long (20%). The chin and/or throat commonly (48%) has light spots on a dark background. The degree of belly mottling varies from light (18%), moderate (60%), to extensive (22%), with an anterior-posterior gradient, darker anteriorly. Several (25%) of the individuals have boldly mottled belly patterns. The toe tips range from just swollen (36%), swollen (38%), to just expanded (26%). In males with black thumb spines, the sizes are medium (48%), moderately large (27%), and large (25%). Three large females (56.9, 59.4, 62.5 mm SVL) have very small single white or two tan-tipped thumb spines. Males range from 37.9 to 55.9 mm SVL; females range from 38.2 to 62.5 mm SVL. The only habitat data available for this cluster of OTUs are for three specimens from one locality for this OTU. Two specimens were collected by a pasture pool and one was taken from a pasture.

A sample of fourteen near-adult and adult specimens comprise the Maracaibo Drainage OTU. The light posterior lip stripes are distinct or indistinct; in only one individual is there no indication of a light stripe. The light stripe extends from under the middle of the eye in some, from just past the middle of the eye in most, and from the posterior corner of the eye in several individuals. The light stripe on the posterior face of the thigh condition is very distinct in one individual, usually distinct or indistinct, and rarely absent. Dorsolateral fold conditions demonstrate the full range of expression for the complex, from (apparently) absent to long. In eight individuals the chin is light spotted. The intensity of belly mottling is either light (6 individuals) or moderate (8). One individual has a boldly mottled belly pattern. The toe tips are scored as swollen (9 individuals), just expanded (1), or expanded (4). Two males have medium-size black thumb spines, four have large spines. Two females (50.4 and 51.2 mm SVL) have two very small white or tan-tipped thumb spines. Eight adult males range from 34.3 to 46.7 mm SVL; three adult females range from 45.0 to 51.2 mm SVL.

The light posterior lip stripe condition of Magdalena Drainage OTU individuals range from distinct (37%), indistinct (29%), to not distinguishable (34%). The light stripe extends from under the middle portion of the eye in some (19%) individuals, from just posterior to the mideye in most (59%), and from the posterior corner of the eye in some (22%). The light stripes on the posterior thighs are sometimes distinct (12%), often indistinct (35%), or usually not indicated (52%). Dorsolateral folds are (apparently) absent (18%), short (10%),

moderate (51%), or long (20%). The chin and/or throat usually (51%) has light spots on a dark background. The intensity of the mottling on the belly ranges from light (29%), moderate (51%), to extensive (20%). A few (10%) individuals have boldly mottled belly patterns. Toe tips are usually just swollen (28%), swollen (43%), just expanded (26%), or rarely expanded (1 individual). Seven males have medium-size black thumb spines, seven have moderately large spines, and three have large spines. Two females, 46.8 and 49.5 mm SVL, have one tiny white thumb spine per thumb and one 48.6 mm SVL female has two tiny tan spines on each thumb. Males range from 37.1 to 50.2 mm SVL; females range from 46.8 to 60.0 mm SVL.

The light posterior eye stripe in Cauca Drainage OTU members is distinct (13%), indistinct (50%), or indistinguishable (37%). In a few specimens (6%), the light stripe extends from under the midportion of the eye, and in many (48%) the stripes extend from just past the mideye region as well as from the posterior corner of the eye (45%). The thighs usually are mottled, with no indication of a light stripe (86%) or with an indistinct light stripe (13%). Dorsolateral folds are (apparently) absent (5%), short (7%), moderate (51%), or long (37%). The chin sometimes has light spots on a dark background (28%). The belly is either moderately (61%) or extensively (39%) mottled. A few individuals (4%) have boldly mottled belly patterns. Toe tips are rarely narrow (one individual), usually just swollen (76%), sometimes swollen (17%), or rarely just expanded (2 individuals). Eight males have medium-size black thumb spines, four have moderately large spines, and two have large spines. One 46.2 mm SVL female has one tiny tan-tipped spine on each thumb. Males range in size from 36.0 to 52.6 mm SVL; females range from 44.9 to 59.1 mm SVL.

There are only two females on hand representing the Atrato Drainage OTU. In both, the light posterior lip stripes are distinct, extending from just posterior to the mideye region in one and from the posterior corner of the eye in the other. One posterior thigh has an indication of a light stripe, the rest are completely mottled. The dorsolateral folds are moderate in length. One specimen has light spots on the chin. Both have moderately mottled bellies; in neither is the mottling boldly patterned. Both have swollen toe tips. Both have two tiny white spines on each thumb. The two are 60.2 and 62.2 mm SVL.

Discriminant function analyses were performed using the measurement data for males and females separately for the following OTUs: Colombian Andes Amazonian Drainage OTU, Maracaibo Drainage OTU, Magdalena Drainage OTU, Cauca Drainage OTU, Region 7 Light Posterior Belly OTU, and Moderate Size Andes OTU. The Atrato Drainage OTU is not included because of its small sample size. The Region 7 Light Posterior Belly OTU and Moderate Size Andes OTU are included to provide perspective for the Colombian OTUs. The results (Tables 41, 42) indicate that the OTUs are rather similar to each other based on analysis of the measurement data, particularly the Colombia Andes Amazonian Drainage OTU and the Magdalena Drainage OTU, whereas the Maracaibo Drainage OTU is rather distinctive.

Comparing all the data and analyses, there is some variation among the Colombian OTUs, but the similarities among the OTUs are more striking than the differences. The differences of degree of expression of posterior lip stripe, light thigh stripe, and boldly patterned bellies among the Colombia Andes Amazonian Drainage OTU, Magdalena Drainage OTU, and Cauca Drainage OTU apparently are geographically related. Canonical discriminant analyses were run for males and females for the Colombia Andes Amazonian Drainage, Magdalena Drainage, Cauca Drainage, and Maracaibo Drain-

TABLE 41.—Generalized squared distances between six Region 7 OTUs. Full names of abbreviated OTUs are: Colombian Andes Amazonian Drainage OTU and Region 7 Light Posterior Belly OTU.

Sex and OTU	Colombia Andes Amazonian	Maracaibo Drainage	Magdalena Drainage	Cauca Drainage	Moderate Size Andes	Light Posterior Belly
Females						
Colombia Andes Amazonian	0	2.5	1.7	1.6	5.8	4.1
Maracaibo Drainage		0	5.7	7.3	5.0	4.5
Magdalena Drainage			0	2.3	6.8	5.9
Cauca Drainage				0	7.3	5.9
Moderate Size Andes					0	1.6
Light Posterior Belly						0
Males						
Colombia Andes Amazonian	0	6.1	0.8	4.0	4.6	2.6
Maracaibo Drainage		0	9.2	15.6	3.5	7.3
Magdalena Drainage			0	2.5	5.4	4.4
Cauca Drainage				0	10.5	8.1
Moderate Size Andes					0	6.7
Light Posterior Belly						0

TABLE 42.—Discriminant analysis of six Region 7 OTUs. Values are the number of observations classified into OTUs. Full names of abbreviated OTUs are: Colombian Andes Amazonian Drainage OTU and Region 7 Light Posterior Belly OTU.

Sex and OTU	Colombia Andes Amazonian	Maracaibo Drainage	Magdalena Drainage	Cauca Drainage	Moderate Size Andes	Light Posterior Belly
Females						
Colombia Andes Amazonian	4	6	5	6	2	3
Maracaibo Drainage	0	2	0	0	0	1
Magdalena Drainage	4	1	7	2	2	0
Cauca Drainage	2	1	4	9	0	0
Moderate Size Andes	2	3	2	1	26	10
Light Posterior Belly	7	5	1	6	16	39
Males						
Colombia Andes Amazonian	21	1	14	5	6	7
Maracaibo Drainage	1	5	0	0	2	0
Magdalena Drainage	6	0	7	3	3	1
Cauca Drainage	2	0	1	17	0	3
Moderate Size Andes	2	6	1	0	18	4
Light Posterior Belly	6	1	1	4	1	30

TABLE 43.—Minima, maxima, and summary statistics for size and measurement ratios for Region 7 Moderate Size Andes OTU. (N = 44 females, 31 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	39.4	57.6	46.6	4.434
SVL	M	34.7	51.3	42.5	4.813
Head length/SVL	F	0.321	0.378	0.354	0.014
Head length/SVL	M	0.337	0.392	0.363	0.014
Head width/SVL	F	0.303	0.372	0.335	0.015
Head width/SVL	M	0.327	0.379	0.350	0.012
Tympanum/SVL	F	0.066	0.087	0.075	0.005
Tympanum/SVL	M	0.072	0.091	0.081	0.006
Thigh/SVL	F	0.396	0.486	0.434	0.024
Thigh/SVL	M	0.392	0.507	0.446	0.028
Shank/SVL	F	0.406	0.509	0.462	0.029
Shank/SVL	M	0.430	0.521	0.473	0.026
Foot/SVL	F	0.472	0.583	0.526	0.028
Foot/SVL	M	0.493	0.591	0.544	0.021

age OTUs to see whether most of the measurement variation among OTUs occurred on the first axis. Virtually all separation of OTUs is on the first axis, which generally is size related, but the Maracaibo Drainage OTU is at the wrong end of the axis as far as size is concerned for both males and females. Re-examination and comparison of the specimens indicates that to my eye the Colombia Andes Amazonian Drainage OTU, the Maracaibo Drainage OTU, the Magdalena Drainage OTU, the Cauca Drainage OTU, and the Atrato Drainage OTU all represent the same species. However, because the Maracaibo Drainage OTU is distinctive based on measurement data analysis, it is kept separate from the other combined Colombian OTUs at this time in order to evaluate its status with OTUs from Regions 4 and 5. For purposes of further analysis, the combined Colombian OTUs are referred to as the Colombian Andes OTU.

To summarize the results for Region 7, the Moderate Size Andes OTU, Large Size Central Peru OTU, Large Size Mid-Andes OTU, Colombia Andes OTU, Region 7 Light Posterior Belly OTU, Region 7 Dark Belly OTU, and Region 7 Anastomotic Belly OTU are each considered to represent distinct species. The Maracaibo Drainage OTU may represent the same species as the Colombian Andes OTU, or it may represent a species from either Region 4 or 5. The summary statistics for each of these OTUs from Region 7 are presented in Tables 43–50.

TABLE 44.—Minima and maxima for size and measurement ratios for Region 7 Large Size Central Peru OTU. (N = 4 females, 3 males.)

Variable	Sex	Minimum	Maximum
SVL	F	52.4	66.6
SVL	M	60.3	61.4
Head length/SVL	F	0.334	0.356
Head length/SVL	M	0.345	0.371
Head width/SVL	F	0.336	0.362
Head width/SVL	M	0.357	0.391
Tympanum/SVL	F	0.071	0.083
Tympanum/SVL	M	0.076	0.089
Thigh/SVL	F	0.413	0.474
Thigh/SVL	M	0.416	0.468
Shank/SVL	F	0.474	0.489
Shank/SVL	M	0.448	0.500
Foot/SVL	F	0.532	0.565
Foot/SVL	M	0.524	0.533

INTERREGIONAL SYNTHESIS

The data and analyses presented above suggest that the Light Posterior Belly OTUs from Regions 4, 5, and 7 represent the same species; the Dark Belly OTUs from Regions 1, 3, 4, and 7 represent the same species; and the Anastomotic Belly OTUs from Regions 4, 5, and 7 represent the same species. For the Light Posterior Belly, Dark Belly, and Anastomotic Belly combined OTUs, the regional representatives are essentially identical in terms of external appearances.

Although the discriminant analyses of the measurement data clearly indicate the closeness of the Region 4 and 7 Light Posterior Belly OTUs, the Region 5 OTU shows a more similar-shape morphology with certain other OTUs (Table 51). This may be an artifact of the small sample size available for the Region 5 OTU. Based on appearances, however, I think the

TABLE 45.—Minima, maxima, and summary statistics for size and measurement ratios for Region 7 Large Size Mid-Andes OTU. (N = 81 females, 110 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	52.3	81.7	65.6	6.521
SVL	M	39.1	60.7	51.6	4.676
Head length/SVL	F	0.322	0.397	0.361	0.016
Head length/SVL	M	0.336	0.410	0.373	0.014
Head width/SVL	F	0.314	0.371	0.344	0.013
Head width/SVL	M	0.328	0.384	0.356	0.011
Tympanum/SVL	F	0.062	0.083	0.069	0.004
Tympanum/SVL	M	0.059	0.089	0.077	0.006
Thigh/SVL	F	0.392	0.506	0.450	0.026
Thigh/SVL	M	0.401	0.503	0.452	0.021
Shank/SVL	F	0.460	0.551	0.508	0.020
Shank/SVL	M	0.457	0.536	0.502	0.016
Foot/SVL	F	0.469	0.605	0.550	0.027
Foot/SVL	M	0.489	0.614	0.545	0.024

TABLE 46.—Minima, maxima, and summary statistics for size and measurement ratios for Region 7 Colombia Andes OTU. (N = 60 females, 97 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	38.2	62.5	52.7	5.842
SVL	M	36.0	55.9	44.5	3.863
Head length/SVL	F	0.318	0.395	0.357	0.017
Head length/SVL	M	0.334	0.402	0.361	0.015
Head width/SVL	F	0.310	0.395	0.340	0.016
Head width/SVL	M	0.305	0.367	0.340	0.010
Tympanum/SVL	F	0.062	0.078	0.069	0.004
Tympanum/SVL	M	0.062	0.087	0.074	0.005
Thigh/SVL	F	0.370	0.498	0.435	0.029
Thigh/SVL	M	0.353	0.486	0.430	0.030
Shank/SVL	F	0.429	0.509	0.465	0.018
Shank/SVL	M	0.416	0.508	0.461	0.021
Foot/SVL	F	0.446	0.581	0.517	0.025
Foot/SVL	M	0.448	0.572	0.516	0.025

TABLE 47.—Minima, maxima, and summary statistics for size and measurement ratios for Region 7 Light Posterior Belly OTU. (N = 74 females, 43 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	34.8	56.2	44.3	4.806
SVL	M	28.3	44.3	37.7	3.735
Head length/SVL	F	0.333	0.394	0.354	0.012
Head length/SVL	M	0.339	0.388	0.363	0.011
Head width/SVL	F	0.312	0.368	0.333	0.012
Head width/SVL	M	0.321	0.395	0.341	0.013
Tympanum/SVL	F	0.062	0.080	0.072	0.004
Tympanum/SVL	M	0.065	0.089	0.074	0.005
Thigh/SVL	F	0.354	0.499	0.428	0.026
Thigh/SVL	M	0.383	0.475	0.431	0.023
Shank/SVL	F	0.421	0.510	0.466	0.020
Shank/SVL	M	0.431	0.508	0.470	0.016
Foot/SVL	F	0.466	0.595	0.523	0.026
Foot/SVL	M	0.468	0.577	0.528	0.023

TABLE 48.—Minima, maxima, and summary statistics for size and measurement ratios for Region 7 Dark Belly OTU. (N = 38 females, 34 males.)

Variable	Sex	Minimum	Maximum	Mean	Standard deviation
SVL	F	34.0	42.5	37.6	2.219
SVL	M	24.5	36.4	32.3	2.260
Head length/SVL	F	0.333	0.381	0.357	0.013
Head length/SVL	M	0.347	0.410	0.368	0.017
Head width/SVL	F	0.313	0.363	0.336	0.012
Head width/SVL	M	0.314	0.375	0.343	0.015
Tympanum/SVL	F	0.062	0.082	0.073	0.005
Tympanum/SVL	M	0.066	0.080	0.074	0.004
Thigh/SVL	F	0.342	0.448	0.395	0.024
Thigh/SVL	M	0.362	0.450	0.415	0.020
Shank/SVL	F	0.351	0.438	0.404	0.018
Shank/SVL	M	0.397	0.450	0.420	0.015
Foot/SVL	F	0.433	0.537	0.499	0.026
Foot/SVL	M	0.474	0.559	0.513	0.022

TABLE 49.—Minima and maxima for size and measurement ratios for Region 7 Anastomotic Belly OTU. (N = 3 females, 5 males.)

Variable	Sex	Minimum	Maximum
SVL	F	36.5	40.8
SVL	M	26.6	32.5
Head length/SVL	F	0.353	0.393
Head length/SVL	M	0.399	0.430
Head width/SVL	F	0.343	0.348
Head width/SVL	M	0.351	0.398
Tympanum/SVL	F	0.061	0.082
Tympanum/SVL	M	0.077	0.113
Thigh/SVL	F	0.417	0.429
Thigh/SVL	M	0.425	0.472
Shank/SVL	F	0.402	0.441
Shank/SVL	M	0.434	0.481
Foot/SVL	F	0.476	0.548
Foot/SVL	M	0.532	0.598

TABLE 50.—Minima and maxima for size and measurement ratios for Region 7 Maracaibo Drainage OTU. (N = 3 females, 8 males.)

Variable	Sex	Minimum	Maximum
SVL	F	45.0	51.2
SVL	M	34.3	46.7
Head length/SVL	F	0.344	0.362
Head length/SVL	M	0.337	0.370
Head width/SVL	F	0.318	0.344
Head width/SVL	M	0.319	0.353
Tympanum/SVL	F	0.068	0.072
Tympanum/SVL	M	0.073	0.083
Thigh/SVL	F	0.442	0.459
Thigh/SVL	M	0.389	0.463
Shank/SVL	F	0.476	0.480
Shank/SVL	M	0.452	0.502
Foot/SVL	F	0.542	0.551
Foot/SVL	M	0.517	0.607

Region 5 Light Posterior Belly OTU represents the same species as the Region 4 and 7 Light Posterior Belly OTUs. Advertisment calls from Region 5 would be instructive.

The available calls of the Dark Belly OTU from Regions 1, 3, and 4 are similar (compare Figures 8, 13, 22, 23). The discriminant analysis of measurement data indicates that the Dark Belly OTUs from Regions 1, 3, 4, and 7 also are very similar (Table 52).

Anastomotic Belly OTU individuals have considerable call repertoires and there is some question as to what the advertisement call is. For the calls analyzed, at least one of the call types is quite similar among all individuals from Regions 4 and 5 (Figures 2, 3, 16–21, 25). Sizes and shapes as analyzed by discriminant analysis of measurement data (Table 53) are essentially identical; however, the size and shape of the Region 7 Anastomotic Belly OTU are more distinctive than anticipated (Table 53), although the sample sizes for Region 7 are really too small to assess meaningfully. Additional specimens and calls from Region 7 should clarify the relationships, but based on overall appearances, I think the Anastomotic Belly OTUs from Regions 4, 5, and 7 all represent the same species.

The Region 2 Small–Moderate Size OTU does not have any single diagnostic feature that separates all individuals of the OTU from all other OTUs 100% of the time, and there are no advertisement calls on hand for it. Nevertheless, the overall appearance of series of specimens of this OTU indicates that it represents a species distinct from all others. It most resembles such OTUs as the Light Posterior Belly OTU and Region 5 Small Size Guianas OTU, from which it is at least distinctive based on discriminant analysis of measurement data (Table 51).

The species status of OTUs between Region 6 and the mainland is unclear, as is the status of the Region 3 Light Belly OTU and of certain OTUs between Regions 4, 5, and 7 in the countries of Colombia and Venezuela. This latter problem is examined first.

Comparison of Certain Colombian and Venezuelan OTUs

The OTUs for which species status are unclear in Colombia and Venezuela are the Light Posterior Belly OTU, the Colombian Andes OTU, the Maracaibo Drainage OTU in Colombia, the Venezuelan Andes OTU, and the Lake Maracaibo OTU in Venezuela. The generalized squared distance results of discriminant analyses of measurement data among males and females of these five OTUs (Table 54) indicate the following. Among these OTUs, the Lake Maracaibo OTU is distinctive. The Light Posterior Belly OTU is distinguishable from the Colombia Andes OTU and the Venezuela Andes OTU based on measurement data. Re-examination and comparison of specimens side by side among these OTUs indicate that the Venezuelan Andes OTU and Colombia Andes OTU appear to represent distinct species, but the problem is compounded by the likelihood that the Venezuelan Andes OTU is composite. It is unclear whether the Light Posterior Belly OTU is the same as either some parts of or all of the Venezuela Andes OTU. The status of the Maracaibo Drainage OTU remains problematical. Based on measurement data, the Maracaibo Drainage OTU is rather distinct within this grouping of five OTUs, but it is not at all clear when comparing specimens side by side that this OTU is distinct from either the Colombia Andes OTU or (parts of)

TABLE 51.—Discriminant analysis generalized squared distances among several mainland and island OTUs. Full OTU names (and sample sizes for females, males) are: Region 4 Light Posterior Belly OTU (313, 181); Region 5 Light Posterior Belly OTU (3, 9); Region 7 Light Posterior Belly OTU (74, 43); Region 2 Small–Moderate Size OTU (50, 55); Small–Moderate Size Island OTU (36, 71); Region 5 Small Size Guianas OTU (147, 93); Region 4 Anastomotic Belly OTU (85, 117).

Sex and OTU	Light Belly 4	Light Belly 5	Light Belly 7	Region 2	Island	Small Size Guianas	Anastomotic Belly 4
Females							
Light Belly 4	0	2.8	1.2	9.5	2.3	12.2	19.5
Light Belly 5		0	4.7	8.6	2.3	14.4	15.3
Light Belly 7			0	7.2	1.9	7.2	18.8
Region 2				0	4.7	3.5	3.5
Island					0	8.5	13.1
Small Size Guianas						0	11.7
Anastomotic Belly 4							0
Males							
Light Belly 4	0	5.6	2.1	10.6	2.2	10.1	26.6
Light Belly 5		0	10.0	12.5	3.9	13.0	20.5
Light Belly 7			0	8.2	2.3	5.3	24.2
Region 2				0	7.5	3.9	5.9
Island					0	5.6	18.8
Small Size Guianas						0	12.5
Anastomotic Belly 4							0

TABLE 52.—Discriminant analysis generalized squared distances among Region 1, 3, 4, 7 Dark Belly OTUs. Full OTU names (and sample sizes for females, males) are: Region 1 Dark Belly OTU (41, 35); Region 3 Dark Belly OTU (177, 120); Region 4 Dark Belly OTU (275, 230); Region 7 Dark Belly OTU (38, 34); Region 4 Anastomotic Belly OTU (85, 117).

Sex and OTU	Dark Belly 1	Dark Belly 3	Dark Belly 4	Dark Belly 7	Anastomotic 4
Females					
Dark Belly 1	0	0.5	1.3	1.0	7.1
Dark Belly 3		0	1.5	1.8	7.2
Dark Belly 4			0	1.1	12.7
Dark Belly 7				0	10.4
Anastomotic 4					0
Males					
Dark Belly 1	0	1.0	1.3	1.2	12.1
Dark Belly 3		0	2.2	2.9	9.8
Dark Belly 4			0	1.5	18.6
Dark Belly 7				0	16.4
Anastomotic 4					0

TABLE 53.—Discriminant analysis generalized squared distances among Region 4, 5, 7 Anastomotic Belly OTUs. Full OTU names (and sample sizes for females, males) are: Region 4 Anastomotic Belly OTU (85, 117); Region 5 Anastomotic Belly OTU (22, 42); Region 7 Anastomotic Belly OTU (3, 5); Region 4 Dark Belly OTU (275, 230).

Sex and OTU	Anastomotic 4	Anastomotic 5	Anastomotic 7	Dark Belly 4
Females				
Anastomotic 4	0	1.6	6.3	12.5
Anastomotic 5		0	8.0	13.4
Anastomotic 7			0	6.5
Dark Belly 4				0
Males				
Anastomotic 4	0	0.6	3.2	17.9
Anastomotic 5		0	4.8	19.3
Anastomotic 7			0	19.9
Dark Belly 4				0

TABLE 54.—Discriminant analysis generalized squared distances among similar Colombian and Venezuelan OTUs. Full OTU names (and sample sizes for females, males) are: Lake Maracaibo OTU (Venezuela) (1 female not analyzed, 4); Light Posterior Belly OTU (388, 233); Maracaibo Drainage OTU (Colombia) (3, 8); Venezuela Andes OTU (27, 20); Colombia Andes OTU (64, 102).

Sex and OTU	Lake Maracaibo	Light Posterior Belly	Maracaibo Drainage	Venezuela Andes	Colombia Andes
Females					
Light Posterior Belly		0	4.8	1.0	2.8
Maracaibo Drainage			0	5.1	5.4
Venezuela Andes				0	5.1
Colombia Andes					0
Males					
Lake Maracaibo	0	9.0	19.0	10.5	16.7
Light Posterior Belly		0	6.8	2.0	2.1
Maracaibo Drainage			0	4.7	7.5
Venezuela Andes				0	5.9
Colombia Andes					0

the Venezuela Andes OTU. Without advertisement call information, the available data are not adequate to resolve completely the species allocations of these five OTUs. The morphological data and side-by-side comparisons of specimens are consistent with recognizing the Colombia Andes OTU and the Light Posterior Belly OTU as two distinct species.

The species status of the Maracaibo Drainage OTU from Colombia, and the Venezuela Andes OTU are left open at this time until further data become available. As discussed earlier, the species status of the Lake Maracaibo OTU relative to the Small Size Guianas OTU requires further data to resolve. Until such data become available, the species status of the Lake Maracaibo OTU is left open. There is one juvenile specimen from Astillero, Norte de Santander, Colombia (USNM 147063), that is most similar to the Lake Maracaibo OTU. The species status of the previously discussed single specimen from near Caripe, Monagas, Venezuela (USNM 216805), is also left as an open question at this time. As indicated, the morphologies among the Colombia Andes OTU and the Light Posterior Belly OTU are similar, such that certain individual specimens can not be allocated to these species with certainty. Re-examination of specimens previously identified as the Colombia Andes OTU or as the Light Posterior Belly OTU from Colombia indicates that some individuals previously were assigned to the incorrect OTU. Specifically, a small series of specimens from the nearby localities of Menegua and Puerto Lopez, Meta, Colombia (ICNMNH 1310–1314, 1322, 18159–18161, USNM 147273, 147274, UTA 8041, 8042), and the nearby localities of Boca del Caño Cabra and Reserva Biológica La Macarena, Meta, Colombia (ICNMNH 2384, IND-AN 2512, UTA 3564), previously identified as belonging to the Region 4 Light Posterior belly OTU probably represent the Colombia Andes OTU and are hereby allocated to the Colombia Andes OTU. A single specimen from Araracuara, Amazonas, Colombia (ICNMNH 18093), also previously was identified as a member of the Light Posterior Belly OTU. Comparison of the specimen with other geographically proximate Light Posterior Belly OTU and Colombia Andes OTU specimens does not lead to a firm conclusion as to OTU identity. The measurement data when run on a discriminant analysis place the specimen in the Colombia Andes OTU. The belly pattern in particular also suggests this allocation; however, the locality of this specimen would suggest membership in the Light Posterior Belly OTU. In order to point out the unresolved nature of this specimen, it is placed in the Colombia Andes OTU; its distinctive geographic location hopefully will serve to stimulate collection of additional material and data to resolve the identification of the frogs of this complex from Araracuara. Two other problematical specimens (MVZ 176010, 176011) from near Río Cuyuní on the road to Santa Elena de Uairén, Bolívar, Venezuela, are very similar to the Region 4 or 5 Light Posterior Belly OTU and are considered as belonging to that species until additional data prove otherwise.

Region 3 Light Belly OTU

The Light Belly Region 3 OTU specimens are morphologically similar to the Anastomotic Belly OTU specimens of Regions 4, 5, and 7, including some specimens with the characteristic anastomotic belly pattern. Based on discriminant analysis of the measurement data, the Light Belly Region 3 OTU males are very similar to Anastomotic Belly Region 4 and 5 OTU males and much more similar to the Region 7 Anastomotic Belly males than to either Dark Belly Region 4 or Light Posterior Belly Region 4 males (Table 55). It is likely that there are different habitat affiliations for the Region 3 Light Belly OTU and Anastomotic Belly OTU individuals. The overwhelming majority of Anastomotic Belly OTU specimens with habitat data were taken from tropical rain forest habitats. Continuous tropical rain forests do not occur where Region 3 Light Belly OTU members have been collected. For example, Mato Verde, Mato Grosso, has typical cerrado with thin or absent gallery forests (P.E. Vanzolini, pers. comm.). It is unknown whether the Region 3 Light Belly OTU is associated with the ciliary forests in the otherwise open cerrado formation landscape (see additional discussion for *Leptodactylus brevipes* in the section on nomenclature). For this paper, the Light Belly Region 3 OTU is considered to represent the same species as the Anastomotic Belly Region 4, 5, and 7 OTU species.

TABLE 55.—Discriminant analysis generalized squared distances among Region 3 Light Belly OTU males with other selected OTUs. Full OTU names (and sample sizes) are: Region 4 Anastomotic Belly OTU (117); Region 5 Anastomotic Belly OTU (42); Region 7 Anastomotic Belly OTU (5); Region 3 Light Belly OTU (29); Region 4 Dark Belly OTU (230); Region 4 Light Posterior Belly OTU (181).

OTU	Anastomotic 4	Anastomotic 5	Anastomotic 7	Light Belly 3	Dark Belly 4	Light Posterior Belly 4
Anastomotic 4	0	0.6	3.1	0.5	17.9	27.0
Anastomotic 5		0	4.7	0.9	19.1	25.7
Anastomotic 7			0	4.9	20.2	41.6
Light Belly 3				0	14.1	22.8
Dark Belly 4					0	27.8
Light Posterior Belly 4						0

Island OTUs

The two OTUs from the Lesser Antilles, Trinidad, and Tobago are similar in some ways to some of the geographically proximate mainland OTUs, but not identical. The advertisement call of the Small–Moderate Size Island OTU is virtually identical with the call of the Region 5 Small Size Guianas OTU (compare Figures 27–29, 31). However, none of the Small–Moderate Size Island OTU individuals have the light lip stripe characteristic of many Region 5 Small Size Guianas OTU specimens. Based on side-by-side comparisons, the Small–Moderate Size Island OTU is most similar to the Region 4 and 5 Light Posterior Belly OTUs, which also is supported by the measurement data (Table 51). The Small Size Trinidad OTU specimen has the same distinctive lip stripe as found in Region 5 Small Size Guianas OTU specimens, but the call is distinct from all others available for analysis. The best resolution of the morphological and call data appears to be to recognize the Small–Moderate Size Island OTU as a distinct species, as well as the Small Size Trinidad OTU as a distinct species. Additional data are needed on advertisement calls to understand the similarity in calls on hand for the Small–Moderate Size Island OTU and the Region 5 Small Size Guianas OTU.

Summary and Identification of Specimens Previously Not Assigned to a Region

In summary, each of the following are recognized as distinct species: (1) Region 6, Small–Moderate Size Island OTU; (2) Region 6, Small Size Trinidad OTU; (3) Region 5 Small Size Guianas OTU; (4) Light Posterior Belly OTUs of Regions 4, 5, 7; (5) Anastomotic Belly OTUs of Regions 4, 5, 7 (including Region 3 Light Belly OTU); (6) Region 2 Small–Moderate Size OTU; (7) Dark Belly OTUs of Regions 1, 3, 4, 7; (8) Region 7 Moderate Size Andes OTU; (9) Region 7 Large Size Central Peru OTU; (10) Region 7 Large Size Mid-Andes OTU; (11) Region 7 Colombia Andes OTU; (12) Region 5 Medium Bolívar OTU; (13) Toe Disked OTU. There remain series of specimens from Colombia and Venezuela (including the Maracaibo Drainage OTU, Lake Maracaibo OTU, and Venezuela Andes OTU) for which species status are unclear.

All of the specimens from areas not contained within the seven defined regions belong to the 13 recognized species. The few specimens from the State of Maranhão, Brazil, all belong to the Anastomotic Belly species. The specimens from the State of Amazonas, Venezuela, belong to the Anastomotic Belly and Region 5 Small Size Guianas species. The single specimen from La Guayacana, Nariño, Colombia, belongs to the Region 7 Large Size Mid-Andes species. The locality is unusual in that it is relatively lowland on the Pacific side of the Andes. All other specimens of this species are from the Amazonian slopes of the Andes.

Nomenclature

Eleven names have been proposed and a twelfth has been used at times for the members of the *podicipinus-wagneri* complex. Each of these names is discussed in the order in which they were proposed.

