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FROGS OF BORACÉIA

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A cassette recording of frog calls from Boracéia is available for $ 5.00 US, including postage. Send checks or postal money orders made out to "Smithsonian Institution." Send order and payment to:

Frogs of Boracéia Tape
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Notes Added in Proof

The Boracéia population of frogs identified as *Hyla albofrenata* throughout the text has been shown to be *Hyla arildae* Cruz and Peixoto (Espécies verdes de *Hyla*: o complexo "Albofrenata" (Amphibia, Anura, Hylidae). Arq. Univ. Fed. Rural, Rio de Janeiro, 8 (1-2) : 59-70, 1985 [published in 1987]).

After the manuscript was submitted, Altig and Johnston developed a generalized scheme of tadpole guilds (Guilds of anuran larvae: Relationships among developmental modes, morphologies, and habitats. Herpetological Monographs, 3: 81-109, 1989). Had this scheme been available to us, we would have used it. As it is, the tadpole guilds recognized in this paper can be placed readily in their system.

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CONTENTS

INTRODUCTION

The "Estação Biologica de Boracéia" was established in 1954 (Travassos and Camargo, 1958) within the Departamento de Zoologia da Secretaria da Agricultura do Estado de São Paulo (now the Museu de Zoologia of the Universidade de São Paulo [MZUSP]). The station, which is surrounded by forested watershed, had formerly been a field site where studies were conducted on growing of cinchona for the production of quinine. The first collections from the station site to be deposited in a museum were made in 1946. Since that time, several herpetologists have worked at the station and a fine collection has been amassed over the years.

The first and most extensive collections were made by P.E. Vanzolini and Werner C.A. Bokermann in the late 1940s and early 1950s. These collections at the MZUSP form the nucleus of the data base that made our studies possible.

A. Stanley and Patricia Rand, then working at the museum in São Paulo, studied the ecology of the frogs of Boracéia during the period of December 1962 through August 1964. They worked the site on an almost monthly basis, concentrating on where the frogs occurred and what they were doing. The voucher specimens are deposited in the MZUSP. A. S. Rand revisited Boracéia in 1983 and 1984.

As part of the International Biological Program, Craig E. Nelson undertook a project to determine the relationship between niche breadth and genetic variation of the frogs at Boracéia with (then) two students, G. Bruce Williamson and Gene Miller. Williamson and Miller were in residence at Boracéia from November 1971 through April 1972. Nelson worked with them at Boracéia in February 1972 and returned (with Sharon and Laura Nelson) from October to december 1972. They collected a body of natural history data, organized the available MZUSP collection data on the frogs from Boracéia, and prepared a preliminary annotated checklist of the frogs of Boracéia. The niche breadth and genetic variation studies have not been published.

W. Ronald Heyer (often with Miriam, Laura, and Elena Heyer) worked the station at intervals from 1975 to the present. The vouchers from these trips are mostly in the USNM (National Museum of Natural History, Smithsonian Institution) collection.

Two other herpetologists have visited the site, making collections associated with their studies. Charles W. Myers worked the station in late February and early March of 1979. The voucher specimens are at the AMNH (American Museum of Natural History). James P. Bogart (with Jo Ellen Bogart) worked at the station in November 1969. His vouchers are in the TNHC (Texas Natural History Collections, Austin) collections.

There have been three others who have added to our knowledge of the frogs of Boracéia through more or less consistent, incidental collecting. Ernesto Rabello (who collected insects), Gertrude Rita Kloss (who studied parasites of amphibians and arthropods) and Francisca Carolina do Val (who studies *Drosophila*) have been administrative officers for Boracéia. Part of their responsibilities include monthly trips to the station. During those trips, they and others accompanying them would collect frogs, particularly any that seemed unusual to them.

These combined field efforts have resulted in an extensive data base for the frogs of Boracéia. The importance of summarizing the accumulated data on the Boracéia frogs has been recognized for many years. At one time, A.S. Rand was planning to publish a summary, based mostly on his field notes. Later, Nelson suggested to Rand that they combine their data to produce a summary. These efforts did not reach fruition. Finally, Heyer proposed a two-step solution that led to this publication. First, all available data were assembled to determine what kinds of data were available and what data were missing. Second, we combined forces with (then) MZUSP graduate students Carlos Alberto Gonçalves da Cruz and Oswaldo L. Peixoto to undertake three additional field seasons of work to fill in as much of the missing data as possible. The field work was concluded in December 1984, 30 years after the station was officially established.

The purpose of this report is to summarize our knowledge of the frogs of Boracéia. This effort represents the first in-depth site analysis of a frog fauna for the entire Atlantic Forest Morphoclimatic Domain of Brasil.

Work at Boracéia

Boracéia has been and remains important because it is logistically easy to work, and although habitats are protected from destruction, careful collecting is permitted. The frog fauna has been sampled repeatedly as new techniques became available that required fresh material. Boracéia has become a reference site for anyone wishing to study the rich endemic frog fauna of the Atlantic Forests of Brasil. In the late 1940s, faunal surveys were initiated and specimens were collected and preserved in alcohol. In the early 1960s, surveys stressed ecological distributions. In the mid 1970s, the Bogarts collected material for the study of chromosomes and Nelson and associates gathered samples for electrophoretic analyses, collected some specimens, and recorded calls. In the late 1970s, Heyer recorded vocalizations and increased sample sizes of museum series and Myers and Daly obtained specimens for the study of skin toxins. In the early 1980s, Cruz and Peixoto concentrated on tadpoles, and Heyer and Maxson collected blood for immunological studies. Techniques now being devoloped and others not yet even thought of will surely be applied to the frogs of Boracéia. Our hope is that this paper will facilitate future studies.

The Fauna

The frog fauna of Boracéia, like that of the rest of the Neotropics, is dominated by hylids and leptodactylids, with a conspicuous but not speciose bufonid element. Unlike much of the Neotropics there are no dendrobatids and only one, rare, microhylid. There are several genera, particularly leptodactylids, that are endemic to the Atlantic Forest and breed in bromeliads, on land or in mountain streams.

The Site

Boracéia is located in the State of São Paulo, about 80 km E of the city of São Paulo, at about 23° 38'S latitude, 45° 52'W longitude. Boracéia is about 900 m above sea level in the Serra do Mar, and about 12 km from the Atlantic coast. It lies in the Atlantic Forest Morphoclimatic Domain (Figure 1); morphoclimatic domains, determined by geomorphological techniques, are defined by the superposition of relief, soil, drainage, climatic and vegetation features (Ab'Sáber, 1977).

The coast adjacent to Boracéia runs east and west. The coastal plain is narrow (ca. 7 km wide), bordered by a steep escarpment rising in 2-3 km to a hilly plateau (ca. 900 m) that slopes gradually to the north. Boracéia sits on the crest of the escarpment. Local relief on the plateau is about 100 m from hilltop to river bed. The escarpment is drained by a series of short steep streams that flow directly into the Atlantic. The plateau is drained by a more complex system of streams that drain north to the Rio Tiete and west, eventually to the Paraná. Boracéia is on the divide between two small rivers: the Rio Claro, which drains to the Rio Tiete, and the Rio Guaratuba, which drains directly into the Atlantic. Many of the larger streams in this area have been dammed to act as reservoirs for the water supply for the city of São Paulo.

The Estação Biológica de Boracéia is in a 16,450 ha reserve of the Departamento de Águas e Esgotos (Travassos and Camargo, 1958). Access to Boracéia is via a dirt road that passes a manned gate house at the water treatment plant at Casa Grande about 7 airline km to the west of Boracéia; the road ends at a reservoir (Represa Ribeirão do Campo) perhaps 5 airline km more to the west. The distances by road are substantially more.

The soil is sandy, with a top layer of 10-15 cm of brown soil and on top of that a thin layer of dead leaves scattered with many dead branches and logs. The forest floor surface is usually damp, often soaking wet, and (at least on our visits) even at its driest, it was damp underneath logs.

The area is among the wettest in Brazil. It gets much rain (the average annual rainfall from 1925-1944 was 3058 mm, [Setzer, 1946], Figure 2) and much moisture as fog. The prevailing wind is from the south, where it originates over

the sea and, as it is pushed up over the escarpment, water condenses as fog or fine rain. The crest of the escarpment where Boracéia is located gets more moisture than the coastal plain or the plateau farther inland. A typical (but not necessarily average) day at Boracéia dawns clear; after an hour or two of sun, the clouds roll in from the south bringing first fog and then rain. The afternoon characteristically is rainy; the rain often stops about sunset and by midnight the sky is clear. Although this is the typical weather pattern, there may be several days without rain or with continuous rain. Generally the period from November through January is warm and wet, the period from May through August is cooler and drier (Figure 2). The other months are quite variable and commonly do not demonstrate a smooth transition between the two major seasons (Figure 2). Temperatures below freezing occur occasionally at Boracéia. Most frosts apparently have few long-term effects on the herpetofauna, although as we have argued elsewhere (Heyer, Rand, Cruz and Peixoto, 1988) the frost of 1979 seems to have resulted in a major reduction in populations of many species.

The coastal plain is largely cultivated, whereas the escarpment and the adjacent portion of the plateau are largely forested because they serve as a catchment area for the water supply to São Paulo. This strip of forest about 10 km wide extends for at least 100 km along the coastal espcarpment.

Access to the reserve is limited to the employees of the Departamento de Águas e Esgotos and visitors to the Estação Biológica de Boracéia. Human trails and tracks show that there is some fishing, particularly in the reservoirs upstream. The high occurrence of tapir tracks, particularly in 1983 and 1984, argues that little hunting occurs. The number of edible palms visible along the road and elsewhere indicates little tree theft.

The forest around Boracéia is continuous except for the breaks formed by the narrow dirt access road, the aqueduct line, several small rivers and the small man-made clearings around the station itself (Figure 3). Though the elevation is low, the topography, wind, high moisture and vegetation have combined to produce a mist forest or cloud forest. The forest has a low, continuous canopy, averaging ca. 5-10 m, highest in the valley bottoms so that the canopy smooths the topography. The forest contains one tree and one bush layer or stratum but the distinction is not marked. The few emergents are mostly palms. There are some trees with buttresses or stilt roots, but not many. Complexes of horizontal moss-covered roots, a few decimeters above the ground, are more conspicuous and characteristic, particularly along the trails (where they may have been created by erosion). The undergrowth is relatively open in most of the forest, but denser along the streams with herbaceous plants including heliconias. One cannot walk far in a straight line, but by detouring around trees and bushes, it is necessary to cut only an occasional vine or climbing bamboo tangle. Slender climbing bamboos are common, as well as several larger species (one *Merostachys* reaching ca. 10 cm in diameter). These large bamboos grow in clumps and flowered simultaneously in the 1970s. There are many palms of several species. *Euterpe edulis* is a conspicuous part of the canopy. Tree ferns and climbing vines are also common, mostly small with many hanging roots of philodendrons; large lianas are rare. Epiphytic mosses of several varieties are conspicuous features, growing on branches, roots, twigs and even old leaves as well as on rocks and logs. Only rarely do mosses form a carpet on the ground. Bromeliads, including some very large ones, grow everywhere — tree, branches and trunks as well as on the ground (Color Figure 1). There are many orchids and epiphytic ferns. Strangler figs occur but not conspicuously. Mistletoe is common. Lichens grow on everything. On many trees the bark is completely covered with epiphytes. Tree trunks tend to be canted from the vertical and are often bent, and usually branch close to the ground; columnar trunks without low branches are not common.

The station's buildings sit in a clearing of about 60,000 sq meters (Figure 3). This clearing was a grassy pasture in 1963-64. By 1971-72 most of the area south of the road except in the immediate vicinity of the buildings was covered by low thickets of second growth as was the area north of the road and to the east of the scientists' residence. In contrast, the cleared area north of the road and west of the scientists' residence was being maintained as a "pasture," despite the

absence of livestock, by frequent cutting. Similar cuttings maintained yards around the buildings. By 1983 the pasture had grown up into young second growth. At times, a small stream in the clearing has been dammed with boards to form a pond (during Nelson's and Heyer's visits in the 1970s it was present; the dam had been removed by our visits in the 1980s). A second, small earthen dammed pond was also present in the pasture in 1971-72. When these ponds were present, such frogs as *Hyla polytaenia* and *Ololygon hayii* reproduced in them. The marsh adjacent to and below the second pond was also occupied by *Leptodactylus fuscus*. An aqueduct parallels the road and the river; it carries water nearly 10 km from the reservoir to the treatment plant at Casa Grande. A strip (perhaps 20 m wide) above the mostly buried aqueduct is cleared regularly, so that it is always very young second growth. A network of trails leads from the station clearing into the forest (Color Figure 2), and to the aqueduct and beyond it through the forest parallel to the Rio Claro. Side trails from the Rio Claro trail lead down to the river at several points, but two are most used, one east and the other west of the station where low falls and large pools make good bathing and fishing spots.

Reference is made in the text to frogs associated with the forests and open formations of Boracéia. "Open formations" include naturally occurring vegetations with open canopies, such as those characteristic of the caatingas and cerrados, as well as man-modified habitats such as pastures. The only open formations we have sampled at Boracéia are man-made as far as we know. One question (presently unanswerable) of interest is whether the open formation frogs of Boracéia are invaders from the adjacent cerrado frog fauna.

Surface water suitable for frog breeding is present in a variety of places including bromeliads, bamboos, tree holes in standing trees and fallen trunks (Color Figure 3), temporary pools in the ridges and slopes of the forest, holes left by tip-ups, low spots on trails and in the ruts of the dirt road. Under closed canopy, surface water is typically associated with streams (Color Figure 4). The headwaters arise in seeps and springs that are always wet and choked with leaves. Small pools and trickles of water feed into small streams. The streambeds may be sandy, rocky or muddy and choked with leaf litter. In some places the streams run over rock walls and in others the streams form a string of small pools. At the edge of the forest and in the pasture, small ponds or pools are open to the sky and are surrounded by bushes and grass (Color Figure 5). The main Rio Claro at Boracéia is 5 to 10 m wide and is a fast flowing stream with a couple of waterfalls spilling over rock outcrops with pothole pools, below which deeper pools are edged by a sand bar overgrown with grass, at least between floods (Color Figure 6).

During most of our visits rain fell, the streams were flowing, the moss and the litter were wet and at least some frogs were active. Even on the driest visits there was water in the river, pools in the stream and the litter in the stream was damp below.

Most collections and observations occurred within 1-2 km of the station buildings, but two more distant sites were regularly visited. One is about 5 km to the west, almost to the end of the road at the Represa Riberão do Campo; it is an abandoned rock quarry with sheer rock walls about 5-7 m high, and a floor of gravel and rock rubble, overgrown with grass clumps and bushes (Figure 4). The walls are usually wet and there are permanent trickles. The floor has a shallow stream and several more or less permanent shallow pools. The second site, Lago do Aterro, lies between the quarry and the station; it is a small artificial reservoir bordered by a band of marsh vegetation, cattails, grass and bushes (Figure 5).

Acknowledgments

Dr. P.E. Vanzolini has continually encouraged our studies at Boracéia. It is due to his encouragement and raising of financial support that this publication has reached completion. Francisca Carolina do Val has been extremely helpful in providing logistic support for our field work at Boracéia. She also provided the frontispiece. James P. Borgart, Gene Miller, Charles W. Myers, and Bruce Williamson freely shared their data from Boracéia with us. George Zug carefully read over the entire manuscript. Ronald Altig, Martha Crump, and Robert Inger reviewed the discussion portion of the paper. Reginald B.

Cocroft improved the English text as he worked with several drafts on the word processor. He also performed the call analyses, producing the oscillograms and audiospectrograms. He suggested several improvements in our treatment of the frog calls and produced the recording of frog calls that is available as an adjunct to this text.

Support for this project has come primarily from the Museu de Zoologia da Universidade de São Paulo (MZUSP). A Scholarly Studies award from the Smithsonian Institution allowed the final work to be done to produce this summary. Additional support has been provided by the Smithsonian's I.E.S.P. Neotropical Lowland Research Program (to Heyer), the Conselho National de Desenvolvimento Científico e Tecnológico (CNPq) (to Cruz and Peixoto), and the U.S. Nacional Science Foundation (GB 18742 to Nelson).

Methods and Materials

Only data gathered from Boracéia have been utilized in framing the descriptions, although other data were used in arriving at taxonomic decisions. The taxonomy of the Atlantic Forest herpetofauna is still in the discovery phase, and there will certainly be further changes in the names used for the Boracéia species. We think we have recognized all Boracéia species currently represented by specimens in the collections and adequately characterized each species, so that future workers should have little trouble in recognizing the taxa we present herein.

For adult morphological analyses, data were gathered for a maximum sample of 10 males and 10 females. Where sample sizes were less than 10 of each sex, data were taken on all available specimens. Heyer gathered these data, analyzed them, and wrote the adult morphology summaries.

For the larval morphologies, characteristic individuals of each species were used for purposes of description and illustration. Cruz and Piexoto took these data and wrote the larval morphology summaries and prepared the tadpole illustrations.

Advertisement calls were analyzed by Reginald Cocroft using a Kay Elemetrics Digital Sona-Graph Model 7800. For certain analyses, calls were filtered (also see glossary) using a Brüel and Kjaer Frequency Analyzer Type 2121.

Ecological data come from field notes from Rand and Rand, with supplementary data from Bogart, Heyer, Myers and Nelson (including Miller and Williamson).

Several potentially confusing features and terms are defined in the glossary section.

The overall responsibility for producing the manuscript was Heyer's.

AN ARTIFICIAL KEY TO THE ADULT FROGS OF BORACEIA

1a. Three toes on each foot ..... *Brachycephalus nodoterga*
1b. Five toes on each foot 2
2a. Pupils vertically elliptical 3
2b. Pupils round or horizontally elliptical 4
3a. Fingers lacking web ..... *Phyllomedusa cochranae*
3b. Reduced but distinct web between fingers III and IV ..... *Phyllomedusa appendiculata*
4a. No inner metatarsal tubercle ..... *Myersiella microps*
4b. Inner metatarsal tubercle present 5
5a. Prominent fleshy triangular extensions (horns) on upper eyelids extending over eyes 6
5b. Upper eyelids lacking such horns 8
6a. Tympanum distinct externally ..... *Ceratophrys aurita*
6b. Tympanum not visible externally 7
7a. Tip of snout with triangular fleshy appendage ..... *Proceratophrys melanopogon*
7b. Tip of snout lacking appendage ..... *Proceratophrys boiei*
8a. Thumb prepollex present 9
8b. Thumb lacking externally visible prepollex 17
9a. Fingers without distinct web; posterior surface of thigh dark with distinct, discrete light spots ..... *Hyla albopunctata*
9b. Fingers usually with noticeable web, at least between fingers III and IV; posterior

surface of thigh uniform or with vertical stripes or ocelli, never with distinct light spots 10

10a. Dorsum uniform brown or lavender (green in life) with distinct pair of white dorsolateral stripes ..... *Hyla prasina*

10b. Dorsum usually striped or blotched, never with distinct single pair of white dorsolateral stripes 11

11a. Upper and outer shank with distinct dark stripe or band extending along length 12

11b. Upper shank without distinct longitudinal stripe or band, may be cross-barred 13

12a. Posterior surface of thigh usually with distinct dark vertical bars or ocelli; larger, males greater than 35 mm SVL, females greater than 50 mm SVL ..... *Hyla multilineata*

12b. Posterior surface of thigh usually uniform or with small spots; smaller, males less than 35 mm SVL, females less than 45 mm SVL ..... *Hyla polytoenia*

13a. Finger webbing extensive, extending at least to base of most distal subanticular tubercle (tubercle number 1) on fourth finger ..... *Hyla pardalis*

13b. Finger webbing present, but not as extensive, not extending beyond second subarticular tubercle on fourth finger 14

14a. At least a finger webbing formula of III 2 1/4-2+IV; large sized (adult SVL of at least 95 mm ..... *hyla faber*

14b. At most a finger webbing formula of III 2 1/2-2 IV; moderate sized (adult SVL no larger than 70 mm) 15

15a. Posterior thigh stripes usually faint; SVL less than 45 mm ..... *Hyla astartea*

15b. Posterior thigh stripes very distinct; SVL greater than 50 mm 16

16a. Tympanum moderate, diameter just less than 1/2 eye diameter *Hyla hylax*

16b. Tympanum large, diameter 3/5-3/4 eye diameter. ..... *Hyla circumdata*

17a. Toes with expanded disks with a circumferential groove or a pair of dorsal scutes .. 18

17b. Toes pointed or expanded, if expanded lacking a circumferential groove or a pair of dorsal scutes 48

18a. Toes with distinct web, at least between toes IV and V 19

18b. Toes without web, toes fringed (fringing may unite basally), or sides of toes smooth or ridged 37

19a. Fingers with distinct web, at least basally between fingers III and IV 20

19b. Fingers lacking web 31

20a. Low, but distinct cranial crests ..... *Osteocephalus langsdorffii*

20b. No cranial crests 21

21a. Dorsum whitish, cream, or lavender (green in life); posterior surface of thigh pigmentless 22

21b. Dorsum with browns or tans; posterior surface of thigh usually with melanophores, may be central pigmentless area 27

22a. Distinct white or dark postocular stripe, canthal stripe usually present 23

22b. No postocular or canthal stripes 24

23a. Snout acute in profile; smaller, males not exceeding 32 mm SVL ..... *Sphaenorhynchus orophilus*

23b. Snout rounded or acutely rounded in profile; larger, males larger than 38 mm SVL ..... *Hyla albofrenata*

24a. Vomerine teeth absent 25

24b. Vomerine teeth present 26

25a. Snout rounded; no upper lip ridge; dorsal pattern of rather regularly spaced pigment cells ..... *Centrolenella eurygnatha*

25b. Snout spatulate; upper lip ridge present, dorsal pattern reticulate ..... *Centrolenella uranoscopa*

26a. White highlighted transverse oval surrounding vent ..... *Hyla albosignata*

26b. Transverse white highlighted ridge above vent only, white highlighted pustules surrounding vent ..... *Hyla leucopygia*

27a. Posterior surface of thigh with distinct pigmentless area (bright orange red in life); white area under eyelang below tympanum ..... *Hyla microps*

27b. Posterior surface of thigh uniform tan, brown, or spotted, or with scattered melanophores; usually no white area under eye and below tympanum 28

28a. Toes more fully webbed, formula of 1 1/3 on inner side of toe IV ..... *Hyla senicula*

28b. Toes with less webbing, maximum index of 2 on inner side of toe IV 29

29a. Posterior surface of thigh usually with distinct light spots on a dark field; larger, size exceeding 39 mm SVL ..... *Ololygon hayii*

29b. Posterior surface of thigh rather uniform; smaller, males not larger then 35 mm SVL 30

30a. Dorsum usually with large dark spots, rarely striped; larger, at least 29 mm SVL ..... *Ololygon crospedospila*

30b. Dorsum usually with a pair of mid-dorsal longitudinal stripes, never spotted, rarely uniform; smaller, less than 25 mm SVL ..... *Hyla minuta*

31a. Posterior surface of thigh rather uniform tan or brown; wrists with a distinct dark band. ..... *Fritziana fissilis*

31b. Posterior surface of thigh with boldly mottled or spotted pattern; wrists lacking a distinct dark stripe 32

32a. Small, males not exceeding 19 mm SVL, females not exceeding 21 mm SVL ..... *Ololygon perpusilla*

32b. Larger, adult males and females at least 22 mm SVL 33

33a. Toe webbing reduced, no more than web of 3^+ on outer side of toe IV and 2 on inner side of toe V ..... *Fritziana ohausi*

33b. Toe webbing more extensive, at least web of 3^- on outer side of toe IV and 1 2/3 on inner side of toe V 34

34a. Dorsal pattern with dark interorbital triangle and light snout and light oblong area on back behind interorbital triangle bordered on either side by usually well defined dark dorsaleral stripes, pattern defined by smooth edges; smaller, males to 25 mm SVL ..... *Ololygon obtriangulata*

34b. Dorsal pattern usually lichenous or with dark chevrons, any pattern approaching that of 34a with irregular or crenulate edges; larger, males greater than 25 mm SVL 35

35a. Belly uniform creamy tan; inner tibia mottled or with light spots ..... *Ololygon x-signata*

35b. Belly distinctly mottled brown and cream; inner tibia with very distinct pattern of alternating dark and light vertical bars or markings 36

36a. Dorsal pattern complexly lichenous, indented light H mark not noticeable ..... *Ololygon brieni*

36b. Dorsal pattern simpler, not noticeably lichenous, with at least a noticeable (although interrupted) light indented H mark extending from the backs of the eyes to past the shoulder region .. *Ololygon flavoguttata*

37a. Sides of toes with fringes 38

37b. Sides of toes smooth or with weak ridges, not with well developed fringes 42

38a. Vomerine teeth absent; cornified spines on inner side of thumb in both sexes 39

38b. Vomerine teeth present; thumb spines usually absent, if present, weakly developed and only on males 40

39a. Canthal stripe sharply defined dorsally, blending into loreal pattern ventrally; 3 spines per thumb ..... *Crossodactylus dispar*

39b. Canthal stripe sharply defined dorsally and ventrally; 2 spines per thumb ..... *Crossodactylus gaudichaudii*

40a. Tympanum hidden; adults large (female 121 mm SVL) ..... *Megaelosia goeldii*

