

# Arquivos de Zoologia

ISSN 0066-7870

ARQ. ZOOL., S. PAULO 30(4): 235-339

25 - VII - 1983

## VARIATION AND SYSTEMATICS OF FROGS OF THE GENUS *CYCLORAMPHUS* (AMPHIBIA, LEPTODACTYLIDAE)

W. Ronald Heyer

### Abstract

*Variation is analyzed among members of the Neotropical frog genus Cycloramphus. The results of the analyses of variation are used in part to delimit species. Twenty one species are recognized, nine of them are described as new. The genus Craspedoglossa is considered a synonym of Cycloramphus. The genus Scythrophrys is not closely related to Cycloramphus, but the genus Zachaenus is.*

*A definition for the genus Cycloramphus is provided, as are taxonomic summaries for each species. The species accounts include a skeletal synonymy, diagnosis of adults, a morphological definition of adults and larvae where known, an advertising call description and a distributional summary with localities and maps. A detailed description of the holotype is provided for each new species. A key to the species distinguishes adult specimens of Cycloramphus.*

*Much of the interspecific variation is of about the same magnitude as intraspecific variation.*

*Natural selection has resulted in changes of both size and shape among species of the genus Cycloramphus.*

*There are no universal patterns of species differentiation and sympatric occurrence. The kinds and degrees of differences among species appear to be geographically specific.*

### Introduction

*This study is a contribution to the understanding of the systematics and zoogeography of the Atlantic Forest fauna. The full richness and beauty of the frogs and forests were not appreciated until a first field experience in the Atlantic Forests, a two week trip to Boracéia, the University of São Paulo field station. That trip proved to be a turning point;*

efforts were then directed towards working with the Atlantic Forest frog fauna and gaining some insights into the origin of its diversity and present distribution. The approach to attaining these goals is through detailed study of taxonomic segments of the frog fauna. Any one such study will give but one view; but by picking a few critical examples, a general picture will hopefully come into focus within my research lifetime.

It was not until the third field season that efforts were concentrated on members of the genus *Cycloramphus*. At that time, it was apparent that many species could still be collected. This was important for two reasons. First, by making critical collections and recordings of advertisement calls, full utilization could be made of the rich museum materials already available. Second, samples for biochemical analysis of the protein albumin (in collaboration with Dr. Linda R. Maxson) to estimate genetic relationships have to come from living frogs. The restricted distributions of *Cycloramphus* species within the Atlantic Forests, the transition from a life cycle involving aquatic stream larvae to a terrestrial life cycle, combined with the fact that the genus had been monographed and appeared to be speciose enough to be interesting but not overwhelming were the final considerations that led to focussed study of this genus.

Historically, members of the genus *Cycloramphus* have been collected and studied intensely by the Brazilian herpetologists W. C. A. Bokermann, Adolfo and Bertha Lutz, and Alipio Miranda-Ribeiro. The early studies were filled with drama and excitement, as shown by the following excerpt from the English translation of Miranda-Ribeiro, 1929, p. 32:

Here, as in everything else that is natural, the absolute identity does not exist. Lutz speaking of the development says that he verified that I, based on the examination of a batch of ova preserved at the Museum and coming from Sta. Catharina, declared that the metamorphosis took place within the egg. He at once concluded that therein lay an error — the batch being perhaps of *Craspedoglossus*, the eggs of which, containing little rana were described and figured at the same time, because he then already knew the evolution of *I. lutzii*, and because the want of natatory membrane in the small frog was sufficient to exclude it from the genus.

I am much afraid of categorical affirmations based on conjectures (or presumption); therefore, when I published my "Notes to serve in the study of the *Gymnobatrachia* of Brazil", I trod the same path in referring to the possible. The attribution of the tadpole to *Craspedoglossus* was mine, at a session of the Brazilian Society of Sciences (*Sociedade Brasileira de Ciências*) the minutes of which should refer thereto.

I well remember that Prof. Lutz impugned it, not omitting his favorite phrase "it is precisely forty years ago that I already knew of the abbreviated metamorphosis", etc. And if the minutes do not record the fact, I can at least remember four witnesses present; the brothers Ozorio de Almeida, Costa Lima and Lauro Travassos. And I believe that his own gentle daughter was also present.

The excitement was due in part to the people who studied the frogs. But the frogs themselves are interesting and their study exhilarating. If the following pages do not reflect this excitement, I recommend the living frogs and the streams and forests where they occur.

The purposes of this paper are to summarize the systematics of members of the genus *Cycloramphus* and to provide the data on morphological variation within and among species that are needed for an understanding of the relationships, zoogeography, and speciation patterns among *Cycloramphus* species.

Two systematic questions need to be answered: (1) How many species are in the genus? (2) What are the generic limits? Bokermann (1951) revised the genus *Cycloramphus* and provided a solid base upon which these two questions can be answered. Four morphological species groupings can be derived from Bokermann's study: (1) the *fuliginosus* group, (2) the *ohausi* group, (3) the *granulosus* group, and (4) the *eleutherodactylus* group. The species level systematic questions are within, not among these groups. For example, Cochran (1955) synonymized some of the taxa which Bokermann (1951) had recognized as distinct within the *fuliginosus* group; Bokermann (1966) in his annotated list of type localities removed several species from the synonymy of the *fuliginosus* group members of his earlier work (1951) as well as some from Cochran's study (1955) and gave them full species status. This paper analyzes the within group morphological variation as an aid to defining species limits. Bokermann (1951) also gave a firm generic definition for *Cycloramphus*, pointing out that *Craspedoglossa* was closely related. Bokermann (pers. comm.) now thinks that *Craspedoglossa stejnegeri* may in fact not be generically distinct from *Cycloramphus*. Thus, the status of *C. stejnegeri* needs to be examined.

The organization of this paper reflects the different methods and goals of dealing with the overall understanding of variation and systematics of members of the genus *Cycloramphus*. The first section treats variation of

external morphology and delimits the species within the four species groups. The second section treats external and internal morphological variation among the species groups and examines *C. stejnegeri* and other closely related taxa to determine the generic limits of *Cycloramphus*. The third section is a taxonomic summary of the genus *Cycloramphus*. The fourth section summarizes interspecific variation.

#### Acknowledgements and museum abbreviations

The following colleagues generously provided information and/or loaned specimens: Werner C. A. Bokermann (WCAB), E. R. Brygoo (MNHP), Antenor Leitão de Carvalho (MNRio), Joseph T. Collins (KU), William E. Duellman (KU), George R. Foley (AMNH), Alice G. C. Grandison (BMNH), Michael Häupl (Vienna), Eugênio Izecksohn (Universidade Federal Rural do Rio de Janeiro), Hans-Wilhelm Koepcke (Zoologisches Institut und Zoologisches Museum, Universität Hamburg), Jean Lescure (MNHP), Charles W. Myers (AMNH), Ronald A. Nussbaum (UMMZ), Günther Peters (Museum für Naturkunde der Humboldt Universität zu Berlin), F. Tiedemann (Vienna), P. E. Vanzolini (MZUSP), Ernest E. Williams (MCZ).

The following companions made the field work in the Atlantic Forests profitable and enjoyable: Ronald I. Crombie (USNM), Maria Christina Duchêne (MZUSP), Annelise Gehrau (Montevideo, Uruguay), Elena D. Heyer, Laura M. Heyer, Miriam H. Heyer, Kazumi Kanno (São Paulo), Frances I. McCullough (USNM), Oswaldo Peixoto (MZUSP), Francisca Carolina do Val (MZUSP).

Charles D. Roberts (Information Systems Division, Smithsonian Institution) aided with

the statistical and multivariate analyses. Frances I. McCullough (USNM) prepared Figures 2-5, 33, 35, 41, 43. Roy W. McDiarmid (U. S. Fish and Wildlife Service, Department of Interior), George R. Zug (USNM), and P. E. Vanzolini (MZUSP) read and criticized the manuscript.

This paper is a contribution to the project, "Evolutionary Zoogeography of the Atlantic Forest System of Brasil: The Anuran Example," supported jointly by the Museu de Zoologia, Universidade de São Paulo, and the I.E.S.P. Amazon Ecosystem Research Program, Smithsonian Institution.

Museum abbreviations as used in the text are:

AL	Adolfo Lutz Collection, MNRio
AMNH	American Museum of Natural History, New York
BMNH	British Museum (Natural History), London
KU	University of Kansas Museum of Natural History, Lawrence
L	Previously unnumbered specimens of the Adolfo Lutz Collection, MNRio
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MNHP	Museum National d'Histoire Naturelle, Paris
MNRio	Museu Nacional, Rio de Janeiro
MZUSP	Museu de Zoologia da Universidade de São Paulo, São Paulo
USNM	United States National Museum Collections, National Museum of Natural History, Smithsonian Institution, Washington, D.C.
Vienna	Naturhistorisches Museum Wien, Wien
WCAB	W. C. A. Bokermann private collection, São Paulo.

## Methods and materials

The methods and materials differ in some aspects for the within group and among group analyses. The museum specimens on which both analyses depend represent the major holdings of *Cycloramphus* in the world. Many museums have small holdings of members of this genus, but no attempt was made to gather all these materials for study.

As with any long-term study, analysis was done in stages. The first stage was the within group analysis. This analysis was used to delimit and describe the species. Upon completion of the initial morphological analysis, a field itinerary was designed to sample critical species for which immunological data were lacking. The results of that field work added appreciably to the numbers of known specimens of some species. These new specimens and material from the Vienna museum (borrowed subsequent to the initial analysis) are included in the taxonomic summary section, but the original within group analysis was not redone to incorporate these specimens.

For the within group analysis, data were taken on the external morphology of all specimens initially assembled. The following data were taken on each specimen: sex, thumb spine number, dorsal pattern, thigh pattern, lip pattern, belly pattern, snout profile, inguinal disk presence or absence, skin texture, foot webbing, and body measurements. Most of these characteristics are either self explanatory or are explained in the within group variation section. However, body and head lengths require some discussion here.

In the within group and taxonomic analyses mensural characters are converted to proportions in order to discern differences in shape (the relationship of head length to body size, not head length itself, is useful in defining shape). The ideal body size

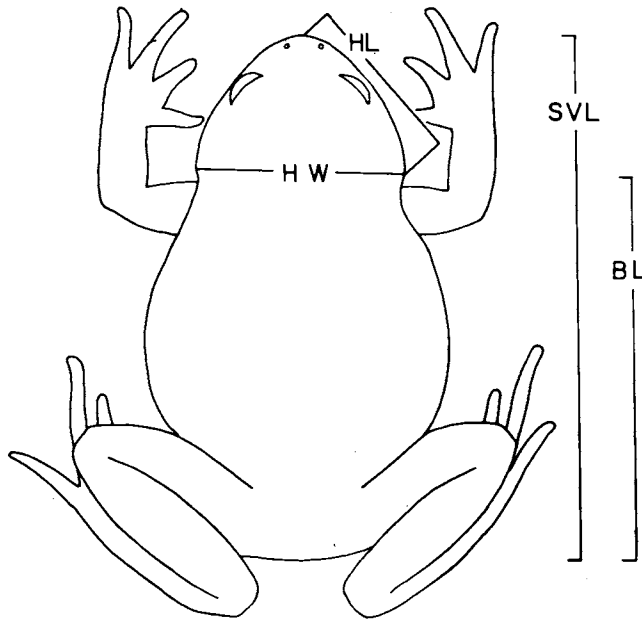


Figure 1. Selected body measurements. SVL = snout vent length (measured), HL = head length (measured), HW = head width (measured), BL = body length (estimated).

measurement is body length (BL) measured from the beginning of the vertebral column to the vent. Because the beginning of the column cannot be accurately located externally in frogs, snout-vent length (SVL) from tip of snout to vent is measured. Estimated body length (BL) is estimated in the following manner (Figure 1). The measured head length (tip of snout to posterior angle of jaw) and 1/2 the measured head width form two sides of a right triangle. With two sides of a right-angle triangle known, the third side can be calculated. This estimated head length is subtracted from SVL to get BL. The trade-off is this: empirically, BL is better to use than SVL for analytic purposes, but SVL is an actual measurement, whereas BL is estimated — this estimation adds noise, so that the information is not as accurate as SVL measurements. Frog measurement data were used for members of the *fuliginosus* group from a small geographic area (Tijuca and Sumaré, Rio de Janeiro) to run correlations of the measurements against SVL and BL to

see how much information was lost by using BL rather than SVL as the estimator of body size. The results (Table 1) indicate that the estimation of BL adds relatively little noise compared to correlations using SVL as an estimator of size. For purposes of analysis, I think the empirical arguments for using BL rather than SVL outweigh the amount of noisy information added by using an estimate of head length to determine BL. Estimated BL is used for the size estimator

Table 1. Correlation coefficients using snout-vent length (SVL) and estimated body length (BL) as size indicators. Sample of 296 frogs from a small geographic region (see text for further information). All correlations significant at the 0.001 level.

	SVL	BL
Head length	0.995	0.998
Head width	0.995	0.990
Eye-nostril distance	0.983	0.979
Eye-eye distance	0.993	0.988
Femur length	0.990	0.986
Tibia length	0.991	0.988
Foot length	0.990	0.986

in the computer aided analyses of within group data, used to described variation. In the taxonomic section, the estimator of overall size used is SVL as it is the measure that can be compared directly by other workers.

### Within group variation

This section examines variation of external morphological characters within groups and uses the results as one basis for determining species limits. Bokermann's (1951) four species groups of *Cycloramphus* are defined as follows:

- C. *fuliginosus* group — foot webbed, individuals lacking thumb spines, dorsum with shagreen and/or tubercles.
- C. *ohausi* group — foot webbed, individuals with thumb spines, dorsum tuberculate.
- C. *granulosus* group — foot not webbed, toes fringed or ridged, individuals lacking thumb spines, skin glandular-warty.
- C. *eleutherodactylus* group — foot not webbed, toes not fringed or ridged, individuals lacking thumb spines, skin smooth or weakly granular, not glandular-warty.

#### *Cycloramphus fuliginosus* group

Core samples, representative of nominate species, are used to analyze within and among sample variation. All core samples are from restricted geographic localities and represent single species with the possible exception of the sample from Rio de Janeiro, where Cochran (1955) suggested that two species might occur. The Tijuca and Sumaré, Rio de Janeiro sample is first analyzed to determine whether it is com-

prised of one or two species, before it is used as a core sample(s) to compare with the remaining core samples. Finally, smaller, outlying population samples are compared with the larger, core samples.

#### Tijuca and Sumaré Sample

All frogs examined except one have more or less uniformly rugose dorsal surfaces. The single exception is a specimen with a heterogeneous dorsal texture, including keratinized tubercles. This specimen, clearly different from all the others, is discussed later. The remaining specimens share the same thumb spine condition, dorsal texture, and male vocal slit condition. The pattern of the dorsum, thigh, lip, and belly, and snout profiles vary, but not discretely. The two characters which do vary and can be characterized meaningfully are foot webbing and measurements.

Foot webbing was examined by plotting the amount of webbing on the distal side of the fourth toe against SVL (Figure 9). Smaller specimens have more foot webbing than larger specimens and most specimens fall into a uniform cluster. Some individuals have more webbing than the vast majority of the specimens, however.

The measurement data were analyzed with the BMD 10 M principal component analysis, identification of outliers. Females, males, and juveniles were treated separately. At the 0.001 level, one female, one male, and three juveniles represented outliers. The female specimen which is a morphological outlier from the other females is the same specimen (L 112) represented by the upper right hand square in Figure 9. The male morphological outlier is the same specimen (AL 565) represented by the second most extreme upper right hand square in Figure 9. Thus, the male and female specimens in question differ in terms of measurements and webbing from all other adults in the sample from Tijuca and Sumaré. The female

specimen (L 112) has the following bottle label information, "morreu no viveiro onde viveu muitos meses." An animal kept alive in the Lutz laboratory if it did not come from Rio, would most likely have come from either Petrópolis or Teresópolis, where Bertha Lutz did much fieldwork. Specimens of the *C. fuliginosus* group were compared from Tijuca-Sumaré with specimens from Teresópolis to find if there were some morphological feature other than webbing or measurements that would distinguish specimens from these two localities. Details of the metacarpal tubercles do differentiate adults from these localities (Figure 55). The metacarpal tubercle arrangement of the female (L 112) and male (AL 565) are of the Teresópolis type. The male occurs as part of a poorly preserved series of five specimens with the same data. The specimen in question visibly differs in degree of fading from the other specimens in the series, suggestive that it was not preserved at the same time as the others. Separation of juvenile specimens is not as distinct by the metacarpal tubercle arrangement. There are four specimens in the same series of specimens as the most distinct juvenile morphological outlier (USNM 96264). The metacarpal tubercle arrangement more closely resembles that of the Teresópolis juveniles than the Tijuca-Sumaré juveniles in USNM 96264. The webbing states of three of the specimens from this series (the fourth is too poorly preserved for evaluation) are indicated in Figure 9. The other two morphologically distinct juveniles have the metacarpal tubercle arrangement more similar to the Tijuca-Sumaré specimens. The juveniles with more webbing than most others as indicated in Figure 9 have the metacarpal tubercle arrangement indistinguishable from the Tijuca-Sumaré juvenile type.

All specimens which are distinctive in terms of webbing and/or measurements are poorly preserved. All well preserved spec-

imens fall into a single morphological series. I conclude that: (1) the distinctive female (L 112) and male (AL 565) labelled from Tijuca and Sumaré respectively are mislabelled and probably came from Teresópolis; (2) one series of juveniles may similarly be mislabelled; and (3) only a single species with a relatively uniform dorsal texture of the *C. fuliginosus* group exists at Tijuca and Sumaré. Specimens L 112, AL 565, and USNM 96264-67 are omitted from further analysis.

#### Geographic Series Samples

There are eight localities from which series of specimens are available for analysis. One to three species of the *C. fuliginosus* group are present at each of these localities. Bokermann (1951) differentiated the sympatric members of this group in the State of São Paulo by dorsal texture and amount of foot webbing. These characters clearly separate all group members occurring sympatrically. Two localities possess adequate series of two sympatric species for analysis. Three members of this group occur in the Cubatão-Paranapiacaba region of São Paulo; of these, two species are represented by series. The third species occurring at this region is discussed in the next section.

The geographic samples of the *C. fuliginosus* group are as follows:

1. Teresópolis
2. Petrópolis
3. Tijuca and Sumaré
4. Barro Branco
5. A - Boracéia
6. B - Boracéia
7. A - Cubatão-Paranapiacaba
8. B - Cubatão-Paranapiacaba
9. A - Morretes
10. B - Morretes
11. Pirabeiraba

The samples from Morretes and Pirabeiraba are actually west of these towns on the slopes where forested mountain

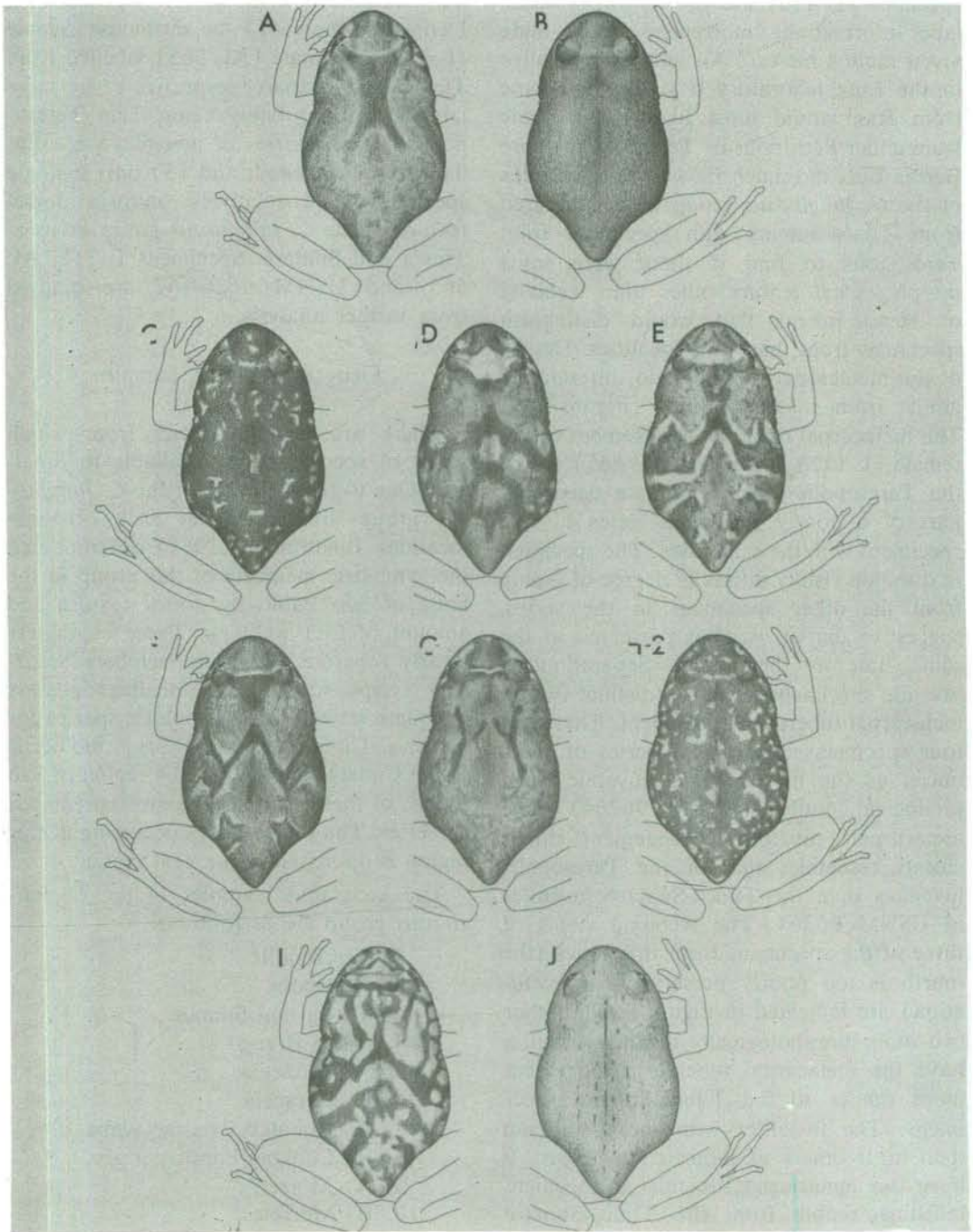


Figure 2. Dorsal pattern standards. Letters as used in text. Additional standards not figured are: A-1, not as distinct as A; D-1, dark blotches larger than in D to coalescing; E-1, not as distinct as E; F-1, broken W; F-2, broad W; H, about half as many spots as H-2, spots larger; H-1, not as distinct as H; I-1, pattern of I, but broken.



Table 2. Distribution of dorsal pattern states among OTUs of the *Cycloramphus fuliginosus* group. Integers are numbers of adult specimens.

	OTUs										
	1	2	3	4	5	6	7	8	9	10	11
± uniform	17	9	73	11	10	23	78	52	9	52	33
Dark with light spots (C)	20	2					1				

streams still occur. These 11 samples are Operational Taxonomic Units (OTUs) for purposes of analysis.

### Character Analysis

*Male Vocal Slits.* — Three character states occur within members of the group. Vocal slits are (1) clearly present, (2) clearly absent, or (3) represented by a vocal fold with no slit leading to a vocal sac. All the males of OTUs 1, 2, 3, 4, 5, and 7 have vocal slits. OTUs 6, 8, and 11 have individuals with all three states within each population. OTU 10 individuals either have or lack vocal slits. OTU 9 individuals have only a vocal fold, but this may be the result of sampling error, as only six males were available.

*Dorsal Pattern.* — Dorsal pattern varies among the OTUs in two ways. In OTUs 1, 2, 3, 5, 7, 10 some juveniles have more distinctive dorsal patterns (Figure 2) than

adults (juvenile pattern same as adult in OTUs 4, 6, 8, 9, 11). Most adult members of this group have similar dorsal patterns, consisting of a nondescript relatively uniform or indistinctly mottled dorsal pattern. Some individuals have a dorsal pattern of a dark background with light spots (Table 2, Figure 2). The other patterns are represented by a total of 10 individuals and are too rare to warrant further comment.

*Thigh Pattern.* — Thigh patterns range from uniform, or mottled, to distinctly spotted (Figure 3). For those OTUs in which adults have distinctly spotted posterior thigh surfaces, the smallest juveniles have mottled thighs, and larger juveniles have more distinctly spotted thighs. The distribution of states among OTUs is shown in Table 3.

*Lip Pattern.* — Lip patterns range from nearly uniformly dark to having distinct light lip bars (Figure 4). This character shows considerable variation within and among OTUs (Table 4).

Table 3. Distribution of posterior thigh surface pattern states among OTUs of the *Cycloramphus fuliginosus* group. Integers are numbers of adult specimens.

	OTUs										
	1	2	3	4	5	6	7	8	9	10	11
Uniform (A)	14	3	21	7	1	7	33	23		3	10
Mottled (B)	5	2	52		3	15	14	24		5	10
Small spots (C-1)	18	5	5	3	4	3	29	5			5
Large spots (C)	1	1	2	1	1		1		9	44	8

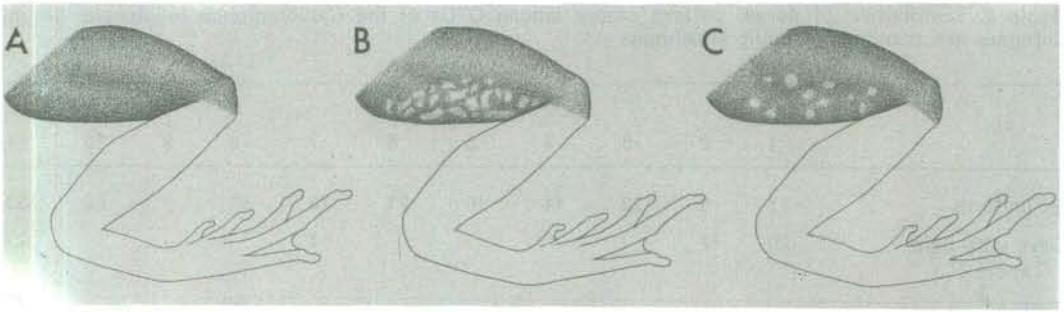


Figure 3. Thigh pattern standards. Letters as used in text. Additional standard not figured: C-1, small spots.

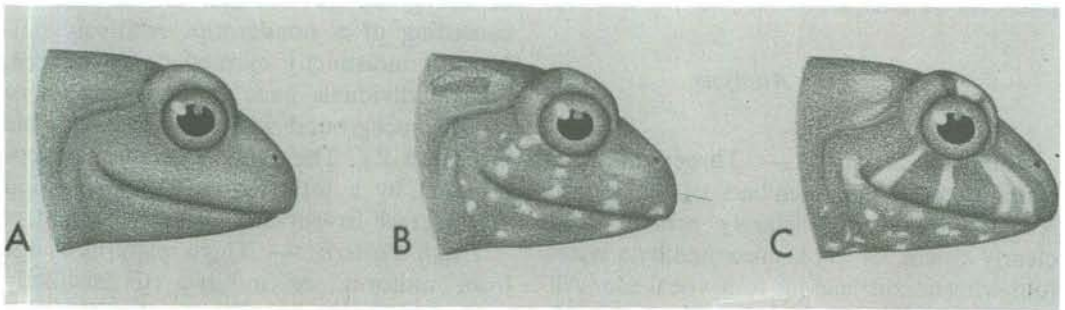


Figure 4. Lip pattern standards. Letters as used in text.

*Belly Pattern.* — Belly patterns range from dark to light and from uniform to light spotted (Figure 5). There is considerable intrapopulational variation, including differences between juveniles and adults. For example, within OTU 3 ( $N = 239$ ), 41% of the juveniles have a uniform belly, whereas only 6% of the adults have uniform bellies. The juvenile patterns are less dis-

tinctive than the adult patterns. The light spots (Figure 5, D) are very distinct in life, and appear like drops of white enamel paint. In preservative, the spots fade. Intrapopulation variation is extreme (Table 5), and precludes detailed comparison among OTUs, other than to point out that some members of OTU 10 have a distinct belly pattern.

Table 4. Distribution of lip pattern states among OTUs of the *Cycloramphus fuliginosus* group. Integers are numbers of adult specimens.

	OTUs										
	1	2	3	4	5	6	7	8	9	10	11
Uniform (A)	14	1	42	3	4	8	43	32	4	37	23
Indistinct bars (B)	14	1	33	7	4	14	28	18	5	12	10
Distinct lip bars (C)	10	9	5	1	1	3	6	2		2	



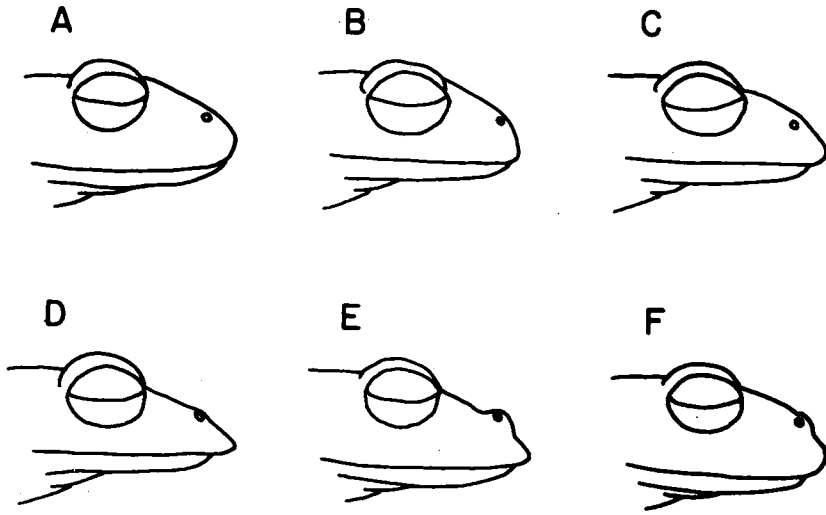


Figure 6. Snout profile standards.

*Snout Profile.* — The snout profile varies considerably (Figure 6), among and within OTUs (Table 6), ranging from rounded to strongly sloping, with lips flared or not.

*Dorsal Texture.* — The dorsal texture differs among the OTUs, but the differences are difficult to quantify. All members of this group have a rugose or warty dorsal surface texture; the few exceptions are

poorly preserved soft specimens. For comparative purposes, the dorsal texture is divided into two characters; (1) the alignment of warts and tubercles; and (2) the kinds of warts and tubercles.

There is considerable variation among OTUs in the alignment of warts and/or tubercles (Table 7). Some OTUs have individuals with regular rows of warts and/or

Table 6. Distribution of snout profile states among OTUs of the *Cycloramphus fuliginosus* group. Integers are numbers of adult specimens.

	OTUs										
	1	2	3	4	5	6	7	8	9	10	11
A	32	1	76	9	5	16	31	14	5	42	15
B	1	10	4	2			3	10		1	17
C							1	6	1		
D								1			
E						2		6			
F					4	7	40	14	3	9	1

Table 7. Distribution of wart alignment states among OTUs of the *Cycloramphus fuliginosus* group. Integers are numbers of specimens.

	OTUs										
	1	2	3	4	5	6	7	8	9	10	11
No alignment	63	13	197	8	57	7	168	31	8	10	30
Irregular rows	4	1	1		6	7	3	67	7	29	11
Regular rows						22		6	5	32	20

tubercles, specimens from other OTUs have no alignment or irregular rows.

In addition to a basically rugose skin, three distinctive textures are recognized: black-tipped tubercles, white-tipped tubercles, and/or a shagreen of fine white tubercles. Certain combinations of these three distinctive texture types are rarely encountered in members of this group. In these cases, categories were combined with the next most similar category. The black and white tipped tubercles represent a real difference that may be confounded by condition. The black tips of poorly preserved specimens can be shed, which tubercles then appear as white. However, some individuals have white tubercles as verified from freshly preserved specimens. The distribution of states among OTUs (Table 8) shows considerable intrapopulation variability in some OTUs and discrete occurrences in other OTUs.

*Webbing.* — In order to determine the amount of variation within OTUs, an indicator of amount of toe webbing is used. This indicator is the amount of webbing on the outer side of the fourth toe. The amount of webbing is determined by use of a webbing formula (Savage and Heyer, 1967), plotted against SVL. The degree of webbing (Figures 7-17) varies in three dif-

ferent ways. First, there is ontogenetic change, most noticeable in those OTUs in which adults have considerable amounts of webbing. An ontogenetic shift of webbing is not obvious for OTUs in which adults have reduced web. Second, there is considerable variation within OTUs, but this is of the same magnitude of variation found intraspecifically in hylid frogs (Savage and Heyer, 1969). Third, OTUs can be associated into three groups: (A) those OTUs with considerable amounts of webbing (OTU 1, Figure 7; OTU 2, Figure 8; OTU 4, Figure 10; OTU 9, Figure 15); (B) those OTUs with moderate amounts of webbing (OTU 3, Figure 9; OTU 5, Figure 11; OTU 7, Figure 13; OTU 11, Figure 17); (C) those OTUs with reduced webbing (OTU 6, Figure 12; OTU 8, Figure 14; OTU 10, Figure 16). There is no overlap of degree of webbing between OTUs with considerable and reduced webbing. There is some overlap between OTUs with considerable and moderate amounts of webbing. There is very little overlap between OTUs with moderate and reduced amounts of webbing. All of the OTUs with moderate and reduced web have the same modal amounts of web on the distal side of the fourth toe ( $3^-$  for moderately webbed OTUs,  $3\ 1/2$  for reduced webbed OTUs). There appears to be somewhat more var-

Table 8. Distribution of dorsal texture states among OTUs of the *Cycloramphus fuliginosus* group. Integers are numbers of specimens.

	OTUs										
	1	2	3	4	5	6	7	8	9	10	11
No tubercles or shagreen	68	14	195	8	1		30				
B, W, S + B, S						29		34		68	50
W, S					59	7		5	19	2	10
B, W + B								24			
W					3	1		30			
S			3				139	3			1

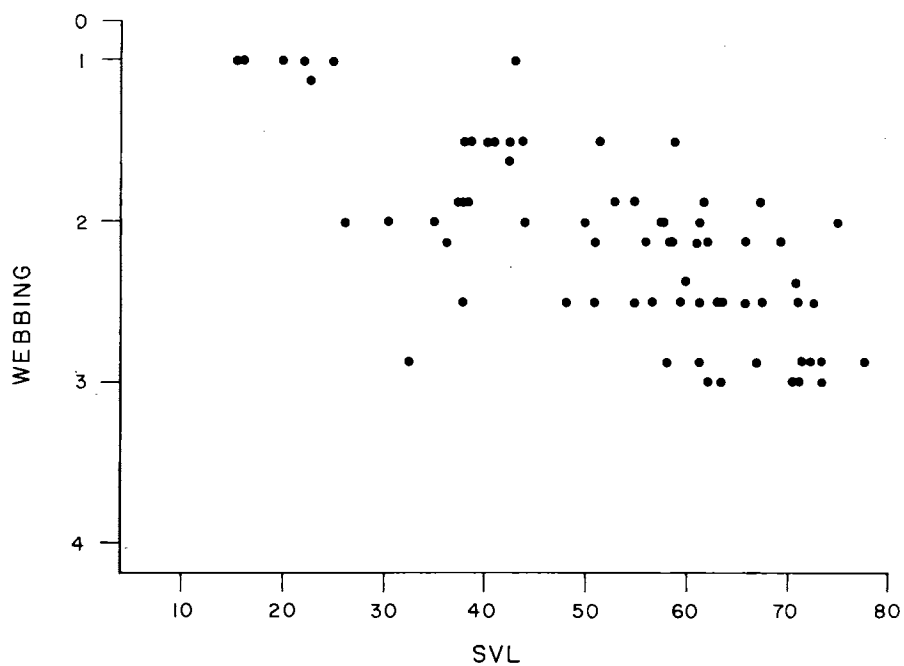


Figure 7. Fourth toe web/SVL plot, OTU 1, *Cycloramphus fuliginosus* group. Numbers on vertical axis represent free subarticular tubercles. Between 0 and 1 is a single descriptor, 1<sup>-</sup>; between other tubercles, seven descriptors are used, e. g., 1<sup>+</sup>, 1 1/4, 1 1/3, 1 1/2, 1 2/3, 1 3/4, 2<sup>-</sup>.

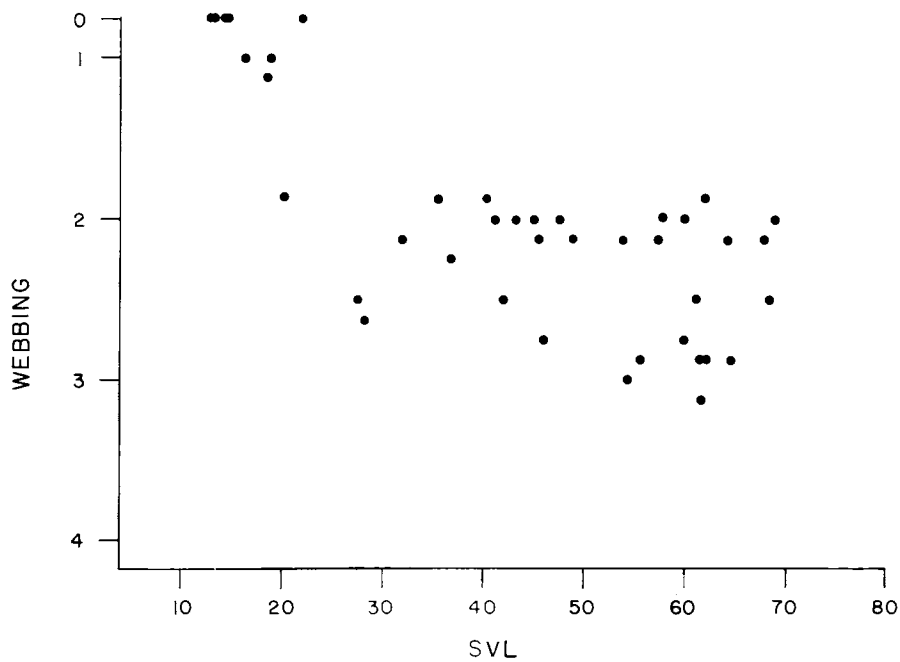


Figure 8. Fourth toe web/SVL plot, OTU 2, *Cycloramphus fuliginosus* group. Also see legend for Figure 7.

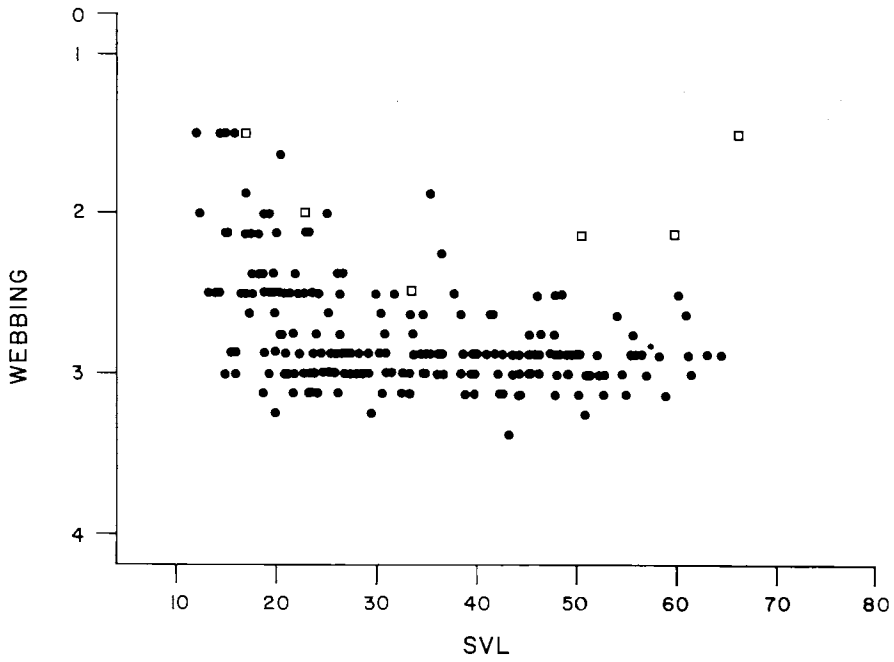


Figure 9. Fourth toe web/SVL plot, OTU 3, *Cycloramphus fuliginosus* group. Each dot represents from one to four individuals. Squares are considered OTU 1 specimens (see text). Also see legend for Figure 7.

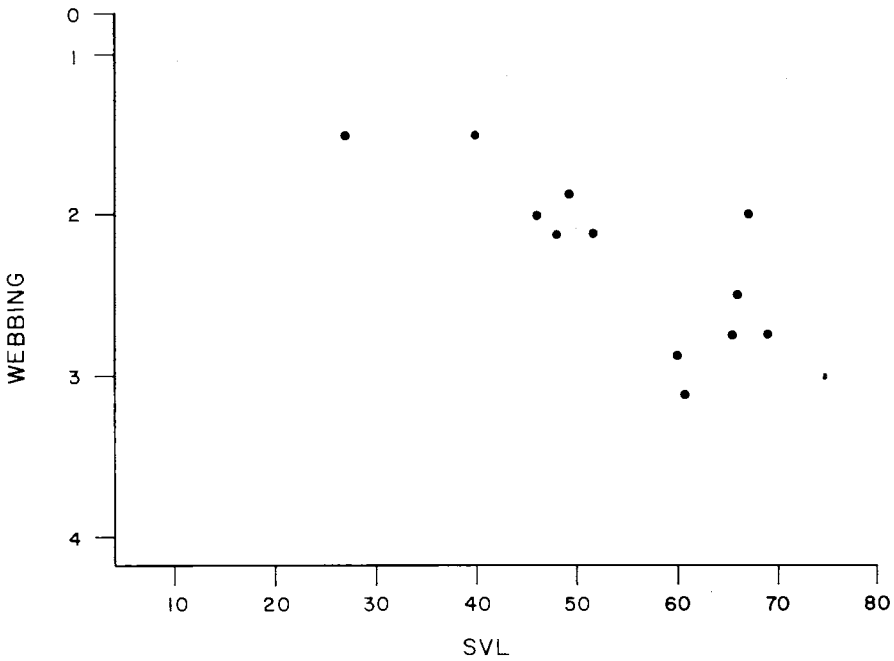


Figure 10. Fourth toe web/SVL plot, OTU 4, *Cycloramphus fuliginosus* group. A dot may represent more than one individual. Also see legend for Figure 7.

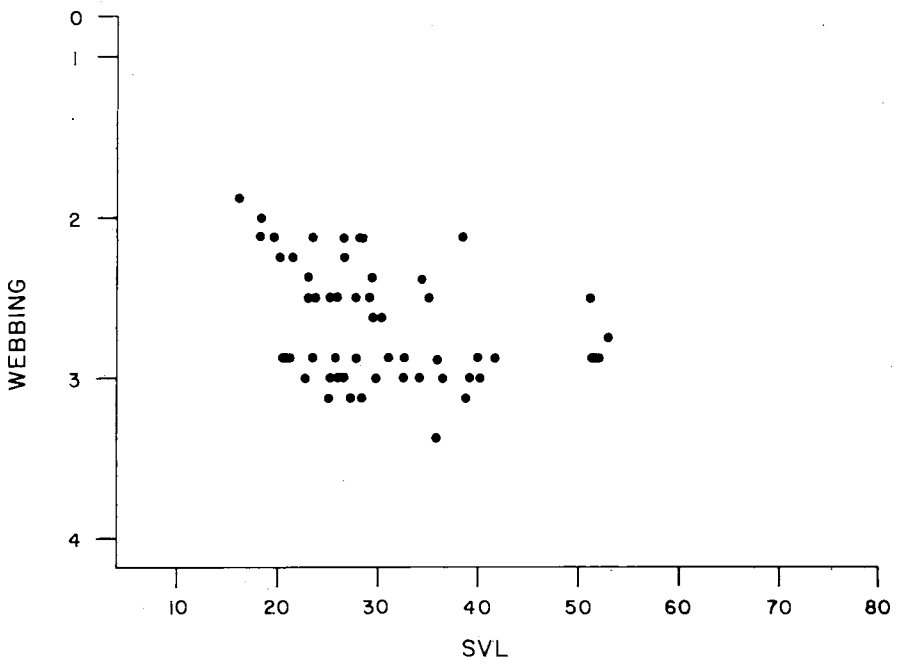


Figure 11. Fourth toe web/SVL plot, OTU 5, *Cycloramphus fuliginosus* group. A dot may represent more than one individual. Also see legend for Figure 7.

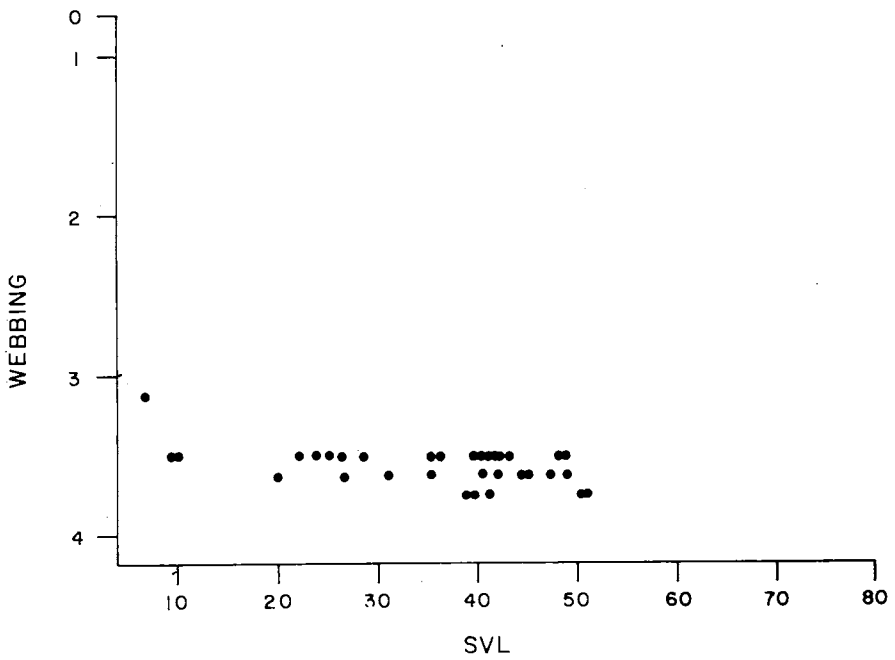


Figure 12. Fourth toe web/SVL plot, OTU 6, *Cycloramphus fuliginosus* group. A dot may represent more than one individual. Also see legend for Figure 7.