Leptodactylus caliginosus Girard, 1853.—*Leptodactylus caliginosus* has appeared most often in the literature in two ways: as a synonym of *Leptodactylus ocellatus* and as a valid name for a species within the *podicipinus-wagneri* cluster. Lutz (1930) was responsible for associating *caliginosus* with a member of the *podicipinus-wagneri* complex. Fortunately, he provided details on the reasons for his action. *Leptodactylus caliginosus* Girard, 1853, is based on two syntypes that were collected by the U.S. Exploring Expedition from Rio de Janeiro. The catalog entry for USNM 7389 (two specimens) has in original handwriting in ink "*Leptodactylus ocellatus*" under the scientific name column, "Rio Janeiro" under the locality column, and "Exp. Exped." under the donor column. Added in pencil in D.M. Cochran's handwriting is the remark that the specimens are cotypes of *Leptodactylus caliginosus* Girard. Girard's (1853:422) description is brief, but it includes the statement, "Skin smooth in the adult, traces of longitudinal folds in the young." These states are still evident in the two specimens with the single number USNM 7389. There is no reason to question the validity of USNM 7389 as anything but the syntypes of *Leptodactylus caliginosus* Girard. Lutz (1930) explained that there were two species of *Leptodactylus* from the Rio de Janeiro region with toe fringes, a common, large species and a much rarer, smaller species. The large species from Rio de Janeiro always has been identified as *Leptodactylus ocellatus,* and, until sometime between 1927 and 1930, Lutz considered that *caliginosus* was a synonym of *ocellatus.* In 1927, Lutz examined the syntypes of *caliginosus* (Lutz, 1930). At that time, he still had not collected any examples of the second, smaller species with toe fringes from Rio de Janeiro. He stated (Lutz, 1930:22): "In 1927 I had an occasion to examine the type and a cotype of Girard's. ... The abdominal pigmentation, the general colour and the size did not exclude small *ocellatus* with somewhat strongly developed pigmentation on the under side and one of the specimens seemed even to show traces of glandular folds; therefore I found no reason to change my opinion." Between 1927, when he examined the types, and 1930, when his paper was published, he found the second species in Rio de Janeiro, for which he thought *caliginosus* was the appropriate name. In his description of what he considered to be topotypes of *L. caliginosus,* Lutz (1930:23) observed, "My biggest male attains a length of about 40 mm. and the largest female (Pl. II) of 42 mm., which I consider near to the maximum. ..." Lutz must not have made notes on the sizes of the syntypes of *caliginosus.* The smaller (presumably juvenile) specimen is about 50 mm SVL and the larger (presumably female) is about 70 mm SVL. The

specimens unquestionably belong to the *ocellatus* complex in my opinion, and I believe that if Lutz had recorded the sizes of the types, he would not have associated them with the smaller species with toe fringes that occurs around Rio de Janeiro. The specimens Lutz (1930) described and figured as topotypes of *caliginosus* definitely are members of the *podicipinus-wagneri* complex and belong to the Region 2 Small–Moderate Size species of this paper. Lutz (1930:22) referred specimens from two other localities as resembling his concept of *caliginosus*. They include "some specimens collected near Avanhadava by J. Venancio and near the Salto do Marimbondo by Dr. C. Pinto. (Both places are in the northwestern part of São Paulo.)" I have not examined the specimens from Avanhadava, but the specimens from near Salto do Marimbondo almost certainly are part of the syntype series of *Leptodactylus nattereri* Lutz, 1926, discussed below and are conspecific with the Dark Belly species of this paper. In short, *Leptodactylus caliginosus* Girard pertains to the *ocellatus* group and does not apply to members of the *podicipinus-wagneri* complex.

Cystignathus podicipinus Cope, 1862.—Cope described *podicipinus* from "Paraguay," apparently based on a single specimen, now ANSP 14539. I examined this type for my previous revision (Heyer, 1970). Based upon notes and photographs I had taken at that time, and especially upon Cope's color pattern description, I conclude there are sufficient similarities for association of *podicipinus* with the Region 1,3,4,7 Dark Belly species. There is only one species of this complex that occurs in Paraguay, and Cope's (1862:156) color pattern description that states that "a yellowish line extends beneath the eye to the angle of the mouth" and the venter is "yellowish brown, with numerous yellow spots," which is diagnostic for the Dark Belly species. The holotype has darkened such that the light posterior lip stripes and belly spots are no longer obvious.

Plectromantis wagneri Peters, 1862.—The holotype, ZSM 1080/0, was destroyed in World War II and was from "Pastassa," not "der Westseide der Anden in Ecuador," as stated by Peters (1862:233) in the type description (Heyer, 1970:19). Peter's description allows unambiguous association with the Region 7 Large Size Mid-Andes species. The destroyed holotype was 68 mm SVL with small black thumb spines, the toes were fringed, the toe tips were expanded into small disks, and the belly was dirty white with more or less extensive black marbeling. Except for size, the characteristics given by Peters for *wagneri* could pertain either to the Light Posterior Belly or the Region 7 Large Size Mid-Andes species; however, only the Region 7 Large Size Mid-Andes species has those character states and large size. The only discrepency between Peters' description and Region 7 Large Size Mid-Andes individuals is, in fact, with detail of size. If the holotype was a female, the SVL fits within the range observed for the Region 7 Large Size Mid-Andes species (Table 45), but the thumb spines are larger than in any other female (given as $1^1/_3$ mm in length in the description of *wagneri;* the small black/tan spines of a 69.5 mm SVL female, KU 120320, from Region 7 Large Size Mid-Andes OTU, are about 0.5 mm in length). If the specimen was a male, the size of the thumb spines, although small, are matched by some males of the Region 7 Large Size Mid-Andes species, but exceed in SVL any of the latter specimens by 7.3 mm (Table 45). It is worth noting that a 23 mm head length as given by Peters for *wagneri* is found in Region 7 Large Size Mid-Andes members of 63 mm SVL, raising the possibility of a typographical error in the type description. The discrepency of size of the type of *wagneri* with specimens of the Region 7 Large Size Mid-Andes species is negligible, in any case. In my earlier revision, I designated as the Neotype for *Plectromantis wagneri* the holotype of *Eleutherodactylus leptodactyloides* Andersson (1945) (Heyer, 1970:21). There is one major difference between Peters' description of *wagneri* and the holotype of *E. leptodactyloides:* the male holotype of *leptodactyloides* is 44 mm SVL, which fits into the area of size overlap between the Region 7 Large Size Mid-Andes species and the Light Posterior belly species, both of which occur along the Rio Pastaza, the type locality of *leptodactyloides.* Rather than stabilize nomenclature, my previous designation of a neotype for *wagneri* added to the confusion of the nomenclature in this complex. Article 75(b) of the International Code of Zoological Nomenclature (1985:157) states: "Circumstances admitted.—A neotype is to be designated only in connection with revisory work, but only in exceptional circumstances when a neotype is necessary in the interests of stability of nomenclature; the designation of a specimen to be a neotype other than in accordance with these conditions is not valid." As designation of a neotype for *Plectromantis wagneri* is not necessary in the interests of nomenclatural stability, my previous designation of the holotype of *Eleutherodactylus leptodactyloides* is invalid. *Plectromantis wagneri* Peters is the oldest available name for the Region 7 Large Size Mid-Andes species.

Platymantis petersii Steindachner, 1864.—The type, originally in the Naturhistorisches Museum Wien, is apparently lost (Heyer, 1970:21; Häupl and Tiedemann, 1978, do not include the specimen in their list of types). Steindachner (1864) described *petersii* on the basis of a single 37 mm SVL adult male from Marabitanas (Amazonas, Brazil). I know of no recent specimens from Marabitanas. There are three species from the area around Marabitanas that include 37 mm SVL males: (1) the Toe Disked species; (2) the Anastomotic Belly Region 4,5,7 species; and (3) the Light Posterior Belly Region 4,5,7 species. The condition of the toe tips of the (lost) holotype, both in the description and figure, is of a state that is found in all three species that are expected to occur at Marabitanas. The overall color pattern, as shown in Steindachner's (1864) plate XVI, fig. 2, also is found in all three species. Steindachner's color description is 17 lines long and as such is detailed in some aspects. A 1 mm wide light posterior eye stripe from the posterior part of the eye to the angle of the mouth is described, but no mention is made of a light stripe on the

posterior thighs, nor is a light thigh stripe evident in plate XVI, fig. 2, although the perspective illustrated could or could not show the lower area of the thigh where a stripe would occur. The most instructive statement of color pattern is that the throat and belly were of a dirty brownish yellow color. Thus, the belly and throat had the same intensity of color pattern, which excludes the Toe Disked species. The illustrations are apparently life-size; at least the SVL of the illustration is 37 mm. There is some perspective in fig. 2, as the legs are not symmetrical, the right side being shorter. Using measurements of the left thigh and shank, together with other measurements from figs. 2, 2a, and 2c, I measure the following for the (lost) holotype: SVL 37.0 mm, head length 14.5 mm, head width 13.8 mm, tympanum 3.5 mm, thigh 18.4 mm, shank 17.2 mm, foot 19.0 mm. Using these measurements in a discriminant analysis, the holotype measurements have a 61% probability of belonging to the Anastomotic Belly species, a 39% probability of belonging to the Toe Disked species, and <1% probability of belonging to the Light Posterior Belly species. Thus, even in the absence of a holotype, I think there is sufficient evidence to positively associate the name *Platymantis petersii* with the Anastomotic Belly species. Designation of a neotype is unnecessary, invalidating my previous designation of AMNH 23182, Río Pescado, Amazonas, Venezuela, a female, as the neotype of *Platymantis petersii*. The locality of Río Pescado, Amazonas, Venezuela, is in the Orinoco drainage, which further destabilizes the nomenclatural stability if my original neotype designation were followed. AMNH 23182 was re-examined. The specimen is a 41.0 mm SVL adult female. The posterior lip stripe is distinct, extending from the posterior corner of the eye. The posterior thigh light stripes are distinct. The dorsolateral folds are moderately developed. The chin, throat, and belly are moderately mottled, with the melanophores becoming scattered quickly on the belly such that the belly is mostly unpigmented. The pattern that is on the belly is not anastomotic. The toe tips are moderately expanded. Comparison of this specimen with others from the same region of Venezuela clearly indicates that it belongs to what I am calling the Small Size Guianas species from the Orinoco drainage, not the Anastomotic Belly species.

Leptodactylus brevipes Cope, 1887.—The holotype, ANSP 11270, remains in quite good condition. The specimen is 50.0 mm SVL and is almost assuredly a female (the specimen has been dissected to examine the sternum; further dissection to examine the sex and reproductive condition could be damaging to the overall integrity of the specimen and should only be done if determined to be critically necessary). The light posterior eye stripe is distinct (especially when viewed with the specimen submersed in alcohol) and does not extend to under the middle of the eye. The dorsolateral folds are interrupted and extend to just beyond the scapular region. The posterior thighs are almost boldly mottled with stronger indications of a light stripe on the left thigh than the right. The ventral pattern appears to be somewhat faded, but it is still clearly discernible. The chin has a few distinct light spots, and the throat and chest regions have a dense profusion of melanophores. The belly pattern consists of an anastomotic melanophore network. The toe tips are just swollen.

The holotype matches the Anastomotic Belly OTU best in terms of extemal morphology, particularly with respect to having the distinctive anastomotic belly pattern. A discriminant analysis was performed using measurement data for females of the three species that occur in the same general geographic region as the provenance of the holotype. The posterior probabilities of membership for the holotype are 99% for the Anastomotic Belly species (*petersii*), 1% for the Dark Belly species (*podicipinus*), and <1% for the Light Posterior Belly species.

The holotype was collected by H.H. Smith from Chapada, Brazil. Herbert Huntingdon Smith was known mostly for his insect collections from South America (see Papavero, 1973, for an interesting summary including Smith's itinerary in South America). There is no doubt that the Chapada where Smith resided from 1882 to 1886 is the locality now known as Chapada dos Guimarães, Mato Grosso, Brazil (as indicated by Bokermann, 1966). Chapada dos Guimarães is considerably further south than other known localities of *L. petersii*. As *L. petersii* is associated with rainforests in the general Amazon basin, I questioned in my own mind whether the holotype of *L. brevipes* really represented the same species I identify as *L. petersii* or whether there might have been a mixup of locality data and the holotype was really from the Amazon region of Brazil and not from Chapada dos Guimarães.

With regard to the possibility of a locality mixup, Smith did in fact collect in the Amazon region of Brazil in 1874 and 1881 (Papavero, 1973). There is no date of collection written in the catalog entry for the holotype in Philadelphia, nor is there any information in the archives about when the collection containing the holotype was received in Philadelphia (J.E. Cadle, pers. comm.); however, many other species in the collection reported on by Cope have been recollected at Chapada dos Guimarães (e.g., the three species of *Pseudopaludicola* Haddad and Cardoso, 1987). Of particular interest is *Leptodactylus mystaceus* (ANSP 14132, collected by H.H. Smith from Chapada), which is also a species with a broad range throughout Amazonia. *Leptodactylus mystaceus* has been recollected from Chapada dos Guimarães by W.C.A Bokermann (Heyer, 1978:41, as *L. amazonicus*) and Adão J. Cardoso (ZUEC 5093). I do not know of any specimens of the *podicipinus-wagneri* complex from Chapada dos Guimarães other than the holotype of *L. brevipes*. All evidence indicates that the holotype of *L. brevipes* came from Chapada dos Guimarães.

The holotype of *L. brevipes* compares extremely well with the Region 3 representatives of *L. petersii* when specimens are compared side by side. As discussed earlier, there must be some different habitat association for the Region 3 specimens of *L. petersii* than for the Region 4 and 5 representatives of *L. petersii*. The habitat differences may be negligable if *brevipes*

was collected from the gallery forests at Chapada dos Guimarães. Up to historical times, there was a continuous network of gallery forests from the southern Amazon rainforests in the State of Mato Grosso to Chapada dos Guimarães (Amaral et al., 1982). If it later is demonstrated that the Region 3 specimens represent a species distinct from the Region 4 and 5 specimens, then *brevipes* will be the oldest available name for that species.

Based on the available data, I conclude that the holotype of *L. brevipes* represents the species recognized herein as the Anastomotic Belly species for which the name *petersii* has priority. Advertisement calls of this taxon from Chapada dos Guimarães could be conclusive in determining whether my conclusion is correct.

Leptodactylus validus Garman, 1887.—Garman described *validus* on the basis of three specimens, ANSP 19425, 26108, and MCZ 2185 from Kingston, St. Vincent. Schwartz and Thomas (1975:44) pointed out that my previous designation of MCZ 71920 as the lectotype (Heyer, 1970:21) is invalid, as MCZ 71920 was not part of the syntypic series. In my folder of data and photographs of *Leptodactylus* types, I have written on the back of a photograph of a ventral view of a frog, "*L. validus* Garman Lectotype MCZ 2185." Why I have the correct number in my type file but cited an incorrect number in the publication is a mystery at this point. MCZ 2185 is an adult male in good condition, and as the Garman article title refers to specimens in the Museum of Comparative Zoology, it is appropriate to designate MCZ 2185 as the lectotype of *Leptodactylus validus* Garman. There is but a single species of the *podicipinus-wagneri* complex on St. Vincent, which I am including in the Small-Moderate Size Island species. *Leptodactylus validus* is the oldest available name for this species.

Leptodactylus nattereri Lutz, 1926.—Lutz (1926) described *L. nattereri* on the basis of three specimens from Ilha Seca, São Paulo, Brazil, and three specimens from Cachoeira do Maribonda (= Marimbondo), São Paulo, Brazil. Bokermann (1966:73) gave the type locality as Ilha Sêca, Itapura, São Paulo, and remarked that Lutz originally cited the two localities involved. Bokermann (1966) further remarked that in the Adolfo Lutz collection there are two examples with the indication of "TIPOS" (n. 1314 and 1315) collected by Joaquim Venancio in April 1926 from Ilha Sêca. The Lutz collection now formally belongs to the Museu Nacional, Rio de Janeiro. Two bottles of specimens pertaining to the types of *nattereri* have been located, which I have examined. The bottle containing the specimens 1314 and 1315 noted by Bokermann no longer has the original bottle labels. The recopied label data gives the date of collection by Joaquim Venancio as May 1926. The other bottle contains three specimens, two of which are tagged with Lutz collection numbers 1015, 1016 (one specimen untagged). The bottle label has "COTIPOS" indicated with the species name, and the collection information is given as "*Leptodactylus* (*nattereri*), S. Paulo [two capital letters I can not decipher], prope Cachoeira Maribondo. leg César Pinto-ded. Maio-1925." This latter bottle of specimens apparently was unavailable to Bokermann but would seem to contain syntypes of *L. nattereri*. Lutz, in his type description, clearly states that his species was based on three examples from Ilha Secca, and, after those were collected, another set of three examples from near Cachoeira do Maribonda (= Marimbondo) were collected. Lutz specimen numbers 1314 and 1315 can not be part of the type series as they were collected later than the specimens from Cachoeira do Maribonda. There appear to be two likely explanations for this discrepancy. First, there could be an error involving the bottle labels for 1314 and 1315, and there still could be a set of three specimens from Ilha Seca collected before May 1925 somewhere in the Lutz collection that are the actual syntypes. Second, one or the other of the Lutzes might have substituted 1314 and 1315 for the original three syntypes and destroyed the original syntypes. The Lutzes did not think of the code of zoological nomenclature as a strictly binding set of rules but rather as a set of general guidelines, and, when there was a conflict, the biological species interpretation was the most important criterion. Thus, for them, what was most important was that future workers would understand what the species were that they described. If better-preserved specimens became available from their type localities, they were likely to replace those specimens as the types. The three syntypes from near the Cachoeira do Marimbondo are in very poor condition. There is a massive ventral incision from the chin through the belly with most of the viscera removed in each. All three are quite faded. Lutz (1926) stated that his specimens of *nattereri* had the same belly pattern as that illustrated by Steindachner (1864, plate XI: figs. 1a-d), which show a dark belly with distinct light spots, the pattern found only in the Dark Belly species. As there is no nomenclatural question that *Leptodactylus nattereri* Lutz is a junior synonym of *Cystignathus podicipinus* (as later recognized by Adolfo Lutz himself), it would seem appropriate to defer designation of a lectotype for *nattereri* until either the syntypes from Ilha Seca are located or until they are known with certainty to no longer exist.

Leptodactylus pallidirostris Lutz, 1930.—Lutz (1930:26) stated that he had numerous specimens from Kartabo collected by Mr. Beebe, from which he described *L. pallidirostris*. Lutz, in addition to a rather general description, provided a color illustration of the dorsum of one individual (1930, plate I: fig. 3). In the Adolfo Lutz collection at the Museu Nacional, there are a series of specimens, Lutz numbers 1829-1836 in two jars, both labelled as "TIPOS-EXÓTICOS" from Kartabo, British Guyana, collected by W. Beebe. Specimens 1830-1835 are either faded, soft, viciously dissected, or all three. The color illustration, plate I: fig. 3, shows quite a distinctively shaped light interorbital spot and toe tips markedly expanded into small disks. None of the Lutz specimen numbers 1829-1836 precisely match the illustration, nor are any of the specimens so close to the illustration as to unambiguously associate one of the syntypes with the figure, as would be desired in the

designation of a lectotype. Specimen 1829 is still in good condition, and I hereby designate it as the lectotype of *Leptodactylus pallidirostris* Lutz. The lectotype is a 33.0 mm SVL male. The light posterior lip stripe is more distinctive on the left and extends to under the middle of the eye. Light posterior thigh stripes are present, highlighted by dark brown ventrally, but the stripes are irregular and the left thigh stripe is not as distinct. The chin has light spots on a brown background. The throat is heavily mottled with brown. The chest and anteriormost belly have scattered, small brown flecks. The remainder of the belly lacks melanophores. The lectotype is from the same population analyzed as the Small Size, Light Posterior Lip Stripe, Kartabo, Guyana OTU, which in turn is part of the Small Size Guianas species. Thus, *Leptodactylus pallidirostris* Lutz is the oldest available name for the Small Size Guianas species.

Leptodactylus natalensis Lutz, 1930.—Lutz (1930:7, 26) based *L. natalensis* on several males and females. In the Portuguese version (1930:7), the type locality is given as "Natal, Rio Grande do Norte, Rio Baldo e outros lugares." The English version gives the type locality as "Rio Bahú and other places near Natal (Rio Grande do Norte)." Bokermann (1966) lists the type locality as "rio Baldo, Natal, Rio Grande do Norte" and gives no indication of specimen numbers, thus suggesting that he was unable to examine any types of *natalensis*. I have examined Lutz numbers 1610–1614, labelled "TIPOS" from Rio Grande do Norte, Natal, Rio Baldo, collected by A. Lutz and J. Venâncio in July 1928, and the specimen I previously designated (Heyer, 1970:22) as the lectotype, USNM 81130, with the minimal catalog data of Natal, Brazil, collected July 1925, received from A. Lutz (no collector given). The lectotype is a 34.5 mm SVL male. The color figure of *natalensis* shows detail adequate to allow one to associate which individual was illustrated, which should have been designated as the lectotype, other things being equal. As AL-MN 1610–1614 and USNM 81130 all represent the same species (in my opinion) and are the same as the other specimens I have examined from around Natal, there is no question in my mind but that *Leptodactylus natalensis* is the oldest available name for the Region 2 Small–Moderate Size species. However, none of the type series at hand matches the color figure. It is worth noting that Lutz stated (1930:27 (English version only, no mention in Portuguese version)), "They [*natalensis*] have much in common with the *caliginosus* Girard from Rio." I consider the specimens that Lutz identified as *caliginosus* from Rio to be conspecific with *natalensis*.

Leptodactylus intermedius Lutz, 1930.—Lutz described *L. intermedius* on the basis of four specimens collected by Erhardt, deposited in the Senckenberg Museum, and subsequently exchanged to Lutz. In both the Portuguese and English versions, Lutz gave the type locality as Manacapuri, near Manaos (1930:8, 27). Bokermann (1966:72) gave the type locality as Manacapurú, Amazonas, which is certainly a correct emendation. Unfortunately, the four syntypes, Lutz numbers 1438–1441 (which are certainly the four specimens used by Lutz as syntypes) are in terrible condition. The bottle label contains the following data: "N° 1438–41. *Leptodactylus intermedius* Lutz, 1930. Amazonas, Manacupari [note different spelling from that given in publication], prope Manáus. Leg. Erhardt. COTIPOS. Recibido 1927." The specimens are dark and extremely brittle. At each handling, the specimens disintegrate further. There is a pile of small body parts in the bottom of the bottle that can not be associated with individual specimens. The main bodies of the four individuals are still intact. Two tags are now dissociated from the main bodies of two specimens. Lutz stated that the largest specimen was a 30 mm female. In the largest specimen, even though the posterior belly interior is exposed, there are no eggs showing and any probing in the area to determine the state of sexual maturity would further destroy the specimen. The figure published by Lutz (plate III: fig. 6) is on a plate with photographs of preserved specimens and illustrations of frogs. It appears that the figure is an illustration, rather than a specimen, and I do not find the illustration particularly informative. On two of the bellies of the syntypes, I discern the anastomotic pattern characteristic of the Anastomotic Belly species. It turns out that USNM 103621 and 103622 also were collected by W. Erhardt, 9 July 1924, from Manacapurú, Amazonas, Brasil. These two specimens are still in good shape and the largest, USNM 103621, 30.5 mm SVL, is a young female with medium-size ova and an oviduct that is beginning to develop. This specimen had not been dissected during previous examinations and had been assumed to be a juvenile, which is why the minimum female size given for the Region 4 Anastomotic Belly OTU (Table 23) is 31.2 mm. Inclusion of USNM 103621 lowers the minimum SVL to 30.5 mm. Both USNM 103621 and 103622 are included in the Anastomotic Belly species. Nomenclaturally, there is no question in my mind that *Leptodactylus intermedius* Lutz is an available name for the Anastomotic Belly species recognized in this paper, but *Platymantis petersii* Steindachner has priority. Stability of nomenclature would not be served by designating one of the syntypes as the lectotype. Rather, it is probable that the syntypes will become totally destroyed due to their poor state of preservation, after which one of the other Erhardt-collected specimens from Manacapurú could be designated as a neotype if circumstances would warrant.

Eleutherodactylus leptodactyloides Andersson, 1945.—The holotype is a 44.0 mm SVL male (medium-size paired black spines on each thumb) from Rio Pastaza, Ecuador. The posterior light lip stripes are distinct and extend from the posterior corner of the eye. The posterior face of the thigh has distinct light stripes. Weak dorsolateral folds, lightly edged in dark brown laterally, extend from the eye to just past mid-distance to the sacrum. The chin has weakly defined light spots; the throat and chest are heavily suffused with contracted melanophores. The belly has more areas without melanophores than with, but the contracted melanophores form an anastomo-

tic pattern. The toe tips are noticeably expanded into small disks.

Two species of the *podicipinus-wagneri* complex occur in the Río Pastaza region of Ecuador, the Region 7 Large Size Mid-Andes OTU (= *L. wagneri*), and the Light Posterior Belly OTU. The holotype of *leptodactyloides* represents the same species as the Light Posterior Belly OTU. This conclusion is based on visual comparison of the type with representatives of the Light Posterior Belly OTU, and a discriminant function analysis of measurement data indicates that the holotype of *leptodactyloides* has a 98% probability of belonging to the Light Posterior Belly OTU and a 2% probability of belonging to the Region 7 Large Size Mid-Andes OTU.

As discussed above, my previous designation of the holotype of *Eleutherodactylus leptodactyloides* as the neotype of *Plectromantis wagneri* is invalid. *Eleutherodactylus leptodactyloides* is the oldest available name for the Light Posterior Belly species.

Adenomera griseigularis Henle, 1981.—Henle based his new species on a single specimen from Tingo Maria, Huanuco, Peru. After examination of the holotype, ZFMK 31800, I determined that the specimen was a juvenile *Leptodactylus*, not an adult *Adenomera*, and synonymized *Adenomera griseigularis* with *Leptodactylus wagneri* (Heyer, 1984). I previously compared the holotype of *A. griseigularis* with a series of juveniles and adults from Tingo Maria (USNM 196019–196025), which includes individuals with the throat and belly pattern described and illustrated by Henle (1981:141, fig. 2). Only one species of the *podicipinus-wagneri* complex has been collected from Tingo Maria as far as I know. *Adenomera griseigularis* Henle is the oldest available name for the Region 7 Moderate Size Andes species.

Species Accounts

A key to identify members of the *podicipinus-wagneri* complex within the *melanonotus* group is premature at this point due to the exclusion of *L. dantasi*, *melanonotus*, and *pustulatus* from this study as well as the fact that not all OTUs can be assigned to species at this time. In order to aid in the identification of the members of this complex that are definable as species, the diagnoses include all *Leptodactylus* with toe fringes except *L. ocellatus* and its closest relatives (*chaquensis*, *macrosternum*, *viridis*). *Leptodactylus ocellatus* and its closest relatives all have at least four well-developed dorsolateral folds, distinguishing them from all members of the *L. podicipinus-wagneri* complex, which at best, have a single pair of dorsolateral folds. Due to the nature of variation exhibited by members of this complex, individual preserved specimens may be unidentifiable. Identifications are facilitated if series of specimens from the same locality are compared directly with representatives of previously identified specimens from the same general locality.

Dorsolateral folds are given as absent, short, moderate, or long. The absent condition does (can) not distinguish between truly absent and poorly preserved (folds present in life but not discernible in preservative) conditions. Short folds are those that extend less than half the distance from the eye to the sacrum; moderate-length folds extend from half the distance from the eye to the full distance to the sacrum; long folds extend from the eye past the sacrum.

Only holotypes of new species are described in detail. In this study, paratypes are designated only for specimens coming from the immediate vicinity of the type locality. The reason for this is to maximize the likelihood that all type material will, in fact, belong to but one species. Referred specimens are those specimens examined that I think belong to the same species, but specifically are not included as types.

The features summarized in the adult characteristics sections are those analyzed for this study. The numbers of specimens indicated are those adult specimens used to summarize the measurement data. Usually the percentages for descriptive characteristics are based on a few more specimens, as the data from subadults also were included.

Because there are so few larval samples available for study in the *podicipinus-wagneri* complex, the larvae were not included as part of the study of variation. The available larval samples and previous descriptions were examined for inclusion in the species accounts sections. There are series for two species that contain both small (Gosner, 1960, stage 25–26) and large (Gosner stage 37–40) tadpoles. There are some size differences in certain proportions and denticle-row configurations that are discussed in larval descriptions. There is one labial tooth row feature that appears to be constant for all larval samples examined. The teeth are added to the rows laterally and the lateralmost teeth are smaller than the more medial teeth; thus, smaller larvae of the same species have fewer teeth per row than larger larvae. However, the number of denticles per 0.1 mm in the middle of the tooth row just anterior to the beak (row A-2 for all *Leptodactylus* in this paper) appears to be constant for Gosner stage 25–40 larvae. Due to the few species samples available as larvae, the problems involved with the island samples (see *L. validus* species account), and the anticipation that the larvae of *L. leptodactyloides* and *petersii* will be illustrated elsewhere (McDiarmid and Cocroft, a publication on the herpetofauna of Tambopata, Peru, pers. comm.), none of the larvae are illustrated for purposes of this paper.

Type locality data for new species are as given on museum loan invoices and are modified only if there has been clarification via correspondence.

Leptodactylus colombiensis, new species

FIGURE 35

HOLOTYPE.—ICNMNH 7409, an adult male from Colombia; Santander; Charalá, Virolín (= Inspección Policía Cañaver-

ales), confluencia del Río Cañaverales con el Río Guillermo, vertiente occidental, 1600–1700 m, 6°13'N, 73°05'W. Collected by Pedro M. Ruiz-C., F. Romero, and L. Martinez, 23 Feb 1981.

PARATYPES (all from Colombia: Santander).—ICNMNH 10516–10518 from Charalá, Cañaverales, collected by Pedro M. Ruiz-C. et al. in Mar 1981; ICNMNH 4493–4495 from Charalá, vereda El Reloj, 1740 m, collected by Pedro M. Ruiz-C., 29 Nov 1978; ICNMNH 6161–6164, 6166, paratopotypes, collected by Pedro M. Ruiz-C., P. Bernal, and V. Rueda, 25 Jan 1980; ICNMNH 7407, 7408, 7410, USNM 313876, 313877, paratopotypes, same data as holotype; ICNMNH 8526 from Charalá, Virolín, carretara a El Olival, collected by Pedro M. Ruiz-C., 7 Mar 1981; ICNMNH 11275, paratopotype, collected by Pedro M. Ruiz-C. and R. Hernández, 15 Apr 1982.

DIAGNOSIS.—*Leptodactylus colombiensis* is associated with the andean slopes of Colombia. The other *Leptodactylus* species that occur in Colombia with toe fringes (except *L. ocellatus* and its closest relatives) are *bolivianus, diedrus, leptodactyloides, melanonotus, petersii, riveroi,* and *wagneri.* For many specimens, identification may have to be made on the basis of geographic distribution, as *L. colombiensis* has not been taken in sympatry with any other member of the *melanonotus* species group. All specimens of *L. bolivianus* and *riveroi* have a pair of well-defined, continuous, smooth, long dorsolateral folds that extend the full length of the body behind the eyes; about 3/4 of the specimens of *colombiensis* have indistinct, short, or moderate-length dorsolateral folds, and in all *colombiensis* the folds are irregular and often interrupted. *Leptodactylus colombiensis* is a moderate–large size species (females to 62 mm SVL, males to 56 mm SVL) in which lip stripes, if present, extend only from the mideye level posteriorly. *Leptodactylus bolivianus* and *riveroi* are large species (*bolivianus* females to 88 mm SVL, males to 94 mm SVL; *riveroi* females to 81 mm SVL, males to 63 mm SVL) in which the entire upper lip and loreal region often has a broad, somewhat ill-defined (*bolivianus*) or well-defined (*riveroi*) light stripe. Most *Leptodactylus colombiensis* individuals have a moderate amount of belly mottling, and all individuals have some belly mottling. Most *L. diedrus* specimens lack a belly pattern or some have light mottling only. Most *L. colombiensis* have just-swollen toe tips; most *L. diedrus* have small, but well-defined toe disks. *Leptodactylus colombiensis* is most similar in appearance to *leptodactyloides. Leptodactylus colombiensis* attains a greater size than *leptodactyloides* (*colombiensis* females 38–62 mm SVL, males 36–56 mm SVL; *leptodactyloides* females 35–56 mm SVL, males 28–48 mm SVL), and more *colombiensis* (44%) have light-spotted chin/throat patterns than do *leptodactyloides* (10%). *Leptodactylus colombiensis* is larger than *L. melanonotus* (*melanonotus* females to 50 mm SVL, males to 46 mm SVL); *Leptodactylus melanonotus* only occurs along Pacific coastal Colombia. *Leptodactylus colombiensis* is larger than *petersii* (*petersii* females 31–51 mm SVL, males 27–41 mm SVL), and, whereas some individuals of *colombiensis* have extensively mottled bellies, none have the extensive anastomotic mottling pattern characteristic of *petersii. Leptodactylus colombiensis* is smaller than *wagneri* (*wagneri* females 52–82 mm SVL, males 39–61 mm SVL), and, whereas only some *colombiensis* have long dorsolateral folds, most *wagneri* have long folds.

DESCRIPTION OF HOLOTYPE.—Snout nearly rounded from

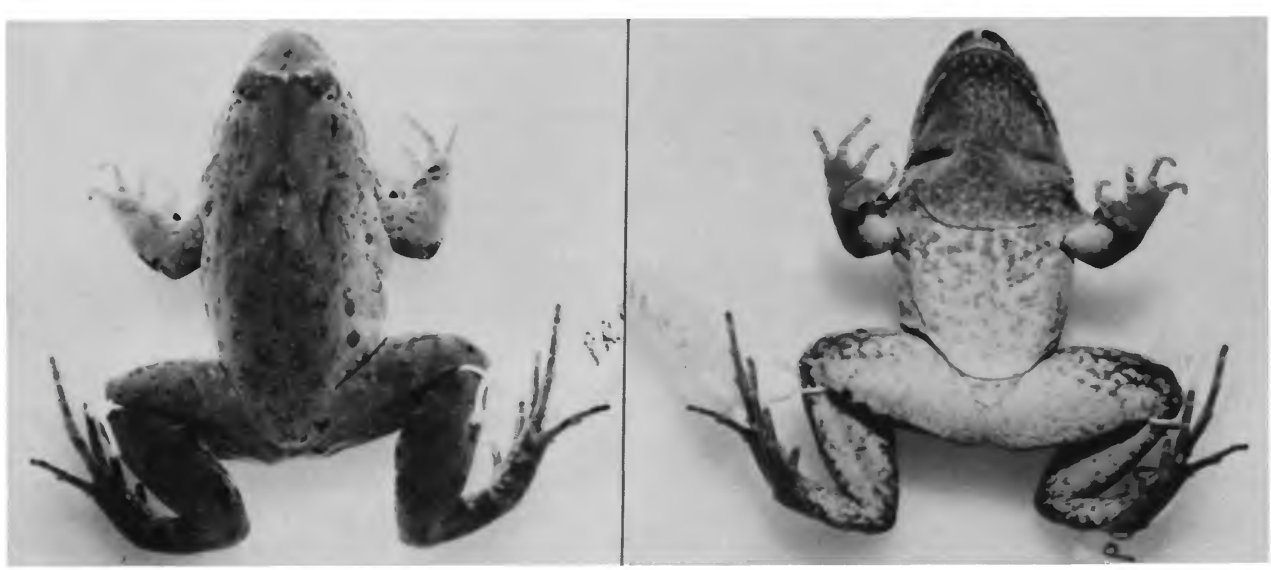

FIGURE 35.—Holotype of *Leptodactylus colombiensis,* new species.

above, rounded in profile; canthus rostralis rounded; lores obtusely concave in cross section; tympanum large, diameter about 3/4 eye diameter; vocal slits well developed, parallel to posterior 1/2 of lower jaw; vocal sac single, internal, no external modification visible; vomerine teeth in two long, almost abutting, almost straight series posterior to and almost entirely between choanae; finger lengths II≈IV<I<III; sides of fingers weakly ridged; each thumb with two medial black spines, distal spine broad, moderately large, proximal spine smaller, medium size; arms somewhat hypertrophied; no ulnar ridge; anterior 1/2 of dorsum with small, scattered white tubercles, posterior 1/2 of dorsum with many, small, heterogeneous-size white tubercles, some brown tipped; supratympanic fold distinct, a pair of weak interrupted dorsolateral folds from behind the eyes to about 2/3 distance to sacrum, outlined by black laterally; mouth commissure gland normal, flanks glandular appearing, very faint, diffuse tan ventrolateral glands bordering anterior 1/2 of belly, no other obvious glands; ventral disk fold distinct, otherwise ventral surfaces smooth; no chest spines; tips of toes slightly swollen; sides of toes extensively fringed; subarticular tubercles rounded, moderately developed; weak but distinct metatarsal fold continuous with fringe on outer toe V; tarsal fold distinct, extending 7/8 distance on tarsus, terminating at inner metatarsal tubercle, not continuous with toe fringe; posterior surface of tarsus and sole of foot with several to many small, heterogeneous-size white tubercles, some tan tipped.