40b. Tympanum distinct; adults smaller (SVL less than 52 mm) 41

41a. Light lateral stripe along upper flank, distinct at least posteriorly .*Hylodes phyllodes*

41b. No light lateral stripe ..... *Hylodes asperus*

42a. Dorsum with series of more or less parallel ridges on body; larger, males exceeding 30 mm SVL, females exceeding 45 mm SVL ..... *Eleutherodacty binotatus*

42b. Dorsum usually lacking ridges, if ridges present, not arranged in more or less parallel rows on body; smaller, males not larger than 28 mm SVL, females not larger than 40 mm SVL. 43

43a. Tips of largest toe disks pointed ..... *Eleutherodactylus parvus*
43b. Tips of largest toe disks ovate or indented 44
44a. Vomerine teeth absent ..... *Eleutherodactylus randorum*
44b. Vomerine teeth present 45
45a. Groin and front of thigh with bold dark and light mottled pattern ..... *Eleutherodactylus nigriventris*
45b. Groin and front of thigh without distinctive pattern 46
46a. Distinct, dark, broad, even eye mask from tip of snout through tympanum to past arm insertion on flank, canthal portion as wide as portion including tympanum ..... *Eleutherodactylus hoehnei*
46b. Eye mask, if present, irregular with canthal portion much narrower that portion in area of tympanum 47
47a. Tympanum distinct; larger, males at least 19 mm SVL, females at least 25 mm SVL ..... *Eleutherodactylus guentheri*
47b. Tympanum indistinct; smaller, males less than 19 mm SVL, females less than 25 mm SVL ..... *Eleutherodactylus spanios*
48a. Toes webbed 49
48b. Toes without web, sides of toes smooth or with fringes that join basally 53
49a. Tympanum distinct 50
49b. Tympanum not visible externally 51
50a. Upper lip with distinct light mark below eye; smaller, less than 100 mm SVL ..... *Bufo crucifer*
50b. Upper lip lacking a distinct light mark below eye; larger, greater than 115 mm SVL ..... *Bufo ictericus*
51a. Iris lacking dorsal meniscus; small, less than 22 mm SVL ..... *Dendrophryniscus brevipollicatus*
51b. Iris with dorsal meniscus; larger, greater than 35 mm SVL 52
52a. Moderate webbing (at least web of 1 on inner side of toe V); not as warty, size of warts rather homogeneous ..... *Cycloramphus boraceiensis*
52b. Reduced webbing (maximum web of 1 1/2 on inner side of toe V); extremely warty, size of warts heterogeneous ..... *Cycloramphus semipalmatus*
53a. Vomerine teeth absent 54
53b. Vomerine teeth present 57
54a. Distinct tarsal tubercle present ..... *Physalaemus cuvieri*
54b. No tarsal tubercle 55
55a. Distinct light pin-stripe from eye to shoulder ..... *Physalaemus* olfersi
55b. No light pin-stripe from eye to shoulder 56
56a. Sole of foot with a few fleshy light tubercles ..... *Physalaemus franciscae*
56b. Sole of foot smooth ..... *Physalaemus maculiventris*
57a. Dorsum uniformly bumpy ..... *Holoaden luederwaldti*
57b. Dorsum smooth or ridged or with folds, or with small tubercles, but never covered with large, uniform bumps 58
58a. Outer tarsus and sole of foot covered with many white tubercles ..... *Adenomera marmorata*
58b. Outer tarsus and sole of foot usually smooth, or, if tuberculate, with a few scattered white tubercles on sole of foot only or with brown-tipped tubercles 59
59a. Fingers flattened; small (SVL not exceeding 20 mm) ..... *Paratelmatobius gaigeae*
59b. Fingers rounded (normal); moderate to large (SVL greater than 35 mm) 60
60a. Tympanum hidden ..... *Cycloramphus eleutherodactylus*
60b. Tympanum distinct 61
61a. Toes distinctly fringed, fringes adpressed to toes ..... *Leptodactylus ocellatus*
61b. Toes smooth or with ridges extending rigidly from sides of toes, never adpressed on toes 62
62a. Back with 6 distinct dorsolateral folds; posterior surface of thigh with light stripe on lower portion; adults smaller, SVL of males less than 50 mm, of females less than 60 mm ..... *Leptodactylus fuscus*
62b. Back with no more than 4 dorsolateral folds; posterior surface of thigh lacking distinct light stripe;

adults larger, SVL of males greater than 50 mm, of females greater than 60 mm 63

63a. Distinct light stripe from under eye, below tympanum, at least to posterior angle of jaw; male thumb with 1 or 2 large dark spines; larger, SVL greater than 120 mm .. .. *Leptodactylus flavopictus*

63b. No distinct light stripe under eye to jaw; male thumb with many dark spines; smaller, SVL less than 85 mm..... ..... *Thoropa miliaris.*

SPECIES ACCOUNTS

Family Brachycephalidae

Brachycephalus nodoterga Miranda-Ribeiro

Color Figure 7

Brachycephalus ephippium nodoterga Miranda-Ribeiro, 1920b.Original description.

Nomenclatural Note. — We disagree with Cochran's (1955:7) statement: "The so-called varieties of *Brachycephalus* described by Miranda-Ribeiro as *atelopoide, nodoterga, garbeana,* and *bufonoides,* said to occur with one another or with typical *ephippium,* are properly synonyms of *ephippium* since there is no valid zoogeographic or structural basis on which to separate them." The *Brachycephalus* at Boracéia differs from the *Brachycephalus* of the Serra da Mantiqueira and Serra dos Órgãos in being smaller and not bright orange in life. The larger, bright orange species is *ephippium.* Re-examination of Miranda-Ribeiro's types (by CEN) confirms many of the structural distinctions he drew. Roy W. McDiarmid, who is studying the complex, informs us (pers. comm.) that the Boracéia *Brachycephalus* may represent a new species. In the meantime, we use *nodoterga* to emphasize that the Boracéia *Brachycephalus* is not conspecific with *ephippium.*

Diagnosis. — *Brachycephalus nodoterga* is the only species at Boracéia with 3 toes on each foot.

Adult Morphology (N = 1 male, 7 females). — Snout outline subovoid to semicircular from above, rounded to vertically rounded in profile; short pair of postorbital crests, a pair of bosses about equidistant between postorbital crests, and a low anteriorly downward sloping ridge behind the eye on the side of the head distinct or not; upper eyelid smooth or with small pustules; no visible external tympanum; male vocal sac fold-like, not expanded; male vocal slits very small, posterior to tongue; no vomerine teeth; fourth finger very reduced, almost absent, third finger longest, first shortest; finger tips pointed, not disked; fingers not webbed, finger with extensive fleshy lateral ridges; finger subarticular tubercles indistinct; male thumb lacking asperities; no forearm fold; no prepollex; no distinctive body glands or folds; small ossification centers scattered over dorsum, concentrated as pebble-like network on head and over vertebral column, additionally, dorsum scattered with small pustules; belly with many to no pustules; feet with 3 toes, inner shortest, outer longest; toe tips pointed, not disked; toes not webbed, toes with fleshy lateral ridges; inner and outer metatarsal tubercles indistinct; heel smooth; posterior surface of tarsus smooth; foot smooth.

Dorsal pattern ranging from pigmentless to background of suffused light brown melanophores highlighted with pigmentless pustules; side of face, flanks, and venter either lacking pigment or with a few scattered melanophores; posterior surface of thigh without pigment, with an outline network of melanophores, or with scattered pustules as on dorsum.

SVL 11.8 mm (male), 12.7-14.5, mean 13.4 mm (females); mean head length 36% SVL (females); mean head width 40% SVL (females); mean thigh length 36% SVL (females); mean shank length 34% SVL (females); mean foot length 29% SVL (females); (all male percentages fall into female ranges).

Life Colors. — Iris black. Dorsum greenish yellow to dark gray-green with yellow warts, warts in regular rows or scattered; front of eye around snout same as dorsal color or yellow orange; arms pale golden yellow to orange with gray green ground color speckled on upper arm,

fading out on forearm; hands and feet same color as limbs or orange; one individual with a large black spot on the posterior dorsum. Undersides of feet, hands, and forearms orange; throat clear; belly clear, yellow with or without white spots, or dirty chrome yellow.

Larval Morphology. — *Brachycephalus ephippium* fom Itatiaia has direct devolopment (Gouvêa, pers. comm.). It is presumed that *B. nodoterga* also has direct development. The larvae described as *Brachycephalus* by Cochran (1955:7) are *Centrolenella eurygnatha* and *Centrolenella uranoscopa* (Heyer, 1985a).

Advertisement Call. — A low buzz, similar to the call of *B. ephippium*. The call has been heard during the day from the forest floor, but has not been tape recorded. Calling individuals were impossible to find.

Ecology. — All specimens were taken from the forest. Of the specimens with ecological data, all were collected on the forest floor surface. One was on a log across the trail and a second was on a forest trail. The rest were collected from the leaf litter: 15 from one small area of exceptionally large trees along a small stream, 9 from two ridgetop litter plots, and isolated individuals from other litter plots. One was collected from forest next to the road 5 km E of the scientists' residence. Specimens have been collected from October through March and May. Most of the specimens were taken in 1969-1972. Although the species was very patchily distributed even then and usually required hand and knee searches, it was likely more abundant then than earlier or later when the same areas were searched.

FAMILY BUFONIDAE

Bufo crucifer Wied

Bufo crucifer Wied, 1821. Original description.

Diagnosis. — The species with any development of cranial crests from Boracéia are *Brachycephalus nodoterga, Bufo crucifer, Bufo ictericus, Dendrophryniscus brevipollicatus,* and *Osteocephalus langsdorffii*. Crests are strongly developed in *Bufo crucifer* and *ictericus,* weakly developed or absent in *B. nodoterga* and *D. brevipollicatus*. Only the two *Bufo* have distinct preocular crests and distinct parotoid glands. *Bufo crucifer* is smaller (males 63-77 mm SVL, females 79-95 mm) than *ictericus* (males 115-140 mm, females 128-154 mm), has smaller parotoid glands than *ictericus,* and has some form of light cream colored bar, stripe, or mark on the upper lip below the eye (no such distinct light mark under the eye in *ictericus*).

Adult Morphology (N = 10 males, 9 females). — Snout outline subelliptical to rounded from above, rounded to rounded-vertical in profile; supraorbital, preparatoid, canthal, and preocular cranial crests well developed, nostril to tip-of-snout crest, parietal, pretympanic and post-tympanic crests present or absent; upper eyelid with a fleshy ridge continuous with canthal crest, surface of upper eyelid covered with brown tipped tubercles; tympanum large and distinct, diameter just larger than 1/2 to about 2/3 diameter of eye; male vocal sac single, subgular, not modified externally; vocal slits in male small or moderate in size; no vomerine teeth,palatine ridges well developed; finger lengths II $\cong$ IV < I $\leq$ III; finger tips lacking disks, pointed or slightly swollen; fingers without webbing, sides of fingers with weak to moderate ridges; basal subarticular tubercles on fingers large and pungent, other subarticular tubercles small, rounded, entire or bifid; males with tan or brown nuptial pad on thumb, with some or quite a bit on the inner side of finger II, inner sides of fingers III with or without nuptial pad; row of tubercles present or absent along outer forearm fold region; no prepollex; parotoid gland well developed with continuous or discontinuous glandular fold extending from paratoid gland to just past mid-body on flank or instead of fold, a distinct to barely discernable row of warts; dorsal texture warty with many brown-tipped tubercles; belly granular with or without small scattered tubercles; toe lengths I<II$\leq$V<III<IV; toe tips slightly swollen or not, not disked; male modal toe webbing formula I 1 1/2-2$^+$ II 1 1/4-3 III 2$^+$-3 2/3 IV 3 3/4-2 V, female I 2$^-$-2$^+$ II 1 1/3-3$^+$ III 2 1/4-3 2/3 IV 4$^-$-2$^+$ V; inner metatarsal tubercle ovoid, same size or slightly larger than rounded pungent or rounded-ovoid non-pungent outer metatarsal tubercle; heel lacking decoration; indistinct to prominent tuberculate inner tarsal fold continuous along 2/3

of tarsus or interrupted; outer tarsus and sole of foot with many large tubercles, tubercles brown tipped or not.

Dorsum characteristically with light mid-dorsal stripe from eye to vent bordered laterally by dark brown pin stripes bordered in turn by brown stripes darker than rest of tan to brown dorsal ground color, light stripe sometimes extending to tip of snout, light stripe sometimes reduced to pin stripe or lighter pin stripe sometimes evident within broader light mid-dorsal stripe, rest of dorsum with or without scattered dark spots, flank fold dark outlined or not, upper limbs uniform, complexly patterned, or indistinctly banded; front of snout tan or brown, same color as dorsal ground color, cream bar under eye on upper lip extensive and distinct to represented by a trace only, cream bar highlighted in front and/or back by dark brown or not, entire upper lip highlighted with cream stripe or not, large dark brown area surrounding and including tympanum with or without extension over parotoid gland; flank pattern an indistinct blending of dorsal and ventral patterns or with dark spots on a tan ground color or with a broken dark stripe along the glandular fold from the parotoid gland to groin; throat gray, belly mostly cream with brown or gray mottling, dark mottle sometimes extensive on front of belly, light mid-ventral stripe on belly present or absent; posterior surface of thigh tan with indistinct light mottling or with a few dark brown spots, light pin stripe from above vent to just inside knee present or absent.

SVL 63.4-76.9, mean 68.4 mm (males), 78.8-95.3, mean 84.8 mm (females); mean head length 33% SVL; mean head width 36% SVL; mean thigh length 44% SVL, mean shank length 45% SVL; mean foot length 47% SVL (males), 45% SVL (females).

Life Colors. — Iris slightly paler than lemon yellow to golden. Dorsum brown (several shades), gold, greenish gold, or green and bronze, mid-dorsal stripe mustard color edged with black, tan streak from eye to upper lip, back and legs sometimes with pink splotches. Venter black with flecks of bronze. Posterior surface of thigh mottled dirty yellow and brown/black. No flash colors.

Larval Morphology. — Body oval in dorsal view, slightly wider than deep; snout broadly rounded in dorsal view; nostril closer to eye than tip of snout; distance between nares 69% interorbital width; nares elliptical; eye 12% body length, situated dorsolaterally and directed laterally; opening of the sinistral spiracle directed posterodorsally on the midline about 68% body length; anal tube median; tail height slightly less than body height; dorsal fin origin on body-tail juncture; dorsal and ventral fins slightly arched; dorsal fin acutely rising at the origin; tail musculature not reaching the rounded tail tip; anteroventral mouth width equal to 40% body width; a single row of oral papillae only on the lateral parts of the lips, some inner scattered papillae present; tooth row formula 2(2)/3; beak moderately developed, finely serrated.

Body and most of the tail musculature uniformly black, a ventral unpigmented longitudinal stripe on tail musculature; fins transparent with few scattered black flecks on dorsal fin. In life, body and tail musculature blackish; fins transparent (Figure 13).

Larval Habitat. — Larvae were collected from temporary pools on the road near the station buildings.

Advertisement Call. — Calls given sporadically; call duration about 4-7 s; about 60-150 notes per call; note duration 0.03-0.06 s; note rate 11.5-15.5 per s; notes pulsed or strongly partially pulsed, each note of 4-7 pulses; note pulse rate about 130-170 per s; calls not noticeably frequency modulated; call beginning quietly, quickly becoming loud and staying loud; dominant frequency range 960-1750 Hz; only first harmonic apparent (Figure 35).

Ecology. — Most calling occurs after dusk in or next to road puddles and ponds in the pasture. Specimens have been collected during the day and at night from almost every terrestrial habitat, including forests, secondary forests, clearings, and pastures. Eleven individuals were taken from forest litter plots. One was recovered from the stomach of a *Liophis*. Specimens have been collected from August through May.

Bufo ictericus Spix

Figure 6

Bufo ictericus Spix, 1824. Original description.

Diagnosis. — The species from Boracéia with any cranial crest development are *Brachycephalus nodoterga, Bufo crucifer, Bufo itericus, Dendrophryniscus brevipollicatus,* and *Osteocephalus langsdorffii.* Crests are strongly developed in *Bufo ictericus* and *crucifer,* weakly developed or absent in *B. nodoterga* and *D. brevipollicatus.* Only the two *Bufo* have distinct preocular crests and parotoid glands. *Bufo ictericus* is larger (males 119-140 mm SVL, females 128-154 mm) than *crucifer* (males 63-77 mm, females 79-95 mm), has larger parotoid glands than *crucifer,* and the upper lip does not have a light cream colored bar, stripe, or mark below the eye such as is found in *crucifer.*

Adult Morphology (N = 10 males, 10 females). — Snout outline rounded-subelliptical to slightly obtuse from above, rounded, rounded-vertical, or vertical in profile; tip of snout to nostril, canthal, preocular, supraorbital, pretympanic, parietal, and preparatoid cranial crests well developed, externally visible maxillary ridge present or absent; upper eyelid with fleshy marginal ridge, upper eyelid surface covered or scattered with black tubercles; small to moderate sized tympanum, diameter less than or equal to 1/2 diameter of eye, posterior portion of tympanum sometimes covered by parotoid gland; male vocal sac single, not noticeably externally modified; males with vocal slits; vomerine teeth absent, palatine ridges present; finger II≤IV<III≤I; no finger disks, finger tips keratinized or not; fingers without webbing, sides of fingers with fleshy ridges; basal finger subarticular tubercles large, somewhat pungent, other finger subarticular tubercles smaller, single or bifid; male nuptial pads brown or black, extensive on inner sides of fingers I and II, extensive to absent on inner side of finger III; no forearm fold; no distinct prepollex; extensive parotoid glands, almost as long as head; dorsum of males warty with black tipped tubercles, dorsum of females with glandular warts, no tubercles, ventral texture granular with numerous small black-tipped tubercles; toe lengths I<II≤V<III<IV; no toe disks, toe tips keratinized or not; modal toe webbing formula I 1^{+}-2 II 1-3^{-} III 2-3 1/2 IV 3 1/2-2^{-} V; inner and outer metatarsal tubercles subequal or inner larger than outer, inner rounded-ovate, outer rounded, not pungent; no heel decoration; tarsus with inner fold extending from <1/2 to 2/3 length of tarsus; outer tarsus warty with black tipped tubercles; sole of foot warty with or without black tipped tubercles.

Color pattern sexually dimorphic; males usually uniform tan, olive green, brown, or gray above, rarely with a broad mid-dorsal light tan stripe and two pairs of symmetrical dark brown blotches on a brown ground color, female dorsal pattern striking with boldly contrasting broad light tan mid-dorsal stripe either straight margined or interdigitating with black ground color, black ground color uniform or with light tan spots, some individuals with a second light stripe including the upper eyelids, parotoid glands to the groin; face of males and females the same as respective dorsal ground colors, upper lip of males with many black tubercles, upper lip of females with some black tubercles; flanks in both sexes a jutaposition of dorsal and ventral colors at mid-body, females with a dark post-tympanic band extending across lower parotoid gland, either bordered above and behind by a light band or light band missing; venters of both sexes light with bold to faint dark marmorations; posterior surface of thighs in both sexes ranging from uniform (same color as dorsal ground color) to boldly dark and light mottled.

SVL 115.3-139.6, mean 128.1 mm (males), 128.0-154.0, mean 137.3 mm (females); mean head length 30% SVL; mean head width 39% SVL; mean thigh length 39% SVL; mean shank length 37% SVL (males), 36% SVL (females); mean foot length 40% SVL.

Life Colors. — Iris metallic green with black band through pupil or fluorescent green yellow with black mottling; dorsum light brown, brown, or black (females), snouts with or without green, sometimes rusty-brown warts near vent; limbs light brown with light to dark brown bands; undersides of toe tips orange, fingers, toes and hand and foot tubercles usually orange; belly white with brown blotches; posterior thigh surface of one male gray with white spots; no flash colors as such but the female dorsal pattern very striking.

Larval Morphology. — Body oval in dorsal view, slightly wider that deep; snout rounded in dorsal view; nostril nearer eye than tip of snout;

distance between nares 84% interorbital width; nares round; eye 13% body length, situated dorsolaterally and directed laterally; opening of the sinistral spiracle directed posterodorsally on the midline about 61% body length; anal tube dextral; tail height slightly less than body height; dorsal fin origin on body-tail juncture; dorsal and ventral fins arched; tail musculature not reaching the rounded tail tip; anteroventral mouth width equal to 33% body width; a single row of oral papillae present only on the lateral parts of the lips, few inner scattered papillae; tooth row formula 2(2)/3; beak moderately developed and finely serrated.

Body and tail musculature uniformly black pigmented; tail fins transparent with faint black flecks on the dorsal and tip of the ventral fin. In life, body and tail musculature black; fins transparent (Figure 14).

Larval Habitat. — Larvae were collected from the (former) pasture pond near the caretaker's house below the scientists' residence and in shallow water at edges of rivers.

Advertisement Call. — Calls given sporadically; call duration about 4-20 s; about 40-180 notes por call; note duration 0.04-0.06 s; note rate 8.5-9.0 per s; notes weakly to strongly partially pulsed, each note of 1-3 pulses, pulse rate about 65-85 per s; calls barely frequency modulated, beginning of call slightly lower in frequency; call intensity constant; dominant frequency range 320-850 Hz; harmonics above the fundamental weak, if present (Figure 36).

Ecology. — Males were heard calling all day on warm, rainy days in October; during the rest of the reproductive season, calling occurs in the early evening after dusk. The most commonly used calling sites are in or next to road puddles, pasture ponds, and a slow pasture stream. Males also call from grass-covered sand banks along the Rio Claro and are seldom seen away from calling sites; boldly patterned females are commonly seen in the forest. Tadpoles have been observed in side pools of the Rio Claro. Specimens have been collected both during the day and at night from the forests, secondary growth, pastures and other clearings, including roads, year-round except July.

Dendrophryniscus brevipollicatus Jimenez de la Espada

Figure 7

Dendrophryniscus brevipollicatus Jimenez de la Espada, 1871. Original description.

Diagnosis. — *Dendrophryniscus brevipollicatus* is the only small species (less than 22 mm SVL) from Boracéia lacking toe disks and vomerine teeth and having a hidden tympanum and pointed-mucronate dorsal snout shape. *Myersiella microps* is also a small species, but has a narrow pointed snout and the hind limbs are much more robust than in *D. brevipollicatus*. Other small species from Boracéia either have toe disks, non-mucronate snouts, distinct tympani, and/or vomerine teeth. The only species from Boracéia that *D. brevipollicatus* is likely to be confused with are small juvenile *Bufo crucifer* or *ictericus*. The thumb of *D. brevipollicatus* is reduced, much shorter than in *Bufo*.

Adult Morphology (N = 6 males, 3 females). — Snout outline pointed and mucronate or pointed-truncate and mucronate from above, strongly acute in profile; cranial crests weakly developed or absent, if present consisting of short preparatoid (supratympanic) crest, canthal crest, or slight boss behind eyes; upper eyelid texture granular or with shagreen and tubercles; tympanum hidden; no male vocal sac; no male vocal slits; no vomerine teeth; thumb rudimentary, finger lengths I<<II≤IV< or <<III; finger tips just broader than digits to expanded and disk-like, but lacking circumferential grooves; fingers without webbing or with a trace of basal webbing, sides of fingers free or with lateral ridges; basal finger subarticular tubercles well developed but not pungent, other subarticular tubercles small to moderate, rounded, single; most males lacking nuptial asperities on thumb, two males with a tan pad on inner thumb; no forearm fold; prepollex not developed; no distinct body glands or folds, weakly developed supratympanic fold, glandular swellings between angle of jaw and shoulder, and/or ill-defined row of larger tubercles from back of eye to groin; dorsal texture with tubercles scattered on a granular or weakly warty, or shagreened ground; belly granular; toe lengths I<II<III<V<IV; no toe

disks; modal toe webbing formula I 1^{+}-2 II 1 1/2-3 III 2-4^{-} IV trace V; inner metatarsal tubercle ovoid, not much larger than relatively large, rounded outer metatarsal tubercle; no heel decoration; no tarsal decoration; outer tarsal surface smooth to warty-glandular; sole of foot smooth.

Dorsal pattern ranging from uniform tan to uniform tan with darker circles around some tubercles to tan and brown with a darker ill-defined dorsal band covering entire snout and interocular region, narrowing in shoulder region to sacrum to pair of distinct darker brown chevrons, one between and posterior to eyes in shoulder region, second in sacral region, chevrons connected by a narrow dark stripe or not, mid-dorsal dark pin stripe present or absent, dorsal tubercles highlighted by dark brown dots or not, dorsolateral tuberculate fold weakly highlighted or not with light above, darker brown below, upper limbs indistinctly cross banded; face area uniform tan, indistinctly mottled, or brown with an ill-defined light area under eye, or with a broken light upper lip stripe from above front of lower jaw to shoulder; flank tan, or mottled with a somewhat darker pattern than adjacent dorsal pattern, or with a distinctly darker band (than adjacent dorsal color) from back of eye to groin; venter lightly scattered with melanophores to light with irregular but symmetrical light tan blotches and stripes of scattered melanophores; posterior surface of thigh indistinctly mottled to boldly mottled, mottle mostly light.

SVL 12.9-16.3, mean 14.5 mm (males), 17.0-21.2, mean 19.3 mm (females); mean head length 37% SVL (males), 33% SVL (females); mean head width 29% SVL (males), 28% SVL (females); mean thigh length 43% SVL (males), 41% SVL (females); mean shank length 44% SVL (males), 41% SVL (females); mean foot length 36% SVL (males), 35% SVL (females).