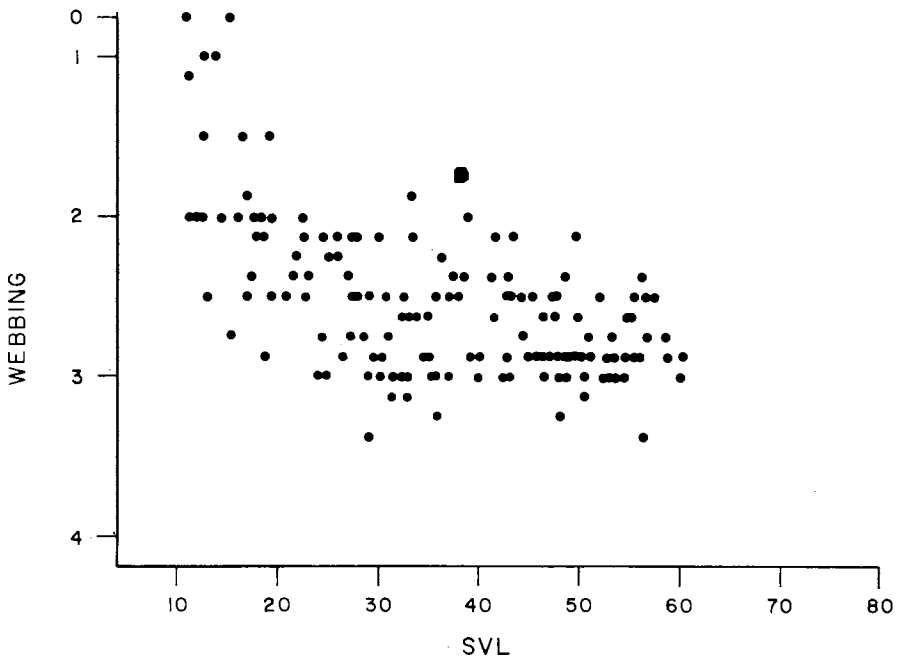


Figure 13. Fourth toe web/SVL plot, OTU 7, *Cycloramphus fuliginosus* group. A dot may represent more than one individual. Also see legend for Figure 7.

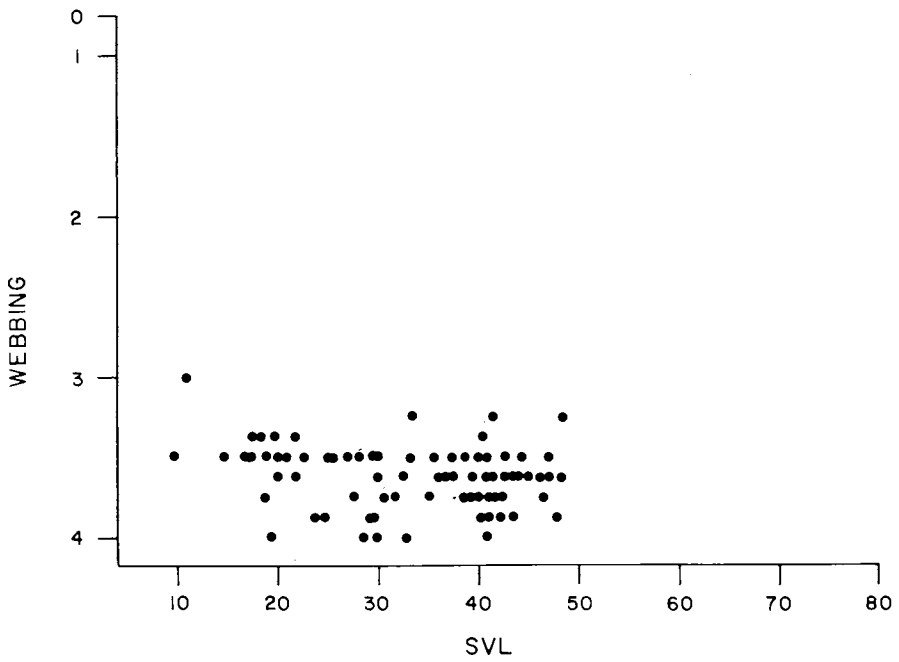


Figure 14. Fourth toe web/SVL plot, OTU 8, *Cycloramphus fuliginosus* group. A dot may represent more than one individual. Also see legend for Figure 7.

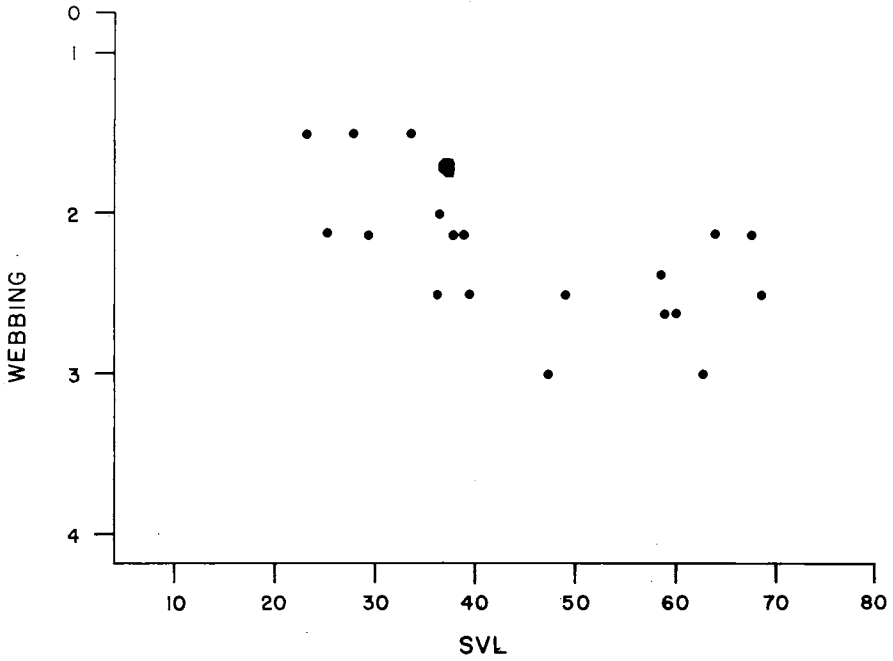


Figure 15. Fourth toe web/SVL plot, OTU 9, *Cycloramphus fuliginosus* group. A dot may represent more than one individual. Also see legend for Figure 7.

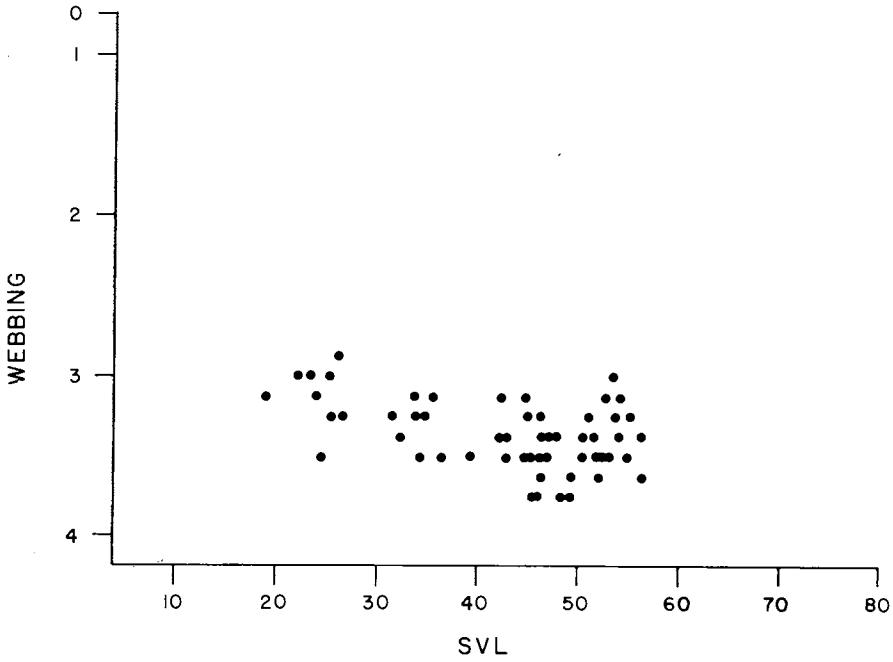


Figure 16. Fourth toe web/SVL plot, OTU 10, *Cycloramphus fuliginosus* group. A dot may represent more than one individual. Also see legend for Figure 7.

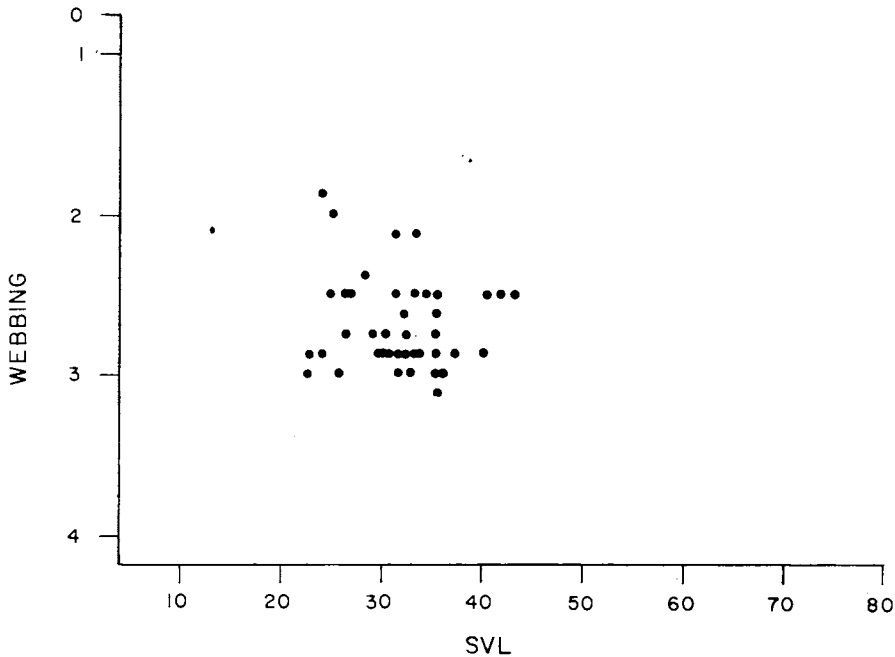


Figure 17. Fourth toe web/SVL plot, OTU 11, *Cycloaramphus fuliginosus* group. A dot may represent more than one individual. Also see legend for Figure 7.

iation among OTUs with considerable web, but the sample sizes are not large enough to clearly demonstrate any differences.

*Measurements.* — The following measurements were taken: snout-vent length (SVL), head length, head width, eye-nostril distance (from the anterior corner of the eye to mid-nostril), eye-eye distance (distance between anterior corners of eyes), femur length, tibia length, foot length (distance from posterior edge of inner metatarsal tubercle to tip of fourth toe). Measurements are examined in two ways: (1) SVL frequency distributions, (2) discriminant function analysis using all measurements except SVL for which the estimated body length is substituted.

The SVL measurements of adult specimens vary considerably among and within OTUs (Figures 18, 19). The size ranges within OTUs is considerable and for those with large samples, two or three size classes are evident. It is likely that both males and

females of this group are long lived and individuals are capable of breeding over several seasons.

The stepwise discriminant function analysis was performed on measurements of adult males and females from the 11 OTUs with the exception of females for OTU 5, for which there is only one female available. The program used was the BMD 07M (Dixon, 1977). The values as recorded from the specimens were used as the variables for analysis with the exception of BL discussed previously. For comments on the meaning and interpretation of results, see Heyer (1977, 1978).

*Males.* — Data for the 11 OTUs were used as the preformed groups for analysis. The variables entered the program in the following order (the F values to enter indicate the relative contribution of each variable to discriminate among the OTUs): Tibia ( $F = 151.8$ ), head length ( $F = 28.7$ ), foot ( $F = 24.5$ ), eye-nostril distance

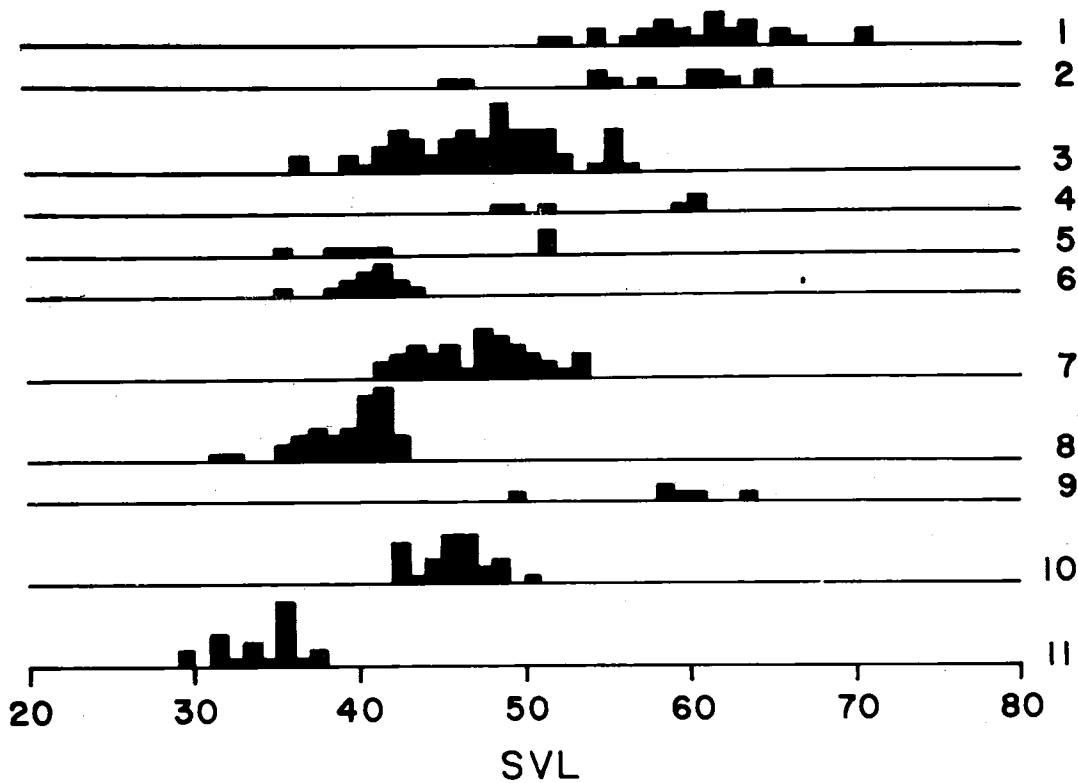


Figure 18. Male size distributions, *Cycloramphus fuliginosus* group OTUs.

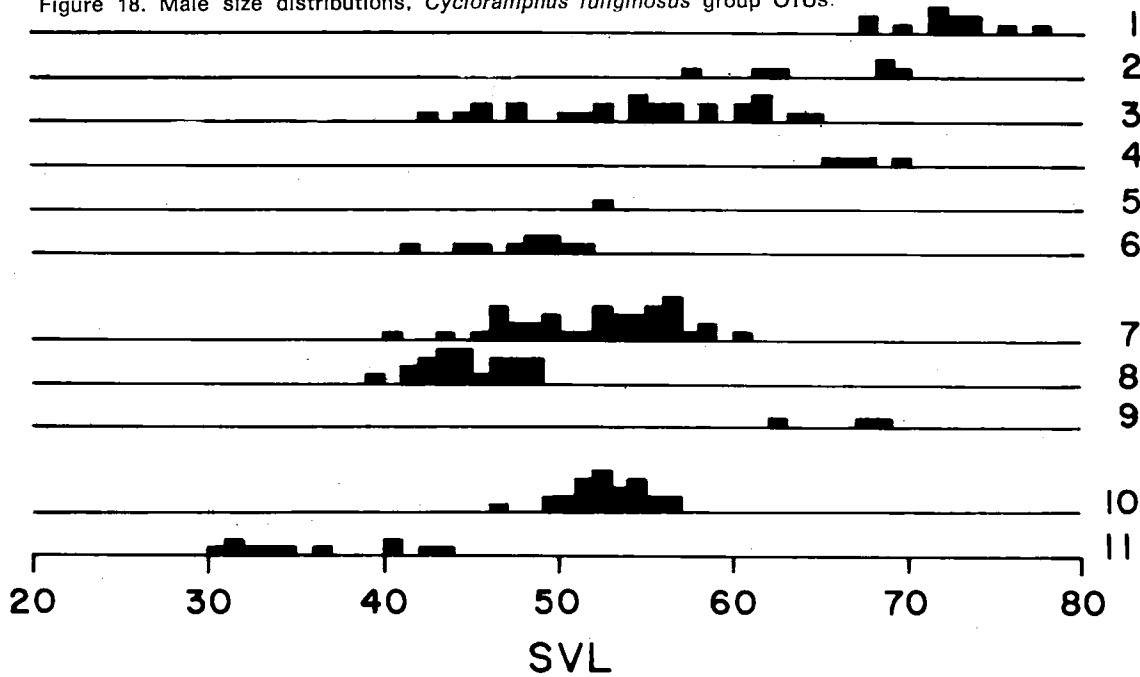


Figure 19. Female size distributions, *Cycloramphus fuliginosus* group OTUs.

( $F = 16.0$ ), head width ( $F = 6.8$ ), eye-eye distance ( $F = 5.8$ ), BL ( $F = 5.6$ ), femur ( $F = 1.5$ ). This is the only  $F$  value for which  $P > .05$ ; the femur data add no information to the analysis).

The classification matrix uses the centroid values for each of the species groupings and determines the probability of each specimen-case belonging to each grouping. The results indicate the discreteness of the groupings. The male results are presented in Table 9.

The plot of the first two discriminant axes gives a visual picture of the phenetic similarities of the species groupings (Figure 20). For the males, the first two axes account for 79% of the total dispersion. The first axis reflects a size component and accounts for 65% of the total dispersion. The variables, head length and foot length, have high coefficient values for the second axis; the second axis accounts for an additional 14% of the total dispersion. The third axis, which accounts for an additional 10% of the total dispersion, also has two variables with high coefficient values, head width and eye-nostril distance. The second and third axes reflect differences in leg length and head shape.

There is one male from OTU 2 that stands out in the analysis, particularly in the graphic plot of the first two discriminant

axes. Specimen AL 2878 comes out in the analysis morphologically the same as members of OTU 3, not as a member of OTU 2. Other members of OTU 2 have the same metacarpal arrangement as members of OTU 1. AL 2878 has the metacarpal arrangement found in members of OTU 3. The webbing is intermediate between that typical of either OTU 2 or 3 and is not diagnostic. The data tag indicates that both collector and date were not known. This specimen is omitted from further analysis and treated as a member of OTU 3 with erroneous locality data.

Females. — Data for 10 OTUs (OTU 5 omitted) were used for the preformed groups for analysis. The variables entered the program in the following order: Tibia ( $F = 115.2$ ), head length ( $F = 29.1$ ), foot ( $F = 27.3$ ), eye-eye distance ( $F = 24.4$ ), eye-nostril distance ( $F = 6.0$ ), BL ( $F = 5.2$ ), head width ( $F = 3.5$ ), femur ( $F = 2.7$ ). All  $F$  values have a  $P < 0.5$ ; all variables add information to the analysis.

The classification matrix (Table 10) indicates the same kind of OTU discreteness as the male analysis.

The plot of the first two discriminant axes is very similar to the male plot and is not figured. There is a better separation of

Table 9. Posterior classification matrix of males of 11 OTUs of the *Cycloramphus fuliginosus* group. Numbers heading columns and rows refer to OTUs as used in text.

	1	2	3	4	5	6	7	8	9	10	11
1 . . . .	19	7	0	0	0	0	0	0	1	0	0
2 . . . .	3	9	1	0	0	0	0	0	0	0	0
3 . . . .	0	0	53	2	1	4	1	2	0	0	0
4 . . . .	0	2	1	4	0	0	0	1	0	0	0
5 . . . .	0	0	0	0	4	1	1	1	0	1	0
6 . . . .	0	0	0	0	1	10	0	2	0	1	0
7 . . . .	0	0	0	1	5	0	30	0	0	3	0
8 . . . .	0	0	0	0	3	7	0	27	0	1	0
9 . . . .	0	0	0	0	0	0	0	0	7	0	0
10 . . . .	0	0	2	0	4	1	2	0	0	19	0
11 . . . .	0	0	0	0	0	1	0	0	0	0	31

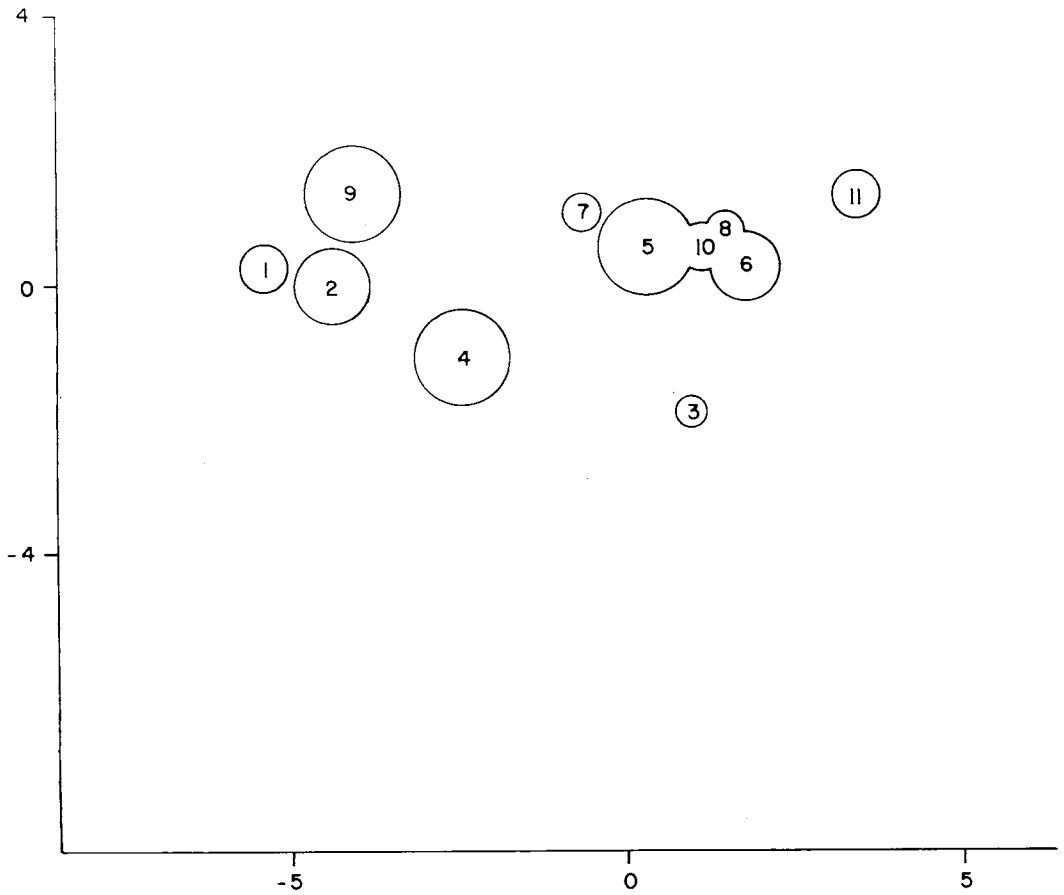


Figure 20. Discriminant axis plot of males of 11 OTUs of the *Cycloramphus fuliginosus* group. Numbers placed at group means refer to OTUs as used in text. Circles indicate 95% confidence interval for group centroids.

Table 10. Posterior classification matrix of females of 10 OTUs of the *Cycloramphus fuliginosus* group. Numbers heading columns and rows refer to OTUs as used in text.

	1	2	3	4	(5)	6	7	8	9	10	11
1 . . .	11	1	0	0		0	0	0	0	0	0
2 . . .	0	6	0	0		0	0	0	0	0	0
3 . . .	0	0	25	1		0	0	0	0	0	0
4 . . .	0	0	0	4		1	0	0	0	1	0
(5)											
6 . . .	0	0	0	0		9	0	1	0	0	0
7 . . .	0	0	2	0		0	33	1	0	3	0
8 . . .	0	0	0	0		3	0	19	0	1	1
9 . . .	0	0	0	0		0	0	0	4	0	0
10 . . .	0	0	0	0		1	2	2	0	23	0
11 . . .	0	0	0	0		0	0	0	0	0	19



examination of these characters can lead to even finer separation of some OTUs in some cases, as detailed below.

There are three localities where two OTUs of the *fuliginosus* group occur together. OTUs 5 and 6 are from the biological station of the University of São Paulo, Boracéia, in the State of São Paulo. OTUs 7 and 8 are from Cubatão, Paranapiacaba and immediate environs in the State of São Paulo. OTUs 9 and 10 are from near Morretes in the State of Paraná. Of the characters examined (Table 11), there is one that is consistent for all three pairs at the localities: webbing differentiates the OTUs. Dorsal texture also differentiates members of OTUs 7 and 8; measurements also differentiate members of OTUs 9 and 10. There are differences in dorsal texture which also separate OTUs 5 and 6, as can be drawn from Tables 7 and 8. The dorsal texture differences are obvious with well preserved specimens; the differences are of kind, not degree. The three OTU pairs that occur at a single locality represent two distinct species at each locality. Using the differences between these sympatric species pairs, any pair-wise combination that differs by webbing or by two characters is considered to represent species level differentiation. There remain three clusters of OTUs which need to be examined in detail to decide whether the differences found among the OTUs represent geographic variation or species differences: (1) OTUs 1, 2, 4, 9, (2) OTUs 3, 5, 7, 11; (3) OTUs 6, 8, 10.

Specimens of OTUs 1, 2, 4, 9 are all large specimens with considerable toe webbing. Examination of the data presented in Tables 2-10 indicates that OTUs 1 and 2 are most similar to each other and OTUs 1 and 2 together are most similar to OTU 4. OTU 9 is the most distinctive within this cluster. Comparison of specimens indicates that OTUs 1, 2, and 4 are similar in dorsal texture (no white or black tubercles, OTU 1 and 2 individuals not shagreened,

some poorly preserved individuals from OTU 4 have what appear to be weak shagreen, but other OTU 4 individuals definitely not with shagreen) and metacarpal arrangement (Figure 55 B) and differ from OTU 9 specimens in these features (white tubercles and strong shagreen, different metacarpal arrangement, Figure 55 A). The differences among OTUs 1, 2, and 4 are differences of degree, not kind and are interpreted as representing geographic variation. With this explanation, OTUs 1 and 2 are more similar to each other than either is to OTU 4. The differences between OTUs 1, 2, 4 and OTU 9 are differences of kind and are interpreted as representing species level differences.

OTU 3, 5, 7, and 11 specimens are of moderate size with moderate toe webbing. OTU 11 is the most distinctive within this cluster (Tables 2-10). Measurements distinguish OTU 11 from OTUs 3 and 7 (Figure 20). Each OTU is distinctive in some aspect of dorsal texture (Tables 7, 8). Examination of freshly preserved specimens indicates that the dorsal texture of each OTU is distinctive. OTU 3 is rugose, but has no distinct tubercles or shagreen. The dorsal texture of OTU 3 appears the same as that of OTUs 1, 2, and 4. The dorsal texture of OTU 5 has in addition to the rugose condition, a shagreen and scattered white-tipped tubercles. The dorsal texture of OTU 7 is rugose and has a shagreen; there are no tubercles. The dorsal texture of OTU 11 has numerous black and/or white tipped tubercles and a shagreen. The metacarpal arrangements found in these four OTUs are similar. OTU 11 is most similar to OTU 5, but direct comparison of the specimens demonstrates that the distinctiveness of the dorsal textures is striking. OTUs 3 and 7 are most similar; direct comparison of specimens indicates that differences between dorsal textures are subtle, but evident. Consistent with other species level decisions, OTUs 3 and 7 are



here considered distinct species. OTUs 5 and 7 have historically been considered conspecific (Bokermann, 1951). The dorsal surfaces are distinct, however and are here considered indicative of species level differences.

OTU 6, 8, and 10 specimens are of moderate size with reduced toe webbing. OTU 10 is the most distinctive of these three (Tables 2-10), especially in the posterior thigh surface pattern (Table 3). The dorsal surface textures are similar in having numerous distinct black and white-tipped tubercles and a shagreen. Direct comparison of well preserved individuals indicates that the tubercles of OTUs 6 and 8 are more raised than those of OTU 10, hence more prominent. This is particularly noticeable when comparing the tubercles on the upper surfaces of the tibia. Specimens from OTU 10 had red bellies in life, whereas specimens from OTUs 6 and 8 lack red on the belly in life. The metacarpal arrangement is similar for all members of these OTUs. OTU 10 is considered specifically distinct from OTUs 6 and 8. The differences between OTUs 6 and 8 are those of degree only and are considered to represent geographic variation.

#### Additional Specimens of the *Cycloramphus fuliginosus* Group

Most of the additional specimens examined were clearly identifiable with the OTUs analyzed in the previous section and were from nearby localities. There are several exceptions, which are discussed in detail. Briefly, the exceptions consist of: (1) a group of specimens from southern São Paulo (State) and the State of Paraná which are not identifiable with any of the recognized OTUs, (2) a few specimens are identifiable with the previously analyzed OTUs, but are not from localities near the OTU they resemble, and (3) two distinctive individual specimens.

The specimens from the states of São Paulo and Paraná are of moderate size, have moderate web and have a dorsal texture of numerous black and/or white tipped tubercles, usually aligned in irregular or regular lines and a shagreen. The dorsal texture is like that expressed by members of OTUs 6 and 8, but the São Paulo and Paraná specimens have more webbing than those of OTUs 6 and 8. Additionally, 11 of the 14 specimens of the São Paulo and Paraná form have large spots on the posterior surface of the thigh, whereas no members of OTUs 6 and 8 have this state (Table 3). The only other OTU with which the São Paulo and Paraná form resembles closely is OTU 11. The dorsal textures differ in that the tubercles of the São Paulo and Paraná form are more pronounced than those of OTU 11. These differences are striking when specimens are compared side by side but are difficult to describe. Additionally, the São Paulo and Paraná form is larger than the OTU 11 form. The differences found between the São Paulo and Paraná form and the other OTUs are of the same magnitude used in recognizing species limits among the OTUs analyzed in the previous section. The São Paulo and Paraná form is considered a distinct species within the *Cycloramphus fuliginosus* group.

The specimen MNRio 1203 was previously mentioned with the Tijuca-Sumaré sample. This specimen is the same as the São Paulo and Paraná species. When specimens were borrowed from the Museu Nacional in Rio de Janeiro, the individuals from each bottle were wrapped separately with the bottle label. Specimen MNRio 1203 was in the same bottle with MNRio 1207, 1210-11. The bottle label gives data only for specimen MNRio 1207. Prof. Antenor Leitão de Carvalho kindly informs me that 1207 was collected from the Serra de Mangaratiba, Rio de Janeiro by Carvalho and Bailey. The Serra de Mangaratiba is next to the coast close to the State of São

Paulo. The specimen is thus not from Tijuca-Sumaré, but it nevertheless represents a disjunct locality from other members of the São Paulo-Paraná species.

All but four specimens of OTU 11 are from the State of Santa Catarina. The other four are from the Paranapiacaba-Cubatão region of São Paulo. Three specimens, MNRio 98, are from Alto da Serra, São Paulo and are clearly the same as OTU 11 specimens. MZUSP 13909 from Paranapiacaba is a juvenile and the identification is not as positive as for MNRio 98(3). The MNRio specimens were collected by F. C. Hoehne and A. Gehrt; there is no known reason to doubt the locality data.

The final outlier is the only specimen reported from the State of Rio Grande do Sul. The locality data for specimen USNM 121318 is Santa Maria, Rio Grande do Sul, received from the Instituto Butantan. The specimen is faded, but is identifiable as the same species as OTU 6 and 8, all other specimens being from the State of São Paulo. Aristoteris T. Leão, a technician of the Section of Parasitology at the Instituto Butantan, kept a frog catalogue in a book originally designed to record autopsies. This book, now at the MZUSP, records that specimen 617, one of a lot of 4, was exchanged to the USNM, and that Cochran had identified all specimens of the lot as *C. asper*. The locality data for the specimen, now USNM 121318, is Rio Grande da Serra, São Paulo, collected in January 1938. Rio Grande, São Paulo is an old railroad station between the cities of Santos and São Paulo. The previously reported locality data, as well as the original USNM ledger data for 121318 are in error. A recent checklist of the amphibians of the State of Rio Grande do Sul (Braun and Braun, 1980), includes *C. asper*. The record for this species occurrence in the State is based on USNM 121318; *Cycloramphus* has otherwise not been collected from Rio Grande do Sul (Pedro Canisio Braun, pers. comm.).

There are three specimens (a female, L 176, and two juveniles, USNM 137680-81) from Santa Catarina that differ from other specimens examined from that region, but are provisionally included in OTU 9 (see later discussion of *C. asper*).

A single specimen from Campos do Jordão (MZUSP 4522) is a moderately large (SVL 46.7) female. The dorsal texture and size are similar to specimens from OTUs 1-4. However, rather than having considerable toe webbing, the specimen has reduced toe webbing. The magnitude of difference is such that it is not likely aberrant. Unfortunately, the sacral region is dissected, so accurate measurements can not be made to compare with the other OTUs. The strikingly different web condition indicates that this specimen represents a distinct species. It is possible that the habitat for this species may have been drastically reduced or obliterated. The specimen was collected in 1944. Werner C. A. Bokermann has collected extensively in the Campos do Jordão region in the 1960-1978 period and has collected no additional material of this species.

A single juvenile specimen of *Cycloramphus* from Caparaó, Pico da Bandeira, Espírito Santo (MZUSP 52924) appears to morphologically bridge the gap between the *fuliginosus* and *granulosus* groups. The toe webbing is reduced, but the dorsal texture is granular, as in members of the *granulosus* group. This individual represents one of the most distinctive species of *Cycloramphus*.

#### Nomenclature

There is considerable confusion concerning the nomenclature of the *Cycloramphus fuliginosus* group (Bokermann, 1951, 1966). Each of the 14 names that have been proposed for the *C. fuliginosus* species group (included in Table 12) are discussed chronologically.

Table 12. Names proposed for members of the genus *Cycloramphus* and the current taxonomic status of each.

Described Name	Current Status
<i>Cycloramphus asper</i> Werner, 1899	<i>Cycloramphus asper</i> Werner
<i>Telmatobius asper</i> Boulenger, 1907	<i>Cycloramphus asper</i> Werner
<i>Cyclorhamphus boulengeri</i> Lutz, 1929	<i>Cycloramphus asper</i> Werner
<i>Telmatobius brasiliensis</i> Steindachner, 1864	<i>Cycloramphus brasiliensis</i> (Steindachner)
<i>Cycloramphus diringshofeni</i> Bokermann, 1957	<i>Cycloramphus diringshofeni</i> Bokermann
<i>Cycloramphus distinctus</i> Lutz, 1932	<i>Cycloramphus ohausi</i> (Wandolleck)
<i>Iliodiscus dubius</i> Miranda-Ribeiro, 1920	<i>Cycloramphus dubius</i> (Miranda-Ribeiro)
<i>Telmatobius duseni</i> Andersson, 1914	<i>Cycloramphus duseni</i> (Andersson)
<i>Iliodiscus eleutherodactylus</i> Miranda-Ribeiro, 1920	<i>Cycloramphus eleutherodactylus</i> (Miranda-Ribeiro)
<i>Cycloramphus eleutherodactylus</i> var. <i>strigilata</i> Lutz, 1929	<i>Cycloramphus eleutherodactylus</i> (Miranda-Ribeiro)
<i>Cycloramphus eleutherodactylus</i> var. <i>variegata</i> Lutz, 1929	<i>Cycloramphus eleutherodactylus</i> (Miranda-Ribeiro)
<i>Cycloramphus fuliginosus</i> Tschudi, 1838	<i>Cycloramphus fuliginosus</i> Tschudi
<i>Cyclorhamphus granulatus</i> Lutz, 1929	<i>Cycloramphus granulatus</i> Lutz
<i>Iliodiscus lutzii</i> Miranda-Ribeiro, 1929	<i>Cycloramphus fuliginosus</i> Tschudi
<i>Cyclorhamphus neglectus</i> Lutz, 1928	<i>Cycloramphus asper</i> Werner
<i>Ceratophrys ohausi</i> Wandolleck, 1907	<i>Cycloramphus ohausi</i> (Wandolleck)
<i>Iliodiscus pinderi</i> Miranda-Ribeiro, 1920	<i>Cycloramphus brasiliensis</i> (Steindachner)
<i>Grypiscus scleromeris</i> Miranda-Ribeiro, 1935	<i>Nomen dubium</i>
<i>Iliodiscus semipalmatus</i> Miranda-Ribeiro, 1920	<i>Cycloramphus semipalmatus</i> (Miranda-Ribeiro)
<i>Niederia spinulifera</i> Ahl, 1923	<i>Cycloramphus asper</i> Werner
<i>Grypiscus umbrinus</i> Cope, 1867	<i>Cycloramphus fuliginosus</i> Tschudi

*Cycloramphus fuliginosus* Tschudi, 1838. — Tschudi proposed the new generic name *Cycloramphus*, in which he included (1838:81) a single species, *fuliginosus*, which is the type species by monotypy. Bokermann (1951) pointed out that *C. fuliginosus* was evidently a *lapsus calami* for *C. fuliginosus*. Duméril and Bibron (1841) retained Tschudi's name for the frogs in the Paris Museum collection upon which Tschudi apparently based his name. Tschudi's description is brief, but all the characteristics pertain to what are now considered to be members of the genus *Cycloramphus*. Tschudi listed *fuliginosus* from India, whereas Duméril and Bibron stated that *fuliginosus* was collected by Delalande from Brasil. Miranda-Ribeiro (1929) concluded that *Cycloramphus fuliginosus* was a *nomen nudum* because of the different localities of Tschudi's and Duméril and Bibron's *fuliginosus* together with the fact that Tschudi did not designate nor figure a type specimen. Miranda-Ribeiro

(1929) further argued that *Cycloramphus fuliginosus* Tschudi could just as well pertain to the Andean genus *Telmatobius* as there was no mention of an inguinal gland by Tschudi, whereas Duméril and Bibron mention this gland in their specimens of *fuliginosus*. Bokermann (1951) correctly pointed out that *Cycloramphus fuliginosus* Tschudi was not a *nomen nudum*, but a valid genus and species as defined by the rules of zoological nomenclature for taxa described prior to 1930, in which no figure or designated specimen was required. Bokermann (1951) concluded that Tschudi considered Duméril and Bibron's 1841 assertion that Tschudi's name was based on the Paris Museum specimens from Brasil to be correct. Bokermann reasoned that Tschudi later treated *Cycloramphus*, citing a name which appeared (and only could have come from) Duméril and Bibron's 1841 work, without arguing Duméril and Bibron's assertions. This negative evidence is suggestive, but not conclusive. The only

firm conclusion that can be drawn concerning *Cycloramphus fuliginosus* Tschudi is that the generic and specific names are nomenclaturally valid and available. Biologically, the data are not adequate to decide whether Tschudi's *Cycloramphus fuliginosus* is the same as Duméril and Bibron's *C. fuliginosus* or whether Tschudi's *C. fuliginosus* pertains to a SE Brazilian or Andean species. However, since Bokermann's revision (1951) the genus name for this group of frogs has been stabilized as *Cycloramphus* Tschudi. As the biological data are equivocal, the best conclusion in terms of nomenclatural stability is to consider that Tschudi based his name upon the specimens in the Paris Museum collected by Delalande from Brasil.

A cotype MNHP 750 is soft and faded but clearly referable to Brazilian frogs herein referred to *Cycloramphus*. There are no tubercles on the dorsum. The webbing is moderate (web 2 2/3 on left, 3+ on right outer fourth toe); but the amount of web is not diagnostic as it falls into the area of overlap between OTU 1, 2, 4 and OTU 3. The male is about 57 mm SVL, which is at the large end of the size distribution for OTU 3. The metacarpal condition is that found in OTU 3. Thus, *Cycloramphus fuliginosus* is considered the oldest available name for OTU 3. MNHP 750 is hereby designated as the lectotype of *Cycloramphus fuliginosus* Tschudi. Papavero (1971, p. 116) documents that all Delalande's specimens originated from the State of Rio de Janeiro.

*Telmatobius brasiliensis* Steindachner, 1864. — The type locality for this species, described on the basis of a single specimen collected by Natterer, is Brasil (probably the environs of Rio Janeiro). The 28.7 mm specimen (Vienna 22922) is still in reasonable condition. The dorsal texture lacks distinct tubercles, aligning the holotype with either the OTU 1, 2, and 4 or OTU 3 species from around Rio de Janeiro. The

foot is extensively webbed, the web state on the outer side of the fourth toe is 1 (compare this state on Figures 7 and 9). The metacarpal condition is equivocal, as expected for juveniles. The webbing is diagnostic of the Organ Mountain species, OTU 1, 2, and 4. *Telmatobius brasiliensis* is the oldest available name for the Organ Mountain species.

*Grypiscus umbrinus* Cope, 1867. — The holotype, MCZ 1497, collected by the Thayer Expedition, is in reasonable condition. The 48 mm specimen has the dorsal texture of rugosity without tubercles, characteristic of OTUs 1, 2, 4 and 3. The metacarpal tubercle condition is that typical of OTU 3. The foot is moderately webbed, the web on the outer side of the fourth toe being a 3- condition, typical of OTU 3 (Figure 9) and less than that typically found in OTUs 1, 2, 4. *Grypiscus umbrinus* Cope is clearly the same species analyzed as OTU 3. *Cycloramphus fuliginosus* is the oldest available name for OTU 3.

*Cyclorhamphus asper* Werner, 1899. — I have been unable to locate the type of *C. asper*. The type is not in the Berlin collections, the most likely repository. Werner's description is brief, but the following diagnostic points are clear in the description: foot 1/2 webbed, dorsum with dense pointed warts, length 54 mm, from Santa Catarina. The webbing, dorsal texture and size are not consistent with any specimens examined in the preceding section. Subsequent to the OTU analysis, I was able to borrow the type of *Telmatobius asper* Boulenger (also see next paragraph), borrow additional material from Santa Catarina from the Vienna Museum, and collect fresh material from Santa Catarina. All of the above mentioned material comes from around Queçaba (Theresópolis), Santa Catarina. The type description is consistent with this material in terms of webbing and dorsal texture. The largest female examined is 53.7 mm, close to the size given by

Werner. It is likely that Werner's specimen was a female as he does not mention an inguinal gland in the description. Nieden (1923, Fig. 291) presented a sketch of the type. The sketch shows less toe webbing than what I would consider one-half webbed. Nieden likely did not critically examine the specimen or drawing with respect to web, because in his key to the genera, he characterized *Cycloramphus* as having web between the metatarsals of the fourth and fifth digits. No *Cycloramphus* has this condition and the drawing does not clearly indicate the extent of web between the metatarsals. Without recourse to direct examination of the type, I follow the description, rather than Nieden's sketch. Based on the description, *Cycloramphus asper* Werner is considered the oldest available name for the species known from around Queçaba, Santa Catarina. Three other species are known from Santa Catarina, but all are considerably smaller than Werner's type and differ in terms of webbing and dorsal texture. The three specimens mentioned previously (L 176, USNM 137680-81) belong to this species, rather than OTU 9.

*Telmatobius asper* Boulenger, 1907. — Lutz (1929) considered Boulenger's *asper* to be a distinct species of *Cycloramphus*. As Boulenger's *asper* is a homonym of Werner's *asper*, Lutz gave the new names *neglectus* (1928) and *boulengeri* (1929) to the species Boulenger named. Bokermann (1966) stated that Lutz had a specimen labeled as "tipo" (specimen 1792, now in collection of MNRio) of *Cycloramphus boulengeri* from São Bento, Santa Catarina and correctly pointed out that as Lutz's name was a replacement name for *Telmatobius asper* Boulenger, the type for *Cycloramphus boulengeri* is the specimen (BMNH 1947.2.15.48) Boulenger described. The species Lutz thought to be the same as Boulenger's *asper* is not. Specimen 1792 is a member of the OTU 11 species. Bou-

lenger's specimens of *asper* are distinct from specimens examined in the OTU analysis, but the same as the Santa Catarina material mentioned above. The dorsal texture is the same as that found in OTUs 6 and 8 and the São Paulo and Paraná species, having pronounced heterogeneous large and small tubercles; however, the feet are extensively webbed, differentiating Boulenger's *asper* from these other taxa. The dorsal texture of Boulenger's *asper* is very different from the texture of the OTU 9 species, which has similar webbing. Both the dorsal texture and webbing differentiate Boulenger's *asper* from OTUs 10 and 11 which also occur in Santa Catarina. Specimen BMNH 1947.2.15.48, a 47.8 mm SVL adult male, collected by J. Michaelis, is hereby selected as the lectotype of *Telmatobius asper* Boulenger.

As indicated above, the type description of *Cycloramphus asper* Werner matches the characteristics of *Telmatobius asper* Boulenger. Thus, *Telmatobius asper* Boulenger is both a homonym and synonym of *Cycloramphus asper* Werner.

*Telmatobius duseni* Andersson, 1914. — Andersson's description of the material collected by the botanist, Dr. P. Dusén, is extensive and complete enough to associate the name with one of OTUs defined recognized in the preceding section. The diagnostic characteristics Andersson describes are: (1) toes one third to scarcely half webbed, (2) "The whole upper surface is provided with densely scattered small tubercles, each usually ending in a rounded horny knob. On the back and the upper parts of the sides the tubercles are to some extent arranged in longitudinal series, forming narrow folds which sometimes are rather regular and angularly bent, or, usually, short, straight or oblique and then numerous.", (3) a large nearly circular disc-shaped inguinal gland, (4) thighs anteriorly and posteriorly spotted with white, (5) male size 31-37 mm. All these features

match individuals of OTU 11 from Santa Catarina. OTU 11 is the smallest species of the *C. fuliginosus* group; the sizes of Andersson's types match exactly. The specimens were taken in crevices and cracks in vertical cliffs. Specimens were taken under similar conditions west of Pirabeiraba, Santa Catarina. The specimens are from Ipiranga, Paraná. OTU 11 specimens are mostly known from Santa Catarina, with a few specimens from São Paulo. If the São Paulo specimens are the same as those in OTU 11, then Andersson's material from Paraná in part fills in a distributional gap. The description indicates that either Andersson's species is the same as the OTU 11 species, or a distinct species closely allied with OTU 11. I take the conservative position and conclude that *Telmatobius duseni* Andersson is the oldest available name for the species recognized as OTU 11 in the preceding section. I have since examined the types, which will be reported on separately.

*Iliodiscus dubius* Miranda-Ribeiro, 1920. — Miranda-Ribeiro described this species based on a series of specimens in the MZUSP from Alto da Serra, São Paulo. I have examined the paratypes of *I. dubius*; the description and paratypes (MZUSP 168, 170, 318, 320, 754, 890) agree in all details with the species analyzed as OTU 7 above. *Iliodiscus dubius* is the oldest available name for the species analyzed as OTU 7.