SVL 46.3 mm, head length 16.7 mm, head width 15.5 mm, tympanum diameter 3.8 mm, thigh length 20.7 mm, shank length 21.3 mm, foot length 22.2 mm.

Dorsum rather uniform gray brown in preservative; irregular white and posteriorly black-bordered interorbital bar; discontinuous, but extensive, narrow mid-dorsal dark stripe; very weak indications of two dorsal chevrons when specimen viewed in fluid, otherwise dorsum with few indistinct darker markings in addition to those already described; upper lip irregularly dark edged with irregular light spotting above, very distinct light stripe from just past lower mideye to posterior extent of mouth commissure gland, black bordered above; upper limbs faintly blotched to weakly cross-barred; edge of chin dark with small light dots, throat and chest almost uniformly dark gray, anterior belly with heavy blotched mottle, becoming lighter posteriorly, lower thighs with same mottle pattern as posterior belly; posterior surface of thigh mottled light and dark gray brown.

COLOR IN LIFE (ICNMNH 7407–7410, USNM 313876, 313877).—Exposed surfaces tan to olive green, with small to medium black spots; interorbital bar yellow; tan bands almost indistinguishable or absent on thigh, shank, and tarsus; labial bars black with narrow yellow intervals; flanks tan yellowish; gular region, chest, belly, tibia, and foot cream color, chin with white dots and some dots grouped in center of throat; chest and belly with tan variegations to reticulations; thigh rose color, anterior surfaces with extensive tan reticulations; concealed surfaces of thigh and foot cream with tan dots or reticulations, medial border of tibia yellowish with small black spots forming a line; iris golden with dense brown dots (translation of field notes provided by Pedro M. Ruiz-C.).

HABITAT (summary for all type specimens).—All from swamps with emergent vegetation of grass and Cyperaceae, in a disturbed secondary forest (Pedro M. Ruiz-C., pers. comm.).

ETYMOLOGY.—Named to indicate that all known specimens of this species are from the country of Colombia.

ADULT CHARACTERISTICS (N = 64 females, 102 males).—Light posterior lip stripes rarely very distinct (1%), often distinct (21%), indistinct (42%), or not discernible (37%), when visible, stripes sometimes extending from just past mideye or usually from posterior corner of eye; light posterior thigh stripe rarely very distinct (2%), often distinct (23%), indistinct (33%), or not discernible (41%); dorsolateral folds sometimes (apparently) absent (11%), sometimes short (10%), usually moderate in length (55%), or often long (24%); toe tips rarely narrow (1%), usually just swollen (45%), often swollen (34%), just expanded (20%), or rarely expanded (1%); male black thumb spines usually medium size (48%), often medium–large (29%), or large (23%); chin/throat often with light spots on a darker field (44%); belly sometimes lightly mottled (16%), usually moderately mottled (59%), often extensively mottled (26%).

Females 38.2–62.5 mm SVL ($\bar{x} = 52.5 \pm 5.7$), males 36.0–55.9 mm SVL ($\bar{x} = 44.3 \pm 3.9$); female head length 32%–40% SVL ($\bar{x} = 36 \pm 2\%$), male head length 33%–40% SVL ($\bar{x} = 36 \pm 2\%$); female head width 31%–40% SVL ($\bar{x} = 34 \pm 2\%$), male head width 30%–37% SVL ($\bar{x} = 34 \pm 1\%$); female tympanum diameter 6%–8% SVL ($\bar{x} = 7 \pm 0\%$), male tympanum diameter 6%–9% SVL ($\bar{x} = 7 \pm 0\%$); female thigh length 37%–50% SVL ($\bar{x} = 43 \pm 3\%$), male thigh length 35%–49% SVL ($\bar{x} = 43 \pm 3\%$); female shank length 43%–51% SVL ($\bar{x} = 46 \pm 2\%$), male shank length 42%–51% SVL ($\bar{x} = 46 \pm 2\%$); female foot length 45%–58% SVL ($\bar{x} = 52 \pm 2\%$), male foot length 45%–57% SVL ($\bar{x} = 52 \pm 2\%$).

LARVAL CHARACTERISTICS.—Unknown.

ADVERTISEMENT CALL.—Unknown.

KARYOTYPE.—Unknown.

GEOGRAPHIC VARIATION.—Variation in adult morphologies was presented by major river drainage systems in "Core Region Analyses, Region 7—Andean Slopes." There is no apparent geographic pattern with respect to size when the largest and smallest adult specimens (those ≤ or ≥ 1.5 standard deviations from mean) are plotted on a map. There are three cases where large and small individuals are geographically close.

DISTRIBUTION.—With the exception of a problematic specimen from Araracuara, Amazonas, Colombia (Figure 36, circle), all other specimens are known from the flanks of the northern Andes in Colombia from altitudes of 180–2600 m (Figure 36; Appendix 2).

FIGURE 36.—Map of localities for *Leptodactylus colombiensis* (dots; circle = ICNMNH 18093 from Araracuara, Colombia, see text), *diedrus* (squares), and *griseigularis* (triangles).

Leptodactylus diedrus, new species

FIGURE 37

HOLOTYPE.—UTA-A 3726, an adult male from Colombia; Vaupés; 1/2 mi NE Timbó, ~1°06′N, 70°01′W. Collected by William F. Pyburn, 23 Jun 1973, in pocket at edge of forest pool.

PARATOPOTYPES.—UTA-A 3723, collected by J.K. Salser, Jr., 23 Jan 1972; UTA-A 3727, same data as holotype; UTA-A 3886, collected by William F. Pyburn, 31 May 1973; UTA-A 3887, collected by William F. Pyburn, 24 Jun 1973; UTA-A 4474, collected by William F. Pyburn, 23 Jul 1972; UTA-A 8592, collected by J.K. Salser, Jr., 28 Jul 1972, calling under water.

DIAGNOSIS.—*Leptodactylus diedrus* occurs in the Amazon basin and is known to occur or might be expected to occur with or near the following *Leptodactylus* species with toe fringes (except for *L. ocellatus* and its closest relatives): *L. bolivianus, colombiensis, dantasi, leptodactyloides, pallidirostris, petersii, podicipinus, riveroi,* and *wagneri. Leptodactylus diedrus* lacks dorsolateral folds, the ventral and posterior thigh patterns abut, the bellies usually lack melanophores, and the toe tips usually are expanded into small disks. In the other *Leptodactylus* from the same geographic region as *diedrus,* well-preserved individuals have at least some indication of dorsolateral folds, the ventral and posterior thigh patterns blend into one another, the bellies usually have melanophores, and only some individuals of *leptodactyloides* and *pallidirostris* have small toe disks.

DESCRIPTION OF HOLOTYPE.—Snout nearly rounded from above, rounded in profile; canthus rostralis rounded; lores weakly obtusely concave in cross section; tympanum large, horizontal diameter about 2/3 eye diameter; vocal slits present, parallel to posterior half of lower jaw; vocal sac single, indicated externally by a pair of lateral folds near jaws; vomerine teeth in two moderately straight series, separated by no more than 1/4 length of single vomerine tooth row from each other, lying posterior to and mostly between small, rounded choanae; finger lengths II just <I≈IV<III; weak ridges on inner sides of fingers II and III only; each thumb with two moderately large black thumb spines; upper arm slightly hypertrophied, no ulnar ridge; dorsum with many rather homogeneously sized, smallish tan/brown-tipped tubercles, denser posteriorly; supratympanic fold present, no indication of dorsolateral folds; flanks glandular appearing, no other glands visible; venter smooth, belly disk fold not evident, ventro-posterior thighs areaolate; no spines or nuptial asperities on chest region; toe tips with small disks, dorsal disk surfaces of largest disks longitudinally creased; toe fringes well developed; subarticular tubercles rounded, moderately developed; low, weak, but distinct light metatarsal fold, continuous with outer toe fringe on toe V; tarsal fold distinct, light, low, extending 7/8 distance of tarsus, terminating at inner metatarsal tubercle, not continuous with toe fringe; posterior surface of tarsus and sole of foot profusely covered with very small to small white tubercles.

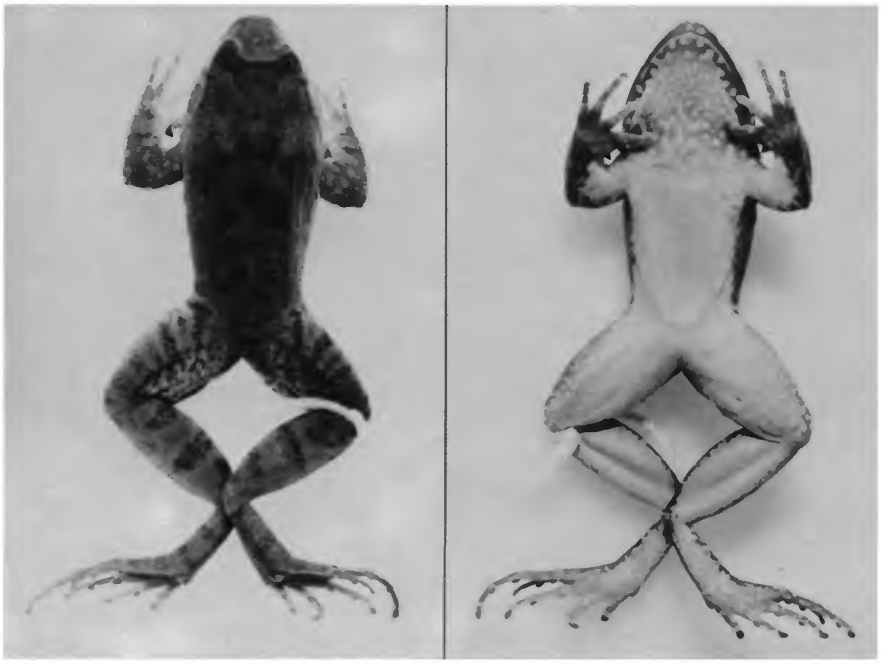

FIGURE 37.—Holotype of *Leptodactylus diedrus*, new species.

SVL 34.3 mm, head length 13.0 mm, head width 12.4 mm, tympanum diameter 2.9 mm, thigh length 14.7 mm, shank length 16.9 mm, foot length 19.0 mm.

Dorsum rather uniform brown in preservative; interorbital blotch distinctly defined anteriorly by dark brown interorbital band, two faint ill-defined darker chevrons in shoulder and sacral area, postsacral region with faint ill-defined darker spots; upper limbs weakly cross-banded; upper lip with dorsally erose dark border, area under eye lighter than darker upper lip pattern, lighter area continuous to angle of jaw, but not developed into distinct light posterior lip stripe; chin with moderately large light spots on a dark brown background, throat and anterior 1/2 of chest boldly mottled tan and white, posterior 1/2 of chest, belly, and ventral limbs devoid of pattern (no melanophores); posterior thigh mottled with distinctive dark transverse stripe bordered above by indistinct light stripe, posterior thigh pattern sharply demarcated (abutting with, no blending) from ventral thigh pattern.

ETYMOLOGY.—From the Greek *diedros,* sitting apart, separated, in allusion to the distinctiveness of this species within the *L. podicipinus-wagneri* cluster.

ADULT CHARACTERISTICS (N = 19 females, 27 males).—Light posterior lip stripes rarely distinct (1 individual), often indistinct (42%), usually not discernible (56%); light posterior thigh stripes rarely indistinct (5%), almost always mottled with no indication of light stripes (95%); dorsolateral folds absent; toe tips rarely swollen (2%), sometimes expanded (10%), usually with small disks (88%); male black thumb spines medium size (55%), medium-large (10%), or large (35%); chin/throat usually with light spots on a darker background (83%); belly sometimes lightly mottled (19%), usually with no melanophores or other pattern (81%).

Females 34.4–47.9 mm SVL ($\bar{x} = 41.1 \pm 3.0$), males 29.7–40.4 mm SVL ($\bar{x} = 36.2 \pm 2.4$); female head length 36%–39% SVL ($\bar{x} = 37 \pm 1\%$), male head length 35%–41% SVL ($\bar{x} = 38 \pm 2\%$); female head width 34%–37% SVL ($\bar{x} = 36 \pm 1\%$), male head width 33%–39% SVL ($\bar{x} = 36 \pm 1\%$); female tympanum diameter 7%–9% SVL ($\bar{x} = 8 \pm 0\%$), male tympanum diameter 8%–10% SVL ($\bar{x} = 9 \pm 1\%$); female thigh length 39%–48% SVL ($\bar{x} = 43 \pm 2\%$), male thigh length 40%–50% SVL ($\bar{x} = 44 \pm 2\%$); female shank length 45%–50% SVL ($\bar{x} = 47 \pm 1\%$), male shank length 42%–52% SVL ($\bar{x} = 47 \pm 2\%$); female foot length 48%–56% SVL ($\bar{x} = 52 \pm 2\%$), male foot length 48%–56% SVL ($\bar{x} = 52 \pm 2\%$).

LARVAL CHARACTERISTICS.—Unknown.

ADVERTISEMENT CALL.—Unknown.

KARYOTYPE.—Unknown.

GEOGRAPHIC VARIATION.—Certain aspects of geographic variation were discussed previously in "Variation within Taxa/Regions, Distinct Taxa" characterizing the Toe Disked OTU. In addition, one of the two specimens from the base of Neblina, Amazonas, Venezuela, is the only adult specimen examined that had distinct light posterior lip stripes.

DISTRIBUTION.—Few localities are known for this species, all of them from the northwestern sector of the Amazon basin (Figure 36; Appendix 2).

Leptodactylus griseigularis (Henle, 1981)

Adenomera griseigularis Henle, 1981:139, fig. 2 [type locality: Botanischer Garten in Tingo Maria, Huanuco, Peru, 641 m; holotype: ZFMK 31800, juvenile].

Leptodactylus wagneri.—Heyer, 1984 [first association of *griseigularis* with the genus *Leptodactylus; griseigularis* considered a synonym of *L. wagneri*].

DIAGNOSIS.—*Leptodactylus griseigularis* occurs in the same region as the following *Leptodactylus* species with toe fringes (except for *L. ocellatus* and its closest relatives): *L. bolivianus, leptodactyloides, pascoensis, petersii,* and *wagneri. Leptodactylus griseigularis* is a moderate-size species (females 39–58 mm SVL, males 35–51 mm SVL) in which most individuals have irregular, moderate-length dorsolateral folds; *Leptodactylus bolivianus* is a large species (females to 88 mm SVL, males to 94 mm SVL) in which the dorsolateral folds are smooth, regular, and long. *Leptodactylus griseigularis* is most likely to be confused with *leptodactyloides.* The commonest thigh pattern in *L. griseigularis* is mottled, without any indication of light stripes; the commonest posterior thigh pattern in *leptodactyloides* is with distinct light stripes. Almost all male *L. griseigularis* have large black thumb spines; almost all male *leptodactyoides* have medium-size black thumb spines. *Leptodactylus griseigularis* is smaller than *pascoensis* (*pascoensis* females 52–67 mm SVL, males 60–61 mm SVL). The commonest posterior lip stripe condition in *L. griseigularis* is indistinct stripes; the commonest condition in *pascoensis* is with no indication of light lip stripes. *Leptodactylus griseigularis* is larger than *petersii* (*petersii* females 31–51 mm SVL, males 27–41 mm SVL). The commonest belly pattern is a light mottle in *L. griseigularis,* whereas the commonest belly pattern in *petersii* is an extensive mottle in an anastomotic pattern. *Leptodactylus griseigularis* is smaller than *wagneri* (*wagneri* females 52–82 mm SVL, males 39–61 mm SVL). The most common dorsolateral-fold condition in *L. griseigularis* is moderate-length folds, and the commonest belly pattern is a lightly mottled state, whereas in *wagneri* the commonest conditions are long dorsolateral folds and moderately mottled bellies.

ADULT CHARACTERISTICS (N = 44 females, 31 males).—Light posterior lip stripes distinct in some individuals (9%), usually indistinct (47%), or not discernible (44%), when discernible, stripes extending from posterior corner of eye; light posterior thigh stripes rarely present (4%), sometimes indistinct (10%), but usually not discernible (86%); dorsolateral folds (apparently) absent (12%), short (7%), usually moderate length (76%), or rarely long (5%); toe tips narrow (11%), just swollen (22%), swollen (39%), just expanded (24%), or rarely expanded (4%, including one individual scored as having almost small disks); male black thumb spines rarely medium size (4%), rarely medium-large (4%), or usually large

(91%); chin/throat sometimes with light spots on a darker field (11%); belly usually lightly mottled (65%), often moderately mottled (27%), and sometimes extensively mottled (7%).

Females 39.4–57.6 mm SVL ($\bar{x} = 46.6 \pm 4.4$), males 34.7–51.3 mm SVL ($\bar{x} = 42.5 \pm 4.8$); female head length 32%–38% SVL ($\bar{x} = 35 \pm 1\%$), male head length 34%–39% SVL ($\bar{x} = 36 \pm 1\%$); female head width 30%–37% SVL ($\bar{x} = 34 \pm 2\%$), male head width 33%–38% SVL ($\bar{x} = 35 \pm 1\%$); female tympanum diameter 7%–9% SVL ($\bar{x} = 8 \pm 0\%$), male tympanum diameter 7%–9% SVL ($\bar{x} = 8 \pm 1\%$); female thigh length 40%–49% SVL ($\bar{x} = 43 \pm 2\%$), male thigh length 39%–51% SVL ($\bar{x} = 45 \pm 3\%$); female shank length 41%–51% SVL ($\bar{x} = 46 \pm 3\%$), male shank length 43%–52% SVL ($\bar{x} = 47 \pm 3\%$); female foot length 47%–58% SVL ($\bar{x} = 53 \pm 3\%$), male foot length 49%–59% SVL ($\bar{x} = 54 \pm 2\%$).

LARVAL CHARACTERISTICS.—Unknown.

ADVERTISEMENT CALL.—Unknown.

KARYOTYPE.—Diploid number 22, 2 pair median, 4 pair submedian, 1 pair subterminal, 4 pair terminal; secondary constriction in chromosome pair 8 (Bogart, 1974; specimens from Huanuco Province, Peru, reported as *Leptodactylus wagneri*).

GEOGRAPHIC VARIATION.—Variation in adult morphologies has been discussed in the "Region 7—Andean Slopes" analysis.

DISTRIBUTION.—The amazonian slopes of the Andes from central Peru to north-central Bolivia, from known altitudes of 100–1800 m (Figure 36; Appendix 2).

Leptodactylus leptodactyloides (Andersson, 1945)

Eleutherodactylus leptodactyloides Andersson 1945:43, fig. 15 [type locality: Rio Pastaza, East Ecuador; holotype NHRM, no number, adult male].

Leptodactylus leptodactyloides.—Heyer, 1970:21, 22 [first association of *leptodactyloides* with the genus *Leptodactylus*].

DIAGNOSIS.—*Leptodactylus leptodactyloides* occurs sympatrically with or in the same general region as the following *Leptodactylus* species with toe fringes (except for *L. ocellatus* and its closest relatives): *L. bolivianus, colombiensis, dantasi, diedrus, griseigularis, pallidirostris, pascoensis, petersii, podicipinus, riveroi, sabanensis,* and *wagneri* (among these, *leptodactyloides* most closely resembles *colombiensis, griseigularis,* and *sabanensis*). *Leptodactylus leptodactyloides* rarely has long dorsolateral folds and the dorsolateral folds are irregular, not smooth; the dorsolateral folds in *bolivianus* and *riveroi* are always long and smooth. *Leptodactylus leptodactyoides* is not as large as *colombiensis* (*leptodactyloides* females 35–56 mm SVL, males 28–48 mm SVL; *colombiensis* females 38–62 mm SVL, males 36–56 mm SVL) and fewer *leptodactyloides* (10%) have light-spotted chins/throats than do *colombiensis* (44%). *Leptodactylus leptodactyloides* never has distinct light belly spots, *dantasi* always has distinct light belly spots, and *podicipinus* often has distinct light belly spots. *Leptodactylus leptodactyloides* can be distinguished further from *podicipinus* by posterior thigh patterns; the thighs of most *leptodactyloides* have distinct light stripes, whereas the thighs of most *podicipinus* are entirely mottled with no indication of light stripes. *Leptodactylus leptodactyloides* almost always has some indication of dorsolateral folds; *diedrus* never has dorsolateral folds. Most *L. diedrus* lack melanophores on the belly; almost all *leptodactyloides* have melanophores on the belly. The posterior and ventral thigh patterns blend into each other in *L. leptodactyloides;* the patterns abut in *diedrus*. The commonest posterior thigh pattern in *L. leptodactyloides* is with distinct light stripes, whereas in *griseigularis* the commonest pattern is mottled, without any indication of light stripes. Almost all male *L. leptodactyloides* have medium-size black thumb spines; almost all male *griseigularis* have large black thumb spines. *Leptodactylus leptodactyloides* is larger than *pallidirostris* (*pallidirostris* females 30–43 mm SVL, males 28–37 mm SVL). The commonest lip stripe condition in *L. leptodactyloides* is indistinct stripes, and all posterior lip stripes extend from the posterior corner of the eye; in *pallidirostris* the commonest condition is distinct stripes, which often extend from under the middle of the eye. Few individuals (10%) of *L. leptodactyloides* have light-spotted chin/throat patterns; many (69%) *pallidirostris* have light chin/throat spots. *Leptodactylus leptodactyloides* is smaller than *pascoensis* (*pascoensis* females 52–67 mm SVL, males 60–61 mm SVL), and *leptodactyloides* individuals usually have at least some indication of light stripes on the posterior thigh, whereas most *pascoensis* specimens have mottled thighs with no indication of light stripes. *Leptodactylus leptodactyloides* usually have at least an indication of light stripes on the posterior thigh, whereas *petersii* usually do not. *Leptodactylus leptodactyloides* have more intense belly patterns anteriorly, and most individuals are moderately mottled; *Leptodactylus petersii* specimens have more uniformly patterned bellies, often in an anastomotic pattern, and most individuals have extensively mottled bellies. More *L. leptodactyloides* have at least indications of posterior lip stripes than *sabanensis*. *Leptodactylus leptodactyloides* differs more from *sabanensis* in advertisement call than in morphological features. In *L. leptodactyloides* the call duration is 0.01–0.04 s with a dominant frequency range of 650–1600 Hz and with maximum energy between 1100–1300 Hz; in *sabanensis* the call duration is 0.04–0.06 s with a dominant frequency range of 900–2300 Hz and with maximum energy between 1400–1800 Hz. *Leptodactylus leptodactyloides* is smaller than *wagneri* (*wagneri* females 52–82 mm SVL, males 39–61 mm SVL). Very few *L. leptodactyloides* specimens have long dorsolateral folds; most *wagneri* do. The bellies of *L. leptodactyloides* characteristically are mottled with a finely mottled pattern; many *wagneri* have boldly mottled bellies.

ADULT CHARACTERISTICS (N = 388 females, 235 males).—Light posterior lip stripes rarely very distinct (1%), sometimes distinct (11%), usually indistinct (52%), and often not discernible (36%), when discernible, stripes extending from

posterior corner of eye; light posterior thigh stripe sometimes very distinct (10%), usually distinct (34%), indistinct (33%), or not discernible (23%); dorsolateral folds (apparently) rarely absent (6%), often short (23%), usually moderate length (65%), or rarely long (5%); toe tips rarely narrow (2%), sometimes just swollen (18%), usually swollen (65%), sometimes just expanded (10%), rarely expanded (4%), and rarely with small disks (1%); male black thumb spines rarely small size (6%) or small/medium (4%), usually medium (87%), and rarely large (2%); chin/throat sometimes with light spots on a darker field (10%); belly rarely lacking melanophores (1%), usually lightly mottled (43%) or moderately mottled (47%), and sometimes extensively mottled (9%).

Females 34.8–56.2 mm SVL ($\bar{x} = 46.3 \pm 3.8$), males 28.3–47.9 mm SVL ($\bar{x} = 40.1 \pm 3.0$); female head length 32%–41% SVL ($\bar{x} = 36 \pm 1\%$), male head length 34%–41% SVL ($\bar{x} = 37 \pm 1\%$); female head width 30%–38% SVL ($\bar{x} = 34 \pm 1\%$), male head width 31%–39% SVL ($\bar{x} = 35 \pm 1\%$); female tympanum diameter 6%–8% SVL ($\bar{x} = 7 \pm 0\%$), male tympanum diameter 6%–9% SVL ($\bar{x} = 8 \pm 0\%$); female thigh length 34%–50% SVL ($\bar{x} = 43 \pm 2\%$), male thigh length 35%–49% SVL ($\bar{x} = 44 \pm 2\%$); female shank length 42%–52% SVL ($\bar{x} = 47 \pm 2\%$), male shank length 42%–51% SVL ($\bar{x} = 47 \pm 2\%$); female foot length 46%–62% SVL ($\bar{x} = 52 \pm 2\%$), male foot length 47%–62% SVL ($\bar{x} = 53 \pm 2\%$).

LARVAL CHARACTERISTICS.—Maximum total length stage 40, 28.3 mm; body length 35%–51% ($\bar{x} = 42.6$) total length; maximum tail depth 32%–51% ($\bar{x} = 41.6$) body length; nostril just nearer snout tip than eye or midway between snout and eye; internarial distance just greater than interorbital distance; eye diameter, stages 25–31, 7%–9% ($\bar{x} = 7.5$) body length, stages 36–40, 8%–12% ($\bar{x} = 9.4$) body length; mouth subterminal; oral disk entire; spiracle sinistral; anal tube median; oral papilla formula 1-2; oral disk width, stages 25–31, 23%–28% ($\bar{x} = 24.9$) body length, stages 36–40, 18%–27% ($\bar{x} = 20.6$) body length; oral papilla gap 24%–43% ($\bar{x} = 35.0$) oral disk width; labial tooth row formula, stages 25–27, 2[2]/3, stages 28–40, 2/3; number of labial teeth in 1/2 row A-2, stages 25–31, 62–75, stages 36–40, 72–113; number of labial teeth in 0.1 mm measured in middle of 1/2 of row A-2, 5.5–9 ($\bar{x} = 7.6$); dorsal body pattern brown, not quite uniform profusion of melanophores; ventral body pattern moderate to heavy mottle anteriorly, light spot just behind oral disk present or absent, very light to moderate scattering of melanophores over guts; melanophores present on oral disk; anal tube with scattered or very few melanophores; tail brown with scattered small flecks, pattern heaviest over musculature, ventralmost edge of fin with or without melanophores.

The preceding larval description is based on samples from Limoncocha, Napo, Ecuador, and from Tambopata, Madre de Dios, Peru.

ADVERTISEMENT CALL.—Call rate of 0.3–3.3 calls per s; call duration 0.01–0.04 s; calls unpulsed or with 3–5 partial pulses; calls frequency modulated with very fast rise times; dominant frequency range 650–1600 Hz, maximum energy 1100–1300 Hz; harmonic structure present or absent (Figures 4, 5, 14, 15). Schneider et al. (1988) described antiphonal calling in a species they identified as *L. wagneri* from the outskirts of Manaus. The scales of analyses are different for the figures they published compared to those in this paper, but the calls they reported appear to be those of *L. leptodactyloides* as recognized in this paper.

KARYOTYPE.—Unknown.

GEOGRAPHIC VARIATION.—Variation has been discussed previously in several sections, and some aspects of geographic variation have been discussed specifically in the "Region 4—Amazonia" analysis. In addition, there does appear to be some geographic variation in size, based on specimens $\geq$ or ≤ 2 standard deviations of mean size for males and females. The largest specimens are found in the west-central portion of the range (Leticia, Amazonas, Colombia; Cusuime, Morona-Santiago, Ecuador; Río Ampiyacu, Estirón, Loreto, Peru), whereas the smallest specimens are found in the south-west portion of the range (Príncipe da Beira, Rondônia, Brazil; Tambopata, Madre de Dios, Peru; several localities in departments of Beni and Santa Cruz, Bolivia).

DISTRIBUTION.—Distributed throughout the greater Amazon basin and the Guianas from known elevations of 15–400 m (Figure 38; Appendix 2).

Leptodactylus natalensis Lutz, 1930

Leptodactylus natalensis Lutz, 1930:7, plate I: figs. 7, 7a; plate III: figs. 1, 2 [type locality: (Brazil) Natal, Rio Grande do Norte, Rio Baldo e outros lugares (Portuguese text, p. 7), Rio Bahú and other places near Natal (Rio Grande do Norte) (English text, p. 26); lectotype USNM 81130, adult male].

DIAGNOSIS.—*Leptodactylus natalensis* occurs along coastal Brazil from the State of Rio Grande do Norte to the State of Rio de Janeiro. The only other *Leptodactylus* (other than *L. ocellatus* and its closest relatives) that occurs in the same general region (but more interiorly) is *podicipinus*. No *L. natalensis* individuals have distinct light belly spots; many *podicipinus* individuals do. Just over half of *L. natalensis* specimens have toe tips larger than the narrow or just-swollen categories; all *podicipinus* have either narrow or just-swollen toe tips.

ADULT CHARACTERISTICS (N = 50 females, 56 males).—Light posterior lip stripe distinct in some individuals (9%), usually indistinct (56%), and often not discernible (34%), when discernible, stripes extending from posterior corner of eye; light posterior thigh stripes rarely distinct (5%), sometimes indistinct (16%), usually not discernible (79%); dorsolateral folds (apparently) rarely absent (2%), usually either short (46%) or moderate length (53%); toe tips narrow (13%), just swollen (31%), swollen (28%), just expanded (22%), or expanded (6%); male black thumb spines sometimes small/medium size (12%), usually medium size (79%), sometimes medium/large (9%); chin/throat usually with light spots on a

FIGURE 38.—Map of localities for *Leptodactylus leptodactyloides* (dots; circle = MVZ 176010, 176011, tentatively identified as *leptodactyloides*, see text) and *nesiotus* (square).

darker field (62%); belly rarely lacking pattern (1%), occasionally lightly mottled (7%), usually moderately mottled (52%) or extensively mottled (40%).

Females 33.1–48.9 mm SVL ($\bar{x} = 39.9 \pm 4.5$), males 28.7–42.1 mm SVL ($\bar{x} = 34.5 \pm 2.7$); female head length 33%–41% SVL ($\bar{x} = 37 \pm 2\%$), male head length 35%–42% SVL ($\bar{x} = 38 \pm 1\%$); female head width 30%–38% SVL ($\bar{x} = 34 \pm 2\%$), male head width 33%–39% SVL ($\bar{x} = 36 \pm 1\%$); female tympanum diameter 6%–9% SVL ($\bar{x} = 8 \pm 0\%$), male tympanum diameter 7%–9% SVL ($\bar{x} = 8 \pm 0\%$); female thigh length 38%–48% SVL ($\bar{x} = 43 \pm 2\%$), male thigh length 39%–49% SVL ($\bar{x} = 44 \pm 2\%$); female shank length 41%–51% SVL ($\bar{x} = 45 \pm 2\%$), male shank length 41%–48% SVL ($\bar{x} = 46 \pm 2\%$); female foot length 46%–57% SVL ($\bar{x} = 53 \pm 2\%$), male foot length 44%–58% SVL ($\bar{x} = 53 \pm 3\%$).

LARVAL CHARACTERISTICS.—Unknown.

ADVERTISEMENT CALL.—Unknown.

KARYOTYPE.—Diploid number 22, 3 pair median, 2 pair submedian, 3 pair subterminal, 3 pair terminal; secondary constriction in chromosome pair 11 (Bogart, 1974; specimens from the State of Rio de Janeiro, Brazil).

GEOGRAPHIC VARIATION.—Geographic variation was discussed above in the section describing variation in "Region 2—East Coast Brazil" for the Small-Moderate Size OTU.

DISTRIBUTION.—Coastal Brazil from the State of Rio Grande do Norte to the vicinity around Rio de Janeiro (Figure 39; Appendix 2).