Life Colors. — Light bronze above, arms and legs banded with darker brown, toes and webbing on hind feet reddish; throat and belly iridescent cream.

Larval Morphology. — Larvae have not been collected at Boracéia. Izecksohn and Cruz (1972) described and figured the larvae from specimens collected from within ground bromeliads at Angra dos Reis, Rio de Janeiro.

Advertisement Call. — Unknown.

Ecology. — Most specimens for which ecological data are available (6) were collected during the day on the forest floor; one specimen was collected from the leaf of a low plant in the morning and three specimens were collected from leaves just above the forest floor at night. The species is apparently active on the forest floor during the day and rests on leaves above the ground at night. Specimens have been collected during the months of October, December, January, and March. This species was taken only once by Rand and Rand and not at all by Nelson et al. Heyer and party found 9 individuals in 1975 and 1976; this may represent a change in abundance although most came from a trail not visited on other trips.

FAMILY CENTROLENIDAE

Centrolenella eurygnatha (A. Lutz)

Hyla eurygnatha A. Lutz, 1925a. Original description.

Cochranella eurygnatha, Taylor, 1951. Transfer of *eurygnatha* to *Cochranella.*

Centrolenella eurygnatha B. Lutz, 1954. Transfer of *eurygnatha* to *Centrolenella.*

Diagnosis. — *Centrolenella eurygnatha* differs from most Boracéia species in being green in life and whitish, lavender, purple or pale blue in preservative. Other species sharing these colors are: *Centrolenella uranoscopa, Hyla albofrenata, H. albosignata, H. leucopygia, H. prasina, Phyllomedusa appendiculata, P. cochranae,* and *Sphaenorhynchus orophilus. Centrolenella eurygnatha* lacks vomerine teeth, *H. albofrenata, albosignata, leucopygia, prasina* and *S. orophilus* have distinct vomerine teeth. The pupils of *C. eurygnatha* are horizontally elliptical; the two species of *Phyllomedusa* have vertically elliptical pupils. *Centrolenella eurygnatha* has a rounded snout lacking an upper lip ridge and a dorsal pattern of rather regularly spaced pigment cells; *C. uranoscopa* has a spatulate shaped snout with an upper lip ridge and a reticulate dorsal pattern.

Adult Morphology (N = 10 males, 1 female). — Snout outline nearly rounded to semicircular from above, rounded to vertically rounded in

profile; no cranial crests; no upper eyelid decoration; tympanum usually partially hidden to almost entirely hidden, diameter about 1/4 eye diameter; male vocal sac single, externally expanded or not; males with vocal slits; no vomerine teeth; finger lengths I≤II≤IV<III; finger disks large, truncate or rounded-truncate, larger than tympanum, disks on fingers III and IV largest, disk on finger I smallest, disk on finger II about equal in size to disk on finger I, or to disk on fingers III and IV, or intermediate in size; modal male finger webbing formula I none II trace III 2 1/2-2^{+} IV, female formula I none II trace III 3^{-}-2 $^{+}$ IV; finger subarticular tubercles small to moderate size, rounded, not pungent; glandular pad on inner side of thumb in males, either tan or same color as thumb; forearm ridge present or absent; no prepollex development; pair of right-angle folds, one on either side of vent, no other body glands or folds; dorsal texture smooth or very finely granular; belly granular; toe lengths I<II<III<V<IV; toe disks large, truncate or rounded-truncate, just smaller than or equal in size to finger disks; modal male toe webbing formula I 2^{-}-2 1/2 II 1 1/2-2 1/2 III 1 1/2-2 1/2 IV 2 3/4-2^{-} V, female webbing formula I 2-2^{+} II 1 3/4-2 1/2 III 2^{-}-3 IV 3^{-}-2^{-} V; ovoid inner metatarsal tubercle, no outer metatarsal tubercle; no heel decoration; tarsus with or without an outer ridge; outer tarsus and sole of foot smooth.

Eyelids with concentration of purple pigment dots, rest of dorsum rather evenly profused with purple pigment dots, forearm and tarsal ridges, when present, white outlined, seat patch white highlighted; side of face with a suffusion of purple pigment dots, upper lip either immaculate or white outlined; dorsal pattern extending to middle of flanks from above, lower half of flanks immaculate; venter immaculate; posterior surface of thigh immaculate.

SVL 19.1-21.7, mean 20.4 mm (males), 20.9 mm (female); (remaining values based on males, values for single female are matched by data for individual males) mean head length 33% SVL; mean head width 36% SVL; mean thigh length 54% SVL; mean shank length 55% SVL; mean foot length 46% SVL.

Life Colors. — Iris variable, including white with a black reticulum and a green stripe through the eye, faint bronze with a light green reticulum, gold with a black reticulum, or silver-green; dorsum green, ranging from transparent green, light jade green, to bright grass green, very fine black dots may or may not be scattered on dorsal surfaces, hands and feet either a lighter green than dorsal color or yellow, fingers and toes yellowish; venter mostly transparent but skin aqua, lime green, or bluish-green, white peritoneum surrounding heart, liver, and digestive tract; posterior surface of thigh translucent yellow green; no flash colors.

Larval Morphology. — Larvae have not been collected from Boracéia. Heyer (1985a) described larval *C. eurygnatha* from the State of Rio de Janeiro. Larvae were collected from within leaf litter on stream bottoms.

Advertisement Call. — Calls given sporadically; call duration 0.12-0.4 s; 1-3 notes per call; note duration 0.12-0.25 s; note rate about 8-12 per s; notes pulsed, each note of 3-12 pulses; note pulse rate 25-70 per s; each note pulse weakly partially pulsed; call intensity constant; notes frequency modulated, frequency barely to noticeably rising throughout notes; dominant frequency range 4200-5500 Hz; only first harmonic apparent (Figure 37).

Ecology. — Males call at night from leaves about 0.1-3.0 m above the ground next to or over small forest streams. Males quickly answer one another so that calls overlap; calling bouts are separated by long silences. The species is nocturnal, only one specimen has been collected during the day. All specimens were collected in the forest. Specimens have been collected from September through March.

Centrolenella uranoscopa (Müller)

Color Figure 8

Hyla uranoscopa Müller, 1924a. Original description.

Cochranella uranoscopa, Taylor and Cochran, 1953. Transfer of *uranoscopa* to *Cochranella.*

Cochranella vanzolinii Taylor and Cochran, 1953. Synonym of *uranoscopa* (Heyer, 1985a), *vanzolinii* described from Boracéia specimen.

Centrolenella uranoscopa, Duellman, 1977. Transfer of *uranoscopa* to *Centrolenella.*

Diagnosis. — The Boracéia species that are green in life and whitish, lavender, purple or pale blue in preservative are *Centrolenella eurygnatha, C. uranoscopa, Hyla albofrenata, H. albosignata, H. leucopygia, H. prasina, Phyllomedusa appendiculata, P. cochranae,* and *Sphaenorhynchus orophilus. Centrolenella uranoscopa* lacks vomerine teeth, *H. albofrenata, albosignata, leucopygia, prasina,* and *S. orophilus* have distinct vomerine teeth. The two species of *Phyllomedusa* have vertically elliptical pupils; the pupils of *C. uranoscopa* are horizontally elliptical. *Centrolenella uranoscopa* has a spatulate shaped snout with an upper lip ridge and a reticulate dorsal pattern; *C. eurygnatha* has a rounded snout lacking an upper lip ridge and a dorsal pattern of rather regularly spaced pigment cells.

Adult Morphology (N = 6 males, 1 female). — Snout shape nearly rounded to semicircular from above, obtuse in profile; no cranial crests; upper eyelid smooth; tympanum small, covered above, distinct below, diameter about 1/4 eye diameter; male vocal sac single, ranging from barely to well expanded externally; males with vocal slits; no vomerine teeth; finger I just <, =, or just > II ≅ to << IV<III; fingers disked, truncate, disks larger than tympanum, disks on fingers III and IV largest, disk on finger I smallest, disk on finger II intermediate in size or equal to disks on III and IV; modal finger webbing formula I none II trace III 2 1/4-2 IV; finger subarticular tubercles small to moderate size, distinct, rounded, not pungent; inner thumb of males with glandular pad; distinct forearm fold, shallowly scalloped or not; prepollex not developed; upper lip with a dermal ridge, scalloped anal flap pronounced or not; dorsum smooth or very weakly granular; belly granular; toe lengths I<II<III<V <IV; toe disks truncate or rounded-truncate, equal to or just smaller in size than finger disks; modal toe webbing formula I 1 1/2-2 II 1-2 1/4 III 1 1/2-2 1/3 IV 2 1/2-2 1/3 V; ovoid inner metatarsal tubercle, no outer metatarsal tubercle; heel with a weak flap to a pronounced scalloped flap; no inner tarsal fold to poorly defined inner tarsal ridge, distinct outer shallowly scalloped tarsal fold; outer tarsus and sole of foot smooth.

Upper eyelids with a concentration of purple pigment, rest of dorsum variegated with violet pigment dots, dorsum may or may not have a few scattered white dots, lower tympanum sometimes highlighted with white, anal flap and scalloped limb fringes highlighted with white or not; side of face with irregularly scattered dark and white pigment dots, lip ridge white highlighted; no distinct flank pattern, dorsal pattern extending down sides about halfway, lower half of flank immaculate; venter immaculate; posterior surface of thigh immaculate.

SVL 19.6-22.5, mean 21.2 mm (males), 23.8 mm (female); mean head length 36% SVL (males), 35% SVL (female); mean head width 36% SVL (males), 34% SVL (female); mean thigh length 56% SVL (males), 49% SVL (female); mean shank length 56% SVL (males), 52% SVL (female); mean foot length 47% SVL (males), 43% SVL (female).

Life Colors. — Iris white with black reticulation, gray stripe through eye; dorsum green with white dots and white around edges of limbs and anus; hands and feet yellow. No flash colors.

Larval Morphology. — Larvae have not been collected from Boracéia. Heyer (1985a) described larval *C. uranoscopa* from the State of Rio de Janeiro. Larvae were collected from within leaf litter on stream bottoms.

Advertisement Call. — Calls given sporadically; call duration 0.04-0.1 s; 1-5 notes per call; note duration 0.03-0.05 s; note rate 0.9-3.2 per s; notes pulsed, each note of 2-3 pulses; pulse rate 80-100 per s; each pulse weakly partially pulsed; call of uniform intensity; notes frequency modulated or not, if modulated, frequency rising throughout notes; dominant frequency range 4100-5400 Hz; only first harmonic apparent (sidebands due to note pulse rate) (Figure 38).

Ecology. — Males call at night from leaves next to or above streams. All specimens were collected at night from small to moderate sized streams in the forest or secondary growth. Specimens were collected from August through January.

Family Hylidae

Fritziana fissilis (Miranda-Ribeiro)

Color Figure 9

Coelonotus fissilis Miranda-Ribeiro, 1920d. Original description.

Fritziana fissilis, Duellman and Gray, 1983. Transfer of *fissilis* to *Fritziana*.

Diagnosis. — *Fritziana fissilis* is a small (SVL 18-25 mm) plain frog with toe disks with circumferential grooves, foot webbing, but no finger webbing. It is distinct from all other Boracéia frogs in having a dark wrist band dorsally.

Adult Morphology (N = 5 males, 3 females). — Snout outline mucronate, semicircular to pointed-nearly rounded from above, acute to rounded-vertical in profile; no cranial crests; upper eyelid surface same texture as dorsum; tympanum distinct, diameter about 1/3 to less than 1/2 diameter of eye; male vocal sac single, internal; males with vocal slits; vomerine teeth in short transverse or obtuse series between or just posterior to choanae; finger I > or =II < or = IV<III; fingers with disks, disks small on fingers I and II, large on fingers III and IV, largest finger disks just larger than, smaller than, or equal to tympanum; fingers without webbing, sides of digits free or with fleshy ridges; finger subarticular tubercles moderately developed, low, round, single or bifid under finger IV; thumb in male lacking nuptial asperities or (usually) with a white, tan, or brown pad on the inner surface of the thumb; forearm fold lacking or delineated by very weak ridge; no prepollex; moderate supratympanic folds, no other body glands or folds; dorsal texture smooth or weakly granular; throat smooth, belly areolate; toe lengths I<II<III≅V <IV; toes disked, largest toe disks equal to or just larger than largest finger disks; modal toe webbing formula I none II trace III 2-3 1/2 IV 3 1/2-2 1/4 V; inner metatarsal tubercle ovoid, not pronounced, outer small and rounded to not visible; heel lacking distinctive decoration; weak inner tarsal fold extending length of tarsus; outer tarsus smooth or granular; sole of foot with large rounded fleshy tubercles.

Dorsal pattern ranging from almost uniform tan with faint dark irregular markings to head tan with body tan dotted with numerous small to moderate sized brown spots to a series of symmetrical dark and light longitudinal stripes, interorbital blotch occasionally present, wrists with a characteristic dark brown band, rest of upper limbs faintly barred, mottled, or almost uniform brown; face ranging from almost uniform to a brown splotch in the loreal region to a distinct canthal stripe or a broad dark canthal and loreal band, supratympanic fold usually dark outlined; flanks lacking distinctive pattern or with a dark band extending from the supratympanic stripe 2/3 posterior along the flank, the flank band rather wide and mottled; venter spotted with brown pinpoint dots, overall aspect cream; posterior surface of the thigh uniform or mottled tan or brown.

SVL 18.1-22.7, mean 20.6 mm (males), 21.1-24.9, mean 22.9 (females); mean head length 36% SVL (males), 37% SVL (females); mean head width 36% SVL; mean thigh length 46% SVL (males), 49% SVL (females); mean shank length 52% SVL (males), 55% SVL (females); mean foot length 42% SVL (males), 46% SVL (females).

Life Colors. — Iris pale bronze with a broad, irregular red horizontal stripe across eye; dorsum dull green, dirty yellow, or bronze, head and nose usually red or pink, stripes and spots, when present, brown or black; some individuals with small orange spots behind armpits on flanks; throat pale green, belly granular white or pale dirty yellow, greenish flesh underneath limbs.

Larval Morphology. — Larvae have not been collected from Boracéia (but see comment for larva of *F. ohausi*). Duellman and Gray (1983) illustrated and briefly described tadpoles from Angra dos Reis, Rio de Janeiro.

Advertisement Call. — Calls heard, but not recorded at Boracéia. Duellman and Gray (1983) published a call of *F. fissilis*, but did not indicate the origin of the call.

Ecology. — All specimens for which data are available were collected at night in the forest sitting on vegetation 1-3 m above the ground, mostly in bromeliads. Individuals have been taken in the months of September through March. Duellman and Gray (1983) infer that females carry eggs in a pouch and release the tadpoles into bromeliads.

Fritziana ohausi (Wandolleck)

Color Figure 10

Hyla ohausi Wandolleck, 1907. Original description.

Fritziana ohausi, Bokermann, 1966a. First use of *ohausi* in *Fritziana*.

Diagnosis. — *Fritziana ohausi* have toe disks with circumferential grooves, no hand webbing, and reduced foot webbing. This moderate sized species (males 24-31 mm SVL, females 29-37 mm SVL) usually has a characteristic dorsal pattern consisting of a dark interorbital triangle fused to two posteriorly diverging dark stripes that extend towards the sacral region. Specimens are almost always taken from bamboo.

Adult Morphology (N = 10 males, 4 females). — Snout outline mucronate and nearly rounded to almost semicircular from above, rounded, vertical, protruding, or acute in profile; no cranial crests; upper eyelid same texture as rest of dorsum, usually slightly warty with a few tubercles; tympanum present, partly hidden, less distinct in females, diameter about 40% diameter of eye in males, about 50% diameter of eye in females; male vocal sac single, internal; males with vocal slits; vomerine teeth in short transverse series between choanae, tooth patches in medial contact to separated by distance equalling length of single tooth patch; finger lengths II<I=IV<III or I=II<IV<III; finger tips with large disks, largest disks on fingers III and IV just larger than or about equal to size of tympanum; fingers without webbing, sides of fingers ridged or rarely fringed; subarticular tubercles moderately developed, single; males usually with extensive creamy tan to brown nuptial pads on inner surface of thumb; no forearm fold; no prepollex; weakly to moderately developed supratympanic fold, no other distinctive body folds or glands; dorsal texture smooth to slightly warty with scattered tubercles; anterior portion of chin smooth, rest of venter areolate; toe lengths I<II<III=V<IV; toe disks large, largest just bigger than or about equal to finger disks; modal toe webbing formula I trace II 2^{-}-3^{+} III 2-3^{+} IV 3^{+}-2 V; inner metatarsal tubercle ovoid, distinct, outer round, distinct, just larger than sole of foot tubercles, about 1/5 to 1/3 size of inner; heel lacking distinctive decoration; tarsus lacking fold or with very weak inner tarsal fold extending length of tarsus; outer tarsal texture smooth, slightly glandular-warty, or slightly warty-tuberculate; sole of foot with many distinct large low round fleshy tubercles.

Dorsal pattern ranging from brown with numerous small darker brown spots to a distinct light and dark outlined dark interorbital triangle, continuous with and expanding posteriorly into a chevron extending to the sacral region, the upper limb surfaces mottled to cross banded; face almost uniform, indistinctly spotted, or upper lip mottled or mottled-barred, weakly defined dark canthal stripe; dark lateral band on anterior flank distinct or not, groin light or light with large dark splotches; venter lightly to moderately mottled brown; posterior surface of thigh with very bold dark and light mottle or large light spots on an almost black ground, bold pattern continuous or not over top of thigh with same bold pattern on front of thigh.

SVL 24.4-30.7, mean 27.6 mm (males), 29.0-36.6, mean 32.1 mm (females); mean head length 36% SVL; mean head width 33% SVL, mean thigh length 44% SVL (males), 43% SVL (females); mean shank length 49% SVL (males), 48% SVL (females); mean foot length 45% SVL.

Life Colors. — Iris gold and black or bronze and black; dorsal colors variable including brown, black, and white, or greenish bronze, or yellow brown, or bronzy brown, may be a pale gold stripe on the side changing to transparent blue gray in the groin, upper limbs clear with dark brown banding, toes and fingers yellow or brown; upper lip bronzy or same as predominant ground color of dorsum; belly gray with cream flecks or transparent with silvery mottling and sparse brown flecks, throat clear with dense brown and silvery mottling or like belly; groin, front and back of thighs colorless or yellow with dark brown, no real flash colors.

Larval Morphology. — The tadpoles of *F. fissilis* and *ohausi* are very similar. Identification of the Boracéia specimens is based primarily on where the larvae were collected.

Body pyriform in dorsal view, slightly wider than deep; snout broadly rounded in profile; nostril nearer tip of snout than eye; distance between nares 48% interorbital width; nares rounded, small, situated dorsally and directed anterolaterally; eye 8% body length, situated dorsolaterally; opening of the ventral spiracle directed posteriorly about 44% body length; anal tube short and median; tail height less than body height; dorsal fin origin on the body-tail juncture; dorsal and ventral fins slightly arched; tail musculature reaching the rounded tail tip; mouth

anteroventral, directed anteriorly, width to 25% body width; a single row of rounded papillae interrupted anteriorly; teeth absent; beak weakly developed.

Body and tail musculature cream; tail fins transparent; intestine full of yolk (Figure 15).

Larval Habitat. — Tadpoles were collected from an open end of a bamboo joint about 3 m high along a forest trail.

Advertisement Call. — Calls given sporadically, duration 0.65-0.90 s; call of 5-6 notes; note duration 0.02-0.04 s; note rate 5.0-6.0 per s; each note of 5-9 pulses, the first 1 or 2 very much stronger than the rest; initial note lower in intensity than remainder; initial notes slightly lower in frequency than final notes; dominant (= fundamental) frequency 2000-3000 Hz; second and third harmonics weakly broadcast or not (Figure 39).

Ecology. — About 2/3 of the specimens for which data are available were found in bamboo clusters, either in cut internodes during the day or on the surface at night. One individual was collected by beating low (1-2 m) roadside vegetation during the day; a juvenile was found on a bromeliad leaf during the day. About 1/3 of the specimens with data were collected from leaves of low vegetation in the primary forest at night. Males have been heard calling from bamboo in the forest at night. Specimens have been collected in August through February, May and June. Females elsewhere carry eggs on their back and deposit the tadpoles in bamboo stems (B. Lutz, 1973).

Hyla albofrenata A. Lutz

Color Figure 11

Hyla albofrenata A. Lutz, 1924. Original description.

Diagnosis. — *Hyla albofrenata* shares the colors of green in life and whitish, lavender, purple or bluish in preservative with *Centrolenella eurygnatha, C. uranoscopa, Hyla albosignata, H.leucopygia, H. prasina, Phyllomedusa appendiculata, P. cochranae,* and *Sphaenorhynchus orophilus. Hyla albofrenata* has vomerine teeth; *Centrolenella* and *Phyllomedusa* lack vomerine teeth. *Hyla albofrenata* lacks a prepollex; *H. prasina* has a prepollex. *Hyla albofrenata* usually has a white canthal stripe and a white supratympanic stripe; *H. albosignata* and *leucopygia* lack such stripes. The supratympanic stripe in *H. albofrenata* curves downward behind the arm insertion; the postorbital stripe in *S. orophilus* is straight, extending as far as the groin.

Adult Morphology (N = 10 males). — Snout outline subelliptical to rounded from above, rounded or slightly acutely rounded in profile; no cranial crests; upper eyelids lacking distinctive features; tympanum present, distinct or covered by skin but visible, large, diameter greater than 1/2 to 2/3 eye diameter; males with single vocal sacs, expanded or not; vocal slits in males elongate; vomerine teeth in acute series lying between posterior half of choanae and extending posteriorly behind choanae; finger I<II< or ≃IV <III; fingers with large disks, largest disk smaller than to just larger than tympanum, disk on finger I smallest, disks about same size on other three fingers; modal finger webbing formula I trace II 1 1/3-2 1/2 III 2 1/4-2 IV; finger subarticular tubercles average size, single; no male thumb asperities; forearm fold weakly developed, weakly scalloped or not; no prepollex on thumb; distinct supratympanic fold curving down behind arm onto side of body, entire dorsum with gland-like structures under skin visible under light microscope, granular seat patch weakly to distinctly developed; dorsal texture finely granular; throat smooth, belly more coarsely granular than dorsum; toe lengths I<II<V< or =III<IV; toe disks large, largest disks just smaller than largest finger disks; modal toe webbing formula I 2^{-}-2^{+}II 1^{+}-2 1/2 III 1 1/3-2 1/2 IV 2 1/3-1^{+} V; inner metatarsal tubercle ovoid, no outer; heel usually with single tubercular calcar, relatively small to moderate in size (absent on right heel of one specimen examined); outer tarsal fold weakly developed, usually present, smooth, inner weak tarsal fold usually absent, if present extending 3/4 length of tarsus; outer tarsal texture smooth; sole of foot smooth or granular with fleshy tubercles.

Dorsum and upper limbs mostly lacking pigment (creamy in preservative) with scattered white enamel dots with brown reticulating pigment emanating from centers of white dots,

brown pigment either contracted to centers of dots and visible only under magnification or expanded such that dorsum with rather large, diffuse brown spots, some brown pigment centers lack overlying white dots, outer forearm and tarsal folds distinctly or indistinctly outlined or highlighted by white, seat patch washed with white; light white canthal stripe usually present, rest of face same as dorsal pattern; supratympanic fold distinctly white, contrasting with surrounding ground color, rest of flank area patternless; venter patternless; posterior surface of thigh patternless.

SVL 38.0-41.6, mean 39.3 (males); mean head length 36% SVL; mean head width 33% SVL; mean thigh length 47% SVL; mean shank length 49% SVL; mean foot length 42% SVL.

Life Colors. — Iris copper to bright orange red, paler around pupil. Dorsum green (light apple or lime), speckled with tan or black spots; canthal and supratympanic folds yellow, also yellow over eyes; bones green. Chin and under sides of feet apple green; throat and around arms, groin, and armpits blue-green; belly yellow; under surfaces of arms and legs transparent dull green; belly peritoneum yellow.

Larval Morphology. — Larvae have not been identified from Boracéia. Peixoto and Cruz (1983) described and figured larvae collected from mountain streams at Tijuca, Rio de Janeiro.

Advertisement Call. — Call a single note given rather regularly at a rate of 0.7-1.7 per s; note duration 0.04-0.06 s; notes not or slightly partially pulsed; call roughly constant in intensity; notes frequency modulated, beginning higher, ending lower; fundamental frequency range 1100-1700 Hz; dominant frequency (second harmonic) range 2200-2800 Hz; first 2 harmonics visible in the waveforms (Figure 40).

Ecology. — Almost all specimens collected have been males calling at night from leaves of trees or shrubs, up to two meters high, next to forest streams; males were regularly heard calling higher. One non-calling individual was taken at night from the center of a bromeliad above a forest stream. Specimens have been collected from October through January.

Hyla albopunctata Spix

Color Figure 12

Hyla albopunctata Spix, 1824. Original description.