*Iliodiscus pinderi* Miranda-Ribeiro, 1920. — Bokermann (1951) discussed the confusion regarding the locality of the type specimen. Miranda-Ribeiro, in the description of *I. pinderi*, listed the locality as Ilha de São Sebastião, São Paulo. The specimen listed as the type in the MZUSP collection, number 1008 (recatalogued from 647) is from Serra de Macaé, Rio de Janeiro. Specimen 1008 appears to be identical with the specimen photographed by Miranda-Ribeiro (1920) as the type and then only known specimen of *Iliodiscus pinderi*

including the nick in the web between the third and fourth toes of the left foot. The 59.4 mm SVL specimen is almost fully webbed, has small distinct spots on the posterior surface of the thigh, and the dorsal texture is rugose lacking tubercles and shagreen. This combination of character states firmly allies MZUSP 1008 with the species recognized above as a combination of OTUs 1, 2, and 4. The only discrepancy is that MZUSP 1008 has more webbing than the other specimens of OTUs 1, 2, and 4. The difference in webbing is slight, however, and could be due to geographic variation. The only specimens of the *C. fuliginosus* group from the Ilha de São Sebastião I have examined belong to the same species as represented by OTU 5. MZUSP 1008 clearly is not the same as the OTU 5 species, differing in thigh pattern, webbing, and dorsal texture. The striking similarity between MZUSP 1008 and Miranda-Ribeiro's photograph of the type, together with the alliance of MZUSP 1008 with the Serra dos Orgãos and not the Ilha de São Sebastião species, leads to the conclusion that Miranda-Ribeiro had incorrect locality data for the specimen he described as *Iliodiscus pinderi* (as also concluded by Bokermann, 1951). The oldest available name for the species is *brasiliensis*.

*Iliodiscus semipalmatus* Miranda-Ribeiro, 1920. — The holotype, MZUSP 737, from Campo Grande, São Paulo is faded, but otherwise in good condition. The 41.9 mm SVL male specimen is characterized by reduced webbing and a dorsal texture of distinct tubercles and shagreen. This combination of states clearly associates this specimen with the species recognized above as a combination of OTUs 6 and 8. *Iliodiscus semipalmatus* is the oldest available name for this species.

*Niedenis spinulifera* Ahl, 1923. — Noble (1926) compared the types of *Niedenis spinulifera* with a specimen identified as *Cycloramphus asper* in the Berlin Museum

and considered them conspecific. Cochran (1955) and Bokermann (1966) followed Noble in this arrangement. The type of *N. spinulifera* is no longer in the Berlin Museum collections (G. Peters, pers. comm.). Ahl described few diagnostic characters: toes with full webbing; dorsum thick with small, pointed white colored warts; 42-46 mm. The associated locality and collector data were lost for the specimen. There are only two species of *Cycloramphus* that have considerable webbing and have white dorsal warts: OTU 9 and the species from Santa Catarina associated with *Cycloramphus asper* above. *Cycloramphus asper* has more webbing than the OTU 9 species individuals. The specimens are likely females or juveniles, as Ahl did not mention an inguinal disk; the sizes of the types could pertain to either species. Very likely, the specimen that Noble compared with the types of *Niederia spinulifera* was *Cycloramphus asper* from Santa Catarina, as many early frog specimens going to European museums originated from Santa Catarina. As the available evidence is consistent with Noble's conclusion, I concur that *N. spinulifera* is a synonym of *C. asper*.

*Cycloramphus neglectus* Lutz, 1928. — Lutz proposed *neglectus* as a new name for *Telmatobius asper* Boulenger, preoccupied by *Cycloramphus asper* Werner. This is the oldest available replacement name for Boulenger's *asper* (see following name), which is here considered a synonym of *Cycloramphus asper* Werner.

*Cycloramphus boulengeri* Lutz, 1929. — Lutz proposed a second replacement name for *Telmatobius asper* Boulenger, for which Lutz designated a type specimen from the MNRio collection (see *Telmatobius asper* Boulenger, above). Lutz often published preliminary descriptions and observations in the Comptes Rendus des Séances de la Société de Biologie, Paris, prior to a more extended treatment in the Memórias do Instituto Oswaldo Cruz series. Lutz also

freely modified the rules of zoological nomenclature, so it is hardly surprising that he should propose two replacement names for the same Boulenger species or designate a type for one of his replacement names. *Cycloramphus boulengeri* has no taxonomic standing, as it is a later replacement name for *T. asper* Boulenger, for which *C. neglectus* has priority.

*Iliodiscus lutzi* Miranda-Ribeiro, 1929. — Miranda-Ribeiro thought that *Cycloramphus fuliginosus* Tschudi pertained to the same frogs recognized today as *Telmatobius* from the Andes of South America. Miranda-Ribeiro accepted Lutz's (1929) recognition of two species in or near Rio de Janeiro, but believed the species Lutz identified as *fuliginosus* lacked a name, and therefore proposed the new name *lutzi*. There is a problem of precise association of *lutzi*, however. Lutz (1929) clearly indicated that the species he called *fuliginosus* was from Tijuca and Corcovado and other localities in or near the city of Rio de Janeiro itself. Lutz (1929) also clearly indicated that the species he identified as *pinderi* came from the Serra de Petrópolis (Organ Mountains) at an average elevation of 800 m. Miranda-Ribeiro (1929) stated that *lutzi* came from the lower slopes of the Petrópolis mountains. Miranda-Ribeiro's (1929) other comments make it clear that he was referring to the city of Rio species (Lutz's *fuliginosus*), however. Bokermann (1966) pointed out that in Miranda-Ribeiro's 1935 treatment, he gave the type-locality of *lutzi* as the lower Serra de Petrópolis, a change from Miranda-Ribeiro's (1929) earlier statement. I find Miranda-Ribeiro's 1929 and 1935 statements consistent, contrary to Bokermann (1966). Aside from the locality, every other indication is clear as what was meant nomenclaturally. It is concluded herein that *Iliodiscus lutzi* refers to the same taxon identified by Lutz as *fuliginosus*, which is the same as the OTU 3 species of the previous analysis.

The situation is sufficiently clear that a neotype need not be designated for *Iliodiscus lutzii*. The oldest available name for this species is *fuliginosus*.

*Grypiscus scleromeris* Miranda-Ribeiro, 1935. — The first use of this name appears on page 415 in the key to the species Miranda-Ribeiro included in *Grypiscus* as: Tibias tuberculadas..... 5 — *Gryp. scleromeris* nom. nov. S. da Bocaina, typo Mus. Inst. Osw. Cruz. (*Gr. umbrinus* Lutz). Bokermann (1966) pointed out that the allocation of this name was most difficult. The specimen from Serra da Bocaina that Lutz identified (but never published) as *umbrinus* has not been located. Neither have additional specimens of *Cycloramphus* with tuberculate tibia been collected from the Serra da Bocaina, although the area has been extensively collected. The name is here treated as a *nomen dubium*, in the hope that additional efforts will locate the Lutz identified *umbrinus* specimen purportedly from the Serra da Bocaina.

#### *Cycloramphus ohausi* group

Samples from three of four localities in the Organ Mountains are too small to analyze intrapopulational variation. As a result, interpopulational variation was not evaluated in detail. All of the pattern, snout profile, dorsal texture, foot webbing and SVL states found in the three small samples are matched by specimens from the large sample. No differences among individuals from the four samples are apparent when the specimens are compared directly. Based on the available evidence, the four samples represent a single species.

Two names have been proposed for this distinctive species; the second would likely have not been proposed had the author been aware of the first name.

*Ceratophrys ohausi* Wandolleck, 1907. — Cochran (1955) pointed out that the species described by Wandolleck as *Ceratophrys ohausi* was a species of *Cycloramphus*. As Cochran (1955) indicated, Wandolleck's

figures (1907, Plate 1, Figure 2, 2a) are diagnostic enough to properly allocate the name. The regular arrangement of tubercles on the dorsum, much as in members of the genus *Proceratophrys*, together with the locality of Petrópolis, indicate that this is the oldest available name for the single species of this group. Cochran (1955, p. 266) stated that Dr. Wandolleck wrote her that the 18 mm SVL type lacked thumb spines. There are several juveniles available; all specimens 18 mm SVL and smaller lack thumb spines. One 18.9 mm specimen has 2 thumb spines, a 19.1 mm individual lacks thumb spines. All specimens 20 mm and larger have thumb spines.

*Cycloramphus distinctus* Lutz, 1932. — Lutz was apparently unaware of the Wandolleck paper and described *distinctus* from specimens also collected at Petrópolis. In the description, Lutz based the name on a series of specimens. In the Lutz collection at MNRio, specimens 2180-2182, 2194, 2242, are indicated as types. The date of collection correspond to the dates given by Lutz in the original description. AL 2180, a 36.1 mm SVL male, is hereby designated as the lectotype of *Cycloramphus distinctus* Lutz.

#### *Cycloramphus granulatus* group

Moderate samples are available from three disjunct areas: (1) Serra da Mantiqueira, in or near the national park of Itatiaia; (2) Serra da Bocaina, (3) two localities in the State of Santa Catarina. As there are but three samples, and as I prefer to avoid the use of the term OTU whenever possible, these three units are referred to as samples using the following abbreviations — M = Serra da Mantiqueira sample, B = Serra da Bocaina sample, S = Santa Catarina sample.

#### Character Analysis

Male Vocal Slits. — All males from the Serra da Bocaina and Serra da Mantiqueira



samples have vocal slits. Five males from the Santa Catarina sample have vocal slits, three males from this sample have vocal folds, but no slit.

**Dorsal Pattern.** — The predominant pattern state for all three samples is a uniform or indistinctly mottled pattern (Figure 2, B; M = 15 individuals, B = 26, S = 12). The M and B samples have a few individuals with more distinctive patterns (M — Figure 2, A = 1 individual, Figure 2, D = 2, Figure 2, G = 1; B — Figure 2, C = 2, Figure 2, D-1 = 1, Figure 2, G = 2).

**Thigh Pattern.** — Most individuals from the three samples have a uniform posterior surface of the thigh pattern; a few individuals have mottled thighs.

**Lip Pattern.** — All three samples have uniform or indistinctly barred upper lips; no differentiation is evident in this character.

**Belly Pattern.** — Most individuals from sample M have a uniformly patterned belly (Figure 5, E); a few individuals have mottled bellies (Figure 5, A, B, C,) or distinct light spots (Figure 5, D). Most individuals of samples B and S have light spotted bellies (Figure 5, D) with mottling also common (Figure 5, A, B, C). The difference between the uniform pattern of sample M and light spotted pattern of samples B and S could be due to preservation, as faded light spots are not visible on a light belly background.

**Snout Profile.** — The snout profiles vary among the samples. Sample M has four individuals with profile A (Figure 6), nine with B, and 6 with C. Sample B has 22 individuals with profile A and 10 with B. Sample S has 11 individuals with profile A and one with B.

**Dorsal Texture.** — The dorsal texture of all specimens is granular, lacking both tubercles and a distinct shagreen. The S sample is unique in that 9 of 11 individuals have distinct regular dorsal lines composed of slightly raised, coalesced granules. Only

one individual of sample B has irregular linear granules; all other individuals of samples M and B lack granular lines.

**Measurements.** — Sufficient data are available only for males of the three samples to use the stepwise discriminant function program. The variables entered the program in the following order (the F values to enter indicate the relative contribution of each variable to discriminate among the samples): Foot (F = 22.5), tibia (F = 9.2), head length (F = 8.1), eye-eye distance (F = 13.0), BL (F = 2.2, P > .05, BL does not add any information to the analysis), head width (F = 1.9, P > .05), femur (F = 1.3, P > .05), eye-nostril distance (F = 0.5, P > .05). The classification matrix has all individuals of each sample posteriorly classified into the appropriate samples. Morphological discrimination among the groups is complete (Figure 21). The first discriminant axis accounts for 86% of the total dispersion; the remaining 14% is accounted for by the second axis. In this kind of analysis the first discriminant axis usually is size related. The male BLs are similar in all three samples so that size alone may not be accounting for the separation of samples along the first axis. The variable with the largest coefficient in both the first and second discriminant axis is eye-eye distance. Thus, head shape apparently is as important as size in discriminating among the three samples.

Variation among the three samples is most noticeable in snout profile and measurements. For both of these characters, the Santa Catarina sample is the most distinctive.

Closer inspection of the data and specimens indicates that the Santa Catarina sample is not homogeneous in all characteristics. Among the three measurement variables that had the highest coefficients for the first two discriminant axes, two show heterogeneity within the Santa Catarina sample and one shows the Santa Catarina sample

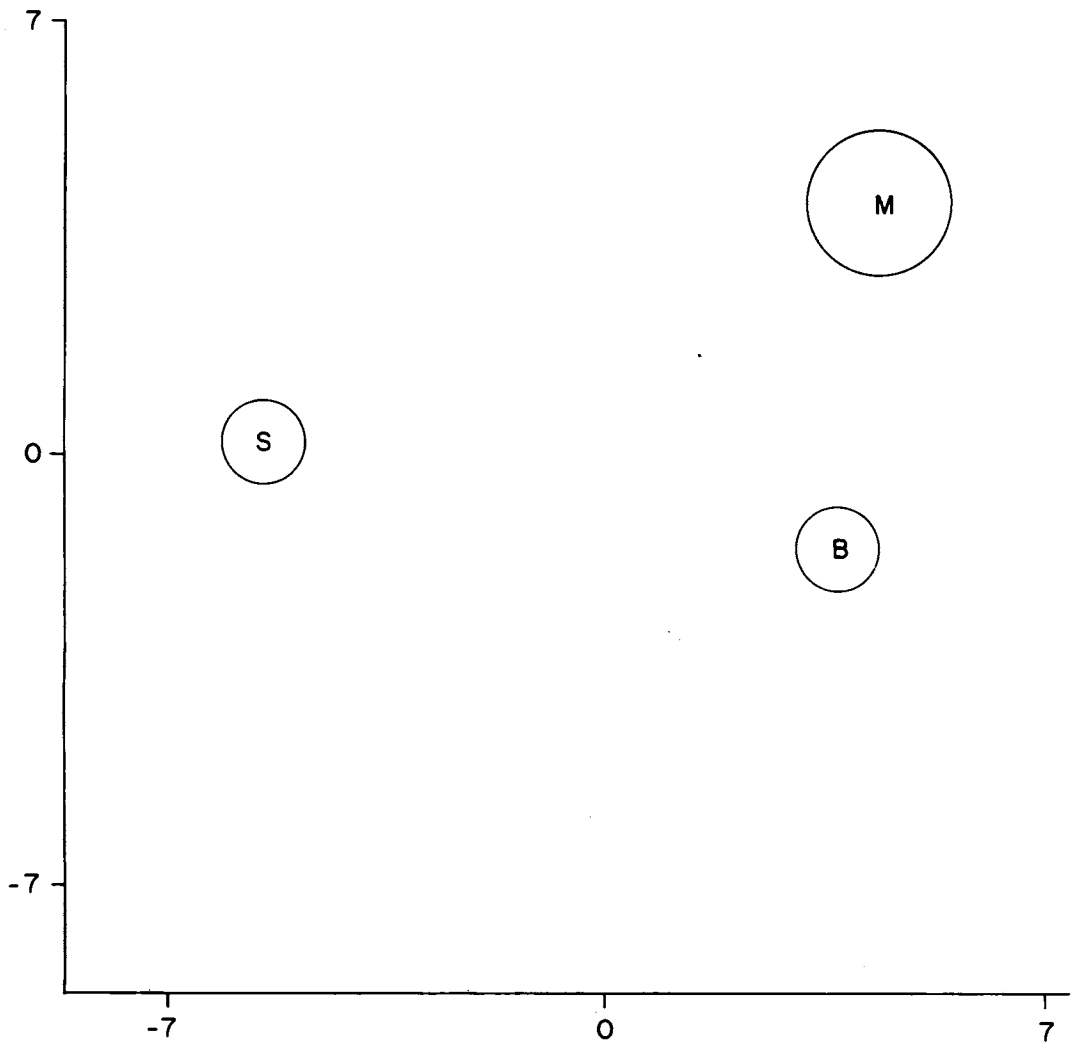


Figure 21. Discriminant axis plot of males of three samples of the *Cycloramphus granulosus* group. M = Serra da Mantiqueira sample, B = Serra da Bocaina sample, S = Santa Catarina sample. Letters placed at group means. Circles indicate 95% confidence interval for group centroids.

homogeneous and differing from the Bocaina and Mantiqueira samples. A plot of eye-eye distance against SVL indicates that the Santa Catarina sample has a slightly broader eye-eye distance than the Bocaina and Mantiqueira samples (Figure 22). Tibia length plotted against SVL indicates that the specimens from Gruta, Santa Catarina, have slightly longer tibias than other members of the group (Figure 23). Foot

length plotted against SVL indicates that the specimens from Petrópolis, Santa Catarina generally have shorter feet than other members of the group (Figure 24). As can be also seen in Figures 22-24, there is a difference among samples for adult size, with specimens from Gruta, Santa Catarina the smallest, and the Bocaina specimens the largest. Direct examination of the specimens provides additional differentiating character-

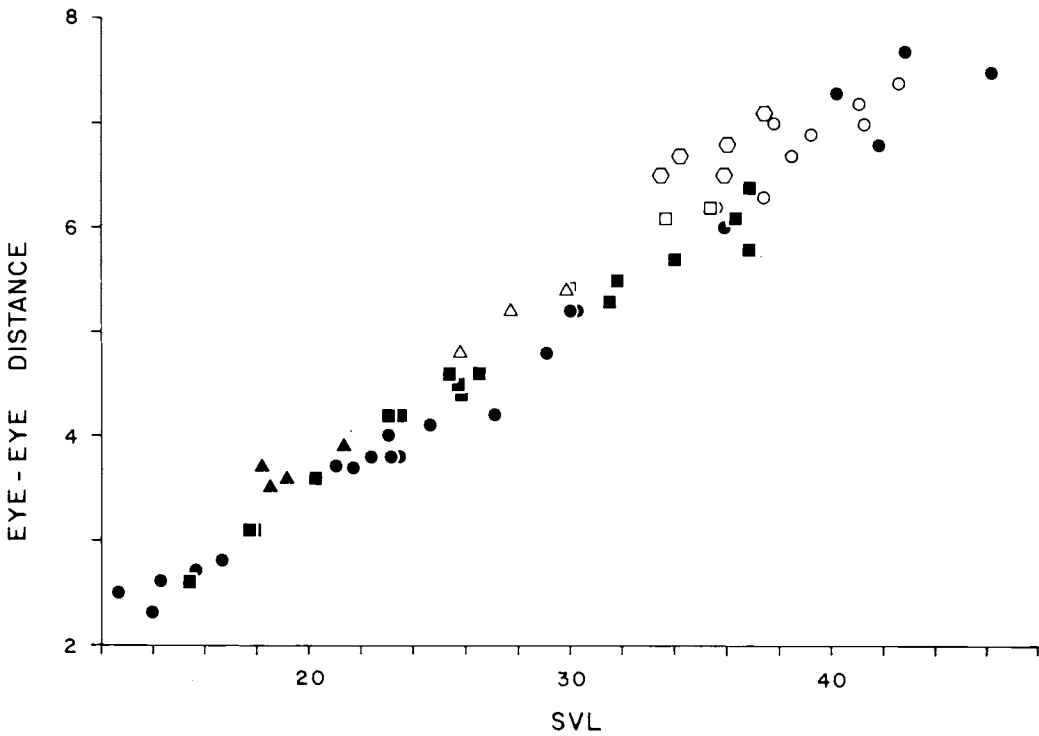


Figure 22. Eye-eye distance plotted against SVL for individuals of the *Cycloramphus granulatus* group. Open hexagons = male Petrópolis specimens; triangles = Gruta specimens, closed = juveniles, open = males; circles = Serra da Bocaina specimens, closed = juveniles and females, open = males; squares = Serra da Mantiqueira specimens, closed = juveniles and females, open = males.

istics. The specimens from Gruta, Santa Catarina lack palmar metacarpal tubercles, 12 of 13 Bocaina adults have palmar metacarpal tubercles, as do all adults from the Mantiqueira and Petrópolis, Santa Catarina. The pebble-like dorsal granules appear to have several mucus glands per granule. This distinctive appearing condition is only found in the Petrópolis, Santa Catarina sample.

Without any comparative life history, habitat, or call data, I think the best taxonomic arrangement that explains the variation is recognition of three species in this group: (1) a species represented by the specimens from Gruta, Santa Catarina, (2) a species represented by the specimens from Petrópolis, Santa Catarina, and (3) a

species represented by specimens from the Serra da Bocaina and Serra da Mantiqueira, recognizing that these latter two samples may well represent distinct species.

Only one name has been proposed for members of this group, *Cycloramphus granulatus* Lutz, 1929. Lutz based the species on two specimens from Serra da Bocaina, 27 and 44 mm SVL respectively. The remains of the 27 mm specimen, AL 1537, are labelled as the tipo of *granulosus* in the Lutz collection at MNRio. The hands and feet of the type are missing, but the distinctive dorsal texture is still evident. AL 2463-65, identified as paratypes of *C. granulatus* from Ouro Preto, Minas Gerais are very poorly preserved but are herein identi-

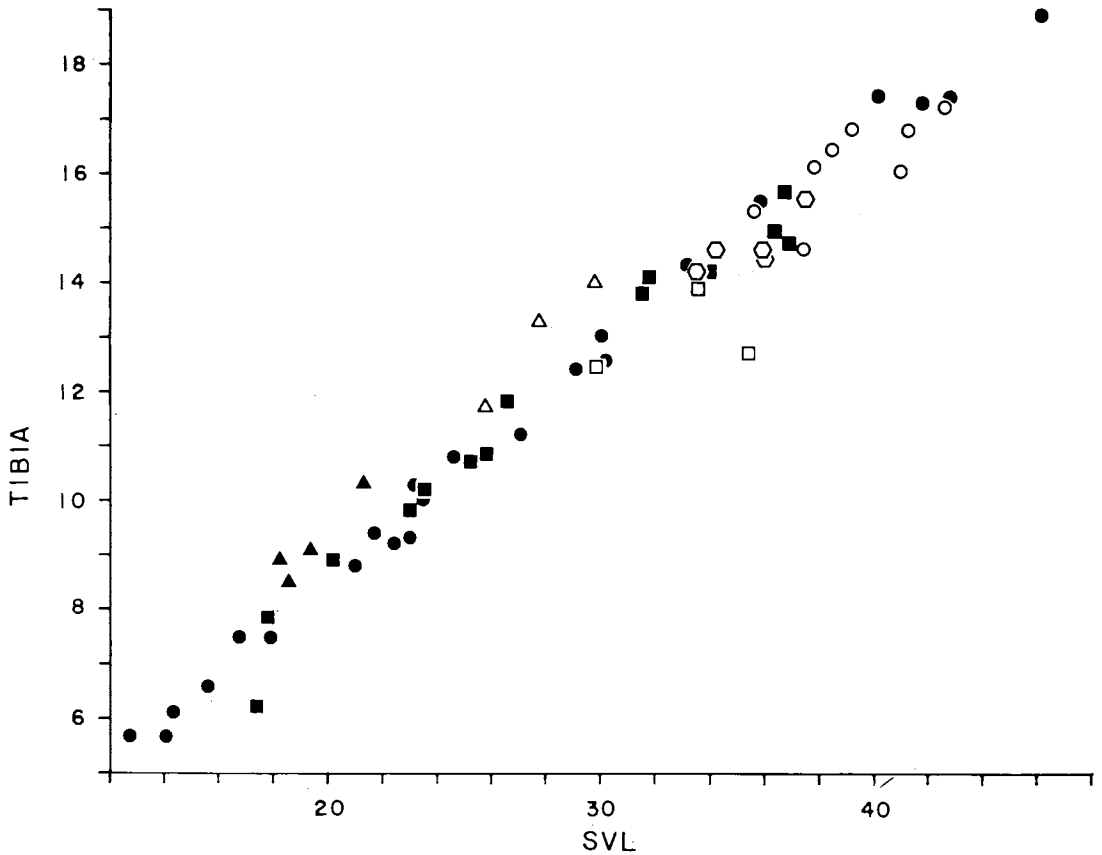


Figure 23. Tibia length plotted against SVL for individuals of the *Cycloramphus granulosus* group. Open hexagons = male Petrópolis specimens; triangles = Gruta specimens, closed = juveniles, open = males; circles = Serra da Bocaina specimens, closed = juveniles and females, open = males; squares = Serra da Mantiqueira specimens, closed = juveniles and females, open = males.

fied as *C. eleutherodactylus*. *Cycloramphus granulosus* is the oldest name for the species recognized herein as that from the Serra da Bocaina and Serra da Mantiqueira.

#### *Cycloramphus eleutherodactylus* group

About 150 specimens of this group are available for analysis, but most samples are of one or a few specimens from scattered localities. For this reason, members of this group are not analyzed in the same detail as members of the *fuliginosus* group, although a similar approach is used. At least three adult males from four loca-

lities are available for a discriminant function analysis. These four samples (OTUs) from the northern and middle part of the geographic range of the group are designated as:

- OTU 21. Tijuca and Sumaré, N = 11
- OTU 22. Teresópolis, N = 9
- OTU 23. Ilha dos Buzios, N = 7
- OTU 24. Iporanga, N = 4.

#### Character Analysis

*Male Vocal Slits.* — All males from OTUs 21 and 22 lack vocal slits and vocal folds. One male each from OTU 23 and

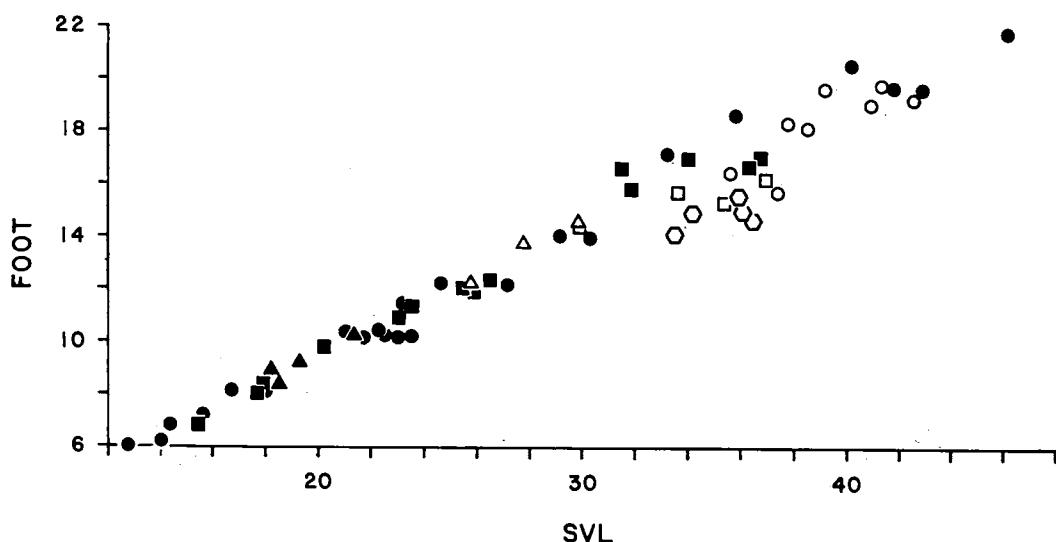


Figure 24. Foot length plotted against SVL for individuals of the *Cycloramphus granulosus* group. Open hexagons = male Petrópolis specimens; triangles = Gruta specimens, closed = juveniles, open = males; circles = Serra da Bocaina specimens, closed = juveniles and females, open = males; squares = Serra da Mantiqueira specimens, closed = juveniles and females, open = males.

OTU 24 has a vocal fold, but no slit. The remainder from OTUs 23 and 24 lacks slits or folds.

*Dorsal Pattern.* — The juveniles from OTU 21 generally have a more distinctive dorsal pattern than the adults. The juvenile patterns of OTU 22 are similar to the adult patterns. Sample sizes from the other OTUs are too small to determine whether the

juvenile pattern differs from the adult. Adult patterns (Table 13) vary among OTUs but because of the small sample sizes, it is uncertain if an inter-OTU component of variation exists.

*Thigh Pattern.* — The juveniles from OTU 21 have less distinct thigh patterns than the adults. Juveniles from OTU 22 have a similar distribution of states as the adults. Comparison of the adult pattern (Table 14) suggests an inter-OTU variation in this character.

Table 13. Distribution of dorsal pattern states among OTUs of the *Cycloramphus eleutherodactylus* group. Integers are numbers of adult specimens. Pattern states correspond to those of Figure 2.

	OTUs			
	21	22	23	24
B . . . .	4	8	1	
C . . . .			1	
E . . . .	3			
E-1 . . .	3		1	1
F . . . .	2	2		
F-1 . . .	1	1	2	
F-2 . . .			2	3
G . . . .	6			
H-2 . . .			1	

Table 14. Distribution of thigh pattern states among OTUs of the *Cycloramphus eleutherodactylus* group. Integers are numbers of adult specimens. Pattern states correspond to those of Figure 3.

	OTUs			
	21	22	23	24
A . . . .		6	7	1
B . . . .		6	1	1
C . . . .	11	2		2
C-1 . . .	2	3		

**Lip Pattern.** — The juveniles of OTU 21 all have patternless or indistinctly barred lips (Figure 4, A, B), similar to the distribution of states of adults (Table 15). Seven of 20 juveniles from OTU 22 have distinct light lip bars, contrasting with the distribution of states among adults (Table 15). Comparison of adult patterns suggests relatively little variation among OTUs.

**Belly Pattern.** — Most juveniles of OTU 21 do not have a distinctly patterned belly (Figure 5, F), contrasting with the adult situation (Table 16). The distribution of juvenile belly pattern states for OTU 22 is similar to that of the adults. Comparison of adult patterns suggests variation among OTUs, particularly with regard to the distinctly patterned belly (Figure 5, F contrasted with A-C).

**Snout Profile.** — There is no discernable variation among OTUs in this character.

**Dorsal Texture.** — The dorsal texture is

either smooth or has a granular or rugose texture, without distinct tubercles. Some or all individuals of all OTUs have a granular or rugose dorsal texture. Most individuals of OTUs 21 and 22 have a smooth dorsal texture. Many individuals from OTUs 21 and 22 have irregular or regular dorsal skin ridges. Individuals from the other two OTUs lack dorsal ridges.

**Measurements.** — Because of small sample sizes, only male measurements for the four OTUs were used as the preformed groups for stepwise discriminant function analysis. The variables entered the program in the following order (the F values to enter indicate the relative contribution of each variable to discriminate among the OTUs): Eye-nostril distance (F = 18.6), tibia (F = 3.6), foot (F = 13.9), head width (F = 3.6), eye-eye distance (F = 2.2, P >.05, eye-eye distance does not add any information to the analysis), head length (F = 2.0, P >.05), BL (F = 0.3, P >.05), femur (F = 0.2, P >.05). The classification matrix using the first four variables that entered the program (Table 17) shows almost complete posterior classification into the proper OTUs. The first discriminant axis accounts for 74% of the total dispersion, the first two axes account for 98%. The plot of the first two discriminant axes (Figure 25) indicates that no one OTU is clearly an outlier. OTUs 22, 23, and 24 are separated best along the first axis, a size axis. OTU 21 is separated along the second axis in which the eye-eye distance

Table 15. Distribution of lip pattern states among OTUs of the *Cycloramphus eleutherodactylus* group. Integers are numbers of adult specimens. Pattern states correspond to those of Figure 4.

	OTUs			
	21	22	23	24
A . . . . .	6	10	4	4
B . . . . .	5	6	4	
C . . . . .	3	1		

Table 16. Distribution of belly pattern states among OTUs of the *Cycloramphus eleutherodactylus* group. Integers are numbers of adult specimens. Pattern states correspond to those of Figure 5.

	OTUs			
	21	22	23	24
A . . . . .	1	9		1
B . . . . .	1	1		
C . . . . .			1	
D . . . . .	1			
E . . . . .		3	7	
F . . . . .	10	1		3

Table 17. Posterior classification matrix of males of four OTUs of the *Cycloramphus eleutherodactylus* group. Numbers heading columns and rows refer to OTUs as used in text.

	OTUs			
	21	22	23	24
21 . . . . .	11	0	0	0
22 . . . . .	0	9	0	0
23 . . . . .	1	0	6	0
24 . . . . .	0	0	0	4

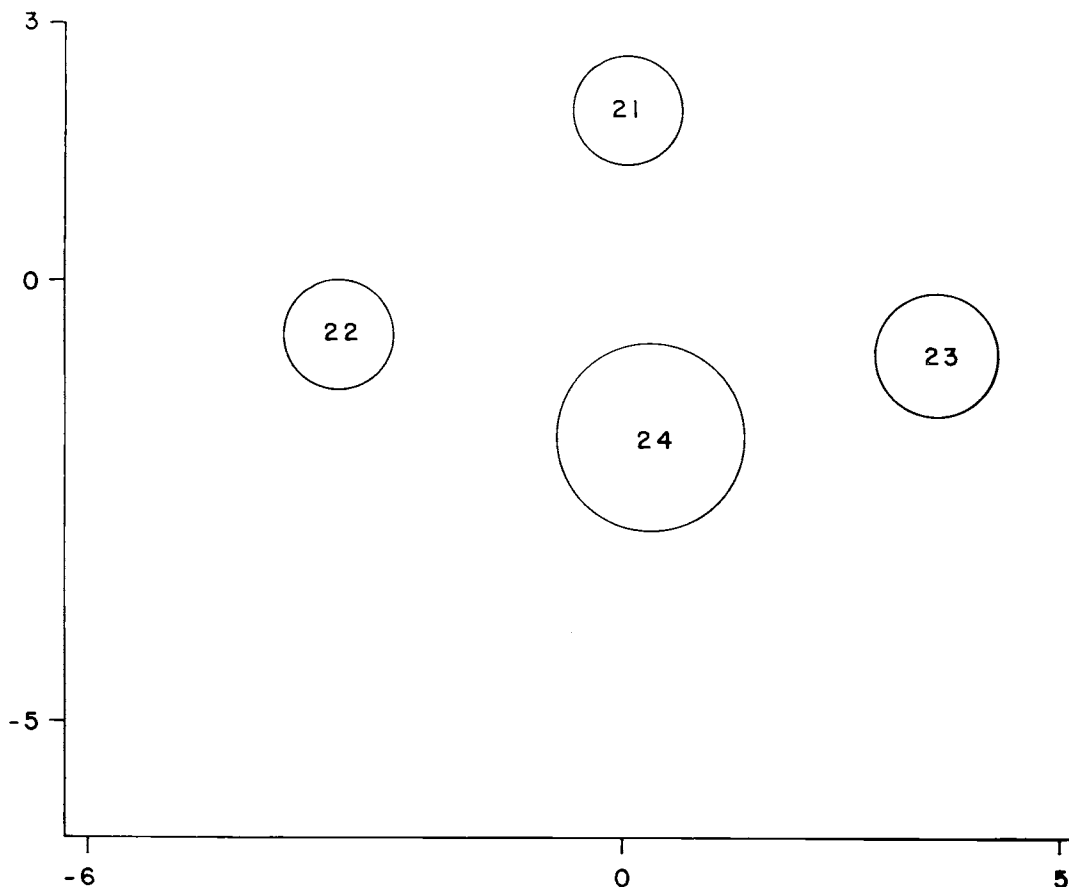


Figure 25. Discriminant axis plot of males of four OTUs of the *Cycloramphus eleutherodactylus* group. Numbers refer to OTUs as used in text, placed at group means. Circles indicate 95% confidence interval for group centroids.

has the highest coefficient. The three variables with the largest coefficients along the first two axes (eye-nostril distance, eye-eye distance, tibia) demonstrate a straight-line relationship when the variables are plotted against SVL (Figure 26 shows the variable with the most variation when plotted against SVL among the three). None of the OTUs is clearly distinguishable from the others on the basis of measurements.

Because of sample sizes the OTU variation is due at least in part to sampling error. However, dorsal ridging distinguishes OTUs 21 and 22 from the remaining two OTUs.

All of the characters treated vary in degree, but none are discrete. All individuals of one OTU can not be distinguished from all individuals of any other OTU. Direct comparison of individuals from the four OTUs does not yield any further distinguishing characteristics.

#### Additional Specimens of the *Cycloramphus eleutherodactylus* Group

Three specimens from Santa Catarina differ from all other specimens of the *C. eleutherodactylus* group in having a distinct

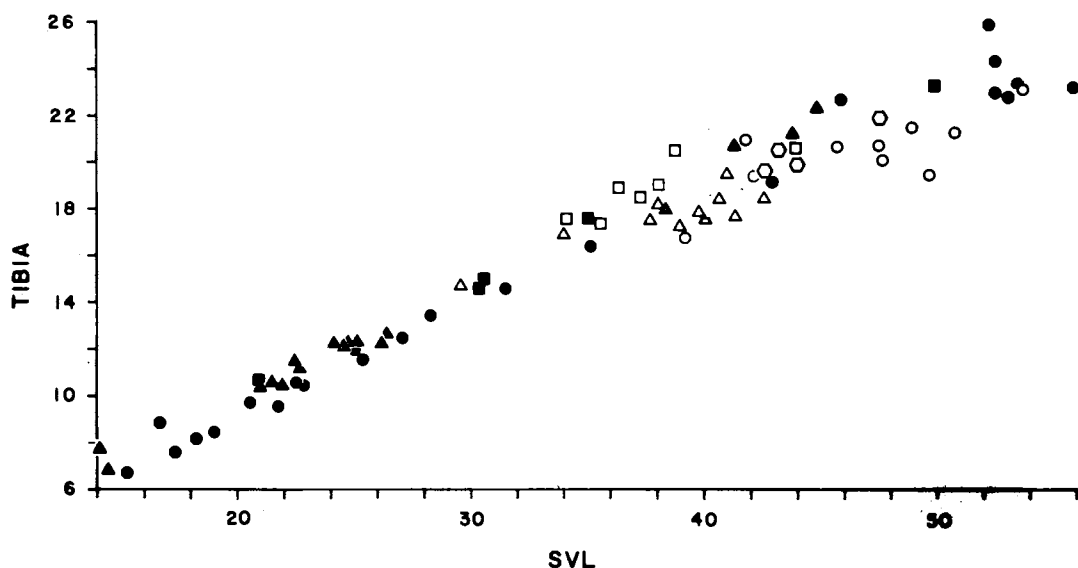


Figure 26. Tibia length plotted against SVL for individuals of four OTUs of the *Cycloramphus eleutherodactylus* group. Triangles = OTU 21 specimens, closed = juveniles and females, open = males; circles = OTU 22 specimens, closed = juveniles and females, open = males; squares = OTU 23 specimens, closed = juveniles and females, open = males; hexagons = OTU 24 male specimens.

sinuous dorsolateral ridge extending from behind the eye to the sacral region, similar to that found in members of the genus *Proceratophrys*. In the individuals from the Organ Mountains and Serra da Bocaina with regular dorsal ridges, the ridges never originate at the posterior eyelid, but always further posteriorly on the dorsum. Two of the three Santa Catarina specimens are males, with well developed vocal slits. Of all other specimens, only two males of the group have vocal folds, which are not broken through. All other males lack folds and slits. The two available males are small and matched in size only by one other male of the group. These differences are interpreted as species level differences.

Geographic variation among the remaining specimens exists. In comparing individuals side by side some individuals obviously have longer fingers and toes than others. This variation in hand and foot length is not easily interpreted (for example,

Figure 27). I find no other differences among the specimens. The populations from each geographic locality or restricted area have some distinguishing characteristics, but the differences are not discrete. There is geographic variation within the remaining members of this group, but with the present sample sizes available, the nature of the variation is difficult to evaluate.

Two species are recognized in this group. One, a variable, rather broad ranging species, is found in the States of Minas Gerais, Rio de Janeiro, São Paulo and Paraná. The second species is known from a few specimens from the State of Santa Catarina.

#### Nomenclature

Four names have been proposed for members of this group.

*Iliodiscus eleutherodactylus* Miranda-Ribeiro, 1920. — The lectotype, designated



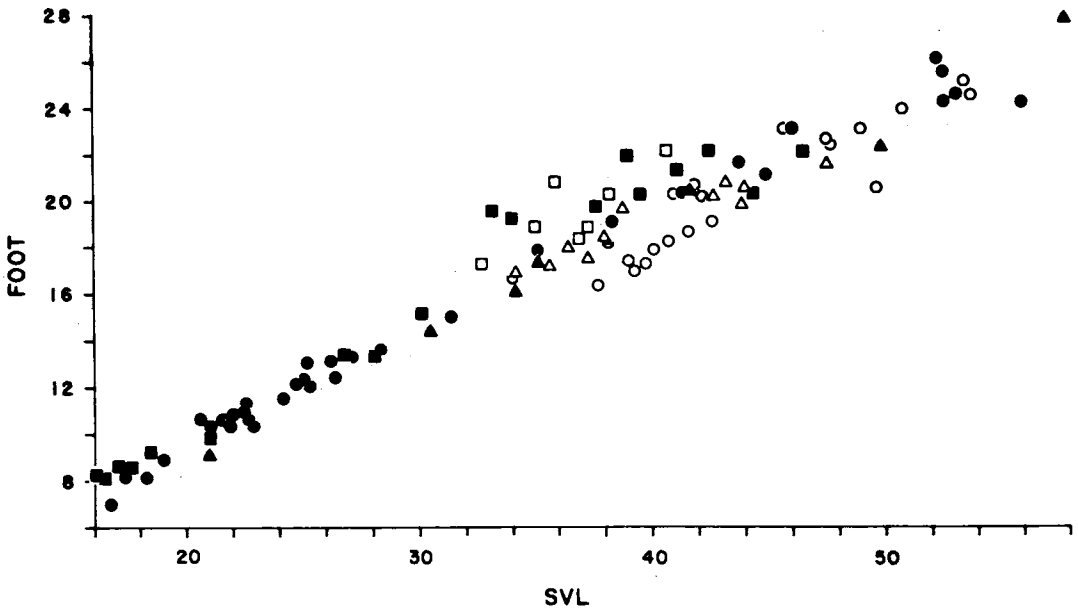


Figure 27. Foot length plotted against SVL for individuals of the *Cycloramphus eleutherodactylus* group. Circles = specimens from OTUs 21 and 22, closed = juveniles and females, open = males; squares = specimens from Boracéia, Cubatão, and the State of Paraná, closed = juveniles and females, open = males; triangles = specimens from Ilha dos Búzios, Iporanga and Juquiá, closed = juveniles and females, open = males.

by Bokermann (1951) as MZUSP 24x, is a female from Alto da Serra, São Paulo. This specimen, as is the allotype, is darkened, but is clearly the same species as that recognized herein as the wide ranging form.

*Cycloramphus eleutherodactylus* var. *variegata* Lutz, 1929. — Lutz described both *variegata* and *strigilata* as varieties of *eleutherodactylus*. He clearly stated that the variation in pattern, size and shape was due to geographic variation, but the differences were of the same magnitude as found within other species of *Cycloramphus*. As the names were proposed prior to 1931 and were clearly associated with published figures, the names are available. Both names refer to the wide ranging species recognized herein. As this study indicates a mosaic pattern of geographic variation within the species, designation of subspecies is inappropriate in this case.

*Cycloramphus eleutherodactylus* var. *strigilata* Lutz, 1929. — This name applies to the wide-ranging species recognized herein (see *C. e. variegata*, above).

*Cycloramphus diringshofeni* Bokermann, 1957. — A juvenile from the Bokermann collection was included in this study as one of the three specimens of the second species of this group from Santa Catarina. The holotype was not examined.

#### TAXONOMIC SUMMARY

Eighteen species of the genus *Cycloramphus* are recognized; twelve in the *fuliginosus* group, one in the *ohausi* group, three in the *granulosus* group, and two in the *eleutherodactylus* group. The oldest available names for species in each group are:

*Cycloramphus fuliginosus* group

- C. asper*
- C. brasiliensis*
- C. dubius*
- C. duseni*
- C. fuliginosus*
- C. semipalmatus*

Six unnamed species

*Cycloramphus ohausi* group

- C. ohausi*

*Cycloramphus granulosis* group

- C. granulosis*

Two unnamed species

*Cycloramphus eleutherodactylus* group

- C. diringshofeni*
- C. eleutherodactylus*

Results of nomenclatural decisions are summarized in Table 12. The unnamed species are described in the taxonomic portion of this paper.

### Generic limits

The relationships of the genus *Cycloramphus* to other leptodactylid genera have been recently discussed by Bokermann (1951), Lynch (1971), and Heyer (1975). Bokermann (1951) consolidated the genera *Cycloramphus*, *Grypiscus*, and *Iliodiscus*, an action followed by Lynch and me. Lynch (1971) placed *Cycloramphus* in the tribe Grypiscini together with the with the genera *Crossodactylodes* and *Zachaenus*. Lynch proposed synonymizing the genus *Craspedoglossa* with *Zachaenus*. Lynch also proposed the new genus *Scythrophrys* for the species described by Cochran as *Zachaenus sawayae*. As *Scythrophrys* was known only from the holotype, Lynch was not able to comment definitively on the relationships, but thought that possibly it was a member of the tribe Grypiscini as he had defined it. Heyer (1975) found *Cycloramphus*, *Craspedoglossa*, and *Zachaenus* to be closely related, but had no further information on

*Scythrophrys*. Bokermann (1951) earlier suggested and later (pers. comm.) strengthened that suggestion that *Cycloramphus* and *Craspedoglossa* might be so closely related as to be congeneric.

This section asks two questions: (1) what are the generic limits of the genus *Cycloramphus*? and (2) what are its closest relatives? These questions are addressed by comparison of morphological features of members of the genera *Cycloramphus* (as defined by Bokermann), *Craspedoglossa*, *Zachaenus* (in the pre-Lynch sense), and *Scythrophrys*.

### THE RELATIONSHIPS OF *SCYTHROPHRYS*

Lynch (1971) proposed the genus *Scythrophrys* on the basis of the only known specimen of *Zachaenus sawayae*. Since that time, four more specimens have become available. Professors Eugênio Izecksohn and Jorge Jim kindly placed at my disposal three individuals collected from Alto Palmeiras, Município de Rio dos Cedros, Santa Catarina. These specimens represent a range extension, as the only other specimen (MZUSP) in addition to the holotype was taken from near the type locality in the State of Paraná. Professor Izecksohn had made superficial dissections on one of the specimens, an adult female, which he allowed me to further dissect to examine the jaw musculature and the hyoid apparatus and associated musculature. Preliminary examination of these features, together with those from the additional specimens lead to the conclusion that *Scythrophrys* is not closely related to the other genera under consideration. Preparation of a skeleton of *Scythrophrys* is not critical to the purposes of this study and is deferred until either additional specimens become available or a suitable hypothesis concerning the relationships of *Scythrophrys* is postulated.

There are several features by which *Scythrophrys* differs from the collective grouping of *Craspedoglossa*, *Cycloramphus*, and *Zachaenus* (referred to as C-C-Z for convenience). All members of C-C-Z have a well developed meniscus on the upper iris. *Scythrophrys* has the smallest indication of a meniscus which would likely be considered absent in a comparative survey. The male thumb of *Scythrophrys* has a keratinized nuptial pad (like that found in *Physalaemus*). No members of C-C-Z have a pad; one species has spines on the thumbs of both sexes. The jaw depressor musculature in *Scythrophrys* is distinctive in having few or no fibers attaching to the dorsal fascia (as noted by Lynch, 1971); all C-C-Z members have a strong origin on the dorsal fascia. The geniohyoideus medialis muscles are separated medially, exposing the hyoglossus, but the distal portions are not covered by the sternohyoideus muscles as is the case for other instances where the geniohyoideus medialis muscles are separated medially. All C-C-Z members have the geniohyoideus medialis muscles in medial contact, covering the hyoglossus in ventral aspect. The sternohyoideus muscle insertion of *Scythrophrys* consists of a narrow band of muscles extending to the midline of the hyoid; the insertion on all C-C-Z members is near the lateral edge of the hyoid. The anterior petrohyoideus muscle of *Scythrophrys* inserts on the ventral body of the hyoid; the insertion is on the edge of the hyoid plate in all C-C-Z members. The omohyoideus muscle is absent in *Scythrophrys*, present in all C-C-Z members. *Scythrophrys* has a shorter iliacus externus muscle than any C-C-Z member. The exterior head of the semitendinosus muscle is reduced and connected by a very long tendon to the interior head of the semitendinosus. This condition is unique among all leptodactylids I have examined. The accessory head of the adductor magnus is absent in *Scythrophrys*, present in all C-C-Z

members. The alary process of the hyoid is broad and winglike in *Scythrophrys*, narrow and stalked in all C-C-Z members.