Leptodactylus nesiotus, new species

FIGURE 40

HOLOTYPE.—USNM 306179, an adult male from Trinidad; St. Patrick; Icacos Peninsula, Icacos. Collected by M. Read, J. Seygagat, and G. White, 18 Jul 1986.

PARATOPOTYPES.—BMNH 1992.147–148, collected by J.R. Downie, 14 Jul 1983.

REMARK.—The paratopotypes were received after the manuscript was completed. The specimens are not included in the preceding analyses sections. Data from the specimens are incorporated only in the species diagnoses and briefly noted later in the species description (below).

DIAGNOSIS.—*Leptodactylus nesiotus* is known from Trinidad, where *bolivianus* and *validus* are the only other *Leptodactylus* with toe fringes (other than either *L. ocellatus* or one of its closest relatives). *Leptodactylus nesiotus* is a small species (males 32–33 mm SVL) with moderate-length, irregular dorsolateral folds; *Leptodactylus bolivianus* is a large species (females to 88 mm SVL, males to 94 mm SVL) with long smooth dorsolateral folds. *Leptodactylus nesiotus* has a broad light stripe on the entire upper lip or at least to under the eye; in those individuals of *validus* with discernible light lip stripes, they extend from the posterior corner of the eye posteriorly.

DESCRIPTION OF HOLOTYPE.—Snout rounded-subovoid from above, rounded in profile; canthus rostralis indistinct; lores weakly obtuse-concave in cross section; tympanum moderate size, horizontal diameter about $^3/_5$ eye diameter; vocal slits well developed, parallel to posterior $^1/_2$ of lower jaw; vocal sac single, internal; vomerine teeth in two arched series separated from each other by distance less than length of single tooth row, lying posterior to and from midchoana to midchoana; finger lengths II≈IV<I<III; fingers with modest lateral ridges; each thumb with two medial moderately small black spines; arms not hypertrophied; no ulnar ridge; dorsum with small black-tipped tubercles, numerous posteriorly, scattered anteriorly; supratympanic fold distinct, weakly developed dorsolateral folds from posterior eye to about midway to sacrum; no obvious body glands; ventral disk fold not visible, venter smooth except for areolate posteroventral thighs; toe tips slightly expanded; lateral toe fringes well developed; subarticular tubercles rounded, moderately developed; weak but distinct metatarsal fold extending to outer toe fringe on toe V; tarsal fold distinct, extending about $^7/_8$ length of tarsus, terminating at inner metatarsal tubercle, not continuous with toe fringe; posterior surface of tarsus and sole of foot with scattered small tan-tipped tubercles.

SVL 33.3 mm, head length 12.4 mm, head width 10.7 mm, tympanum diameter 2.7 mm, thigh length 14.6 mm, shank length 15.6 mm, foot length 19.4 mm.

Dorsum darker and lighter brown grays in preservative; dark triangular interorbital blotch followed by one complete chevron in scapular region and an incomplete chevron in front of sacral region, posterior dorsum with two dark elongate spots; upper limbs with dark cross bands; entire upper lip with broad light stripe area, well-defined dorsally from eye to under tympanum, otherwise borders ill defined; chin with distinct light spots on a darker ground color, throat and chest profused with melanophores, belly speckled; posterior surfaces of thighs boldly dark-and-light mottled, no real indications of distinct light stripes.

VARIATION.—The paratopotypes are males, 31.7 and 31.8 mm SVL. The upper lip stripes are not as distinct as in the holotype, but the upper border of the stripe is well defined from the eye to the tympanum and the stripes extend anteriorly to under the eye. The bellies are speckled as in the holotype. One specimen has distinct light stripes on both posterior thighs, whereas the other has a distinct stripe on only one thigh.

ETYMOLOGY.—From the Greek *nesiotes*, islander, in reference to its only known occurrence on the Island of Trinidad.

LARVAL CHARACTERISTICS.—Unknown.

ADVERTISEMENT CALL.—Call rate about 3.8 calls per s; call duration 0.03 s; calls partially pulsed with 4–5 partial pulses; calls frequency modulated with fast rise times; broadcast frequency 1500–2000 Hz, maximum energy 1800–2000 Hz;

FIGURE 39.—Map of localities for *Leptodactylus natalensis* (triangles), *pallidirostris* (dots), and *pascoensis* (squares).

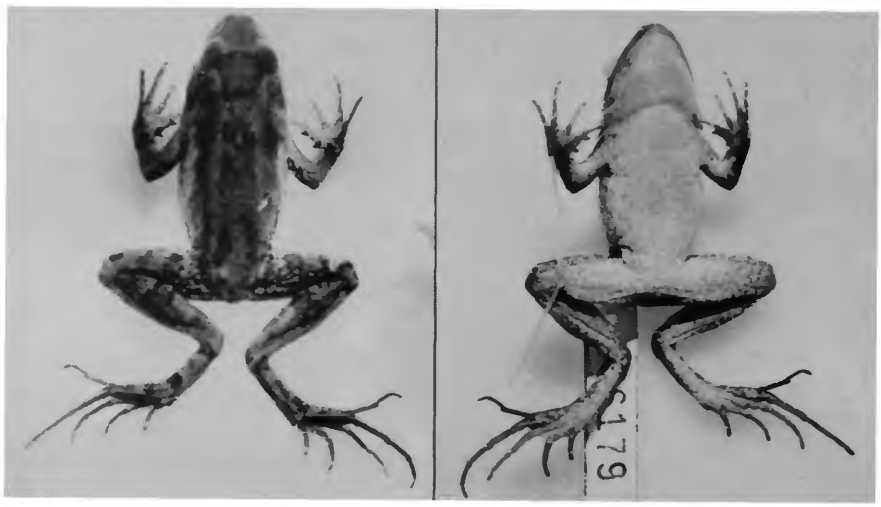

FIGURE 40.—Holotype of *Leptodactylus nesiotus*, new species.

harmonic structure ambiguous for recording available (Figure 30).

KARYOTYPE.—Unknown.

GEOGRAPHIC VARIATION.—Known only from the holotype.

DISTRIBUTION.—Known only from the type locality (Figure 38; Appendix 2).

Leptodactylus pallidirostris Lutz, 1930

Leptodactylus pallidirostris Lutz, 1930, plate I: fig. 3 [type locality: British Guiana; Kartabo; lectotype AL-MN 1829, adult male].

DIAGNOSIS.—*Leptodactylus pallidirostris* occurs in the Guiana shield region. The other species of *Leptodactylus* that occur in the same area with toe fringes (except *L. ocellatus* and its closest relatives) are *L. bolivianus, diedrus, leptodactyloides, petersii,* and *sabanensis. Leptodactylus pallidirostris* is a small species (females 30–43 mm SVL, males 28–37 mm SVL) with short to medium dorsolateral folds; *L. bolivianus* is a large species (females to 88 mm SVL, males to 94 mm SVL) with a pair of long, well-developed dorsolateral folds. Some individuals of *L. pallidirostris* appear to lack dorsolateral folds and the ventral and posterior thigh patterns merge; all *diedrus* lack dorsolateral folds and the ventral and posterior thigh patterns abut. *Leptodactylus pallidirostris* is smaller than *leptodactyloides* (*leptodactyloides* females 35–56 mm SVL, males 28–48 mm SVL). The commonest lip stripe condition in *pallidirostris* is distinct stripes that often extend from under the middle of the eye; the commonest condition in *leptodactyloides* is indistinct, and all stripes extend from the posterior corner of the eye. Many *L. pallidirostris* individuals (69%) have light chin/throat spots; few (10%) *leptodactyloides* do. The belly of *L. pallidirostris* usually is lightly mottled with the pattern ranging from a fine mottle to distinct, rather dark blotches; the belly of *petersii* usually is extensively mottled and often in an anastomotic pattern. The commonest toe-tip condition in *L. pallidirostris* is swollen with some individuals having expanded tips or small disks; the commonest toe-tip condition in *petersii* is just swollen and no individuals have expanded toe tips or small toe disks. *Leptodactylus pallidirostris* is smaller than *sabanensis* (*sabanensis* females 42–57 mm SVL, males 35–46 mm SVL). The most common lip stripe condition in *sabanensis* is indiscernible, and, when lip stripes are discernible, they extend from the posterior corner of the eye (see comparison with *leptodactyloides* above for *pallidirostris* condition). The advertisement call of *L. pallidirostris* has a broadcast frequency range of 1500–3500 Hz with maximum energy of 2500–3500 Hz; the broadcast frequency range of the advertisement call of *sabanensis* is 900–2300 Hz with maximum energy of 1400–1800 Hz.

ADULT CHARACTERISTICS (N = 152 females, 100 males).—Light posterior lip stripes rarely very distinct (3%), usually distinct (46%) or indistinct (42%), occasionally not discernible (8%), when discernible, the stripes extending from under mideye or from posterior corner of eye; light posterior thigh stripes rarely very distinct (2%), often distinct (23%) or indistinct (23%), usually not discernible (51%); dorsolateral folds occasionally (apparently) absent (7%), usually short (79%), sometimes moderate length (15%); toe tips just swollen (13%), swollen (28%), just expanded (25%), expanded (22%), or with small disks (12%); male black thumb spines occasionally small size (6%), rarely small–medium size (1%), usually medium size (89%), rarely medium–large size (4%); chin/throat usually with light spots on a darker background (69%); belly patternless (11%), lightly mottled (43%), moderately

mottled (35%), or extensively mottled (10%).

Females 29.5–42.8 mm SVL ($\bar{x} = 36.9 \pm 2.6$), males 27.8–37.3 mm SVL ($\bar{x} = 33.2 \pm 1.9$); female head length 32%–40% SVL ($\bar{x} = 37 \pm 1\%$), male head length 34%–42% SVL ($\bar{x} = 38 \pm 2\%$); female head width 30%–40% SVL ($\bar{x} = 32 \pm 2\%$), male head width 30%–38% SVL ($\bar{x} = 34 \pm 2\%$); female tympanum diameter 6%–9% SVL ($\bar{x} = 7 \pm 0\%$), male tympanum diameter 7%–9% SVL ($\bar{x} = 8 \pm 0\%$); female thigh length 36%–48% SVL ($\bar{x} = 42 \pm 3\%$), male thigh length 35%–53% SVL ($\bar{x} = 43 \pm 3\%$); female shank length 42%–52% SVL ($\bar{x} = 46 \pm 2\%$), male shank length 42%–54% SVL ($\bar{x} = 47 \pm 2\%$); female foot length 48%–60% SVL ($\bar{x} = 53 \pm 2\%$), male foot length 50%–61% SVL ($\bar{x} = 55 \pm 2\%$).

LARVAL CHARACTERISTICS.—Unknown.

ADVERTISEMENT CALL.—Call rate 0.8–2.7 calls per s; call duration 0.03–0.05 s; calls of two notes, first note a single pulse, second note partially pulsed with 2–5 partial pulses; calls frequency modulated with very fast rise times; broadcast frequency range 1500–3500 Hz, maximum energy in higher portion of frequency range; weak harmonic structure indicated but evidence for harmonics not decisive (Figures 27–29).

KARYOTYPE.—Unknown.

GEOGRAPHIC VARIATION.—Geographic variation for this species has been discussed in the analysis of "Region 5—Guiana Shield" OTUs.

DISTRIBUTION.—The Guianas, north-central Roraima, Brazil, and Venezuela from known elevations of sea level to 360 m (Figure 39; Appendix 2).

Leptodactylus pascoensis, new species

FIGURE 41

HOLOTYPE.—LACM 40665, an adult male from Peru; Pasco; Iscozazin Valley, Chontilla, 780 m, ~10°17'S, 75°13'W. Collected by Richard Etheridge and David B. Wake, 13 Aug 1961.

PARATOPOTYPES.—All collected by Richard Etheridge: LACM 40660, 9 Jul 1961; LACM 40661–40663, USNM 313875, 11 Aug 1961.

DIAGNOSIS.—*Leptodactylus pascoensis* presently is known only from a restricted region along the amazonian flanks of the Andes in central Peru. Other *Leptodactylus* with toe fringes (other than *L. ocellatus* and its closest relatives) that might be expected to occur near or with *pascoensis* are *L. bolivianus, diedrus, griseigularis, leptodactyloides, petersii,* and *wagneri.* Dorsolateral folds in *L. pascoensis* are never long nor do *pascoensis* have distinct lip stripes; all *bolivianus* have long dorsolateral folds and many individuals have distinct light lip stripes. *Leptodactylus pascoensis* is larger than *diedrus* (*pascoensis* females 52–67 mm SVL, males 60–61 mm SVL; *diedrus* females 34–48 mm SVL, males 30–40 mm SVL), and the ventral and posterior thigh patterns merge in *pascoensis* whereas they abut in *diedrus. Leptodactylus pascoensis* is also larger than *griseigularis* (*griseigularis* females 39–58 mm SVL, males 35–51 mm SVL). The commonest light posterior lip stripe condition in *pascoensis* is with no indication of stripes; the commonest condition in *griseigularis* is indistinct. *Leptodactylus pascoensis* is larger than *leptodactyloides* as well (*leptodactyloides* females 35–56 mm SVL, males 28–48 mm SVL), and most *pascoensis* individuals have mottled posterior thigh surfaces with no indication of light stripes, whereas *leptodactyloides* individuals usually have at least some indication of light posterior thigh stripes. *Leptodactylus pascoensis* is larger than *petersii* (*petersii* females 31–51 mm SVL, males 27–41 mm SVL), and the belly is never extensively mottled in an anastomotic pattern whereas most *petersii* have extensively patterned bellies and often in an anstomotic pattern. No *L. pascoensis* have long dorsolateral folds; the commonest condition in *wagneri* is long dorsolateral folds. The bellies of *L. pascoensis* are lightly to moderately mottled, but never in a bold mottle; the bellies of most *wagneri* are moderately mottled and some are extensively mottled, and the bellies are often with a boldly mottled pattern, approaching an anastomotic pattern.

DESCRIPTION OF HOLOTYPE.—Snout rounded from above, rounded in profile; canthus rostralis indistinct; lores weakly obtuse-concave in cross section; tympanum large, diameter about 3/4 eye diameter; vocal slits well developed, parallel to posterior 1/2 of lower jaw; vocal sac single, internal, no external modification visible; vomerine teeth in two long, almost abutting arched series extending posterior to choanae, from midchoana to midchoana; finger lengths II≈IV<I<III; inner sides of fingers II and III with well-developed ridges; each thumb with two large black spines; upper arms moderately hypertrophied; no ulnar ridge; dorsum with many very small and small white- or tan-tipped tubercles, denser posteriorly; supratympanic fold distinct, barest indication of interrupted dorsolateral folds from eye to mid-distance to sacrum; orange-tan ventrolateral glands most developed just behind anterior belly fold, extending in a diffuse manner to thighs on sides of belly; ventral disk fold distinct, otherwise ventral surfaces smooth except ventroposterior thighs areolate; no chest spines; tips of toes swollen; toe fringes well developed; subarticular tubercles rounded, moderately developed; metatarsal fold developed into an extensive fringe, continuous with fringe on toe V; tarsal fold distinct, extending about 7/8 length of tarsus, terminating at inner metatarsal tubercle, not continuous with toe fringe; outer tarsus profused with medium-size and small white tubercles, sole of foot with shagreen and scattered small white tubercles.

SVL 60.3 mm, head length 20.8 mm, head width 21.8 mm, tympanum diameter 4.7 mm, thigh length 25.1 mm, shank length 27.0 mm, foot length 31.6 mm.

Dorsum almost uniform brown with faint pattern of light interorbital bar bordered behind by darker interorbital triangular blotch, rest of dorsum with larger and smaller darker blotches, upper lip with medial light bar, two light vertical lip

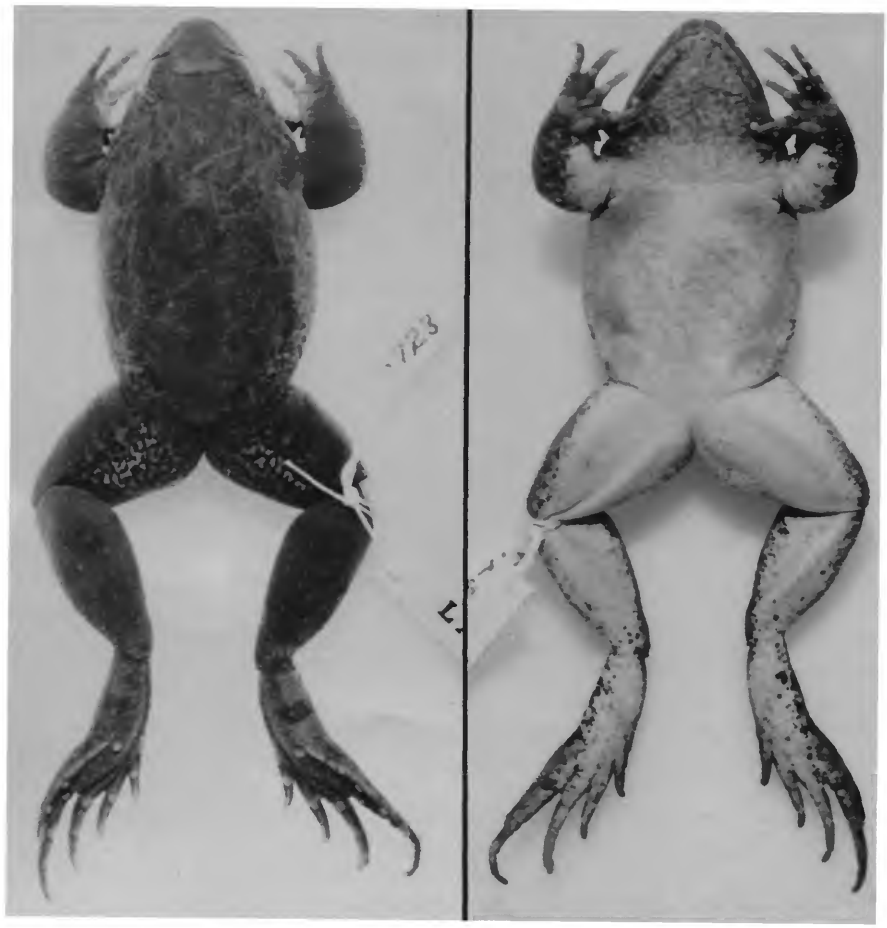

FIGURE 41.—Holotype of *Leptodactylus pascoensis*, new species.

bars between naris and eye, somewhat distinct light stripe from posterior corner of eye, under tympanum through jaw commissure, upper limbs very weakly cross barred or spotted; chin and throat with somewhat ill-defined light spots on a darker ground, belly with only a very few scattered melanophores; posterior surface of thigh boldly mottled dark brown and almost white, no real indication of light stripes.

ETYMOLOGY.—Named for the Peruvian Department of Pasco, where most of the known specimens have been collected.

ADULT CHARACTERISTICS (N = 4 females, 3 males).—Posterior light lip stripes somewhat distinct or not discernible, when discemible stripes extending from posterior corner of eye; posterior thigh light stripe indistinct or usually not discernible; dorsolateral folds (apparently) absent, short, or medium length; toe tips just swollen or swollen; male black thumb spines large; chin/throat with light spots on a darker field or usually absent; belly lightly to moderately mottled.

Females 52.4–66.6 mm SVL, males 60.3–61.4 mm SVL; female head length 33%–36% SVL, male head length 34%–37% SVL; female head width 34%–36% SVL, male head width 36%–39% SVL; female tympanum diameter 7%–8% SVL, male tympanum diameter 8%–9% SVL; female thigh length 41%–47% SVL, male thigh length 42%–47% SVL; female shank length 47%–49% SVL, male shank length 45%–50% SVL; female foot length 53%–56% SVL, male foot length 52%–53% SVL.

HABITAT AND COLOR NOTES.—"Wet forest floor. Dorsum olive with lighter olive-gray markings mid-dorsally and between eyes. Ventral ground color whitish with yellowish overlap posteriorly, yellow most intense on posterior thigh. Throat dark. (LACM 40660). Above dark gray-green with indistinct darker gray markings; a light gray interorbital bar; throat and chest white marbled with gray-brown; posterior belly and lower limb surfaces dirty yellow. (LACM 40661–40663, USNM 313875)." (Field notes of Richard Etheridge and

David B. Wake, pers. comm.)

LARVAL CHARACTERISTICS.—Unknown.

ADVERTISEMENT CALL.—Unknown.

KARYOTYPE.—Unknown.

DISTRIBUTION.—Known only from two localities from 780–2500 m from central Peru east of the Andes (Figure 39; Appendix 2).

Leptodactylus petersii (Steindachner, 1864)

Platymantis petersii Steindachner, 1864:254, plate 16: figs. 2, 2a–c [type locality: (Brazil; Amazonas) Marabitanas; holotype lost, originally in NMW collection].—Boulenger, 1882:247 [apparent first association of *petersii* with the genus *Leptodactylus*, as a synonym of *Leptodactylus caliginosus*].

Leptodactylus brevipes Cope, 1887:51 [type locality: Chapada, Brazil (= Chapada dos Guimarães, Mato Grosso, Brazil); holotype ANSP 11270, female (?)].

Leptodactylus intermedius Lutz, 1930:8, plate 3: fig. 6 [type locality: Manacapuri (= Manacapurú) perto do Manaos (Amazonas, Brazil); syntypes MN-AL 1438–1441].

Leptodactylus podicipinus petersii.—Gorham, 1966:136 [apparent first proposal of *petersii* as a subspecies of *podicipinus*].

DIAGNOSIS.—*Leptodactylus petersii* occurs in greater Amazonia and the Guiana shield region. The other *Leptodactylus* species with toe fringes (except *L. ocellatus* and its closest relatives) that are known to occur sympatrically with *petersii* or that are from the same region are *L. bolivianus, dantasi, diedrus, griseigularis, leptodactyloides, pallidirostris, pascoensis, podicipinus, riveroi, sabanensis,* and *wagneri*. *Leptodactylus petersii* is smaller than *bolivianus* and *riveroi* (*petersii* females 31–51 mm SVL, males 27–41 mm SVL; *bolivianus* females to 88 mm SVL, males to 94 mm SVL; *riveroi* females to 81 mm SVL, males to 63 mm SVL), and *petersii* individuals have at most a pair of medium-length, moderately developed dorsolateral folds whereas all *bolivianus* and *riveroi* have a pair of long, well-developed dorsolateral folds. *Leptodactylus petersii* does not have distinct light spots on a dark belly; *dantasi* does. The belly of *L. petersii* usually is extensively mottled, whereas the belly of *diedrus* usually lacks melanophores. In addition, the ventral and posterior thigh patterns merge in *L. petersii*, whereas they abut in *diedrus*. *Leptodactylus petersii*, is smaller than *griseigularis* (*griseigularis* females 39–58 mm SVL, males 35–51 mm SVL), and the commonest belly pattern in *petersii* is an extensive mottle in an anastomotic pattern, whereas the commonest belly pattern in *griseigularis* is a light mottle that is not developed into an anastomotic pattern. *Leptodactylus petersii* individuals have relatively uniformly and extensively patterned bellies, often in an anastomotic pattern; *leptodactyloides* have more intense belly patterns anteriorly, and most individuals have moderate mottling but not in an anastomotic pattern; *pallidirostris* usually have lightly mottled bellies with a pattern ranging from a fine mottle to distinct, rather dark blotches, with the pattern usually more intense anteriorly. Almost no *L. petersii* have distinct light posterior thigh stripes; most *leptodactyloides* do. *Leptodactylus petersii* is smaller than *pascoensis* (*pascoensis* females 52–67 mm SVL, males 60–61 mm SVL), and the belly is usually darker in *petersii* than in *pascoensis* (*pascoensis* bellies never extensively mottled nor in an anastomotic pattern). No *L. petersii* have distinct light spots on the belly, whereas *podicipinus* commonly does. The commonest toe-tip state in *L. petersii* is just swollen, and some individuals have swollen and just-expanded toe tips; the commonest toe-tip state in *podicipinus* is narrow, and no *podicipinus* have swollen or just-expanded toe tips. *Leptodactylus petersii* is smaller than *sabanensis* (*sabanensis* females 42–57 mm SVL, males 35–46 mm SVL). Most *L. petersii* (56%) have light chin/throat spots; few *sabanensis* (15%) have light chin/throat spots, and no *sabanensis* have anastomotic or speckled belly patterns. *Leptodactylus petersii* is smaller than *wagneri* (*wagneri* females 52–82 mm SVL, males 39–61 mm SVL), and no *petersii* have long dorsolateral folds, whereas most *wagneri* do.

ADULT CHARACTERISTICS (N = 121 females, 197 males).—Light posterior lip stripes rarely very distinct (1%), sometimes distinct (12%), usually indistinct (44%) or not discernible (43%), when discernible, stripes extending from posterior comer of eye; light posterior thigh stripes rarely distinct (2%), occasionally indistinct (8%), usually absent (90%); dorsolateral folds sometimes (apparently) absent (10%), usually short (70%), sometimes moderate length (20%); toe tips narrow (14%), just swollen (62%), swollen (13%), or just expanded (11%); male black thumb spines small (16%), small–medium (15%), medium (64%), rarely medium–large (2%) or large (2%); chin/throat usually with light spots on a darker background (56%); belly rarely lightly mottled (4%), often moderately mottled (30%), usually extensively mottled (66%).

Females 31.2–51.3 mm SVL ($\bar{x} = 39.1 \pm 3.9$), males 26.6–41.1 mm SVL ($\bar{x} = 32.9 \pm 2.6$); female head length 35%–43% SVL ($\bar{x} = 39 \pm 2\%$), male head length 36%–44% SVL ($\bar{x} = 40 \pm 2\%$); female head width 32%–38% SVL ($\bar{x} = 35 \pm 1\%$), male head width 33%–40% SVL ($\bar{x} = 36 \pm 1\%$); female tympanum diameter 6%–10% SVL ($\bar{x} = 8 \pm 1\%$), male tympanum diameter 8%–11% SVL ($\bar{x} = 10 \pm 1\%$); female thigh length 36%–51% SVL ($\bar{x} = 43 \pm 2\%$), male thigh length 36%–50% SVL ($\bar{x} = 43 \pm 3\%$); female shank length 40%–50% SVL ($\bar{x} = 44 \pm 2\%$), male shank length 41%–49% SVL ($\bar{x} = 45 \pm 2\%$); female foot length 47%–60% SVL ($\bar{x} = 53 \pm 2\%$), male foot length 48%–60% SVL ($\bar{x} = 54 \pm 2\%$).

LARVAL CHARACTERISTICS.—Maximum total length stage 36, 20.8 mm; body length 36%–44% ($\bar{x} = 40.3$) total length; maximum tail depth 39%–46% ($\bar{x} = 42.4$) body length; nostril just nearer eye or midway from eye to tip of snout; internarial distance about equal to or just greater than interorbital distance; eye diameter 7%–11% ($\bar{x} = 9.4$) body length; mouth subterminal; oral disk entire; spiracle sinistral; anal tube median; oral papilla formula 1-2 or 1-2-1; oral disk width 18%–28% ($\bar{x} = 20.9$) body length; oral papilla gap 42%–55% ($\bar{x} = 49.3$) oral disk width; labial tooth row formula 2(2)/3; number of labial teeth in a single split row of A-2, stages 29–37, 60–78;

number of labial teeth in 0.1 mm measured in middle of one split tooth row in A-2, 5.5–8 ($\bar{x} = 6.6$); dorsal body brown, heavily and uniformly mottled or uniform brown uppermost, moderately mottled laterally extending to eyes; ventral body brown, moderately mottled entirely or heavier mottling anteriorly; light to moderate profusion of melanophores on oral disk; light to moderate profusion of melanophores on anal tube; tail either almost uniformly brown or musculature moderately mottled brown, dorsal fin lightly sprinkled with melanophores, dorsalmost fin clear and very few melanophores on ventral fin, only next to musculature.

The preceding larval description is based on samples from Tambopata, Madre de Dios, Peru. The tadpole illustrated by Hero (1990:252) as *Leptodactylus wagneri/podicipinus* (not examined by me) is most certainly *petersii*, as *petersii* is the only member of the complex that occurs within the forests in the areas Hero studied.

ADVERTISEMENT CALL.—There are apparently two major types of calls given by *Leptodactylus petersii*. Further study is needed in order to determine what the functions of these calls are.

Type 1: Call rate 2.9–4.2 calls per s; call duration 0.04–0.05 s; calls of single pulsatile notes, about 3–4 partial pulses per note/call; calls not noticeably frequency modulated; broadcast frequency range 700–1200 Hz, maximum energy 750–800 Hz; harmonics weakly to strongly developed (Figure 16).

Type 2: Call rate 0.6–1.3 calls per s; call duration 0.03–0.05 s; calls of two juxtaposed notes, first note noticeably pulsatile, with 2–4 partial pulses, second note not noticeably pulsed; first note frequency modulated upward with a fast rise time, second note often frequency modulated downward with a slower fall time than rise time of first note; broadcast frequency range of first note 800–1600 Hz, of second note 1800–2800 Hz; first note with harmonic structure, second note apparently without harmonic structure (Figures 3, 20, 21, 25).

KARYOTYPE.—Unknown.

GEOGRAPHIC VARIATION.—Geographic variation has been discussed within the analyses for "Region 3—Interior Brazil" and "Region 4—Amazonia" and apply to the species as a unit. There is no obvious geographic variation in size when the largest and smallest individuals (> and < 2 standard deviations from mean) are examined with the exception that all the smallest individuals come from the Peruvian Department of Madre de Dios and the Bolivian Department of Beni. The largest individuals occur in the Brazilian states of Amazonas, Goiás, Mato Grosso, Pará, and the Department of Loreto in Peru.

REMARK.—Hoogmoed and Cadle (1991:131) reported on *Leptodactylus* from Cocha Cashu, Peru, and stated that "several adults of a *wagneri*-group *Leptodactylus* (FMNH 228256...) were observed on the logs around the pools, at the edge of the water, or under loose bark on other parts of the logs. ...*Leptodactylus* larvae (USNM 298934), presumably of the same species, were present in pools at sites 1 and 2." FMNH 228256 is *L. petersii;* USNM 298934 is definitely not a larval *petersii*, but rather, it is a member of the *L. pentadactylus* group.

DISTRIBUTION.—Known from the Guianas, the Amazon basin, and isolated localities from the Cerrado open formations in central Brazil (Figure 42; Appendix 2).

Leptodactylus podicipinus (Cope, 1862)

Cystignathus podicipinus Cope, 1862:156 [type locality: Paraguay; holotype ANSP 14539, adult male].

Leptodactylus podicipinus.—Boulenger, 1882:248 [apparent first association of *podicipinus* with *Leptodactylus*].

Leptodactylus nattereri Lutz, 1926:1011 [type localities: Ilha Secca and Cachoeira do Maribonda, São Paulo, Brazil; unquestioned syntypes MN-AL 1015, 1016, plus unnumbered specimen in same jar with 1015, 1016].

DIAGNOSIS.—*Leptodactylus podicipinus* has the southernmost distribution of members of the *podicipinus-wagneri* complex but the range extends into Amazonia, central Brazil and extends toward northeast Brazil. Other *Leptodactylus* with toe fringes (other than *L. ocellatus* and its closest relatives) known to occur sympatrically with *podicipinus* or are from the same region as *podicipinus* are *L. bolivianus, dantasi, diedrus, griseigularis, leptodactyloides, natalensis, petersii, pustulatus,* and *riveroi. Leptodactylus podicipinus* is smaller than *bolivianus* or *riveroi* (*podicipinus* females 30–54 mm SVL, males 24–43 mm SVL; *bolivianus* females to 88 mm SVL, males to 94 mm SVL; *riveroi* females to 81 mm SVL, males to 63 mm SVL), and the dorsolateral folds are rarely long in *podicipinus* and never well developed, whereas all *bolivianus* and *riveroi* have a pair of long, well-developed dorsolateral folds. Although many *L. podicipinus* have small, distinct, light belly spots, not all do; *dantasi* has large, distinct, light belly spots and is larger than *podicipinus* (only known female *dantasi* 68 mm SVL). The bellies of *L. podicipinus* usually are extensively mottled and the ventral and posterior thigh patterns merge; the bellies of *diedrus* usually lack melanophores and the ventral and posterior thigh patterns abut. *Leptodactylus podicipinus* is smaller than *griseigularis* (*griseigularis* females 39–58 mm SVL, males 35–51 mm SVL), and the bellies of *podicipinus* are usually darker than those of *griseigularis* (*griseigularis* bellies usually lightly mottled and no individuals have distinct light belly spots). The posterior thighs of most *podicipinus* are mottled with no indication of light stripes; the commonest posterior thigh state in *leptodactyloides* is a distinct stripe, and no *leptodactyloides* have distinct light belly spots. All *L. podicipinus* have either narrow or just-swollen toe tips; just over half of all *natalensis* have toe tips larger than the just-swollen category, and no *natalensis* have distinct light belly spots. The most common toe-tip state in *L. podicipinus* is narrow; the most common toe-tip state in *petersii* is just swollen and some individuals have swollen and just-expanded toe tips. No *petersii* have distinct belly spots. No *L. podicipinus*

FIGURE 42.—Map of localities for *Leptodactylus petersii*.

have discrete, distinct light spots on the posterior face of the thigh; all *pustulatus* do.

ADULT CHARACTERISTICS (N = 532 females, 419 males).—Light posterior lip stripes rarely very distinct (2%), sometimes distinct (20%), usually indistinct (43%), often indiscernible (35%), when discernible, stripe extending from either under midportion of eye or posterior corner of eye; light posterior thigh stripes rarely distinct (4%), sometimes indistinct (17%), usually posterior thighs completely mottled with no indication of light stripes (79%); dorsolateral folds (apparently) sometimes absent (9%), usually short (44%) or moderate length (46%), rarely long (1%); toe tips usually narrow (75%) or just swollen (25%); male black thumb spines rarely small (3%), small-medium (2%), medium-large (3%), or large (2%), usually medium size (91%); chin/throat usually with distinct spots on a darker background (58%), distinct light spots often extending to cover belly (42%); belly rarely with a light scattering of melanophores (4%), sometimes with a moderate profusion of melanophores (20%), usually dark, extensively profused with melanophores (75%).