Diagnosis. — The Boracéia species with distinct prepollices are *Hyla albopunctata, H. astartea, H. circumdata, H. faber, H. hylax, H. multilineata, H. pardalis, H. polytaenia,* and *Hyla prasina.* In all of these species, the prepollex is present in both sexes (although proportionately larger in males) and a slender bony spine is covered or projecting only at the tip. In *Leptodactylus flavopictus* and *ocellatus,* cornified, fully exposed spines are present in the prepollical area only in males. *Hyla albopunctata* has a dark eye mask, lacks finger webbing, and has distinct light spots on dark posterior surfaces of the thighs, differing in each of these features from the other Boracéia *Hyla* with prepollices.

Adult Morphology (N = 10 males). — Snout outline subelliptical from above, rounded or protruding in profile; no cranial crests; no distinctive features on upper eyelids; tympanum large, distinct, diameter 2/3 to 3/4 eye diameter; male vocal sac single, slightly or moderately expanded on posterior 1/2 of throat and chest; males with vocal slits; vomerine teeth in acute arches, almost in medial contact, medial portions lying between posterior extent of choanae, lateral portions of vomerine teeth extending posterior to choanae; finger I<II just <, =, or >IV <III; finger disks large, largest on fingers II, III, IV, largest disks much smaller than tympanum; modal finger webbing formula I none II trace III trace IV, sides of fingers ridged; finger subarticular tubercles moderate, single; no thumb asperities in males; distinct smooth outer forearm ridge; males with modest prepollex, bony spine exposed or not; supratympanic fold extending to about 1/3 length of body anteriorly, dermal fold over vent; dorsum smooth or very finely granular-glandular; chin smooth, rest of belly granular; toe lengths I<II<III=V<IV; toe disks large, equal to or just smaller than finger disks; modal toe webbing formula I 1 1/2-2$^+$ II 1$^+$-2 1/2 III I 2/3-3 IV 2 3/4-1 1/4 V; inner metatarsal tubercle average size, ovoid, outer metatarsal tubercle (if in fact present) indistinguishable from

other tubercles in area; heel with smooth or interrupted dermal ridge; weak inner and outer tarsal folds extending length of tarsus; outer tarsal texture smooth; sole of foot with low, round tubercles.

Dorsum almost uniform brown to brown mottled, to brown with darker brown transverse bands or longitudinal bands, or a mixture, scattered whitish dots present or absent, dark middorsal pin stripe rarely indicated, outer forearm and tarsal folds white, vent fold white, upper arm surfaces and shank almost uniform brown or banded, upper surface of thigh cross banded brown, outer surface of shank with broad, dark gray-brown stripe; broad dark brown canthal stripe involving whole face or not extending over tympanum to shoulder region, rest of face uniform brown except tip or most of upper jaw white outlined; lower flanks with light spots, most extensive in groin; lower jaw outlined, brown to gray network on throat and chest, rest of belly cream or dirty orange-yellow; posterior surfaces of thigh with distinct light spots on a dark brown field.

Male SVL 53.7-65.4, mean 58.0 mm; mean head length 35% SVL; mean head width 30% SVL; mean thigh length 50% SVL; mean shank length 55% SVL; mean foot length 45% SVL.

Life Colors. — Iris bronze, some individuals with a blue ring around the iris. Lip stripe cream or yellow; canthal stripe dark brown; dorsum tan or brown, sometimes with enamel yellow dots; flanks with bright yellow bars or spots on a light purple ground color. Throat yellow; belly dirty yellow; undersides of hind legs with a yellow-orange wash. Posterior surface of thighs with discrete, distinct bright yellow or orange-yellow spots on a lavender to lavender-brown field. Flank and posterior thigh patterns definitely flash color patterned.

Larval Morphology. — Body oval in dorsal view, wider than deep; snout rounded in dorsal view; nostril nearer eye than tip of snout; distance between nares 61% interorbital width; nares reniform; dorsolateral eye 11% body length; opening of the sinistral spiracle directed posterodorslly on the midline at about 90% body length; anal tube dextral; tail higher than body; dorsal fin origin extending slightly onto the body; dorsal and ventral fins arched; tail musculature reaching the pointed tail tip; anteroventral mouth width equal to 34% body width; a single row of oral papillae shortly interrupted in upper lip; tooth row formula 2(1,2)/3(1); beak moderately developed and finely serrated.

Body brown with few darker brown spots; venter light brown anteriorly; tail brown marbled with a longitudinal median brown stripe on first third of the musculature. In life, body deep tan with dark spots on dorsum and white flecks on belly; tail musculature with superior half red brown, inferior grayish and a longitudinal median blackish stripe on first third; fins red brown marbled (Figure 16).

Larval Habitat. — Tadpoles were collected from the large permanent pond, "Lago do Aterro" (Figure 5).

Advertisement Call. — Calls given sporadically; call duration 0.4-0.7 s; of two types; in type I (Figure 41) only a single note; in type II (Figure 42) 6-20 "pseudonotes" (i.e., not completely separated), modulation producing these "pseudonotes" is fairly weak at the beginning of the call but approaches 100% by the end of the call; otherwise both have the same basic structure, both strongly partially pulsed; pulse rate of 100-200 per s; 40-80 pulses per call; call about constant loudness throughout, shows no frequency modulation; dominant frequency range 700-2400 Hz, within which the sonogram shows 2 harmonics, the fundamental at about 900-1000, the second harmonic at 1800-2000 Hz; pulsatile nature of the call produces a strong side band series.

Ecology. — All specimens were collected in November, calling at night on vegetation at the edge of Lago do Aterro. This species was first heard and collected in 1982, although the Lago do Aterro was intensively worked previously, especially in 1963-1964.

Hyla albosignata A. Lutz and B. Lutz

Hyla albosignata A. Lutz and B. Lutz, 1938. Original description.

Diagnosis. — *Hyla albosignata* shares the colors of green in life and whitish, lavender, purple, or bluish in preservative with *Centrolenella euryganatha, C. uranoscopa, Hyla albofrenata, H. leucopygia, H. prasina, Phyllomedusa*

appendiculata, P. cochranae, and *Sphaenorhynchus orophilus. Hyla albosignata* has vomerine teeth; *Centrolenella* and *Phyllomedusa* lack vomerine teeth. *Hyla albosignata* lacks a prepollex; *H. prasina* has a prepollex. *Hyla albosignata* lacks a distinct postorbital stripe; such stripes occur in *H. albofrenata* and *S. orophilus.* The vent is completely encircled by a white outlined, broken, transversely oval ridge in *H. albosignata;* in *H. leucopygia* a white outlined transverse ridge occurs above the vent only.

Adult Morphology (N = 1 male). — Snout outline subelliptical from above, rounded-vertical in profile; no cranial crests; no distinctive features on upper eyelids; tympanum large, distinct, diameter about 2/3 diameter of eye; male with single, internal vocal sac; vocal slits present in male; vomerine teeth in acute series between and posterior to choanae; finger length I<IV<II<III; finger disks present, large, largest disk smaller than tympanum; finger webbing formula I trace II 1 1/2-2 2/3 III 2-2 IV; finger subarticular tubercles moderate, single; no thumb asperities on male; outer forearm fold distinct, smooth; no prepollex; supratympanic fold of average development, fields of glandular tissue visible in skin (under magnification) extending from behind tympanum to 2/3 distance posteriorly on flank, circumvent fold, continuous above vent, broken on sides and below; dorsum smooth; venter granular; toe lengths I<II<V<III<IV; toe disks large, distinct, largest just smaller than largest finger disks; toe webbing formula I 1 3/4-2^{+} II 1-2 1/2 III 1-2 2/3 IV 2 1/4-1^{+}V;inner metatarsal tubercle rounded-ovate, prominent, outer not visible;heel with prominent calcar continuous with a fold; no inner tarsal fold, smooth outer tarsal fold continuous with heel calcar; outer tarsal texture smooth; sole of foot with low, round fleshy tubercles.

Dorsum overall lacking pigment but with randomly uniform scattered profusion of black dots and 20-30 white dots; folds on outer forearm, tarsus, and around vent white highlighted; face mostly pigmentless except for a few white dots in area in front of tympanum extending to underneath the eye; flanks lacking pigment; lower lip light outlined, rest of venter pigmentless; posterior surface of thigh pigmentless.

SVL 41.5 mm (male); head length 36% SVL; head width 32% SVL, thigh length 47% SVL, shank length 52% SVL; foot length 41% SVL.

Life Colors. — Not available.

Larval Morphology. — Tadpoles not collected at Boracéia. Peixoto and Cruz (1983) described and figured larvae collected from mountain streams at Paranapiacaba, São Paulo.

Advertisement Call.— Not recorded, but similar to those of *H. leucopygia* and *H. albofrenata.*

Ecology. — The single male was observed calling and collected at night from a leaf 1 m up on a bush 3 m from a forest stream in October 1963.

Hyla astartea Bokermann

Hyla astartea Bokermann, 1967. Original description.

Diagnosis. — The Boracéia species with distinct prepollices are *Hyla albopunctata, H. astartea, H. circumdata, H. faber, H. hylax, H. multilineata, H. pardalis, H. polytaenia,* and *H. prasina.* In all of these species, the prepollex is present in both sexes (although larger in males) and a slender bony spine is covered or projects only at the tip. In *Leptodactylus flavopictus* and *L. ocellatus,* cornified, fully exposed spines are present in the prepollical area only in males. *Hyla astartea* lacks the parallel dorsal stripes found in *H. multilineata* and *polytaenia. Hyla astartea* has finger webbing; *Hyla albopunctata* does not. *Hyla astartea* lacks the distinct pair of white dorsolateral stripes evident in *H. prasina. Hyla astartea* (SVL 39-44 mm) is smaller than *H. circumdata, faber, hylax,* and *pardalis* (SVL at least 55 mm). *Hyla astartea* has less finger webbing (maximum web of 2 1/2 on outer side of finger III) than *H. faber* and *H. pardalis* (at least web of 2 1/4 on outer side of finger III). *Hyla astartea* is creamy tan dorsally (in preservative) and lacks distinct transverse dorsal bands; *H. circumdata* and *hylax* are tan to brown dorsally and often have dark transverse dorsal bands.

Adult Morphology (N = 10 males, 1 female). — Snout outline subovoid, rounded, to almost semicircular from above, rounded or vertically rounded in profile; no cranial crests; edge of upper eyelid with a slightly thickened ridge, upper

eyelid surface indistinct from dorsal texture; tympanum visible, sometimes distinct, diameter less than 1/2 eye diameter; male vocal sac single, not expanded to moderately expanded; vocal slits in males; vomerine teeth in arched acute series between and posterior to choanae, contiguous medially; finger lengths I<II<IV<III; finger disks large, largest equal to or just larger than tympanum; modal finger webbing formula I none II trace III 2 3/4-2 1/2 IV; finger subarticular tubercles moderately developed, single or slightly bifid under finger IV; no male thumb asperities; outer forearm with glandular, scalloped ridge; prepollex present, smaller in female, spine exposed or not; supratympanic fold of average development, no other obvious body folds or glands; dorsum smooth; front of throat smooth, rest of belly pebble-granular; toe lengths I<II <V= or <III<IV; largest toe disks just larger than largest finger disks; modal male toe webbing formula I 2-2 1/2 II 1 1/2-3 III 1 1/2-3 IV 2 1/2-1 1/2 V, female toe webbing formula I 1 1/2-2$^+$ II 1-2 1/2 III 1$^+$-2 1/2 IV 2 1/2-1$^+$ V; inner metatarsal tubercle moderate, ovoid, outer indistinct;heel glandular or glandular warty, one wart prominent as calcar or not; weak inner tarsal fold running length of tarsus; outer tarsal texture glandular warty; sole of foot with fleshy tubercles.

Dorsal pattern variable including uniform tan with small brown and white dots or brown or white blotches or lichenous tan and white or tan and brown or with indistinct dark transverse bands, upper limb surfaces indistinctly cross barred or with lichenous blotches, forearm ridge cream highlighted, elbow with or without a cream splotch, broken or continuous cream or white supra-vent stripe present or absent, heel with or without white stripe and heel tubercles cream or not; face with weak dark canthal stripe, rest of face uniform tan with brown dots; narrow to broad vertical brown stripes along flanks, interspaces equal to 4-5 times width of stripes, flank pattern distinct to barely evident; chin with a few scattered brown dots, rest of venter lacking melanophores; dark cross stripes on front of thigh continuous over top of thigh with stripes on back of thigh, light areas 2-5 times width of stripes or stripes on top and posterior surfaces of thigh only or stripes on top of thigh only, posterior surfaces of thigh patternless.

SVL 39.4-41.5, mean 40.4 (males), 44.1 mm (female); mean head length 37% SVL; mean head width 36% SVL; mean thigh length 49% SVL (males), 53% SVL (female); mean shank length 52% SVL (males), 58% SVL (female); mean foot length 41% SVL (males), 43% SVL (female).

Life Colors. — Iris golden, outlined in black. Dorsum cream, leaf brown, or red brown with brown or black dots or spots, mostly on head and back, few on limbs, with or without dorsal white or cream spots or blotches; top of thigh bronze or red; tops of hands and feet reddish, salmon pink, or brick red; white line across vent and heels present or absent; sides of body with gray bars; bones light green. Undersides of feet salmon pink. Posterior surface of thigh salmon pink to brick red, with or without dark brown vertical stripes.

Larval Morphology. — Tadpoles have not been collected from Boracéia, nor have they been described from other localities.

Advertisment Call. — Calls given sporadically; call duration about 0.35-0.95 s; calls of 1-3 note groups, each note group containing 2-5 notes of increasing duration, 0.02-0.12 s; each note group initiated by single pulse note, concluded by multiple pulsed note; note rate 9.1-16.7 per s; multiple pulsed notes of 2-20 pulses; pulse rate about 100-400 per s; complex frequency modulation within longer notes; initial notes of note groups quieter than following notes within note groups, following note groups of apparent equal intensity; dominant frequency range 800-2400 Hz; distinct sidebands on pulsed notes, no apparent harmonics (Figure 43).

Ecology. — Males were observed calling at night from bromeliads 1 to 2 m above ground near streams in primary or secondary forest. A few other non-calling specimens were collected at night 1-3 m high on vegetation in the forest away from streams. Specimens have been collected from October through February.

Hyla circumdata (Cope)

Color Figure 13

Hypsiboas circumdatus Cope, 1871. Original description based on this publication, not *nomen nudum* of Cope, 1867.

Hyla crepitans, Cochran, 1955. Cochran (p. 70) listed two specimens from Boracéia in the Paris Museum collected by Bokermann (not examined by us); the specimens are probably either *H. circumdata* or *hylax*.

Diagnosis. — The Boracéia species with distinct prepollices are *Hyla albopunctata, H. astartea, H. circumdata, H faber, H. hylax, H. multilineata, H. pardalis, H. polytaenia*, and *H. prasina*. In all of these species, the prepollex is present in both sexes (although larger in males) and a slender bony spine is covered or projects only at the tip. In *Leptodactylus flavopictus* and *L. ocellatus*, cornified, fully exposed spines are present in the prepollical area only in males. *Hyla circumdata* lacks the parallel dorsal stripes of *H. multilineata* and *polytaenia*. *Hyla circumdata* has finger webbing; *Hyla albopunctata* does not. *Hyla circumdata* lacks the distinct pair of white dorsolateral stripes evident in *H. prasina*. *Hyla circumdata* has less finger webbing (maximum web of 2 1/2 on outer side of finger III) than *H. faber* and *pardalis* (minimum web of 2 1/4 on outer side of finger III). *Hyla circumdata* further differs from *H. faber* in being smaller (maximum SVL for *circumdata* 67 mm; minimum SVL for *faber* 95 mm); the ulnar and tarsal fringes are much better developed in *pardalis* than in *circumdata*. *Hyla circumdata* is larger (minimum SVL 55 mm) than *H. astartea* (maximum SVL 44 mm) and has a tan or brown dorsum usually with distinct dark cross bands; *H. astartea* is creamy tan dorsally and lacks dark transverse bands. The tympanum is large in *H. circumdata* (diameter 3/5-3/4 eye diameter), moderate in *H. hylax* (diameter just less than 1/2 eye diameter).

Adult Morphology (N = 10 males, 10 females). — Snout outline rounded or nearly rounded from above, rounded or vertically rounded in profile; no cranial crests; upper eyelids lacking distinctive features; tympanum large, distinct, diameter 2/3-3/5 eye diameter; male vocal sac single, slightly or not expanded externally; males with vocal slits; vomerine teeth in transverse or arched-acute series, usually between choanae, sometimes partly extending posterior beyond choanae; finger lengths I<II<IV <III; finger disks large, but much smaller than tympanum; modal finger webbing formula for males I trace II 2^{-}-3 III 2 1/2-2^{+} IV, for females I trace II 2^{+}-3^{+} III 2 2/3-2^{+} IV; subarticular tubercles well developed, rounded, single or bifid under fingers III and IV; brown nuptial pad on base of thumb in males, forearm hypertrophied in males; outer forearm with a distinct to weak warty fold; prepollex large in males, distinct but smaller in females, spines exposed or not in males; moderately developed supratympanic fold, weakly to moderately developed horizontal supra-vent fold; dorsum smooth; chin smooth, chest striated or granular, belly and under thighs granular; toe lengths I<II<III=V<IV or V<III; toe disks large, largest equal to or just smaller than largest finger disks; modal toe webbing formula in males I 1 1/2-2 II 1-2 2/3 III 1 1/3-2 1/2 IV 2^{+}-1^{-} V, in females I 2^{-}-2^{+} II 1 1/4-2 2/3 III 1 1/2-3^{-} IV 2 1/2-1^{+} V; large ovoid inner metatarsal tubercle; outer indistinct or very small and round; heel usually with a single tubercle or small calcar, rarely smooth; weak to distinct inner tarsal fold along length of tarsus; outer tarsal texture smooth or slightly warty; sole of foot smooth or (usually) with scattered regular large fleshy tubercles.

Dorsal pattern variable, usually including some combination of tan, brown, or gray cross bands or stripes on body or anastomosing patterns, cross stripes or bands, when present, more regular posteriorly, cream spots present or absent, upper limbs tan with brown cross bands; dark mid-dorsal stripe from tip of snout extending to sacral region, vent, or absent, dorsal and ventral colors sharply to indistincty demarcated along outer hand and forearm fold and outer foot and outer tarsus; heels, elbows, and supra-vent region sometimes with bold enamel cream spots; canthal stripe faint or absent, rest of face uniform tan or brown; flanks with vertical tan and brown or cream and brown stripes, stripes sometimes anastomosing, distinct along entire flank or more distinct posteriorly; throat and chest speckled brown, front of belly with scattered melanophores, posterior belly mostly lacking melanophores; some vertical brown stripes on posterior surface of thighs continuous with stripes of front of thighs, latter stripes sometimes faint.

SVL 56.1-66.6, mean 62.2 mm (males), 56.3-64.8, mean 60.0 mm (females); mean head

length 36% SVL; mean head width 37% SVL (males), 36% SVl (females); mean thigh length 51% SVL (males), 50% SVL (females); mean shank length 53% SVL; mean foot length 45% SVL (males), 43% SVL (females).

Life Colors. — Dorsum tan with darker brown markings; cream spots on back, elbows, heels, and vent; upper limb surfaces banded with gray or orange-tan; flanks golden yellow, more intense in groin with pale transverse banding. Throat and chest cream or yellow with black dots; belly and undersides of thigh orange, under surfaces of arms, hands, and rest of legs pink flesh color. Thigh with narrow dark gray bands continuous from front across top to rear surfaces, front and rear ground color transparent purplish or thigh with narrow tan bands dorsally and dark gray bands on a pink flesh colored ground on front and backs of thighs, same pattern continuing on concealed surface of shank.

Larval Morphology. — Tadpoles unknown from Boracéia.

Advertisement Call. — Call unknown.

Ecology. — No specimens have been heard calling. Is is surprising that we have no record of the call of this species at Boracéia because the Rands and Heyer made special efforts to track down unfamiliar calls. This is made more curious because we are unable to find any description of the call of the species in the literature though there are descriptions of its close relatives. At Boracéia the closely related *H. hylax* is common and conspicuous since the calls are loud and it calls for much of the year. Possibly *H. circumdata* has a call so similar to that of *H. hylax* that we did not distinghuish them, or because *H. circumdata* is shyer and called from places that were more difficult to reach, or was rarer or perhaps just on chance alone we found only *H. hylax* when we searched for the origins of the calls. However, it would be most unusual for two sympatric species to have calls so similar that they could be consistently confused. Another possibility is that *H. circumdata* is voiceless; this is possible but unlikely because it has fully developed vocal sacs. A third possibility is that *H. circumdata* calls at a time (perhaps very late at night, during the winter) or in a place that we did not sample adequately. Whatever the reason, the call of *H. circumdata* remains to be described.

All specimens have been taken at night from vegetation in the forest and in clearings, mostly away from any streams or ponds. Specimens have been collected in November through March.

Hyla faber Wied

Color Figure 14

Hyla faber Wied, 1821. Original description.

Diagnosis. — The Boracéia species with distinct prepollices are *Hyla albopunctata, H. astartea, H. circumdata, H. faber, H. hylax, H. multilineata, H. pardalis, H. polytaenia,* and *H. prasina*. In all of these species, the prepollex is present in both sexes (although larger in males) and a slender bony spine is covered or projects only at the tip. In *Leptodactylus flavopictus* and *L. ocellatus,* cornified, fully exposed spines are present in the prepollical area only in males. Of the Boracéia hylids with prepollices, *H. faber* is the largest, with an adult SVL of at least 95 mm (no other member of this cluster exceeds 75 mm SVL). *Hyla faber* also has a smooth heel; most other species with prepollices usually have a tubercle, calcar, and/or flap on the heel.

Adult Morphology (N = 10 males, 1 female). — Snout outline almost subelliptical to rounded from above, rounded in profile; no cranial crests; upper eyelid lacking distinctive features; tympanum distinct, largest diameter greater than 1/2 to 2/3 diameter of eye; male vocal sac single, not expanded externally; males with vocal slits; vomerine teeth in acute or arched-acute series, lying mostly between choanae, lateral most portions extending posterior to choanae; finger lengths I<II<IV<III; finger disks large but largest disks smaller than tympanum; modal finger webbing formula I trace II 1 1/2-2 1/3 III 2^{+}-2^{-} IV; finger subarticular tubercles moderately developed, single or slightly bifid, males without thumb asperities; outer forearm lacking a fold or with a slight to noticeble fold; prepollex present in both sexes, spines exposed or covered in males; very weak to moderately developed supratympanic fold; dorsal texture smooth or very slightly granular; front of throat smooth, belly granular; toe lengths I<II<V<III<IV; toe disks

large, largest disks noticeably smaller than largest finger disks to same size as finger disks; modal toe webbing formula I 1-2⁻ II 1⁻-2 III 1-2⁺ IV 2-1⁻ V; inner metatarsal tubercle oval, much larger than round indistinct outer metatarsal tubercle; heels lacking distinctive features; weak but distinct inner tarsal fold along entire length of tarsus; outer tarsal texture smooth or glandular; sole of foot with light fleshy tubercles.

Dorsal pattern variable, mottled or lichenous tans, browns and/or grays, scattered (or not) with large or small dark dots, dark mid-dorsal stripe from top of snout to scapula or ilial region, upper limb surfaces faintly to distinctly banded, outer fingers, forearms, tarsi, heels, toes with sharp demarcation of dorsal pattern by light pin stripe, bordered by dark below, outer shank with dark longitudinal band, supratympanic fold dark outlined or not, dark vent seat patch distinctly bordered above by cream pin stripe, sharply blending into surrounding pattern below; face uniform, same as dorsal color; flanks with faint to distinct dark and light vertical lines, blending in with dorsal and ventral patterns, on lower flanks, light granules with dark interstices; males with dark gray throats, chest light or dark gray, arm insertion areas and belly cream, female with dirty cream throat with light brown dots, belly creamy orange; posterior surface of thigh light with indications of dark vertical stripes or dark with indistinct darker vertical stripes or so dark that almost uniform.

SVL 97.0-104.0, mean 99.2 mm (males), 103.8 mm (female); mean head length 36% SVL (males), 35% SVL (female); mean head width 38% SVL (males), 39% SVL (female); mean thigh length 53% SVL (males), 55% SVL (female), mean shank length 55% SVL (males), 56% SVL (female); mean foot length 44% SVL (males), 45% SVL (female).

Life Colors. — Iris white with black reticulations. Dorsum dirty green brown with darker brown markings or gray-pink to walnut brown with lighter and darker blotching; cream stripe along outside of foot to around heel, on forearm and above vent; mid-dorsal stripe dark brown. Throat opalescent pink or dark gray; lower lip white outlined; belly bright orange-yellow; under surfaces of legs transparent yellow to bright orange-yellow.

Larval Morphology. — Tadpoles not collected from Boracéia. Cei (1980) described and figured the larvae from specimens collected at Tijuca, Rio de Janeiro.

Advertisement Call. — Calls of individual notes given sporadically or at a rate of 1.0-1.6 per s; call/note duration 0.10-0.12 s; call/note structure complex, initial portion of call of strongest intensity and of 2 or 3 partial pulses producing a broad dominant frequency range of about 250-1800 Hz immediately followed by quieter portion, frequency modulated, starting with a dominant (=fundamental) frequency of about 300-400 Hz, descending slightly but perceptibly (on audiospectrograms) during reminder of call, latter call portion with harmonics distinctly or indistinctly visible (Figure 44).