The differences document that *Scythrophrys* is not closely related to the C-C-Z complex. Character states which were previously unknown, but which are the same as demonstrated by some or all C-C-Z members are: ovarian eggs with melanophores; only adductor mandibulae posterior subexternus muscle present; tensor fasciae latae muscle inserts posterior to the anterior extent of the iliacus externus muscle on the ilium; the sartorius muscle is narrow as in most leptodactylids; the adductor longus muscle is strap like, extending about 3/4 the length of the adductor magnus muscle and attaching to it; a broad anterior process of the hyale is present.

The jaw depressor muscle condition of *Scythrophrys* is approached only in *Euparkerella* and *Batrachyla*. *Scythrophrys* is not an eleutherodactyline as the eggs have melanophores and most probably have a free living larval stage. *Scythrophrys* differs from *Batrachyla* in hyoid morphology and musculature. Externally, *Scythrophrys* resembles *Zachaenus*, *Paratelmatobius*, and *Physalaemus*. In addition to jaw musculature, *Scythrophrys* differs from *Paratelmatobius* in hyoid morphology and musculature and from *Physalaemus* in sternal morphology. *Scythrophrys* is a very distinctive leptodactylid genus whose affinities are obscure.

#### CHARACTER ANALYSIS

All members of the genera *Craspedoglossa*, *Cycloramphus*, and *Zachaenus* share the following derived character states (as defined in Heyer, 1975 or Heyer and Liem, 1976): iris meniscus present; tympanum hidden; depressor muscle origin from dorsal fascia and squamosal region with little or no attachment to tympanic annulus; geniohyoideus medialis muscle contiguous me-

dially; sternohyoideus muscle insertion near lateral edge of hyoid; anterior petrohyoideus muscle insertion on lateral edge of hyoid plate; alary process of hyoid narrow and stalked; terminal phalanges knobbed. This combination of derived states, emphasized by the unique character of the iris meniscus indicates that the members of these three genera form a natural unit whose closest relationships are to each other.

External characteristics were examined for all species of the three genera. Muscle and osteological (Appendix 1) features were examined for at least one member of each of the species groupings based on external morphology except for the two species known from single specimens at the time of analysis. If there was no variation in the characters examined among these samples, or if the variation corroborated the previously defined units, additional data were not taken. Only in the case of the thigh musculature was it thought necessary to examine the condition in all species for which more than one individual was available.

Following is a discussion of characters that have either been used historically in determining generic affinities in this group or were found to vary in this study. Primitive and derived character states are defined as appropriate and follow Heyer (1975) or Heyer and Liem (1976) unless otherwise noted.

**Tongue.** — The tongue shape differs slightly among members of this group, but the basic form is a round tongue, contrasting with the elliptical tongue of most other leptodactylids. Regal and Gans (1976) pointed out major differences in frog tongue morphologies. The kinds of dissections necessary to document these differences were not made for this study. Bokermann (1951) stated that *Craspedoglossa* differed from *Cycloramphus* by a corneal fringe on the tongue. I find no differences in tongues among members of these genera.

**Thumb spines.** — Thumb spines are absent in all species of the three genera examined with the notable exception of *C. ohausi*, which has spines in both sexes. To my knowledge, thumb spines on both sexes in leptodactylids only occurs elsewhere in the genus *Crossodactylus*. Character 1: state 0 (primitive), thumb spines absent; state 1 (derived), thumb spines present.

**Male Inguinal Gland.** — Contrary to Lynch (1971, p. 140), *Craspedoglossa* has inguinal glands. Character 2: state 0, no male inguinal glands; state 1, male inguinal glands present.

**Toe Webbing.** — Three states are recognized among these three genera, webbed, fringed or ridged, and free. The fringed or ridged state has lateral prominences on the toes which may join at the base of the toes, but they do not form distinct membranous webs. The fringe/ridge condition found here is considered a distinctly derived condition which is likely not an intermediate condition between webbed and free toes. Character 3: state 0, toes webbed; state 1, toes with lateral fringes or ridges; state 2, toes free. The directions of change of character states are:

$$1 \leftarrow 0 \rightarrow 2$$

**Egg Melanophores.** — Late ovarian eggs were examined where possible. Character 4: state 0, melanophores present; state 1, melanophores absent.

**Iliacus Externus Muscle.** — Character 5: state 0, muscle extends from one-half to three-fourths anterior on ilium; state 1, muscle extends less than one-half anterior on ilium.

**Tensor Fasciae Latae Muscle.** — Character 6: state 0, insertion posterior to the anterior extent of the iliacus externus on the ilium; state 1, insertion anterior to the anterior extent of the iliacus externus on the ilium.

**Semitendinosus Muscle.** — Variation in the interior and exterior heads of this muscle

is slight among the three genera, ranging from exterior head smaller than and attached by a tendon to the interior head (Heyer, 1975, Fig. 3 B) to interior and exterior heads about equal, exterior head attached by a tendon to the interior, bulks of two heads displaced (Heyer, 1975, Fig. 3 D). The variation is continuous between these states, precluding meaningful coding of this character.

**Adductor Longus Muscle.** — The muscle is present in species of the three genera and variation in its development is slight. The muscle ranges from about one-half to full length of the adductor magnus muscle, and attaching in part or entirely (usual situation) on the adductor magnus. The muscle is shortest in *C. eleutherodactylus*, one-half to two-thirds the length of the adductor magnus. Variation is minimal in this character, precluding meaningful coding.

**Omohyoideus Muscle.** — Character 7: state 0, omohyoideus insertion in part or entirely on ventral body of hyoid plate; state 1, omohyoideus insertion on edge of hyoid plate adjacent to the posteromedial process. Although not specifically categorized previously, state 1 is considered the derived state as it is limited to the New World leptodactylids (Heyer, 1975, Table 16, p. 11).

**Anterior Process of the Hyale.** — The variation observed ranges from a well defined swelling on the hyale to absence. There is no definite, narrow process as seen in other leptodactylid frogs. The process is clearly absent in *Zachaenus parvulus*, ambiguous in *Craspedoglossa bolitoglossa*, *C. stejnegeri*, and *Cycloramphus dubius*, small in *C. fuliginosus*, and a clear indication of an anterior swelling is found in *C. duseni*, *C. ohausi*, *C. granulatus* group — Petrópolis, Santa Catarina, and *C. eleutherodactylus*. The variation observed is not great and continuous, precluding meaningful coding of this character.

**Posterior Sternum.** — Character 8:

state 0, mesosternum cartilaginous (Heyer, 1975, Figure 4 F, H); state 1, mesosternum with mineral deposition (Heyer, 1975, Figure 4 L).

**Nasal Contact with Frontoparietal.** — Character 9: state 0, no contact; state 1, contact.

**Zygomatic Ramus of Squamosal.** — The zygomatic ramus varies from just noticeably elongate (*fuliginosus*, *brasiliensis*, *ohausi*, *granulosus*) to elongate (*Boracéia dubius*, *semipalmatus*, *dubius*, *eleutherodactylus*, *Z. parvulus*) to very elongate (*bolitoglossa*, *stejnegeri*). The variation is so continuous in this characteristic that recognition of discrete states is not meaningful.

**Otic Ramus of Squamosal.** — Character 10: state 0, otic ramus slender or very slightly broadened; state 1, ramus expanded into small otic plate.

**Posterior Maxilla.** — Character 11: state 0, posterior portion narrower than anterior portion, or with very slight development of flange; state 1, posterior maxilla with definite flange, not contacting squamosal; state 2, posterior maxilla with extremely developed flange, articulating with zygomatic process of squamosal. The direction of change of character state is:

0 → 1 → 2

**Frontoparietal Process.** — Character 12: state 0, no process; state 1, small lateral process present (Lynch, 1971, p. 140, Fig. 91).

**Mid-sagittal Crest.** — There is some intraspecific variation in this character: two specimens of *C. fuliginosus* lack a mid-sagittal crest, one specimen has a small, but definite mid-sagittal crest. The presence of a low crest contrasts with the extreme crest development, however. Character 13: state 0, mid-sagittal crest low or absent; state 1, high mid-sagittal crest.

**Pterygoidal Flange.** — Character 14: state 0, pterygoidal ridge not developed into

definite flange; state 1, pronounced pterygoidal flange.

Extent of Sphenethmoid. — The intra-specific variation is as great as that observed among species, ranging from a short sphenethmoid, separated by about two diameters of the optic foramen from the optic foramen, to a long sphenethmoid, contacting the optic foramen.

### GENERIC LIMITS

This section evaluates the characters discussed in the previous section to determine the similarities and differences among species clusters based on shared derived character states. All derived states are utilized in this process, even though they may have little or no phyletic information.

The relative distinctiveness of a species or species cluster is an important piece of information in determining where generic lines should be drawn. Once the generic units are determined, the characters offering little or no phyletic information can be dropped (Hecht and Edwards, 1976) and an analysis of relationships can be made.

Not all species were sampled for all characters for the good reason that it seemed unnecessary. The species groups of *Cycloramphus* based on external characteristics show uniform muscle and bone conditions for the species sampled with the single exception of the *C. eleutherodactylus* group (Table 18). There are too few good specimens of *C. diringshofeni* to allow complete examination of all systems. There are several differences between *Craspedoglossa bolitoglossa* and *stejnegeri*; these species are

Table 18. Distribution of character states used in species group analysis. See text for definition of characters and states.

	Characters													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Craspedoglossa</i>														
<i>bolitoglossa</i>	0	1	2	1	1	0	0	1	1	1	2	0	1	1
<i>stejnegeri</i>	0	1	2	1	0	0	0	0	1	1	1	0	1	1
<i>Cycloramphus</i>														
<i>fuliginosus</i> group														
<i>fuliginosus</i>	0	1	0	0	0	0	0	0	1	0	0	0	0	1
<i>brasiliensis</i>	0	1	0	0	0	0			1	0	0	0	0	1
<i>Boracéia "dubius"</i>	0	1	0	0	0	0			1	0	0	0	0	1
<i>semipalmatus</i>	0	1	0	0	0	0			1	0	0	0	0	1
<i>dubius</i>	0	1	0	0	0	0	0	0	1	0	0	0	0	1
Iporanga species	0	1	0	0	0	0								
OTU 10	0	1	0	0	0	0								
OTU 9	0	1	0	0	0	0								
<i>duseni</i>	0	1	0	0	0	0	0	0						
<i>asper</i>	0	1	0	0	0	0								
<i>ohausi</i> group														
<i>ohausi</i>	1	1	0	0	0	1	0	0	0	0	0	0	0	0
<i>granulosus</i> group														
<i>granulosus</i>	0	1	1	0	0	0			1	0	0	0	0	1
Gruta species	0	1	1	0	0	0	0	0						
"Petrópolis" species	0	1	1		0	0								
<i>eleutherodactylus</i> group														
<i>diringshofeni</i>	0	1	2		0	0								
<i>eleutherodactylus</i>	0	1	2	1	1	0	0	0	1	0	1	0	1	1
<i>Zachaenus parvulus</i>	0	0	2	1	0	0	1	1	1	1	0	1	0	1

treated individually in the analysis. The following seven taxa are used for further analysis: *bolitoglossa*, *stejnegeri*, *fuliginosus* (group), *ohausi*, *granulosus* (group), *eleutherodactylus*, *parvulus*.

Four of these taxa share the most states: *bolitoglossa*, *stejnegeri*, *eleutherodactylus*, and *parvulus*. Every derived state that *stejnegeri* has is shared with *bolitoglossa*; every derived state that *eleutherodactylus* has is also shared with *bolitoglossa*. Discounting unique states, *parvulus* shares all derived states with *bolitoglossa*. The first choice to be made is whether *bolitoglossa* is best grouped with *stejnegeri*, *eleutherodactylus*, or *parvulus*. Four characters are shared among all four taxa (states of toe webbing, egg melanophores, nasal-frontoparietal contact, and pterygoidal flange). Three additional characters are shared among *bolitoglossa*, *stejnegeri*, and *eleutherodactylus* (states of inguinal gland, maxilla, mid-sagittal crest). Additionally, *bolitoglossa* shares one character with *stejnegeri* (state of otic ramus of squamosal) and *eleutherodactylus* (state of iliacus externus muscle). Beyond the four states shared by all four taxa, *bolitoglossa* shares an additional two with *parvulus* (states of sternum and otic ramus of squamosal), one of which (squamosal) is also shared with *stejnegeri*. The choice reduces to a cluster of (A) *bolitoglossa*, *stejnegeri*, and *eleutherodactylus* on the one hand and (B) *bolitoglossa*, *stejnegeri*, and *parvulus* on the other. The states differentially defining these two groupings are (A) inguinal gland, maxilla, and mid-sagittal crest versus (B) otic ramus of squamosal. I think the cluster of *bolitoglossa*, *stejnegeri*, and *eleutherodactylus* is the more robust and assume that these three taxa are most closely related to each other.

The next decision is whether the cluster of *bolitoglossa*, *stejnegeri*, and *eleutherodactylus* is most closely related to (A) *fuliginosus* and *granulosus*, or (B) *parvulus*.

The cluster of *bolitoglossa*, *stejnegeri*, and *eleutherodactylus* shares derived states of the nasal-frontoparietal contact and pterygoidal flange with *fuliginosus*, *granulosus*, and *parvulus*. The differentially defining characteristics are (A) inguinal gland, and (B) toe webbing and egg melanophores. The function of inguinal glands is unknown, but the lack of toe webbing and egg melanophores are associated with terrestriality. The basic question is whether the trend towards terrestriality occurred once (*bolitoglossa-stejnegeri-eleutherodactylus* most closely related to *parvulus*) or twice (*bolitoglossa-stejnegeri-eleutherodactylus* most closely related to *fuliginosus* and *granulosus*) in this assemblage of seven taxa.

There is some life history information available on this group of frogs. Free living tadpoles are known for some members of the *fuliginosus* group. Terrestrial larvae are known for *stejnegeri* and *parvulus*. No unquestioned information is available for *bolitoglossa*, *ohausi*, or the *granulosus* or *eleutherodactylus* groups. Miranda-Ribeiro (1926) published two figures of direct development stages attributed to *Iiodiscus asper* and *Craspedoglossa sanctae-catharinae* (= *bolitoglossa*), which became the subject of debate between Adolfo Lutz and Miranda-Ribeiro. The direct development eggs were taken at the same time as adults of the associated species. It is likely that both figured developmental series belong to the genus *Eleutherodactylus*. Of all available information, the most critical is the comparison of the terrestrial larvae of *stejnegeri* and *parvulus*. The larvae of both species are laid on land and have large yolk stores. The larvae hatch out of the egg capsules. The larvae do not feed in *parvulus*; yolk stores provide sufficient energy through metamorphosis (Lutz, 1944). The same is probable for *stejnegeri* (Heyer and Crombie, 1979). The overall morphologies of the larvae of *stejnegeri* and *parvulus* are quite similar (Heyer and Crombie, 1979). The

larvae are not identical however, differing in tooth row number and presence or absence of marginal papillae on the lower lip. The tooth rows of both larvae are reduced in comparison to free living larvae and characters of reduction or loss bear little information on relationships (Hecht and Edwards, 1976). The reductions of tooth rows and marginal papillae are not in the same direction for both species. The more specialized tooth row condition is found in *parvulus*, the more specialized papilla condition in *stejnegeri*. A common ancestor would have to have had a more generalized larva than either, but that ancestral condition could still be a terrestrial larval form. The other life history difference is the form of the egg mass; *stejnegeri* eggs are in a string, *parvulus* eggs in a clump.

The available life history data are compatible with either relationship grouping calling for the terrestrial larvae to have evolved once or twice in the group. The differences in larval form and egg mass shape are of a large enough magnitude to have evolved independently from a common ancestor with a free living, feeding larva, such as found in members of the *fuliginosus* group. Alternatively, the overall similarities could be indicative of the terrestrial larvae evolving but once in this group.

Although the data are consistent with alternative interpretations, I think the evidence favors the grouping of *bolitoglossa-stejnegeri-eleutherodactylus* with *fuliginosus* and *granulosus*, which decision rests on the inguinal gland demonstrating relationship among this group and the terrestrial larvae having evolved twice.

The last decision is whether *ohausi* or *parvulus* is the more closely related to the remainder of the taxa. The evidence for *ohausi* showing relationship is the sharing of the inguinal gland characteristic. The evidence for *parvulus* being related to the other taxa is the sharing of character states of the nasal-frontoparietal contact and

pterygoidal flange. The nasal-frontoparietal contact and pterygoidal flange characteristics are not associated with terrestriality *per se*. The pterygoidal flange only occurs in *Hydrotaetare* among other leptodactylids, strongly suggesting that this characteristic indicates close relationship among the taxa possessing the state in the group under study. Alternatively, inguinal glands are not common in leptodactylid frogs and also argue for close relationship among the taxa possessing them in the group under study. Recognizing that the evidence could be interpreted either way, I prefer the arrangement with *ohausi* showing closer relationship to the other taxa than *parvulus*. The easiest way to explain the double origin of nasal-frontoparietal contact and development of the pterygoidal flange is to assume that the immediate ancestor to all seven taxa had these states and that through a paedogenetic process, the "primitive" states of these characters evolutionarily reappeared in *ohausi*.

#### RELATIONSHIPS AND TAXONOMIC CONCLUSIONS

A phylogeny consistent with the above conclusions is presented in Figure 28. Also indicated are the character states that appear once in the phylogeny and the character states that have the most possible phylogenetic content. These latter are the characters remaining after deletion of characters that are unique to one taxa or that the derived states are states of reduction or loss, following the arguments of Hecht and Edwards (1976).

It should be re-emphasized that a slightly more parsimonious phylogeny, using the characters as analyzed, combines *parvulus* with the cluster *bolitoglossa-eleutherodactylus-stejnegeri*. The data as analyzed do not discriminate effectively between these alternatives. The reasons I prefer the arrange-



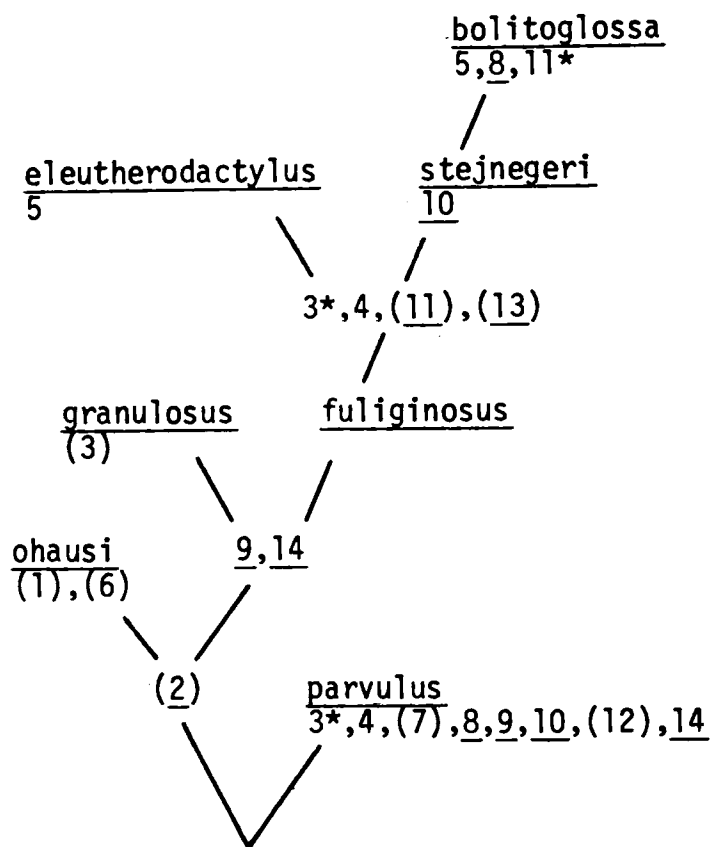


Figure 28. Proposed relationships among seven groups of frogs formerly placed in the genera *Cycloramphus*, *Craspedoglossa* and *Zachaenus*. Character numbers in parentheses represent unique state appearances within the phylogeny. Underlined character numbers represent character states with possible phylogenetic information (see text). Plain numbers are derived states for characters described in text; asterisks indicate secondary derivation.

ment represented in Figure 28 are that the overall gross morphology of *parvulus* differs from all other *Cycloramphus* and the nature of the egg masses differs between *parvulus* and *stejnegeri*.

Little can be stated in terms of relationships. The cluster of *bolitoglossa*, *stejnegeri*, and *eleutherodactylus* is the most robust in the phylogeny. Other relationships in the proposed phylogeny are supportable, but as discussed above, other schemes could be defended with the available morphological data.

The decision where to draw generic boundaries on the phylogeny (Figure 28) is perhaps more a case of personal preference

than evidence. I prefer to recognize two genera for the taxa figured: *Zachaenus* for *parvulus* and *Cycloramphus* for the other taxa. If the proposed relationships are correct, then terrestriality has been approached twice within this group and such a shift is best represented by recognizing two genera. The differences between the *fuliginosis* and *granulosus* group and *bolitoglossa-stejnegeri-eleutherodactylus* are in large part differences of degree; I believe these groups grade one into the other. Another alternative would be to recognize *ohausi* as a distinct genus. Certainly the thumb spines and tensor fasciae latae conditions are unique to *ohausi*. If *ohausi* shows

a paedogenetic trend in the skull, that would be further evidence of the distinctive evolutionary direction of *ohausi* in this complex. The overall morphology of *ohausi* is very similar to members of the *fuliginosus* group, this gestalt impression adds to the decision to include *ohausi* in the same genus with the other taxa exclusive of *parvulus*.

The available genetic data indicate that *Zachaenus* is part of the same evolutionary lineage as *Cycloramphus*, but the available data are not appropriate to use as the sole basis for generic classification (Maxson, et al., 1981).

#### COMPARISON WITH PREVIOUS SCHEMES

From 1920 and 1935 there was a raging controversy in print on the genera and generic names associated with *Cycloramphus* (A. Lutz, 1929; Miranda-Ribeiro, 1920, 1929, 1935). From 1935 to 1971, three genera were recognized for the taxa studied herein: *Craspedoglossa*, *Cycloramphus*, and *Zachaenus*. The only character listed by various authors (summarized in Bokermann, 1951) separating *Craspedoglossa* from *Cycloramphus* involved the tongue. As stated previously, I find no differences in tongue shape or structure among the species historically partitioned in these two genera.

Lynch (1971) proposed a new scheme, in which he synonymized the genus *Craspedoglossa* with *Zachaenus*. As his study is the most detailed recent study, careful comparison is required between his conclusions and those resulting from the present study. Lynch lists only two characters which differentiate the species usually associated with *Craspedoglossa* and *Zachaenus*: snout shape and a patagium. Lynch (1971, p. 142) stated that, "In all other characters used in the generic diagnoses, *Craspedoglossa* and *Zachaenus* are identical." The following discussion lists Lynch's character

numbers and his description. These are followed by my interpretation.

19) "Frontoparietals not ornamented except for prominent sagittal crest and supraorbital processes." *Zachaenus parvulus* has a moderate sagittal crest, but not prominent as in *Craspedoglossa*. *Zachaenus parvulus* has supraorbital processes, *Craspedoglossa* lacks them (compare Lynch, 1971, Fig. 91 with 92).

43) "Body lacking glands." This is true for *Zachaenus*, but males of *Craspedoglossa* have well developed inguinal glands.

46) "Development abbreviated, tadpole semi-aquatic, vent median, 1/1 tooth rows, labial papillae broadly interrupted anteriorly." Now that the larva of *C. stejnegeri* is known, the differences discussed previously require redefinition of this character if the synonymy of *Craspedoglossa* with *Zachaenus* is to be maintained.

49) "Adults less than 30 mm SVL." *Craspedoglossa* exceeds this size (*C. stejnegeri* to 55 mm SVL).

Of these characters, I think what most influenced Lynch was that the thought *Craspedoglossa* lacked inguinal glands. Comparison of Lynch's Fig. 90, the skull of *Cycloramphus eleutherodactylus* with Fig. 92, the skull of *stejnegeri*, shows them to be very similar and markedly different in details of shape from his Fig. 91, the skull of *Z. parvulus*.

It is important to review the differences that Lynch found between *Cycloramphus* and *Craspedoglossa* which allowed him to maintain *bolitoglossa* and *stejnegeri* outside of the genus containing *eleutherodactylus*. A list follows of character numbers and conditions first for *Cycloramphus* (first) versus those for *Zachaenus* (sensu Lynch, including *Craspedoglossa*) for the characters that differ. Where appropriate, my observations are also listed.

7) Omosternum moderate-sized versus omosternum relatively large.

8) Sacral diapophyses rounded to very

slightly dilated *versus* sacral diapophyses rounded.

11) Palatal shelf of premaxilla of moderate depth, not notched, palatal process short *versus* palatal shelf of maxilla relatively deep, not notched, palatal process moderate sized.

13) Palatal shelf of maxilla relatively narrow, pterygoid process large *versus* palatal shelf of maxilla of moderate width, pterygoid process lacking. I find no difference in maxillary palatal shelf shape or pterygoid process either among specimens or between Lynch's Figures 90 and 92.

19) Frontoparietals not ornamented, bearing large sagittal crest *versus* frontoparietals not ornamented except for prominent sagittal crest and supraorbital processes. Much more variation in sagittal crest exists within both groups than Lynch recognized, invalidating this characteristic as diagnostic. The species *bolitoglossa* and *stejnegeri* lack supraorbital processes.

22) Epiotic eminences prominent posteriorly, obsolete anteriorly *versus* epiotic eminences obsolete.

29) Palatines broad, widely separated medially, bearing small odontoid ridges *versus* palatines slender, widely separated medially, no odontoid ridges. I find no differences in palatine width either in specimens or between Lynch's Figures 90 and 92. I do find an odontoid ridge on the palatine of *stejnegeri*, not figured by Lynch.

31) Anterior ramus of parasphenoid broad, not keeled *versus* anterior ramus of parasphenoid narrow, not keeled. I would characterize the anterior ramus as narrow in *Cycloramphus* plus *bolitoglossa* and *stejnegeri*, broad in *parvulus*. These characterizations agree with Lynch's figures.

43) Inguinal glands present *versus* body lacking glands. As stated above, *bolitoglossa* and *stejnegeri* have inguinal glands.

46) Larvae with very brief tadpole stage, semi-aquatic, vent median, 1/1 tooth rows, labial papillae broadly interrupted anteriorly

*versus* development abbreviated, tadpole semi-aquatic, vent median, 1/1 tooth rows, labial papillae broadly interrupted anteriorly. I would characterize the larvae of such species as *Cycloramphus* Boracéia "dubius" as aquatic and the larvae of *parvulus* and *stejnegeri* as terrestrial. The larval type of *C. eleutherodactylus* is not known.

49) Adults 30-55 mm SVL *versus* adults less than 30 mm SVL. Examination of additional material demonstrates that this diagnostic break does not occur.

Re-evaluation of the characters Lynch used to separate *C. eleutherodactylus* and *bolitoglossa-stejnegeri* into different genera indicates many fewer differences exist than Lynch described. I conclude that the remaining differences are trivial and do not negate the conclusions drawn in this paper.

#### GENERIC NOMENCLATURE NOTES

Lynch (1971, p. 139) incorrectly summarized the generic nomenclature associated with the species Bokermann considered to be the single genus *Cycloramphus*. Lynch indicated that in 1926 Miranda-Ribeiro thought there were three genera involved: *Cycloramphus*, *Grypiscus*, and *Iliodiscus*. Lynch thought this generic partitioning was based on toe webbing variation and mandibular pseudoteeth in *Grypiscus*. This is not correct, but was apparently based on Lynch's belief that, "Six species of the genus (*asper*, *diringshoefensi* [sic], *dubius*, *eleutherodactylus*, *granulosus*, and *pinderi*) lack webbing or lateral fringes on the toes; three species (*boulengeri*, *fulginosus* [sic], and *neglectus*) have one-half to fully webbed toes." Three of the species in the first list have unquestionable webbing (*asper*, *dubius*, *pinderi*). Miranda-Ribeiro's (1935) final assessment of the genera was that there was but a single genus involved, for which the oldest name was *Grypiscus*, as he thought

*Cycloramphus* was based on an Andean species. Bokermann (1951) followed the one genus concept for *Cycloramphus*, but, as Lynch pointed out, made an incorrect type-species designation for *Iliodiscus*.

### Species previously placed in the genus *Craspedoglossa*

Representatives of species previously placed in the genus *Craspedoglossa* were not included in the early stages of this study. When it was determined that *Craspedoglossa* was a synonym of *Cycloramphus*, easily obtainable representatives were gathered. As specimens of this group are generally rare in collections, in all likelihood an effort to borrow additional material would not add appreciably to the knowledge of species or their distributions. Rather than delay the present paper, only those specimens at hand are used for analysis.

Three samples are available: (1) a moderate sample from near Teresópolis in the Organ Mountains, (2) a small sample from Brejo da Lapa in the Serra da Mantiqueira, and (3) a small sample from the Serra do Mar in the State of Santa Catarina. As sample sizes are small, variation is discussed in summary fashion.

**Color Pattern.** — The Organ Mountains sample dorsal pattern ranges from uniform to narrowly chevroned (Figure 2, B, E, F, G) with an indistinct or absent light interorbital bar. The lip is uniform or has indistinct light bars. The thigh is spotted or rarely uniform. The belly is mostly light with some dark mottle (Figure 5, C).

The Brejo da Lapa sample has a uniform or slightly blotched dorsal pattern (Figure 2, B, D) with very distinctive light interorbital bars. The lips are distinctly light barred. The thighs are spotted. The belly is uniform (Figure 5, E).

The Santa Catarina sample has a uniform or dotted and lined dorsal pattern (Figure 2, B, J) lacking interorbital bars. The lips are not barred. The thigh ranges from uniform to spotted. The belly has light spots or is uniform to distinctly patterned (Figure 5, D, E, F).

**Measurements.** — The samples differ in adult size, head and hind limb proportions (Figure 29 shows size and head width differences. The head width of the Brejo da Lapa sample is distinctive. The foot length/SVL plot [not figured] indicates that the Santa Catarina sample is distinct from the other two samples.)

Each sample is distinct in size, color pattern, and body and limb proportions. Historically, two species have been recognized for the Organ Mountain and Santa Catarina samples. The Brejo da Lapa sample is as distinct from the other two samples as the other two are from each other. Each sample is recognized as a distinct species.

Three names have been proposed for the species under discussion: *Borborocoetes bolitoglossus* Werner, 1897; *Craspedoglossa santaecatharinae* Müller, 1922; and *Borborocoetes stejnegeri* Noble, 1924.

The holotype of *B. bolitoglossus* was collected from Blumenau, Santa Catarina. The type is not in the collections of either the Vienna or Hamburg Museums. If the type were in the Hamburg collection, it was destroyed in World War II. The description is brief and inconclusive; the pattern and morphological features described do not allow association of this name with any given species of *Cycloramphus* with free toes. The tongue description is similar to those of *Cycloramphus* in terms of shape and attachment, but differs in referring to horny rows on the tongue surface. The type locality of Blumenau is within the geographic range of the species historically associated with this name. Until either the type is located or toptotypic series collected,

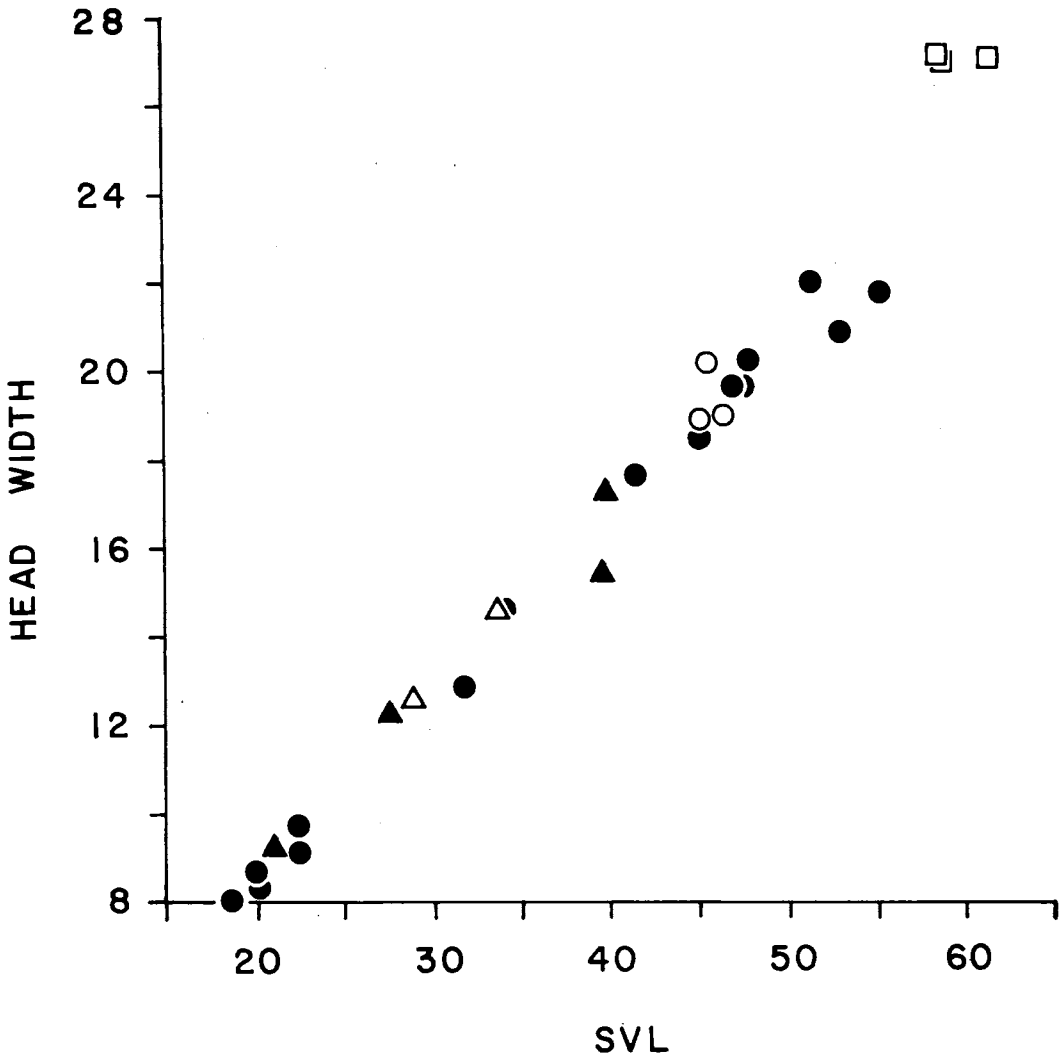


Figure 29. Head width plotted against SVL for individuals previously placed in the genus *Craspedoglossa*. Triangles = *C. bolitoglossa*, closed = juveniles and females, open = males, circles = *C. stejnegeri*, closed = juveniles and females, open = males; squares = males from Brejo da Lapa.

the best procedure is to consider *Borboro-coetes bolitoglossus* as the oldest name for the Santa Catarina species.

Müller described *Craspedoglossa santaecatharinae* from Rio Novo, Santa Catarina. The description and figures are adequate to associate this name with the Santa Catarina species. The thin dark vertebral line Müller mentioned is diagnostic. Müller indicated that some of his specimens had

light interorbital bars, extending the pattern state from that discussed above. *Craspedoglossa santaecatharinae* is a synonym of *B. bolitoglossus*.

Noble described *B. stejnegeri* on the basis of a single specimen from the Organ Mountains. The description and the type, USNM 52608, clearly allocate the name with the Organ Mountains species. The uniform dorsal pattern and texture (finely granular)

together with the curved dorsal folds are diagnostic. Re-examination of the specimen indicates that it is a female, not a male as stated by Noble. Noble indicated a SVL of 42 mm, I measure 45.6. The specimen is a young female with small ovaries, apparently entering the first breeding season. This size of the frog and condition of the ovaries is comparable to other specimens examined (Figure 29). *Borborocoetes stejneri* is the oldest available name for the Organ Mountains species.

Two of the three species have available names, the third is named in the next section.

### Taxonomy

The purposes of this section are (1) to provide a definition for the genus *Cycloramphus* as recognized herein, (2) to provide adequate diagnoses, descriptions and keys to differentiate the species, and (3) summarize the known morphological, call, and distributional data for each of the species.

#### GENERIC DEFINITION

##### *Cycloramphus* Tschudi, 1838

*Cycloramphus* Tschudi, 1838:81. Type-species by monotypy, *Cycloramphus fuliginosus* Tschudi, 1838.

*Cyclorhamphus* Agassiz, 1847:110. Emendation of *Cycloramphus* Tschudi, 1838.

*Pithecopsis* Günther, 1859:22. Type-species *Pithecopsis fuliginosus* (Tschudi, 1838). Duméril and Bibron (1841:454) include *Pithecopsis fuliginosus*, a Duméril and Bibron manuscript name, in the synonymy of *Cycloramphus fuliginosus* Tschudi. Günther used *Pithecopsis* in association with a generic definition, thus the name dates from Günther rather than Duméril and Bibron.

*Grypiscus* Cope, 1867:206. Type-species by monotypy *Grypiscus umbrinus* Cope, 1867.

*Iliodiscus* Miranda-Ribeiro, 1920:267. Type-species by subsequent designation (Lynch, 1971:137, see also remarks on Lynch, page 139) *Iliodiscus dubius* Miranda-Ribeiro, 1920.

*Craspedoglossa* Müller, 1922:167. Type-species by monotypy, *Craspedoglossa santaecatharinae* Müller, 1922.

*Niedenis* Ahl, 1924:107. Type-species by monotypy, *Niedenis spinulifer* Ahl, 1924.

Pupil horizontal with distinct meniscus; tympanum hidden; thumbs lacking asperities except for *C. ohausi* with black spines on thumbs of both sexes; well defined circular inguinal glands in males; toe tips simple or swollen, no circumferential groove; tarsal fold distinct or not, if distinct, extending nearly the length of tarsus, no tarsal tubercles; inner and outer metatarsal tubercles rounded; toes free, ridged, or webbed; adductor mandibularis muscle s only (adductor mandibulae posterior subexternus only present); depressor mandibulae condition dfsq, DFsq, or DFsq(at) (origin from dorsal fascia and squamosal and otic region, slip from squamosal and otic region usually larger, few fibers from annulus tympanicus present or absent); geniohyoideus medialis muscle contiguous medially; anterior petrohyoideus muscle insertion on lateral edge of hyoid plate; sternohyoideus muscle insertion entirely near edge of hyoid plate; omohyoideus muscle insertion on hyoid plate or on hyoid plate and fascia lateral to posteromedial process; iliacus externus muscle extending from 1/3 to 3/4 length of ilium, tensor fasciae latae muscle insertion posterior to the anterior extent of the iliacus externus on the ilium, exterior head of semitendinosus muscle about equal in bulk to interior head, attached by tendon to interior portion or not; adductor longus muscle strap-like, attaching on adductor magnus

muscle from about 1/2 length of adductor magnus to almost full length near the knee; quadratojugal present, contacting maxilla; posterior maxilla expanded or not, often in proximity or contacting (*bolitoglossus*) zygomatic ramus of squamosal; nasals large, contacting each other, the maxillae, and usually the frontoparietals; frontoparietals in contact (usually) or not (*ohausi*), usually not exposing frontoparietal fontanelle; zygomatic process of squamosal elongate; otic process of squamosal shorter than zygomatic process, slightly expanded into a very small plate or not; vomer with teeth; pterygoid flange usually prominent; prootic not fused with frontoparietal; occipital condyles widely separated; cervical cotyles widely separated, not stalked; anterior process of hyale barely present to well developed; alary process of hyoid stalked, distally expanded; posterior sternum cartilaginous, distally expanded into two discrete lobes (Heyer, 1975, Fig. 4, H); sacral diapophyses rounded or slightly expanded; terminal phalanges knobbed; ilium with dorsal crest.

#### SPECIES ACCOUNTS

Except for the detailed descriptions of holotypes, only those characteristics that differentiate the species are described.

In the Adult Specimen Definition sections, N refers to the number of adult individuals used for statistical analyses. Numerical summaries are means plus or minus one standard deviation. Webbing formulae follow Savage and Heyer (1967) and are the modal values based on adult specimens. Male and female modal values are presented separately only if they differ.

The larval stages are according to Gosner (1960).

Distributions are based on locality data associated with specimens examined in this study unless otherwise noted. The locality data are recorded in the same manner as the original catalog data (or invoices) and are not standardized in terms of distances

or elevations. A gazetteer (Appendix 2) is provided as a further aid to finding the localities on maps. Numbers in parentheses after museum numbers indicate the number of specimens with the same museum number.

#### *Cycloramphus asper* Werner, 1899

*Cycloramphus asper* Werner, 1899:482.

Type-Locality: Sta. Catarina, Brasil. Holotype: Presumably formerly in Berlin Museum, probably destroyed.

*Telmatobius asper* Boulenger, 1907:394.

Type-Locality: Theresopolis, Santa Catharina, Brazil. Lectotype: BMNH 1947.2.15.48, adult male.

*Niedenia spinulifer* Ahl, 1924:107. Type-Locality: Label lost; perhaps Ndjiri swamps, Schillings (free translation). Types: Berlin Museum, probably destroyed.

*Cyclorhamphus neglectus* Lutz, 1928:640.

Replacement name for *Telmatobius asper* Boulenger.

*Cyclorhamphus boulengeri* Lutz, 1929:9.

Replacement name for *Telmatobius asper* Boulenger.

**Diagnosis.** — The species with toe webbing and distinct black and/or white tubercles on the dorsum are *C. asper*, *boraceiensis*, *duseni*, *lutzorum*, *mirandaribeiroi*, *ohausi*, *rhyakonastes*, *semipalmatus*. *Cycloramphus asper* has considerable toe webbing, distinguishing *asper* from *ohausi*, *rhyakonastes*, and *semipalmatus*, which have reduced webbing. *Cycloramphus asper* is larger (males 38-48 mm, females 44-54 mm SVL) than the moderately webbed *C. duseni* (males 29-38 mm, females 31-44 mm SVL). *Cycloramphus asper* is smaller and most individuals lack distinct spots on the posterior surface of the thigh; *C. mirandaribeiroi* is larger (males 49-61 mm, females 62-69 mm SVL) and all individuals have large discrete thigh spots. The considerably webbed *C. asper* differs from both *C. boraceiensis* and *lutzorum* in that they have

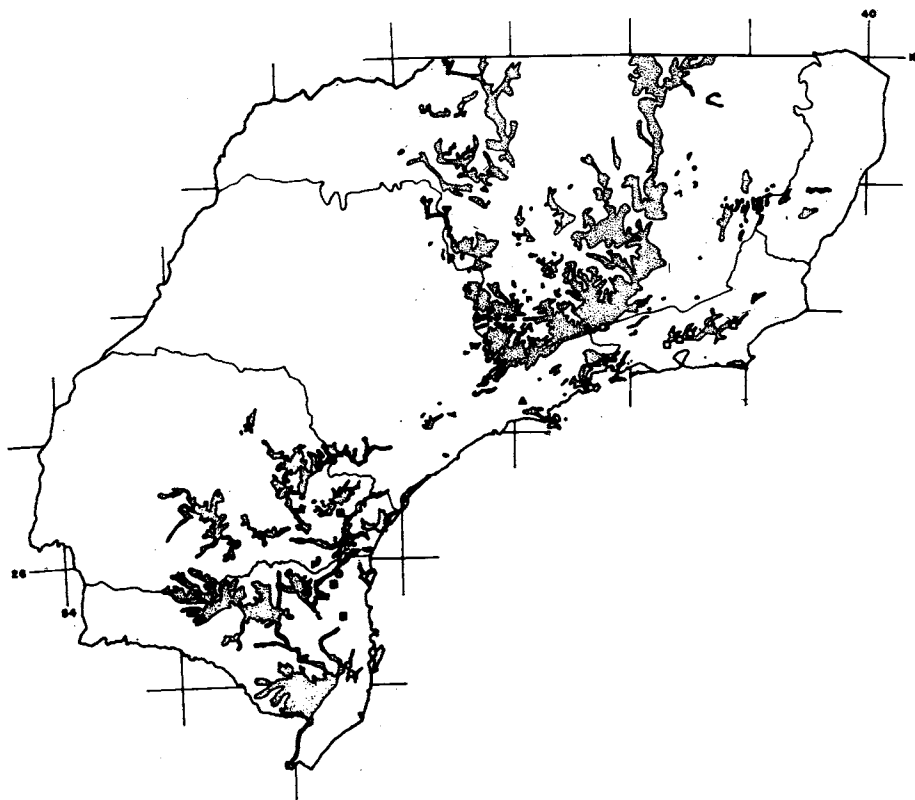


Figure 30. Distribution map of *Cycloramphus asper* (open circles), *bandeirensis* (closed circle), *boltoglossus* (closed squares), *boraceiensis* (open triangles), *brasiliensis* (open squares), *carvalhoi* (closed triangle). Stippled areas join approximate 1000 meter contours.

moderate web. The dorsal tubercles of *C. asper* are borne on high relief warts; the tubercles of *C. boraceiensis* are on low relief warts. Most individuals of *C. asper* do not have distinct light spots on the posterior surface of the thigh; most *C. lutzorum* have distinct light thigh spots.

**Adult Specimen Definition** (N = 33). — No thumb spines; snout profile rounded, blunt, or lip pronounced (Figure 6, A, B, F); dorsal pattern blotched to almost uniformly dark brown (Figure 2, B, D-1); posterior surface of thigh usually uniformly patterned, mottled to sometimes distinctly light spotted; no distinctive colors in life; dorsum with high relief warts bearing shagreen and black and/or white tubercles, warts sometimes aligned in irregular to regular lines; male foot web I 0 — 1 1/2 II 0 — 2 III 0 — 2- IV 2- — 0 V,

female I 0 — 2- II 0 — 2+ III 0 — 2 1/4 IV 2- — 0 V; male SVL  $44.3 \pm 3.0$ , maximum 47.8 mm, female SVL  $49.4 \pm 3.1$ , maximum 53.7 mm, females larger than males ( $t = 4.81$ ,  $P < .001$ ); male head length/SVL ratio  $0.39 \pm .02$ ; female  $0.38 \pm .01$ ; male head width/SVL ratio  $0.42 \pm .02$ , female  $0.42 \pm .01$ ; male eye-nostril distance/SVL ratio  $0.09 \pm .01$ , female  $0.09 \pm .01$ ; male eye-eye distance/SVL ratio  $0.19 \pm .01$ , female  $0.18 \pm .01$ ; male femur/SVL ratio  $0.43 \pm .02$ , female  $0.44 \pm .03$ ; male tibia/SVL ratio  $0.45 \pm .03$ , female  $0.45 \pm .02$ ; male foot/SVL ratio  $0.49 \pm .03$ , female  $0.50 \pm .02$ .