Females 29.5–54.3 mm SVL ($\bar{x} = 38.8 \pm 3.8$), males 24.5–43.3 mm SVL ($\bar{x} = 34.0 \pm 3.1$); female head length 30%–40% SVL ($\bar{x} = 35 \pm 2\%$), male head length 31%–41% SVL ($\bar{x} = 36 \pm 2\%$); female head width 30%–42% SVL ($\bar{x} = 33 \pm 1\%$), male head width 29%–39% SVL ($\bar{x} = 34 \pm 1\%$); female tympanum diameter 6%–9% SVL ($\bar{x} = 7 \pm 0\%$), male tympanum diameter 6%–9% SVL ($\bar{x} = 8 \pm 0\%$); female thigh length 32%–47% SVL ($\bar{x} = 39 \pm 3\%$), male thigh length 31%–47% SVL ($\bar{x} = 41 \pm 3\%$); female shank length 35%–46% SVL ($\bar{x} = 41 \pm 2\%$), male shank length 36%–48% SVL ($\bar{x} = 42 \pm 2\%$); female foot length 40%–59% SVL ($\bar{x} = 50 \pm 3\%$), male foot length 43%–57% SVL ($\bar{x} = 52 \pm 2\%$).

LARVAL CHARACTERISTICS.—Maximum total length stage 38, 28.2 mm; body length 34%–41% ($\bar{x} = 38.2$) total length; maximum tail depth 48%–56% ($\bar{x} = 51.4$) body length; nostril just nearer eye than tip of snout or about midway between tip of snout and eye; internarial distance just greater than or about equal to interorbital distance; eye diameter 9%–12% ($\bar{x} = 10.8$) body length; mouth subterminal; oral disk entire; spiracle sinistral; anal tube median; oral papilla formula 1-2; oral disk width 17%–21% ($\bar{x} = 19.2$) body length; oral papilla gap 38%–57% ($\bar{x} = 44.4$) oral disk width; labial tooth row formula 2(2)/3; number of labial teeth in a single split row of A-2, stages 37–38, 63–78; number of labial teeth in 0.1 mm measured in middle of one split tooth row in A-2, 6–7 ($\bar{x} = 6.3$); tadpole essentially uniform brown with heavy suffusion of melanophores including oral disk, anal tube, and dorsal and ventral tail fins; tail either uniform brown or with very few, small light flecks.

The preceding larval description is based on samples from Curuçá, Amazonas, and Estancia Caiman near Miranda, Mato Grosso do Sul, Brazil. Vizotto (1967) described and figured larval *L. podicipinus* from the interior of the State of São Paulo, Brazil.

ADVERTISEMENT CALL.—Call rate 0.5–8.4 calls per s; call duration 0.02–0.04 s; calls with distinct initial pulses and rest of call pulsatile or entire call pulsatile, with 3–7 pulses/partial pulses; calls markedly frequency modulated with extremely sharp attacks and fast rise times, short terminal frequency downsweep present or absent; broadcast frequency range 1000–3500 Hz with greater intensity of call either in lower frequency range at beginning of call or higher frequency range at end of call; harmonics weakly to moderately developed (Figures 8, 13, 22, 23).

KARYOTYPE.—Diploid number 22, 3 pair median, 2 pair submedian, 2 pair subterminal, 4 pair terminal; secondary constriction in chromosome pair 8 (Bogart, 1974; specimens from São José do Rio Prêto, São Paulo, Brazil).

GEOGRAPHIC VARIATION.—Variation for *L. podicipinus* within Regions 3 and 4 already has been discussed (as the Dark Belly OTUs). Among regions, there is variation in expression of the light stripe on the posterior thighs. In Region 4, only 5% of the individuals show any indication of light stripes, whereas 30% of the individuals in Regions 1, 3, and 7 (combined) have at least indications of light stripes if not distinct light stripes. There is no obvious geographic variation in size (based on specimens $\leq$ or $\geq$ 2 standard deviations of the mean). Both large and small females occur in the large sample from Porto Velho, Rondônia, Brazil. It is worth noting that 13 of the 17 males and all 14 females $\geq$ 2 standard deviations from the mean occur in the single sample from Alejandria, Beni, Bolivia.

DISTRIBUTION.—Open formations of Paraguay, adjacent Argentina, Bolivia, central Brazil, and extending along the Rio Madeira and Rio Amazonas within the Amazon basin, with a problematical outlier (discussed later) from Igarapé Belém, Amazonas, Brazil, with a known altitudinal range up to 550 m (Figure 43, Igarapé Belém = circle; Appendix 2).

Leptodactylus sabanensis, new species

FIGURE 44

HOLOTYPE.—KU 166559, an adult male from Venezuela; Bolívar; km 127, El Dorado–Santa Elena de Uairen road, 1250 m, −6°00′N, 61°30′W. Collected by William E. Duellman, Linda Trueb, and Dana K. Duellman, 24 Jul 1974.

PARATOPOTYPES.—KU 166545–166547, collected by William E. Duellman, John E. Simmons, and Juan R. León, 16 Jul 1974; KU 166553–166558, 166560, 166561, collected by William E. Duellman, Linda Trueb, and Dana K. Duellman, 24 Jul 1974; KU 181031, collected by Stefan Gorzula, 27 Jan 1979.

DIAGNOSIS.—*Leptodactylus sabanensis* currently is known only from the Gran Sabana of Venezuela and has yet to be taken in sympatry with other *Leptodactylus* species with toe fringes. The other *Leptodactylus* with toe fringes (excluding *L.*

FIGURE 43.—Map of localities for *Leptodactylus podicipinus* (circle = problematical locality of Igarapé Belém, Amazonas, Brazil).

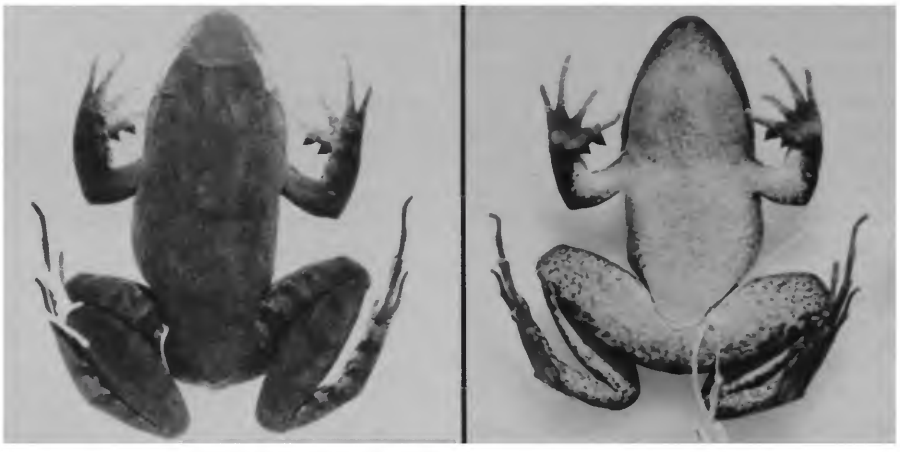

FIGURE 44.—Holotype of *Leptodactylus sabanensis*, new species.

ocellatus and its closest relatives) that occur next to the Gran Sabana are *L. bolivianus, diedrus, leptodactyloides, pallidirostris, petersii,* and *riveroi. Leptodactylus sabanensis* is smaller than *bolivianus* and *riveroi* (*sabanensis* females 42–57 mm SVL, males 35–46 mm SVL; *bolivianus* females to 88 mm SVL, males to 94 mm SVL; *riveroi* females to 81 mm SVL, males to 63 mm SVL); most *sabanensis* do not have long dorsolateral folds, and, among those that do the folds are not well developed and smooth, whereas all *bolivianus* and *riveroi* have a pair of long, smooth, well-developed dorsolateral folds. The ventral and posterior thigh patterns merge in *L. sabanensis;* in *diedrus* the patterns abut. Fewer *L. sabanensis* have indications of light posterior lip stripes than in *leptodactyloides. Leptodactylus sabanensis* differs more from *leptodactyloides* in advertisement calls than in morphological features. In *L. sabanensis,* call duration is 0.04–0.06 s with a dominant frequency range of 900–2300 Hz with maximum energy between 1400–1800 Hz; in *leptodactyloides,* call duration is 0.01–0.04 s with a dominant frequency range of 650–1600 Hz with maximum energy between 1100–1300 Hz. *Leptodactylus sabanensis* is larger than *pallidirostris* (*pallidirostris* females 30–43 mm SVL, males 28–37 mm SVL). The most common lip stripe condition in *L. sabanensis* is indiscernible, but when the lip stripes are discernible, they extend from the posterior corner of the eye; the commonest lip stripe condition in *pallidirostris* is distinct stripes that often extend from under the middle of the eye. The broadcast frequency range of the advertisement call of *L. pallidirostris* is 1500–3500 Hz with maximum energy at 2500–3500 Hz (see comparison with *leptodactyloides* above for *sabanensis* call data). *Leptodactylus sabanensis* is larger than *petersii* (*petersii* females 31–51 mm SVL, males 27–41 mm SVL). Few *L. sabanensis* (15%) have light chin/throat spots; most *petersii* (56%) do. *Leptodactylus sabanensis* do not have anastomotic or speckled belly patterns, which are characteristically found in *petersii.*

DESCRIPTION OF HOLOTYPE.—Snout rounded from above, rounded in profile; canthus rostralis rounded; lores weakly obtusely concave in cross section; tympanum large, diameter about 3/4 eye diameter; vocal slits well developed, lying from under posterior portion of tongue to angle of jaw; vocal sac single, essentially internal, but very slightly expanded externally; vomerine teeth in two moderate, almost straight series, separated by distance about 1/3 length of a single vomerine tooth row, lying posterior to and mostly between choanae; finger lengths II≈IV<I<III; sides of fingers weakly ridged; each thumb with two large medial black spines; arms very slightly hypertrophied; no ulnar ridge; dorsum with small white- or black-tipped tubercles, sparse anteriorly, dense posteriorly; supratympanic fold distinct, weak interrupted dorsolateral fold from eye to sacrum; no obvious glands; ventral disk fold not discernible, venter smooth; no chest spines; tips of toes noticeably swollen; sides of toes extensively fringed; subarticular tubercles rounded, moderately developed; well-developed metatarsal fold continuous with fringe on outer toe V; tarsal fold well developed, extending about 7/8 distance on tarsus, terminating at inner metatarsal tubercle, not continuous with toe fringe; outer surface of tarsus shagreened with several small brown-tipped tubercles, sole of foot shagreened with scattered small white-tipped tubercles.

SVL 45.1 mm, head length 17.8 mm, head width 16.0 mm, tympanum diameter 3.9 mm, thigh length 21.6 mm, shank length 22.2 mm, foot length 25.7 mm.

Dorsum mostly uniform brown with a light interorbital stripe interruptedly bordered posteriorly by a darker brown stripe, dorsolateral folds interruptedly outlined with darker brown; flanks with small, indistinct dark brown spots/blotches; upper limbs weakly to noticeably cross-banded with dark brown; upper lip rather uniform brown; chin and throat extensively

mottled brown; chest and belly heavily speckled brown, more extensively anteriorly; posterior surface of thigh boldly mottled dark brown and tan, row of tan spots in area where light stripe found in other individuals.

HABITAT AND COLOR NOTES.—KU 166545-166550 were "under rocks and logs by day and on ground by night. Dorsum grayish tan with brown spots. Labial and dorsolateral stripes pinkish cream. Males with cream throat and yellow belly. Females with cream belly with gray flecks. Iris dull reddish bronze." (William E. Duellman field notes, pers. comm.)

ETYMOLOGY.—Named to indicate this species is geographically centered on the Gran Sabana of Venezuela.

ADULT CHARACTERISTICS (N = 10 females, 22 males).—Light posterior lip stripes distinct (15%), indistinct (36%), or not discernible (48%), when discernible, stripes extending from posterior corner of eye; light posterior thigh stripe distinct (23%), indistinct (45%), or not discernible (32%); dorsolateral folds (apparently) absent (6%), rarely short (3%), usually moderate length (61%), often long (30%); toe tips just swollen (42%), swollen (36%), just expanded (18%) or expanded (3%); male black thumb spines medium size (64%), medium-large (32%), or large (4%); chin/throat occasionally with light spots on a darker field (15%); belly lightly mottled (15%), usually moderately mottled (61%), or sometimes extensively mottled (24%).

Females 42.1-56.9 mm SVL ($\bar{x} = 51.0 \pm 4.8$), males 35.0-46.4 mm SVL ($\bar{x} = 43.0 \pm 2.7$); female head length 34%-39% SVL ($\bar{x} = 37 \pm 2\%$), male head length 35%-40% SVL ($\bar{x} = 38 \pm 1\%$); female head width 33%-36% SVL ($\bar{x} = 34 \pm 1\%$), male head width 32%-38% SVL ($\bar{x} = 35 \pm 1\%$); female tympanum diameter 7%-8% SVL ($\bar{x} = 8 \pm 0\%$), male tympanum diameter 8%-10% SVL ($\bar{x} = 9 \pm 0\%$); female thigh length 43%-49% SVL ($\bar{x} = 46 \pm 2\%$), male thigh length 41%-49% SVL ($\bar{x} = 45 \pm 2\%$); female shank length 44%-52% SVL ($\bar{x} = 49 \pm 2\%$), male shank length 45%-52% SVL ($\bar{x} = 48 \pm 2\%$); female foot length 49%-61% SVL ($\bar{x} = 56 \pm 4\%$), male foot length 51%-60% SVL ($\bar{x} = 55 \pm 2\%$).

LARVAL CHARACTERISTICS.—Unknown.

ADVERTISEMENT CALL.—Call rate 1.2 calls per s; call duration 0.04-0.06 s; call slightly pulsatile; calls markedly frequency modulated without a sharp attack, with a moderately fast rise time; broadcast frequency range 900-2300 Hz with greatest intensity of call in 1400-1800 Hz range; weak harmonic structure (Figure 26).

KARYOTYPE.—Unknown.

DISTRIBUTION.—Known only from and near the Gran Sabana of Venezuela (Figure 45; Appendix 2).

Leptodactylus validus Garman, 1887

Leptodactylus validus Garman, 1887:14 [type locality: Kingston, St. Vincent; lectotype MCZ 2185, adult male].

DIAGNOSIS.—*Leptodactylus validus* is only known to occur with or near to the fringe-toed *Leptodactylus* species *bolivianus* and *nesiotus* (excluding *L. ocellatus* or one of its closest relatives). *Leptodactylus validus* is smaller than *bolivianus* (*validus* females 38-52 mm SVL, males 30-43 mm SVL; *bolivianus* females to 88 mm SVL, males to 94 mm SVL), and no *validus* have long dorsolateral folds whereas all *bolivianus* do. In those individuals of *L. validus* with discernible lip stripes, the stripes extend from the posterior corner of the eye posteriorly; *L. nesiotus* has a broad light stripe that extends from at least under the eye.

ADULT CHARACTERISTICS (N = 36 females, 71 males).—Light posterior lip stripes rarely very distinct (2%), often distinct (30%), usually indistinct (55%), sometimes not discernible (14%), when discernible, stripes extending from posterior corner of eye; light posterior thigh stripes rarely very distinct (3%), otherwise distinct (37%), indistinct (23%), or not discernible (38%); dorsolateral folds (apparently) rarely absent (1%), usually short (91%), occasionally medium length (8%); toe tips just swollen (3%), swollen (53%), just expanded (4%), expanded (27%), or small disked (14%); male black thumb spines small-medium size (2%), medium (65%), medium-large (21%), or large (13%); chin/throat rarely with light spots on a darker field (4%); belly rarely essentially lacking pattern (3%), usually lightly mottled (66%), often moderately mottled (29%), rarely extensively mottled (2%).

Females 38.1-51.5 mm SVL ($\bar{x} = 44.3 \pm 2.9$), males 30.5-42.9 mm SVL ($\bar{x} = 37.8 \pm 2.6$); female head length 35%-39% SVL ($\bar{x} = 36 \pm 1\%$), male head length 34%-41% SVL ($\bar{x} = 37 \pm 2\%$); female head width 32%-36% SVL ($\bar{x} = 34 \pm 1\%$), male head width 32%-39% SVL ($\bar{x} = 35 \pm 1\%$); female tympanum diameter 7%-9% SVL ($\bar{x} = 8 \pm 0\%$), male tympanum diameter 7%-9% SVL ($\bar{x} = 8 \pm 0\%$); female thigh length 40%-49% SVL ($\bar{x} = 44 \pm 2\%$), male thigh length 41%-52% SVL ($\bar{x} = 45 \pm 2\%$); female shank length 44%-50% SVL ($\bar{x} = 47 \pm 2\%$), male shank length 45%-53% SVL ($\bar{x} = 48 \pm 1\%$); female foot length 48%-58% SVL ($\bar{x} = 53 \pm 2\%$), male foot length 50%-59% SVL ($\bar{x} = 54 \pm 2\%$).

LARVAL CHARACTERISTICS.—The available tadpole data require discussion. Kenny described the larvae of a member of the *podicipinus-wagneri* complex from Trinidad as *L. podicipinus petersi* (1969:75, fig. 36), and samples of larvae are on hand from Tobago and St. Vincent. The larvae from the three islands are each very distinct from each other, certainly at the species level of difference. At least for the samples from St. Vincent and Tobago, the identification of the larvae is not certain; identification is based on known adult occurrences and known *Leptodactylus* larval morphologies. The larval type described by Kenny from Trinidad is unique for all other known *Leptodactylus* in having a ventral papillary gap in the oral disk, suggesting either that the larvae described and figured are abnormal or that the larvae in fact are not *Leptodactylus*, but represent some other genus. The larvae described by Kenny further differ from the Tobago and St. Vincent larvae in that the A-2 labial tooth row is split in the stage 29 Trinidad larvae (stage based on published figure), whereas for all similar stage

FIGURE 45.—Map of localities for *Leptodactylus sabanensis* (triangles), *validus* (squares), and *wagneri* (dots, single record from near La Guayacana, Nariño, Colombia, indicated by circle).

(and greater) larvae from Tobago and St. Vincent, the A-2 labial tooth row is entire. The larvae from Tobago correspond in total size and proportions (particularly the oral disk) with the *L. bolivianus-ocellatus* group larvae on the mainland of South America rather than with the *podicipinus-wagneri* complex. As far as is known, no member of the *L. bolivianus-ocellatus* group occurs on Tobago (Hardy, 1982); however, Hardy (1982:68–69) discussed reports of a large frog (which provided frog legs for human consumption) on Tobago that was said to live in holes in the forest and come out at night. No voucher specimens of this reported frog have been taken, although there is a large femur from the Robinson Crusoe Cave that is leptodactylid, not bufonid (Hardy, 1982; R.I. Crombie, pers. comm.). Hardy (1982:69) thought the reports might refer to *L. pentadactylus*, but has since discounted that species allocation for the reports (Hardy, 1984). It is possible that the reports referred to a member of the *bolivianus-ocellatus* complex, but as no transformed specimens of this complex are known as vouchers from Tobago, nothing of certainty can be stated at this time. For present purposes, larval descriptions are provided for the Tobago and St. Vincent samples separately.

Tobago Larvae: Maximum total length stage 37, 34.8 mm; body length 36%–41% ($\bar{x}$ = 38.1) total length; maximum tail depth 56%–62% ($\bar{x}$ = 59.5) body length; nostril mid-distance between tip of snout and eye or just closer to either tip of snout or eye; internarial distance just greater than or about equal to interorbital distance; eye diameter 8%–10% ($\bar{x}$ = 9.2) body length; mouth subterminal; oral disk entire; spiracle sinistral; anal tube median; oral papilla formula 1-2 or 1-2-3-2; oral disk width 17%–20% ($\bar{x}$ = 18.9) body length; oral papilla gap 26%–33% ($\bar{x}$ = 29.7) oral disk width; labial tooth row formula 2/3; number of labial teeth in 1/2 of row A-2, stages 36–37, about 95; number of labial teeth in 0.1 mm measured in middle of 1/2 of row A-2, 5.5–8 ($\bar{x}$ = 6.4); tadpole entirely uniform brown, heavily suffused with melanophores, including oral disk, anal tube, and entire tail.

St. Vincent Larvae: Maximum total length stage 36, 25.8 mm; body length, stage 25, 41%–46% ($\bar{x}$ = 43.7) total length, stages 29–38, 38%–44% ($\bar{x}$ = 41.0) total length; maximum tail depth, stage 25, 41%–52% ($\bar{x}$ = 44.7) body length, stages 29–38, 49%–58% ($\bar{x}$ = 53.5) body length; nostril mid-distance between tip of snout and eye or just closer to eye (some stage 25 individuals only); stage 25 larvae internarial distance about equal to or just less than interorbital distance, stage 29–38 larvae internarial distance just greater than interorbital distance; eye diameter, stage 25, 6%–8% ($\bar{x}$ = 6.3) body length, stages 29–38, 8%–12% ($\bar{x}$ = 10.7) body length; mouth subterminal; oral disk entire; spiracle sinistral; anal tube median; oral papilla formula 1-2; oral disk width 23%–29% ($\bar{x}$ = 25.5) body length; oral papilla gap, stage 25, 39%–56% ($\bar{x}$ = 46.3) body length, stages 29–38, 28%–39% ($\bar{x}$ = 33.2) body length; labial tooth row formula, stage 25, 2(2)/3, stages 29–38, 2/3; number of labial teeth in one split row of A-2, stage 25, 45–60; number of labial teeth in 1/2 row A-2, stages 29–38, 100–115; number of labial teeth in 0.1 mm measured in middle of 1/2 of row A-2, 7.5–12 ($\bar{x}$ = 9.2); stage 25 larvae light with scattering of melanophores on body and tail, either lacking or very few on oral disk, no melanophores on anal tube, melanophores not extending to uppermost or lowermost tail fins; stage 29–38 larvae gray, dorsal body uniform with heavy profusion of melanophores, ventral body almost uniform to distinctly mottled, with profusion of melanophores, heavier behind oral disk than over guts, oral disk with melanophores, anal tube with melanophores, tail gray with heavy profusion of melanophores on entire tail except for a large very distinct to indistinct light spot over anterior tail musculature.

ADVERTISEMENT CALL.—Call rate of 1.1–1.9 calls per s; call duration 0.03–0.06 s; calls usually of two notes, first note a single pulse occasionally weak or apparently absent, second note with 2–6 partial pulses; calls frequency modulated with very fast rise times; broadcast frequency range 1300–3500 Hz, with maximum energy in 2300–3500 Hz range; harmonic structure equivocal, but second note perhaps representing a shift to a harmonic of the first note (Figures 31–33).

KARYOTYPE.—Unknown.

GEOGRAPHIC VARIATION.—Variation among the various island populations has been discussed in the section analyzing specimens from "Region 6—Trinidad, Tobago, Lesser Antilles."

DISTRIBUTION.—The Lesser Antilles islands of St. Vincent, Bequia, Grenada, and the continental islands of Tobago and Trinidad (Figure 45; Appendix 2).

Leptodactylus wagneri (Peters, 1862)

Plectromantis wagneri Peters, 1862:232 [type locality: "der Westseite der Anden in Ecuador (Peters, 1862:233)" in error, catalog entry for the holotype "Pastassa;" holotype destroyed, formerly in ZSM collection, Munich].

Leptodactylus wagneri.—Nieden, 1923:479 [first apparent association of *wagneri* with *Leptodactylus*].

DIAGNOSIS.—*Leptodactylus wagneri* occurs along the amazonian flanks of the Andes and is known to occur with or in the same general region as the following *Leptodactylus* species with toe fringes (excepting *L. ocellatus* and its closest relatives): *L. bolivianus, colombiensis, dantasi, diedrus, griseigularis, leptodactyloides, pascoensis,* and *petersii. Leptodactylus wagneri* does not reach the same size as *bolivianus* (*wagneri* females 52–82 mm SVL, males 39–61 mm SVL; *bolivianus* females to 88 mm SVL, males to 94 mm SVL). Few *L. wagneri* have distinct posterior lip stripes, and all discernible lip stripes in *wagneri* extend from the posterior corner of the eye; many *bolivianus* have light stripes on the entire upper lip including under the eye. *Leptodactylus wagneri* is larger than *colombiensis* (*colombiensis* females 38–62 mm SVL, males 36–56 mm SVL), and most *wagneri* have long dorsolateral

folds whereas only some *colombiensis* do. *Leptodactylus wagneri* do not have distinct light belly spots; *L. dantasi* does. *Leptodactylus wagneri* is larger than *diedrus* (*diedrus* females 34–48 mm SVL, males 30–40 mm SVL), and the ventral and posterior thigh patterns merge in *wagneri* whereas the patterns abut in *diedrus*. *Leptodactylus wagneri* is larger than *griseigularis* (*griseigularis* females 39–58 mm SVL, males 35–51 mm SVL). The most common condition for dorsolateral folds in *wagneri* is long, and the most common belly pattern is moderately mottled. The most common fold condition in *griseigularis* is moderate length, and the most common belly pattern is the lightly mottled state. *Leptodactylus wagneri* is larger than *leptodactyloides* (*leptodactyloides* females 35–56 mm SVL, males 28–48 mm SVL). Most *L. wagneri* have long dorsolateral folds; few *L. leptodactyloides* have long folds. Many *L. wagneri* have boldly mottled bellies, whereas the bellies of *leptodactyloides* characteristically are finely mottled. In addition to the bold pattern, the bellies of most *L. wagneri* are moderately mottled and some are extensively mottled; the bellies of *pascoensis* are lightly to moderately, but never boldly, mottled. Characteristically, *L. wagneri* is larger than *petersii* (*petersii* females 31–51 mm SVL, males 27–41 mm SVL), and no *petersii* have long dorsolateral folds.

ADULT CHARACTERISTICS (N = 82 females, 110 males).—Light posterior lip stripes distinct (27%), indistinct (54%), or indiscernible (19%), when discernible, stripe extending from posterior corner of eye; light posterior thigh stripes rarely very distinct (1%), often distinct (32%), indistinct (28%), or indiscernible (39%); dorsolateral folds rarely (apparently) absent (2%) or short (1%), often medium length (21%), usually long (75%); toe tips rarely narrow (2%), usually either just swollen (43%) or swollen (54%), rarely just expanded (1%); male black thumb spines rarely small size (1%) or medium-small (5%), usually medium (68%), sometimes medium-large (18%), occasionally large (8%); chin/throat sometimes with light spots on a darker background (27%); belly rarely lightly mottled (3%), usually either moderately mottled (49%) or extensively mottled (48%), mottle usually in a strikingly bold pattern (57%).

Females 52.3–81.7 mm SVL ($\bar{x} = 65.5 \pm 6.5$), males 39.1–60.7 mm SVL ($\bar{x} = 51.6 \pm 4.7$); female head length 32%–40% SVL ($\bar{x} = 36 \pm 2\%$), male head length 34%–41% SVL ($\bar{x} = 37 \pm 1\%$); female head width 31%–37% SVL ($\bar{x} = 34 \pm 1\%$), male head width 33%–38% SVL ($\bar{x} = 36 \pm 1\%$); female tympanum diameter 6%–8% SVL ($\bar{x} = 7 \pm 0\%$), male tympanum diameter 6%–9% SVL ($\bar{x} = 8 \pm 0\%$); female thigh length 39%–51% SVL ($\bar{x} = 45 \pm 3\%$), male thigh length 40%–50% SVL ($\bar{x} = 45 \pm 2\%$); female shank length 45%–55% SVL ($\bar{x} = 51 \pm 2\%$), male shank length 46%–54% SVL ($\bar{x} = 55 \pm 2\%$); female foot length 47%–60% SVL ($\bar{x} = 55 \pm 3\%$), male foot length 49%–61% SVL ($\bar{x} = 55 \pm 2\%$).

LARVAL CHARACTERISTICS.—Unknown.

ADVERTISEMENT CALL.—Unknown.

KARYOTYPE.—Unknown.

DISTRIBUTION.—Most specimens are from the amazonian slopes of the Andes in southern Colombia, Ecuador, and northern Peru; there are a few records from lowland Amazon localities in Ecuador, Peru, and Colombia, and a single specimen is known from the low Pacific slopes of the Andes in Colombia (Figure 45; Appendix 2).

Distributions

Understanding the distribution patterns of the *podicipinus-wagneri* complex is still at an early stage. This is due in part to unresolved systematic problems and to undercollected regions where members of the complex occur. Until the status of the Venezuelan Andes OTUs are resolved, the distributions of *L. colombiensis, leptodactyloides,* and *sabanensis* can not be understood adequately. Similarly, if the geographic samples currently included in *L. griseigularis* prove to contain more than one species, the distribution patterns involved will change significantly. Additional collecting efforts could change the distribution of *L. diedrus* as documented in this paper (Figure 36). There are two species for which the systematic understanding and collecting efforts are adequate such that additional data are unlikely to change the distribution patterns described in this paper: *L. natalensis* and *podicipinus*. Before commenting further on the distributions of these latter two species, discussion is required for a locality from which I believe the provenance of specimens in museum collections is problematical.

Borys Malkin collected the specimens from Igarapé Belém, Rio Solimões, Amazonas, Brazil, that are the basis of all *Leptodactylus* records for that locality. The Malkin specimens for Igarapé Belém are in the American Museum of Natural History (AMNH) and Museu de Zoologia da Universidade de São Paulo (MZUSP) collections. The following members of the *podicipinus-wagneri* complex are recorded from Igarapé Belém: *L. diedrus* (Figure 36), *leptodactyloides* (Figure 38), *petersii* (Figure 42), *podicipinus* (Figure 43), and *wagneri* (Figure 45). The locality is well within the known distributional limits of *L. leptodactyloides* and *petersii*, and it forms part of the known distributional limit of *L. diedrus*, but unremarkably so (Figure 36). Igarapé Belém is an outlier locality for *L. wagneri*, but the presence of *wagneri* (as currently understood) in other lowland Peruvian localities that are somewhat geographically removed from the Andean slopes suggests either that all of the lowland localities are in error (probably due to identification errors) or that the Igarapé Belém record may be valid for *wagneri* (Figure 45). However, in the case of *L. podicipinus*, Igarapé Belém is well removed from the rest of the *podicipinus* localities (Figure 43), and I believe this record represents an error. *Leptodactylus podicipinus* occurs in open formations. It is not a particularly difficult species to collect. Collections are available between Igarapé Belém and the other

known localities for *podicipinus;* if *podicipinus* occurs in the mapped hiatus (Figure 43), it should have been collected by now. There is an additional member of the *L. melanonotus* group in Malkin's collection from Igarapé Belém: *L. pustulatus.* There are no habitat data available for *pustulatus* to my knowledge, but the other known localities for *pustulatus* all occur in open vegetation domains, geographically distant from Igarapé Belém (Figure 46). *Leptodactylus pustulatus* is arguably the most distinctive species in the *melanonotus* group, i.e., there is no doubt about identification for this species. The distributions of both *L. podicipinus* and *pustulatus* provide, in my opinion, conclusive evidence that the locality data for Igarapé Belém are in error for those two species at least. The problem is to discern which records *are* valid for Igarapé Belém.

There is no question that Malkin collected frogs from Igarapé Belém. The likeliest answer is that Malkin combined, by mistake, collections made from another locality with those from Igarapé Belém. Malkin did not individually field tag his specimens. Malkin collected at Igarapé Belém from 8 to 28 April 1966. He also collected at Barra do Tapirapés, Mato Grosso, Brazil, from 29 December 1965 to 16 January 1966, from which locality both *L. podicipinus* and *pustulatus* are known to occur. Both of these collections were sold to the museums simultaneously by Malkin. Dr. P.E. Vanzolini indicates that there is a possibility of specimen mixing at the MZUSP between the Malkin collections labelled as from Estirón, Peru (whence both *L. diedrus* and *wagneri* also are known), and Igarapé Belém, but not from collections labelled as from Igarapé Belém and Barra do Tapirapés (pers. comm.). I conclude that Malkin did mix some specimens from Barra do Tapirapés with those from Igarapé Belém in both the AMNH and MZUSP collections. The evidence is not as strong that Malkin also mixed in some specimens from Estirón, Peru, with the Igarapé Belém collection, but the possibility has interesting consequences in our understanding of distributions. For further work, Igarapé Belém is excluded as a locality for *Leptodactylus podicipinus* and *pustulatus,* but questionably included as a locality for *L. diedrus, leptodactyloides, petersii,* and *wagneri.*

The distribution of *Leptodactylus natalensis* follows the Atlantic Forest Morphoclimatic Domain from its northern extent, ending in the State of Rio de Janeiro (Figure 39). Given the level of collecting effort in the states of Rio de Janeiro and São Paulo, that southern distributional limit is believable. Interestingly, Serra dos Cavalos, Pernambuco, one of the northern localities that on a map lies outside the Atlantic Forest Morphoclimatic Domain (Ab'Sáber, 1977) is a "brejo," containing a mesic forest that was connected with the Atlantic Forest vegetation during the last, wettest phase of the glacial cycle (see Vanzolini, 1981, for a general discussion of brejos in northeastern Brazil).

The distribution of *L. podicipinus* suggests a basic adaptation of *podicipinus* to the open formation vegetations of Argentina (northeast), Bolivia, Paraguay, and Brazil with limited invasion of the southern Amazon basin only along the major river systems of the Rio Madeira and Amazonas. The limited distribution of *L. podicipinus* in Amazonia suggests that it may be a relatively recent invader in that region.