Ecology. — Males were heard calling at night from the edge of Lago do Aterro and the quarry. All specimens were collected at night, mostly from the quarry or Lago do Aterro. In 1963-64 a chorus was heard in the quarry. Several individuals have been found in the clearing at the station, but no calling has been heard there. Sometimes males called from shallow circular depressions; eggs and tadpoles occurred in such depressions that were probably made or at least modified by the frogs. One individual was taken from a leaf on low vegetation in the forest away from water. Specimens have been taken from September through March.

Hyla hylax Heyer

Color figure 15

Hyla hylax Heyer, 1985b. Original description.

Diagnosis. — The Boracéia species with distinct prepollices are *Hyla albopunctata, H. astartea, H. circumdata, H. faber, H. hylax, H. multilineata, H. pardalis, H. polytaenia,* and *H. prasina.* In all of these species, the prepollex is present in both sexes (although larger in males) and a slender bony spine is covered or projects only at the tip. In *Leptodactylus flavopictus* and *L. ocellatus,* cornified, fully exposed spines are present in the prepollical area only in males. *Hyla hylax* lacks the parallel dorsal stripes of *H. multilineata* and *H. polytaenia. Hyla hylax* has finger webbing; *Hyla albopunctata* does not.

Hyla hylax lacks the distinct pair of white dorsolateral stripes evident in *H. prasina*. *Hyla hylax* has less finger webbing (maximum web of 2 1/2 on outer side of finger III) than *H. faber* and *pardalis* (minimum web of 2 1/4 on outer side of finger III). *Hyla hylax* further differs from *H. faber* in being smaller (maximum SVL for *hylax* 64 mm; minimum SVL for *faber* 95 mm); the ulnar and tarsal fringes are much better developed in *pardalis* than in *hylax*. *Hyla hylax* is larger (minimum SVL 55 mm) than *H. astartea* (maximum SVL 44 mm) and has a tan or brown dorsum usually with distinct transverse bars; *H.astertea* is creamy tan dorsally and lacks transverse bands. The tympanum is moderate in *H. hylax* (diameter just less than 1/2 eye diameter), large in *H. circumdata* (diameter 3/5-3/4 eye diameter).

Adult Morphology (N = 10 males, 2 females). — Snout outline subovoid to semicircular from above, rounded or rounded-vertical in profile; no cranial crests; no distinctive features on upper eyelids; tympanum distinct, moderate, diameter equal to or just greater than 1/2 diameter of eye; male vocal sac single, slightly inflated externally; males with vocal slits; vomerine teeth in arched acute series, medial portions almost in contact, medial extent between choanae, lateral portions extending posterior to choanae; finger lengths I<II<IV<III; finger disks large, largest same size or just larger or just smaller than tympanum; modal finger webbing formula I trace II 2-3^{+} III 2 2/3-2 1/2 IV; finger subarticular tubercles moderately developed, single or barely bifid under finger IV; males with small brown nuptial pad on base of thumb medial to prepollex, male forearm slightly to moderately hypertrophied; outer forearm with a weak series of warts or a warty ridge; prepollex well developed, somewhat less so in females, spine exposed or not in males; supratympanic fold weakly developed, glandular supra-anal fold; dorsum smooth; chin smooth, chest striated, belly granular; toe lengths I<II<V< or =III<IV; toe disks large, largest just smaller than or equal to largest finger disks; modal toe webbing formula I 2^{-}-2 II 1^{-}-2 1/4 III 1-21/2 IV 2^{+}-1 V; inner metatarsal tubercle large, ovoid, outer metatasal tubercle very small, round or not visible; heel with a small to moderate sized calcar, other tubercles sometimes present; inner tarsal fold present or absent, if present, extending full length of tarsus; outer surface of tarsus smooth or slightly warty; sole of foot with low, rounded fleshy tubercles.

Dorsal pattern variable, ranging from almost uniform tan to distinctly dark cross banded or lichenous brown, dark mid-dorsal stripe from tip of snout to scapular region or sacral region present or absent, upper limb surfaces brown with darker brown cross bands, slight dark demarcation of dorsal and ventral color along outer forearm, black outlined cream on vent fold, heel calcar, and spots in elbow present or absent, light tan stripe on outside edge of foot and tarsus to calcar present or absent; face tan or brown with dark speckles or streaks; flanks light tan with dark brown vertical stripes of equal width or lighter areas 3-4 times as wide as dark stripes, in some individuals every other dark flank stripe continuous with dark transverse dorsal bands; chin with heavy or light speckling of brown, rest of belly uniform cream or with very scattered melanophores; posterior surface of thigh with dark vertical stripes on a lighter uniform ground, some individuals with dark stripes continuous over upper thigh with stripes on front of thigh.

SVL 55-3.61.5 mean 58.1 mm (males), 60.0-63.4 (females); [remaining values for males only; the values for females all fall within the ranges found for males] mean head length 35% SVL; mean head width 34% SVL; mean thigh length 48% SVL; mean shank length 51% SVL; mean foot length 40% SVL.

Life Colors. — Iris golden. Dorsum khaki (reddish at night) with darker cross bands, with or without cream blotches; dark brown mid-dorsal stripe; flanks yellow with dark brown bars; upper hands orange. Chin, throat, belly and patch on under thigh with salmon pink cast; rest of underlimbs fleshy purple. Front and back of thighs, concealed portion of shank yellow, orange, or purple with black lines.

Larval Morphology. — Tadpoles unknown.

Advertisement Call. — Calls given sporadically; call duration about 0.5-1.0 s; calls pulsed, pulses grouped together forming 5-10 notes within call initially, note duration about 0.03-0.08 s, note rate about 10 per s, more continuous but still not evenly pulsed at end of call; pulse rate about 110-175 per s, not completely uniform

within a call; first half of call most intense; calls not noticeably frequency modulated; dominant frequency range 400-2300 Hz; no apparent harmonic structure; distinct sidebands due to pulsatile nature of call (Figure 45).

Ecology. — Males call from the ground or on low vegetation near forest streams; calling sites include rolled up palm frond, stem of a shrub, mouth of a hole, center of a bromeliad, a cavity under a rock or stick or on the ground. Almost all individuals were collected at night from the forest, some well away from any stream, presumably foraging in the understory; one individual was collected from a clearing and a few individuals were collected during the day. The few individuals collected during the day were apparently inactive, either on vegetation or in rolled up leaves. Specimens have been collected from September through March and June.

Hyla leucopygia Cruz and Peixoto

Color Figure 16

Hyla leucopygia Cruz and Peixoto, 1985. Original description.

Diagnosis. — *Hyla leucopygia* shares the colors of green in life and whitish, lavender, purple, or bluish in preservative with *Centrolenella eurygnatha, C. uranoscopa, Hyla albofrenata, H. albosignata, H. prasina, Phyllomedusa appendiculata, P. cochranae,* and *Sphaenorhynchus orophilus. Hyla leucopygia* has vomerine teeth; *Centrolenella* and *Phyllomedusa* lack vomerine teeth. *Hyla leucopygia* lacks a prepollex; *H. prasina* has a prepollex. *Hyla leucopygia* lacks a distinct postorbital stripe; such stripes occur in *H. albofrenta* and *S. orophilus. Hyla leucopygia* has a white outlined transverse ridge above the vent; the vent is completely encircled by a white outlined, broken, transversely oval ridge in *H. albosignata.*

Adult Morphology (N = 7 males). — Snout outline subelliptical to subovoid from above, rounded in profile; no cranial crests; upper eyelids lacking distinctive features; tympanum large, distinct, diameter about 2/3 to 3/4 eye diameter; male vocal sac single, slightly expanded or not; males with vocal slits; vomerine teeth in acute or acutely arched series between choanae (MZUSP 30835 lacking vomerine teeth); finger lengths I<II< or =IV<III; finger disks large, largest on fingers II, III, IV, largest disks much smaller than tympanum (due to large tympanum); modal finger webbing formula I trace II 1 1/3-2 1/3 III 2⁻-1 1/2 IV; finger subarticular tubercles moderately developed, single; no male thumb asperities; outer forearm with distinct, smooth fold; no prepollex; moderate supratympanic fold, supravent dermal ridge, diffuse glands along entire flanks; dorsum smooth; venter granular; toe lengths I<II<III< or =V<IV; toe disks of moderate size, largest just smaller than largest finger disks; modal toe webbing formula I 2⁻-2 1/3 II 1⁺-2 1/2 III 1⁺-2 1/2 IV 2⁺-1 V; prominent ovate inner metatarsal tubercle, outer not visible or round and indistinct; heel with a fold and well developed calcar; weak inner tarsal fold present or absent, well developed smooth fold on outer tarsus for entire length; outer tarsal texture smooth or with glandular appearing cells; sole of foot granular with fleshy rounded tubercl s.

Dorsum mostly pigmentless with a scattering of small brown and white dots, outer ulnar, tarsal, and supra-vent folds white highlighted. white sometimes spreading laterally onto hands, feet, ventral forearm and tarsus; face same pattern as dorsum; dorsal and ventral patterns meeting low on flanks; chin white outlined, belly creamy yellow with bits of white pigment flecks; posterior surface of thigh pigmentless.

SVL 38.2 - 44.2, mean 41.0 mm (males); mean head length 36% SVL, mean head width 35% SVL; mean thigh length 46% SVL; mean shank length 48% SVL; mean foot length 44% SVL.

Life Colors. — Iris gold or silver centrally, red or golden bronze peripherally. Dorsum bright grass green with small white spots, sides lighter; vent fold, heels, outsides of feet, forearms and hands white; vent papillae yellow; sides near groin yellow; bones green. Lower lip white outlined; chin chartreuse; chest bluish; belly green on sides and pale yellow in center; under arms and base of belly Prussian blue, lighter at joints and under thigh and shank. Posterior thigh same color as dorsum, lacking white spots.

Larval Morphology. — Tadpoles unknown.

Advertisement Call. — Calls of individual notes, given sporadically or frequently up to a

rate of 1-3 notes per s; note duration 0.08.0-15 s; notes not pulsed; calls gradually increasing and fading in intensity; notes usually not frequency modulated, occasionally rising sharply in frequency initially then either constant in frequency or descending in frequency for remainder of note; notes with strong harmonic structure, with up to at least 7 harmonics visible; dominant frequency spread among fundamental and second and third harmonics, loudest band varying among notes but usually the third harmonic, fundamental frequency range 650-1000 Hz, second harmonic range 1250-1800 Hz, third harmonic range 2000-2700 Hz (Figure 46).

Ecology. — This species, like *H. albofrenata*, is a persistent caller, usually in small groups of 4 to 5 males high in trees in forest near streams. One male was recorded at night in the forest away from water from a leaf on a small tree. All other specimens have been taken at night from vegetation in the forest or at the forest edge. Specimens have been collected in December and February and heard calling from August to May.

Hyla microps Peters

Color Figure 17

Hyla microps Peters, 1872. Original description.

Diagnosis. — The combination of small size (less than 30 mm SVL), toe disks with circumferential grooves, hand and foot webbing, a black axillary membrane, a distinct pigmentless area on the posterior surface of the thigh (bright orange-red in life), and a white area under the eye and below the tympanum distinguishes *H. microps* from all other Boracéia frogs.

Adult Morphology (N = 10 males, 1 female). — Snout outline nearly rounded to semicircular from above, vertical, slightly vertically acute, or vertically rounded in profile; no cranial crests; upper eyelids with small warts in well preserved specimens; tympanum distinct, diameter just less than or about equal eye diameter; vocal sac in males single, greatly expanded externally, extending onto chest; males with vocal slits; vomerine teeth in transverse series just posterior to choanae, contiguous or slightly separated medially; finger lengths I<IV= or <II<III; finger disks moderately large, largest about same size as tympanum; modal finger webbing formula I trace II 1 1/2-3⁻ III 2 1/2 -2 IV; finger subarticular tubercles moderately developed, bifid at least under finger IV; no male thumb asperities; outer forearm with rugose fold or series of low warts; no prepollex; distinct axillary membrane; supratympanic fold indistinct; dorsum smooth; venter granular; toe lengths I<II<V< or =III<IV; largest toe disks about same size as largest finger disks; modal toe webbing formula I 2⁻-2⁺ II 1⁺-2 1/3 III 1⁺-2 1/2 IV 2 1/2-1⁺ V; inner metatarsal tubercle oval, outer small and round or indistinct; heel with 1-4 warty protuberances, prominent or not; no inner tarsal fold, outer rugose tarsal fold or series of low warts on outer tarsus; outer tarsal texture smooth or glandular; sole of foot distinctly or indistinctly granular.

Dorsal pattern complex lichenous brown with irregular dark interorbital and sacral markings to almost uniform, upper limbs barred to almost uniform, outer forearm, tarsal, foot and hand folds continuously highlighted in white or by series of white spots; white seat patch; face with distinct white mark below tympanum and under eye, rest of face complex pattern of browns or almost uniform; flanks form almost same pattern as on dorsum to bold contrasting pattern of brilliant white with dark brown irregular blotches; anterior edge of throat brownish or brown and white, vocal sac mostly unpigmented, belly whitish with scattered brown dots; posterior surface of thigh with central oblong pigmentless area bordered medially by dark brown, light spot on inner surface of shank in males, bold light and dark pattern on inner surface of shank in female.

SVL 20.8-23.6, mean 22.5 mm (males), 29.3 mm (female); mean head length 31% SVL (males), 29% SVL (female); mean head width 30% SVL (males), 29% SVL (female); mean thigh length 44% SVL (males),46% SVL (female); mean shank length 47% SVL (males), 49% SVL (female); mean foot length 41% SVL.

Life Colors — Iris dark silver, yellow, or golden centrally, copper colored peripherally. Dorsum brown, sometimes with dirty red spots; subocular spot cream-yellow; some with scattered metallic green spots on face and, less often, sides of back. Inner two toes bright orange. Flanks brown with white or yellow mottle. Throat black with salt and pepper on lower lip

fringe; chest gray; belly white with black markings; seat patch white, outlined with broad black lines. Front and back of thighs bright orange red.

Larval Morphology. — Body oval in dorsal view, as wide as deep; snout broadly rounded in dorsal view; nostril nearer tip of snout than eye; distance between nares 94% interorbital width; nares small, round and directed anteriorly; eye 20% body length, situated dorsolaterally; opening of the sinistral spiracle directed posteriorly on the midline about 66% body length; anal tube short and dextral; tail higher than body; dorsal fin origin midway on body length; dorsal and ventral fin arched; tail musculature reaching the tip of the xiphicercal tail; anteroventral mouth width equal to 18% body width; upper lip absent, lower lip with a single row of oral papillae; teeth absent; beak strongly developed and finely serrated.

Body and tail musculature brownish with creamy areas, fins creamy with brownish marbling (Figure 17).

Larval Habitat. — Tadpoles were collected from the small, deep, black-water pond next to the road, bordered by forest and road, near the scientists' residence. This pond is apparently permanent.

Advertisement Call. — Two kinds of calls were heard and recorded.

The predominant call (type A) given sporadically to frequently, of 1-3 notes, the first note longest, about 0.20-0-0.35 s, pulsed at a rate of 130-150 per s, the following 1 or 2 secondary notes (when present) shorter, about 0.09-0.10 s, given at a rate of just less than 2 per s; secondary notes also pulsatile, given at a rate of about 70-90 pulses per s; structure of pulses complex; individual notes intensity modulated, increasing in loudness; no frequency modulation; dominant (= fundamental) frequency range 4500-5800 Hz; calls without harmonic structure; sidebands due to pulsatile nature of call (Figure 47, upper wave form and A).

The type B call (interaction?) given sporadically; duration about 0.5-0.6 s; call of distinct notes/pulses, given at a rate of about 45-55 per s; structure of pulse/notes complex, very like that of pulses in call type A; calls with modest intensity changes, beginning of call quieter; no frequency modulation; dominant (= fundamental) frequency range 4700-5500 Hz; calls without harmonic structure; sidebands evident, apparently due to complex structure of notes/pulses (Figure 47, lower wave form and B).

Ecology. — Males call at night from grass or low vegetation over or next to ponds at the forest edge or in clearings. All specimens have been collected at night from similar situations as the calling males described above. Specimens have been collected in October through February.

Hyla minuta Peters

Color Figure 18

Hyla minuta Peters, 1872. Original description.

Diagnosis. — *Hyla minuta* is a small species (less than 24 mm SVL) with toe disks with circumferential grooves, hand and foot webbing, and a distinctive dorsal pattern of a usually distinct dark interorbital triangle with two dark lined extensions to the sacral region.

Adult Morphology (N = 10 males, 6 females). — Snout outline nearly rounded to almost semicircular from above, rounded in profile; no cranial crests; upper eyelids same texture as rest of dorsum, without distinctive features; tympanum indistinctly visible or hidden, moderate size, diameter just less than 1/2 diameter of eye; male vocal sac single, greatly expanded externally; males with vocal slits; vomerine teeth in short obtuse or transverse series between choanae or on line at posterior edge of choanae; finger lengths I<II<IV<III; finger disks moderate sized, largest disks about equal to or smaller than tympanum; modal finger webbing formula I trace II 1 3/4-3$^-$ III 2 1/2-2$^+$ IV; no thumb asperities in males; outer forearm fold absent or very weakly developed; no prepollex; weak supratympanic fold, pronounced vent sheath extending over vent from above; dorsum smooth or with scattered, small, indistinct tubercles; venter granular; toe lengths I<II<III=V<IV: toe disks moderate sized, largest about same size as largest finger disks; modal toe webbing formula I 1-2 II 1-2 III 1-2$^+$ IV 2$^+$-1 V; inner metatarsal tubercle oval, outer indistinct or absent; heel smooth or with a glandular ridge or indistinct glandular appearing bumps; weakly developed inner tarsal fold extending length of tarsus, incomplete outer tarsal

fold near heel present or absent; outer tarsal texture smooth; sole of foot smooth or granular.

Dorsal pattern yellow tan or tan with scattered black dots with gray or brown interorbital triangle from which two narrow to posteriorly expanded stripes extending to sacral region, forming with the triangle a distinctive dark hourglass, or dorsal stripes and interorbital triangle so faint the pattern is hardly visible, upper limbs barred or uniform, heel, outer tarsus and foot (but not outer forearm) with contrasting dark and light patterns meeting sharply, often with stripe between, dark seat patch bordered above by light or white line, ill-defined but a most always visible dark stripe from back of eye, over tympanum, ending either above shoulder or mid-body; face with indistinct or distinct loreal stripe, sharply defined above, ill-defined below, concentration of melanophores in loreal region, distinctive or ill-defined light area on upper lip, particularly under the eye; flanks with joining of dorsal and ventral patterns on lower portions; undersides of males with scattered melanophores around chin and throat, chest lacking pigment and a mid-ventral white pigment band down belly; undersides of females with brown dotted chin and entire belly, throat and chest whitish; posterior surface of thigh with scattered melanophores or with an indistict proximal pigmentless spot.

SVL 19.2-21.4, mean 19.9 mm (males), 20.0-22.2, mean 21.1 mm (females); mean head length 32% SVL (males), 33% SVL (females); mean head width 31% SVL (males), 32% SVL (females); mean thigh length 47% SVL; mean shank length 51% SVL (males), 52% (females); mean foot length 45% SVL (males), 44% SVL (females).

Life Colors. — Iris bronze to pale gold. Dorsum dirty cream or yellow with khaki or brown dorsal pattern; upper limbs dirty yellow with brown bands or marks; fingers and toes yellow, orange, or red; some individuals with cream stripe over vent and on heels; undersides of males with yellow throats, cream bellies, undersurfaces of limbs flesh colored with fine black dots, undersides of females with white chin and throat, dark white belly, undersurfaces of limbs tranparent orange red. Posterior surface of thigh fleshy orange color.

Larval Morphology. — Body oval in dorsal view, deeper than wide; snout broadly rounded in dorsal view; nostril closer to tip of snout than eye; distance between nares 85% interorbital width; nares elliptical, situated laterally and directed anteriorly; eye dorsolateral, 19% body length; opening of the sinistral spiracle directed posteriorly on the inferior half of the body about 73% body length; anal tube very short and dextral; tail higher than body; dorsal fin origin midway on the body length; fins arched; tail musculature reaching the tip of xiphicercal tail; mouth anteroventral, width 30% body width; mouth directed anteriorly; two rows of oral papillae broadly interrupted on upper lip; tooth row formula 1/2; teeth weakly developed; beak moderately developed and finely serrated.

Body and tail white with brown scattered spots; brown stripe from eye to snout; longitudinal median brown stripe on first third of tail musculature; brown fringe on dorsal and ventral fins; silvery-white belly. In life, body and tail lemon-yellow with black spots; dorsum of the body more olive; black stripe from eye to snout; red sometimes occurring on tail; iris golden (Figure 18).

Larval Habitat. — Tadpoles were collected from the deeper ponds on the quarry floor and from a seasonally algae-filled water reservoir tank in a clearing.

Advertisement Call. — Calls given sporadically, of 1-3 notes, call duration 0.3-1.0 s, first note longest 0.13-0.16 s duration, following secondary notes, if present, shorter, about 0.05 s duration; note rate 2-3 per s; notes pulsed at about 160-180 pulses per s; note wave form complex; primary notes beginning quietly, ending loudly; primary notes slightly frequency modulated in a complex fashion; fundamental frequency centering on 3000 Hz, dominant frequency (5500-6500 Hz) centering on 6000 Hz; notes with harmonic structure; side bands due to pulsatile nature of notes (Figure 48).

Ecology. — This is a common species at Boracéia. All specimens have been collected at night from clearings, mostly on low vegetation over or next to temporary and permanent ponds including the quarry. It overlaps in places with *H. microps* but also occurs in more open microhabitats. Specimens have been collected in October through March.

Hyla multilineata A. Lutz and B. Lutz

Color Figure 19

Hyla multilineata A. Lutz and B. Lutz, 1939. Original description.

Nomenclatural Note. — Cohran (1955:84) and Duellman (1977:38), among others, consider *multilineata* a subspecies of *Hyla bischoffi* Boulenger. We have not evaluated the species level status of *multilineata* with respect to *bischoffi*, but use the name *multilineata* solely because the Boracéia specimens are conspecific with *multilineata* described from Alto da Serra, São Paulo.

Diagnosis. — The Boracéia species with distinct prepollices are *Hyla albopunctata, H. astartea, H. circumdata, H. faber, H. hylax, H. multilineata, H. pardalis, H. polytaenia,* and *H. prasina.* In all of these species, the prepollex is present in both sexes (although larger in males) and a slender bony spine is covered or projecting only at the tip. In *Leptodactylus flavopictus* and *ocellatus*, cornified, fully exposed spines are present in the prepollical area only in males. *Hyla multilineata* has a series of light and dark dorsolateral stripes and a distinct dark band on the tibia; it shares these features only with *H. polytaenia* of the Boracéia frogs with prepollices. The posterior surface of the thigh usually has distinct dark vertical bars or ocelli in *H. multilineata; H. polytaenia* usually has a uniform posterior surface of the thigh. *Hyla multilineata* is larger (males 36-47 mm SVL, females 57-60 mm SVL) than *H. polytaenia* (males 27-33 mm SVL, females 35-40 mm SVL).

Adult Morphology (N = 10 males, 2 females). — Snout outline subovoid to nearly rounded from above, rounded in profile; no cranial crests; upper eyelids usually lacking ornamentation, rarely with a single ridge; tympanum sometimes difficult to see but usually visible externally, diameter about 1/2 eye diameter; male vocal sac single, small; males with vocal slits; vomerine teeth in short acute series, between or just posterior to choanae, in medial contact or separated by less than length of one vomerine tooth row; finger lengths I<II< or =IV< or <<III; finger disks moderate to large, largest disks smaller than or about same size as tympanum; modal finger webbing formula I none II 2-3^{+} III 2 2/3-2 1/2 IV; finger subarticular tubercles moderately developed, single or bifid; no thumb asperities; outer forearm with a weak glandular fold to a distinct rugose fold; prepollex large in males, spines usually not exposed, prepollex rudimentary in females; weakly developed pair of dorsolateral folds, supratympanic fold extending to dorsolateral fold and ending at 1/3 body length, vent flaps slightly to moderately pronounced; dorsum smooth; venter granular; toe lengths I< or =II<III=V<IV; toe disks moderately developed, largest about same size as finger disks; modal toe webbing formula I 2-2 1/2 II 1 3/4-3 III 2-3 IV 2 1/2-1^{+}V; inner metatarsal tubercle oval, outer absent or very indistinct; heel with moderate to large calcar; weakly to distinctly developed inner tarsal fold extending full length of tarsus, less well developed outer tarsal fold; outer tarsal texture smooth to weakly granular; sole of foot granular.

Dorsal pattern striped, ranging from almost uniform tan with small random dots and two broad indistinct dark stripes on either side of midline from scapula to groin to a pattern of distinct series of narrow darker and lighter tan and brown stripes randomly dotted with small brown spots, upper limbs striped to uniform cream with random small dots, outer shank with a complete (sometimes irregular) dark stripe bordered above by a light thin stripe, vent flaps dark highlighted as a small seat patch; dark canthal stripe from tip of snout to eye, upper lip with or without a narrow dark brown highlight bordered above by a light stripe or light area; flanks with light brown band from behind eye through tympanum and fading out in mid-flank, with or without dark flecks in groin; venter cream, periphery of throat and chin to entire chin and chest area with small dark dots; posterior surface of thigh pattern quite variable, from a very distinct series of ocelli, to a series of ocelli open below, to a series of dark elongate spots on the upper portion and scattered smaller dark spots on the lower portion to random small dark marks on the upper portion and no pigment on most of the posterior thigh surface.