**Advertising Call.** — Unknown.

**Larval Definition.** — Larvae unknown.

**Distribution.** — Serra do Mar in the State of Santa Catarina (Figure 30).



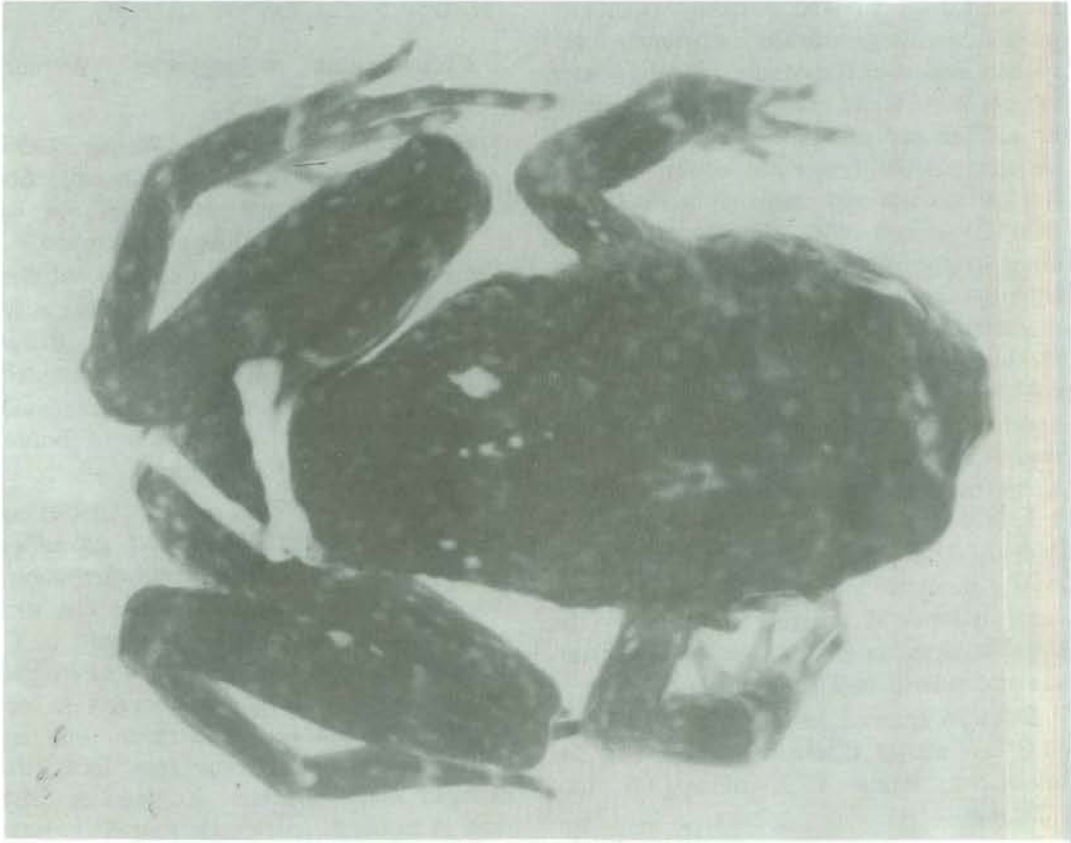


Figure 31. Holotype of *Cycloramphus bandeirensis*.

**SANTA CATARINA.** Petrópolis (probably in error and same as next locality) (USNM 137680-81, Vienna 4120, 4122:1-23, 15822); Queçaba (= Theresópolis) (BMNH 1947.2.1548-1549, Vienna 4121:1-8, 4123:1-7, 4124:1-7); 40 km from Santo Amaro da Imperatriz on road to São Bonifácio (between Queçaba and São Bonifácio) (MZUSP 57748-754, USNM 217844-851); Município de Serra Alta (São Bento do Sul) córrego na região Rio Vermelho, Serra do Mar (L 176).

***Cycloramphus bandeirensis*, new species**  
Figure 31

Holotype: MZUSP 52924, a juvenile from Brasil: Espírito Santo, Pico da Ban-

deira, 2450 m. Collected by Lyn C. Branch in November 1977. Paratopotype: USNM 220073.

**Diagnosis.** — The species that have toe webbing and lack black and/or white dorsal tubercles are *C. bandeirensis*, *brasiliensis*, *dubius*, *fuliginosus* and *jordanensis*. The reduced toe webbing of *C. bandeirensis* differs from the moderate webbing of *dubius* and *fuliginosus* and distinguishes *bandeirensis* from the considerably webbed *brasiliensis*. The dorsum of *bandeirensis* lacks a shagreen, distinguishing it from *dubius*, which has a shagreen. The posterior surface of the thigh has distinct light spots in *bandeirensis*; *jordanensis* lacks such spots as do almost all individuals of *C. fuliginosus*.

**Description of Holotype.** — Snout rounded from above, vertically sloping in profile; canthus rostralis indistinct; loreal slightly concave; tympanum hidden; vomerine teeth in short transverse series almost in medial contact posterior and between choanae; second finger just longer than first; flat ovoid inner metacarpal tubercle smaller than flat ovoid outer metacarpal tubercle, inner metacarpal tubercle separated from subarticular tubercle of thumb by almost diameter of subarticular tubercle; thumbs lacking asperities; dorsal texture granular, cobblestone-like, granules lack shargreen and tubercles; chin granulate, belly smooth, ventral thigh granulate; toe tips nearly same width as digits; toe webbing I 1 3/4 — 2 1/2 II 2- — 3+ III 2 3/4 — 4- IV 3 3/4 — 2+ V; subarticular tubercles moderate; elongate inner metatarsal tubercle, outer metatarsal tubercle indistinct; weak tarsal fold; metatarsal ridge; posterior tarsus and sole of foot smooth.

SVL 26.9, head length 9.2, head width 11.2, eye-nostril distance 2.4, eye-eye distance 5.3, femur 13.3, tibia 13.6, foot 12.4 mm.

Dorsum dark brown with light brown mottling and spots; loreal area tan, contrasting with darker dorsal color, no distinct lip bars or stripes; upper limbs faintly barred and light spotted; chin and belly dark with light spots; front and back of thighs and tibias with distinct light spots.

**Paratopotype.** — A 33.1 mm SVL male. Color in life: dorsum and posterior surfaces of thighs dark purplish brown, almost black, with yellow spots; belly flecked white and flesh, iris black with silvery radiating network.

**Etymology.** — Named after the type locality.

**Advertising Call.** — Unknown.

**Larval Definition.** — Larvae unknown.

**Distribution.** — Known only from the type locality (Figure 30).

**ESPÍRITO SANTO.** Pico da Bandeira, (MZUSP 52924, USNM 220073).

**Cycloramphus bolitoglossus** (Werner), 1897, new combination

*Borborocoetes bolitoglossus* Werner, 1897: 265. Type-Locality: Blumenau, Sta. Catharina, Brasil. Holotype: not examined, may be lost or destroyed.

*Craspedoglossa santaecatharinae* Müller, 1922:168, Figs. 1-3. Type-Locality: Rio Novo, Sta. Catharina, Brasil. Type: Munich Museum, not examined.

*Craspedoglossa bolitoglossa*: Bokermann, 1966:16. First association of *bolitoglossa* with *Craspedoglossa*.

**Diagnosis.** — The webless species of *Cycloramphus* are *bolitoglossus*, *carvalhoi*, *catarinensis*, *diringshofeni*, *eleutherodactylus*, *granulosus*, *stejnegeri*, *valae*. The toes are free and the dorsum is smooth in *C. bolitoglossus*; the toes are ridged or fringed and the dorsum is glandular-warty in *catarinensis*, *granulosus*, and *valae*. The leg is shorter in *bolitoglossus* (e.g. foot/SVL ratio in males average .40, females .36) than in *diringshofeni* (male foot/SVL ratio average .50) or *eleutherodactylus* (male foot/SVL .48 ± .03 (one standard deviation), female .49 ± .04). *Cycloramphus bolitoglossus* is smaller (males 28-34 mm, females 39-40 mm SVL) than either *carvalhoi* (males 58-62 mm SVL) or *stejnegeri* (males 45-47 mm, females 45-56 mm SVL). The dorsal pattern of a dark mid-vertebral pin stripe and scattered small dark spots (Figure 2, J) occurs only in some individuals of *C. bolitoglossus*.

**Adult Specimen Definition** (N = 4). — Thumbs lacking spines; snout rounded or vertical (Figure 6, A, B); dorsal pattern uniform or with small scattered dots and a hairline mid-dorsal stripe (Figure 2, B, J) posterior surface of thigh uniform, mottled, to distinctly light spotted; dorsal texture smooth or slightly granular; foot without web, toes free; male SVL 28.8-33.6 mm,

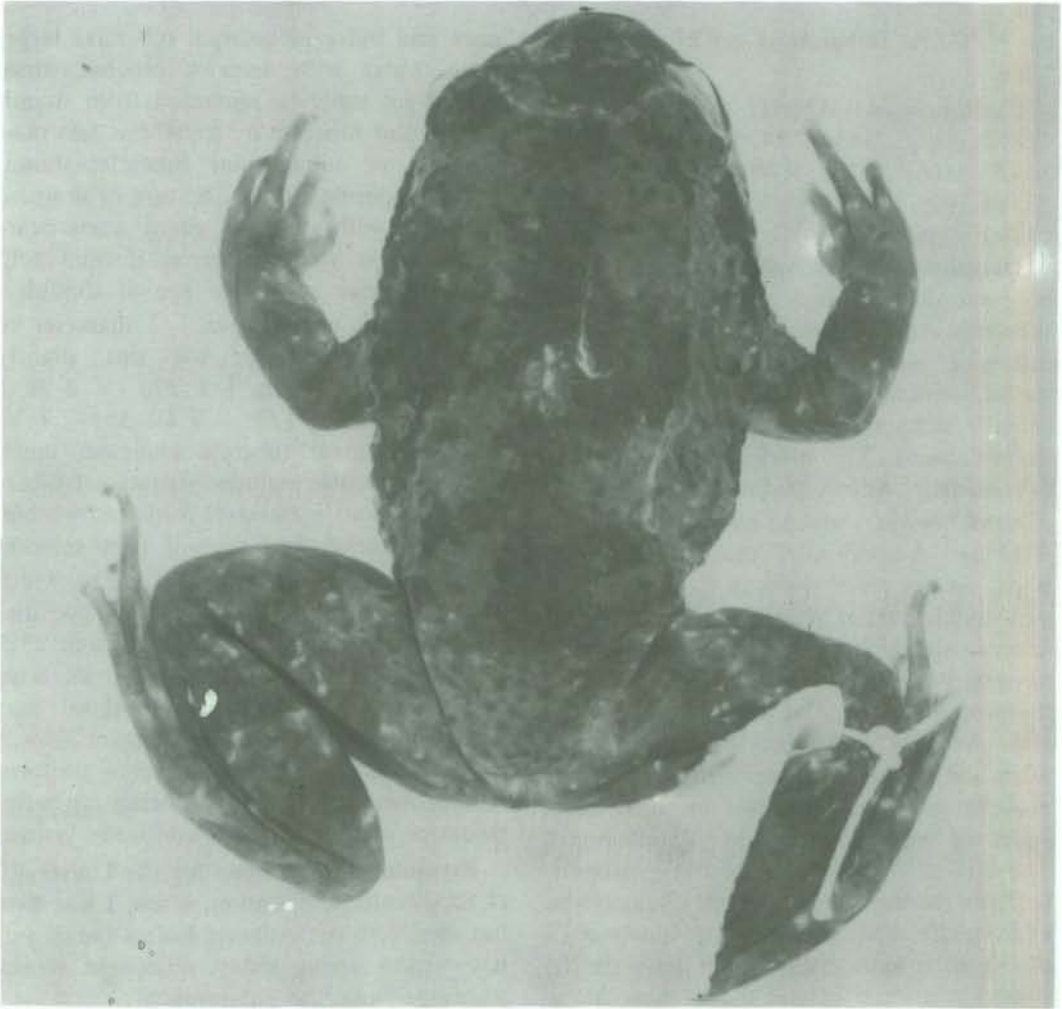


Figure 32. Holotype of *Cycloramphus boraceiensis*.

female 39.4-39.8 mm; male head length/SVL ratio 0.37, female 0.33; male head width/SVL ratio 0.43, female 0.41; male eye-nostril distance/SVL ratio 0.08, female 0.08; male eye-eye distance/SVL ratio 0.15, female 0.14; male femur/SVL ratio 0.38, female 0.37; male tibia/SVL ratio 0.35, female 0.34; male foot/SVL ratio 0.40, female 0.36.

**Advertising Call.** — Unknown.

**Larval Definition.** — Larvae unknown.

**Distribution.** — Serra do Mar in the states of Paraná and Santa Catarina (Figure 30).

**PARANÁ.** Volta Grande (USNM 125487-492).

**SANTA CATARINA.** Blumenau (type locality of *C. santaecatharinae*); Humboldt (= Corupá) (USNM 66573); Rio Novo (= Corupá) (type locality of *B. bolitoglossus*).

*Cycloramphus boraceiensis* new species  
Figure 32

Holotype: MZUSP 3934, an adult male from Brasil: São Paulo; Boracéia. Collected

by W. C. A. Bokermann on 27 December 1948.

Paratopotypes: AMNH 54546, MZUSP 2287, 3050, 3430, 3433-34, 3439-441, 3443, 3866, 3923, 4048, 16199, 23038, 23784-792, 37652-58, USNM 129150, 217936-966.

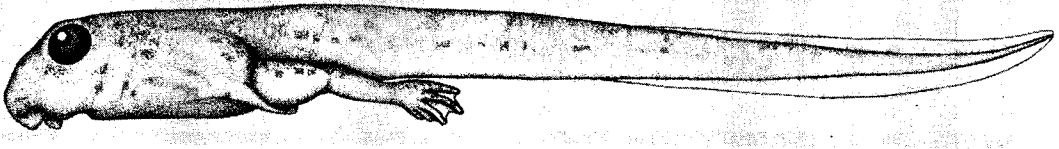
**Diagnosis.** — The species with toe webbing and distinct black and/or white dorsal tubercles are *C. asper*, *boraceiensis*, *duseni*, *lutzorum*, *mirandaribeiroi*, *ohausi*, *rhyakonastes*, *semipalmatus*. *Cycloramphus boraceiensis* lacks thumb spines, *C. ohausi* has thumb spines. The moderately webbed *C. boraceiensis* differs from *C. asper* and *mirandaribeiroi*, which have considerable webbing. Additionally, the tubercles are borne on low relief warts in *C. boraceiensis* and on high relief warts in *asper*; most *C. boraceiensis* lack thigh spots, all *mirandaribeiroi* have large light distinct spots on the posterior surface of the thigh. The moderate webbing and tubercles on low relief warts of *C. boraceiensis* differs from the reduced web and tubercles on high relief warts of *rhyakonastes* and *semipalmatus*. The low relief warts of *C. boraceiensis* differ from the high relief warts of *C. lutzorum*; additionally, whereas some individuals of *C. boraceiensis* have distinct light spots on the posterior surface of the thigh, most *lutzorum* have such spots. *Cycloramphus boraceiensis* is a larger species (males 35-55 mm, females 52-59 mm SVL) than *C. duseni* (males 29-38 mm, females 31-44 mm SVL). *Cycloramphus boraceiensis* most closely resembles *C. dubius*, but *dubius* lacks distinct dorsal black and/or white tubercles.

**Description of Holotype.** — Snout weakly semicircular from above, rounded with a flared lip in profile; canthus rostralis indistinct; loreal very slightly concave; tympanum hidden; vomerine teeth in transverse almost contiguous series posterior to and between choanae; elongate vocal slits present; first finger just shorter than second;

inner and outer metacarpal tubercles large, ovate, outer with anterior process, inner metacarpal tubercle separated from thumb subarticular tubercle by somewhat less than diameter of subarticular tubercle; thumb lacking asperities; dorsal texture of uniform low warts with shagreen, many warts bearing a single white tubercle; distinct fold from posterior corner of eye to shoulder; inguinal disk ovoid, over 1/2 diameter of eye; venter granular; toe tips slightly swollen; toe webbing I 1 1/3 — 2 II 1 1/3 — 3— III 1 1/3 — 3 IV 3— — 1 V; inner metatarsal tubercle elongate, much larger than outer rounded metatarsal tubercle; tarsal and metatarsal folds not visible; posterior tarsus and sole of foot smooth. SVL 51.3, head length 19.6, head width 21.2, eye-nostril distance 3.8, eye-eye distance 9.7, femur 22.3, tibia 22.9, foot 23.5 mm. Dorsum almost uniform brown with lighter central spot and interorbital bar; loreal and upper lip region uniform brown; upper limbs slightly barred; chin uniform light brown, darker than uniformly tan belly; posterior surface of thigh uniformly brown.

**Etymology.** — Named for the University of São Paulo field station, where I was first introduced to the Atlantic Forest fauna and have since spent many enjoyable weeks learning about the environment.

**Adult Specimen Definition** (N = 11). — Thumbs lacking asperities; snout rounded, vertically sloping or upper lip flared in profile (Figure 6, A, B, F); dorsal pattern uniform or with large dark coalesced blotches (Figure 2, B, D-1); posterior surface of thigh uniform, mottled, or rarely with small distinct light spots; no distinctive colors in life; dorsal texture of more or less uniform low profile granular warts bearing shagreen and a single white tubercle, warts rarely aligned into short irregular series; foot web I 1 — 2 II 1 1/3 — 2 1/2 III 1 1/2 — 3 IV 3— — 1 V; male SVL 44.9 ± 7.1, maximum 54.7 mm, female 55.4, maximum 58.1 mm; male head length/

Figure 33. Larva of *Cycloramphus boraceiensis*.

SVL ratio  $0.39 \pm .01$ , female 0.40; male head width/SVL ratio  $0.42 \pm .01$ , female 0.42; male eye-nostril distance/SVL ratio  $0.08 \pm .01$ , female 0.08; male eye-eye distance/SVL  $0.18 \pm .01$ , female 0.19; male femur/SVL ratio  $0.46 \pm 0.02$ , female 0.47; male tibia/SVL ratio  $0.46 \pm .02$ , female 0.46; male foot/SVL ratio  $0.47 \pm .02$ , female 0.48.

**Advertising Call.** — Call short, about 0.03 s duration; not finely tuned, energy distributed between 500 and 3500 Hz with energy peaks at about 1400 and 2000 Hz (Heyer and Mello, Fig. 1 B, 2 C, Figure 59A); sharp click sound.

**Larval Definition.** — Larva elongate, depressed; belly flattened with shelf extending past body; neither spiracle nor anus visible in single example at hand (USNM 217933); eye large, 18% head-body length; oral disk broad, 39% head-body length; oral disk entire, anterior papilla gap broad, almost width of disk, oral papillae in single row, continuous posteriorly; tooth row formula  $\frac{2}{3}$ ; beak with chisel-like central cusp; head-body length 23% total length; total length 27.2 mm, stage 42; body rather uniformly patterned, tail with dorsal series of light continuous spots (Figure 33).

**Distribution.** — The Serra do Mar in the southeastern part of the State of Rio de Janeiro and the northern half of the State of São Paulo; the offshore islands of Ilha Grande and São Sebastião (Figure 30).

**RIO DE JANEIRO.** Ilha Grande (MNRio 2241); Parati (MNRio 1635(3), 1638).

**SÃO PAULO.** Boracéia (AMNH 54546, MZUSP 2287, 3050, 3426, 3430, 3433-34, 3439-441, 3443, 3866, 3923, 3934, 4048,

16199, 23037-38, 23784-792, 37652-58, USNM 129150, 217933, 217936-966; Ilha de São Sebastião (MZUSP 8107, 9986, 23373, USNM 217934-35.

**Cycloramphus brasiliensis** (Steindachner), 1864

*Telmatobius brasiliensis* Steindachner, 1864: 282, Plate XVI, Figs. 3, 3a-3c. Type-Locality: region around Rio de Janeiro, Brasil. Holotype: Vienna Museum 22922, juvenile.

*Iliodiscus pinderi* Miranda-Ribeiro, 1920: 269, Plates 3-5. Type-Locality: Ilha de S. Sebastião, S. Paulo as originally published in error; correct type-locality is Serra de Macaé, Rio de Janeiro, Brasil. Holotype: MZUSP 1008, adult male.

**Diagnosis.** — The species that have toe webbing and lack black and/or white dorsal tubercles are *C. bandeirensis*, *brasiliensis*, *dubius*, *fuliginosus*, and *jordanensis*. The considerable toe webbing of *brasiliensis* differs from the moderate webbing of *dubius* and *fuliginosus* and distinguishes *brasiliensis* from *bandeirensis* and *jordanensis*, which have reduced web. The dorsum of *C. brasiliensis* lacks shagreen, contrasting with the dorsal shagreen of *C. dubius*. Arrangement of metacarpal tubercles (Figure 55) further distinguishes *C. brasiliensis* from *fuliginosus*.

**Adult Specimen Definition** (N = 67). — Thumbs lacking asperities; snout usually rounded, sometimes vertically sloping in profile (Figure 6, A, B); dorsal pattern uniform, light spotted, or blotched (Figure 2, B, C, D, D-1); posterior surface of thigh uniform, mottled, or with small, distinct light spots; no distinctive colors in life;

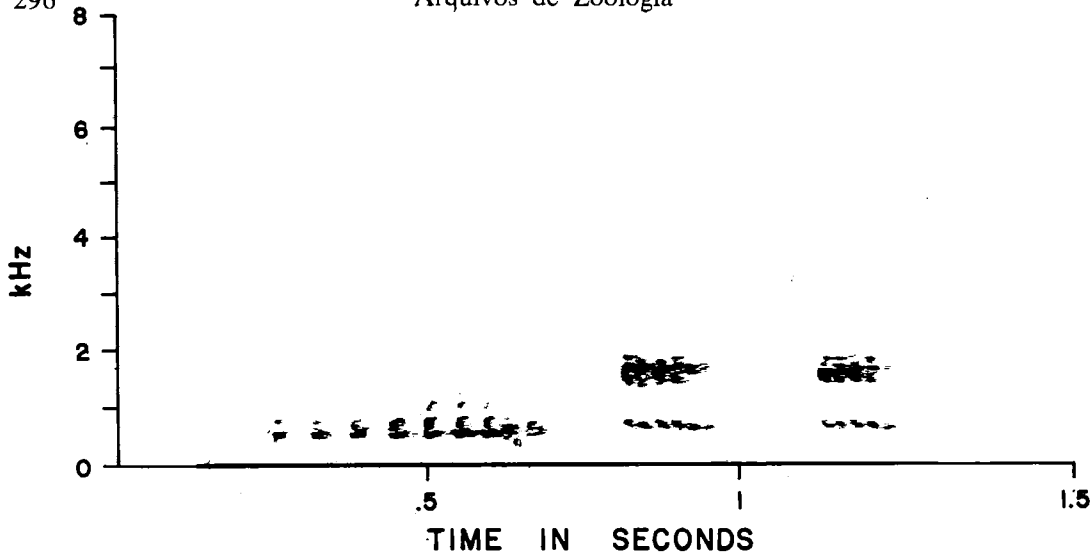


Figure 34. Audiospectrogram of the advertising call of *Cycloramphus brasiliensis*. Specimen recorded at 20:50 h on 3 December 1977 from Brasil: Rio de Janeiro; near Teresópolis. Specimen USNM 217858.

dorsal texture more or less uniformly rugose-granular lacking shagreen and tubercles, rarely rugosities aligned in short, irregular ridges; male web I 1 – 2 II 1 – 2 1/2 III 1 1/2 – 2 1/2 IV 2+ – 1 V, female I 1 – 2 II 1 – 2 1/2 III 1 1/2 – 2 1/2 IV 2 1/2 – 1 V; male SVL  $59.3 \pm 5.4$ , maximum 70.8 mm, female  $68.9 \pm 4.7$ , maximum 77.8 mm; male head length/SVL ratio  $0.39 \pm .01$ , female  $0.39 \pm .01$ ; male head width/SVL ratio  $0.42 \pm .01$ , female  $0.42 \pm .01$ ; male eye-nostril distance/SVL ratio  $0.09 \pm .01$ , female  $0.09 \pm .01$ ; male eye-eye distance /SVL ratio  $0.19 \pm .01$ , female  $0.19 \pm .01$ ; male femur/SVL ratio  $0.50 \pm .02$ , female  $0.49 \pm .01$ ; male tibia/SVL ratio  $0.49 \pm .02$ , female  $0.48 \pm .01$ ; male foot/SVL ratio  $0.46 \pm .02$ , female  $0.45 \pm .02$ .

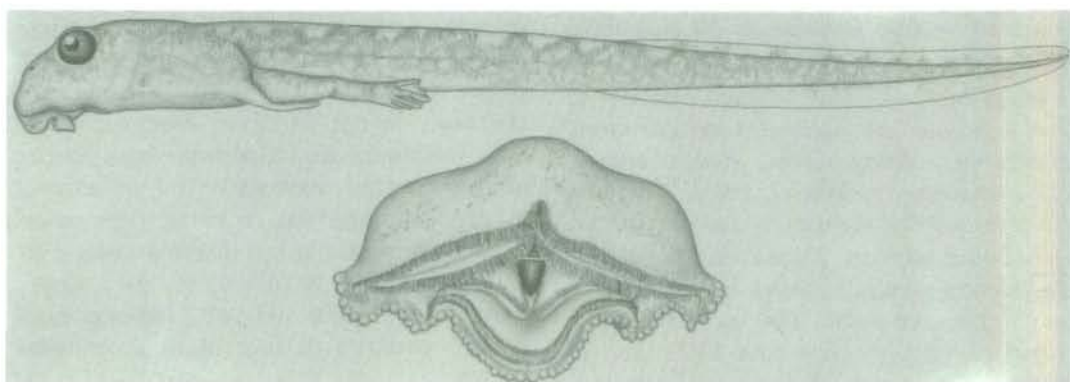
**Advertising Call.** — Call of three notes, first note quite different from second two; call duration about 1:0 s, duration of first note about 0.43 s, duration of second and third notes 0.12-0.14 s; first note a series of about 9 pulses at a dominant frequency of 540 Hz; second and third notes of about 5-6 pulses each at a dominant frequency of 1600-1800 Hz, with peak intensity at 1700 Hz (Figure 34).

**Larval Definition.** — Larva elongate, depressed; tail fins low, present only on distal half of tail; belly flattened with bilobed shelf extending posteriorly past body; spiracle very small, sinistral; anus not visible in single example at hand (AMNH 104139); eye large, 17% head-body length; oral disk broad, 37% head-body length; oral disk entire, anterior papilla gap broad, almost width of disk, oral papillae in single row, continuous posteriorly; tooth row formula  $\frac{2}{1-1}$ ; beak with chisel-like central cusp; head-body length 25% total length; total length 37.5 mm, stage 41; body mottled, tail with series of light ocelli dorsally (Figure 35).

**Remarks.** — The larval material reported by Lutz (1929) is too poorly preserved to study.

**Distribution.** — Serra dos Órgãos and Serra da Mantiqueira (Figure 30).

**RIO DE JANEIRO.** Barro Branco (L 115, MNRio 1491, 1566, 1591(2), 1592(4), 2039(2), 2250, USNM 132994-95); Serra de Macaé (AL 1723); Nova Friburgo (AL 2720, WCAB 18530, 19405-07); Petrópolis (AL 1693-94, 1694a, 1724, 2877, 2879,

Figure 35. Larva of *Cycloramphus brasiliensis*.Figure 36. Holotype of *Cycloramphus carvalhoi*.

MNRio 2871, USNM 96418, 96428); Petrópolis, Independência (AL 1352-54, 1404-05, 3630-37; 3150-52); Teresópolis (AL 1842, 4125-131, AMNH 104139, L 1-25, MNRio 97, 2444(2), MZUSP 155, 34653, 57755-770, USNM 164124, 217852-866, WCAB 4730-31); Tinguá, Serra Vilna (MNRio 3562(10).

***Cycloramphus carvalhoi*** new species  
Figure 36

Holotype: L 132, an adult male from Brasil; Rio de Janeiro, Brejo da Lapa, Alto Itatiaia, 2200 m. Collected by Bertha Lutz and Elio Gouvêa on 3 November 1951.

Paratopotypes: L 133-34, adult males

collected by Elio Gouvêa on 30 November 1959 at the type locality.

**Diagnosis.** — The webless species of *Cycloramphus* are *bolitoglossus*, *carvalhoi*, *catarinensis*, *diringshofeni*, *eleutherodactylus*, *granulosus*, *stejnegeri*, *valae*. The toes are free and the dorsum is smooth in *carvalhoi*; the toes are ridged or fringed and the dorsum glandular-warty in *catarinensis*, *granulosus*, and *valae*. The leg is shorter in *carvalhoi* (e.g. average foot/SVL ratio in males 0.39) than in *diringshofeni* (average male foot/SVL 0.50) or *eleutherodactylus* (male foot/SVL  $0.48 \pm .03$  (one standard deviation) female  $0.49 \pm .04$ ). *Cycloramphus carvalhoi* is larger (males 58-62 mm SVL) than *bolitoglossus* (males 28-34 mm, females 39-40 mm SVL) or *stejnegeri* (males 45-47 mm, females 45-56 mm SVL).

**Description of Holotype.** — Snout rounded from above, sloping in profile; canthus rostralis rounded-obtuse; loreal obtusely concave in cross section; tympanum hidden; vomerine teeth in transverse series in medial contact, between and posterior to choanae; no vocal fold or slit; first finger just longer than second; outer metacarpal tubercle large, rounded, inner metacarpal tubercle ovoid, separated from subarticular tubercle of thumb by diameter of subarticular tubercle; thumbs without asperities; dorsal texture smooth; fold from posterior corner of eye over hidden tympanum to shoulder; inguinal gland large, disk shaped, diameter of gland greater than 1/2 femur length; venter smooth; toe tips about width of digits, not noticeably expanded; toes free; subarticular tubercles under toes moderately developed; outer metatarsal tubercle rounded, smaller than globose-ovoid inner metatarsal tubercle; no tarsal or metatarsal folds; posterior surface of tarsus and sole of foot smooth. SVL 58.8, head length 23.4, head width 27.1, eye-nostril distance 4.0, eye-eye distance 9.3, femur 21.1, tibia 18.7, foot 23.7 mm. Dorsum dark lichenous brown with light tan spot in mid-post

scapular region and distinct light tan inter-orbital bar; loreal region mottled, light stripes on upper lip indistinct anteriorly (between tip of snout to front of eye), narrow obtuse light stripe from front corner of eye directed downward and posteriorly to edge of upper lip, a broad light stripe from lower posterior eye directed downward and posteriorly to angle of jaw; upper limbs barred; chin and belly uniform light brown; posterior surface of thigh uniform brown.

**Etymology.** — Named for Professor Antenor Leitão de Carvalho who has facilitated work on specimens in the National Museum in Rio for at least two generations of herpetologists.

**Adult Specimen Definition** (N = 3). — Thumb lacking asperities; snout profile rounded or vertically sloping (Figure 6, A, B); dorsal pattern uniform or blotched (Figure 2, B, D-1); posterior surface of thigh uniform; dorsal texture smooth; toes free; male SVL 58.8-61.7 mm; male head length/SVL ratio 0.38; male head width/SVL ratio 0.45; male eye-nostril distance/SVL ratio 0.06; male eye-eye distance/SVL ratio 0.15; male femur/SVL ratio 0.37; male tibia/SVL ratio 0.30; male foot/SVL ratio 0.39.

**Advertising Call.** — Unknown.

**Larval Definition.** — Larvae unknown.

**Distribution.** — Presently known from the type locality (Figure 30).

**RIO DE JANEIRO.** Brejo da Lapa (L 132-134).

#### *Cycloramphus catarinensis* new species Figure 37

Holotype: USNM 137675, an adult male from Brasil; Santa Catarina, Petrópolis (probably in error for Theresópolis = Queçaba) collected by J. Michaelis on 19 March 1905.

Paratopotypes: MZUSP 57771, USNM 137676-79, Vienna 15823:1-9.



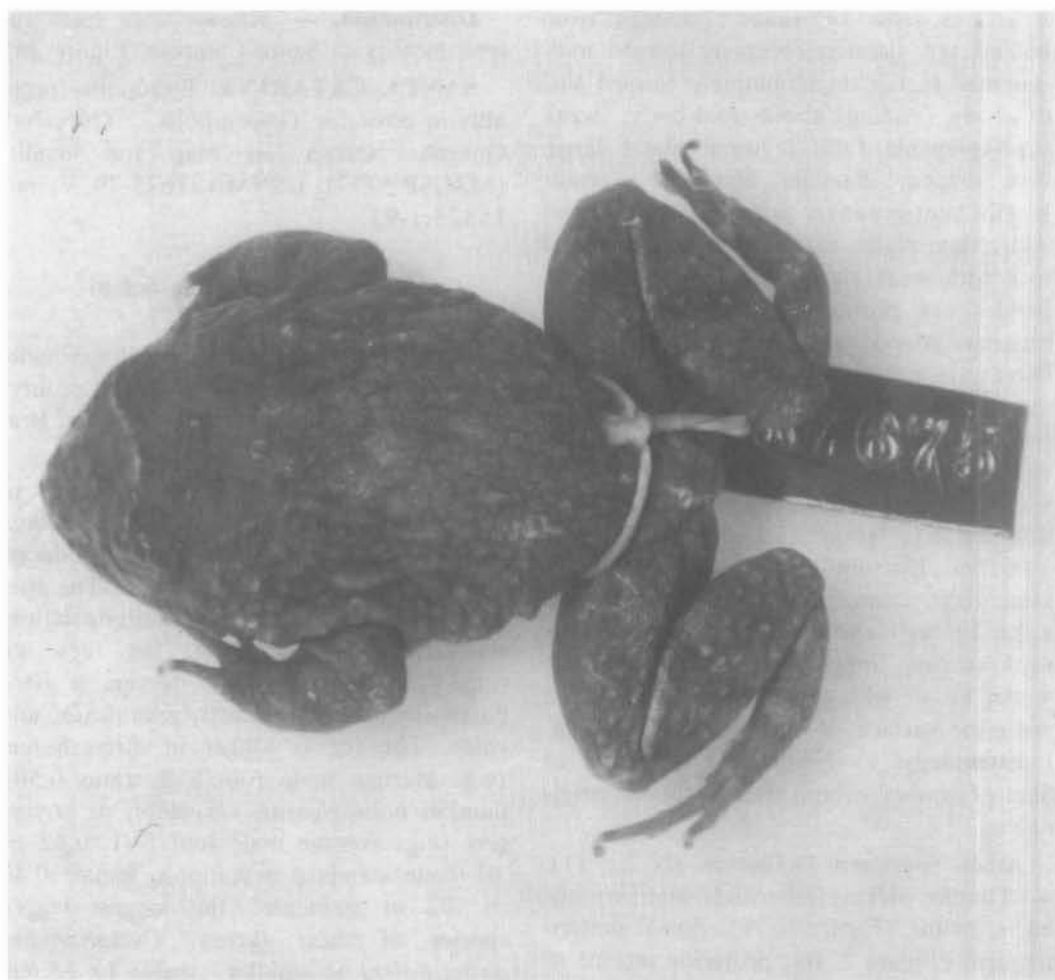


Figure 37. Holotype of *Cycloramphus catarinensis*.

**Diagnosis.** — The webless species of *Cycloramphus* are *bolitoglossus*, *carvalhoi*, *catarinensis*, *diringshofeni*, *eleutherodactylus*, *granulosus*, *stejnegeri*, *valae*. The toes are ridged or fringed and the dorsum is warty-glandular in *catarinensis*, the toes are free and the dorsum is smooth, weakly crenulate or weakly granular in *bolitoglossus*, *carvalhoi*, *diringshofeni*, *eleutherodactylus* and *stejnegeri*. Each dorsal wart has several structures that appear to be mucus glands, giving each wart a mosaic pattern; these glandular structures are not present in *granulosus* and *valae*.

**Description of Holotype.** — Snout rounded from above and in profile; canthus rostralis indistinct; loreal slightly concave in cross section; tympanum hidden, vomerine teeth in transverse series almost in medial contact, between and posterior to choanae; vocal fold present, but vocal slits absent; first finger just longer than second; outer metacarpal tubercle heart shaped, inner ovoid, separated from subarticular tubercle of thumb by diameter of subarticular tubercle; thumb lacking asperities; dorsal texture roughly granular, each granule covered with small glandular appearing

structures; row of raised granules from behind eye directed obliquely toward mid-scapular region then obliquely toward side of body, ending about mid-body; weak supratympanic fold; inguinal gland large, disk shaped, diameter about 1/3 femur length; venter weakly granular; toe tips just wider than digits; toes not webbed, sides of toes with weak ridges; toe subarticular tubercles not pronounced; outer metatarsal tubercle round, smaller than low ovoid inner metatarsal tubercle; no tarsal or metatarsal folds; outer tarsus and sole of foot glandular appearing, but not tuberculate. SVL 37.5, head length 14.3, head width 16.0, eye-nostril distance 3.4, eye-eye distance 7.1, femur 15.5, tibia 15.5, foot 14.6 mm. Dorsum rather uniform brown, faint light interorbital stripe; loreal and upper lip region with four faint narrow vertical stripes; upper limbs faintly barred; venter brown with small distinct light spots; posterior surface of thigh uniform brown.

**Etymology.** — Named for the State of Santa Catarina, where the specimens originated.

**Adult Specimen Definition** (N = 11). — Thumbs lacking asperities; snout rounded in profile (Figure 6, A); dorsal pattern uniform (Figure 2, B); posterior surface of thigh usually uniform, sometimes mottled; dorsal texture strongly granular, each granule with gland-like structures, regular short dorsolateral folds usually present; foot lacking web, toes weakly to strongly ridged or fringed laterally; male SVL  $35.3 \pm 2.3$ , maximum 39.2 mm; male head length/SVL ratio  $0.37 \pm .01$ ; male head width/SVL ratio  $0.41 \pm .02$ ; male eye-nostril distance/SVL ratio  $0.08 \pm .01$ ; male eye-eye distance/SVL ratio  $0.19 \pm .01$ ; male femur/SVL ratio  $0.44 \pm .03$ ; male tibia/SVL ratio  $0.42 \pm .02$ ; male foot/SVL ratio  $0.42 \pm .02$ .

**Advertising Call.** — Unknown.

**Larval Definition.** — Larvae unknown.

**Distribution.** — Known only from the type locality in Santa Catarina (Figure 38).

**SANTA CATARINA.** Petrópolis (probably in error for Theresópolis = Queçaba), Queçaba shown on map for locality (MZUSP 57771, USNM 137675-79, Vienna 15823:1-9).

### **Cycloramphus diringshofeni**

Bokermann, 1957

*Cycloramphus diringshofeni* Bokermann, 1957:249, Figs. 2, 4-6. Type-Locality: São Bento do Sul, Santa Catarina, Brasil. Holotype: WCAB 548, male.

**Diagnosis.** — The webless species of *Cycloramphus* are *bolitoglossus*, *carvalhoi*, *catarinensis*, *diringshofeni*, *eleuthero-dactylus*, *granulosus*, *stejnegeri*, *valae*. The toes are free and the dorsum is smooth or slightly granular in *diringshofeni*; the toes are ridged or fringed and the dorsum is glandular-warty in *catarinensis*, *granulosus*, and *valae*. The leg is longer in *diringshofeni* (e.g. average male foot/SVL ratio 0.50) than in *bolitoglossus*, *carvalhoi*, or *stejnegeri* (e.g. average male foot/SVL  $0.42 \pm .01$  (one standard deviation), female  $0.42 \pm .02$  in *stejnegeri*, the longest legged species of these three). *Cycloramphus diringshofeni* is smaller (males to 31 mm SVL), has a sinuous dorsolateral ridge, and the males have vocal slits; *C. eleuthero-dactylus* is larger (males to 54 mm SVL), short dorsal ridges are occasionally present, never elongate or sinuous to the extent of *diringshofeni*, and the males lack vocal slits.

**Adult Specimen Definition** (N = 2). — Thumbs lacking asperities; snout rounded or vertically sloping in profile (Figure 6, A, B); dorsal pattern uniform with dark outlines of dorsolateral folds and posterior small spots (Figure 2, G); posterior surface of thigh uniform, mottled, or with small distinct light spots; dorsal texture usually smooth, rarely with glandular warts; toes free; male SVL 29.2-30.6 mm, male head

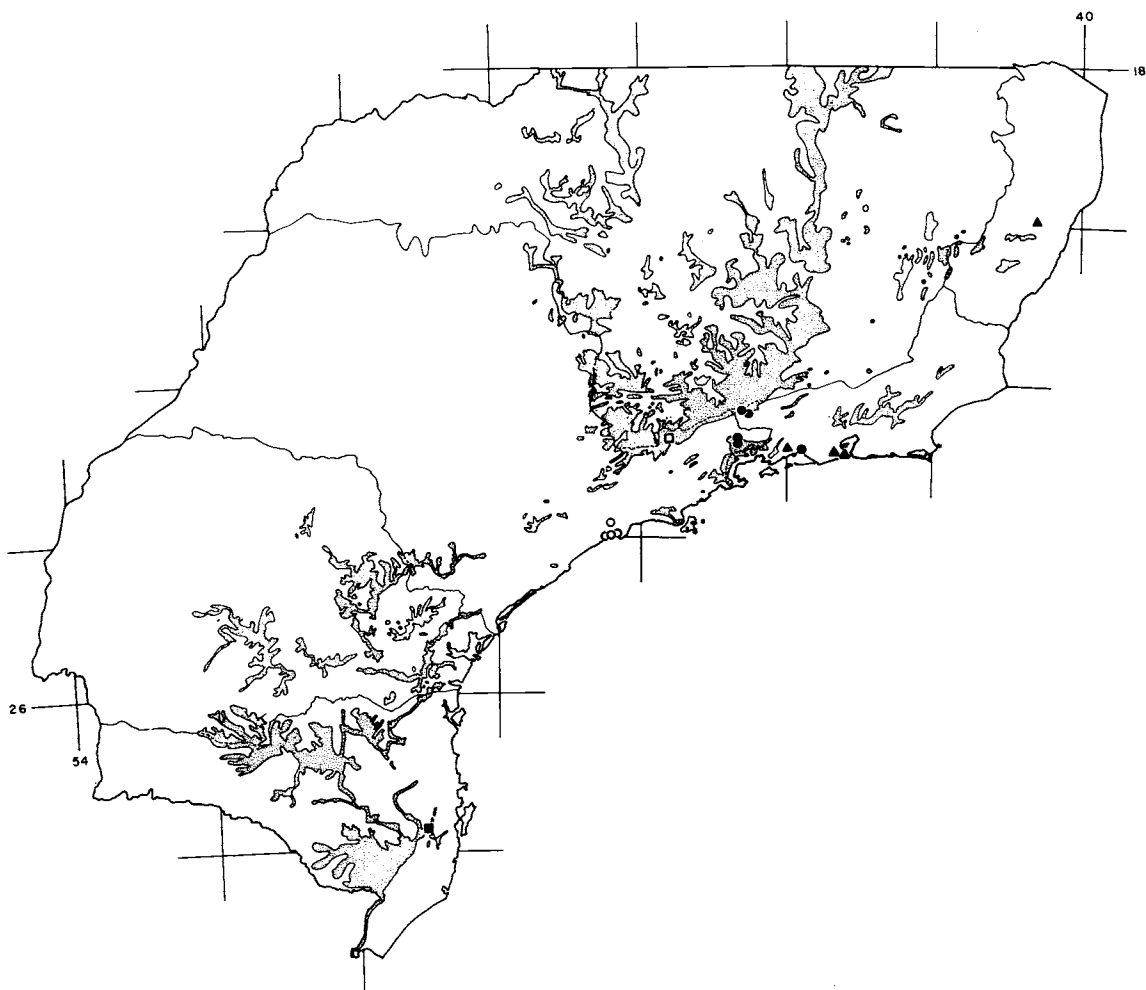


Figure 38. Distribution map of *Cycloramphus catarinensis* (closed squares), *dubius* (open circles), *fuliginosus* (closed triangles), *granulosus* (closed circles), and *jordanensis* (open square). Stippled areas join approximate 1000 meter contours.

length/SVL ratio 0.38; male head width/SVL ratio 0.40; male eye-nostril distance/SVL ratio 0.09; male eye-eye distance/SVL ratio 0.17; male femur/SVL ratio 0.45; male tibia/SVL ratio 0.50; male foot/SVL ratio 0.50.

**Advertising Call.** — Unknown.

**Larval Definition.** — Larvae unknown.

**Distribution.** — Serra do Mar in the State of Santa Catarina (Figure 39).

**SANTA CATARINA.** Petrópolis (probably in error for Theresópolis = Queçaba) (Vienna 4117:1-3); São Bento (AL

1863); Rio Vermelho, São Bento do Sul (L 177, WCAB 3723).

***Cycloramphus dubius***  
(Miranda-Ribeiro), 1920

*Ilidiscus dubius* Miranda-Ribeiro, 1920: 268, Plates 1-3. Type-Locality: Alto da Serra, São Paulo, Brasil. Lectotype: MZUSP 647, adult male.