Differentiation

Variation of types of characters among taxa of the *podicipinus-wagneri* complex is in itself variable. For example, the same adult morphological character that has discrete states and that is consistently different between two species may well demonstrate a continuous variation between two other species. Also, some taxa seem better defined by advertisement call differences, others by larval morphologies. The differentiation patterns of the character complexes analyzed for this paper can be summarized as follows.

Size is among the adult morphological features that shows the most interspecific and least intraspecific variation. Size differences among taxa usually are not discrete, however, including taxa that have extensive sympatric distributions. Measurement data, as well as the morphological features of dorsolateral folds, toe tips, and size of male thumb spines, demonstrate intraspecific variation that sometimes equals that found interspecifically, but usually each species has a distinctive (but not discretely distinct) distribution of character states. Adult pattern characters also often vary as much intraspecifically as interspecifically, but some species may have distinct character states. For example, the *L. podicipinus* with distinct light belly spots are distinct from all *L. leptodactyloides,* which never have distinct light belly spots; however, some individual *L. podicipinus* without distinct belly spots have the same belly patterns found in some *L. leptodactyloides.*

Although few larval samples have been analyzed for members of this complex, the available data suggest that interspecific variation may be more discrete than for adult morphological characters. Features of size, tooth row morphology, and tail pattern appear to characterize each species (for those species for which identifications are not in doubt).

Advertisement calls are quite species-specific in *Leptodactylus* species in general (Heyer and Straughan, 1976; Heyer, 1978, 1979). However, advertisement calls of the *podicipinus-wagneri* complex are not as distinct as those found in the other species groups. For one thing, individuals of the *podicipinus-wagneri* complex demonstrate a broad array of vocalization types, the functions of which are not well understood at present. At the least, individual males are capable of producing distinct advertisement and aggressive calls, but it is not clear which are which for all species. Theoretically, one would expect advertisement calls to demonstrate the greatest interspecific differences because males should attract only females of their same species, but they may defend their calling site against any intruding male independent of species. More work needs to be done to evaluate the call functions so that calls with the same

FIGURE 46.—Map of localities for *Leptodactylus pustulatus* (square = problematical locality of Igarapé Belém, Amazonas, Brazil).

functions are compared among species. It is possible that members of this complex are using the advertisement call more as a location signal than as a species coding signal. Typically, the calls of these frogs are quieter than those of other *Leptodactylus* species and have wide broadcast frequency bands. The latter feature facilitates point location of the sound source and the quieter call may be a consequence of producing a call with wider broadcast frequency bands.

Karyotypes have been described for only three members of the *podicipinus-wagneri* complex. The karyotypes of *griseigularis* and *podicipinus* are quite similar, but they are rather distinct from that of *natalensis,* differing in number of telocentric pairs and location of secondary constrictions (Bogart, 1974). Karyotype analysis of additional species might be fruitful in terms of understanding the patterns of evolutionary differentiation occurring in the complex.

There appears to be a modest degree of habitat differentiation among members of the complex. Some species, such as *L. leptodactyloides, pallidirostris,* and *wagneri* occur both in open vegetation formations and closed forests. Others appear to demonstrate greater habitat specialization: *Leptodactylus podicipinus* and *validus* only occur in open vegetation formations or situations; *L. diedrus, pascoensis,* and *petersii* occur exclusively (or almost so) in closed forest habitats. Whether these habitat distributions are related to processes of species differentiation is unknown at present.

Comment on Relationships

Morphological data are inadequate to perform a robust cladistic analysis for the members of the *podicipinus-wagneri* complex in at least two ways. All of the morphological data that could be used to evaluate relationships are the data presented in this paper. I know of no other morphological data that could be used. These data are very difficult, if not impossible, to categorize in distinct, polarized states. That is the first inadequacy. The second is that for a cladistic analysis to be robust, one should have more states than taxa. At present, that is not the case for the frogs in question. When more complete data sets are available for larvae, karyotypes, and behavior, then a cladistic analysis may well be instructive.

At this time, in order to evaluate relationships in *Leptodactylus* (in general), I prefer to obtain genetic-estimate data from appropriate molecular analyses. Materials are being gathered toward this end.

Unresolved Problems and Their Consequences in Understanding Evolutionary Processes

Data are insufficient to resolve all species boundaries questions in the *podicipinus-wagneri* complex at this time. Some of these problems have serious consequences relative to our understanding of distribution patterns and speciation processes within this complex. The unresolved problems are discussed in descending order of severity of consequences, in my opinion.

The series of populations occurring along the Venezuelan Andes and in the coastal mountains of Venezuela represent the largest unresolved problem. There is considerable morphological variation among the few available samples for these populations, and it is not at all clear how many species of the complex occur in the montane slope regions of Venezuela. A second-level problem is whether any of the Venezuela montane slope populations are conspecific with either *L. colombiensis* or *leptodactyloides*. The distributions of either *L. colombiensis* or *leptodactyloides* would be significantly expanded if either occurred along the Venezuelan montane slopes. This problem must be resolved before we can understand the role of mountain building and geographic isolation in the differentiation and speciation processes of the taxa that occur in northern South America. Data needed to resolve this problem are new intensive collections all along the Venezuelan montane slopes, concentrating not only on obtaining adequate series of specimens to analyze adult morphological variation but also on obtaining recordings of calls, larval samples, and tissue samples for molecular analysis. The data at hand are so inadequate that sampling needs to be done as if no materials existed to aid in resolution of the problem.

The second major unresolved problem involves the taxa considered as *L. validus* and *pallidirostris* in this paper. The current recognition of *L. validus* as a species occurring on the Lesser Antilles, Trinidad, and Tobago, but not on the mainland of South America runs counter to almost all other distribution patterns for the islands involved. As Trinidad and Tobago are continental islands and the Lesser Antilles are oceanic islands, the expected distribution patterns for a single species occurring on any combination of Trinidad, Tobago, and the Lesser Antilles are as follows: (1) the species occurs on the mainland, Trinidad and Tobago, and the Lesser Antilles; (2) the species occurs on the mainland and Trinidad and Tobago but not on the Lesser Antilles; (3) the species occurs only on Trinidad and/or Tobago; (4) the species occurs only on the Lesser Antilles. Thus, in terms of *validus,* one would expect that either (1) *validus* should be restricted to the Lesser Antilles, and the Trinidad and Tobago populations represent a closely related, but distinct, species that either is found only on Trinidad and Tobago or also occurs on the mainland of South America; or (2) *validus* also occurs on the mainland of South America. The adult morphological analyses indicate that there is slight differentiation of the Lesser Antilles populations from the Trinidad and Tobago populations. If the tadpoles analyzed have been correctly associated with species, then the larval data clearly support alternative (1). The mainland species that would be expected to be conspecific with *validus* (either as defined in this paper, or only the Trinidad and Tobago populations) is *pallidirostris.* The available call data are consistent with a single species, *pallidirostris* plus *validus,* occurring on the mainland, Trinidad and Tobago, and the Lesser Antilles; the adult morphological data are not. This conflict of call and adult morphological data could be due to combining of two (or more?) species within *pallidirostris.* There is no doubt in my mind, in comparing *pallidirostris* from the Guianas with *validus* from the islands, that different species are represented. There are no call data on hand for *pallidirostris* from the Guianas. The available calls for *pallidirostris* all come from Venezuela. There is certainly color pattern variation differences

between at least some of the Venezuelan populations I have included in *pallidirostris* (including those for which call data are available); the taxonomic decision I took was conservative, and I would not be surprized if at least some of the Venezuelan populations I included in *pallidirostris* are distinct at the species level and in fact are conspecific with the populations on Trinidad and Tobago I assigned to *validus*. The available adult morphological data are probably sufficient; that is, analysis of additional adult morphological data is not likely to resolve this problem. The problem should be resolvable with either call data or molecular analyses. Call data from throughout the entire range of *pallidirostris* would be needed to determine whether two or more species have been included (available call data are adequate for *validus*). Molecular analysis of samples from *validus* from the Lesser Antilles and Trinidad and Tobago, and samples of *pallidirostris* at least from the Guianas and Venezuela proximate to Trinidad would be required. Adequate tissue samples are available for the various populations of *validus* as recognized in this paper; analysis of those should determine whether the Lesser Antilles populations are conspecific with the Trinidad and Tobago populations. Available tissue samples for *pallidirostris* are inadequate to resolve the relationships between *pallidirostris* and *validus*.

It is unlikely that *Leptodactylus nesiotus* occurs only on Trinidad. Read (1986) pointed out that frogs that are known only from the Icacos peninsula on Trinidad occur in the (adjacent) Orinoco floodplain of Venezuela (e.g., *Adenomera hylaedactyla, Leptodactylus macrosternum*) or the llanos of Venezuela (e.g., *Hyla miniscula*). The latter distribution is zoogeographically difficult to explain, but it would be worth field time to explore the Orinoco floodplain and the llanos in the State of Yaracay, Venezuela, for the presence of *Leptodactylus nesiotus*.

A series of geographically isolated populations along the Amazonian flanks of the Andes in Peru and Bolivia has been included in a single species, *L. griseigularis*. There is some differentiation among these populations as indicated by adult morphological data. Isolation of populations of *L. griseigularis* likely has been due to mountain-building activities. In this situation, where populations have become geographically isolated without subsequent contact, advertisement calls may not have differentiated to include species-coding information. It is likely that understanding of differentiation within *L. griseigularis* will depend entirely on molecular analytic techniques. To my knowledge, tissue samples are available for a couple of geographically close localities in Peru. Additional tissue samples throughout the entire range of *L. griseigularis* are needed.

The final problem worth comment is whether the Region 3 representatives of *L. petersii* are in fact conspecific with the other region representatives of *petersii*. All specimen-related data suggests that they are; however, the lack of habitat data for any of the Region 3 *petersii* raises the question of conspecificity. Almost all species of *L. petersii* with habitat data are from closed forests. Extensive closed forests do not exist as such in the area where the Region 3 representatives of *petersii* occur; the only forests are gallery forests along streams. My prediction is that the Region 3 *petersii* were collected in and are restricted to gallery forest habitats. Probably a single new collection of any population of Region 3 *petersii* with habitat and call data would resolve this problem.

The above problems are detailed for two reasons. First, although considerable progress has been made in understanding variation in the *podicipinus-wagneri* complex, I do not wish to leave the impression that all problems have been resolved. Second, by summarizing the problems, I hope to encourage others to gather the data needed for their resolution and to report their results.

Appendix 1

OTU (Operational Taxonomic Unit) Assignments

Part A: Single-taxon and sympatric species population OTUs. Because of the large number of OTUs designated in the "Single taxon and sympatric species analyses," these OTUs are organized by country localities alphabetically.

Single-taxon and sympatric species Population analyses OTU names	Taxa/Region analyses OTU Names	Final (species) assignment
Bolivia		
Alejandria		
Moderate Size, Light Posterior Thigh Stripe	Region 4 Light Posterior Belly	*leptodactyloides*
Small/Moderate Size, Dark Belly	Region 4 Dark Belly	*podicipinus*
Buenavista		
Small Size, Dark Belly	Region 7 Dark Belly	*podicipinus*
Small/Moderate Size, Light Thigh Stripe	Region 7 Light Posterior Belly	*leptodactyloides*
Rurrenabaque		
Small Size, Dark Belly	Region 7 Dark Belly	*podicipinus*
Tumi Chucua		
Small Size, Dark Belly (part)	Region 4 Anastomotic Belly	*petersii*
Small Size, Dark Belly (part)	Region 4 Dark Belly	*podicipinus*
Moderate Size, Light Posterior Thigh Stripe	Region 4 Light Posterior Belly	*leptodactyloides*
Brazil		
Boca do Acre		
Moderate Size, Lightly Speckled Belly	Region 4 Light Posterior Belly	*leptodactyloides*
Small Size, Moderately Speckled Belly	Region 4 Anastomotic Belly	*petersii*
Borba		
Small Size, Dark Belly	Region 4 Dark Belly	*podicipinus*
Small Size, Speckled Belly	Region 4 Anastomotic Belly	*petersii*
Cachoeira do Espelho		
Moderate Size, Light Posterior Thigh Stripe	Region 4 Light Posterior Belly	*leptodactyloides*
Small Size, Anastomotic Belly	Region 4 Anastomotic Belly	*petersii*
Curuçá		
Small Size, Dark Belly	Region 4 Dark Belly	*podicipinus*
Igarapé Belém		
Large Size, Flecked Belly*	Region 7 Large Size Mid-Andes	*wagneri*
Moderate Size, Light Posterior Belly	Region 4 Light Posterior Belly	*leptodactyloides*
Moderate Size, Toe Disked	Toe Disked	*diedrus*
Small Size, Dark Belly	Region 4 Dark Belly	*podicipinus*
Iquiri		
Moderate Size, Light Belly	Region 4 Light Posterior Belly	*leptodactyloides*
Small Size, Dark Belly	Region 4 Anastomotic Belly	*petersii*
Lago Amanã		
Moderate Size, Light Belly	Region 4 Light Posterior Belly	*leptodactyloides*
Small Size, Anastomotic Belly	Region 4 Anastomotic Belly	*petersii*
Porto Velho		
Small Size, Dark Belly	Region 4 Dark Belly	*podicipinus*
Santa Cruz da Serra		
Moderate Size, Lightly Mottled Belly	Region 4 Light Posterior Belly	*leptodactyloides*
Small/Moderate Size, Anastomotic Belly	Region 4 Anastomotic Belly	*petersii*
Colombia		
Leticia		
Moderate Size, Light Posterior Belly	Region 4 Light Posterior Belly	*leptodactyloides*
Small Size, Speckled Belly	Region 4 Anastomotic Belly	*petersii*
Quebrada Tucuchira		
Moderate Size, Light Posterior Belly	Region 4 Light Posterior Belly	*leptodactyloides*
Small Size, Anastomotic Belly	Region 4 Anastomotic Belly	*petersii*

Single-taxon and sympatric species Population analyses OTU names	Taxa/Region analyses OTU Names	Final (species) assignment
Ecuador		
Limoncocha		
Moderate Size, Light Posterior Belly	Region 4 Light Posterior Belly	*leptodactyloides*
Santa Cecilia		
Large Size, Boldly Mottled Belly	Region 7 Large Size Mid-Andes	*wagneri*
Moderate Size, Light Posterior Belly	Region 7 Light Posterior Belly	*leptodactyloides*
Guyana		
Kartabo		
Moderate Size, Light Posterior Belly	Region 5 Moderate Size, Light Posterior Belly, Guianas	*leptodactyloides*
Small Size, Light Posterior Lip Stripe	Region 5 Small Size Guianas	*pallidirostris*
Peru		
Cuzco Amazonico		
Moderate Size, Light Posterior Belly	Region 4 Light Posterior Belly	*leptodactyloides*
Small Size, Dark Belly	Region 4 Anastomotic Belly	*petersii*
Divisoria		
Moderate Size, Light Posterior Belly	Region 7 Light Posterior Belly	*leptodactyloides*
Moderate/Large Size, Mottled Thigh	Region 7 Moderate Size Andes	*griseigularis*
Estirón		
Large Size, Mottled Thigh*	Region 7 Large Size Mid-Andes	*wagneri*
Moderate Size, Light Posterior Belly	Region 4 Light Posterior Belly	*leptodactyloides*
Small Size, Anastomotic Belly	Region 4 Anastomotic Belly	*petersii*
Small/Moderate Size, Toe Disked	Toe Disked	*diedrus*
Tambopata		
Moderate Size, Light Posterior Belly	Region 4 Light Posterior Belly	*leptodactyloides*
Small Size, Dark Belly	Region 4 Anastomotic Belly	*petersii*
Surinam		
Amotopo		
Juvenile, Small Toe Disked	Region 5 Small Size Guianas	*pallidirostris*
Small Size, Anastomotic Belly	Region 5 Anastomotic Belly	*petersii*
Langaman Kondre		
Small Size, Light Posterior Lip Stripe	Region 5 Small Size Guianas	*pallidirostris*
Loëkreek		
Moderate Size, Light Belly	Region 5 Moderate Size, Light Posterior Belly, Guianas	*leptodactyloides*
Small Size, Anastomotic Belly	Region 5 Anastomotic Belly	*petersii*
Paloemeu		
Moderate Size, Light Belly	Region 5 Moderate Size, Light Posterior Belly, Guianas	*leptodactyloides*
Small Size, Anastomotic Belly	Region 5 Anastomotic Belly	*petersii*

Part B: Regional Analyses OTU Assignments

Region	Final (species) assignment
Region 1—South	
Small Size, Dark Belly	*podicipinus*
Region 2—East Coast Brazil	
Small–Moderate Size	*natalensis*
Region 3—Interior Brazil	
Dark Belly	*podicipinus*
Light Belly	*petersii*
Southern and Eastern (included in Dark Belly)	*podicipinus*
Region 4—Amazonia	
Anastomotic Belly	*petersii*
Dark Belly	*podicipinus*
Light Posterior Belly	*leptodactyloides*

Region	Final (species) assignment
Region 5—Guiana Shield	
Anastomotic Belly	*petersii*
Aragua (included in Venezuela Andes)	Venezuela Andes OTU
Lake Maracaibo	Lake Maracaibo OTU
Medium Size Bolívar	*sabanensis*
Moderate Size, Light Posterior Belly, Guianas	*leptodactyloides*
Small Size Bolívar (included in Small Size Guianas)	*pallidirostris*
Small Size Guianas	*pallidirostris*
Venezuela Andes	Venezuela Andes OTU
Region 6—Trinidad, Tobago, Lesser Antilles	
Bequia (included in Small–Moderate Size Island)	*validus*
Grenada (included in Small–Moderate Size Island)	*validus*
St. Vincent (included in Small–Moderate Size Island)	*validus*
Small Size Trinidad	*nesiotus*
Small–Moderate Size Island	*validus*
Small–Moderate Size Trinidad (included in Small–Moderate Size Island)	*validus*
Tobago (included in Small–Moderate Size Island)	*validus*
Region 7—Andean Slopes	
Anastomotic Belly	*petersii*
Atrato Drainage (included in Colombia Andes)	*colombiensis*
Cauca Drainage (included in Colombia Andes)	*colombiensis*
Colombia Andes	*colombiensis*
Colombia Andes Amazonian Drainage (included in Colombia Andes)	*colombiensis*
Dark Belly	*podicipinus*
Large Size Central Peru	*pascoensis*
Large Size Mid-Andes	*wagneri*
Light Posterior Belly	*leptodactyloides*
Magdalena Drainage (included in Colombian Andes)	*colombiensis*
Maracaibo Drainage	Maracaibo Drainage OTU
Moderate Size Andes	*griseigularis*
Moderate Size Bolivia (included in Moderate Size Andes)	*griseigularis*
Moderate Size Central Peru (included in Moderate Size Andes)	*griseigularis*
Moderate/Large Size South-Central Peru (included in Moderate Size Andes)	*griseigularis*
Inter-Regional Synthesis	
Anastomotic Belly	*petersii*
Colombian Andes	*colombiensis*
Dark Belly	*podicipinus*
Lake Maracaibo	Lake Maracaibo OTU
Light Posterior Belly	*leptodactyloides*
Maracaibo Drainage	Maracaibo Drainage OTU
Region 1 Dark Belly (included in Dark Belly)	*podicipinus*
Region 3 Dark Belly (included in Dark Belly)	*podicipinus*
Region 3 Light Belly (included in Anastomotic Belly)	*petersii*
Region 4 Anastomotic Belly (included in Anastomotic Belly)	*petersii*
Region 4 Dark Belly (included in Dark Belly)	*podicipinus*
Region 4 Light Posterior Belly (included in Light Posterior Belly)	*leptodactyloides*
Region 5 Anastomotic Belly (included in Anastomotic Belly)	*petersii*
Region 5 Light Posterior Belly (included in Light Posterior Belly)	*leptodactyloides*
Region 5 Moderate Size, Light Posterior Belly, Guianas (included in Light Posterior Belly)	*leptodactyloides*
Region 7 Anastomotic Belly (included in Anastomotic Belly)	*petersii*
Region 7 Dark Belly (included in Dark Belly)	*podicipinus*
Region 7 Light Posterior Belly (included in Light Posterior Belly)	*leptodactyloides*
Venezuela Andes	Venezuela Andes OTU

* These population samples from Region 4 were deferred for study with the Region 7 analysis (see text for further explanation).

Appendix 2

Specimens Examined and Locality Data

Museum collection codes follow Leviton et al. (1985) with the following additions: AJCardoso = Adão J. Cardoso field numbers; AL-MN = Adolfo Lutz collection maintained as a discrete collection at the Museu Nacional, Rio de Janeiro; Ergueta = Patricia Ergueta field numbers; IND-AN = INDERENA, Ministerio de Agricultura, Bogotá; MHNSM = Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (not MHNJP as in Leviton et al., 1985); ULABG = Universidad de Los Andes, Laboratorio de Biogeografia, Mérida.

Locality names and determinations for the distribution map point localities were derived as follows. Locality names originally came from museum specimen invoices and generally have been modified only if there was reason to do so. The goal has been to correct errors (but to be confident they really are errors), to have the locality data as precise and correct as possible, and to keep the data as close to the original data in museum catalogs as possible. If elevations and distances were recorded in the English system in the catalogs (and invoices) they have not been converted to the metric system. I have been building a *Leptodactylus* locality file since the beginning of my studies on the genus, which has been used for this study as well. Early on, I translated words that modified the locality if they were in any language other than English (such as "boca del Rio X" to "mouth of River X"); generally, I no longer do such translations, as my translation may subtly change the meaning intended originally. Diacritical marks are essential, as several place names differ only by such marks. I have attempted to include diacritical marks accurately. Latitude and longitude data were used as an aid to determine point localities on maps. The coordinate data came from the following sources: invoice data; gazetteers; maps with the place names identified; written queries to museum curators; and, as likely as not, P.E. Vanzolini's locality card file of some 10,000 South American herpetological localities. Prior to this study my working locality file was a manual operation on sheets of paper. At the beginning of this study, the file was converted to an electronic database, which includes a remarks field for the locality. The remarks are essential. For example, there may be several Santo Antonio's from Amazonia. Which Santo Antonio is the collection site for specimens at hand may be known for specimens in some museum collections and not for others. My computerized file was checked against P.E. Vanzolini's card file through several iterations.

The coordinates for the localities have not been included in this appendix for the following reasons. In earlier studies, I used coordinates to produce computer generated maps (e.g., Heyer, 1978, 1979). I find that I learn much more about distributions by hand plotting each locality and would encourage others to do the same. Many times coordinates imply a level of precision that the original locality data lack. For example, if the data state "40 km NE Manaus," in order to use a computer mapping program, one has to determine the coordinates from a map and feed those coordinates into a computer. However, usually one does not know whether the collector determined the distance by asking local residents how far it was from Manaus, by guessing how far she or he had travelled by rivers and in which direction from Manaus, or by looking at a map afterward and giving a straight-line map distance for the 40 km figure. Usually for the scale involved, there is not a problem; however, if someone else were to later use those coordinate data to plot the fine-scale distribution of the biota within a 50 km radius of Manaus, the guessed coordinate data could be wildly inaccurate at that scale. I prefer to use the coordinates for Manaus as the reference point in this example and place the locality on the map at the time I am doing the distribution map so that I know the accuracy of the locality data is appropriate for the scale of the map being used. I also have not included the coordinates and associated remarks for the localities herein, as P.E. Vanzolini is anticipating making his verified locality file available, of which mine is really a subset. In the interim, hard copies of my locality database will be provided upon request.

Unassignable to OTU (N = 1)

VENEZUELA. *Monagas:* Caripe, 5 km NW of, San Agustin, 1150 m, USNM 216805.

Lake Maracaibo OTU (N = 19)

COLOMBIA. *Norte de Santander:* Astillero, 55 m, USNM 147063 (questionable assignment).

VENEZUELA. *Mérida:* Caño Zancudo, km 14 rodovia, al sur del Lago (~9 km após Santa Elena), 850 m, AJCardoso 402. *Zulia:* El Tukuko (= Tucuco), cerca, Sierra de Perijá, > 1000 m, ULABG 2571-2575; El Tukuko (= Tucuco), 5 km SW, via Misión de San Miguel, Sierra de Perijá, 150 m, ULABG 1339; El Tukuko (= Tucuco), río a 34 km S de, por carretera, 260 m, ULABG 1369-1377 (questionable assignment); Santa Barbara de Zulia, bosques ao lado do Canal Birimbay, 50 m, AJCardoso 305, 306.

Maracaibo Drainage OTU (N = 24)

COLOMBIA. *Norte de Santander:* Chinácota, veredas Paramito y Alto Meguey, 1390–2270 m, ICNMNH 15141–15156; La Selva, ~1100 m, USNM 147064–147069; Pamplonita, KU 150748, 150749.

Venezuela Andes OTU (N = 64)

VENEZUELA. *State Unknown:* Maracaibo Drainage, Río Bonicito, UMMZ 100056. *Amazonas:* Río Pescado (= Sabana Grande), 100 m, ULABG 1413. *Aragua:* Cumboto, 70 m, UMMZ 113975 (2); Ocumare (de la Costa), near, 25 m, UMMZ 122373, 171832; Rancho Grande (now Parque Nacional Henri Pittier), near Maracay, 910–1170 m, AMNH 70687, KU 132808–132814, RMNH 23620; Coastal side of mountains on road between Rancho Grande and Ocumare-Turiamo, UMMZ 156930, 156931. *Barinas:* Quebrada de Las Palmas, MNRJ 4891. *Distrito Federal:* Caracas, 920 m, MZUSP 6398; El Junquito, 1900 m, MZUSP 8318–8324; El Limon (= Hacienda El Limon), 600 m, USNM 121146; El Limon, 5 km S, road to Colonia Tovar, 800 m, KU 132807; Río Cotiza, road from San José de Galipan, USNM 117526, 128837. *Falcón:* Carora, 84 km NW of, Cerro Socopó, 1260 m, USNM 216804; Cerro Cosme, MCZ 26144–26146, 59751–59753; Palma Sola, 5 km S, 25 m, UMMZ 55551. *Guárico:* Parque Nacional Guatopo, 250–1550 m, TCWC 60402. *Mérida:* Chama, Río, AMNH 10685–10688; Mérida, 1640 m, AMNH 3136, MCZ 2640, TCWC 58966, 58968, USNM 118176; Parque Yohama, Lagunillas, ULABG 2611, 2612; Río Albarregas, near Mérida, AMNH 10517–10519. *Miranda:* Altagracia de Orituco, 27 km N, 1700′, TCWC 60400; Los Canales, Planta Electrica de Narguita, USNM 128838; Petare, 850 m, USNM 121147. *Táchira:* La Fria Pueblo Nuevo, rt. fork Río Oropito, UMMZ 55552, 55553. *Trujillo:* Boconó, 3 km E, 1575 m, KU 132815–132820; La Loma, 4 km desde el puente de San Jacinto, ciudad de Trujillo, ULABG 1140.

Leptodactylus colombiensis (N = 274)

COLOMBIA. *Amazonas:* Araracuara (= Rápidos Araracuara), ICNMNH 18093. *Antioquia:* Cocorná, Vda. La Veta, 15 km S Medellin, 800 m, ICNMNH 15779; Envigado, ~1600 m, AMNH 39265, 39274, 39281; Medellin, near, 1500 m, AMNH 38785, 38808–38815, 39465; Parque Nacional Natural Las Orquideas, Urrao, IND-AN 2010, 2011; San Carlos, 1040 m, KU 150747; Urrao, 1875 m, ICNMNH 1252. *Boyacá:* Corocito, 6 km N, 1820 m, KU 169093; Muzo, 1240 m, FMNH 69744, MCZ 24920, USNM 147076; Pajarito, Corinto, 1600 m, ICNMNH 5150, 5151, 9558–9562, 9722–9729. *Casanare:* Agua Azul (= Aguazul), 860 m, ICNMNH 9563. *Cauca:* Popayán, 1760 m, FMNH 54377–54383, TCWC 24051, USNM 145781. *Cundinamarca:* Anapoima, Qda. Socotá, carretera a San Antonio, ICNMNH 18115, 18116; Anolaima, near Bogotá, ~1500 m, AMNH 13471, USNM 147054, 147055; Fusagasugá, 1750 m, AMNH 71581, USNM 153944; La Mesa, 1000–1300 m, USNM 144892, 144893; Medina, Colegio Deptal., 520 m, ICNMNH 14630–14635; Medina, Vda. Choapal, approx. km 7 NNE carretera Medina—Gachalá, 620 m, ICNMNH 14628; Páratebueno, Vda. Palomares, sitio Brisas del Llano, km 6 Páratebueno—Villanueva, ICNMNH 14649; Sasaima, Vda. Santa Ana, finca Sacaita, 1630 m, ICNMNH 3236; Sasaima, near, 1120 m, LACM 9284–9288; Tena, Laguna Pedro Palo, 2040 m, ICNMNH 18077–18079. *Huila:* Parque Nacional Natural Cueva de los Guacharos, Municipio Acevedo, IND-AN 3607, 3611, San Agustin, 1600 m, AMNH 88581, 88582; San Agustin, 3 km S, Parque Arqueologica, 1750 m, KU 169095. *Meta:* Acacías, 500 m, ICNMNH 14119–14125, 14127; Boca del Caño La Cabra, UTA 3564; 92 km from Bogotá, road to Villavicencio, 900 m, KU 132822; Buenavista, 1100 m, MVZ 63067–63073, USNM 144867–144882; Finca El Borrego, ~20 km W Pajure, E Villavicencio, MCZ 96979; Finca Santa Terrasita, 15 km NE Villavicencio, ICNMNH 594, UTA 2729, 2731, 2738, 8043; Fuente de Oro, inspeccíon Puerto Limón, km 9 carretera Pto. Limón—Pto. Lleras, ICNMNH 18146, 18147; Granada, on Río Ariari, S of Villavicencio, ~200 m, USNM 151494; Hacienda La Guardia, 0.5 km NE Villavicencio, 450 m, UMMZ 132464 (4), 132465 (2); Hda. Santa Ana, km 9 carretera Villavicencio /cio Puerto López, ICNMNH 14629; La Macarena (Serranía de), ICNMNH 2451, 2952–2954, 2957; Menegua, E. Puerto López, ~200 m, USNM 147273, 147274; Parque Nacional Natural La Macarena, Canaña Bocas Caño Cabra, IND-AN 2384; Parque Nacional Natural La Macarena, Río Cafre, IND-AN 2512; Pozo Azul, between Villavicencio and Restrepo, MCZ 96980; Pozo Azul, km 7 carretera Villavicencio—Restrepo, ICNMNH 18082–18084, 18088, 18092; Puerto López, near, ~200 m, UTA 8041, 8042; Puerto López, Hda. Mozambique, 181 m, ICNMNH 1310–1314, 1322; Puerto López, Vda. Menegua, 250 m, ICNMNH 18159–18161; Vía a Puerto López, Hda. El Hachón (Sena), ICNMNH 18089; Restrepo, 500 m, ICNMNH 18158; San Martín, 46 km S, 22 km E, 1600′, MVZ 63076; Villavicencio, ~500 m, FMNH 30571, 81788, 81789, 81799, 81800, 174079, ICNMNH 2356, 2357, 18107, 18109, 18110, KU 110411, 110425, 110426, MCZ 16277, 96975–96978, MVZ 63074, 63075, 63738, 63739, UMMZ 74811, USNM 144848–144866, 146382–146384, 147056–147062, 158041; Villavicencio, 5 km SE, 480 m, KU 110412, 110413, 150750. *Santander:* Charalá, Cañaverales, 1400 m, ICNMNH 10516–10518; Charalá, vereda El Rejos, 1740 m, ICNMNH 4493–4495; Charalá, Virolín, 1700 m, ICNMNH 6161–6164, 6166, 11275; Charalá, Virolín, approx. Río a Guillermo, 2600 m, ICNMNH 7407–7510, USNM 313876, 313877; Charalá, Virolín, carretera a El Olival, ICNMNH 8526; El Socorro, Vda. San Lorenzo, Hda. La Esmeralda, 950 m, ICNMNH 1275, 1425; Lagos del Cacique, 4.7 km SE

Bucaramanga, USNM 146250; Lebrija, 1080 m, USNM 144883–144888; San Gil, ICNMNH 3557, 3560, UMMZ 74799. *Tolima:* Icononzo, 50 km E, Qda. Laja, 1130–1180 m, ICNMNH 18081; Mariquita, 530 m, AMNH 84868; Quindio Mts., MCZ 8217. *Valle:* Cali, near, 950 m, USNM 148800–148823; Ingenio El Saman, Pradera, CAS-SU 21865; Río Ponce (= Pance), E slope Farallones de Cali, 1670 m, KU 169096–169098.

Leptodactylus diedrus (N = 127)

BRAZIL. *Amazonas:* Igarapé Belém, Rio Solimões, AMNH 97059, 97062–97065, 97068, 97070, 97072–97076, MZUSP 24904, 24922; Rio Enuixi (= Uneuixi or Inuixi), afl. Tea, MZUSP 39540.

COLOMBIA. *Amazonas:* La Chorrera, 50 km N, ICNMNH 4804; Puerto Rastrojo, Río Mirití-Paraná, IND-AN 3535. *Vaupés:* Timbó, IND-AN 3410, UTA 3723, 3726, 3727, 3886, 3887, 4474, 8592; Wacará, UTA 3720, 4473, 8361, 8591, 8594; Yapima, near, UTA 4296–4298, 4378, 4910–4915, 8593.

PERU. *Loreto:* Estirón, Río Ampiyacu, AMNH 115673, 115675–115682, 115685, 115687, 115689, 115690, 115692, 115695, 115701, 115702, 115705, 115706, 115708, 115717–115719, 115721–115728, MZUSP 24002, 24005, 24007, 24008, 24781, 24787–24790, 24794, 24795, 24799, 24801, 24806, 24808, 24809, 24811, 24813, 24815, 24817, 24819, 24821, 24823, 24824, 24826, 24828–24830, 24837, 24845, 24848, 24850, 24853, 24855–24865, 24867, 24868, 24870–24874; Iquitos, 100 m, FMNH 45399; Mishana on Río Nanay (3 km airline SSW Mishana), 150 m, AMNH 102993.