SVL 36.9-46.1, mean 42.8 (males), 57.0-59.6 mm (females); [remaining measurements data for males, the values for the two females fall within

the male value ranges] mean head length 35% SVL; mean head width 33% SVL; mean thigh length 49% SVL; mean shank length 53% SVL; mean foot length 43% SVL.

Life Colors. — Iris light banana yellow above and below, or silvery tan below, or uniform bronze. Dorsum cream to pale gold with brown stripes (distinct at night, sometimes very faint by day), in some individuals the darker dorsal stripes green tinged; elbows, vent, outer shank and heels green; canthal stripe green, small green spot behind tympanum; groin red; front of thighs, tarsus and foot burnt orange. Undersides of thigh and shank red. Posterior surface of thigh burnt orange with black or translucent purple or blue dark markings and light iridescent blue dots.

Larval Morphology. — Body oval in dorsal view, wider than deep; snout rounded in dorsal view; nostril midway between eye and tip of snout; distance between nares 79% interorbital width; nares reniform; eye dorsolateral, 14% body length; opening of the sinistral spiracle directed posterodorsally on the midline about 75% body length; anal tube dextral; tail as high as body; dorsal fin origin extending slightly onto the body; dorsal fin slightly arched and ventral fin relatively straight; tail musculature reaching the pointed tail tip; mouth anteroventral, width 45% body width; a single row of briefly interrupted papillae on upper lip; tooth row formula 2(2)/3(1); beak moderately developed and finely serrated.

Body and tail dark gray, first third of tail musculature less pigmented. In life, body and tail black with scattered white flecks (Figure 19).

Larval Habitat. — Tadpoles were collected from the large permanent pond, "Lago do Aterro" (Figure 5).

Advertisement Call. — Two types of calls are given. Both are surprisingly quiet for a frog of this size.

Call type 1. Calls of 1 or 2 notes, 2 note calls given almost as frequently as 1 note calls. When actively calling, calls given at a rate of about 1 every 4 s; call duration 0.07-0.45 s; note duration 0.07-0.10 s; notes pulsed, 8-11 pulses per note, given at a rate of about 100-200 pulses per s, decreasing through note; notes with no frequency modulation; notes of same intensity through beginning and middle, quieter at very end of call; dominant (= fundamental) frequency broadcast channel 1100-2000 Hz; very weak third harmonic sometimes broadcast; sidebands due to pulsatile nature of note (Figure 49).

Call type 2. Call given infrequently, consisting of a single note with structure similar to that of type 1 call, but of briefer duration (about 0.08) and a high pulse rate (about 200-250 pulses per s) and followed by a series of 9-14 notes; call duration 0.07-1.05 s; secondary note duration about 0.02 s; secondary notes given at a rate of 16-33 per s; each secondary note of a single pulse; series of notes not intensity modulated; no frequency modulation; dominant (= fundamental) frequency broadcast channel 1200-2200 Hz (Figure 50).

Ecology. — All specimens were collected at night, mostly from low vegetation or grass in pasture ponds or at the quarry. One individual was taken on a bromeliad leaf at the edge of a forest stream. This species resembles *H. polytaenia*. It is less frequently seen, and less abundant when present — typically only one or two males per night were found at a pond. Specimens were collected from December through March.

Hyla pardalis Spix

Color Figure 20

Hyla pardalis Spix, 1824. Original description.

Diagnosis. — The Boracéia species with distinct prepollices are *Hyla albopunctata, H. astartea, H. circumdata, H. faber, H. hylax, H. multilineata, H. pardalis, H. polytaenia,* and *H. prasina*. In all of these species, the prepollex is present in both sexes (although larger in males) and a slender bony spine is covered or projecting only at the tip. In *Leptodactylus flavopictus* and *L. ocellatus*, cornified, fully exposed spines are present in the prepollical area only in males. *Hyla pardalis* has more extensively developed scalloped forearm and tarsal flaps and more hand webbing, with the webbing reaching at least to the base of the first subarticualar tubercle on the fourth finger, than the other *Hyla* with distinct prepollices, in which the finger webbing does not extend beyond the second subarticular tubercle of the fourth finger.

Adult Morphology (N = 10 males, 8 females). — Snout outline rounded to nearly rounded from above, rounded to rounded-vertical in profile; no cranial crests; upper eyelid with one prominent warty tubercle in some individuals, in other individuals the upper eyelid texture same as dorsal texture; tympanum distinct, large, diameter about 2/3 eye diameter; male vocal sac single, somewhat expanded; males with vocal slits; vomerine teeth in long gently arched acute series between and on level of posterior borders of choanae, in medial contact or barely separated; finger lengths I<II<IV<III; finger disks large, largest disks just smaller than tympanum; modal finger webbing formula I 2⁺-2⁺ II 1⁻-2 III 1 1/2-1⁻IV; finger subarticular tubercles moderately large, pungent or not, single or bifid; no thumb asperities; outer forearm with distinct, scalloped fold, fold continuous with fold on edge of outer finger; prepollex well developed in males, spine exposed or not, prepollex present but not as well developed in females; supratympanic fold moderately developed, a pair of scalloped folds under vent; dorsal texture granular to very pronounced warty-granular; belly areolate; toe lengths I<II<V< or =III<IV; largest toe disks just smaller than to noticeably smaller than largest finger disks; modal toe webbing formula I 1⁻-1 1/2 II 1⁻-1 2/3 III1⁻-2⁻ IV 1 2/3-1⁻V; inner metatarsal tubercle oval, outer very small, round, indistinct; heel with scalloped fold developed into distinct calcar at end; weak inner tarsal fold along length of tarsus, sometimes indistinct near foot, strongly developed scalloped outer tarsal fold continous with fold on edge of outer toe; outer tarsal texture smooth; sole of foot granular or with series of small fleshy tubercles.

Dorsal pattern usually complex lichenous brown, sometimes irregularly spotted or almost uniform brown, upper limbs weakly banded to uniform, limb fringes barely highlighted; face pattern usually same as dorsal pattern, sometimes with indistinct dark loreal stripe, or supratympanic fold dark highlighted; flanks with series of alternating narrow to somewhat broad dark and light vertical stripes; chin speckled with brown, belly uniform cream; posterior surface of thigh with scattered melanophores, usually superimposed by dark vertical stripes.

SVL 59.3-68.4, mean 63.7 mm (males), 66.3-73.6, mean 68.7 mm (females); mean head length 34% SVL; mean head width 34% SVL; mean thigh length 50% SVL (males), 48% SVL (females); mean shank length 52% SVL (males), 51% SVL (females); mean foot length 43% SVL (males), 42% SVL (females).

Life Colors. — Iris entirely silver or yellow peripherally and silver in center or yellow above and silvery bronze below or greenish yellow above with a tan horizontal stripe below. Dorsum greenish gray. Flanks light green; groin lavender. Inside of mouth bluish green. Bones green. Belly dirty green-white-gray with salmon wash in places; underside of hands and feet (webbing and skin) deep brown-red; undersides of disks green. Posterior surface of thigh brown or lavender (no flash color on thigh or groin).

Larval Morphology. — Body oval in dorsal view, wider than deep; snout rounded in dorsal view; nostril closer to eye than tip of snout; distance between nares equal to or just less than interorbital distance; nares reniform; eye dorsolateral, 15% body length; opening of the sinistral spiracle directed posterodorsally on the midline about 69% body length; anal tube median; tail as high as body; dorsal fin origin extending slightly onto the body; dorsal fin slightly arched and ventral fin relatively straight; tail musculature reaching the pointed tail tip; anteroventral mouth width equal to 44% body width; a single row of oral papillae, except on a small section of the upper and lower lips; tooth row formula 2(2)/3-4(1); beak moderately developed and finely serrated.

Body and tail musculature brown, with transverse darker brown bands on dorsum of the tail musculature; dorsal fin light brown, ventral fin and venter unpigmented. In life, body tan or grayish-brown with small golden flecks; belly blackish with many silvery dots; tail musculature brown with transverse brown bands on the dorsum; dorsal fin light brown, ventral fin unpigmented; tail musculature and dorsal fin with silvery dots; iris golden with an outer gray ring (Figure 20).

Larval Habitat. — Tadpoles were collected from shallow ponds on the quarry floor.

Advertisement Call. — Calls given sporadically; call duration about 0.15-0.35 s; calls

strongly pulsed; pulse rate about 50-175 pulses per s; at slowest pulse rate call pulses are completely separated and appear as notes; calls beginning quietly and rapidly becoming loud with maximal intensity just before end of call; calls not noticeably frequency modulated; dominant frequency range 400-1800 Hz; no apparent harmonics; sidebands due to pulsatile nature of call (Figure 51).

Ecology. — Males were observed calling at night from shallow water or land in open marshy situations at the quarry and pastures in or adjacent to small puddles as small as cow hoofprints. Active individuals were taken at night from similar situations as calling males. Inactive individuals were collected during the day from a rock wall seep on a road cut and under rocks and wood on the quarry floor. Specimens were collected from September through February.

Hyla polytaenia Cope

Color Figure 21

Hyla polytaenia Cope, 1870. Original description.

Diagnosis. — *Hyla polytaenia* has a series of light and dark dorsolateral stripes and a distinct dark band on the shank; it shares these features only with *H. multilineata* among the Boracéia frogs with distinctly developed prepollices. The posterior surface of the thigh in *H. polytaenia* is usually uniform; in *H. multilineata* the posterior surface of the thigh usually has distinct vertical bars or ocelli. *Hyla polytaenia* is smaller (males 27-33 mm SVL, females 35-40 mm SVL) than *H. multilineata* (males 36-47 mm SVL, females 57-60 mm SVL).

Adult Morphology (N = 10 males, 9 females). — Snout outline rounded or nearly rounded from above, rounded to vertically rounded in profile; no cranial crests; no distinctive features on upper eyelids; tympanum usually with distinct color pattern although annulus not distinct, moderate size, diameter about 1/2 diameter of eye; males with single externally expanded large thin vocal sac; males with vocal slits; vomerine teeth in short transverse series lying just posterior to, but between choanae; finger lengths I<II<IV <III; finger disks moderate size, disks largest on fingers II, III, IV, largest disks just smaller than or about equal to tympanum; modal finger webbing formula I trace II trace III 2 2/3-2 1/3 IV; finger subarticular tubercles moderate, single; no thumb asperities; outer forearm with modest shallowly scalloped or straight glandular fold; prepollex well developed in males, spine covered, prepollex reduced in females, but present; weak supratympanic fold, low glandular supravent ridge sometimes developed into a short vent sheath; dorsum smooth; throat smooth, rest of belly granular; toe lengths I<II<III< or = or >V<IV; largest toe disks equal to or just smaller than largest finger disks; modal toe webbing formula I 2-2 1/2 II 1 3/4-3 III 2^{-}-3^{+} IV 3-1 1/2 V; inner metatarsal tubercle ovoid, no outer; heel smooth or with a weak transverse glandular fold; weakly to distinctly developed inner tarsal fold extending length of tarsus, very weak outer tarsal fold present or absent; outer tarsal texture smooth or glandular; sole of foot granular.

Dorsal pattern with very regular, usually very distinct, longitudinal stripes, consisting of three cream outlined broad brown stripes (rarely interrupted), one from snout to above vent, other two from around eyelids to above and to side of vent, two narrow stripes, partly or entirely interrupted, between the three broad stripes, two dark lines and incomplete stripes lateral to broad stripes, upper limbs with interrupted longitudinal stripes, outer forearm and shank with a dark longitudinal band, heel with light transverse stripe, cream stripe above vent bordered below by brown; white outlined dark canthal stripe from (almost) tip of snout through nostril to eye and extending posteriorly as broad band through tympanum to groin, upper lip with thin brown stripe, bordered above by light stripe, narrow sinuous brown stripe between canthal and lip stripes present or absent; flanks with a distinct or indistinct light stripe near belly from around arm insertion to groin region, in addition to brown band mentioned above; chin white with scattered brown dots, same pattern sometimes extending to front of chest and sides of otherwise unmarked belly; posterior surface of thigh usually lacking pigment or with a few scattered brown dots, area next to vent white with brown dots.

SVL 27.3-32.6, mean 30.0 (males), 35.7-40.0, mean 38.1 (females); mean head length 32%

SVL; mean head width 30% SVL (males), 31% SVL (females); mean thigh length 46% SVL (males), 47% SVL (females); mean shank length 50% SVL; mean foot length 43% SVL (males), 41% SVL (females).

Life Colors. — Iris gold or bronze, sometimes with a faint horizontal dark bar. Dorsum tan, brown, and dirty cream with darker brown longitudinal stripes; hands and feet orange or red; heel and vent stripes white; groin red. Belly cream; bottoms of hands and feet orange. Anterior and posterior surfaces of thighs salmon pink to transparent red.

Larval Morphology. — Body oval in dorsal view, wider than deep; snout rounded in dorsal view; nostril nearer eye than tip of snout; distance between nares 76% interorbital width; nares reniform, situated dorsolaterally; eye dorsolateral, 14% body length; opening of the sinistral spiracle directed posterodorsally on the midline about 80% body length; anal tube median, anal tube opening dextral; tail higher than body; dorsal fin origin barely at end of body; fins slightly arched; tail musculature reaching the pointed tail tip; anteroventral mouth width equal to 37% body width; a single row of oral papillae interrupted on upper lip; tooth row formula 2(2)/3(1,2); beak moderately developed and finely serrated.

Dorsum of the body brown; venter unpigmented; tail brown marbled; longitudinal median brown stripe on first third and transverse bars on dorsum of tail musculature. In life, dorsum of the body olive with black flecks; venter black with silvery flecks; tail brown marbled; silvery flecks on ventral fin; longitudinal median dark brown stripe on first third and transverse dark brown bars on dorsum of tail musculature; iris with golden ring and outer gray ring (Figure 21).

Larval Habitat. — Tadpoles were collected from the deeper ponds on the floor of the quarry, from the permanent pond "Lago do Aterro" (Figure 5), and from a seasonal, algae-filled water reservoir tank in a clearing.

Advertisement Call. — A typical call sequence consists of alternating calls of 2 distinct types. One type consists of longer harsh notes, the second is a trill of brief notes very much quieter than the harsh notes (Figure 52).

The harsh noted call of 1-6 notes; call lasting from 0.1-1.0 s; each note 0.05-0.15 s duration; given at a rate of up to 5 notes per s; notes pulsatile, ranging in rate about 250 pulses pers at the start of a longer note to 150 pulses per s at the end; frequency modulation noticeable or not; intensity modulation not marked; dominant (= fundamental) frequency 4800-6700 Hz; no apparent harmonics; sidebands due to pulsatile nature of call.

The trilled call of 4-13 notes; each note 0.02-0.03 s duration; given at rates of about 6-20 notes per s; notes apparently of a single pulse; intensity modulation not noticeable; frequency modulation among notes noticeable but unpredictable; dominant (= fundamental) frequency 4500-6600 Hz, any given note with a frequency bandwidth of 500-1000 Hz; no apparent harmonics.

Ecology. — Males were collected calling from stems and leaves of reeds, grass, and low shrubs around open ponds in meadows and the quarry at night. Most other individuals were collected from similar situations as the calling males. A very few individuals have been taken from leaves of small trees or bushes in the forest at night away from water. One individual was collected from a bush by the road while beating vegetation for insects. Specimens have been collected in every month of the year except June.

Hyla prasina Burmeister

Hyla prasina Burmeister, 1856. Original description.

Nomenclatural Note. — The relationships among *Hyla prasina, pulchella,* and *raddiana* are not clear. We follow Duellman (1977:86) in using *prasina* for the Boracéia population.

Diagnosis. — *Hyla prasina* is the only Boracéia species that has both an externally distinct prepollex and is green in life and whitish, lavender, purple or bluish in preservative.

Adult Morphology (N = 6 males). — Snout outline subovoid to nearly rounded from above, rounded in profile; no cranial crests; no distinctive features on upper eyelids; tympanum distinct, diameter about 1/2 or just larger than 1/2 eye diameter; male vocal sac single, externally

expanded; males with vocal slits; vomerine teeth in short acute or transverse series between and at posterior extent of choanae; finger lengths I<II<IV<III; finger disks large, largest disks on fingers II, III, IV just smaller than or about same size as tympanum; modal finger webbing formula I none II trace III 2 3/4-2 1/2 IV; finger subarticular tubercles moderately developed, single or bifid under finger IV; no thumb asperities; smooth or scalloped weak glandular forearm fold, more distinct on proximal half; prepollex modest but present; weakly developed supratympanic fold, weakly to moderately developed supra-vent fold; dorsal texture slightly glandular, almost smooth; front and/or sides of chin smooth, rest of belly granular; toe lengths I<II<V< or =III<IV; largest toe disks just smaller than or about equal to largest finger disks; modal toe webbing formula I 1 1/2-2 II 1-2 1/2 III 1 1/2-2 3/4 IV 2 1/2-1+ V; inner ovoid metatarsal tubercle prominent, outer small and round, indistinctly visible or not; heel smooth or with granular texture, no distinctive features; distinct inner tarsal fold along length of tarsus, weak glandular ridge on outer tarsus present or absent; outer tarsal texture smooth or weakly glandular; sole of foot weakly granular.

Dorsum uniform slate gray with distinct dark brown outlined enamel white irregular stripe from eye above tympanum reaching to groin (but not to thigh), short dark brown outlined stripe (or purplish brown and tan) on dorsal surface of forearm extending from near elbow to wrist, outer forearm and tarsal ridges lighter than dorsal color, heel with dark outlined light stripe, longitudinal dark brown outlined white stripe in middle of or towards outer dorsal surface of shank, supra-vent fold dark brown outlined with white; loreal region dark purple above, sharply defined from dorsal color by light stripe or not, fading to light lip below or distinct white stripe on upper lip; groin and anterior 1/3-1/2 of thigh with distinct vertical brown stripes on a light field, anterior portions of flanks a blending of the dorsal and ventral colors, chin white-purple, central throat and belly dirty cream yellow; posterior surface of thigh with series of irregular vertical brown stripes on a light field.

SVL 41.2-49.6, mean 44.7 mm (males); mean head length 32% SVL; mean head width 31% SVL; mean thigh length 49% SVL; mean shank length 51% SVL; mean foot length 45% SVL.

Life Colors. — Iris copper. Enamel green to olive green above including limbs; light lines metallic golden; light snout, flank stripe edged below with dark brown, other light lines brown outlined; flanks below light lines paler green fading to cream belly; purple behind shoulder; tympanum copper. Chin yellow to chartreuse; throat dirty orange; belly cream, pale pink posteriorly; cream on underside of thigh around vent, rest of undersides of limbs translucent purple-flesh colored; feet and hands gray underneath; faint brown banding on concealed surfaces of shank and foot. At groin some dark brown and white transverse lines on transparent purple ground, brown lines continuing faintly onto anterior surface of upper thigh and repeated on posterior surface of thigh more distinctly.

Larval Morphology. — Tadpoles unknown.

Advertisement Call. — Call not recorded from Boracéia; described by Rands as loud harsh "chrraa."

Ecology. — One individual was collected from the quarry wall; others were calling at night from more or less exposed sites on vegetation in ponds on the quarry floor or calling in vegetation at the edge of the "Lago do Aterro" and on vegetation in a pond 3 km east of the scientists' residence. Specimens were collected in October and March.

Hyla senicula Cope

Hyla senicula Cope, 1868. Original description.

Diagnosis. — *Hyla senicula* is the only Boracéia species with a patagium that also has toe disks with circumferential grooves, hand and foot webbing, a lichenous dorsal pattern, and a uniform brown posterior thigh pattern.

Adult Morphology (N = 1 male). — Snout outline semicircular from above, rounded in profile; no cranial crests; upper eyelids warty; tympanum distinct, diameter about 1/2 eye diameter; male vocal sac single, large and expanded externally; male with vocal slits; vomerine teeth in short transverse series lying between the choanae; finger lengths I<II<IV<III; finger disks large, largest on fingers II,III and IV larger than

tympanum; finger webbing formula I 2-2 1/3 II 1-2 III 1 2/3-1 1/2 IV; finger subarticular tubercles moderate size, double under all digits; no thumb asperities; well developed scalloped fringe on outer forearm; no prepollex; moderately developed supratympanic fold; dorsal texture warty; throat and chest smooth, belly granular; toe lengths I<II<V<III<IV; toe disks large, largest about same size as finger disks; toe webbing formula I 1^{-}-1 1/3 II 1^{-}-1^{+} III 1-1 1/3 IV 1 1/3-1 V; inner metartasal tubercle elongately oval, no visible outer; heel with fleshy warts; distinct inner tarsal fold and outer broken tarsal fringe; outer tarsal texture smooth; sole of foot granular.

Dorsum a complex pattern of light and dark leaf brown variegations, upper limbs cross banded, most indistinctly so, but top of thigh (and somewhat less so, on foot and tarsus) very boldly banded white and dark; face mostly with same pattern as back, small light area under eye; anterior half of flanks with a joining of dorsal and ventral patterns, posterior half of flanks with a bold, distinct, black and white mottle; tip of chin brown and white, front of vocal sac brown, most of vocal sac pigmentless, chest white, belly dirty orange yellow; posterior surface of thigh uniform brown.

SVL 37.7 mm; head length 30% SVL; head width 33% SVL; thigh length 47% SVL; shank length 50% SVL; foot length 45% SVL.

Life Colors. — Iris silver with brown reticulation. Dorsum lichenous brown. Flanks and tops of thighs with cream yellow markings. Posterior surface of thigh brown.

Larval Morphology. — Tadpoles unknown.

Advertisement Call. — Call not recorded from Boracéia.

Ecology. — The single individual was taken from low vegetation on the floor of the quarry at night in December.

Ololygon Fitzinger

Taxonomic Note. — The proposal erecting *Ololygon* by Fouquette and Delahoussaye (1977) has not been accepted by all herpetologists. Some are concerned that Fouquette and Delahoussaye recognized the genus on the basis of a single character, sperm morphology. Almeida and Cardoso (1985) indicated that some species possess variation encompassing the range of sperm morphology used to separate *Hyla* and *Ololygon*. One of us (WRH) is of the opinion than the members of the *Hyla rubra* group (= *Ololygon*) are recognizable as distinct from *Hyla*, are monophyletic, and that further study will demonstrate other characters that define the group. Consequently, we recognize *Ololygon*.

Ololygon brieni (de Witte)

Color Figure 22

Hyla brieni de Witte, 1930. Original description.
Ololygon brieni, Fouquette and Delahoussaye, 1977. Transfer of *Hyla catherinae brieni* to *Ololygon.*

Nomenclatural Note. — We have compared the Boracéia form with specimens of *O. catherinae* from Santa Catarina and find them distinct. As *brieni* is an available name, we use it for the Boracéia population; this allocation may be premature, as we have not compared the type of *brieni* with Boracéia specimens.

Diagnosis. — *Ololygon brieni* is a moderate sized species (males 30-33 mm SVL, females 32-38 mm SVL) with toe disks with circumferential grooves, toe webbing but no finger webbing. Of the species sharing the above characteristics, *O. brieni* is most likely to be confused with *O. flavoguttata* and *O. obtriangulata* (Figure 8), which, like it, have the front and back of the thighs and hidden portion of the shank with very distinct alternating dark and white bands. *Ololygon brieni* has the most complexly lichenous dorsal pattern of these three. almost always with irregular or crenulate edged markings; *O. obtriangulata* has smooth edged dorsal markings; *O. flavoguttata* has a noticeable narrowly defined light indented H-shaped mark from behind the eyes to past the shoulder region, not seen in *O. brieni.*

Adult Morphology (N = 10 males, 7 females). — Snout outline rounded or nearly rounded, tip with or without a tubercle from above, acute, vertically acute, or rounded acute in profile; no cranial crests; upper eyelid usually with scattered tubercles, rarely smooth; tympanum distinct, diameter just less than or about equal 1/2 eye diameter; male vocal sac single, internal; males

with vocal slits; vomerine teeth in short transverse or slightly oblique series lying between or just posterior to choanae; finger lengths I<II<IV<III; finger disks large, distinct, largest on fingers II, III, IV, larger than or about equal to tympanum; fingers usually free, rarely with trace of web, sides of fingers ridged; finger subarticular tubercles moderately developed, single or slightly bifid under finger IV; no thumb asperities; outer forearm with very faint fold or not; no prepollex; weakly to moderately developed supratympanic fold; dorsal texture usually smooth with scattered tubercles, rarely entirely smooth; throat smooth or weakly granular, belly granular; toe lengths I<II<III< or =V<IV; toe disks large, largest disks just smaller than or same size as largest finger disks; male modal toe webbing formula I 2^{+}-2 1/2 II 1 1/3-2 1/2 III 1^{+}-2 1/2 IV 2 1/3-1^{+}V, female modal toe webbing formula I 2^{+}-2 1/2 II 1 3/4-3 III 1^{+}-2 3/4 IV 2 1/2-1^{+}V; inner metatarsal tubercle ovate to almost round, outer rounded, rather indistinct, 1/4-1/3 size of inner; heel rarely almost smooth to usually with a few prominent fleshy tubercles; no tarsal decoration; outer surface of tarsus usually smooth, rarely weakly glandular; sole of foot with low rounded fleshy tubercles.