**Diagnosis.** — The species that have toe webbing and black and/or white dorsal tubercles are *C. bandeirensis*, *brasiliensis*, *dubius*, *fuliginosus*, and *jordanensis*; of

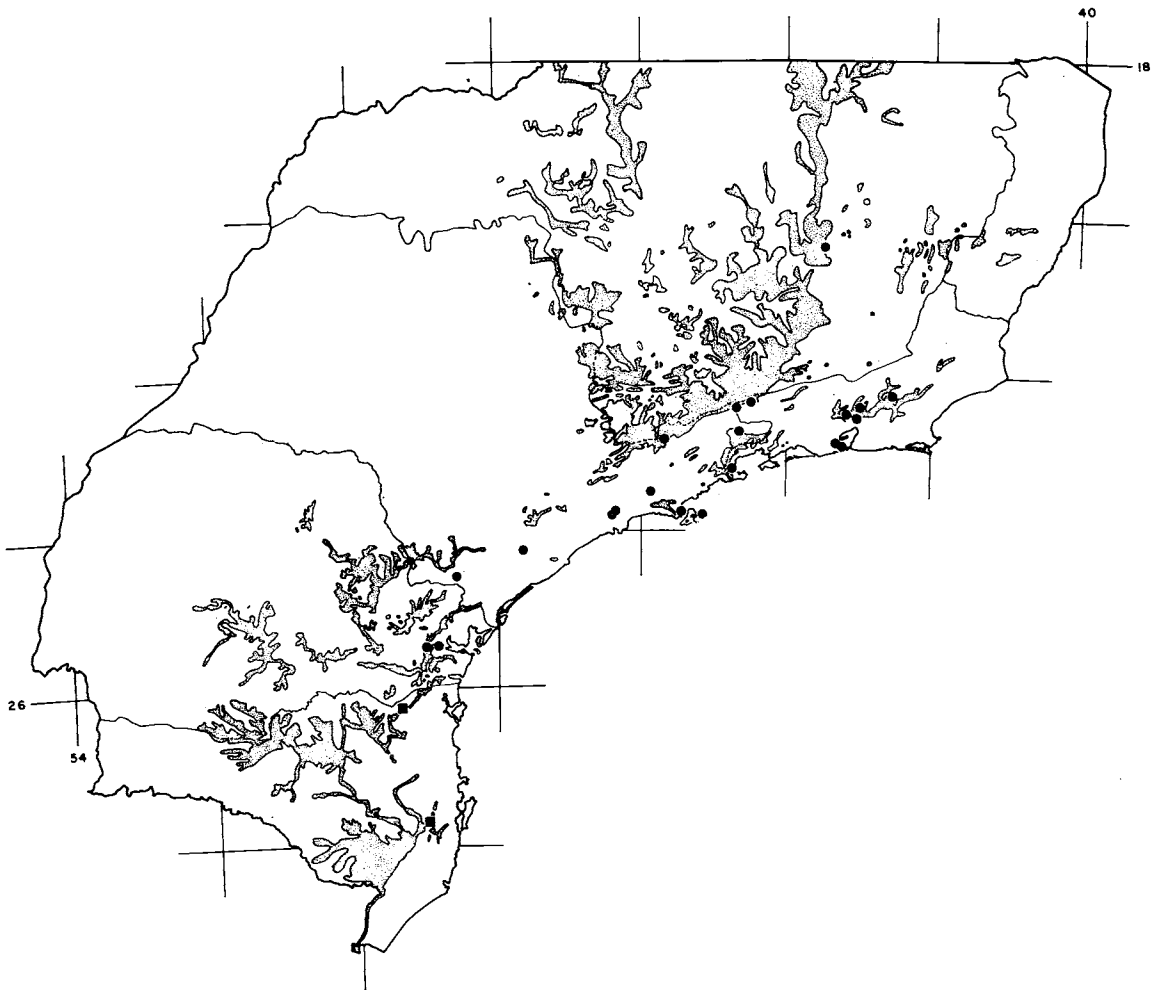


Figure 39. Distribution map of *Cycloramphus diringshofeni* (squares) and *eleutherodactylus* (circles). Stippled areas join approximate 1000 meter contours.

these, *dubius* is the only one to have a shagreen on the dorsum.

**Adult Specimen Definition** (N = 78). — Thumbs lacking asperities; snout rounded or with flared lip, rarely vertically sloping in profile (Figure 6, A, B, F); dorsum uniform, rarely blotched (Figure 2, B, D-1); posterior surface of thigh uniform, mottled, or with small, distinct, light spots; no distinctive colors in life; dorsum granular-rugose, overlain with shagreen, lacking black or white tubercles, almost never with irregular short ridges; male foot web I 1 – 2 II 1 – 2 1/2 III 1 1/2 – 3– IV 3– – 1 V, female I 1 – 2 II 1 – 2 1/2 III 1 1/2 –

3 IV 3– – 1 V; male SVL  $47.5 \pm 3.4$ , maximum 53.7 mm, females  $52.4 \pm 4.8$ , maximum 60.3 mm, females larger than males ( $t = 5.1$ ,  $P < .001$ ); male head length/SVL ratio  $0.40 \pm .01$ , female  $0.40 \pm .01$ ; male head width/SVL ratio  $0.44 \pm .01$ , female  $0.44 \pm .01$ ; male eye-nostril distance/SVL ratio  $0.08 \pm .01$ , female  $0.09 \pm .01$ ; male eye-eye distance/SVL ratio  $0.20 \pm .01$ , female  $0.19 \pm .01$ ; male femur/SVL ratio  $0.48 \pm .02$ , female  $0.50 \pm .02$ ; male tibia/SVL ratio  $0.48 \pm .02$ , female  $0.48 \pm .02$ ; male foot/SVL ratio  $0.50 \pm .02$ , female  $0.51 \pm .03$ .

**Advertising Call.** — Unknown.

**Larval Definition.** — Larvae unknown.

**Distribution.** — A portion of the State of São Paulo (Figure 38).

**SÃO PAULO.** Alto da Serra de Cubatão (USNM 164117-18); Engenheiro Ferraz (MZUSP 23039, 23068); Paranapiacaba (AL 4057-58, L 138-147, 149-150, MZUSP 8864, 9005, 10591, 10648, 10788, 11001, 13910, 23416-17, 23488, WCAB 45681-5740, 45742-49, 45756, 45758); Santos (L 152);  $\pm$  4 miles N Santos on escarpment from plateau,  $\pm$  600' (USNM 196325(3); 4 miles N Santos on road from São Paulo to Santos, edge of escarpment,  $\pm$  2000' (USNM 196323(2), 196324(6), 196326); km 47 on old São Paulo-Santos road (MZUSP 10026, 10155-169, 10269, 10271-74, 10277-78, 10281-89, 10291-0308, 10848-51, 10853-56, 20444-45, 20449, 20451, 20454, 20456-57, 20459, 22433-36 USNM 217867-68); Voturuá (MZUSP 2290, 2293).

**Cycloramphus duseni** (Andersson), 1914

*Telmatobius duseni* Andersson, 1914:1.

Type-Locality: Ypiranga, Sierra do mar, Parana, Brazil. Types: Stockholm Museum, five specimens, not examined.

**Diagnosis.** — The species with toe webbing and distinct black and/or white dorsal tubercles are *C. asper*, *boraceiensis*, *duseni*, *lutzorum*, *mirandaribeiroi*, *ohausi*, *rhyakonastes*, *semipalmatus*. *Cycloramphus duseni* individuals lack thumb spines, *C. ohausi* individuals have thumb spines. The moderate web of *C. duseni* differs from the reduced web of *C. rhyakonastes* and *semipalmatus* and the considerable web of *asper* and *mirandaribeiroi*. *Cycloramphus duseni* is smaller (males 29-38 mm, females 31-44 mm SVL) than *asper*, *boraceiensis*, *lutzorum*, *mirandaribeiroi*, and *rhyakonastes* (smallest male 35.9 mm, smallest female 42.6 mm SVL).

**Adult Specimen Definition** (N = 53). — Thumb lacking asperities; snout rounded or vertically sloping (Figure 6, A, B), rarely

sloping or with flared lip (Figure 6, C, F); dorsal pattern uniform; posterior surface of thigh uniform, mottled, or sometimes with discrete light large or small spots; no distinctive colors in life; dorsal texture of warts covered by shagreen with large and small black and/or white tubercles, warts often aligned into regular or irregular rows; male foot web I 1 – 2 II 1 – 2 1/2 III 1 1/2 – 3 IV 3 – 1 V, female I 1 – 2 II 1 – 2 1/2 III 1 1/2 – 3 – IV 2 1/2 – 1 V; male SVL 33.4  $\pm$  2.6, maximum 37.7 mm, female 38.4  $\pm$  4.1, maximum 43.7 mm, females larger than males ( $t = 4.8$ ,  $P < .001$ ); male head length/SVL ratio 0.38  $\pm$  .02, female 0.38  $\pm$  .02; male head width/SVL ratio 0.41  $\pm$  .02, female 0.41  $\pm$  .02; male eye-nostril distance/SVL ratio 0.09  $\pm$  .01, female 0.09  $\pm$  .01; male eye-eye distance/SVL ratio 0.19  $\pm$  .01, female 0.19  $\pm$  .01; male femur/SVL ratio 0.48  $\pm$  .02, female 0.49  $\pm$  .03; male tibia/SVL ratio 0.47  $\pm$  .02, female 0.48  $\pm$  .03; male foot/SVL ratio 0.48  $\pm$  .03, female 0.49  $\pm$  .04.

**Advertising Call.** — Call of individual notes given sporadically; call short, about 0.03 s; call not well tuned, frequency from about 1300-2700 Hz with strongest intensity about 2200-2400 Hz (Figure 40).

**Larval Definition.** — Larva elongate, depressed; tail fins low, present only on distal half of tail; belly flattened with flap extending posteriorly past body, flap shallowly bilobed or not; spiracle very small, sinistral; anus median; eye moderately large, 13-18% head-body length; oral disk broad, 31-39% head-body length; oral disk entire, anterior papilla gap broad, almost width of disk; oral papillae in single row, continuous posteriorly: tooth row formula  $\frac{2}{3}$ ; beak with strong and deep central cusps; head-body length 23-28% total length; largest total length 32.0 mm, stage 41; body mottled, tail with series of light mid-dorsal ocelli (Figure 41).

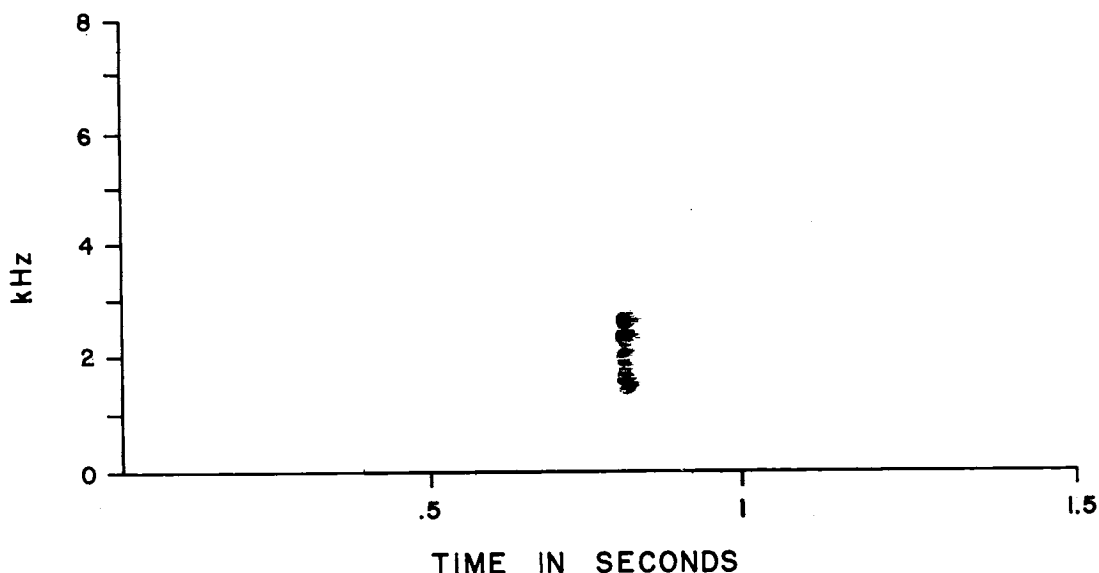


Figure 40. Audiospectrogram of the advertising call of *Cycloramphus duseni*. Specimen (not captured) recorded at 21:15 h on 15 December 1978 from Brasil: Santa Catarina; 17 km (by road) W Pirabeiraba on BR 280 to Campo Alegre. Air temperature 22.2° C.



Figure 41. Larva of *Cycloramphus duseni*.

**Distribution.** — Serra do Mar in the States of São Paulo, Paraná and Santa Catarina (Figure 42).

**PARANÁ.** Ypiranga (= Ipiranga) (type locality of *Telmatobius duseni*, specimens not examined).

**SANTA CATARINA.** Colonia Hansa, Joinville (AL 1795-96); Humboldt (= Corupá) MNRio 99(9), 712, UMMZ 58508 (6), USNM 66578-79, Vienna 6154); Joinville (MNRio 3947(8)); 13-17 km W Pirabeiraba (MZUSP 57772-57798, USNM 217869-896, 217931); Rio do Teste (L 168); Rio Vermelho, São Bento do Sul (MZUSP 20620); São Bento (AL 1792-94, L 175); Município de Serra Alta (São Bento do Sul), córrego na região Rio Vermelho, Serra do Mar (L 163-64, 169-174); Serra da Subida, caminho de Blumenau

a Lages (L 165-67); Timbó (Eugenio Izecksohn collection).

**SÃO PAULO.** Alto da Serra de Cubatão (MNRio 98(3)); Paranapiacaba (MZUSP 13909).

***Cycloramphus eleutherodactylus***  
(Miranda-Ribeiro), 1920

*Iliodiscus eleutherodactylus* Miranda-Ribeiro, 1920:270, Plates 5-6. Type-Local-ity: Alto da Serra, São Paulo, Brasil. Lectotype: MZUSP 24x, adult female.

*Cycloramphus eleutherodactylus* var. *variegata* Lutz, 1929:12, Plate 1, Figs. 5-6 Type(s) and type-locality not specifically designated.

*Cycloramphus eleutherodactylus* var. *strigilata* Lutz, 1929:13, Plate 3, Fig. 5.

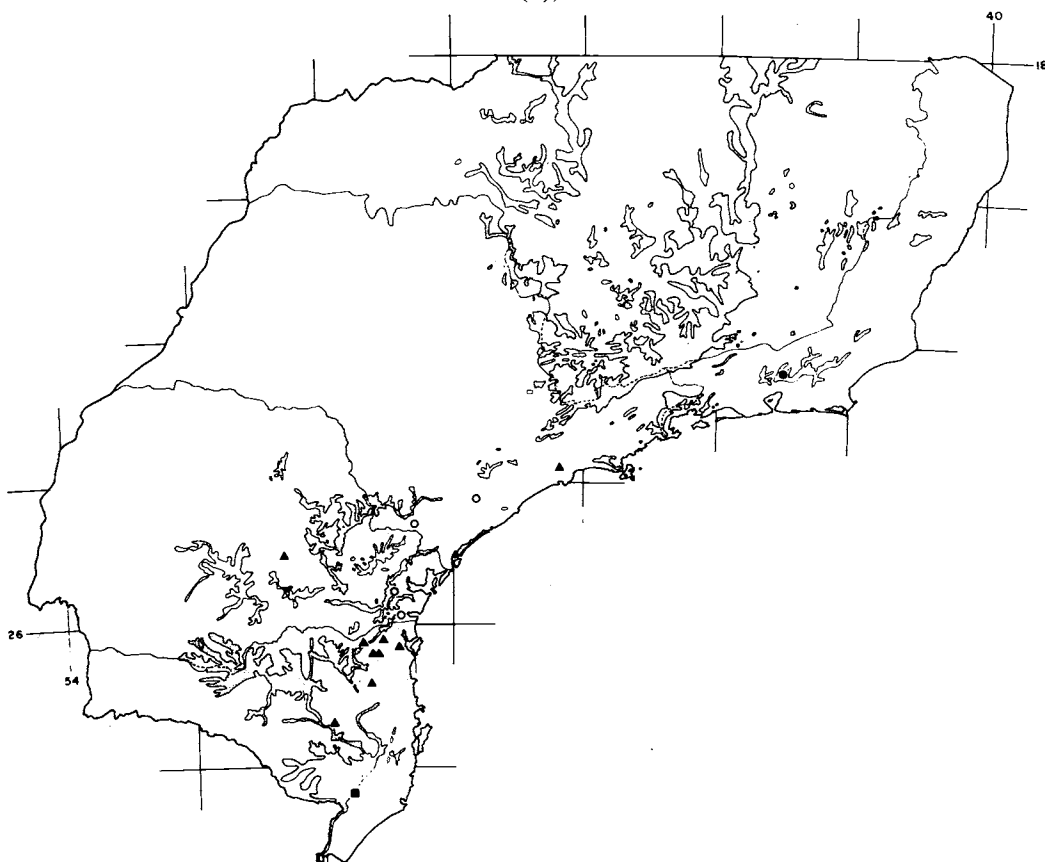


Figure 42. Distribution map of *Cycloramphus duseni* (closed triangles), *lutzorom* (open circles), *stejnegeri* (closed circle), and *valae* (closed square). Stippled areas join approximate 1000 meter contours.

Type(s) and type-locality not specifically designated.

**Diagnosis.** — The webless species of *Cycloramphus* are *bolitoglossus*, *carvalhoi*, *catarinensis*, *diringshofeni*, *eleutherodactylus*, *granulosus*, *stejnegeri*, *valae*. The toes are free and the dorsum is smooth, weakly rugose, or slightly granular in *eleutherodactylus*, the toes are ridged or fringed and the dorsum is glandular-warty in *catarinensis*, *granulosus*, and *valae*. The leg is longer in *eleutherodactylus* (e.g. average foot/SVL ratio in males  $0.48 \pm .03$  (one standard deviation), female  $0.49 \pm .04$ ) than in *bolitoglossus*, *carvalhoi*, or *stejnegeri* (e.g. average male foot/SVL  $0.42 \pm .01$ , female  $0.42 \pm .02$  for *stejnegeri*, the longest legged species of the three). *Cycloramphus eleuthe-*

*rodactylus* is larger (males to 54 mm SVL) than *diringshofeni* (males to 31 mm SVL); *eleutherodactylus* occasionally have short dorsal ridges, but never elongate and sinuous as in *diringshofeni*; male *eleutherodactylus* lack vocal slits, male *diringshofeni* have vocal slits.

**Adult Specimen Definition** (N = 64). — Thumbs lacking asperities; snout rounded or vertically sloping (Figure 6, A, B), rarely obliquely sloping (Figure 6, C) in profile; dorsal pattern uniform to distinctly patterned, patterns with regular dark markings or irregular variegations (Figure 2, B, E, E-1, F, F-1, F-2, G, H, H-1, H-2, I, I-1, J); posterior surface of thigh uniform, mottled or with distinct light spots; no distinctive life colors; dorsum smooth or weakly rugose.

often with irregular or short regular ridges; toes lacking web, sides of toes free; male SVL  $41.1 \pm 5.3$ , maximum 53.7 mm, females  $46.2 \pm 6.4$ , maximum 58.3 mm, females larger than males ( $t = 3.4$ ,  $P = .001$ ); male head length/SVL ratio  $0.40 \pm .02$ , female  $0.40 \pm .02$ ; male head width/SVL ratio  $0.44 \pm .02$ , female  $0.44 \pm .02$ ; male eye-nostril distance/SVL ratio  $0.09 \pm .01$ , female  $0.09 \pm .01$ ; male eye-eye distance/SVL ratio  $0.18 \pm .01$ , female  $0.18 \pm .01$ ; male femur/SVL ratio  $0.45 \pm .03$ , female  $0.45 \pm .03$ ; male tibia/SVL ratio  $0.47 \pm .04$ , female  $0.48 \pm .04$ ; male foot/SVL ratio  $0.48 \pm .03$ , female  $0.49 \pm .04$ .

**Advertising Call.** — Known to have a call, but not recorded on magnetic tape.

**Larval Definition.** — Unquestionable larvae unknown.

**Distribution.** — This species is known from the Serra dos Orgãos, Serra da Mantiqueira, Serra da Bocaina, and Serra do Mar (Figure 39).

**MINAS GERAIS.** Ouro Preto (UMMZ 92448, USNM 98084).

**PARANÁ.** Banhado (USNM 123897-98); Morretes, Anhaia (L 162).

**RIO DE JANEIRO.** Campo Belo (MZUSP 7905); Corcovado, Panheiros (AL 3925-26, L 114); Guapi, Alcindo Guanabara (AL 3008-09); Macieiras e Maromba, descida entre (L 116); Novo Frigburgo, Alto da Serra (AL 4352); Parati (MNRio 1648); Petrópolis, Independência (L 111); Rio de Janeiro, Sumaré (AL 446); Rio de Janeiro, Tijuca (AL 474-75, 550-52, 3551-52, 3608-617, 3672, L 113, MNRio 1278(2), USNM 96262); Rio de Janeiro, Sumaré or Tijuca (WCAB 14429, 14467-69, 27477-78, 27480, 27548, 27551); Teresópolis (L 26-32, 35-56, MZUSP 57799-7801, USNM 217898-7900).

**SÃO PAULO.** Serra da Bocaina (MNRio 2419(a, b), MZUSP 1070, 1486); Bonito, Serra da Bocaina (AL 908, 2310, L 136-37); Boracéia (L 153-54, MZUSP 3428-29,

3432, 22642, 22997, 23793, 36875, 37564, USNM 217897); Ilha dos Búzios (MZUSP 23040, 23069, 23830-36, 23839-841, 23956); Serra de Caraguatatuba, rd. from Caraguatatuba to São Sebastião (MZUSP 9987); Serra de Cubatão, Alto da (AL 711-12, MNRio 101); Eugênio Lefèvre (MZUSP 15351); Iporanga (MZUSP 23828-29, 23866-67); Juquiá, 8 km N (UMMZ 104267(2)); Paranapiacaba (AL 4059, L 151, MZUSP 6476, 8865, 10592, WCAB 1724, 3275, 5758, 6565, 8865); 4 miles N Santos on road from São Paulo to Santos, edge of escarpment,  $\pm 2000'$  (USNM 196320(2)); km 47 on old São Paulo — Santos road (MZUSP 10144-45, 10221-22, 10373).

### *Cycloramphus fuliginosus*

Tschudi, 1838

*Cycloramphus fuliginosus* Tschudi, 1838:81.

Type-Locality: India, in error; corrected locality Brasil, State of Rio de Janeiro. Lectotype: MNHP 750, adult male. *Cycloramphus fuliginosus a lapsus calami* for *C. fuliginosus* (Bokermann, 1951).

*Grypiscus umbrinus* Cope, 1867:206 Type-Locality: Rio de Janeiro, Brasil. Holotype: MCZ 1497, adult female.

*Iliodiscus lutzi* Miranda-Ribeiro, 1929:15.

Type-Locality: lower slopes of Petrópolis mountains, Brasil. Type(s) not designated.

**Diagnosis.** — The species that have toe webbing and lack black and/or white dorsal tubercles are *C. bandeirensis*, *brasiliensis*, *dubius*, *fuliginosus*, *jordanensis*. The moderate web of *fuliginosus* contrasts with the reduced web of *bandeirensis* and *jordanensis*. The dorsum of *fuliginosus* lacks a shagreen, contrasting with the dorsal shagreen of *dubius*. Arrangement of metacarpal tubercles (Figure 55) distinguishes *fuliginosus* from the considerably webbed *brasiliensis*.



Figure 43. Larva of *Cycloramphus fuliginosus*.

**Adult Specimen Definition** (N = 93). — Thumbs without asperities; snout rounded (Figure 6, A), sometimes vertically sloping (Figure 6, B) in profile; dorsal pattern uniform or blotched (Figure 2, B, D, D-1, H-1); posterior surface of thigh usually uniform or mottled, rarely with distinct light spots; no distinctive colors in life; dorsal texture of low relief granular warts lacking shagreen or tubercles; male toe web I 1 – 2 – II 1+ – 2 1/2 III 1 1/2 – 3 – IV 3 – 1 V, female I 1 – 2 II 1 – 2 1/2 III 1 1/2 – 3+ IV 3 – 1 V, male SVL  $47.3 \pm 4.6$ , maximum 56.3 mm, female  $54.7 \pm 6.0$ , maximum 64.3 mm, females larger than males ( $t = 6.4$ ,  $P < .001$ ); male head length /SVL ratio  $0.41 \pm .01$ , female  $0.40 \pm .02$ ; male head width/SVL ratio  $0.43 \pm .01$ , female  $0.43 \pm .02$ ; male eye-nostril distance /SVL ratio  $0.08 \pm .01$ , female  $0.08 \pm .01$ ; male eye-eye distance/SVL ratio  $0.20 \pm .01$ , female  $0.20 \pm .01$ ; male femur/SVL ratio  $0.46 \pm .02$ , female  $0.46 \pm .02$ ; male tibia/SVL ratio  $0.44 \pm .01$ , female  $0.44 \pm .02$ ; male foot/SVL ratio  $0.44 \pm .02$ , female  $0.43 \pm .02$ .

**Advertising Call.** — Known to have a call, but unrecorded on magnetic tape.

**Larval Definition.** — Larva elongate, depressed; tail fins low, present only on distal half of tail; belly flattened with shelf extending posteriorly past body; spiracle small, sinistral; anus median; eye moderate, 12% head-body length; oral disk broad, 33% head-body length; oral disk entire, anterior papilla gap broad, almost width of disk; oral papillae in single row, continuous posteriorly; tooth row formula  $\frac{2}{3}$ ; upper and lower beak with strong and deep central

cuspid regions; head-body length 19% total length; total length about 43.5 mm, stage 41; body not distinctively patterned, tail with series of light ocelli dorsally (Figure 43).

**Distribution.** — Coastal forests from the State of Rio de Janeiro to mid-Espírito Santo (Figure 38).

**ESPÍRITO SANTO.** Santa Tereza (MNRio 1317, USNM 200441).

**RIO DE JANEIRO.** Corcovado, Paineiros (AL 553, 3933-35); Represa Piraguara-Realengo (MNRio 1752); Realengo (MNRio 2109, 3946); Rio de Janeiro (MZUSP 160, 164, 3114, 3130-31, 3140, 3150, 3156, 3619, 3621-22, 3624, 3850, 9836, 9838-843, 9846-48, 9851, 20676, 23305, USNM 81144, 217901-02); Rio de Janeiro, Sumaré (AL 530-32, 1406-07, 1494-97, MNRio 2329); Rio de Janeiro, Tijuca (AL 296a, 1691-92, 2200-08, 2243, 2485-86, 2913-14, 3234, 3600, MNRio 357, 1852, USNM 164120-22, 217932); Rio de Janeiro, Sumaré or Tijuca (WCAB 13392-97, 13679-684, 14169-175, 14423-28, 14920-26, 14928-29, 14935-940, 16722-25, 16807-815, 17039-046, 17081-84, 17193-7264, 17495-96, 17680-84, 17688-696, 18414-16, 18500, 18690-91, 27263, 27267, 27269, 27271-73, 27285, 27483-492, 27617, 27619-262, 36100); Serra de Mangaratiba (MNRio 1207, 1210-11).

#### *Cycloramphus granulosus* Lutz, 1929

*Cycloramphus granulosus* Lutz, 1929:13, Plate 3, Figs. 3-4. Type-Locality: Serra da Bocaina, Brasil. Lectotype: AL 1537.

**Diagnosis** — The webless species of *Cycloramphus* are *bolitoglossus*, *carvalhoi*,

*catarinensis*, *diringshofeni*, *eleutherodactylus*, *granulosus*, *stejnegeri*, and *valae*. The toes are ridged or fringed and the dorsum is glandular-warty in *C. granulosus*; the toes are free and the dorsum is smooth, slightly rugose or weakly granular in *bolitoglossus*, *carvalhoi*, *diringshofeni*, *eleutherodactylus*, *stejnegeri*. *Cycloramphus granulosus* lacks mucus-gland (like) structures on the dorsal warts; such structures are present in *catarinensis*. The leg is shorter in *granulosus* (e.g. average tibia/SVL ratio  $0.42 \pm 02$  (one standard deviation) in males,  $0.41 \pm .02$  in females) than in *valae* (average tibia/SVL ratio  $0.48 \pm .01$  in males,  $0.45 \pm .02$  in females); *granulosus* are generally larger (males to 43 mm, females to 47 mm SVL) than *valae* (males to 33 mm, females to 40 mm SVL).

**Adult Specimen Definition** (N = 20). — Thumb lacking asperities; snout usually rounded (Figure 6, A), rarely sloping (Figure 6, B, C) in profile; dorsal pattern uniform, blotched, spotted, or rarely with indications of dark-lined pattern (Figure 2, B, C, D, D-1, G); posterior surface of thigh uniform or mottled; in life, dorsum brown with yellow-green punctations, chest tan with white dots (USNM 217903); dorsal texture granular-warty, lacking both shagreen and tubercles; foot lacking web, toes with lateral ridges or fringes; male SVL  $38.2 \pm 2.9$ , maximum 42.6 mm, females  $37.8 \pm 4.8$ , maximum 46.2 mm, male head length/SVL ratio  $0.38 \pm 01$ , female  $0.38 \pm .02$ ; male head width/SVL ratio  $0.42 \pm .02$ , female  $0.41 \pm .02$ ; male eye-nostril distance/SVL ratio  $0.07 \pm .01$ , female  $0.07 \pm .01$ ; male eye-eye distance/SVL ratio  $0.18 \pm .01$ , female  $0.17 \pm .01$ ; male femur/SVL ratio  $0.44 \pm .02$ , female  $0.44 \pm 0.1$ ; male tibia/SVL ratio  $0.41 \pm .02$ , female  $0.42 \pm .02$ ; male foot/SVL ratio  $0.46 \pm .02$ , female  $0.48 \pm .03$ .

**Advertising Call.** Unknown.

**Larval Definition.** — Larvae unknown.

**Distribution.** — This species is known

from portions of the Serra da Bocaina, Serra da Mantiqueira, and Serra do Mar (Figure 38).

**RIO DE JANEIRO.** Campo Belo (MZUSP 13628-29, 13635, 15826); Itaguaí (L 118-19); Itatiaia (L 117, 120-23, 129-131); Maromba, km 3 da estrada para Alto Itatiaia (L 124-28).

**SÃO PAULO.** Serra da Bocaina (MZUSP 101, WCAB 31232-35, 42205-06, 42503-512); Bonito, Serra da Bocaina (AL 2510-12, 2513(2), USNM 96743, 96745-46, 96748-751); Corrego Mãe d'Água, Serra da Bocaina (L 135); Fazenda do Veado, Serra da Bocaina (MZUSP 57802-04, USNM 217903-05).

***Cycloramphus jordanensis* new species**  
Figure 44

Holotype: MZUSP 4522, and adult female from Brasil; São Paulo, Campos do Jordão. Collected by F. Lane on 23 December 1944.

**Diagnosis.** — The species that have toe webbing and lack black and/or white dorsal tubercles are *C. bandeirensis*, *brasiliensis*, *dubius*, *fuliginosus*, and *jordanensis*. The reduced webbing of *jordanensis* distinguishes it from the moderately webbed *dubius* and *fuliginosus* and the considerably webbed *brasiliensis*. The posterior surface of the thigh lacks distinct light spots in *jordanensis*; such spots are present in *bandeirensis*.

**Description of Holotype.** — Snout rounded from above and in profile; canthus rostralis indistinct; loreal region concave; tympanum hidden; vomerine teeth of a single tooth on each vomer, between the choanae; first finger just longer than second; outer metacarpal tubercle large, heart-shaped, inner metacarpal tubercle ovoid, separated from thumb subarticular tubercle by distance of greater than diameter of subarticular tubercle; thumbs lacking asperities; dorsal texture rugose, lacking shagreen or tubercles; supratympanic fold present; no



Figure 44. Holotype of *Cycloramphus jordanensis*.

inguinal gland; ventral texture smooth; toe tips expanded into small ungrooved disks; toe fringed, webbing reduced I  $2^-$  —  $2\frac{1}{2}$  II  $2^-$  — 3 III  $2\frac{3}{4}$  —  $3\frac{3}{4}$  IV 4 —  $2\frac{3}{4}$  V; subarticular tubercles moderately developed; rounded outer metatarsal tubercle smaller than ovoid inner metatarsal tubercle; tarsal fold present, extending  $\frac{3}{4}$  length of tarsus, continuous with inner metatarsal fold; outer metatarsal fold present on distal half of metatarsal region, continuous with toe fringe; outer tarsus smooth; sole of foot smooth.

SVL approximately 47, head length 20.5, head width 20.6, eye-nostril distance 3.8, eye-eye distance 9.0, femur 20.4, tibia 23.0, foot 24.7 mm.

Dorsum uniform brown, upper lip and loreal region mottled, not striped; upper limbs faintly barred; chin and belly of large

anastomosing brown network on a light background; posterior surface of thigh faintly mottled, almost uniform brown.

**Etymology.** — Named for the type locality.

**Advertising Call.** Unknown.

**Larval Definition.** — Larvae unknown.

**Distribution.** — Known only from the type locality (Figure 38).

**SÃO PAULO.** Campos do Jordão (MZUSP 4522).

***Cycloramphus lutzorum* new species**  
Figure 45

Holotype: MZUSP 57805, an adult male from Brasil; São Paulo, about 11 km W of Iporanga on road to Apiaí. Collected by W. Ronald Heyer, Frances I. McCullough and Francisca Carolina do Val on 16 November 1979.



Figure 45. Holotype of *Cycloramphus lutzorum*.

Paratopotypes: MZUSP 57806-08, USNM 217967-69.

**Diagnosis.** — The species with toe webbing and distinct black and/or white dorsal tubercles are *C. asper*, *boraceienseis*, *duseni*, *lutzorum*, *mirandaribeiroi*, *ohausi*, *rhyakonastes*, *semipalmatus*. *Cycloramphus lutzorum* lacks thumb spines; *C. ohausi* has thumb spines. The moderate webbing of *C. lutzorum* differs from the considerable webbing of *asper* and *mirandaribeiroi* and the reduced webbing of *rhyakonastes* and *semipalmatus*. The dorsal tubercles on high relief warts of *C. lutzorum* contrast with the low relief wart bearing tubercles of *boraceienseis*. *Cycloramphus lutzorum* is larger (males 41-47 mm, females 42-58 mm SVL) than *duseni* (males 29-38 mm, females 31-44 mm SVL).

**Description of Holotype.** — Snout weakly semicircular from above, rounded in profile; canthus rostralis indistinct; loreal region slightly concave; tympanum hidden; vomerine teeth in short transverse series, separated by less than length of one series, lying between and posterior to choanae; vocal slits present, vocal sac internal; first

and second fingers about equal lengths; outer metacarpal tubercle large, rounded with anterior projection, inner metacarpal tubercle ovoid, separated from thumb subarticular tubercle by just less than diameter of subarticular tubercle; thumbs lacking asperities; dorsal texture of high relief warts, shagreened, each wart bearing one or more black tipped tubercles; warts aligned into more or less regular short rows; supratympanic fold present; inguinal gland moderate sized, disk shaped, diameter  $1/4 - 1/3$  femur length; venter weakly granular; toe tips just wider than digit width; toes fringed, webbing I  $1\ 2/3 - 2^+$  II  $2^- - 3$  III  $2 - 3\ 1/4$  IV  $3 - 1\ 1/4$  V; toe subarticular tubercles moderate; outer rounded metatarsal tubercle smaller than inner ovoid metatarsal tubercle; indistinct tarsal and metatarsal folds; lower tarsus covered with small, low, rounded brown tubercles; sole of foot with small, low, tubercles on outer half, smooth on inner half.

SVL 45.1, head length 18.6, head width 19.2, eye-nostril distance 4.5, eye-eye distance 8.7, femur 22.1, tibia 22.1, foot 23.3 mm.

Dorsum uniform; upper lip with faint light stripes from under eye to edge of lip; upper limbs barred; chin dark grey with distinct light spots, belly and limbs light gray with distinct light spots; posterior surface of thigh dark with distinct, large light spots.

**Etymology.** — Named for Adolfo and Bertha Lutz who added much to our knowledge of *Cycloramphus* through publications and collections.

**Adult Specimen Definition** (N = 15). — Thumbs lacking asperities; snout rounded or vertically sloping in profile, lip flared or not (Figure 6, A, B, F); posterior surface of thigh almost always with distinct large light spots, rarely uniform or mottled; dorsal texture of high relief warts bearing shagreen and black and/or white tubercles, warts often aligned into irregular or regular short rows; male foot webbing I 1 1/3 — 2 II 1 1/3 — 3 III 1 2/3 — 3 1/4 IV 3 — 1 1/4 V, female I 1 1/2 — 2+ II 1 1/2 — 3— III 2 — 3 IV 3+ — 1 1/2 V; male SVL  $43.5 \pm 2.0$ , maximum 46.8 mm, female  $48.8 \pm 5.5$ , maximum 58.0 mm, females larger than males ( $t = 2.4$ ,  $P = .047$ ); male head length/SVL ratio  $0.41 \pm .01$ , female  $0.40 \pm .02$ ; male head width/SVL ratio  $0.42 \pm .01$ , female  $0.43 \pm .02$ ; male eye-nostril distance/SVL ratio  $0.09 \pm .01$ , female  $0.09 \pm .01$ ; male eye-eye distance/SVL ratio  $0.19 \pm .01$ , female  $0.18 \pm .01$ ; male femur/SVL ratio  $0.47 \pm .01$ , female  $0.45 \pm .04$ ; male tibia/SVL ratio  $0.47 \pm .01$ , female  $0.46 \pm .04$ ; male foot/SVL ratio  $0.50 \pm .03$ , female  $0.49 \pm .05$ .

**Advertising Call.** — Not recorded.

**Larval Definition.** — Larvae unknown.

**Distribution.** — Serra do Mar in the states of Paraná, Rio de Janeiro, and São Paulo (Figure 42).

**PARANÁ.** Banhado (USNM 163462); Serra de Araraquara (MNRio 1791(2)); Rio Taquaral em Marumbi, Serra do Mar na estrada de ferro de Curitiba (AL 160-61).

**RIO DE JANEIRO.** Serra de Mangaratiba (MNRio 1203).

**SÃO PAULO.** Iporanga (MZUSP 10005, 21822-23, 21889, 23826-27, 57805-08 USNM 217967-971); 8 km N Juquiá (UMMZ 104266(3); USNM 132993).

***Cycloramphus mirandaribeiroi* new species**  
Figure 46

**Holotype:** MZUSP 57809, an adult male from Brasil; Paraná, 9 km W São João da Graciosa on PR 410 to Curitiba. Collected by W. Ronald Heyer, Kazumi Kanno and Francisca Carolina do Val on 27 December 1978.

**Paratypes:** MZUSP 57810-14, USNM 217972-77, a series of adults and juveniles from 9-16 km W São João da Graciosa on PR 410 to Curitiba. Collected by same collectors from 23-27 December 1978.

**Diagnosis.** — The species with toe webbing and distinct black and/or white dorsal tubercles are *C. asper*, *boraceiensis*, *duseni*, *lutzorum*, *mirandaribeiroi*, *ohausi*, *rhyakonastes*, *semipalmatus*. The considerable toe webbing of *C. mirandaribeiroi* differs from the moderate webbing of *boraceiensis*, *duseni*, *lutzorum*, and distinguishes from the reduced webbing of *ohausi*, *rhyakonastes*, and *semipalmatus*. Additionally, *C. mirandaribeiroi* has distinct light spots on the posterior surface of the thigh, most individuals of *boraceiensis* and *duseni* lack distinct thigh spots. *Cycloramphus mirandaribeiroi* is a larger species (males 49-61 mm, females 62-69 mm SVL) than *lutzorum* (males 41-47 mm, females 42-58 mm SVL). *Cycloramphus mirandaribeiroi* is also larger than the similarly webbed *asper* (males 38-48 mm, females 44-54 mm SVL), most *asper* lack the distinct thigh spots characteristic of *mirandaribeiroi*.

**Description of Holotype.** — Snout rounded from above and in profile; canthus rostralis indistinct; loreal slightly concave in cross section; tympanum hidden; vomerine teeth in slightly obtuse angulate series, in close proximity medially, lying between and posterior to choanae; vocal fold present,



Figure 46. Holotype of *Cycloramphus mirandaribeiroi*.

not opening to a pouch; second finger just longer than first; outer metacarpal tubercle large, rounded with anterior projection, inner metacarpal tubercle ovoid, separated from thumb subarticular tubercle by less than diameter of subarticular tubercle; thumbs lacking asperities; dorsal texture of low relief warts bearing shagreen and white tipped tubercles, warts not aligned; indistinct supratympanic fold; inguinal gland large, disk-shaped, diameter about  $1/3$  femur length; venter weakly granulate; toe tips expanded into small ungrooved disks just wider than digit; toes fringed, webbing I 1 – 2 II 1 –  $2\frac{3}{4}$  III 1+ – 3– IV  $2\frac{2}{3}$  – 1 V; toe subarticular tubercles moderate; outer rounded metatarsal tubercle smaller than ovoid inner metatarsal tubercle; no tarsal or metatarsal folds; posterior surface of tarsus with shagreen and small tubercles; sole of foot with fine shagreen.

SVL 60.2, head length 25.3, head width 27.0, eye-nostril distance 6.1, eye-eye dis-

tance 12.6, femur 30.3, tibia 29.7, foot 31.3 mm.

Dorsum uniform with light spot in middle of back and light interorbital bar; upper lip with faint light stripes from under eye to edge of lip; upper limbs faintly barred; venter dark brownish gray with small distinct light spots; posterior surface of thigh dark with contrasting light distinct spots.

**Etymology.** — Named for Alipio Miranda-Ribeiro, a major contributor to the understanding of this group of frogs.

**Adult Specimen Definition** (N = 11). — Thumbs lacking asperities; snout rounded or sloping in profile, lip flared or not (Figure 6, A, C, F); dorsal pattern uniform; posterior surface of thigh usually with large distinct light spots, rarely mottled; light spots under eyes, on belly and on posterior face of thigh yellow in life; dorsal texture of warts with shagreen and white tipped tubercles, warts often aligned into irregular or regular short rows; foot webbing I 1 – 2

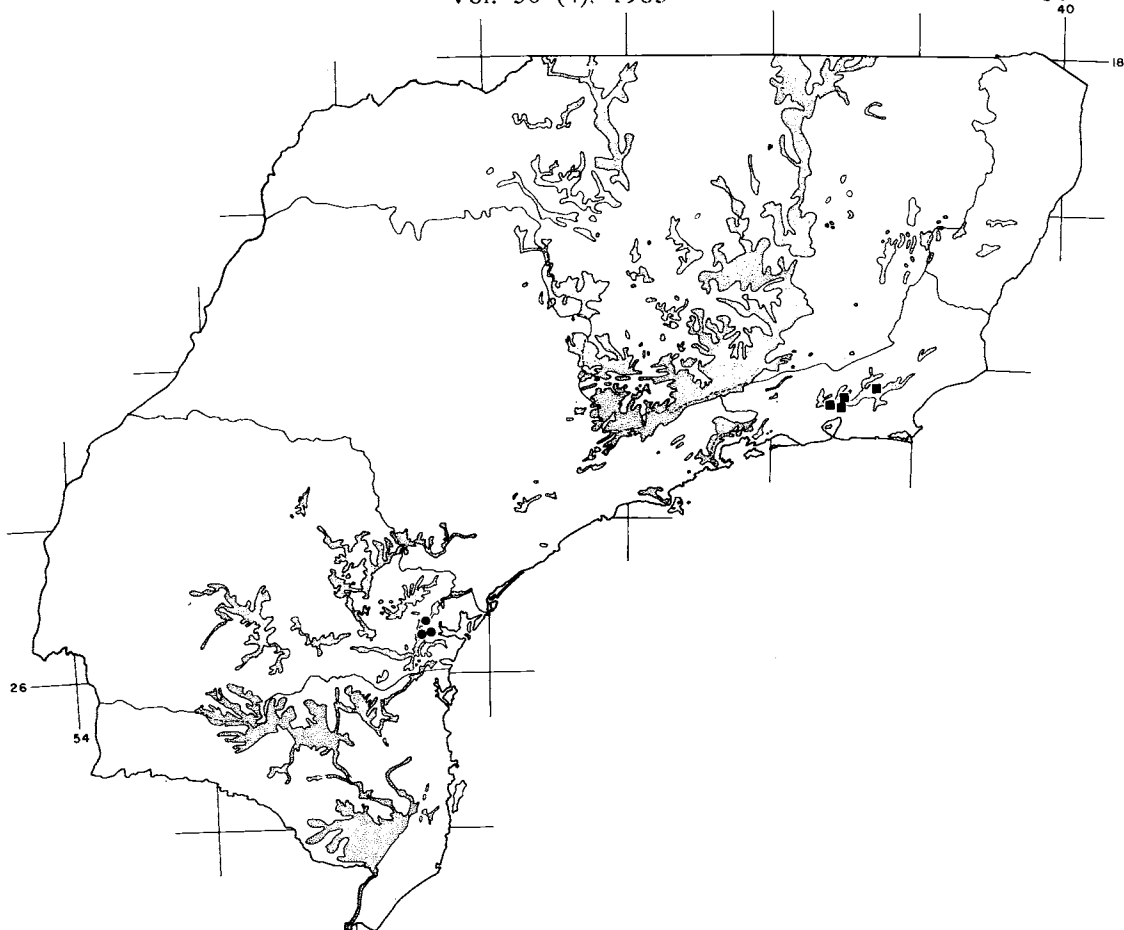


Figure 47. Distribution map of *Cycloramphus mirandaribeiroi* (circles) and *ohausi* (squares). Stippled areas join approximate 1000 meter contours.

II 1 - 2 1/2 III 1 - 3 - IV 2 1/2 - 1 V;  
 male SVL  $58.2 \pm 4.5$ , maximum 63.8 mm,  
 females  $66.5 \pm 2.7$ , maximum 68.6 mm,  
 females larger than males ( $t = 3.3$ ,  $P =$   
 $.009$ ); male head length/SVL ratio  $0.40 \pm$   
 $.01$ , female  $0.41 \pm .01$ ; male head width/  
 SVL ratio  $0.43 \pm .01$ , female  $0.44 \pm .02$ ;  
 male eye-nostril distance/SVL ratio  $0.10 \pm$   
 $.01$ , female  $0.10 \pm .01$ ; male eye-eye dis-  
 tance/SVL ratio  $0.20 \pm .01$ , female  $0.20$   
 $\pm .01$ ; male femur/SVL ratio  $0.49 \pm .02$ ,  
 female  $0.48 \pm .02$ ; male tibia/SVL ratio  
 $0.49 \pm .02$ , female  $0.50 \pm .02$ ; male foot/  
 SVL ratio  $0.51 \pm .03$ , female  $0.51 \pm .02$ .

**Advertising Call.** — Known to have a  
 call, but not recorded on magnetic tape.

**Larval Definition.** — Larvae unknown.

**Distribution.** — Serra do Mar in the  
 State of Paraná (Figure 47).

**PARANÁ.** Morretes (USNM 160311-18);  
 9-16 km W São João da Graciosa (MZUSP  
 57809-814, USNM 217972-77); Rio Ta-  
 quaral em Marumbi, Serra do Mar, na  
 estrada de ferro de Curitiba (L 157-59).

***Cycloramphus ohausi*** (Wandolleck), 1907

*Ceratophrys ohausi* Wandolleck, 1907:10,  
 Plate 1, Figs. 2, 2a. Type-Locality:  
 Petrópolis, Brasil. Holotype: Originally  
 in Dresden Museum, presumed lost.

*Cyclorhamphus distinctus* Lutz, 1932:71,  
 Plate 32, Figs. 1-4. Type-Locality:  
 near Petrópolis, 800 m, Brasil. Lecto-  
 type: AL 2180, adult male.