VENEZUELA. *Amazonas:* Cerro Neblina (= Cerro de la Neblina), USNM 307105, 307106.

Leptodactylus griseigularis (N = 306)

BOLIVIA. *La Paz:* Caranavi, 600 m, KU 183030, MCZ 97075–97092, 97094–97103, 97105–97121, 97123–97126, 97128–97136, 97138–97153, 97155–97173, 97175, 97177, 97179–97193, 97195–97204, 97206–97216, 97218–97220; Caranavi, 15.7 km S, 900 m, KU 183029; Huachi (= San Miguel de Huachi), UMMZ 64103 (3), 64104; Ixiamas, UMMZ 74816 (2); Puerto Linares, near, USNM 281176–281187.

PERU. *Ayacucho:* Ayna, Provincia La Mar, FMNH 39726; Candalosa, Provincia La Mar, FMNH 39727–39732, 39734–39744; Sivia on Apurimac River, Provincia La Mar, FMNH 39725, 39746. *Huanuco:* Aucayacu, 600 m, USNM 196018, 306381–306383; Ganzo Azul (= Ganso Azul), FMNH 45144; La Divisoria, AMNH 86498–86500, FMNH 56314–56317, 56319; Tingo María, 650–770 m, AMNH 91926, 109340, MVZ 123096, USNM 196012, 196013, 196016, 196019–196025, 306347–306359, USNM 306376–306380, 306384–306390; Tingo María, 30 km NE (air), Cordillera Azul, 1330 m, AMNH 91921–91925. *Junin:* Chancharia, on Río Perene, 2.5 hrs by motor boat below Pampa Silva and approx. 0.5 miles above the entrance of Río Ipoki, ~700 m, USNM 196017; La Merced, ~800 m, RMNH 23866; Palmapata, FMNH 36827–36830; San Luis de Shuaro, near, 780 m, KU 181286, 181287; San Ramon, 800 m, KU 135507; Satipo (= San Francisco de Satipo), 630 m, MCZ 24424–24428, UMMZ 89476 (6); Tarma, valley of Vitoc River, 1200–1400 m, FMNH 36817–36826. *Pasco:* Cacazú, 900 m, USNM 306765; Oxapampa and environs, 1825–2120 m, USNM 306766–306776. *San Martín:* La Morada, USNM 196014, 306360–306372; Tocache Nuevo, Río Huallaga, ~500 m, AMNH 42627, USNM 196015, 306373–306375. *Ucayali:* Iparía, MCZ 75021, 75024; Yarinacocha, 100–170 m, RMNH 23853–23863, 23872, 23873.

Leptodactylus leptodactyloides (N = 1384)

BOLIVIA. *Beni:* Alejandria, Río Mamoré, AMNH 79116–79119, 79121, 79122; Beni Reserve, Río Cureraba, Provincia Yacuma, US Field 173805, 173806, 173810–173812, 173815, 173817, 173821, 173822, 173829–173833 (to Bolivia), USNM 283260, 283261, 283265–283271, 306605–306616; Upper Beni below mouth of Río Mapiri (also Cousata), UMMZ 64098 (8); Carasco, Río Itenez (Guaporé), AMNH 79142–79151, 79165; Opposite Costa Marques (Brazil), AMNH 84794; Espiritu, Provincia Ballivián, Ergueta 1145–1147, USNM 306647, 306648; Puerto Almacen (= Mayor Pedro Vaca Diez), 260 m, AMNH 72251, 72254, 72398–72402, 92599; Reyes, 230 m, UMMZ 201343; Confluence of Río Blanco and Río Itenez (Guaporé), AMNH 79100, 79101; Río Grande, 5 km NW boca, Río Mamoré, AMNH 79104, 79124–79131; Río Ibarre (Ibare), boca del, Río Mamoré, AMNH 79098; Río Itenez (Guaporé), between Puerto Capitan Vasquez and Santa Fe, AMNH 79138–79141; Río Mamoré at 13°35′S, AMNH 79110; Río Mamoré, 10 km E San Antonio, AMNH 79097, 79106, 79107; Río Mamoré, 10 km S Camiaco, AMNH 79105; Río Mamoré, 15 km SE Puerto Julio, AMNH 79102, 79103; Río Mamoré, ~8 km N Exaltación, AMNH 79111–79113; Río Mamoré, near Santa Cruz, AMNH 79099, 79114, 79115, 79177; Río Quiquibey, USNM 280989; Santa Rosa, Río Mamoré, AMNH 72403–72413, 128449–128464, 128466–128468; Trinidad, 235 m, AMNH 79108, 79109; Tumi Chucua, 170 m, USNM 280221–280226. *Cochabamba:* Puerto Chipiriri, 300 m, AMNH 72242, 72243. *Santa Cruz:* Buenavista (= Buena Vista), 400 m, AMNH 34003, 34005, 34007, 34009, 34011, 34013–34015, 34017–34019, 34073, UMMZ 63833 (40), 63834 (19), 63835 (14), 64028, 64029, 64030 (2), 64037 (5), 64038 (2), 64039 (9), 66613, 66614 (7), 66615 (2), 66616 (4), 66617 (4), 66618 (8), 66619 (3), 66620, 66621, 66622 (4), 66623 (22), USNM 118687, 118688, 146523, 146524; Cotoca, near, 1233′, USNM 142110–142120; 5 km N Boca Río Chaparé, AMNH 79132, 79133; Río Ichilo, 54 km S Boca Río Chaparé, AMNH

79134–79137; Tunas, 335 m, MCZ 30136.

BRAZIL. *Acre:* Cruzeiro do Sul (Igarapé Formoso), ZUEC 8481; Iquiri, MZUSP 6512–6515, 6613; Plácido de Castro, MZUSP 6533–6546; Porto Walter, MZUSP 51622, 51623; Rio Branco, ZUEC 5639. *Amazonas:* UHE Balbina, Rio Uatumã, INPA 200, 201, 203; Benjamin Constant, MNRJ 2976; Beruri, MZUSP 50531–50536, 50538–50542, USNM 202529–202537; Boca do Acre, USNM 202519; Boca do Auati-paraná, MZUSP 40539; Boca do Pauini, USNM 202522, 202523; Canutama, MZUSP 50502; Codajáz, MCZ 90819–90821, MZUSP 39643–39645, 42192; Costa do Batalha, prox. Rio Juruá, MCZ 90831, 90832, MZUSP 39926, 39927; Ilha próx. Costa do Tarará, entre Fonteboa e Auati-paraná, MCZ 90839–90861, MZUSP 40432–40455; Fonteboa, Alto Solimões, MCZ 90834–90838, MZUSP 40058–40062; Fortaleza, médio Purus, MZUSP 4470, 4472, 4477, 4494, INPA-WWF-SI Reserves, N of Manaus, MZUSP 69048, 69049; Igarapé Belém, Rio Solimões, AMNH 97060, 97066, 97067, 97069, 97071, MZUSP 24898, 24900, 24905–24908, 24911, 24913, 24916–24921, 24923, 24924, 24926–24930, 24932–24935; Ilha da Marchantaria, entrada Lago dos Reis (= Rei), prox. Manaus, INPA 773, 775; Lago Aiapuá, MZUSP 53756; Lago Amanã, MZUSP 58546, 58547, 59502, 59503, 59506, 59509–59511; Manaus, MZUSP 4483–4489; Mucuripe, USNM 202526; Pauini, USNM 202524, 202525; Tefé, MZUSP 39920. *Pará:* Cachoeira do Espelho, Rio Xingú, MZUSP 63357–63360, 63362–63372, 63403, 63405, 63421–63423, 63425, 69050–69064, USNM 303448–303463, 303521; Juruá, Rio Xingú, MZUSP 64260–64267; Largo do Souza, Rio Iriri, MZUSP 63386–63391, 63432–63447, USNM 303500–303508; Tucuruí, 50 km S, MZUSP 60304. *Rondônia:* Forte Príncipe da Beira (= Príncipe da Beira), MZUSP 25162–25168; Foz do Jamari, MZUSP 51478, USNM 202542, 202543; San Antonio de Guaporé, along Rio Guaporé, USNM 115973; Santa Cruz da Serra, MZUSP 61564–61581, USNM 303994, 303995.

COLOMBIA. *Amazonas:* Isla Santa Sofia II, 2 mi NE, on Colombian mainland, MVZ 172046; Isla Santa Sofia II, 20 km NW Leticia, MCZ 85772, 85773, 85779, 85783–85791, 85793–85796, 85798–85804, 85806, 90823, MVZ 172043–172045, 172097–172100, MZUSP 39165; Leticia, ~100 m, ICNMNH 18097, 18098, KU 124748–124758, USNM 142179–142194, 146252, 147031; Parque Nacional Natural Amacayacú, IND-AN 2085, 2086, 2089, 2092, 2202, 2203, 3885, 3886, 3889, 3890; Puerto Nariño, ICNMNH 11285, KU 153309–153311; Puerto Nariño, 50 km NW, MCZ 96859; Quebrada Tucuchirá, 20 mi NW Leticia, IND-AN 3411–3413, 3415–3418, 3422, MVZ 172077–172083, 172086–172094, 172101. *Vaupés:* Bocas del Ariari, ICNMNH 587, UTA 3563, 4471, 4472; Río Ariari and Río Guaviare, UTA 3718, 8044–8046; Timbó, UTA 3885.

ECUADOR. *Morona-Santiago:* Ashuara Village on Río Macuma, 300 m, AMNH 94710–94719; Cusuime, 320 m, AMNH 93731, 93733, 93737, 93738, 93740–93746, 93748–93769, 93771–93775, 93777, 93779, 93781, 93782, 93784–93788, 93793–93795, 93797, 93798. *Napo:* Coca, MCZ 106040–106042; Lagarto Cocha (= Río Lagartococha), ~300 m, USNM 196819; Limoncocha, 300 m, KU 99107–99114, 178254–178257, 183526, LACM 92132–92183, 92185–92230, 92232–92337, 92339–92347, 92349–92365, 92367–92412, MCZ 56322–56327, USNM 313544–313548 (larvae); Santa Cecilia, 340 m, KU 104645, 104655, 104660, 104662, 104669, 104678, 104680, 104696, 104699, 104702, 109144, MCZ 56385, 56386, 56389, 56409, 56419, 56426–56428, 56430, 56432; Zancudo, FMNH 218490. *Pastaza:* Montalvo, 250 m, RMNH 23982–23989, 23991–24004, 24009–24012, USNM 196820.

FRENCH GUIANA. Ipoucin Crique, trib. Fleuve Approuague, 27 m, LACM 44628; Lac des Américains, Mont Grand Matoury, SW Cayenne, 15 m, RMNH 23874.

GUYANA. *Mazaruni-Potaro:* Kartabo (= Kartabu Point), 100 m, AMNH 39625.

PERU. *Amazonas:* Galilea, Río Santiago, 180 m, MVZ 173877–173882; La Poza, 180 m, MVZ 173829–173836, 173838–173864, 173868–173870, 173872–173875, 173884, 173887–173898, 173900–173903, 173907–173921, 173923–173925. *Huanuco:* La Divisoria, FMNH 56320; Monte Alegre, Río Pachitea, AMNH 43013; Panguana, KU 154887–154895, 171902, RMNH 23865. *Loreto:* Centro Union, TCWC 41690–41694, 41696; Estación Biologica Pithecia, Río Samiria, KU 191997–191999; Estirón, Río Ampiyacu, AMNH 115674, 115683, 115684, 115686, 115694, 115696–115700, 115703, 115704, 115707, 115709–115716, 115720, CAS 93320, MZUSP 24791, 24798, 24800, 24805, 24820, 24822, 24827, 24846, 24849; Iquitos, 100 m, TCWC 52501; 50 river mi NE Iquitos, 0.5 miles N Explorama Lodge, 0.1 mile E Río Yanacano, 0.7 mile N Río Amazonas, ~100 m, USNM 234007; Isla Pasto, ~80 km NE Iquitos, Río Amazonas opposite Ayana, 80 m, KU 206115–206117; Marañon, mouth of Pastaza, AMNH 42221–42227, 42229–42235; Pampa Hermosa, AMNH 42142–42144, 42661; Pebas, 100 m, CAS-SU 6344; Río Amazonas, S bank, SE Isla Nazaria, ~83 km NE Iquitos, 80 m, KU 206118; Mouth of Río Contaya (Río Alto Tapiche), AMNH 42988; Río Pastaza, above mouth, AMNH 42713, 42714, 43059; Middle Río Utoquinia, AMNH 42779; Upper Río Utoquinia, AMNH 42599; Roaboya, ~100 m, AMNH 42823, 42824; "San Antonia" above mouth of Río Pastaza, AMNH 43060–43062; Tibi Playa (above mouth of Río Ucayali), AMNH 42783; Yanamona, TCWC 41486. *Madre de Dios:* Aguas Calientes, Río Alto Madre de Dios, 1 km downstream from Shintuya, FMNH 228255; Cocha Cashu, Río Manú between Río Panagua and Río Cachiri, ~400 m, MNHSM 9088, USNM 247784, 321214–321221; Cuzco Amazonico, ~15 km E Puerto Maldonado, 200 m, KU 194912, 205043–205048, 205050, 205051, 205057–205059, 205222–205232, 207747, 207748, 209187, MVZ 197092, 197093; Lago Valencia, extreme W bank, house of Alfred Gompinjer, MVZ 197094, 197095; Manu, 360 m, FMNH 141056; Pakitza,

USNM 307138; Tambopata, BMNH 1987.566–567, 1987.620–622, USF 153207 (larvae), 153213 (larvae), 153364 (larvae), USNM 222294, 222295, 222297, 222298, 222302, 222303, 247372–247386, 247389–247406, 247408, 247409, 247411, 247654–247657, 268980–268986, 307123–307137. *Ucayali:* Balta, Río Curanja, 300 m, KU 196570–196577; Colonia Callaría, Río Callaría, 15 km from Ucayali, 154 m, CAS 93138, 93194, 93195; Igarapé Champuia, Alto Curanja, MZUSP 10341, 10342; Iparía, MCZ 75022, 75023; Pucallpa, 150 m, FMNH 56322, TCWC 24070; Pucallpa, 20–40 km SE, 300–500′, TCWC 24071; Río Suhayo, AMNH 42321.

SURINAM. *Marowijne:* Loëkreek Kamp, Hofwijks, 120 m, RMNH 23898; Paloemeu, RMNH 24013, 24014. *Nickerie:* Kabalebo Rivier, RMNH 23877–23879, 23893, 23894, 23899.

VENEZUELA. *Bolívar:* Río Cuyuní, 69 km SE, on road to Santa Elena, ~700′, MVZ 176010, 176011.

Leptodactylus natalensis (N = 211)

BRAZIL. *Alagoas:* Manimbu, MZUSP 11982, 11983; Murici, MNRJ 9718, 9743; Rio Largo, Fazenda Canoas, MZUSP 9279; São Miguel dos Campos, MNRJ 9591, MZUSP 9250. *Bahia:* CEPLAC, 5 km W Itabuna, 50 m, MNRJ 4971–4980, 4982–4987, RMNH 23608–23610; Cumuruxatiba (Fazenda Imbaçuaba), MZUSP 59442–59445; Estrada Alcobaça—Prado, MNRJ 4989; Fazenda Luzitania, near Itajuipe, RMNH 23612–23614; Fazenda Santa Barbara, near Itacara, RMNH 23611; Salvador, MZUSP 9131, 9550, 9551. *Espírito Santo:* Linhares, MNRJ 4913–4917. *Paraíba:* João Pessoa, MZUSP 59410, 63102–63114; Mamanguape, MZUSP 62975. *Pernambuco:* Igarassú, MNRJ 2365; Serra dos Cavalos, MZUSP 63169–63172. *Rio Grande do Norte:* Natal, Areia Preta, AL-MN 1610–1614 (Paralectotypes), AMNH 36261, MCZ 15847, UMMZ 68791, USNM 81130 (lectotype). *Rio de Janeiro:* BR 040, km 31, MZUSP 12034, 12035; BR 040, km 36, AL-MN 3744–3747, MZUSP 124; Barro Branco, MNRJ 1658; Covanca, Serra da Piedade (= Represa da Covanca), MNRJ 4869, 4870; Duque de Caxias, MNRJ 1808, 2325, 9820–9823, 9825; Estrela (= "Estrella"), mun. de Magé, AL-MN 1882, 1883, MNRJ 4871; Itaguaí, MNRJ 4908, 4929; Represa da Covanca, near Jacarepaguá, AL-MN 1876–1881; Rio Baby (= Babi), Baixada Fluminense, AL-MN 2684; São Vicente de Paulo, Araruama, Lagoa Juturnaíba, MNRJ 4118, 4139, 9827–9831, 9842, 9843; Sernambetiba, Recreio dos Bandeirantes, AL-MN 2721, 2821–2823; Tijuca, AL-MN 3684. *Sergipe:* Areia Branca, MZUSP 37838–37892, 37894–37918; Santo Amaro das Brotas (Usina Limoeiro), MZUSP 56733–56753, USNM 209621–209625.

Leptodactylus nesiotus (N = 3)

TRINIDAD. Icacos (Point), BMNH 1992.147–148, USNM 306179.

Leptodactylus pallidirostris (N = 468)

BRAZIL. *Roraima:* Marco de fronteira BV 8, INPA 1302, 1304; Boa Vista, MZUSP 66050–66052, 66054–66057; Colonia Apiaú, MZUSP 66312, 66315, 66316, USNM 302207; Igarapé Cocal, USNM 302408, 302409; Ilha de Maracá, MZUSP 65574, 65589.

FRENCH GUIANA. Cayenne, LACM 44629–44631; Cayenne, between, and Tonate, CAS 146926, 146927; Iracoubo, near, sea level, TCWC 65573, 65575, 65577–65579; Kaw (= Caux), ~100 m, MCZ 99132; Mana, 11.2 km E, TCWC 65569–65571; Monte Cabassou, near Cayenne, LACM 44632, 44633; Rémire, USNM 291358; Sophie, MCZ 44564.

GUYANA. *District Unknown:* No specific locality, AMNH 13551; Anowine Cr., Essequibo River, UMMZ 79475; Mocho Mocho, USNM 146366, 146367; Santa Rosa Island, Moruco River, UMMZ 55833 (2). *East Demerara-West Coast Berbice:* Atkinson, McKensie Trail, USNM 162872–162879; Enmore Estate, sea level, USNM 162966, 162967; Georgetown, sea level, FMNH 172021–172026, 172028–172030, UMMZ 80497; Wismar, ~100 m, AMNH 45750, UMMZ 77517, 80417 (2). *Mazaruni-Potaro:* Kartabo (= Kartabu Point), 100 m, AMNH 10377, 10379–10383, 11656, 11657, 11659, 11661, 11662, 11672, 11673, 11675, 11683, 11687, 11688, 11717, 13518–13523, 39628, 39629, 39632, 39634, 39657, 39660, 39663, 39669, 39670, 39676, 39705, 70882–70901, 128531–128544, USNM 118059–118062. *Rupununi:* Isheartun, AMNH 53435–53437; Kuyuwini Landing, AMNH 49352, 92629; Lethem, 107 m, MCZ 50708. *West Demerara-Essequibo Coast:* Demerara River, Camueni (= Kamuni) Creek, AMNH 34050; Dunoon, Demerara River, CAS 54768–54772, UMMZ 50180, 50181 (2), 50182–50207, 50209, 50210, 50212–50214, 50216–50227; Oko Mountains, FMNH 26691.

SURINAM. *District Unknown:* No specific locality, RMNH 16729; Coronie Road, RMNH 23644, 23677–23679, 23691–23695. *Commewijne:* Meerzorg, near, RMNH 23615; Nieuw Grond (Plantation), MCZ 99130. *Coronie:* Wayambo River, RMNH 23646. *Marowijne:* Albina-Paramaribo Road, 100 km E Paramaribo, MCZ 97281; Djaikreek (= Djai Creek), RMNH 23680, 23681; Galibi Nature Reserve, sea level, MCZ 89590; Langaman Kondre, MZUSP 24001, 24696–24756; Moengo Tapoe (= Mongotapoe), sea level, RMNH 15090 (3), 23671, 23672, 23850; Moengo, 9 km W, RMNH 23901; Wia Wia, RMNH 23683–23690. *Nickerie:* 3rd Camp, RMNH 23676, 23682; Amatopo, near (near Wonotobo), 100 m, RMNH 23839; Apoera, near, RMNH 18625; Arrawarra (= Arawarra kreek), MCZ 92372, RMNH 23664, 23665; Blanche-Marie-vallen, Nickerie River, RMNH 23645; Kaiserberg Airstrip (= Kayser Gebergte Airstrip), Zuid River, 278 m, FMNH 128925, 128928, 128936, 128940, RMNH 16754, 16756 (2); Matapi, Corantijn Rivier, RMNH 16759, 23650, USNM 220068; Moko Moko Creek (now Paris Jacob Creek), Marowijne River, RMNH 23675; Sipaliwini,

~360 m, RMNH 23700; Zwampenkamp (Swamp-camp), near 3rd camp, RMNH 23674; Tapoeripa, near, Nickerie River, MCZ 92370, 92371; Utrecht, MCZ 92367–92369; Wageningen, RMNH 23647, 23887; Wakay of Matapi, RMNH 23648; Wakay, Corintijn River, RMNH 23649, 23651–23663. *Para:* Hoek Meursweg, Paramaribo—Zanderij road, km 7.2, RMNH 23666; Paramaribo, 36 km S, on Paramaribo—Zanderij road, RMNH 23903; Santigron, near, RMNH 23668–23670. *Para/Saramacca:* Garnizoenpad, W Paramaribo, RMNH 23632–23640. *Paramaribo:* Paramaribo, sea level, RMNH 23667, 23696, 23697, 23900, 23904, 23905. *Saramacca:* Witagron (= Bitagron), 30 m, RMNH 23902. *Suriname:* 2e rijweg, RMNH 23698; Blakkawatra, between, and Java, MCZ 89667, 89703; Leonsberg, sea level, RMNH 23895, 23896; Tawajari (= Tawaiari Kreek), RMNH 23884.

VENEZUELA. *Amazonas:* Atabapo, Santa Barbara, 90 m, AMNH 100637–100647, RMNH 23616–23618, 23625–23628, 23980; Capibara, 106 km SW Esmeralda, Brazo Casiquiare, 130 m, AMNH 23166; Cerro Yapacana, base, AMNH 100636, 100648–100653, RMNH 23622–23624; Río Pescado (= Sabana Grande), 100 m, AMNH 23182 (invalidly designated neotype of *petersii*). *Apure:* Bruzual, ~10 km SW, TCWC 47488; Hato La Guanota, 4 km W San Fernando de Apure, TCWC 45261; Mantecal, Modulo Experimental Fernando Corrales, 100 m, AJCardoso 225–227. *Barinas:* Hato San Martin, approx. 30 km ENE Puerto de Nutrias, Distrito Sosa, ULABG 1694, 1695. *Bolívar:* El Manteco and immediate environs, ~300 m, RMNH 18396, 18397, 18399–18405; El Manteco, 23 km S, RMNH 18398; 28 km SE El Manteco, Los Patos, 350 m, USNM 216803; El Manteco, ~35 miles S, TCWC 60165; El Palmar, 28 km E, Río Grande, TCWC 60183, 60184; just below mouth of Río Horeda, 100 m, AMNH 62170–62174; floodplain of Río Orinoco, AMNH 62945–62949. *Delta Amacuro:* Barrancas, 140 km NE, LACM 31382–31397; Castillos de Guayana (= Los Castillos), 32 km W of San Felex, 50 m, RMNH 23619; Mission of San Francisco de los Guayos (= Misión de Guayo), sea level, RMNH 18406. *Guárico:* Corozo Pando, near, TCWC 47489, 47491. *Monagas:* Caripito, ~100 m, AMNH 70669–70686, USNM 117088, 117089. *Sucre:* Bohordal, 15 km S Río Caribe, RMNH 23629–23631; Guaraúnos, ~100 m, RMNH 23621.

Leptodactylus pascoensis (N = 7)

PERU. *Huanuco:* Serranía Sira, ~2500 m, KU 154896. *Pasco:* Chontilla, Iscozazin Valley, LACM 40660–40663, 40665, USNM 313875.

Leptodactylus petersii (N = 860)

BOLIVIA. *Beni:* Ivon, BMNH 1967.2087–2088, 1967.2090, 1967.2092; Lago Versalles, Río Itenez (Guaporé), AMNH 79152–79161, 128469–128502; Tumi Chucua, 170 m, USNM 280216, 280219. *Pando:* Cobija, USNM 281759; confronte Plácido de Castro (Brazil), MZUSP 6529–6531.

BRAZIL. *Acre:* No specific locality, BMNH 1970.2042; Cruzeiro do Sul (Igarapé Formoso), MZUSP 58288, ZUEC 4387, 8432; Igarapé do Nico, Rio Acre, MZUSP 50226; Iquiri, MZUSP 6581, 6614–6685, 6688, 6689; Porto Walter, MZUSP 51576, 51642. *Amazonas:* AM-010, km 12, MZUSP 60316–60324; AM-010, km 60, MZUSP 60331, 60332; Anavilhanas (Arquipélago), INPA 1215–1218; Auati-paraná, MZUSP 40644; UHE Balbina, Rio Uatumã, INPA 021, 023, 085, 151, 152, 192, 789, 790; Beruri, MZUSP 50529, 50530, 50537, USNM 202528, 202538–202541; Boca do Acre, MZUSP 56723–56725, USNM 202520, 202521; Boca do Pauini, MZUSP 50318–50321; Boca do Rio Preto da Eva, MZUSP 24886; Borba, CAS-SU 11848, MZUSP 51244–51248, USNM 202597–202599; Cantagalo, Rio Negro, MZUSP 37043; Costa da Altamira, Rio Japurá, MZUSP 50882, 51149–51155; Foz do Purus, MZUSP 24885; Igarapé Belém, Rio Solimões, MZUSP 24902, 24910, 24931; Igarapé Puruzinho, MZUSP 51337, 51500–51502, USNM 202550–202552; Igarapé Tucuxi, Auati-Paraná, MZUSP 28122, 28123, Ilha da Marchantaria, entrada Lago dos Reis (= Rei), prox. Manaus, INPA 771, 774, 776, 777; Ilha do Mojuí, Rio Japurá, MZUSP 51121, 51179–51182; INPA-WWF-SI Reserves, N of Manaus, MZUSP 57361–57363, 60078, 60105; Itapiranga, MZUSP 27759, 27766, 27768; Lago Aiapuá, MZUSP 53755; Lago Amanã, MZUSP 58099, 58100, 58521–58524, 58544, 58545, 59504, 59505, 59507, 59508, 59512, 59513; Lago Januari, MZUSP 53752; Lago Miuá, margem esquerda do Solimões, abre ~15 km acima de Codajás, MZUSP 42177–42179; Lago Miuá, prox. Codajás, MCZ 90826–90830; Lago Pantaleão, Rio Japurá, MZUSP 58132; Maguarizinho, Rio Japurá, MZUSP 51143; Manacapurú, USNM 103621, 103622; Manacapurú, 15 km N, 72 km W Manaus, RMNH 23838; Paraná Amanã, MZUSP 58129–58131; Restauração, MZUSP 51335; Seringal Americá, MZUSP 50417; Tapauá, Rio Purus, USNM 202527; Tapera, Rio Negro, MZUSP 37514. *Goiás:* Amaro Leite, MNRJ 2971, 9824. *Maranhão:* Aldeia Araçu, Igarapé Gurupi-Una, MZUSP 24956; Aldeia Jauaruhu (or Yavaruhu), Igarapé Gurupi-Una, MZUSP 25013; Aldeia do Ponto, MZUSP 21232; Carolina, MNRJ 433, MZUSP 21664, 21665. *Mato Grosso:* Aldeia dos Tapirapés, 30 leagues up Rio Tapirapé and 14 to the NW, CAS-SU 12774–12778, MNRJ 3142, 9832–9841; Chapada dos Guimarães, Salgadeira, 400 m, ANSP 11270 (holotype of *brevipes*); Mato Verde, Rio Araguaia, MZUSP 6588–6612. *Pará:* Alegre, 15 km NE Marapanim, MZUSP 24996; Alter do Chão, INPA 1292, MZUSP 59007; BR-10, km 93 (Anápolis-Belém), MZUSP 30518; Barreirinha, Rio Tapajós, near São Luis (Cachoeiras), MZUSP 35725; Belém, AMNH 113840, 113841, CAS-SU 11829, FMNH 83264, 83265, MCZ 36010, 36011, MNRJ 1451, 4887–4889, 4906, 4907, 8057, USNM 154067, 154068; Cachimbo, MZUSP

21656–21661; Cachoeira do Espelho, Rio Xingú, MZUSP 63356, 63361, 63404, 63406, 63424, 69065–69067, USNM 303442–303447; UHE Cachoeira Porteira, Rio Trombetas, INPA 050, 052, 081, 084, 097, 204, 205, 324, 424, 425, 448, 462–464, 467–469, 473, 630, 631, 636, 833, 834, 841–844; Curuá-Una, MZUSP 58438–58440, 58458; Ilha de Nova Olinda, Rio Tapajós, MZUSP 53992; IPEAN, KU 127409–127418, 128337, 128338; Monte Cristo, Rio Tapajós, MCZ 90824, 90825, MZUSP 38898, 38922, 38928, 39829; Parque Nacional da Amazônia, Rio Tapajós, USNM 288751–288754; Piratuba (= Igarapé Piratuba), AL-MN 2868, 2869; Reserva Biológica Rio Trombetas, MZUSP 69003–69044, USNM 306455–306495; Rio Mapuera, at equator, AMNH 46181; Reserva Florestal da Sudam, 74 km SE Santarém, KU 129953; Taboleiro Leonardo, Rio Trombetas, MZUSP 49668. *Rondônia:* Alto Paraíso, MZUSP 60395; Cachoeira de Nazaré, Rio Machado, MZUSP 63828; Calama, MZUSP 51392–51395, USNM 202547–202549; Nova Brasilia, MZUSP 60496, USNM 304113; Nova Colina, MZUSP 60454; Santa Barbara, MZUSP 62039–62042; Santa Cruz da Serra, MZUSP 61557–61563. *Roraima:* Alto Alegre, MZUSP 66033; Colonia Apiaú, MZUSP 65927, 66313, 66314; Ilha de Maracá, MZUSP 60627, 62430, 65588, 65590, 65749, 65750.

COLOMBIA. *Amazonas:* Isla Santa Sofia II, 20 km NW Leticia, MCZ 85770, 85771, 85774–85777, 85805, 90822, MVZ 172039, MZUSP 39163; Leticia, ~100 m, ICNMNH 18096, 18099, IND-AN 2866, KU 153304–153306; Puerto Nariño, KU 153307, 153308; Puerto Nariño, 50 km NW, MCZ 93781; Quebrada Tucuchirá, 20 mi NW Leticia, IND-AN 3414, 3420, MVZ 164232–164262, 172048, 172076; Río Caiwima, ~60 km NNE Puerto Nariño, MCZ 97004; headwaters Río Caiwima, ~70 km NNE Puerto Nariño, MCZ 97023, 97024, 97026–97032. *Meta:* Fuente de Oro, inspección Puerto Limón, km 9 carretera Pto. Limón—Pto. Lleras, ICNMNH 11473; Loma Linda (= Lomalinda), UTA 3714, 3715, 3880–3882, 4242, 4243, 4250, 4251, 4317, 4318, 7946, 8590. *Vaupés:* Río Ariari and Río Guaviare, UTA 8047.

FRENCH GUIANA. Cayenne, between, and Tonate, CAS 146925; Iracoubo, near, sea level, TCWC 65568, 65572, 65574, 65576; Kaw (= Caux), ~100 m, RMNH 23852; Régina, 25 m, LACM 44624–44627; Rémire—Cabassou road, SE Cayenne, RMNH 23890.

GUYANA. *District Unknown:* Marudi, AMNH 46238, 92620; upper Rupununi River, AMNH 43682, 46270, 46271, 46437, 128267–128289. *East Berbice-Corentyne:* Shudikar-wau (River), AMNH 46274, 80029–80037, 87889, 92621–92628, 128245–128266. *East Demerara-West Coast Berbice:* Enmore Estate, sea level, USNM 162950. *Mazaruni-Potaro:* Kartabo (= Kartabu Point), 100 m, AMNH 25233, 39630, 39631, 39633, 39697. *Rupununi:* Isheartun, AMNH 53438; Kuyuwini Landing, AMNH 46281, 49355, 92630–92633; N of Acarahy (= Acarai) Mts., W of New River, KU 69690; Parabam, AMNH 46425.

PERU. *Loreto:* Estirón, Río Ampiyacu, MZUSP 24003, 24004, 24854; 50 river mi NE Iquitos, 0.5 mi N Explorama Lodge, 0.1 mi E Río Yanacano, 0.7 mi N Río Amazonas, ~100 m, MCZ 85781; Mishana on Río Nanay (3 km airline SSW Mishana), 150 m, USNM 321224; Pebas, 100 m, AMNH 102996; Quebrada Órán, ~5 km N Río Amazonas, 85 km NE Iquitos, 110 m, KU 206112–206114; Quistococha, few miles outside Iquitos, UMMZ 182567; Río Napo, 1 km N, 157 km by river NNW Iquitos, 350 m, KU 206111; Río Yanayacu, ~20 miles downstream Iquitos, KU 157808; Sobral, Río Tamaya, AMNH 43238; Yagua Indian village, headwaters of Río Loretoyacu, 100+ km NW Leticia, AMNH 96353–96359. *Madre de Dios:* Cocha Cashu, Río Manú between Río Panagua and Río Cachiri, ~400 m, KU 154897–154899, MHMSM 9089, USNM 321222, 321223; Cuzco Amazonico, ~15 km E Puerto Maldonado, 200 m, KU 205195–205204, 209188, MVZ 199502; Río Manú, 70 km up from mouth, FMNH 228256; Tambopata, USF 153384 (larvae), USNM 222293, 222296, 222299–222301, 247371, 247387, 247388, 247407, 247410, 247412–247421, 268973–268979, 269067 (larvae), 307120–307122; (Lago) Sandoval, MVZ 173728, 173729. *Ucayali:* Colonia Callaría, Río Callaría, 15 km from Ucayali, 154 m, CAS 93189, 93199; Río Suhayo, AMNH 42325; Yarinacocha, 100–170 m, RMNH 23867–23871.