Dorsal pattern variable including a distinct but irregular chocolate posteriorly directed triangular interorbital spot, anastomosing darker brown stripes on light tan on rest of back, or complex lichenous brown stripes from behind eye or axilla to as far as sacrum on each side, or well defined dark stripes to sacrum and lighter ladder-like brown stripes mid-dorsally, or complexly variegated brown and tan pattern, upper limbs cross barred; face with irregular dark, broad canthal stripe, distinct or indistict dark and light oblique bars on upper lip below eye area; anterior 2/3 of flanks with a meeting of the dorsal and ventral patterns, groin with bold black and white mottle, white sometimes in form of large spot; belly brown mottle on creamy tan; anterior, dorsal, and posterior surface of thighs with alternating dark and light bands, black and tan dorsally, black and white anteriorly and posteriorly, dark bands up to twice as wide as light, bands usually very regular, rarely irregular.

SVL 30.5-32.7, mean 32.0 mm (males), 32.3-37.6, mean 34.5 mm (females); mean head length 35% SVL; mean head width 32% SVL (males), 33% SVL (females); mean thigh length 45% SVL; mean shank length 50% SVL (males), 51% SVL (females); mean foot length 43% SVL (males), 42% SVL (females).

Life Colors. — Iris creamy yellow. Dorsum tan and brown; groin and anterior surface of thigh light areas colorless or with a pale turquoise wash. Bones white. Venter cream with mottled tan and brown. Posterior surface of thighs black and white.

Larval Morphology. — Tadpoles unknown.

Advertisement Call. — Call not recorded from Boracéia. Described by Rand as low quiet "krink krank" and "krk rick rick."

Ecology. — Males were calling in April and August from low grass and vegetation near the edge of a stream in low secondary growth at night. All individuals with data were collected at night mostly from leaves or stems of low vegetation both near and away from streams or ponds in forests, secondary growth, or clearings. Specimens were collected in July, August, October, and December through April.

Ololygon crospedospila (A. Lutz)

Color Figure 23

Hyla crospedospila A. Lutz, 1925b. Original description.

Ololygon crospedospila, Fouquette and Delahoussaye, 1977. Transfer of *crospedospila* to *Ololygon*.

Diagnosis. — *Ololygon crospedospila* is a moderate sized species (males 29-34 mm SVL) characteristically with several pairs of large white edged dark brown spots on the dorsum. It is the only species to have these distinct dorsal spots and an almost uniform brown or tan posterior surface of the thigh with webbing on both the hands and feet.

Adult Morphology (N = 10 males). — Snout outline subelliptical to subovoid with a pointed tip from above, rounded-acute in profile; no cranial crests; upper eyelid lacking distinctive features; tympanum distinct, diameter just less than or about equal 1/2 eye diameter; males with single, large, externally expanded vocal sac; males with vocal slits; vomerine teeth in short

transverse series lying between the choanae; finger lengths I<II<IV<III; finger disks large, largest on fingers II, III, and IV just less than or about equal to size of tympanum; modal finger webbing formula I trace II 2-3^{+} III 2 2/3-2 1/2 IV; finger subarticular tubercles moderately developed, slightly or distinctly bifid under finger IV; male thumb with somewhat indistinct cream or white glandular patch on inner surface; forearm fold lacking or represented by a series of low tubercles; no prepollex; weakly to moderately developed supratympanic fold; dorsum smooth or weakly granular, flanks granular, particularly posteriorly; throat and chest smooth, belly granular; toe lengths I<II<V= or <III<IV; toe disks large, largest just smaller than or about equal to largest finger disks; modal toe webbing formula I 2^{-}-2 II 1^{-}-2 III 1-2 IV 2^{+}-1^{-} V; inner ovate metatarsal tubercle moderately developed, outer rounded tubercles 1/4-1/3 size inner, prominent or moderately so; heel with moderately pronounced fleshy tubercles; broken inner tarsal fold on proximal 1/2 to 2/3 of tarsus, of 3-4 fleshy tabs to almost continuous; outer tarsal texture with scattered to many pronounced fleshy tubercles; sole of foot with fleshy tubercles.

Dorsal pattern tan with paired white outlined (interrupted or continuous, somewhat or very distinct) dark brown spots between eyes, above shoulders and sacrum with a few other scattered small spots to a similar pattern but dark spots coalesced to form a pair of white outlined dorsal stripes; upper limbs distinctly blotched or cross banded with white outlined dark brown on tan; face with narrow to broad dark canthal stripe, rest of face uniform tan with prominent to almost indistinct white highlighting on area between under eye and front of tympanum; flanks with dark irregular stripe from behind eye to mid-body or almost to leg in groin, most of flanks with meeting of dorsal and ventral patterns low on flanks, groin mottled; front of throat with many scattered brown dots or not, belly cream with white wash anteriorly, with very few scattered brown dots; posterior surface of thigh uniform brown to weakly mottled.

SVL 29.6-33.3, mean 31.0 mm (males); mean head length 34% SVL; mean head width 32% SVL; mean thigh length 42% SVL; mean shank length 51% SVL; mean foot length 43% SVL.

Life Colors. — Iris copper or dark bronze. Dorsum brown with yellow highlighting sometimes with green. Flanks yellow or chartreuse. Tips of digits yellow. Throat yellow; belly whitish. Posterior surface of thighs brown or translucent flesh color.

Larval Morphology. — Body oval in dorsal view, deeper than wide; snout slightly truncate in dorsal view; nostril midway between eye and tip of snout; distance between nares 66% interorbital width; nares elliptical; eye dorsolateral, 17% body length; opening of the sinistral spiracle directed posterodorsally on the midline about 76% body length; anal tube short and dextral; tail as high as body; dorsal fin origin midway on body length; fins slightly arched; tail musculature reaching the pointed tail tip; anteroventral mouth width equal to 33% body width; a single row of oral papillae broadly interrupted on upper and lower lips, one to two inner lateral rows; tooth row formula 2(1,2)/3(1); third lower row very short, appearing as modified part of the lower lip; beak strongly developed and finely serrated; lower beak keeled.

Body and tail gray; fins and tail musculature brown marbled. In life, general aspect lemon-yellow; fins light brown marbled. Advanced stages (38 onward) turning dark brown marbled (Figure 22).

Larval habitat. — Tadpoles were collected from the deeper ponds on the floor of the quarry and from the permanent pond, "Lago do Aterro" (Figure 5).

Advertisement Call. — Calls given sporadically at a rate up to 1.4 per s; call duration 0.25-0.32 s; 5-7 notes per call, given at rates of about 22-33 per s; note duration 0.02-0.05 s; notes weakly partially pulsed at basic pulse rate of 425-470 per s (one third of carrier frequency); calls not noticeably frequency modulated; beginning and ending of calls quieter than mid-portion; individual notes beginning and ending rather abruptly; dominant (= fundamental) frequency range 1200-1500 Hz; prominent sidebands due to partial pulsing of notes (Figure 53).

Ecology. — Males have been observed calling at the quarry on low vegetation or on boul-

ders associated with ponds. All specimens were collected at night from the same open situations as calling males at the quarry, Lago do Aterro, or the pond 3 km east of the scientists' residence. Specimens were collected during the months of November through February. The species is common now but was rare earlier; all specimens but one were taken after 1965.

Ololygon flavoguttata (A. Lutz and B. Lutz)

Color Figure 24

Hyla flavoguttata A. Lutz and B. Lutz, 1939. Original description.

Ololygon flavoguttata, Fouquette and Delahoussaye, 1977. Transfer of *flavoguttata* to *Ololygon.*

Diagnosis. — *Oloygon flavoguttata* is a moderate sized species (29-41 mm SVL) with toe disks and circumferential grooves and toe webbing but no finger webbing. Of the species sharing these characteristics, *O. flavoguttata* is most likely to be confused with *O. brieni* (Figure 8). *Ololygon flavoguttata* has a noticeable (but sometimes interrupted) light indented H-mark extending from the eye to past the shoulder; this mark does notoccur in *O. brieni.* The dorsal pattern of *O. brieni* is also more complexly lichenous than that of. *O. flavoguttata.*

Adult Morphology (N = 1 male, 3 females). — Snout outline rounded or nearly rounded with a tuberculate tip (in well preserved individuals) from above, acute or rounded-acute in profile; no cranial crests; upper eyelid with scattered tubercles (as on back); tympanum distinct, diameter just less than 1/2 eye diameter; male vocal sac single, internal; males with vocal slits; vomerine teeth in two short transverse patches lying between choanae; finger lengths I<II<IV<III; finger disks very large, largest on fingers II, III, IV about same size as tympanum; no finger webbing, sides of fingers with fleshy ridges; finger subarticular tubercles moderately developed, single; male with creamy glandular nuptial pad on inner surface of thumb; no forearm fold; no prepollex; modest supratympanic fold; dorsum with scattered tubercles; venter granular; toe lengths I<II<V< or =III<IV; toe disks large, largest just smaller or about equal largest finger disks; modal toe webbing formula I trace II 1 1/2-3- III 1 1/3-2 3/4 IV 3--1 1/2 V; inner metatarsal tubercle ovate, average size, outer small, round, about 1/5-1/6 size of inner, not distinct from other tubercles in area; heel with scattered tubercles with one prominent or not; inner and outer tarsal folds absent or, rarely, weakly developed; outer tarsal texture with scattered tubercules; sole of foot with low, round, fleshy tubercles.

Dorsal pattern complex dark and light browns including a series of light outlined or light confluent or separate chevrons with dark brown tubercles surrounded by dark circles, upper limbs distinctly or indistinctly cross barred; loreal region mottled or brown with blackish circles with tubercles in centers, two distinct oblique light stripes, one directed forward under eye, one directed posteriorly from posterior corner of eye, two more or less distinct light spots on upper lip between eyes and tip of snout present or absent; anterior 1/2 to 3/5 of flanks a blending of dorsal and ventral patterns, remainder of flanks with bold black and white pattern with large spot in groin next to leg; venter mottled brown-black or brown and dirty tan-cream; posterior surface of thigh with oblong large white spots on a black-brown field, white spots connecting with light cross bars on top of thighs and large oblong white spots on anterior surface of thighs, same bold pattern on concealed portion of shank.

SVL 29.3 mm (male), 37.2-40.4 mm (females); head length 37-39% SVL; head width 35-37% SVL; thigh length 46-48% SVL; shank length 53-54% SVL; foot length 42-45% SVL.

Life Colors. — Iris bronze. Dorsum complex pattern of tans, browns, yellowish tan. Belly pale yellow-green with brown marks. Groin, front and back of thighs and concealed portion of shank with bright orange flash colors.

Larval Morphology. — Body oval in dorsal view, slightly wider than deep; snout broadly rounded in dorsal outline; nostril nearer eye than tip of snout; distance between nares 69% interorbital width; nares rounded and dorsal; eye dorsolateral, 11% body length; opening of the sinistral spiracle directed posterodorsally on the midline about 73% body length; anal tube short and dextral; tail slightly higher than body; dorsal

fin origin slightly onto the body; dorsal and ventral fins arched; tail musculature reaching the pointed tail tip; anteroventral mouth width equal to 47% body width; two rows of oral papillae, absent on the upper lip and some inner papillae on the lateral parts; tooth row formula 2(2)/3; beak moderately developed and finely serrated.

Body gray brown; fins and tail musculature brown marbled (Figure 23).

Larval Habitat. — Rabello collected the larvae from the Rio Claro.

Advertisement Call. — Call not recorded from Boracéia. Described by Rand as a harsh (but high) "raack" and/or "tick tick tick".

Ecology. — A small chorus of males was heard calling from dense bushes at the edge of the pasture stream at night on two occasions in September and October. The only other individuals with data were collected at night from leaves or stems of vegetation 1-2 m high by streams or away from water in the forest. Specimens were collected in August, September, December, January, and March.

Ololygon hayii (Barbour)

Color Figure 25

Hyla hayii, Barbour, 1909. Original description. - Cochran, 1955. Citation of specimens from Boracéia.

Ololygon hayii, Fouquette and Delahoussaye, 1977. Transfer of *hayii* to *Ololygon.*

Diagnosis. — *Ololygon hayii* has a uniform dorsal pattern with uniform upper limbs. Most other frogs at Boracéia have cross bars, bands or stripes on the upper lips. *Ololygon hayii* can be distinguished from all other Boracéia frogs with uniform dorsal limb patterns in having a combination of moderate size (males 39-43 mm SVL, females 44-51 mm SVL), toe disks with circumferential grooves, finger and toe webbing, and the posterior surface of the thigh with light spots on a dark background.

Adult Morphology (N = 10 males, 10 females). — Snout outline pointed-rounded, pointed-subovoid, rounded or subovoid from above, rounded or rounded-acute in profile; no cranial crests; upper eyelid texture same as dorsal texture, no distinctive features; tympanum distinct, diameter 1/2-2/3 eye diameter; vocal sac single, externally expanded; males with vocal slits; vomerine teeth usually in short transverse series in medial contact lying between choanae, occasionally barely separated medially or with a slightly acute orientation; finger lengths I<II< or = IV<III; finger disks large, largest disks on fingers II, III, IV about same size as tympanum (or a bit larger or smaller); modal finger webbing formula I trace II trace III 3^{-}-2 1/2 IV; finger subarticular tubercles well developed, somewhat pungent, single or very slightly bifid under finger IV; males with cream nuptial pad on inner side of thumb; no ulnar fold; no prepollex; moderate supratympanic fold; dorsal texture smooth to moderately granular, sometimes weakly glandular appearing, with or without scattered tubercles; throat weakly tuberculate or weakly granular, vocal sac smooth, belly granular; toe lengths I<II<III< or = V<IV; toe disks large, largest about same size as largest finger disks; male modal toe webbing formula I 2^{-}-2^{+} II 1-2 III 1-2^{+} IV 2-1 V, female I 2^{-}-2 II 1^{-}-2 III 1-2 IV 2-1^{-} V; inner metatarsal tubercle ovoid, outer 1/3-1/2 size of inner, ovoid; heel weakly to moderately grandular, with or without scattered tubercles; broken or entire inner tarsal fold from proximal 1/3 of tarsus to entire length; outer tarsal texture smooth or with scattered tubercles; sole of foot with low fleshy tubercles, sometimes also granular.

Dorsal pattern usually almost uniform, sometimes with indistinct scattered small dark or light spots or weak darker mottle-network, upper limbs same as back, not banded; side of face with same pattern as dorsum, upper lip sometimes lighter than rest of face; axilla and groin (posterior half of flanks) with large distinct or confluent light blotchy spots dark highlighted (axilla pattern sometimes not as distinct as groin), rest of flanks with blending of dorsal and ventral patterns; venter cream with scattered brown network on throat and chest or sometimes on entire belly, some females with moderately brown speckled bellies; large distinct or confluent light spots (rarely muted, but always present) on a dark brown field on the anterior and posterior surfaces of the thigh and the hidden portion of the shank pattern sometimes not as distinct on anterior surface of thigh and hidden portion of shank.

SVL 39.3-43.0, mean 41.6 mm (males), 44.6-50.2, mean 48.0 mm (females); mean head length 36% SVL; mean head width 33% SVL (males), 34% SVL (females); mean thigh length 43% SVL (males), 44% SVL (females); mean shank length 49% SVL (males), 52% SVL (females); mean foot length 44% SVL (males), 45% SVL (females).

Life Colors. — Iris reddish gold with a horizontal black smudge across the middle. Dorsum walnut brown, lustrous khaki, coppery brown, or brown, sometimes with small yellow spots. Belly greenish yellow to bright yellow, sometimes flecked with brown or black, chin and throat darker; under limbs pale green or dirty yellow; hands and feet brown. Axilla, groin, anterior and posterior surfaces of thigh and hidden portion of shank with bright deep yellow, chrome yellow, or orange yellow flash colors.

Larval Morphology. — Body sub-cylindrical in dorsal view, deeper than wide; snout broadly rounded in dorsal view; nostril closer to eye than tip of snout; distance between nares 72% interorbital width; nares dorsolateral, rounded; eye dorsolateral, 18% body length; opening of the sinistral spiracle directed posteriorly on the inferior half of the body about 78% body length; anal tube short and dextral; tail higher than body; dorsal fin origin midway on the body length; fins arched; tail musculature reaching the pointed tail tip; mouth anteroventral, width 44% body width; a single row of oral papillae interrupted on the upper lip; scattered papillae on lateral portions; tooth row formula 2(2)/3(1); beak strongly developed and finely serrated; lower beak keeled.

Body on dorsum and tail musculature lightly brown pigmented; venter transparent; fins transparent with brown reticulations. In life, body musculature lemon-yellow; venter white; fins yellowish with blackish reticulations; iris golden with a median longitudinal red stripe (Figure 24).

Larval Habitat. — Tadpoles were collected from the deeper ponds on the floor of the quarry, the permanent pond "Lago do Aterro" (Figure 5), and a seasonal, algae-filled water resevoir tank in a clearing.

Advertisement Call. — Two kinds of calls are commonly given: an advertisement call and an occasional call. A day call is heard infrequently and has not been recorded.

The advertisement call given sporadically, up to 3 per s; duration 0.20-0.26 s; call of almost distinct notes ("pseudonotes"), note duration 0.05-0.10 s; note rate of about 60-70 per s; each note weakly partially pulsed at a rate of about 350-380 per s; 3-4 pulses per note; calls initially of slightly weaker intensity; calls with weak frequency modulation at beginning of calls, starting at a slightly lower frequency; dominant (= fundamental) frequency range 1200-2800 Hz; harmonic structure; sidebands prominent due to complexly pulsatile nature of call (Figure 54).

The occasional call consists of 1-2 short notes given singly or, more often, repeated up to 4 times; call duration 0.05-0.18 s; note duration 0.03-0.09 s; call rate up to 6 per s; notes pulsatile, given at a rate of 300-500 pulses per s; dominant frequency range about 1200-2800 Hz; no apparent harmonics; sidebands due to pulsatile nature of call (Figure 54).

Ecology. — Males were heard calling from low vegetation around streams and ponds at night in open situations or second growth; the species is common at night in these habitats, including the quarry and "Lago do Aterro". All active specimens were found at night, mostly from low vegetation near water. Only one specimen was captured in primary forest. This is the most common frog in the bathrooms, from where they occasionally call at dusk or during the day. A few individuals were collected from under rocks on the quarry floor in the day. Specimens have been collected in all months except July.

Ololygon obtriangulata (B. Lutz)

Figure 8

Hyla obtriangulata B. Lutz, 1973. Replacement name for *Hyla catherinae simplex* B. Lutz, 1968.

Ololygon obtriangulata, Fouquette and Delahoussaye, 1977. Transfer of *obtriangulata* to *Ololygon.*

Remarks. — The few adult specimens from Boracéia compare very well with topotypic specimens from Brejo da Lapa, particularly in dorsal pattern and overall morphology. The samples differ somewhat in size, as the largest male specimen from Boracéia is 24.5 mm SLV;

the males in the topotypic series (USNM 207850-895) range from 24.3-31.2 mm SVL. The venters are slightly darker in the topotypic series and the groin gland patch is not as distinct in all topotypic specimens as it is in the Boracéia individuals.

Diagnosis. — This moderately small species (males 22-25 mm SVL) with toe disks with circumferential grooves, no hand webbing and with foot webbing has an invariant, characteristic dorsal pattern. There is a dark interorbital triangle; the snout and the mid-central back region behind the interorbital triangle are light. The mid-back light area is bordered on the edges by dark and usually by well defined dark dorsolateral stripes. The only other species with which *O. obtriangulata* is likely to be confused is *O. brieni* (Figure 8), in which a few individuals have a dorsal pattern approaching that observed in *O. obtriangulata*. *Ololygon brieni* is larger (males 30-33 mm SVL, females 32-38 mm SVL), and the patterns are usually defined by irregular or crenulate lines, rather than the smoothly defined patterns seen in *O. obtriangulata*.

Adult Morphology (N = 4 males). — Snout outline rounded and pointed or subovoid from above, rounded-acute in profile; no cranial crests; upper eyelid without distinctive features, same texture as surrounding dorsum; tympanum distinct, moderate size, diameter somewhat less than 1/2 diameter of eye; male vocal sac single, internal; males with vocal slits; vomerine teeth in short transverse series lying between choanae; finger lengths I<II<IV<III; finger disks moderate to somewhat large, largest disks on fingers II, III, IV about same size as tympanum; fingers without webbing, sides of fingers ridged; finger subarticular tubercles not pronounced, single; male thumb with or without a cream pad on inner surface; no forearm fold; no prepollex; moderate supratympanic fold, patch of glandular cells in groin; dorsal texture smooth or smooth with very few scattered tubercles; throat and chest weakly granular, belly granular; toe lengths I<II <III<V<IV; largest toe disks just smaller than largest finger disks; modal toe webbbing formula I trace II 1 3/4-2 1/2 III 1^{+}-2 1/2 IV 2^{+}-1 1/4 V; inner metatarsal tubercle ovoid, outer not visible or very small and round; heel with one to a few fleshy tubercles; no tarsal decoration; outer surface of tarsus smooth; sole of foot smooth or (usually) with low round fleshy tubercles.

Two basic dorsal patterns, each with light tan snout, light outlined darker brown posteriorly directed interorbital triangle and broad light tan central band extending from either side of interorbital triangle to vent with indistinct small dark brown markings, light central band either bordered by relatively uniform darker brown laterally or a pair of distinct light-outlined dorsolateral bands from behind eye to groin, upper limbs faintly cross banded; faint dark canthal stripe, dark forwardly directed oblique bar from under front of eye to edge of upper lip present or absent, area immediately under eye somewhat lighter; flanks with blending of dorsal and ventral patterns on anterior 2/3, with or without a dark stripe from behind tympanum to mid-body, groin white with large dark irregular spots; venter cream with brown reticulation on throat and chest or extending onto entire belly; anterior and posterior surfaces of thighs and hidden portion of shank light with large bold irregular dark spots or transverse bars.

SVL 22.1-24.5 mm (males); mean head length 37% SVL; mean head width 32% SVL; mean thigh length 45% SVL; mean shank length 53% SVL; mean foot length 43% SVL.

Life Colors. — No life colors available for Boracéia specimens.

Larval Morphology. — Body oval in dorsal view, slightly wider than deep; snout broadly rounded in dorsal outline; nostril nearer eye than tip of snout; distance between nares 72% interorbital width; nares rounded and dorsal; eye dorsolateral, 14% body length; opening of the sinistral spiracle directed posterodorsally on the midline about 73% body length; anal tube short and dextral; tail slightly higher than body; dorsal fin origin on body-tail juncture; dorsal and ventral fins arched; tail musculature reaching the pointed tail tip; mouth anteroventral, width equal to 43% body width; a single row of oral papillae shortly interrupted anteriorly and some inner scattered papillae on lateral parts; tooth row formula 2(2)/3; beak moderately developed and finely serrated.

Body brown; fins and tail musculature brownish marbled (Figure 25).

Larval Habitat. — Tadpoles were collected in an isolated pool of a small stream in the forest. The larvae were exposed on the bottom of the pool.

Advertisement Call. — Not recorded for Boracéia specimens.

Ecology. — Four specimens were collected from leaves on low vegetation at night in the forest. One individual was taken at night on a fern in a clearing. Individuals were collected in December and April.

Ololygon perpusilla (A Lutz and B. Lutz)

Figure 9

Hyla perpusilla A. Lutz and B. Lutz, 1939. Original description. - Cochran, 1955. Citation of specimens from Boracéia.

Ololygon perpusilla, Fouquette and Delahoussaye, 1977. Transfer of *perpusilla* to *Ololygon.*

Nomenclatural Note. — There are several species within the species identified currently as *O. perpusilla* (Peixoto, 1986). There is a single unnammed new species at Boracéia; currently, the best name to use for it is *perpusilla.*

Diagnosis. — *Ololygon perpusilla* is one of the smallest frog species at Boracéia (males 16-19 mm SVL, females 19-21 mm SVL), essentially found only on or in large, terrestrial, forest bromeliads. *Ololygon perpusilla* has toe disks with circumferential grooves, no hand webbing, and reduced toe webbing with webbing distinct only between the outer three toes. The combination of small size and reduced webbing separate *O. perpusilla* from the other taxa with which it is likely to be confused, namely *Fritziana ohausi* and several other *Ololygon* species.

Adult Morphology (N = 10 males, 6 females). — Snout outline pointed-mucronate to rounded-mucronate from above, acute in profile; no cranial crests; upper eyelid glandular or with scattered warts, same texture as back; tympanum distinct, diameter just less than or about equal to eye diameter; male vocal sac single, slightly to greatly expanded including chest region; males with vocal slits; vomerine teeth in small rounded or short obtuse series lying between choanae or between posterior borders of choanae; finger lengths I just <II< or =IV<III; finger disks largest on finger III, smallest on finger I, size on fingers II and IV intermediate or same size as III, largest disks about same size as tympanum; fingers without webbing, sides of fingers slightly fringed; finger subarticular tubercles moderately developed, single or bifid under finger IV; indistinct white glandular nuptial pad on inner thumb of males, visible only under high magnification (absent in USNM 209061); outer forearm usually smooth or with a row of small warts; no prepollex; supratympanic fold weakly developed; dorsal texture almost smooth or with scattered warts; throat and chest relatively smooth, belly granular; toe lengths I<II<V< or =III<IV; toe disks distinct, largest disks just smaller than or about equal to largest finger disks; modal toe webbing formula I none II trace III 2-3^{+} IV 3^{+}-2^{-}V; inner metatarsal tubercle ovoid, outer round, about 1/2 size of inner; no heel decoration; no tarsal decoration; outer surface of tarsus smooth or with scattered warts, rarely warts aligned in a row on outer tarsus; sole of foot with fleshy tubercles.