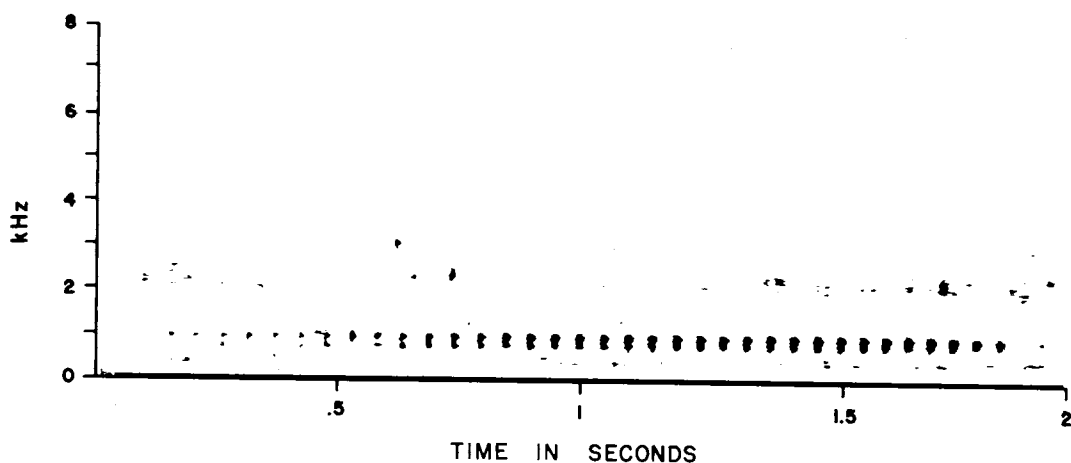


Figure 48. Audiospectrogram of the advertising call of *Cycloramphus ohausi*. Specimen (not captured) recorded about 20:00 h on 14 December 1977 from Brasil: Rio de Janeiro; near Teresópolis. Air temperature 15-16° C.

**Diagnosis.** — *Cycloramphus ohausi* is the only species which has black cornified thumb spines. Such spines are lacking in members of both sexes of all other *Cycloramphus* species.

**Adult Specimen Definition** (N = 74). — Male thumb with from 2-11 black cornified spines, female 2-9 spines; snout moderately to strongly sloping in profile (Figure 6, B, C, D, E); dorsal pattern sometimes uniform, usually with distinct pattern of dark interorbital triangle with apex extended and forked posteriorly, outlined in light (Figure 2, A, A-1, B); posterior surface of thigh uniform or mottled; no distinctive colors in life; dorsal texture of shagreen and large and small white-tipped tubercles on the apices of warts, some warts aligned in 2-6 dorsolateral rows, rows not straight, but symmetrically arranged; toes fringed, male web I 2<sup>-</sup> — 2<sup>+</sup> II 2<sup>-</sup> — 3<sup>+</sup> III 2 1/2 — 4<sup>-</sup> IV 3 1/2 — 2<sup>+</sup> V, female I 1 1/2 — 2<sup>+</sup> II 2<sup>-</sup> — 3<sup>+</sup> III 2 1/2 — 4<sup>-</sup> IV 3 3/4 — 2 V; male SVL 32.0 ± 3.9, maximum 38.6 mm, female 36.2 ± 2.8, maximum 41.6 mm, females larger than males ( $t = 5.0$ ,  $P < .001$ ); male head length/SVL ratio 0.40 ± .02, female 0.40 ± .01; male head width/SVL ratio 0.43 ± .02, female

0.43 ± .01; male eye-nostril distance/SVL ratio 0.09 ± .01, female 0.09 ± .01; male eye-eye distance/SVL ratio 0.16 ± .01, female 0.16 ± .01; male femur/SVL ratio 0.46 ± .03, female 0.45 ± .03; male tibia/SVL ratio 0.44 ± .02, female 0.43 ± .02; male foot/SVL ratio 0.50 ± .02, female 0.48 ± .03.

**Advertising Call.** — Call of about 34-37 pulsed notes lasting from 1.2-1.5 s; dominant frequency between 800-1000 Hz; call intensity modulated, beginning quietly, ending loudly (Figure 48).

**Larval Definition.** — Larvae unknown.

**Distribution.** — Serra dos Orgãos (Figure 47).

**RIO DE JANEIRO.** Guapi, Alcindo Guanabara (AL 3006-07); Nova Friburgo (WCAB 18531-32); Petrópolis (L 110); Petrópolis, Independência (AL 2180-82, 2194, 2242, 3237, L 108-09); Teresópolis (AL 4322, L 57-107, MZUSP 61, 99, 6400, 20617, 20621, 57815-826 USNM 118998-99, 159094-95, 217906-917, WCAB 17714, 17725-26, 19377).

***Cycloramphus rhyakonastes* new species**  
Figure 49

Holotype: MZUSP 57827, an adult male





Figure 49. Holotype of *Cycloramphus rhyakonastes*.

from Brasil; Paraná, 15 km W of São João da Graciosa on PR 410 to Curitiba. Collected by W. Ronald Heyer, Kazumi Kanno, and Francisca Carolina do Val on 23 December 1978.

Paratypes: MCZ 100109, MZUSP 57828-859, USNM 217978-18011.

**Diagnosis.** — The species with toe webbing and distinct black and/or white dorsal tubercles are *C. asper*, *boraceiensis*, *duseni*, *lutzorum*, *mirandaribeiroi*, *ohausi*, *rhyakonastes*, *semipalmatus*. *Cycloramphus rhyakonastes* individuals lack thumb spines, *C. ohausi* individuals have thumb spines. The reduced webbing of *C. rhyakonastes* differs from the moderate webbing of *boraceiensis*, *duseni*, and *lutzorum*, and distinguishes *rhyakonastes* from the considerably webbed *asper* and *mirandaribeiroi*. Most individuals of *C. rhyakonastes* have large light distinct spots on the posterior surface of the thigh and red bellies in life; most individuals of *semipalmatus* have uniform thighs, some individuals have small thigh spots, no *semipalmatus* have red bellies in life.

**Description of Holotype.** — Snout rounded from above and in profile, lip flared; canthus rostralis indistinct; loreal shallowly

concave in cross section; tympanum hidden; vomerine tooth bearing process obtuse angulate, between and posterior to choanae, vomerine teeth not visible; vocal fold, not a slit; first and second fingers about equal, second just longer than first when equally adpressed; outer metacarpal tubercle modified cordiform, inner metacarpal tubercle ovoid, separated from thumb subarticular tubercle by distance greater than diameter of subarticular tubercle; thumbs lacking asperities; dorsal texture shagreened with high relief warts bearing brown tipped tubercles, warts arranged in short, symmetrical series; supratympanic fold discernable; inguinal gland small, disk shaped, diameter  $1/5 - 1/4$  length of femur; venter weakly granular; toe tips slightly swollen, just broader than digit width; toes fringed, web I  $1 \frac{2}{3} - 2+$  II  $1 \frac{1}{2} - 3-$  III  $2+ - 3 \frac{1}{3}$  IV  $3 \frac{1}{3} - 2-$  V; subarticular tubercles moderate; prominent, rounded outer metatarsal tubercle smaller than ovoid inner metatarsal tubercle; no tarsal or metatarsal folds; posterior tarsus shagreened and covered with brown tubercles; sole of foot shagreened, lacking tubercles.

SVL 42.2, head length 16.1 head width

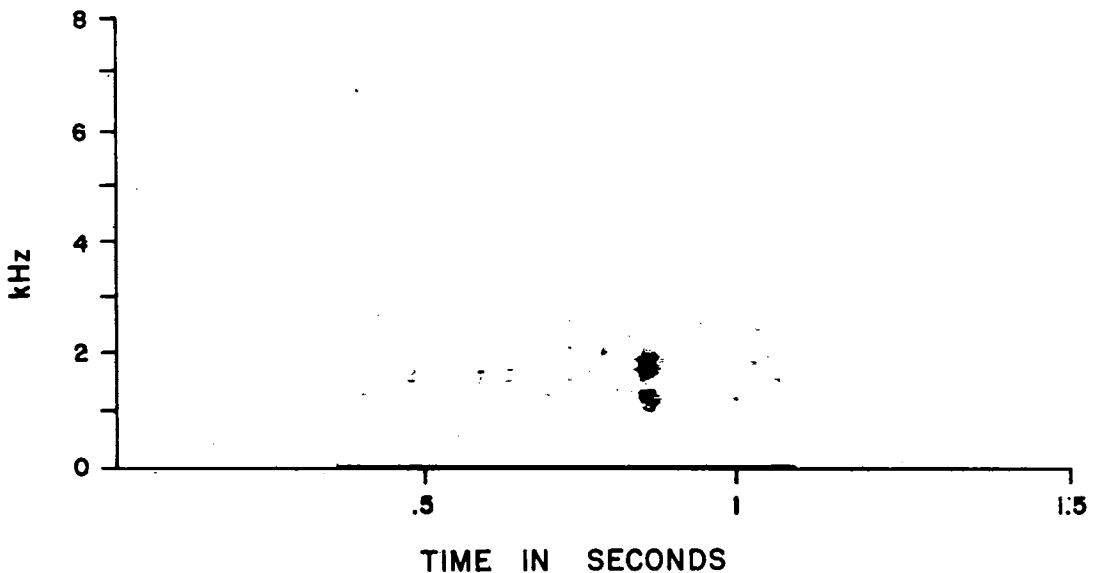


Figure 50. Audiospectrogram of the advertising call of *Cycloramphus rhyakonastes*. Specimen (not captured) recorded 20:15 h on 26 December 1978 from Brasil: Paraná, 12 km W São João da Graciosa on PR 410 to Curitiba. Air temperature 17.4° C.

17.8, eye-nostril distance 3.8, eye-eye distance 7.7, femur 22.7, tibia 21.6, foot 21.8 mm.

Dorsal pattern mottled with light spot in middle of back and light interorbital bar; upper lip with light stripes from below eye to edge of lip; upper limbs barred, chin gray with contrasting small light spots; chest mottled, belly and under limb surfaces lightly mottled, red in life; posterior surface of thigh dark with distinct light spots, yellow in life.

**Etymology.** — From the Greek *rhyakos*, rushing stream and *nastes*, inhabitant.

**Adult Specimen Definition** (N = 57). — Thumbs lacking asperities; snout usually rounded, rarely vertically sloping in profile, lip flared or not (Figure 6, A, B, F); dorsal pattern uniform or mottled; posterior surface of thigh usually dark with distinct light spots, rarely uniform or mottled; lip stripes, chin spots and thigh spots faded to bright yellow in life, belly and under limbs dirty yellow-red (sometimes) to vivid brick red in life; dorsal texture shagreened with high

relief warts bearing white or brown tipped tubercles, warts often arranged in short irregular or regular rows; toes fringed, male web I trace II 1 3/4 — 3 III 2+ — 3 1/3 IV 3 1/3 — 2- V, female I trace II 2- — 3 III 2 1/2 — 3 1/2 IV 3 1/2 — 2 V; male SVL 45.2 ± 2.5, maximum 50.6 mm, female 52.2 ± 3.0, maximum 56.4, females larger than males ( $t = 9.7$ ,  $P < .001$ ); male head length/SVL ratio 0.40 ± .01; female 0.39 ± .01; male head width/SVL ratio 0.42 ± .01, female 0.41 ± .01; male eye-nostril distance/SVL ratio 0.09 ± .01, female 0.08 ± .01; male eye-eye distance/SVL ratio 0.18 ± .01, female 0.18 ± .01; male femur/SVL ratio 0.47 ± .05, female 0.46 ± .02; male tibia/SVL ratio 0.47 ± .03, female 0.46 ± .02; male foot/SVL ratio 0.49 ± .04, female 0.48 ± .02.

**Advertising Call.** — Call of sporadic single notes; call short, duration 0.04-0.05 s; call not well tuned, energy spread over range of 1000-2500 Hz, with maximum energy between 1500-2100 Hz (Figure 50).

**Larval Definition.** — Larvae unknown.

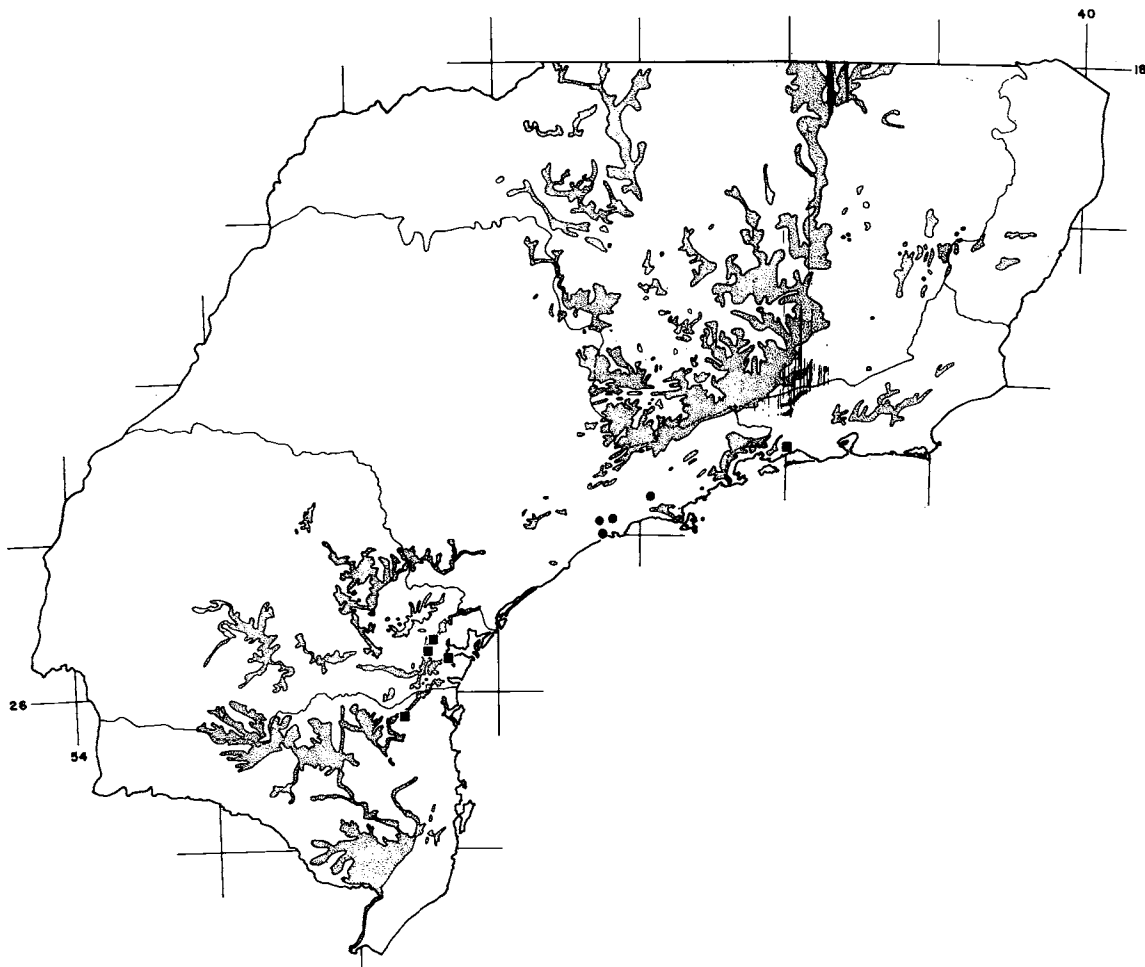


Figure 51. Distribution map of *Cycloramphus rhyakonastes* (squares) and *semipalmatus* (circles). Stippled areas join approximate 1000 meter contours.

**Distribution.** — Serra do Mar in the states of Paraná and Santa Catarina (Figure 51).

**PARANÁ.** Banhado (USNM 163463, 164119); Morretes (USNM 160310); 9-16 km W São João da Graciosa on PR 410 to Curitiba (MCZ 100109, MZUSP 57827-859, USNM 217978-18011); Rio Taquaral em Marumbi, Serra do Mar na estrada de ferro de Curitiba (L 155-56, 160-61).

**SANTA CATARINA.** Rio Vermelho, São Bento do Sul (WCAB 36155-162).

***Cycloramphus semipalmatus***  
(Miranda-Ribeiro), 1920

*Iliodiscus semipalmatus* Miranda-Ribeiro, 1920:269, Plates 3, 5-6. Type-Local-ity: Campo Grande, São Paulo, Brasil. Holotype: MZUSP 737, adult male.

**Diagnosis.** — The species with toe webbing and distinct black and/or white dorsal tubercles are *C. asper*, *boraceiensis*, *duseni*, *lutzorum*, *mirandaribeiroi*, *ohausi*, *rhyakonastes*, *semipalmatus*. *Cycloramphus semipalmatus* individuals lack thumb spines, *C. ohausi* individuals have thumb spines. The reduced webbing of *C. semipalmatus* differs

from the moderate webbing of *boraceiensis*, *duseni*, and *lutzorum*, and distinguishes from the considerable webbing of *asper* and *mirandaribeiroi*. Most individuals of *C. semipalmatus* have uniform thighs, some have small spots on the posterior surface of the thigh, no individuals of *C. semipalmatus* have red bellies in life; most individuals of *rhyakonastes* have large light distinct thigh spots and red bellies in life.

**Adult Specimen Definition** (N = 86). — Thumbs lacking asperities; snout rounded or sloping in profile, lip flared or not (Figure 6, A, B, C, E, F); dorsal pattern usually uniform (Figure 2, B), sometimes with dark interorbital triangle extending onto back (Figure 2, A-1); posterior surface of thigh uniform or mottled, rarely with small distinct light spots; no distinctive colors in life; dorsal texture shagreened with high profile warts bearing black and/or white tipped tubercles, warts of different sizes, warts usually aligned in short irregular rows; toes ridged or fringed, male web I trace II trace III trace IV 3 3/4 — 2 V, female I trace II trace III trace IV 3 2/3 — 2- V; male SVL  $39.6 \pm 2.5$ , maximum 43.4 mm, female SVL  $45.5 \pm 2.9$ , maximum 51.0 mm, females larger than males ( $t = 10.11$ ,  $P < .001$ ); male head length/SVL ratio  $0.40 \pm .01$ , female  $0.40 \pm .01$ ; male head width/SVL ratio  $0.44 \pm .01$ , female  $0.43 \pm .01$ ; male eye-nostril distance/SVL ratio  $0.08 \pm .01$ , female  $0.08 \pm .01$ ; male eye-eye distance/SVL ratio  $0.17 \pm .01$ , female  $0.17 \pm .01$ ; male femur/SVL ratio  $0.48 \pm .02$ , female  $0.47 \pm .03$ ; male tibia/SVL ratio  $0.48 \pm .02$ , female  $0.46 \pm .02$ ; male foot/SVL ratio  $0.49 \pm .02$ , female  $0.47 \pm .03$ .

**Advertising Call.** — Call consisting of sporadic notes; short, duration 0.03-0.04 s; call not finely tuned, energy from 200 — 5000 Hz, energy peak about 800 Hz (Heyer and Mello, 1979, Figs. 1 A, 2, A, B, 4, Figure 59 D).

**Larval Definition.** — Larvae unknown.

**Distribution.** — Serra do Mar in the state of São Paulo (Figure 51).

**SÃO PAULO.** Boracéia (MZSUP 1575, 3060, 3424-25, 23394-96, 23398-99, 23766-783, 37563, 37766, USNM 217918-928; Alto da Serra de Cubatão (AL 183, 186, 189a, 191-93, 378, 380-82, 694-709, 1310-12, 3348-350, MNRio 100, USNM 81143, 96820-835, 96841-46, 217929-930); Engenheiro Ferraz (MZUSP 23066-67); Paranapiacaba (AL 4041-056, L 148, MZUSP 8996-98, 9000-04, 10567, 10593-94, 10608-611, 10655, 10786, 11002, 13912, 13914-17, WCAB 1085, 3203, 4234, 9116, 9118-19, 34828, 36215-17, 45136-38); Rio Grande (MZUSP 23254-57, 23259-262, 23264-67);  $\pm 4$  miles N Santos on escarpment from plateau,  $\pm 600'$  (USNM 196322(2)); km 47 on old São Paulo — Santos road (MZUSP 10027-28, 10219).

**Cycloramphus stejneri** (Noble), 1924, new combination

*Borborocoetes stejneri* Noble, 1924:68.  
Type-Locality: Organ Mountains, Brazil, 1500 meters. Holotype: USNM 52608, female.

*Craspedoglossa stejneri*: Cochran, 1955: 235. First association of *stejnegeri* with *Craspedoglossa*.

**Diagnosis.** — The webless species of *Cycloramphus* are *bolitoglossus*, *carvalhoi*, *catarinensis*, *diringshofeni*, *eleutherodactylus*, *granulosus*, *stejnegeri*, *valae*. The toes are free and the dorsum is smooth in *C. stejneri*; the toes are ridged or fringed and the dorsum is glandular-warty in *catarinensis*, *granulosus*, and *valae*. The leg is shorter in *stejnegeri* (e.g. average foot/SVL ratio  $0.42 \pm .01$  (one standard deviation) in males,  $0.42 \pm .02$  in females) than in *diringshofeni* (male foot/SVL average 0.50) or *eleutherodactylus* (foot/SVL ratio  $0.48 \pm .03$  in males,  $0.49 \pm .04$  in females). *Cycloramphus stejneri* (males 45-47 mm, females 45-56 mm SVL) is larger than

*bolitoglossus* (males 28-34 mm, females 39-40 mm SVL) and smaller than *carvalhoi* (males 58-62 mm SVL).

**Adult Specimen Definition** (N = 10). — Thumbs lacking asperities; snout rounded or vertically sloping in profile (Figure 6, A, B); dorsal pattern uniform to distinctly chevroned (Figure 2, B, E-1, F, F-1, G); posterior surface of thigh with small or larger distinct light spots; no distinctive colors in life; dorsal texture smooth or granular, usually with regular dorsal ridges; toes lacking ridge, fringe, or web; male SVL  $45.7 \pm 0.7$ , maximum 46.5 mm, female  $49.6 \pm 3.7$ , maximum 55.4 mm; male head length/SVL ratio 0.40, female  $0.38 \pm .01$ ; male head width/SVL ratio 0.42, female  $0.42 \pm .01$ ; male eye-nostril distance/SVL ratio 0.09, female  $0.08 \pm .01$ ; male femur/SVL ratio 0.35, female  $0.34 \pm .01$ ; male tibia/SVL ratio 0.34, female  $0.34 \pm .01$ , male foot/SVL ratio 0.42, female  $0.42 \pm .02$ .

**Advertising Call.** — Call unknown.

**Larval Definition.** — Larva elongate; tail fins low, on distal two thirds of tail dorsally, complete ventrally; belly not flattened; spiracle absent; anus median, usually bifid; oral disk small, with two large papillae laterally, no anterior or posterior papillae; tooth row formula  $\frac{2-2}{1-1}$ ; largest individual, stage 31, 25.2 mm; body and tail lack pigmentation (Heyer and Crombie, 1979, Fig. 1).

**Distribution.** — Organ Mountains (Figure 42).

**RIO DE JANEIRO.** Teresópolis (USNM 164116, 208491-8504, WCAB 19457- 460, 19472).

***Cycloramphus valae* new species**  
Figure 52

Holotype: MZUSP 57860, an adult female from Brasil; Santa Catarina, Gruta,

20 km E Bom Jardim on road to Lauro Müller. Collected by W. Ronald Heyer, Frances I. McCullough, and Francisca Carolina do Val on 23 November 1979.

Paratopotypes: MCZ 100110, MZUSP 35471-77, 57861-888, USNM 218012-037, Vienna 25195.

**Diagnosis.** — The webless species of *Cycloramphus* are *bolitoglossus*, *carvalhoi*, *catarinensis*, *diringshofeni*, *eleutherodactylus*, *granulosus*, *stejnegeri*, *valae*. The toes are ridged or fringed and the dorsum is glandular-warty in *C. valae*; the toes are free and the dorsum smooth, slightly rugose, or weakly granular in *bolitoglossus*, *carvalhoi*, *diringshofeni*, *eleutherodactylus*, *stejnegeri*. *Cycloramphus valae* lacks mucus gland (like) structures on the dorsal warts; such structures are present in *catarinensis*. The leg is longer in *valae* (e.g. average tibia/SVL ratio  $0.48 \pm .01$  (one standard deviation) in males,  $0.45 \pm .02$  in females) than in *granulosus* (average tibia/SVL ratio  $0.42 \pm .02$  in males,  $0.41 \pm .02$  in females); *valae* are generally smaller (males to 33 mm, females to 40 mm SVL) than *granulosus* (males to 43 mm, females to 47 mm SVL).

**Description of Holotype.** — Snout rounded from above and in profile; canthus rostralis indistinct; loreal region slightly concave in profile; tympanum hidden; vomerine teeth in short transverse series, almost contiguous medially, lying between and posterior to choanae; first and second fingers about equal length, second just longer than first when equally adpressed; outer metacarpal tubercle rounded-ovate, inner metacarpal tubercle ovoid, separated from thumb subarticular tubercle by distance equal to less than diameter of subarticular tubercle; thumb lacking asperities; dorsal texture strongly granular, lacking shagreen and tubercles; very indistinct supratympanic fold; ventral texture weakly granular; toe tips not or just slightly swollen, about same diameter as digit width; toes



Figure 52. Holotype of *Cycloramphus valae*.

with lateral ridges, no web; moderate sub-articular tubercles; rounded, outer metatarsal tubercle smaller than ovoid inner metatarsal tubercle; no tarsal or metatarsal folds; posterior tarsus granular; sole of foot smooth.

SVL 36.2, head length 12.3, head width 13.4, eye-nostril distance 3.0, eye-eye distance 6.1, femur 16.0, tibia 16.3, foot 16.6 mm.

Pattern uniform dark brown gray above, lighter uniform brown gray below and on posterior surface of thigh.

**Etymology.** — Named for my friend and field companion, Dra. Francisca Carolina do Val, who has consistently aided our night collecting after she collected drosophilid flies by day. Her help and friendship have made my introduction to the Atlantic Forest fauna possible and enjoyable.

**Adult Specimen Definition** (N = 35). — Thumbs lacking asperities; snout rounded in profile; dorsum uniform or blotched (Figure 2, A, D-1); posterior surface of thigh uniform; no distinctive colors in life; dorsal texture strongly granular, lacking shagreen

or tubercles, usually no dorsal ridges present, rarely short irregular ridges present; toes with lateral ridges, rarely almost free, foot usually without web, rarely trace of basal webbing present; male SVL  $29.8 \pm 2.3$ , maximum 32.4 mm, female  $35.6 \pm 2.4$ , maximum 39.6 mm, females larger than males ( $t = 6.0$ ,  $P < .001$ ); male head length/SVL ratio  $0.36 \pm .01$ , female  $0.34 \pm .01$ ; male head width/SVL ratio  $0.39 \pm .01$ , female  $0.38 \pm .01$ ; male eye-nostril distance/SVL ratio  $0.08 \pm .01$ ; female  $0.08 \pm .01$ ; male eye-eye distance/SVL

ratio  $0.19 \pm .01$ , female  $0.18 \pm .01$ ; male femur/SVL ratio  $0.47 \pm .02$ , female  $0.44 \pm .02$ ; male tibia/SVL ratio  $0.48 \pm .01$ , female  $0.45 \pm .02$ ; male foot/SVL ratio  $0.50 \pm .02$ , female  $0.47 \pm .02$ .

**Advertising Call.** — Unknown.

**Larval Definition.** — Larvae unknown.

**Distribution.** — Known from the type locality (Figure 42).

**SANTA CATARINA.** Gruta, município de Lauro Müller (MCZ 100110, MZUSP 35471-77, 57860-888, USNM 218012-037, Vienna 25195).

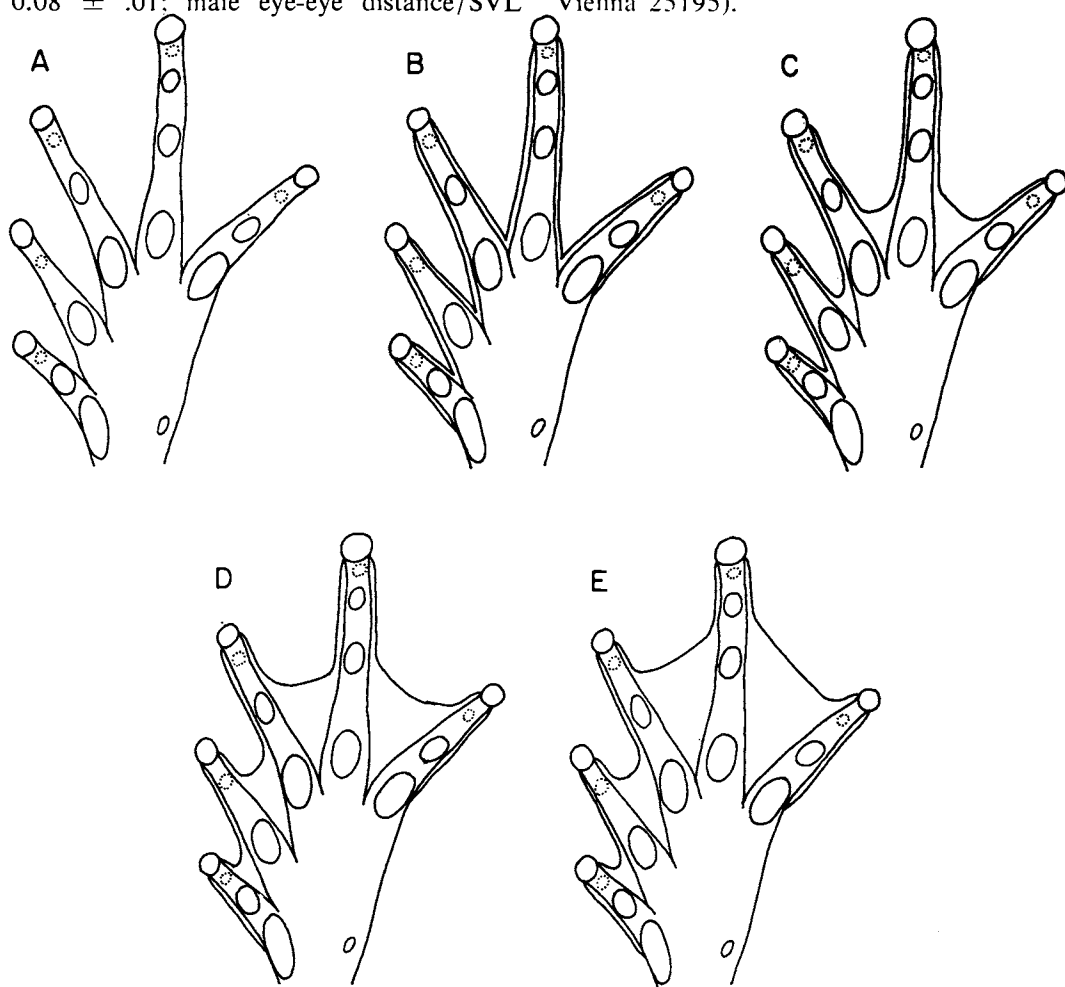


Figure 53. Ventral views of representative feet. A — free toes, B — fringed toes, C — reduced toe webbing, modal formula for female *C. rhyakonastes* I trace II 2- — 3 III 2 1/2 — 3 1/2 IV 3 1/2 — 2 V, D — moderate toe webbing, modal formula of female *C. fuliginosus* I 1 — 2 II 1 — 2 1/2 III 1 1/2 — 3+ IV 3 — 1 V, E — considerable toe webbing, modal formula for male *C. brasiliensis* I 1 — 2 II 1 — 2 1/2 III 1 1/2 — 2 1/2 IV 2+ — 1 V.

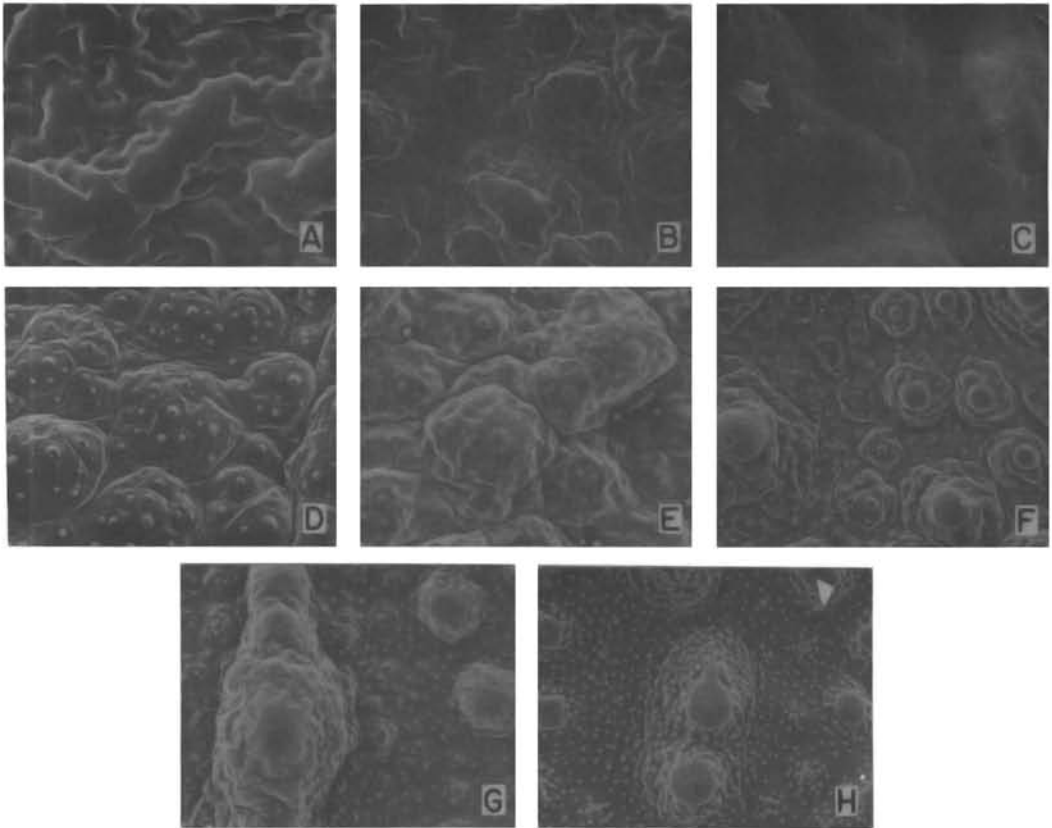


Figure 54. Dorsal textures, scanning electron micrographs. All from pieces of skin taken from dorsal shoulder area. A = *C. brasiliensis*, USNM 217857; B = *C. granulatus*, USNM 217903; C = *C. catarinensis*, USNM 137676; D = *C. dubius*, USNM 217868; E = *C. boraceiensis*, USNM 217940; F = *C. duseni*, MZUSP 57774, G = *C. semipalmatus*, USNM 217930, H = *C. ohausi*, USNM 217912.

AN ARTIFICIAL KEY TO ADULT MEMBERS OF THE GENUS *CYCLORAMPHUS*

- |                                                                                                                                                                                                                                   |                                                                                                                                                                                                                                                                                                                                                                                     |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <p>1 A. Toes not webbed (Figure 53, A, B) . . . . . 2</p> <p>1 B. Toes webbed (Figure 53, C, D, E) . . . . . 9</p> <p>2 A. Toes ridged or fringed (Figure 53 B), dorsum granular or glandular-warty (Figure 54, B, C) . . . 3</p> | <p>2 B. Toes free (Figure 53, A), dorsum usually smooth or slightly rugose . . . . . 5</p> <p>3 A. Dorsal granules with mucus gland-like structures, giving each granule a mosaic pattern . . . . . <i>catarinensis</i></p> <p>3 B. Dorsal granules not having a mosaic pattern . . . . . 4</p> <p>4 A. Leg shorter (mean male tibia 42% SVL, female 41), size larger (males to</p> |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|



- 43 mm SVL, females 47 mm), States of Rio de Janeiro and São Paulo ..... *granulosus*
- 4 B. Leg longer (mean male tibia 48% SVL, female 45), size smaller (males to 33 SVL, females 40 mm), State of Santa Catarina ..... *valae*
- 5 A. Leg longer (mean femur length 45% SVL, mean tibia length 47-50% SVL, mean foot length 48-50% SVL) ..... 6
- 5 B. Leg shorter (mean femur length 34-38% SVL, mean tibia length 30-35% SVL, mean foot length 36-42% SVL) ..... 7
- 6 A. Dorsum with elongate sinuous symmetrical dorsolateral ridges, males with vocal slits, size smaller (males to 31 mm SVL) ..... *diringshofeni*
- 6 B. Dorsum smooth or if short ridges present, not sinuous, males lack vocal slits, size larger (males to 54 mm SVL) ..... *eleutherodactylus*
- 7 A. Size smaller (males to 34 mm, females 40 mm SVL), dorsum often with mid-dorsal dark pin stripe, States of Paraná and Santa Catarina ..... *bolitoglossus*
- 7 B. Size larger (males and females at least 45 mm SVL), dorsum never with mid-dorsal dark pin strip, States of Minas Gerais and Rio de Janeiro ..... 8
- 8 A. Size larger (males at least 58 mm SVL, females unknown), Serra da Mantiqueira ..... *carvalhoi*
- 8 B. Size smaller (males to 47 mm, females 56 mm SVL), Serra dos Órgãos ..... *stejnegeri*
- 9 A. Dorsum lacking brown, black or white tipped tubercles (Figure 54, A, D) ..... 10
- 9 B. Dorsum with brown, black, or white tipped tubercles (Figure 54, E-H) ..... 14
- 10 A. Dorsum with shagreen (Figure 54, D) ..... *dubius*
- 10 B. Dorsum lacking shagreen (Figure 54, A) .... 11
- 11 A. Reduced toe webbing (Figure 53 C) ..... 12
- 11 B. Moderate or considerable toe webbing (Figure 53, D, E)... 13
- 12 A. Distinct tarsal fold pronounced into a flap, short distinct outer metatarsal flap, posterior surface of thigh lacking distinct light spots ..... *jordanensis*
- 12 B. Tarsal fold weak, outer metatarsal ridge not pronounced, posterior surface of thigh with distinct light spots ..... *bandeirensis*
- 13 A. Moderate foot webbing (Figure 53, D), inner metacarpal tubercle separated from subarticular tubercle of thumb by distance about equal to diameter of subarticular tubercle (Figure 55, A) ..... *fuliginosus*
- 13 B. Considerable foot webbing (Figure 53, E), inner metacarpal tubercle separated from subarticular tubercle of thumb by distance much less than diameter of subarticular tubercle (Figure 55, B) ..... *brasiliensis*
- 14 A. Thumbs with cornified spines ..... *ohausi*
- 14 B. Thumbs lacking spines 15

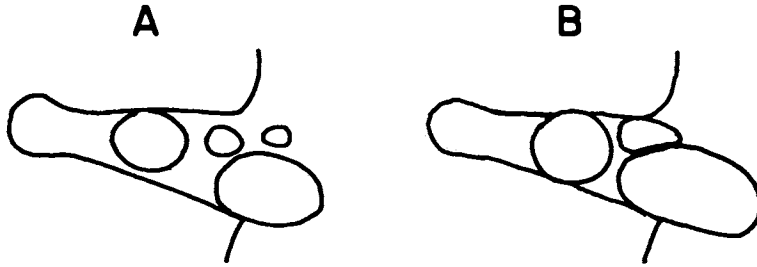


Figure 55. Metacarpal-thumb subarticular tubercle relationship. A = *C. fuliginosus* type, B = *C. brasiliensis* type.

- 15 A. Reduced webbing (Figure 53, C) ..... 16
- 15 B. Moderate to considerable webbing (Figure 53, D, E) .... 17
- 16 A. Red bellies in life, most individuals with distinct light spots on the posterior surface of the thigh, States of Paraná and Santa Catarina ....  
..... *rhyakonastes*
- 16 B. Bellies not red in life, most individuals with uniform posterior thigh surfaces, State of São Paulo  
..... *semipalmatus*
- 17 A. Toes moderately webbed (Figure 53, D) ..... 18
- 17 B. Toes considerably webbed (Figure 53, E) ..... 20
- 18 A. Size smaller (males to 38 mm SVL, females to 44 mm) ..... *duseni*
- 18 B. Size larger (minimum male 36, maximum 55 mm SVL, minimum female 42, maximum 58 mm SVL) ..... 19
- 19 A. Low profile dorsal warts (Figure 54, E) ..... *boraceiensis*
- 19 B. High profile dorsal warts (Figure 54, G) ..... *lutzorom*
- 20 A. Size smaller (males to 48 mm SVL, females to 54), most with posterior surface of thigh lacking

- distinct light spots .....  
..... *asper*
- 20 B. Size larger (minimum male size 48 mm SVL, minimum female size 62 mm SVL, posterior surface of thigh with large distinct light spots .....  
..... *mirandaribeiroi*

### Degree and nature of interspecific variation

This section summarizes interspecific variation, focussing on minimum and maximum variation among species. Discussion seeks plausible answers to two questions. First, what is the nature and magnitude of differences among species, that is, is interspecific variation of the same magnitude as intraspecific variation? Second, what are the premating isolating mechanisms that operate among the species of *Cycloramphus*?

### LARVAL MORPHOLOGY

Unquestioned larvae are known for only five species. Of these, four are *C. fuliginosus* group members with aquatic larvae; the fifth species has terrestrial larvae.

The aquatic larvae are remarkably similar morphologically. They are elongate and depressed with similar oral structures and color patterns. The only differences are in

size; *boraceiensis* and *duseni* with the smallest larvae, *brasiliensis* with the next largest, and *fuliginosus* with the largest. These sizes do not correlate well with adult sizes.

The terrestrial larva of *C. stejneri* is similar in the elongate habitus but differs in other major features from the four aquatic larvae. They have large yolk stores, (probably carrying them through to metamorphosis, as in *Zachaenus*), and an oral apparatus distinct from the aquatic *Cycloramphus* larvae in terms of oral papillae, tooth row numbers, and beak structure. The oral apparatus appears embryonic and may be similar to the embryonic oral apparatus of *Cycloramphus* aquatic larvae. If this is true, then the magnitude of differences between larval types diminishes, as the differences can be accounted for by minor adjustments in developmental rates. Unfortunately, adequately preserved late embryonic and hatchling larval states of aquatic *Cycloramphus* larvae are not available. The developing series of *C. brasiliensis* (reported as *pinderi*) and *fuliginosus* larvae reported by Lutz (1929) are too poorly preserved for study. His figures lack the views and detail needed for comparison.

#### JUVENILE MORPHOLOGY

The smallest available juveniles of members of the *C. fuliginosus* and *granulosus* groups are essentially indistinguishable. All have indistinguishably mottled or uniform dorsal lip, thigh, and belly patterns. The dorsal textures are more similar in the juveniles than adults. There are some toe webbing differences, paralleling the adult webbing differences. The youngest *C. ohausi* have the distinctive dorsal pattern and light lip bars of the adult; body form is similar to juveniles of the *C. fuliginosus* and *granulosus* groups. The smallest *C. eleutherodactylus* and *stejnegeri* have nondescript patterns, but the body shapes and toe web-

bing are very similar to each other and distinctive from the body shapes of young juveniles of the *C. fuliginosus*, *granulosus*, and *ohausi* groups.

#### ADULT MORPHOLOGY

##### Pattern

There is relatively little pattern difference among species of *Cycloramphus*, particularly when compared with certain other genera, such as *Leptodactylus*, in which posterior thigh surface patterns are diverse and diagnostic for many species.

The dorsal patterns of most *Cycloramphus* are variations of an uniform or irregularly blotched pattern. Relatively few species have characteristically different and defining patterns in some, most, or all individuals. The species with the most distinctive dorsal patterns are *C. bandeirensis*, *bolitoglossus*, *eleutherodactylus*, and *ohausi*. The variation in dorsal pattern within *C. eleutherodactylus* is of the same magnitude as the most distinctive patterns exhibited among the other species.

The pattern of the loreal and upper lip varies from essentially uniform to boldly marked with vertically oriented light stripes. Some species exhibit intraspecific variation that encompasses as much variation as seen among species. This same characterization is true for posterior surface of the thigh and the belly patterns; whereas some species may have only one extreme state or the other, some species demonstrate the extreme states with all intermediates.

Pattern variation among *Cycloramphus* species is not extensive; intraspecific variation approaches that of interspecific variation. The variation available in some species seems adequate for selection to have produced the patterns found in most members of this genus. Although no genetic data are available, it is difficult to imagine more than a very few alleles accounting for the differences observed in pattern.

### Dorsal Texture

Whereas intraspecific variation is pronounced in terms of pattern, there is little intraspecific variation and marked interspecific variation in dorsal texture. Each species is uniform in terms of presence or absence of shagreen and tubercles. The degree of wartiness is almost an invariate within a species. There is some intraspecific variation in arrangement and distribution of warts and/or tubercles into regular or irregular rows or ridges. The degree of intraspecific variation in this latter aspect does not include the extreme conditions found either in *C. diringshofeni* or *ohausi*, where ridges or tuberculate rows are long, sinuous, and symmetrical.

Although variation in dorsal texture is discrete among species, the most complex textures combining all extreme states are found in some species. This suggests that the genetic potential for the range of dorsal textures seen is present within at least some extant species and that selection has operated on variation within ancestral forms to produce the mosaic distribution of discrete texture states found in the extant *Cycloramphus* species. The magnitude of differences in dorsal texture found among extant species probably is the same as occurred within the ancestral forms.

### Toe Webbing

Each species has a characteristic toe webbing state. No one species encompasses the range of variation found among all species. All species considered collectively form a smooth morphocline ranging from completely free toes to toes with considerable webbing. There are no discrete gaps but rather an overlap between adjacent species on the morphocline.

Assuming a correlation of genetic differentiation with degree of toe webbing, a single genetic change event could produce the differences seen between species with considerable and moderate webbing, where-

as a series of genetic differentiation events would likely be involved in the extremes of free toes versus considerable toe webbing.

### Size and Shape

The data and the way they were taken are best discussed in terms of snout profile shape, adult size, and proportional or shape differences.

There is considerable intraspecific variation in snout shape profile ranging from rounded, vertically sloping to sloping, with or without flared lips. The range of intraspecific variation equals the range of interspecific variation in all species except for *C. ohausi*, in which many individuals have more strongly sloping snouts than the other species.

Size is sexually dimorphic in *Cycloramphus* species, with females being larger than males. There are clear interspecific size differences in addition to the intraspecific variation observed. Each species has a characteristic adult size, but all species can be arranged along a continuum from small to large, with overlap between adjacent species along the continuum.

It is clear that selection has resulted in size differences among species. The measurement data are now examined to determine whether selection has resulted in proportional or shape differences among species.

The SPSS (Nie, et al., 1975) program SCATTERGRAM was used for each size variable for each species for which more than a single individual was available at the time of analysis. Each variable was plotted against BL (estimated body length). Correlations are high, most  $r^2$  values in the .95-.99 range. The worst correlation for a sample size of >15 specimens is an  $r^2 = .71$ .