SURINAM. *Brokopondo:* Brownsweg, ~50 m, RMNH 23642, 23833–23835; Maikaboeka Kreek, NW Brownsweg, 20 m, RMNH 23844; Phedra, RMNH 23836, 23837. *Commewijne:* Mapanekreek (= Mapane Kreek), Camp 8, RMNH 15074. *Marowijne:* Albina, 3 km S, Parabam, RMNH 23840; Lely Mountains (= Lely Gebergte), 690 m, RMNH 23876, 23885, 23897; Loëkreek Kamp, Hofwijks, 120 m, RMNH 23888; Paloemeu, RMNH 23849; Wia Wia, RMNH 23851. *Nickerie:* 3rd Camp, RMNH 23673; Amatopo, near (near Wonotobo), 100 m; RMNH 23848, 23962, 23963; Avanavero a/d Kabalebo, RMNH 16760; Evakreek, 20 km N Lucie Rivier, 200 m, RMNH 23842, 23843, 23846, 23847, 23881, 23882; Kabalebo Rivier, RMNH 23889, 23891, 23892; Kaboeri Kreek (= Kapoeiri Kreek), RMNH 16758 (7), 16761; Kaiserberg Airstrip (= Kayser Gebergte Airstrip), Zuid River, 278 m, FMNH 128927, 128933–128935, 128937–128939, RMNH 16754 (5), 23643; Mozeskreek, 90 m, RMNH 23880; Sipaliwini, ~360 m, RMNH 15173, 15188, 16725 (3), 16748, 23641, 23699, 24015, 24016; Vreedzaamkreek, Lucie Rivier, 200 m, RMNH 23845, 23875, 23883, 23886. *Saramacca:* Raleighvallen-Voltzberg Nature Reserve, Voltzberg Camp, W bank Coppename River, 360 m, MCZ 92373.

VENEZUELA. *Amazonas:* Cerro Neblina (= Cerro de la Neblina), USNM 307107–307119. *Bolívar:* Las Claritas, 85 km S El Dorado, RMNH 23701.

Leptodactylus podicipinus (N = 1518)

ARGENTINA. *Chaco:* Barranqueras, MZUSP 24561–24566; General Vedia, Río de Oro, 60 m, BMNH 1963.649; Resistencia, 50 m, KU 84732–84734. *Corrientes:* Itatí, 30

km W, CAS 100504; Manantiales, 50 m, MCZ 35589, 35590. *Formosa:* Laguna Oca, esteros, MCZ 32775, 32776; Monte Lindo, CAS-SU 11284. *Misiones:* Iguazu Falls, 175 m, FMNH 9271.

BOLIVIA. *Beni:* Alejandria, Río Mamoré, AMNH 79120, 79179–79187, 128380–128448; Beni Reserve, Río Cureraba, Provincia Yacuma, USF 173799, 173852, 173892, 173894 (to Bolivia), USNM 283262–283264, 306620–306622; Cachuela Esperanza, 165 m, UMMZ 64102 (2); Carasco, Río Itenez (Guaporé), AMNH 79162–79164, 79166; Espiritu, Provincia Ballivián, USNM 283292, 306649, Ergueta 584; Guayaramerin (Guayará Merí), USNM 280906–280910; Ivon, BMNH 1967.2086, 1967.2089, 1967.2091, UMMZ 64099 (7); Lake Rogagua, UMMZ 64100 (7); Puerto Almacen (= Mayor Pedro Vaca Diez), 260 m, AMNH 72245–72250, 72252, 72253, 72255, 79169, 92558–92598; Puerto Siles, Río Mamoré, AMNH 79460; Reyes, 230 m, UMMZ 64101; confluence of Río Blanco and Río Itenez (Guaporé), AMNH 79168; Río Grande, 5 km NW boca, Río Mamoré, AMNH 79123, 79172–79174; Río Ibarre (Ibare), boca del, Río Mamoré, AMNH 79170; Río Itenez (Guaporé), 9 km SE Costa Marques (Brazil), AMNH 98139; Río Itenez (Guaporé), El Remanso, AMNH 79167; Río Itenez (Guaporé), ~20 km above mouth, AMNH 79175-79176; Río Mamoré at 13°35'S, AMNH 79178; Rurrenabaque, 220 m, AMNH 108318, UMMZ 64097 (3), USNM 280681–280710, 280716–280753; Santa Rosa, Río Mamoré, AMNH 72414–72424, 92600–92619, 128465; Trinidad, 235 m, CAS 152206, USNM 280995; Trinidad, 25 km NW, Río Mamoré AMNH 79171; Tumi Chucua, 170 m, USNM 208215, 208217, 208218. *La Paz:* San Buenaventura, 5 km W, USNM 280711–280715. *Santa Cruz:* Aguas Calientes, MZUSP 21343–21353; Amboró National Park, Buena Vista, 450 m, BMNH 1987.1078; Buenavista (= Buena Vista), 400 m, AMNH 39538, UMMZ 74353 (3), 74354 (3), 74355, 74356 (2), 74357 (2), 74358 (3), 74359; El Carmen, MCZ 30020–30022; El Portón, 550 m, MCZ 30027; Roboré, MCZ 30023–30026; San José de Chiquitos, ~300 m, MCZ 30028, 30029, MZUSP 21319–21336, 21376; Santa Cruz de la Sierra (Santa Cruz), 480 m, BMNH 1940.4.6.74–75; Santistebán, Naranjal, USNM 146551; Warnes, Río Pailoncito bridge, 35 km from river on road to Puerto Lacey, USNM 146552.

BRAZIL. *State Unknown:* Boa Hora (State of Rondônia?), UMMZ 64096; Igarapé Totemino, MNRJ 4894. *Amazonas:* Borba, MZUSP 51249–51253, USNM 202590–202596; Curuçá, MZUSP 51270–51304, USNM 202554–202588, 241307 (larvae); Humaitá, MNRJ 4924–4928, 4930–4970; Igarapé Belém, Rio Solimões, MZUSP 24030, 24031; Ilha da Marchantaria, entrada Lago dos Reis (= Rei), prox. Manaus, INPA 772, 778, 779; Itacoatiara, CAS 49731, MZUSP 39496; Itapiranga, MZUSP 27767, 44286; Lago Januari, MZUSP 53751, 53753; Lago Marinheiro, MZUSP 53757; Manicoré, MZUSP 51254, USNM 202589; Nova Olinda, MZUSP 37146; Restauração, USNM 202553. *Bahia:* Barreiras, at or near, MNRJ 1039, UMMZ 109986; São José do Rio Grande, MNRJ 1045, 1046, UMMZ 109989. *Goiás:* 40–50 miles up Araguaya River from mouth of Rio Toribero, UTA 8349; Aruanã, MZUSP 24011–24014, 24018, 24019; GO-164, km 72, near Jeroaquara, MZUSP 1518; Luis Alves, Rio Araguaia, MZUSP 10834–10836, 10838; Nerópolis, MZUSP 25346; Rio Verde, MZUSP 12518–12522, 25343. *Mato Grosso:* Barra do Tapirapés, AMNH 68093, 70176–70179, 73692–73696, 73698–73710, 73718, 128339, 128503–128530, CAS-SU 11806–11809, MNRJ 2377, 9826, MZUSP 24028, 24029, 25283, 25284; Cáceres, MZUSP 22180, 22181, 22184–22189, 22191; Descalvado, FMNH 9097, 9100–9114; 1 day's run below Descalvado, USNM 132736, 132737; Dumbá, MZUSP 1448; Ilha de Taiamã, MZUSP 57406–57410; Lagoa Ipavu, Parque Indígena do Xingú, MZUSP 25212; Mato Verde, Rio Araguaia, MZUSP 24023, 24024, 24026, 25236–25240, 25311–25319; Poconé (Fazenda Jofre), MZUSP 52747; Porto Conceição, Paraguay River, FMNH 9161; Porto Esperidião, MZUSP 52177–52190, 59742, 59744, 59745, 60551, USNM 303761; Porto Jofre, MZUSP 61249, 61250, USNM 303706, 303707; Posto Diauarum, Parque Indígena do Xingú, MZUSP 49501–49517; Posto Leonardo, Parque Indígena do Xingú, MZUSP 44301; Rio Culuene, 40 km acima da confluencia com o Xingú, MNRJ 2364; Rio Pixaím, MZUSP 56726–56728, 61251; São Domingos, Rio das Mortes, MZUSP 988, 989, 991, 993, 1072, 1076, 1085, 1132, 1133, 1135–1137, 1139–1141, 1143–1148, 1151–1154, 1156, 1171, 1192, 1224, 1227, 1231, 1236, 1242, 1244, 1247–1253, 1255, 1257, 1278, 1281–1283, 1287, 1289–1292, 1298, 1329, 1345, 1347, 1348, 1354, 1366, 1369–1371, 1374–1379, 1381, 1385, 4241–4245, 4249, 4251–4253, 4256, 4258–4270, 10891, 10892, 10894–10900, 14755–14761, 14763–14783, USNM 148677–148691; São Luiz de Cáceres (now Cáceres), CAS-SU 22918; Vila Bela da Santíssima Trinidade, MZUSP 52104, 56729–56732. *Mato Grosso do Sul:* Agua Clara, FMNH 67088; Aquidauana, MZUSP 16203, 16204; Corumbá, UMMZ 104225 (2); Coxim; MZUSP 61018, 61019, 61037; Dourados, MNRJ 4903–4905; Estancia Caiman, MZUSP 67419–67441, USNM 302516 (larvae), 302814–302848; Fazenda Canaã, Três Lagoas, MZUSP 25231–25233; Jupiá, MZUSP 24009, 24010; Maracaju, USNM 107705–107708, 107710, 107711; Porto Esperança, no Rio Paraguay (margem esquerda) 60 km da fronteira, UMMZ 104232 (11), USNM 133005–133008; Salobra, CAS-SU 11802, 11803, UMMZ 104227 (2); Santa Luzia, MZUSP 28550, 28551. *Minas Gerais:* Januária, Rio dos Pandeiros, UMMZ 109984; Pirapora, MNRJ 1038, 1040–1044, 1393, UMMZ 109982 (10), 109983 (2), 109985 (2), 109987 (3), 109988, USNM 98001–98003; Uberlândia, MZUSP 12055–12063; Unaí, MZUSP 64423, 64424. *Pará:* Alter do Chão, INPA 1244, 1245, 1247–1249, 1252, 1291; Boca do Figueiredo, Rio Nhamundá, MZUSP 24983, 24985–24988; Cachoeira do Ararí (now Arariuna), Ilha Marajó, MZUSP 24975; Ereré, MNRJ 4896;

Fazenda Paciencia, Rio Nhamundá, MCZ 90833, MZUSP 44311; Lago Urariá, prx. Oriximiná, MZUSP 24993-24995, 32313-32317; "Maloca Jorge" no Rio Maicurú, MNRJ 4897; Óbidos, KU 129947-129952; Oriximiná, MNRJ 4898-4902; Rio Andirá, MCZ 32725, 32726. *Paraná:* Guaíra, MZUSP 28546, 28547; Parque Nacional de Iguaçu, MNRJ 4892, 4893; Rio Paracaí, MZUSP 15827. *Piauí:* Teresina, MZUSP 25015. *Rio Grande do Sul:* Cêrro Largo, MZUSP 24032. *Rondônia:* Porto Velho, KU 92933-92937, MZUSP 16685-16690, 16694-16696, 16700-16716, 16718-16721, 16723-16730, 16732-16734, 16736-16749, 16751-16760, 16763-16785, 16787-16805, 16807, 16809-16811, 16813-16820, 16823-16827, 16829-16832, 16834-16843, 16845-16848, 16851-16916, 24559, 62110-62175, RMNH 23841, ZUEC 5381; São Carlos, MZUSP 51464, 51465, USNM 202545. *São Paulo:* Anhembi, USNM 227657, 227658; Baurú, MNRJ 4874-4886, MZUSP 53, 54; Edgardia, Botucatu, MNRJ 4909-4912; Emas, Cachoeira de, MZUSP 3067, 4636-4642, 9038, 9041-9043, 11223; Lins, MZUSP 9024; Luis Antonio, USNM 303207, 303208; Panorama, MZUSP 25433-25435; estrada Pirajú-Manduri, km 61, divisa de municípios, MNRJ 4918-4923; Porto Marcondes, Rio Paranapanema, MZUSP 1980, 1981, 1983, 1984, 1987-1997; Posto 75, prope. Toledo Pisa (= Piza), MNRJ 4872, 4873. *Tocantins:* Santa Isabel do Morro, MZUSP 24022, 25326.

PARAGUAY. *Department Unknown:* Río Paraguay, MCZ 15670. *Alto Paraguay:* Estancia Primavera, BMNH 1955.1.5.29-33, 1971.1912, 1971.1914-1915, 1972.2381-2387, 1972.2388-2391; Paso Río Tapiricuay, BMNH 1972.2392. *Amambay:* Bella Vista, 2 km (by road) SSE of, Estancia Apami de Ocariz, USNM 253182; Parque Nacional Cerro Corá, ~32 km WSW of Pedro Juan Caballero, ~500 m, USNM 253116-253122, 253124, 253125. *Caaguazu:* Pastoreo, NE of Caaguazu, MCZ 17902-17909, 17911-17916. *Central:* Areguá, Lago Ypacaraí, 62 m, LACM 126435, 126436, UMMZ 166939, USNM 205598; Asunción, 77 m, MNRJ 4895; Caacupé, Arroyo Ytyguazu, BMNH 1972.2397-2399; Colonia Nueva Italia, ~100 m, AMNH 50654-50656; Puente Remanso, 1 km S, ~100 m, UMMZ 166959; Río Salado, below bridge on road from Luque to San Bernardino, 60 m, LACM 126459, USNM 205601. *Itapua:* Arroyo Pirayu-í, LACM 126460; El Tirol, 19.5 km NNE Encarnación by road, 200-240 m, LACM 126437, USNM 253123, 253440-253457. *La Cordillera:* Caraguatay, Estáncia Saladillo, LACM 126438-126458, USNM 205599, 205600. *Presidente Hayes:* Chaco-í, 75 m, MCZ 25827-25833; Estancia La Golondrina and vicinity, 34.8 km NW toll booth on puente Remanso, ~75 m, UMMZ 166910, 166931, 166937, 166944, 166947-166949, 166951, 166952, 166962-166969; Río Pilcomayo at Puerto Falcon bridge (to Argentina) 12 km WSW Chaco-í, UMMZ 166960. *San Pedro:* Colonia Friesland, Rüchenau, near Itacurubí del Rosario, KU 73411; Primavera, KU 186834; Puerto Rosario, 100 m, BMNH 1971.1913.

Leptodactylus sabanensis (N = 49)

BRAZIL. *Roraima:* BV 8, INPA 1303.

VENEZUELA. *Bolívar:* Arabopó (= Arabupu), 1200-1300 m, AMNH 39758, 39759, UMMZ 85197 (5); Cabanayen (= Kavanayen), KU 185694, RMNH 18407, 18408; El Dorado, 85 km SSE, km 125, KU 166545-166561, 181031; Gran Savana (Sabana), 145 km S El Dorado, 1380 m, KU 166562-166571, TCWC 60148-60152; km 137 rodovia 10, a lado del Monumento al Soldado Pionero, 2 km do limite N da Gran Sabana, 1100 m, AJCardoso 346; La Escalera, 121 km S El Dorado, RMNH 23981; La Escalera, 18 km N, 126 km S El Dorado, 1400 m, RMNH 23979; Las Claritas, 85 km S El Dorado, TCWC 60155; Paulo, Mt. Roraima, 5100′, AMNH 39753.

Leptodactylus validus (N = 350)

LOCALITY UNCERTAIN. "British Guiana" "Grenada Island," AMNH 18961, 18970-18972, 18992.

TOBAGO. *St. Andrew:* Bacolet River, AMNH 55873. *St. John:* Anse Fourmi, near, on Charlotteville-Bloody Bay Road, USNM 192762; Bloody Bay, near mouth of Bloody Bay River, USNM 167494-167496, 227853; Charlotteville, near, USNM 167503, 167504, 227847-227852; Hills above Man-of-War Bay, 2 km ENE Charlotteville, ~100 m, AMNH 87403-87406; Speyside, ~600′, MCZ 27788, 27789, USNM 306081-306084, 306088, 306092. *St. Patrick:* Buccoo Bay, AMNH 55863-55865, 128545, 128546. *St. Paul:* Louis d'Or Land Settlement, USNM 195012-195016; Speyside, near, USNM 306098 (larvae); Windward Road, about milestone 22.5 near Lambeau Hill Crown Trace, USNM 195030, 195104-195107, 195129, 195130.

TRINIDAD. *District Unknown:* No specific locality, FMNH 42073, 42074; Four Roads, MCZ 3244-3254, 6083; Galiba River, MCZ 4090; Manzanilla—Mayaro Road, AMNH 79843; Mara Forest, MCZ 3239; San Rafael, FMNH 49664, 49665. *Nariva:* Brickfield, FMNH 49656, 49657, 49659, 49660. *St. Andrew:* Mt. Harris, FMNH 49654, 49655; Sangre Grande, MCZ 3295-3298. *St. George:* Arena, near San Rafael, AMNH 55812; Arima Valley, above Simla (on Arima-Blanchisseuse Road), AMNH 55811, 70483-70485, 79844, MVZ 199699, USNM 166622-166624, 286948, 286959, 286960, 286964, 287018, 306103; Brasso Seco, USNM 306104-306110; Carapo, near, USNM 314671, 314672; Churchill-Roosevelt Highway, AMNH 55813, 55814; Saint Augustine, MCZ 17901; St. Joseph, MCZ 11777, 11778; Tucker Valley, AMNH 51605, USNM 119055-119060. *St. Patrick:* Chatham Beach, USNM 314627-314670.

WINDWARD ISLANDS. *Bequia:* No specific locality, MVZ 83786, 83787, USNM 103976-103978; Road between Admiralty Bay and Spring Bay, MVZ 83788. *Grenada:* Grand Anse Bay and beach, St. George Parish, USNM 314785-314851; Grand Etang, St. Andrews Parish, LACM

64144, 64145, MCZ 2963–2971, 2974, RMNH 9999, UMMZ 60257 (2), USNM 67183, 67184, 67186–67194, 67199, 67201–67203, 67205, 67208, 67212; Lower Pearls, SDSNH 66647–66657; Mt. Horn, Weedy Ditch, MCZ 31555. *St. Vincent:* Arnos Vale, St. George Parish, USNM 314718–314770, 314513–314515, 314854, 314855 (larvae); Brighton, USNM 79068–79075; Rose Cottage, SDSNH 67834, USNM 314516–314520; 1 mi NE Vermont, St. Andrew Parish, USNM 314512.

Leptodactylus wagneri (N = 603)

BRAZIL. *Amazonas:* Igarapé Belém, Rio Solimões, AMNH 97061.

COLOMBIA. *Caquetá:* Florencia, 450 m, KU 124744–124747. *Nariño:* La Guayacana, near, 260 m, FMNH 61754. *Putumayo:* El Pepino, 10.3 km W, KU 169094; Mocoa, ~15 km airline SW, 1180 m, AMNH 84869; Puerto Asís, near, 260 m, LACM 50199; Puesto de Bombeo Guamues, near Puerto Asís, 1000 m, KU 140313; Río Rumiyacu, FMNH 54376; Santa Rosa de Sucumbíos (Kofan Village), upper Río San Miguel, 700 m, AMNH 116300–116325.

ECUADOR. *Morona-Santiago:* Agua Rica, a one-house posada on trail between Limon and Gualeceo, slightly south of west of Limon, 6200′, USNM 287897; Arapicos, Río Llushin, USNM 196814, 306325–306329; Copal, USNM 196790, 306330; Cusuime, 320 m, AMNH 93729, 93730, 93732, 93734–93736, 93739, 93747, 93770, 93776, 93778, 93780, 93783, 93789–93792, 93796; Limon, USNM 196799, 196800, 196822, 306331; Mendez, USNM 196791–196796, 196798, 283832, 283833, 306339–306346; Mision Bomboiza, 840 m, KU 147060–147067; Plan Grande, 2900′, USNM 196797; Plan de Milagro, 1980 m, KU 202643, USNM 196801–196805, 287895, 287896, 306332–306338; San José, USNM 283834, 283835; Sucúa, 2 miles E of, on trail from Sucúa to Río Upano, 2700′, MCZ 88577, 88578, 91272, 91273, USNM 196780, 196781, 283836–283880. *Napo:* Avila, 600 m, UMMZ 92145; Cascada San Rafael (Salto de Agua), FMNH 218489; Coca, KU 158608, MCZ 106034–106039, 106043, 106044; Dureno, 320 m, LACM 92184, 92231, 92348; Lago Agrio, 340 m, KU 126262–126266; Llanganates area, NE of Riobamba, FMNH 23509 (8); Loreto, 550 m, USNM 196816; Mount Sumaco (= Volcán Sumaco), S slope, USNM 196807; Puerto Libre, Río Aguarico, 570 m, KU 122584; Reventador, Volcan, MCZ 105818, RMNH 23977; Río Napo, UMMZ 92146; Río Salado bridge, 0.7 km NE, on Lago Agrio road, 1380 m, KU 189998, 189999; Río Yasuní (150 km upstream from Río Napo), 180 m, KU 175124; Santa Cecilia, 340 m, KU 104630–104644, 104646–104654, 104656–104659, 104661, 104663–104665, 104667, 104668, 104670–104677, 104679, 104681–104695, 104697, 104698, 104700, 104701, 104703–104712, 106968, 109142, 109143, 109145–109151, 111400–111402, 111425, 119343, 119351, 122583, 126261, 146188–146190, 149359–149363, 152397, 152398, 175457–175459, 175461, 175462, MCZ 56373–56384, 56387, 56388, 56390–56399, 56401–56408, 56410–56418, 56420–56425, 56429, 56431, 56433–56436, UMMZ 129284 (2); Tena, 1–5 km N, Tena-Archidona road, 640 m, RMNH 23978. *Pastaza:* Abitagua (= Cerros de Abitagua), 1100 m, FMNH 25789, 26899, UMMZ 92147; upper Bobonaza, USNM 196806; Canelos, 600 m, MCZ 17950; Canelos to Maranon, MCZ 19648–19650; Chichirota, Bobonaza, ~300 m, USNM 196818; Mera, 1160 m, KU 120304–120315, 120317–120319, 132821, RMNH 24005–24008, UMMZ 177952–177955; Puyo, 975 m, FMNH 172638–172640, 172642, KU 127035, 127036, UMMZ 132456, USNM 196770, 196777, 196778, 196784–196789, 196809, 196811, 196815, 286487, 286497, 286498, 306248–306317; Puyo, 5.6 km N, 1150 m, KU 202644–202650; Puyo, 25 km N, USNM 205031; region of upper Río Curaray, USNM 196821; Río Llushin, N of Arapicos, USNM 196782; Río Oglan, USNM 196817; Río Pindo, USNM 196808, 196813, 306323, 306324; Río Villano, USNM 196783, 196810, 287898, 306318–306322; Shell Mera, KU 99051–99068, 99070–99080, 99083, 99084, 99086–99089, 99091–99106, 109140, 109141, USNM 196779, 196812; Union Base (= Tambo Unión), trail from to Rosario Yacu, 920 m, MCZ 95642; Veracruz, 950 m, KU 120316. *Tungurahua:* Baños, FMNH 172978, 172979; Río Negro, 1260 m, KU 120320–120334; Río Negro, 8 km E, 1240 m, KU 146191. *Zamora-Chinchipe:* Zamora, near, 1000 m, KU 120298–120302, MCZ 85360.

PERU. *Amazonas:* Galilea, Río Santiago, 180 m, MVZ 173885, 173886; Huampami, Río Cenepa, 215 m, MVZ 162640; La Poza, 180 m, MVZ 173837, 173865–173867, 173871, 173885, 173886, 173899, 173922; Shiringa, Quebrada Yutipis, Río Santiago, 200–400 m, MVZ 173883, 173904–173906. *Loreto:* Estirón, Río Ampiyacu, AMNH 115688, 115693, MZUSP 24792, 24807, 24812; Mishana on Río Nanay, 3 km airline SSW Mishana, AMNH 102991, 102992; Lower Río Napo region, E bank Río Yanayacu, ~90 km N Iquitos, 120 m, KU 206119. *San Martín:* Rioja-Pucatambo trail, 9 km from Rioja, 3 km from Río Negro, 840 m, MCZ 100075.

Literature Cited

Ab'Sáber, A.N.

1977. Os domínios morfoclimáticos na América do Sul. Primeira aproximação. *Geomorfologia*, 52:1–22, 1 map.

Amaral, D.A., B.C. Fonzar, and L.C. Oliveira Filho

1982. Vegetação: As regiões fitoecológicas, sua natureza e seus recursos econômicos. In *Projeto Radambrasil, Levantamento de Recursos Naturais, Cuiabá*, 26(21):401–452. Rio de Janeiro: Ministério das Minas e Energia.

Andersson, L.G.

1945. Batrachians from East Ecuador Collected 1937, 1938 by Wm. Clarke-Macintyre and Rolf Blomberg. *Arkiv för Zoologi*, 37A(2):1–88.

Bogart, J.P.

1974. A Karyosystematic Study of Frogs in the Genus *Leptodactylus* (Anura: Leptodactylidae). *Copeia*, 1974:728–737.

Bokermann, W.C.A.

1966. *Lista anotada das localidades tipo de anfíbios Brasileiros*. 183 pages. São Paulo: Serviço de Documentação.

Boulenger, G.A.

1882. *Catalogue of the Batrachia Salientia s. Ecaudata in the Collection of the British Museum*. Second edition, 495 pages, 30 plates. London: British Museum (Natural History).

Cardoso, A.J., and J. Vielliard

1990. Vocalizações de anfíbios anuros de um ambiente aberto, em Cruzeiro do Sul, Estado do Acre. *Revista Brasileira de Biologia*, 50:229–242.

Cope, E.D.

1862. On Some New and Little Known American Anura. *Proceedings of The Academy of Natural Sciences of Philadelphia*, 14:151–159.

1887. Synopsis of the Batrachia and Reptilia Obtained by H.H. Smith, in the Province of Mato Grosso, Brazil. *Proceedings of the American Philosophical Society*, 24:44–60.

Fugler, C.M., and A.B. Walls

1979. The Anura (Amphibia) of Rio Upano Valley of Eastern Ecuador. *Journal of the Tennessee Academy of Science*, 54:149–156.

Garman, S.

1887. On West Indian Reptiles and Batrachians in the Museum of Comparative Zoology at Cambridge, Mass. *Bulletin of the Essex Institute*, 19:1–24.

Girard, C.

1853. Descriptions of New Species of Reptiles, Collected by the U.S. Exploring Expedition, Under the Command of Capt. Charles Wilkes, U.S.N., Second Part, Including the Species of Batrachians, Exotic to North America. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 6:420–424.

Gorham, S.W.

1966. Liste der rezenten Amphibien und Reptilien: Ascaphidae, Leiopelmatidea [sic], Pipidae, Discoglossidae, Pelobatidae, Leptodactylidae, Rhinophrynidae. *Das Tierreich*, 85:1–222.

Gosner, K.L.

1960. A Simplified Table for Staging Anuran Embryos and Larvae with Notes on Identification. *Herpetologica*, 16:183–190.

Haddad, C.F.B., and A.J. Cardoso

1987. Taxonomia de três espécies de *Pseudopaludicola* (Anura, Leptodactylidae). *Papéis Avulsos de Zoologia*, 36:287–300.

Hardy, J.D., Jr.

1982. Biogeography of Tobago, West Indies, with Special Reference to Amphibians and Reptiles: A Review. *Bulletin of the Maryland Herpetological Society*, 18:37–142.

1984. Herpetology of Tobago: Additions, Deletions, and Taxonomic Changes. *Bulletin of the Maryland Herpetological Society*, 20:12–19.

Häupl, M., and F. Tiedemann

1978. Typenkatalog der Herpetologischen Sammlung, Amphibia. *Kataloge der Wissenschaftlichen Sammlungen des Naturhistorischen Museums in Wien, Vertebrata*, 2:1–34.

Henle, K.

1981. *Adenomera griseigularis*, eine neue Leptodactyliden-Art aus Peru (Amphibia: Salientia: Leptodactylidae). *Amphibia-Reptilia*, 2:139–142.

Hero, J.-M.

1990. An Illustrated Key to Tadpoles Occurring in the Central Amazon Rainforest, Manaus, Amazonas, Brasil. *Amazoniana*, 11:201–262.

Heyer, W. R.

1970. Studies on the Frogs of the Genus *Leptodactylus* (Amphibia: Leptodactylidae), VI: Biosystematics of the Melanonotus Group. *Contributions in Science, Los Angeles County Museum*, 191:1–48.

1974. *Vanzolinius*, a New Genus Proposed for *Leptodactylus discodactylus* (Amphibia, Leptodactylidae). *Proceedings of the Biological Society of Washington*, 87:81–90.

1978. Systematics of the *fuscus* Group of the Frog Genus *Leptodactylus* (Amphibia, Leptodactylidae). *Science Bulletin, Natural History Museum of Los Angeles County*, 29:1–85.

1979. Systematics of the *pentadactylus* Species Group of the Frog Genus *Leptodactylus* (Amphibia: Leptodactylidae). *Smithsonian Contributions to Zoology*, 301:1–43.

1984. The Systematic Status of *Adenomera griseigularis* Henle, with Comments on Systematic Problems in the Genus *Adenomera* (Amphibia: Leptodactylidae). *Amphibia-Reptilia*, 5:97–100.

Heyer, W.R., A.S. Rand, C.A.G. Cruz, O.L. Peixoto, and C.E. Nelson

1990. Frogs of Boracéia. *Arquivos de Zoologia*, 31:231–410.

Heyer, W.R., and I.R. Straughan

1976. A Functional Analysis of the Mating Calls of the Neotropical Frog Genera of the *Leptodactylus* Complex (Amphibia, Leptodactylidae). *Papéis Avulsos de Zoologia*, 29:221–245.

Hoogmoed, M.S., and J.E. Cadle

1991. Natural History and Distribution of *Agalychnis craspedopus* (Funkhouser, 1957) (Amphibia: Anura: Hylidae). *Zoologische Mededelingen Leiden*, 65:129–142.

International Trust for Zoological Nomenclature

1985. *International Code of Zoological Nomenclature, Third Edition, Adopted by the XX General Assembly of the International Union of Biological Sciences*. 338 pages. Huddersfield, England: H. Charlesworth & Co. Ltd.

Kenny, J.S.

1969. The Amphibia of Trinidad. *Studies on the Fauna of Curaçao and Other Caribbean Islands*, 29:1–78, 15 plates.

Leviton, A.E., R.H. Gibbs, Jr., E. Heal, and C.E. Dawson

1985. Standards in Herpetology and Ichthyology, Part I: Standard Symbolic Codes for Institutional Resource Collections in Herpetology and Ichthyology. *Copeia*, 1985:802–832.

Lutz, A.

1926. Sur deux espèces nouvelles de Batraciens brésiliens. *Comptes Rendus de la Société de Biologie, Paris*, 95:1011–1012.

1930. Segunda memoria sobre especies brasileiras do genero Leptodactylus, incluindo outras alliadas. *Memorias do Instituto Oswaldo Cruz*,

23:1-20 [in Portuguese], 21-34 [in English], 5 plates.

Nieden, F.

1923. Amphibia, Anura I: Subordo Aglossa und Phaneroglossa Sectio I Arcifera. *Das Tierreich*, 46:1-584.

Papavero, N.

1973. *Essays on the History of Neotropical Dipterology with Special Reference to Collectors (1750-1905)*. Volume II, 446 pages. São Paulo: Museu de Zoologia, Universidade de São Paulo.

Peters, W.

1862. Eine neue Gattung von Laubfröschen, *Plectromantis*, aus Ecuador. *Monatsbericht der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, 1862:232-233.

Read, V.M. St. J.

1986. Two New Anurans Form [sic] Trinidad. *Bulletin of the Chicago Herpetological Society*, 21:29-31.

Schneider, H., G. Joermann, and W. Hödl

1988. Calling and Antiphonal Calling in Four Neotropical Anuran Species of the Family Leptodactylidae. *Zoologische Jahrbücher, Abteilung für Allgemeine Zoologie und Physiologie der Tiere*, 92:77-103.

Schwartz, A., and R. Thomas

1975. A Check-list of West Indian Amphibians and Reptiles. *Special Publication, Carnegie Museum of Natural History*, 1:1-216.

Steindachner, F.

1864. Batrachologische Mittheilungen. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien*, 14:239-288, plates IX-XVII.

Vanzolini, P.E.

1981. A Quasi-Historical Approach to the Natural History of the Differentiation of Reptiles in Tropical Geographic Isolates. *Papéis Avulsos de Zoologia*, 34:189-204.

Vizotto, L.D.

1967. *Desenvolvimento de anuros da Região Norte-Ocidental do Estado de São Paulo*. 161 pages. São José do Rio Prêto, São Paulo: Tipografia Rio Prêto.

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