Regression lines were drawn for each variable for the 16 species represented by a sample size of at least 15 individuals. Individual values were plotted for the three species represented by 3-6 individuals. The results indicate that there are differences in

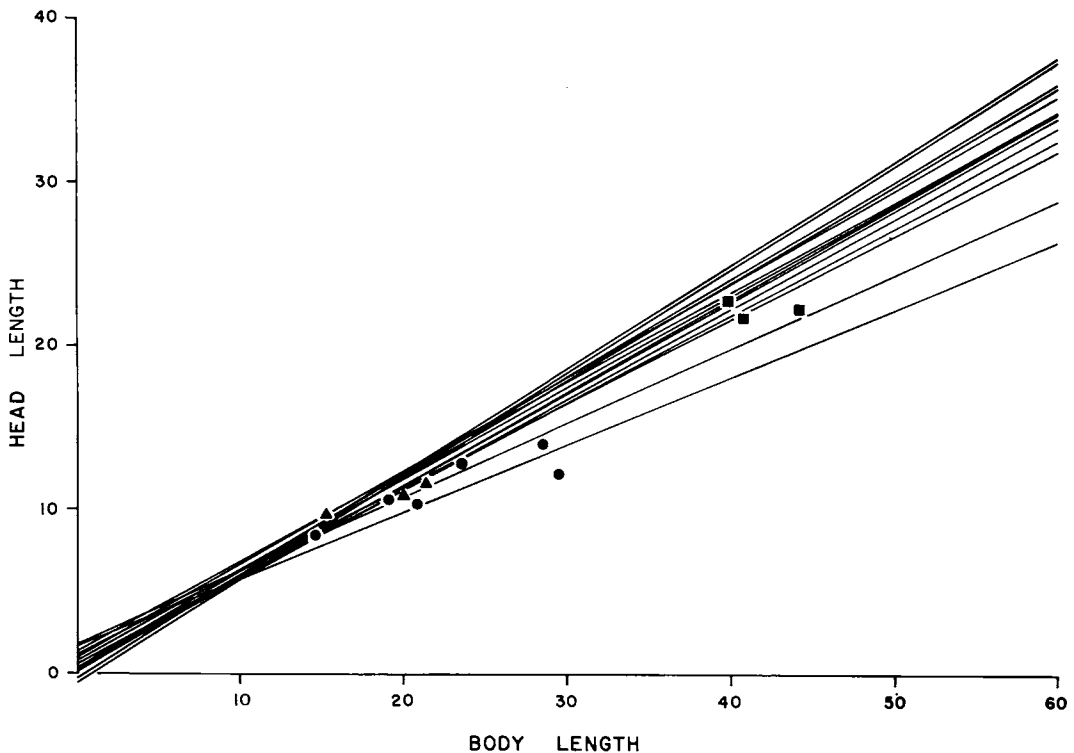


Figure 56. Regression lines of head length plotted against body length for 16 species of *Cycloramphus* with individual values for *C. bolitoglossus* (circles), *carvalhoi* (squares), and *diringshofeni* (triangles). A line may represent more than one species.

variable proportions among species. The general patterns of regression lines are similar; head length vs. BL, eye-eye distance vs. BL and tibia length vs. BL are figured (Figures 56-58) as examples. These examples, together with the rank order of intercept at a body length of 60 mm (Table 19) summarize the variation encountered.

The variables group into three general patterns. First, the head length and head width variables show a basic similarity, in that those species with longer heads also have wider heads, vice versa. The only notable exception is *C. eleutherodactylus*, which only has a moderately long head, but has one of the widest heads in the sample. A second pattern is comprised of the variables of eye-nostril and eye-eye distances. Again, generally, those species having the greatest eye-nostril distances also have the greatest

eye-eye distances, vice-versa. The two most notable exceptions are *C. ohausi*, which has a moderate eye-nostril to body length relationship, but has the lowest eye-eye to body length relationship, and *C. fuliginosus*, which has a moderately low eye-nostril to body length relationship and a high eye-eye to body length relationship. Third, the femur, tibia, and foot to body length relationship patterns are similar, lacking notable exceptions.

In terms of species, several conclusions can be drawn. First, there is a core of species that all have the same proportional relationships: *C. asper*, *boraceiensis*, *brasilienis*, *diringshofeni*, *duseni*, *lutzorum*, *rhakonastes* and *semipalmatus*. Second, *C. mirandaribeiroi* is distinctive in having consistently high proportional relationships for all variables. Third, *C. bolitoglossus*, *catari-*

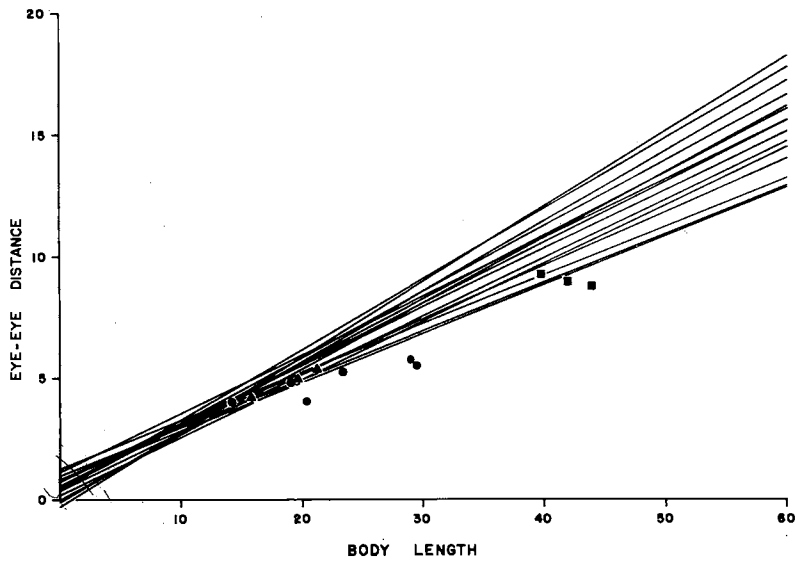


Figure 57. Regression lines of eye-eye distance plotted against body length for 16 species of *Cyclo-ramphus* with individual values for *C. bolitoglossus* (circles), *carvalhoi* (squares), and *diringshofeni* (triangles). A line may represent more than one species.

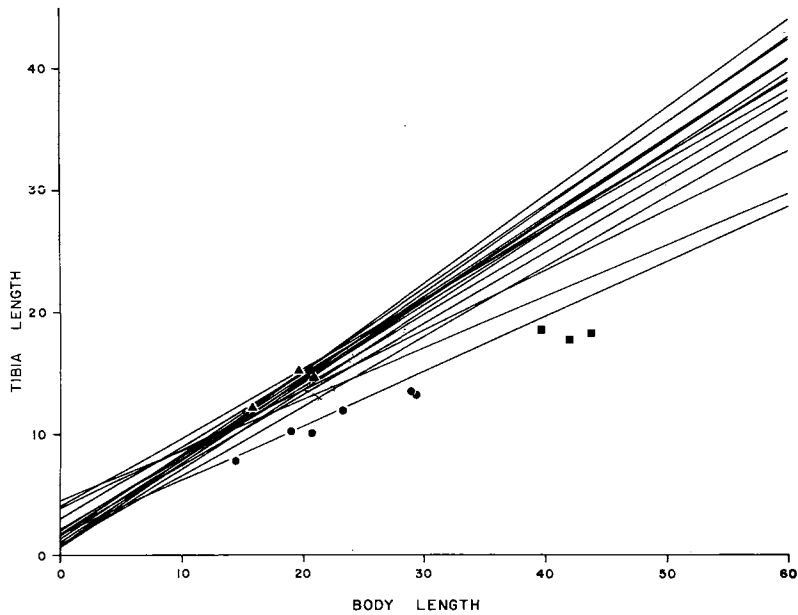


Figure 58. Regression lines of the tibia length plotted against body length for 16 species of *Cyclo-ramphus* with individual values for *C. bolitoglossus* (circles), *carvalhoi* (squares), and *diringshofeni* (triangles). A line may represent more than one species.

Table 19. Rank order (largest to smallest variable values) for each variable at a body length of 60 mm.

Head Length	Head Width	Eye-Nostril	Eye-Eye	Femur	Tibia	Foot
<i>fuliginosus</i>	<i>eleutherodactylus</i>	<i>mirandaribeiroi</i>	<i>mirandaribeiroi</i>	<i>mirandaribeiroi</i>	<i>mirandaribeiroi</i>	<i>mirandaribeiroi</i>
<i>mirandaribeiroi</i>	<i>mirandaribeiroi</i>	<i>dubius</i>	<i>fuliginosus</i>	<i>brasiliensis</i>	<i>dubius</i>	<i>dubius</i>
<i>dubius</i>	<i>fuliginosus</i>	<i>ohausi</i>	<i>dubius</i>	<i>dubius</i>	<i>brasiliensis</i>	<i>eleutherodactylus</i>
<i>semipalmatus</i>	<i>dubius</i>	<i>asper</i>	<i>brasiliensis</i>	<i>fuliginosus</i>	<i>boracelensis</i>	<i>ohausi</i>
<i>lutzorum</i>	<i>semipalmatus</i>	<i>boracelensis</i>	<i>asper</i>	<i>semipalmatus</i>	<i>semipalmatus</i>	<i>boracelensis</i>
<i>ohausi</i>	<i>boracelensis</i>	<i>eleutherodactylus</i>	<i>boracelensis</i>	<i>boracelensis</i>	<i>eleutherodactylus</i>	<i>asper</i>
<i>rhyakonastes</i>	<i>ohausi</i>	<i>lutzorum</i>	<i>duseni</i>	<i>duseni</i>	<i>fuliginosus</i>	<i>semipalmatus</i>
<i>boracelensis</i>	<i>brasiliensis</i>	<i>brasiliensis</i>	<i>eleutherodactylus</i>	<i>eleutherodactylus</i>	<i>duseni</i>	<i>lutzorum</i>
<i>brasiliensis</i>	<i>asper</i>	<i>duseni</i>	<i>lutzorum</i>	<i>granulosus</i>	<i>rhyakonastes</i>	<i>granulosus</i>
<i>stejnegeri</i>	<i>rhyakonastes</i>	<i>rhyakonastes</i>	<i>rhyakonastes</i>	<i>rhyakonastes</i>	<i>lutzorum</i>	<i>rhyakonastes</i>
<i>asper</i>	<i>stejnegeri</i>	<i>fuliginosus</i>	<i>semipalmatus</i>	<i>ohausi</i>	<i>asper</i>	<i>duseni</i>
<i>eleutherodactylus</i>	<i>lutzorum</i>	<i>semipalmatus</i>	<i>granulosus</i>	<i>asper</i>	<i>ohausi</i>	<i>brasiliensis</i>
<i>granulosus</i>	<i>granulosus</i>	<i>stejnegeri</i>	<i>catarinensis</i>	<i>lutzorum</i>	<i>granulosus</i>	<i>fuliginosus</i>
<i>duseni</i>	<i>duseni</i>	<i>catarinensis</i>	<i>valae</i>	<i>catarinensis</i>	<i>valae</i>	<i>stejnegeri</i>
<i>catarinensis</i>	<i>catarinensis</i>	<i>granulosus</i>	<i>stejnegeri</i>	<i>valae</i>	<i>catarinensis</i>	<i>valae</i>
<i>valae</i>	<i>valae</i>	<i>valae</i>	<i>ohausi</i>	<i>stejnegeri</i>	<i>stejnegeri</i>	<i>catarinensis</i>

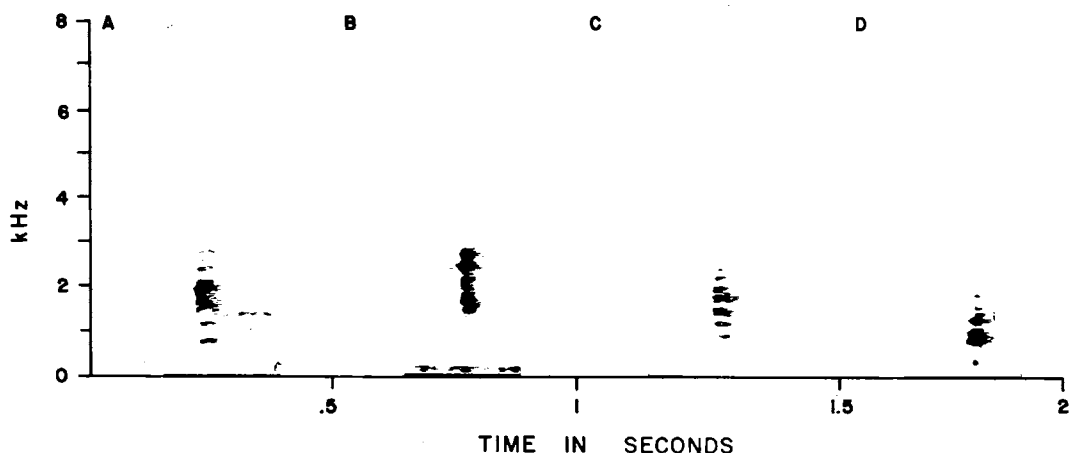


Figure 59. Audiospectrograms of calls of (A) *C. boraceiensis*, (B) *duseni*, (C) *rhyakonastes*, and (D) *semipalmatus*.

*nensis*, and *valae* are distinctive in having consistently low proportional relationships for all variables. Fourth, *C. carvalhoi* and *stejnegeri* have moderate head length and width to body length proportional relationships, but low proportional relationships for the remaining variables. Fifth, the remaining species are distinctive in only one or two variables.

Selection has resulted in changes of both size and shape among species of the genus *Cycloramphus*.

#### ADVERTISING CALLS

Calls have been tape recorded for only

six species. For these six species, there is a common unit to the call: the pulse. The pulse structure appears to maximize location information, perhaps at the expense of species coding information (Heyer and Mello, 1979). Pulses are organized in three ways producing three distinctive call types. In the first, the entire call consists of a single pulse, which is given sporadically. In the second, the call consists of a number of individual pulses; the calls are given sporadically. In the third, the pulses are organized into notes and a call consists of three notes, the first note differing in sound from the second two notes. Calls are given sporadically. These three call types are distinctive (compare Figures 34, 48, 59, and Table 20).

Table 20. Comparison of features of advertising calls for six species of *Cycloramphus*. Call type A = call = note = single pulse; Call type B = call of several pulses; Call type C = call of pulses organized into three notes, the first distinctive from the second and third.

	Call Type	Call Duration in s	Dominant Frequency in Hz		Pulse Modulation
			Range	Peak	
<i>C. boraceiensis</i>	A	.03-.04	500-3500	1700-2300	pulsatile, $\pm$ 400 Hz
<i>C. brasiliensis</i>	C	1.00			
1st note		.43		540	pulsatile, $\pm$ 250-300 Hz
2nd & 3rd notes		.12-.14	1600-1800	1700	pulsatile, $\pm$ 125-200 Hz
<i>C. duseni</i>	A	.02	1400-3000		pulsatile, $\pm$ 300 Hz
<i>C. ohausi</i>	B	1.76	750-1100	910	
individ. pulse		.02	750-1100	910	not pulsatile
<i>C. rhyakonastes</i>	A	.04	1300-2200	1850	pulsatile, $\pm$ 250-350 Hz
<i>C. semipalmatus</i>	A	.03-.04	200-5000	800-1500	pulsatile, $\pm$ 250-300 Hz



Audiospectrograms indicate that either sidebands or harmonics are present in all calls except for *C. ohausi*. In the *C. ohausi* call, the audiospectrograms and oscillographic strip chart recordings indicate that each pulse is made of a single smooth sine wave lacking internal intensity modulation. This suggests that the dominant frequency is the fundamental and is the frequency broadcast. All other calls have indications of sideband or harmonic structure in the audiospectrograms, in the range from 125-400 Hz, with the majority ranging from 250-350 Hz. This suggests that the fundamental frequencies for these calls may actually be these lower frequencies and that harmonics of these frequencies are broadcast. This explanation is consistent with the vocal sac of *Cycloramphus*, which is not large, but rather is an unremarkable expansion of the floor of the mouth. A large expanded vocal sac that is not stretched to its elastic limits is more efficient in coupling low frequencies with the air. A small vocal sac, stretched tightly, can efficiently couple higher frequencies to the air (see Drewry, Heyer, and Rand, 1982, for another example). Thus, the vocal sacs of *Cycloramphus* would be predicted to act as tuned resonators, coupling higher frequencies to the air, but absorbing lower frequencies, including the fundamental produced by the laryngeal apparatus.

The magnitude of differences among the three types of calls analyzed suggests that structural as well as behavioral differences are involved. These kinds of call differences, with attendant differences of production mechanisms, in turn suggest longer term genetic isolation than expected for very closely related species.

In contrast, the differences among the four species analyzed having the single pulse call are of a smaller magnitude. Comparison of the calls (Figure 59, Table 20) indicates broad overlap of call duration and broadcast frequencies. The similarities of audiospec-

trograms suggests that the calls are produced in the same way. There is a difference in intensity modulation among the calls, but the differences are difficult to quantify (Figure 60). The differences among these calls are in fact much smaller than those found among closely related species of frogs in several other genera (for example Straughan and Heyer, 1976 for the genus *Leptodactylus*, and Heyer, 1980, for hylid frogs). Presumably, the kinds of differences evidenced among these four species calls are about the same magnitude as intraspecific differences.

## HABITATS

Few habitat data are available. The following information is presented as a beginning; most observations are from single localities per species where all potential habitat types were not available.

Larval habitats fall into two distinct types. The first is a terrestrial burrow and is used by *C. stejnegeri*, which has terrestrial larvae (Heyer and Crombie, 1979). The second habitat is associated with running water. In all cases, larvae were taken on rocks which were covered with a film of running water, either on exposed rocks in or next to streams (*C. brasiliensis*, *fuliginosus*), or vertical rock wall seeps at quarries or road cuts (*C. boraceiensis*, *duseni*). All of the rock wall seeps that I have examined are man made, but comparable conditions likely occur naturally at certain kinds of waterfalls and/or rock outcroppings with an outflow of ground water.

Juvenile and adult habitats fall into two categories.

In the first, juveniles and adults are found away from running water by day and night. *Cycloramphus eleutherodactylus* has been found under logs and rocks in the forest by day as well as active on the forest floor at night. *Cycloramphus stejnegeri* is

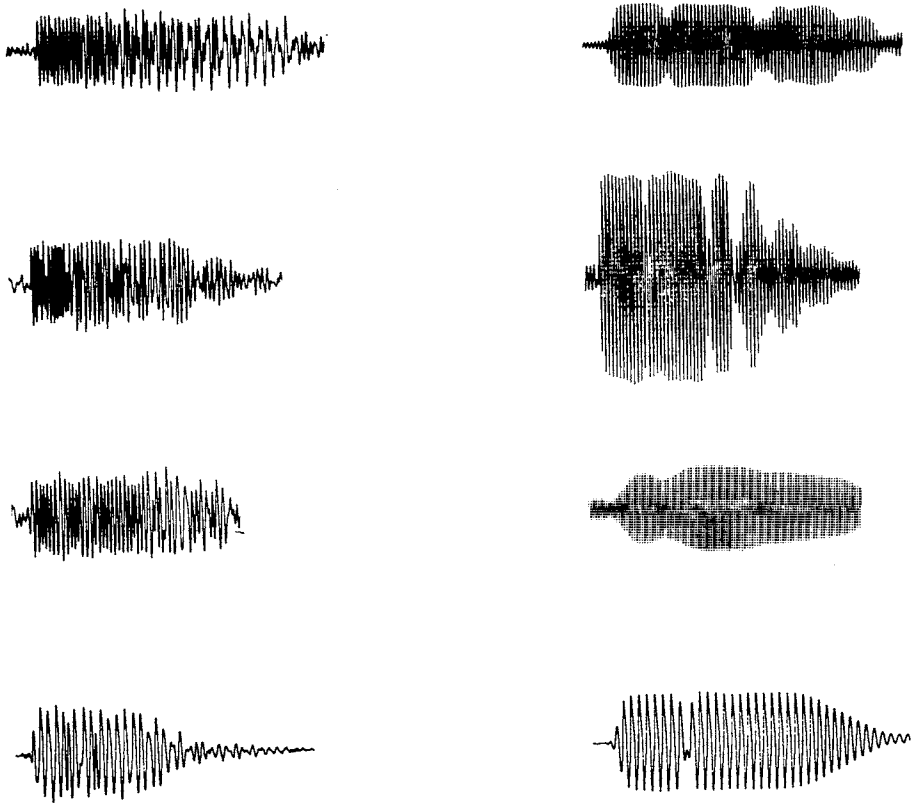


Figure 60. Oscillographic strip chart recordings of, top to bottom, *C. boraceiensis*, *duseni*, *rhyakonastes*, and *semipalmatus*. Because of the amount of background stream noise, the straight analyses (left) are compared with bandpass filtered analyses centering on the maximum energy of the call. From top to bottom on the right, the calls are filtered at 10% bandpass at 1950 Hz, 10% bandpass at 2000 Hz, 1% bandpass at 1900 Hz, and 10% bandpass at 900 Hz. Dark line equals 0.01 s.

associated with burrows in the forest floor, near or far from streams (Heyer and Crombie, 1979).

In the second category, juveniles and adults are associated with running water, essentially either streams, waterfalls, or rock wall seeps. The streams are all small to moderate, rocky streams where the water flow is fast enough that the stream can be heard. No *Cycloramphus* have been taken from large streams or rivers, although few efforts have been made to sample these habitats.

Comparison of the known habitat data (Table 21) suggests the following tentative summaries. First, apparently no species is restricted to the rock wall seep habitat. Second, some species appear to be restricted to either streams or waterfalls. The breakdown in categories is rather artificial, however, as many of the streams in which *Cycloramphus* occur are on hillsides and the drop in elevation results in alternation between a stream and waterfall situation. Third, there is broad overlap in the habitat categories as defined. Further refining of

Table 21. Known occurrences of juveniles and adult *Cycloramphus* species associated with running water among major habitat categories. For stream or waterfall widths, S = small stream, 1 m or less in width, M = moderate streams, 1-4 m in width.

	Rock Wall Seep	Stream	Waterfall	Stream or Waterfall Width
<i>C. asper</i> . . . . .			X	M
<i>C. boraceiensis</i> . . . . .	X	X		M
<i>C. brasiliensis</i> . . . . .	X	X		M
<i>C. dubius</i> . . . . .		X		S
<i>C. duseni</i> . . . . .	X	X		S,M
<i>C. fuliginosus</i> . . . . .		X		S
<i>C. granulosis</i> . . . . .			X	M
<i>C. lutzorum</i> . . . . .			X	S
<i>C. mirandaribeiroi</i> . . . . .		X		M
<i>C. ohausi</i> . . . . .		X		S,M
<i>C. rhyakonastes</i> . . . . .		X		M
<i>C. semipalmatus</i> . . . . .		X		S
<i>C. valae</i> . . . . .	X		X	S

these categories would likely not change the extensive habitat overlap conclusion. At any given locality, someone with previous collecting experience can quite accurately predict which streams will have *Cycloramphus*. Among and within these broad categories, there may be some habitat partitioning.

#### SUMMARY OF INTERSPECIFIC VARIATION

##### Differences Among Species

In some species the interspecific variation appears to be of the same magnitude as intraspecific variation for all of the characteristics examined. These are (1) a group of stream associated species within the *C. fuliginosus* morphological group, (2) *C. diringshofeni* and *eleutherodactylus*, (3) *C. catarinensis* and *valae*, and (4) *C. bolitoglossus*, *carvalhoi*, and *stejnegeri*. At the other extreme, certain species differ from each other by a magnitude much greater than the range of variation found within species. The differences between *C. bolitoglossus* and *ohausi* are pronounced and

must involve considerable genetic differentiation.

Many stream associated *Cycloramphus* are crevice dwellers apparently hiding among rocks and in rock holes and fissures in the day and active near these same places at night. When approached at night, individuals of *C. granulosis*, *lutzorum*, and *valae* often back into crevices about the same size as the frog. A crevice dwelling morphology as represented by *C. valae* (Figures 56-58) with a small head and short limbs is similar in some respects to the shape of the terrestrial burrow associated *C. stejnegeri* (Figures 57, 58). Assuming fossoriality is a derived condition in *Cycloramphus*, the precursor to a fossorial morphology can be found among other non-fossorial *Cycloramphus* species.

The terrestrial species of *Cycloramphus* show about the same range of variation in morphology as the stream associated species. For example, the forest floor *C. diringshofeni* and *eleutherodactylus* differ considerably from the presumably fossorial *C. bolitoglossus*, *carvalhoi*, and *stejnegeri*, but the same kinds of differences are matched

in the stream associated species. The terrestrial *C. eleutherodactylus* has a morphology similar to several members of the stream associated *C. fuliginosus* group. Thus, an adaptive shift in terms of one character (riparian to terrestrial ecology) does not require an accompanying adaptive shift in another character (morphological proportions).

#### Sympatric Occurrences

Comparison of distributions suggests the generalization that a terrestrial species and a stream associated species often occur at the same localities. This generalization is supported by field observations.

Further comment on sympatric occurrences is restricted to those associations which involve more than a single terrestrial and single stream associated species for which I have personal field experience.

Four species of *Cycloramphus* occur at Teresópolis, Rio de Janeiro: *C. brasiliensis*, *eleutherodactylus*, *ohausi*, and *stejnegeri*. Both *C. eleutherodactylus* and *stejnegeri* are terrestrial species. *Cycloramphus eleutherodactylus* is a forest floor species, *C. stejnegeri* is a burrow dweller. The distinctive morphological differences correlate well with the habitat differences. The calls of the two are not available. *Cycloramphus brasiliensis* and *ohausi* are stream associated species. Both occur along the same streams, but *C. brasiliensis* occurs only along the moderate sized streams; *C. ohausi* occurs along both moderate and small streams. Although habitat separation is partial, the morphologies (size, webbing, dorsal texture, dorsal pattern) and calls of these two species are very different.

Boracéia, São Paulo has three species of *Cycloramphus*: *boraceiensis*, *eleutherodactylus*, and *semipalmatus*. The two stream associated species have similar calls (also see Heyer and Mello, 1979), but differ in terms of webbing, dorsal texture, and habitat. At Boracéia, the habitat separation is

striking, with *C. semipalmatus* found along small streams and *C. boraceiensis* at rock wall seeps.

The Cubatão-Paranapiacaba area of São Paulo also commonly has three *Cycloramphus*: *dubius*, *eleutherodactylus*, and *semipalmatus*. The call of *C. dubius* is not available for detailed comparison, but sounds similar to *semipalmatus* in the field. There is no habitat separation between these two species; both occur along the same streams. The two species differ in terms of webbing and dorsal texture.

Two species of stream dwelling *Cycloramphus* occur near Morretes, Paraná: *mirandaribeiroi* and *rhyakonastes*. Both species occur together in the larger streams, only *rhyakonastes* occurs in the smaller streams. The *C. rhyakonastes* call from rocks in or next to the stream. A single *mirandaribeiroi* was heard (but not recorded) calling from the ground two meters from the stream bed. The call sounded similar to the call of *rhyakonastes*, but perhaps with a lower dominant frequency. The two species differ in terms of webbing, dorsal texture, belly color, and partially differ in size.

There are no universal patterns of species differentiation and sympatric occurrence. Stream associated species differ in calls at some places but not others; habitat in some places, but not others, etc. The kinds and degrees of differences among species appear to be geographically specific.

#### Possible Premating Isolating Mechanisms

Pattern is an effective visual premating isolating mechanism in some groups of frogs (Straughan, 1966). The dorsal and belly patterns of most of the *Cycloramphus* species are so similar that these pattern differences are likely not involved in premating isolating mechanism coding features. The most likely patterns functioning as visual

preparing isolating mechanisms are the discrete light lip stripes and discrete light spots on the posterior surface of the thighs in some *Cycloramphus*. Both pattern types apparently carry little or no species coding information in *Cycloramphus*, however. Intraspecific variation in these states is as great for some species as between species. There are no known sympatric instances where one species of *Cycloramphus* invariably has one pattern state and a second species has a contrasting state. In fact, the opposite is true in the case of thigh spots. Most species do not have distinct thigh spots, so one might expect that if one species of a sympatric pair has thigh spots, the second would lack spots. Around Morretes, Paraná, two species occur sympatrically, both of which are characterized by having distinct light thigh spots.

Toe webbing is qualitatively different among several sympatric species, but it seems more likely that the webbing differences relate to ecological adaptations rather than function as a preparing isolating mechanism in a visual or tactile sense.

Size differences would act as preparing isolating mechanisms in some, but not all cases of sympatry.

Habitat differences and effectiveness as preparing isolating mechanisms range from non-existent, to partial, to complete for sympatric species.

Advertising calls are qualitatively different for some sympatric species and only quantitatively different for others. Although advertising calls should serve as very effective preparing isolating mechanisms for some species, the calls must be only partially effective in others (also see Heyer and Mello, 1979).

The only consistent differences observed among all cases of sympatry are differences of webbing (already discussed) and dorsal texture. The differences in dorsal texture among sympatric species are discrete and

qualitatively different and may function as tactile cues for species identification.

To summarize, it appears that no one preparing isolating mechanism is totally effective among all species of *Cycloramphus*. Rather several preparing isolating mechanisms apparently function among sympatric species, each of which may be partially effective by itself, but which are totally effective only in combination with each other.

## References

- Agassiz, L. 1847 Nomenclatoris zoologici index universalis continens nomina systematica classium, ordinum, familiarum et generum animalium omnium . . . . Soloduri. 393 pp.
- Ahl, E. 1924. Über eine neue Cystignathiden-Gattung. Zoologischer Anzeiger, 58:107-108.
- Andersson, L. G. 1914. A New *Telmatobius* and new Teiidoid lizards from South America. Arkiv för Zoologi, 9:1-12.
- Bokermann, W. C. A. 1951. Sinopse das espécies brasileiras do gênero *Cycloramphus* Tschudi, 1838 (Amphibia, Salientia-Leptodactylidae). Arquivos do Museu Nacional, Rio de Janeiro, 42:77-106.
- Bokermann, W. C. A. 1957. Sobre uma nova espécie de "*Cycloramphus*" do Estado de Santa Catarina, Brasil. Revista Brasileira de Biologia, 17:249-252.
- Bokermann, W. C. A. 1966. Lista anotada das localidades tipo de anfíbios brasileiros. Serviço de Documentação, São Paulo. 183 pp.
- Boulenger, G. A. 1907. Description of a new frog of the genus *Telmatobius* from Brazil. Annals and Magazine of Natural History, ser. 7, 19:394.
- Braun, P. C. and C. A. S. Braun. 1980. Lista prévia dos anfíbios do Estado do Rio Grande do Sul, Brasil. Iheringia, 56:121-146.
- Cochran, D. M. 1955. Frogs of southeastern Brazil. United States National Museum Bulletin, 206:1-423.
- Cope, E. D. 1867. On the families of the Raniform Anura. Journal of the Academy of Natural Sciences, Philadelphia, 1867, part II:189-206.

- Dixon, W. J., series editor. 1977. Biomedical computer programs P-series. Berkeley: University of California Press. 880 pp.
- Drewry, G. E., W. R. Heyer, and A. S. Rand. 1982. A functional analysis of the complex call of the frog *Physalaemus pustulosus*. *Copeia*, 1982(3):636-645.
- Duméril, A. M. C. and G. Bibron. 1841. *Erpétologie générale ou histoire naturelle complète des reptiles*. Vol. 8. Paris: Librairie Encyclopédique de Roret. 784 pp.
- Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, 16:183-190.
- Günther, A. 1859. Catalogue of the Batrachia Salientia in the collection of the British Museum. London: Taylor and Francis. 160 pp. + 12 plates.
- Hecht, M. K. and J. L. Edwards. 1976. The determination of parallel or monophyletic relationships: The proteid salamanders — a test case. *The American Naturalist*, 110:653-677.
- Heyer, W. R. 1975. A preliminary analysis of intergeneric relationships of the frog family Leptodactylidae. *Smithsonian Contributions to Zoology*, 199:1-55.
- Heyer, W. R. 1977. A discriminant function analysis of the frogs of the genus *Adenomera* (Amphibia: Leptodactylidae). *Proceedings of the Biological Society of Washington*, 89:581-592.
- Heyer, W. R. 1978. Systematics of the *fuscus* group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). *Natural History Museum of Los Angeles County, Science Bulletin*, 29: 1-85.
- Heyer, W. R. 1980. The calls and taxonomic positions of *Hyla giesleri* and *Oloolygon opalina* (Amphibia, Anura, Hylidae). *Proceedings of the Biological Society of Washington*, 93:655-661.
- Heyer, W. R. and R. I. Crombie. 1979. Natural history notes on *Craspedoglossa stejnegeri* and *Thoropa petropolitana* (Amphibia: Salientia, Leptodactylidae). *Journal of the Washington Academy of Sciences*, 69:17-20.
- Heyer, W. R. and D. S. Liem. 1976. Analysis of the intergeneric relationships of the Australian frog family Myobatrachidae. *Smithsonian Contributions to Zoology*, 233:1-29.
- Heyer, W. R. and C. C. Mello. 1979. Descriptions of the advertising calls of *Cycloramphus asper* and *Cycloramphus dubius* (Amphibia: Leptodactylidae). *Papéis Avulsos de Zoologia, São Paulo*, 32:193-200.
- International Code of Zoological Nomenclature. 1964. International code of zoological nomenclature adopted by the XV International Congress of Zoology. International Trust for Zoological Nomenclature. 176 pp.
- Lutz, A. 1928. Biologie et métamorphose des Batraciens du genre *Cyclorhamphus*. *Comptes rendus des séances de la Société de Biologie*, 98:640.
- Lutz, A. 1929. Taxonomia e biologia do genero *Cyclorhamphus*. *Memorias do Instituto Oswaldo Cruz*, 22:5-16 (Portuguese), 17-25 (English) + 5 plates.
- Lutz, A. 1932. Uma nova espécie de *Cyclorhamphus*. *Memorias do Instituto Oswaldo Cruz*, 26:71-73 (Portuguese), 74-76 (English) + plate 32.
- Lutz, B. 1944. Biologia e taxonomia de *Zachaenus parvulus*. *Boletim do Museu Nacional, Zoologia*, 17:1-66.
- Lynch, J. D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactylid frogs. *University of Kansas Museum of Natural History Miscellaneous Publication*, 53:1-238.
- Maxson, L. R., W. R. Heyer and R. D. Maxson. 1981. Phylogenetic relationships of the Brazilian leptodactylid frog genera *Craspedoglossa*, *Cycloramphus*, and *Zachaenus*. *Experientia*, 37:144-145.
- Miranda-Ribeiro, A. 1920. O gênero *Telmatobius* já foi constatado no Brasil? *Revista do Museu Paulista*, 12:261-278 + 6 plates.
- Miranda-Ribeiro, A. 1926. Notas para servirem ao estudo dos Gymnobatrachios (Anura) brasileiros. Tomo primeiro. *Arquivos do Museu Nacional, Rio de Janeiro*, 27:1-227 + 22 plates.
- Miranda-Ribeiro, A. 1929. *Cycloramphus*, *Grypiscus* e *Iliodiscus*. *Boletim do Museu Nacional, Rio de Janeiro*, 5:5-19 (Portuguese), 20-34 (English) + one page addenda.
- Miranda-Ribeiro, A. 1935. *Cycloramphus*, *Grypiscus* e *Iliodiscus* e as leis de prioridade. *Revista do Museu Paulista*, 19:399-416 + 3 plates.
- Müller, L. 1922. Über eine Sammlung Froschlurche von Sta. Catarina nebst Beschreibung zweier neuer Arten. *Blätter für Aquarien- und Terrarienkunde*, 33:167-171.
- Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. *Statistical package for the social sciences*. Second edition. New York: McGraw-Hill Book Company. 675 pp.

- Nieden, F. 1923. Anura I. Subordo Aglossa und Phaneroglossa Sectio I Arcifera. Das Tierreich, 46:1-584.
- Noble, G. K. 1924. Some Neotropical batrachians preserved in the United States National Museum with a note on the secondary sexual characters of these and other amphibians. Proceedings of the Biological Society of Washington, 37:65-72.
- Noble, G. K. 1926. An analysis of the remarkable cases of distribution among the Amphibia, with descriptions of new genera. American Museum Novitates, 212:1-24.
- Papavero, N. 1971. Essays on the history of Neotropical Dipterology, with special reference to collectors (1750-1905). Vol. I. Empresa Gráfica da Revista dos Tribunais S.A., São Paulo. 216 pp.
- Regal, P. J. and C. Gans. 1976. Functional aspects of the evolution of frog tongues. Evolution, 30:718-734.
- Savage, J. M. and W. R. Heyer. 1967. Variation and distribution in the tree-frog genus *Phyllomedusa* in Costa Rica, Central America. Beitrage zur Neotropischen Fauna, 5:111-131.
- Savage, J. M. and W. R. Heyer. 1969. The tree-frogs (Family Hylidae) of Costa Rica: diagnosis and distribution. Revista de Biología Tropical 16:1-127.
- Steindachner, F. 1864. Batrachologische Mitteilungen. Verhandlungen der Kaiserlich-königlichen Zoologisch-Botanischen Gesellschaft in Wien, 14:239-288 + 9 plates.
- Straughan, I. R. 1966. An analysis of species recognition and species isolation in certain Queensland frogs. Part 2. Species isolation. PhD. dissertation, University of Queensland, 80 pp.
- Straughan, I. R. and W. R. Heyer. 1976. A functional analysis of the mating calls of the Neotropical frog genera of the *Leptodactylus* complex (Amphibia, Leptodactylidae). Papéis Avulsos de Zoologia, São Paulo 29:221-245.
- Tschudi, J. J. 1838. Classification der Batrachier, mit Berücksichtigung der fossilen Thiere dieser Abtheilung der Reptilien. Neuchâtel. 102 pp + 6 plates.
- Wandolleck, B. 1907. Einige neue und weniger bekannte Batrachier von Brasilien. Abhandlungen und Berichte des Königl. Zoologischen und Anthropologisch-Ethnographischen Museums zu Dresden, 11:1-15 + 1 plate.
- Werner, F. 1897. Über einige noch unbeschriebene Reptilien und Batrachier. Zoologischer Anzeiger, 20:261-267.
- Werner, F. 1899. Beschreibung neuer Reptilien und Batrachier. Zoologischer Anzeiger, 22:479-484.

Appendix 1. List of skeletal material examined. CS = cleared and stained; no designation = dry skeleton.

- Cycloramphus bolitoglossus*, USNM 125492 (CS)
- C. boraceiensis*, MZUSP 4541
- C. brasiliensis*, KU 92807, MZUSP 155
- C. dubius*, KU 92780
- C. eleutherodactylus*, KU 92785
- C. fuliginosus*, KU 92790-91, MZUSP 3625,9850
- C. granulosus*, KU 92795 (CS)
- C. ohausi*, KU 92801 (CS), MZUSP 65
- C. semipalmatus*, KU 92773, MZUSP 3436
- C. stejnegeri*, KU 92742 (CS) 92747
- Zachaeus parvulus*, KU 93082 (CS), 107090 (CS), 107091.

Appendix 2. Gazetteer of *Cycloramphus* localities. Alphabetized by specific localities. Order is specific locality; state; approximate latitude and longitude.

- Alto da Serra (= Paranapiacaba); São Paulo; 23 47 S, 46 19 W.
- Apiaiá; São Paulo; 24 31 S, 48 50 W.
- Araraquara, Serra de; Paraná; 25 53 S, 48 50 W.
- Banhado; Paraná; 25 29 S, 49 00 W.
- Barro Branco; Rio de Janeiro; 22 35 S, 43 15 W.
- Blumenau; Santa Catarina; 25 56 S, 49 03 W.
- Bonito, Serra da Bocaina; São Paulo; 22 46 S, 44 35 W.
- Boracéia; São Paulo; 23 38 S, 45 50 W.
- Brejo da Lapa, Alto Itatiaia; Rio de Janeiro; 22 22 S, 44 44 W.
- Búzios, Ilha dos; São Paulo; 23 48 S, 45 08 W.

- Campo Belo; Rio de Janeiro; 22 30 S, 44 34 W.
- Campo Grande (= Campo Grande da Serra); São Paulo; 23 46 S, 46 21 W.
- Campo Grande da Serra; São Paulo, 23 46 S, 46 21 W.
- Campos do Jordão; São Paulo; 22 44 S, 45 35 W.
- Caraguatatuba, Serra de, road from Caraguatatuba — S. Sebastião; São Paulo; 23 45 S, 45 27 W.
- Colônia Hansa, Joinville (= Corupá); Santa Catarina; 26 18 S, 48 50 W.
- Corcovado, Paineiras; Rio de Janeiro; 22 57 S, 43 13 W.
- Córrego Mãe d'Água, Serra da Bocaina; São Paulo; 22 46 S, 44 35 W.
- Corupá; Santa Catarina; 26 26 S, 49 14 W.
- Cubatão, Alto da Serra de; São Paulo; 22 28 S, 45 15 W.
- Engenheiro Ferraz; São Paulo; 23 59 S, 46 36 W.
- Eugenio Lefèvre; São Paulo; 22 49 S, 45 38 W.
- Fazenda do Veado, Serra da Bocaina; São Paulo; 22 49 S, 44 39 W.
- Grande, Ilha; Rio de Janeiro; 23 09 S, 44 30 W.
- Grande, Rio; São Paulo; 23 47 S, 46 37 W.
- Gruta, município de Lauro Müller, 20 km E Bom Jardim on road to Lauro Müller; Santa Catarina; 28 28 S, 49 33 W.
- Guapi, Rio de Janeiro; 22 32 S, 42 59 W.
- Humboldt (= Corupá); Santa Catarina; 26 26 S, 49 14 W.
- Ilha dos Búzios; São Paulo; 23 48 S, 45 08 W.
- Ilha Grande; Rio de Janeiro; 23 09 S, 44 30 W.
- Ilha São Sebastião; São Paulo; 23 46 S, 45 20 W.
- Independência, Petrópolis; Rio de Janeiro; 22 31 S, 43 10 W.
- Ipiranga; Paraná; 25 01 S, 50 35 W.
- Iporanga; São Paulo; 24 35 S, 48 35 W.
- Itaguaí; Rio de Janeiro; 22 52 S, 43 47 W.
- Itatiaia, Vale do Paraíba; Rio de Janeiro; 22 30 S, 44 34 W.
- Joinville, Santa Catarina; 26 18 S, 48 50 W.
- Juquiá, 8 km N; São Paulo; 24 18 S, 47 37 W.
- Macaé, Serra de; Rio de Janeiro; 22 10 S, 41 50 W.
- Macieiras, Est. de, km 10, Parque Nacional Itatiaia; Rio de Janeiro; 22 25 S, 44 38 W.
- Mãe d'Água, Córrego, Serra da Bocaina; São Paulo; 22 46 S, 44 35 W.
- Mangaratiba, Serra de; Rio de Janeiro; 22 57 S, 44 02 W.
- Maromba, Rio de Janeiro; 22 25 S, 44 38 W.
- Marumbi, Rio Taquaral em, Serra do Mar na estrada de ferro de Curitiba; Paraná; 25 38 S, 48 42 W.
- Morretes; Paraná; 25 28 S, 48 49 W.
- Nova Friburgo; Rio de Janeiro; 22 16 S, 42 32 W.
- Novo Friburgo (= Nova Friburgo); Rio de Janeiro; 22 16 S, 42 32 W.
- Novo, Rio (= Corupá); Santa Catarina; 26 26 S, 49 14 W.
- Ouro Preto; Minas Gerais; 20 23 S, 43 30 W.
- Paranapiacaba; São Paulo; 23 47 S, 46 19 W.
- Parati; Rio de Janeiro; 23 13 S, 44 34 W.
- Paraty (= Parati); Rio de Janeiro; 23 13 S, 44 34 W.
- Petrópolis; Rio de Janeiro; 22 31 S, 43 10 W.
- Petrópolis; (probably = Theresópolis = Queçaba); Santa Catarina; 27 44 S, 48 56 W.
- Pico da Bandeira; Espírito Santo; 20 26 S, 41 47 W.
- Pirabeiraba, 13-17 km W; Santa Catarina; 26 12 S, 49 07 W.
- Piraguara-Realengo, Represa; Rio de Janeiro; 22 52 S, 43 26 W.
- Queçaba; Santa Catarina; 27 44 S, 48 56 W.
- Realengo; Rio de Janeiro; 22 52 S, 43 26 W.
- Realengo-Piraguara, Represa; Rio de Janeiro; 22 52 S, 43 26 W.
- Represa Piraguara-Realengo; Rio de Janeiro; 22 52 S, 43 26 W.
- Rio de Janeiro; Rio de Janeiro; 22 48 S, 43 22 W.



- Rio Grande (= Rio Grande da Serra); São Paulo; 32 47 S, 46 37 W.
- Rio Grande da Serra; São Paulo; 23 47 S, 46 37 W.
- Rio Novo (= Corupá); Santa Catarina; 26 26 S, 49 14 W.
- Rio Taquaral em Marumbi, Serra do Mar na estrada de ferro de Curitiba; Paraná 25 38 S, 48 42 W.
- Rio do Testo; Santa Catarina; 26 45 S, 49 11 W.
- Rio Vermelho; Santa Catarina; 26 17 S, 49 20 W.
- Santa Teresa; Espírito Santo; 19 55 S, 40 36 W.
- Santo Amaro da Imperatriz, 40 km from, on road to São Bonifácio (between Queçaba and São Bonifácio); Santa Catarina; 27 52 S, 48 57 W.
- Santos; São Paulo; 23 53 S, 46 28 W.
- São Bento (= São Bento do Sul); Santa Catarina; 26 16 S, 49 23 W.
- São Bonifácio, on road to, 40 km from Santo Amaro da Imperatriz (between Queçaba and São Bonifácio); Santa Catarina; 27 52 S, 48 57 W.
- São João da Graciosa. 9-16 km W, on PR 410 to Curitiba; Paraná; 25 21 S, 48 53 W.
- São Paulo — Santos old road, km 47; São Paulo; 23 42 S, 46 27 W.
- São Sebastião, Ilha; São Paulo; 23 46 S, 45 20 W.
- Serra Alta, Município de, (São Bento do Sul), córrego na região Rio Vermelho, Serra do Mar; Santa Catarina; 26 16 S, 49 23 W.
- Serra de Araraquara; Paraná; 25 53 S, 48 50 W.
- Serra de Caraguatatuba, road from Caraguatatuba — S. Sebastião; São Paulo; 23 45 S, 45 27 W.
- Serra de Cubatão, Alto da; São Paulo; 22 28 S, 45 15 W.
- Serra de Macaé; Rio de Janeiro; 22 10 S, 41 50 W.
- Serra de Mangaratiba; Rio de Janeiro; 22 57 S, 44 02 W.
- Serra da Subida, caminho de Blumenau a Lages; Santa Catarina; 27 06 S, 49 27 W.
- Subida, Serra da, caminho de Blumenau a Lages; Santa Catarina; 27 06 S, 49 27 W.
- Sumaré; Rio de Janeiro; 22 48 S, 43 32 W.
- Taquaral, Rio, em Marumbi, Serra do Mar na estrada de ferro de Curitiba; Paraná; 25 38 S, 48 42 W.
- Teresópolis; Rio de Janeiro; 22 26 S, 42 59 W.
- Testo, Rio do; Santa Catarina; 26 45 S, 49 11 W.
- Theresópolis (= Queçaba); Santa Catarina; 27 44 S, 48 56 W.
- Tijuca; Rio de Janeiro; 22 48 S, 43 32 W.
- Timbó; Santa Catarina; 26 50 S, 49 18 W.
- Tinguá, Serra Vilna; Rio de Janeiro; 22 36 S, 43 26 W.
- Vermelho, Rio; Santa Catarina; 26 17 S, 49 20 W.
- Volta Grande; Paraná; 25 15 S, 49 05 W.
- Voturuá; São Paulo; 23 58 S, 46 23 W.
- Ypiranga (= Ipiranga); Paraná; 25 01 S, 50 35 W.