Dorsal pattern of complexly mottled browns with a well- to ill-defined dark interorbital bar, sometimes with a broad but indistinctly defined partial to compete light band from in between eyes to just past sacrum, upper limbs complexly mottled; indistinct dark canthal stripe present or absent, indistinct series of light and dark bars or triangles on upper lip and under eye, large light area under eye usually visible; anterior flank with or without an indistinct dark oblique bar, posteriorly, large cream spot in groin or edges of cream spot slightly mottled; throat and chest speckled with brown, posterior belly dirty cream; anterior and posterior surfaces of thigh and hidden portion of shank with large light irregular (and sometimes coalescing) spots on a brown background (spots not distinct in one female examined).

SVL 16.7-18.3, mean 17.4 mm (males), 19.0-20.2, mean 19.8 mm (females); mean head length 39% SVL (males), 38% SVL (females); mean head width 34% SVL (males), 33% SVL (females); mean thigh length 43% SVL (males), 42% SVL (females), mean shank length 50% SVL (males),51% SVL (females); mean foot length 37% SVL (males), 39% SVL (females).

Life Colors. — Iris bronze or yellow, often with symmetrically placed small dark red or brown spots. Dorsal colors dark and light brown, and/or grey brown, mid-dorsal stripe (when present) and subocular spot cream. Greenish tinge to sides of belly near groin. Bright yellow-orange, or orange flash colors in groin, front and back of thighs, and hidden portion of shank.

Larval Morphology. — Body oval in dorsal view, slightly elongated, wider than deep; snout rounded in dorsal view; nostrils midway between eye and tip of snout; distance between nares 69% interorbital width; nares small, rounded; eyes dorsolateral, small, 8.7% body length; opening of the sinistral spiracle directed posterodorsally at 60% of body length; anal tube elongated, median, anal tube opening dextral; tail and body height equivalent; dorsal fin origin at body and tail juncture; dorsal and ventral fins very slightly arched; tail musculature not reaching the round tail tip; mouth width equal to 40% body width; oral papillae occurring in a single anterior row, broadly interrupted, two posterior rows and up to 4 rows in lateral portions; tooth row formula 2(2)/3; beak moderately developed and finely serrated.

Body and tail brownish, tail lighter than body, tail fin transparent. In life body dark gray and tail light gray (Figure 26).

Larval Habitat. — A tadpole was collected from the water-filled axils of a large ground bromeliad.

Advertisement Call. — Calls given frequently when actively calling, in series of 10-20 at a rate of about 0.3-0.4 per s; call duration 0.25-0.40 s; each call of 4-5 notes; note duration 0.03-0.07 s; note rate 11-15 per s; each note pulsed, 4-11 pulses per note, pulse rate 180-290 per s, pulses amplitude modulated 4 times per pulse; call not notably intensity or frequency modulated; dominant (= fundamental) frequency range 3500-5900 Hz; call apparently without harmonic structure; strong sideband structure due to pulsatile nature of call (Figure 55).

Ecology. — Males commonly call at night on leaves of large, usually terrestrial bromeliads close to the ground in both secondary and mature forest. All active specimens were taken at night; most specimens from the same places as calling males, some individuals have been taken from leaves or stems of other types of low vegetation from primary or secondary forest. One specimen was collected in the daytime from low roadside vegetation that was beaten to collect insects. Specimens were collected from September through April.

Ololygon x-signata (Spix)

Hyla x-signata Spix, 1824. Original description.
Ololygon x-signata, Fouquette and Delahoussaye, 1977. Transfer of *x-signata* to *Ololygon*.

Remarks. — *Ololygon x-signata* is only represented by a single specimen from Boracéia. This is unusual, as *x-signata* typically is common where it occurs. It is possible that the specimen (MZUSP 54382) is not from Boracéia, but it was misidentified and catalogued as part of a series of *O. hayii*. As there is no valid reason to doubt the locality data of this specimen, the species is included in the Boracéia fauna.

Diagnosis. — *Ololygon x-signata* is a moderate sized species (male 42 mm SVL) with toe disks with circumferential grooves, foot webbing, but no hand webbing. *Ololygon x-signata* has a relatively simple dorsal pattern, of dark chevrons; most taxa with which it might be confused have lichenous or complex dorsal patterns including dorsolateral stripes. *Ololygon x-signata* is most likely to be confused with *Ololygon hayii* at Boracéia. *Ololygon x-signata* has banded upper limb surfaces; the upper limb surfaces of *O. hayii* are uniform, not banded.

Adult Morphology (N = 1 male). — Snout outline subelliptical-subovoid from above, rounded in profile; no cranial crests; no upper eyelid decoration; tympanum distinct, large, diameter about 2/3 eye diameter; male vocal sac single, externally expanded; male with vocal slits; vomerine teeth in short, contiguous, transverse series lying between choanae; finger lengths I<II<IV<III; finger disks large, but largest disks much smaller than tympanum due to large tympanum size; fingers without webbing, sides of fingers slightly ridged; finger subarticular tubercles moderately developed, single; ill-defined cream glandular pad on inner thumb of male; no forearm fold; no prepollex; weak supratympanic fold; dorsum slightly glandular; throat

finely granular, belly granular; toe lengths I<II<III=V<IV; toe disks well developed, largest just smaller than largest finger disks; toe webbing formula I 2^{+}-2^{+} II 1 1/2-2 1/2 III 1 1/2-2 2/3 IV 2^{+}-1 V; inner and outer metatarsal tubercles rounded-ovoid, outer less pronounced and just smaller than inner; no heel decoration; no tarsal decoration; outer surface of tarsus smooth; sole of foot with low rounded low rounded fleshy tubercles.

Dorsal pattern tan with darker brown faint irregular interorbital bar and two chevrons, one above shoulders, a second above sacrum, upper limbs faintly cross-banded; face more or less uniform tan; light area above arm insertion, faint mottle of large light indistinct markings on darker background in groin, rest of flanks a blending of dorsal and ventral patterns; throat and chest cream, speckled with brown, belly cream; posterior surface of thigh with indistinct but large light spots on a dark background, pattern less distinct on front of thighs and hidden portions of shanks.

SVL 42.5 mm (male); head length 34% SVL; head width 32% SVL; thigh length 44% SVL; shank length 50% SVL; foot length 41% SVL.

Life Colors. — Unknown for Boracéia specimen.

Larval Morphology. — Tadpoles not collected from Boracéia.

Leon (1975) described larva ascribed to *x-signata* from Venezuela.

Advertisement Call. — Calls not recorded from Boracéia.

Ecology. — The single individual was collected in December 1947.

Osteocephalus langsdorffii (Duméril and Bibron)

Hyla langsdorffii Duméril and Bibron, 1841. Original description.

Osteocephalus langsdorffii, Cope, 1867. First use of *langsdorffii* with *Osteocephalus*.

Diagnosis. — *Osteocephalus langsdorffii* is the only species of frog from Boracéia to have the combination of toe disks with circumferential grooves, toe and finger webbing, and cranial crests.

Adult Morphology (N = 1 male). — Snout outline almost semicircular from above, rounded in profile; low but distinct preocular, supraorbital, preparatoid, and pretympanic cranial crests; upper eyelid same texture as back, lacking distinctive features; tympanum distinct, large, diameter about 3/4 eye diameter; male vocal sac single, but externally expanded as bilobed sac; males with vocal slits; vomerine teeth in forwardly arched transverse series lying between choanae; finger lengths I<II<IV<III; finger disks large, largest disks on fingers II, III, IV much smaller than tympanum due to large tympanum size; finger webbing formula I trace II 1 1/2-2 1/2 III 2^{+}-2^{+} IV; finger subarticular tubercles well developed, bifid under finger IV; extensive brown nuptial pad on inner thumb of male; extensive, scalloped forearm fringe; no prepollex; weak supratympanic fold, extensive scalloped transverse flap under vent; dorsal texture glandular with scattered, indistinct tubercles; throat and chest weakly granular, belly granular; toe lengths I<II<III=V<IV; toe disks large, largest disks smaller than largest finger disks; toe webbing formula I 1-2 II 1^{-}-2^{+} III 1-2 IV 1 2/3-1^{-} V; inner metatarsal tubercle ovoid, outer small, round, about 1/5 size of inner; heel with well developed calcar-fold; smooth inner and outer tarsal folds along length of tarsus, outer fold more extensive than inner; outer surface of tarsus with slightly glandular texture; sole of foot granular with low, round fleshy tubercles.

Dorsal pattern lichenous tan and brown, upper limbs irregularly cross banded in tan and brown; face tan with dark brown irregular small spots and marks, ill-defined light area on lower half of posterior eyelid extending to tympanum; flanks with a blending of the dorsal and ventral pattterns; ventral pattern cream; posterior surface of thigh almost uniformly light tan.

SVL 74.9 mm (male); head length 30% SVL; head width 29% SVL; thigh length 50% SVL, shank length 54% SVL, foot length 41% SVL.

Life Colors. — Unknown for Boracéia specimens.

Larval Morphology. — Tadpoles unknown from Boracéia. Duellman (1974) described and figured tadpoles of this species from Guarujá, São Paulo.

Advertisement Call. — Call unrecorded.

Ecology. — The single specimen from Boracéia was collected in March 1948.

Phyllomedusa appendiculata A. Lutz

Phyllomedusa appendiculata A. Lutz, 1925a. Original description.

Nomenclatural Note. — Brasilian members of the genus *Phyllomedusa* are being studied by one of us (Cruz). Justification for the use of *P. cohranae* for species occurring at Boracéia will be published elsewhere. The use of *P. appendiculata* for the Boracéia population is provisional.

Diagnosis. — The Boracéia species *Centrolenella eurygnatha*, *C. uranoscopa*, *Hyla albofrenata*, *H. albosignata*, *H. leucopygia*, *H. prasina*, *Phyllomedusa appendiculata*, *P. cochranae*,and *Sphaenorhynchus orophilus* are red or green in life and whitish, lavander, pink, or bluish in preservative. The *Phyllomedusa* species have vertically elliptical pupils; all other green Boracéia frogs (in life) have horizontally elliptical pupils. *Phyllomedusa appendiculata* has reduced but distinct finger webbing, especially between the third and fourth fingers; *P. cochranae* lacks finger webbing.

Adult Morphology (N = 2 females). — Snout outline subovoid from above, vertical in profile; no cranial crests; upper eyelid without distinctive features; tympanum hidden above, distinct below, diamater about 1/2 diameter of eye; male vocal sac and slit condition unknown; no vomerine teeth; finger lengths I<II<IV<III; finger disks large, largest disks on fingers II, III, IV just larger than tympanum; finger webbing formula I trace II trace III 2 2/3-2 1/2 IV; finger subarticular tubercles moderate, single; male thumb asperity condition unknown; forearm fold distinct; no prepollex; supratympanic fold most distinct from tympanum to shoulder; dorsal texture smooth; chin smooth, belly granular; toe lengths I<II<III<V<IV; toe disks large, largest about same size as largest finger disks; toe webbing formula I 2^{+}-2 1/2 II 2-3 III 2-3^{-} IV 2 1/2-1^{+} V; inner metatarsal tubercle ovoid, outer not visible; heel with long prominent calcar; inner and outer tarsal folds along length of tarsus; outer tarsal texture smooth; sole of foot with fleshy tubercles.

Dorsal pattern almost uniform purple with a few small enamel white dots, purple on forearm, shank, and tarsus white outlined; face almost uniform purple or brown with light stripe from eye through tympanum to beyond angle of jaw bordered above by supratympanic fold; flank with dorsal pattern bordered by white stripe dorsally, with a band of pigmentless area along length of flank with a few spots of white pigment anteriorly; venter whitish anteriorly, cream posteriorly; posterior surface of thigh pigmentless.

SVL 36.8-37.4 mm (females); head length 36% SVL, head width 34% SVL, thigh length 43-45% SVL; shank length 47-49% SVL; foot length 32-38% SVL.

Life Colors. — Unknown for specimens from Boracéia.

Larval Morphology. — Body sub-cylindrical in dorsal view, slightly wider than deep; snout broadly rounded in dorsal outline; nostril nearer the tip of snout than eye; distance between nares 75% interorbital width; nares rounded, small, situated dorsolaterally and directed laterally; opening of the ventral spiracle directed posteriorly about 58% body length; anal tube short, attached to the ventral fin and dextral; tail slightly higher than body; dorsal fin origin on body-tail juncture; dorsal fin almost straight, ventral arched; tail musculature reaching the pointed tail tip; mouth anteroventral, width equal to 49% body width; two interrupted rows of oral papillae, except for the lateral portions with about five rows, few inner scattered papillae; tooth row formula 2(2)/3(1); beak moderately developed and finely serrated.

Body and tail musculature uniformly faded brownish; tail fins transparent with blackish fringe (Figure 27).

Larval Habitat. — Tadpoles were collected from wide portions of a forested stream.

Advertisement Call. — Unrecorded at Boracéia.

Ecology. — Two were collected from small trees at night next to forest streams. Specimens have been collected in October and December through February.

Pyllomedusa cochranae Bokermann

Color Figure 26

Pyllomedusa cochranae Bokermann, 1966b. Original description.

Diagnosis. — The Boracéia species *Centrolenella eurygnatha, C. uranoscopa, Hyla albofrenata, H. albosignata, H. leucopygia, H. prasina, Phyllomedusa appendiculata, P. cochranae,* and *Sphaenorhynchus orophilus* are reddish or green in life and whitish, lavender, pink, purple, or bluish in preservative. The *Phyllomedusa* species have vertically elliptical pupils; all of the other green (in life) Boracéia frogs have horizontally elliptical pupils. *Phyllomedusa cochranae* lacks finger web; *P. appendiculata* has reduced, but distinct finger web, especially between the third and fourth fingers.

Adult Morphology (N = 6 males). — Snout outline rounded or nearly rounded from above, vertical in profile, no cranial crests; upper eyelid smooth or with very slight wartiness; tympanum hidden above, distinct below, diameter about equal to or just less than 1/2 eye diameter; males without vocal sacs; males lacking vocal slits; no vomerine teeth; finger lengths I<II< or = IV<III; finger disks distinct, largest disks on fingers II, III, IV about same size or just smaller than tympanum; fingers free, webbing absent; finger subarticular tubercles moderately developed, bifid under finger IV (sometimes under III); males with dark patch of spinules on base of inner thumb; forearm fold distinct, glandular, not scalloped; no prepollex; supratympanic fold distinct only from posterior edge of tympanum to shoulder, long pair of broad dorsolateral glandular folds in mid-body distinct or not; dorsal texture smooth-glandular; throat and chest weakly granular to granular, belly granular; toe lengths I<II<III< or >V<IV; toe disks distinct, largest about same size as largest finger disks; trace of web only between toes III-IV-V; inner metatarsal tubercle ovoid, outer not visible; heel with small calcar; weak to pronounced outer glandular tarsal fold, no inner; outer tarsal texture smooth; sole of foot with fleshy tubercles.

Dorsum uniform pink with scattered small or moderate brown spots and a few enamel white spots on back and upper limbs, outer forearm and tarsal folds white highlighted, outer arm and tarsus with lots of brown dots, white in vent region or not; face same pattern as dorsum or with a line of brown dots along the edge of the upper lip; flank with distinct to indistinct large brownish spots on a white ground; venter uniformy creamy white; posterior surface of thigh variable, from mostly lacking pigment to almost uniformly washed with a wgute suffusion to a red pigment dot wash.

SVL 28.6-33.9 mm (males); mean head length 36% SVL; mean head width 36% SVL; mean thigh length 46% SVL; mean shank length 49% SVL; mean foot length 31% SVL.

Life Colors. — Iris silver with black reticulations. Dorsum bright enamel green with either scattered small blue dots or scattered brown pinpoint spots over head, body, arms, and legs. Concealed surfaces of sides, arms (all of upper arm), legs, fingers and toes orange with irregular rounded purple spots, the purple darker at groin. Belly and lower surfaces of arms and legs flesh colored, transparent posteriorly.

On newly captured specimens (MZUSP 32075-76), the body colors were deep rich red brown. The change from green to brown was observed in captivity. Color change can be quite rapid (less than 3 minutes) or color may remain for some time an intermediate olive-brown shade, sometimes mottled. This color change does not seem to affect the colors of the concealed surfaces.

Larval Morphology. — Body sub-cylindrical in dorsal view, slightly deeper than wide; snout broad in dorsal outline; nostril midway between eye and tip of snout; distance between nares 114% interorbital width; nares rounded, small and situated dorsolaterally; eye dorsolateral and directed laterally, 17% body length; opening of the ventral spiracle directed posteriorly about 55% body length; anal tube long, free from the ventral fin and dextral; tail slightly higher than body; dorsal fin origin extending slightly onto the body; dorsal and ventral fins arched; tail musculature reaching the pointed tail tip; anterodorsal mouth with a funnel-shaped dermal fold equal to 80% body width and showing two distinct sizes of papillae; tooth row formula 1/2(1); beak moderately developed and finely serrated.

Body and tail musculature uniformly gray brownish; tail fins transparent with flecks (Figure 28).

Larval Habitat. — Tadpoles were collected from wide portions of a forested stream.

Advertisement Call. — Call not recorded from Boracéia. Males have been heard calling, answering each other with a single quiet "churrup."

Ecology. — One individual was observed calling at night from 1 m up on a forest vine 1 m from the edge of a pool in a stream; it was part of a small chorus of *P. cochranae* at this pond. Individuals walked slowly rather than hopping; the flash colors were exposed while walking. Individuals were collected in August, September, December and February.

Sphaenorhynchus orophilus (A. Lutz and B. Lutz)

Color Figure 27

Hyla (Sphoenohyla) orophila A. Lutz and B. Lutz, 1938. Original description.

Sphaenorhynchus orophilus, Rivero, 1969. Transfer of *orophila* to *Sphaenorhynchus*.

Diagnosis. — *Sphaenorhynchus orophilus* shares the colors of green in life and whitish, lavender, purple or bluish in preservative with *Centrolenella eurygnatha, C. uranoscopa, Hyla albofrenata, H. albosignata, H. leucopygia, H. prasina, Phyllomedusa appendiculata,* and *P. cochranae*. *Sphaenorhynchus orophilus* has vomerine teeth; the *Centrolenella* and *Phyllomedusa* species lack vomerine teeth. *Sphaenorhynchus orophilus* lacks a prepollex; *H. prasina* has an externally developed prepollex. *Sphaenorhynchus orophilus* has a distinct canthal and post-orbital stripe extending as far as the groin; *H. albosignata* and *leucopygia* lack canthal or postorbital stripes. The postorbital stripe in *S. orophilus* continues straight behind the eye; the postorbital stripe in *H. albofrenata* curves downward behind the arm insertion.

Adult morphology (N = 5 males). — Snout outline pointed or truncate-subovoid from above, acute in profile; no cranial crests; no special features on upper eyelids; tympanum covered; male vocal sac single, externally expanded, extending from posterior half of throat through chest region; males with vocal slits; vomerine teeth in short transverse series lying between and just posterior to choanae; finger lengths I<II<IV<III; finger disks present, moderate, largest on fingers II, III, IV; modal finger webbing formula I 2-2^{+} II 1 1/2-2 1/2 III 2^{+}-2 IV; finger subarticular tubercles low, rounded, single, or bifid under fingers III, IV; male thumb with light tan nuptial pad on inner base; outer forearm fold weakly developed, smooth; no prepollex; fold from eye to mid-body high on flank, modest transverse vent fold covering top of vent; dorsum granular; venter granular; toe lengths I<II<III< or =V<IV; largest toe disks just smaller than or about same size as finger disks; modal toe webbing formula I 1^{-}-2^{-} II 1^{-}-2 III 1-2 IV 2-1 V; inner metatarsal tubercle ovoid, outer round and flat, about 1/4 size inner, or indistinct; heel granular; weakly developed inner and outer tarsal folds extending length of tarsus distinct or not; outer tarsal texture granular or smooth; sole of foot granular with a few round fleshy tubercles.

Dorsal pattern creamy white with a pale suffusion of brown pigment dots with more pigment anteriorly or indistinct brown spots on back (and limbs) and on upper eyelids, sometimes with a dark, indistinctly defined mid-dorsal band on head extending to shoulder region; upper limbs mostly lacking pigment, with a scattering of brown dots or spots, outer forearm and tarsal fold regions weakly white highlighted or not, seat patch area washed with white or not; face with a dark stripe from tip of snout, across canthus to eye, white patch under eye distinct or not, rest of face same pattern as back; light stripe (on fold) distinct or not from eye to groin, bordered below by brown dots anteriorly to about mid-body or to groin; venter creamy white, front of vocal sac with or without brown dots; posterior surface of thigh lacking pattern.

SVL 28.7 -32.0, mean 30.3 mm (males); mean head length 27% SVL; mean head width 29% SVL; mean thigh length 43% SVL; mean shank length 44% SVL; mean foot length 43% SVL.

Life Colors. — Iris bronze to yellow-bronze. Dorsum green with or without black mottling or spots; dorsolateral stripes yellow above, black below; outer foream, foot and tarsus highlighted

with white stripe; white pebbled seat patch. Belly green or greenish yellow; white-sheathed guts visible through belly wall. Posterior surface of thigh green (as rest of limbs).

Larval Morphology. — Body subcylindrical in dorsal view; wider than deep; snout broadly rounded in dorsal view; nostril midway between eye and tip of snout; distance between nares 84% interorbital width; nares elliptical, directed anteriorly; eye dorsolateral and directed laterally, 13% body length; opening of the sinistral spiracle directed posteriorly on the midline about 80% body length; anal tube median; tail slightly higher than body; dorsal fin origin extending slightly onto the body; dorsal and ventral fins arched; tail musculature reaching the pointed tail tip; mouth anteroventral, directed anteriorly, width 32% body width; two rows of oral papillae, the first broadly interrupted anteriorly and the second restricted to the lateral and ventral portions; tooth row formula 2(2)/3(1); beak moderately developed and finely serrated.

Body and tail brown with two longitudinal unpigmented stripes on first half of tail musculature; an unpigmented longitudinal stripe from the mouth passing under the eye; dorsal and ventral fins marbled; venter light brown. In life, dorsum of the body brown fading to a pale yellow venter; a conspicuous yellow longitudinal stripe from the mouth passing under the eye; tail musculature brown with two longitudinal yellow stripes on the first half; dorsal and ventral fins brown marbled over a yellow background; iris golden with two blackish areas converging on the pupil (Figure 29).

Larval Habitat. — Tadpoles were collected from the permanent pond "Lago do Aterro" (Figure 5).

Advertisement Call. — Two call types were heard and recorded.

The predominant call heard of 2-12 notes of about 0.30-1.80 s duration; note rate 4-7 per s; each note 0.01-0.03 s duration; notes with complex wave form modulated at about 200 Hz; call about the same loudness throughout; call not noticeably frequency modulated; dominant (= fundamental) frequency about 2000-2700 Hz; no obvious harmonic structure evident in wave form; sidebands due to modulation of note (Figure 56).

The second call about 0.25 s duration, of about 20-25 notes/pulses, unevenly spaced to a maximum rate of about 150 pulses/notes per s; initial pulse quieter than remainder of call; wave form of pulses complex, weakly partially pulsed at about 1200 Hz; call not noticeably frequency modulated; dominant (= fundamental) frequency about 1500-2700 Hz; sidebands produced by close set notes of various spacing and their pulsatile nature (Figure 56).

The more rarely heard call apparently is given before the more commonly heard calls and is not given by itself, unlike the more commonly heard call.

Ecology. — Males call at night from vegetation just at or partly above the water of large ponds or lakes in open vegetation. Specimens have been collected only from Lago do Aterro and one from the quarry, the same habitats where calling males were found. Specimens were collected in November and January or February.

Family Leptodactylidae

Adenomera marmorata Fitzinger *in* Steindachener

Color Figure 28

Adenomera marmorata Fitzinger *in* Steindachner, 1867. Original description. — Wassersug and Heyer, 1988. Description of internal oral morphology of larvae from Boracéia.

Leptodactylus marmoratus, Cochran, 1955. Specimens cited from Boracéia.

Diagnosis. — *Adenomera marmorata* is the only small Boracéia frog (SVL less than 23 mm) lacking toe web or fringe but with a distinct tympanum and vomerine teeth and with a profusion of white-tipped tubercles on the outer tarsus and sole of foot.

Adult Morphology (N = 10 males, 10 females). — Snout outline from above in males subelliptical to nearly rounded, in females nearly rounded to almost semicircular, snout profile rounded, in large males rounded-acute to acute; no cranial crests; no distinctive upper eyelid decoration; tympanum distinct, diameter about equal to or just larger than 1/2 eye diameter; male vocal sac present, single, internal or barely

expanded externally; males with vocal slits; vomerine teeth in short transverse (slightly obtuse in one specimen) series, separated from each other by about length of one tooth row, lying well posterior to choanae; finger lengths IV<I just <, just >, or ≡II<III; finger tips rounded or very slightly swollen, not disked; fingers free, without fringes or webbing; basal finger subarticular tubercles rounded, more prominent than low, rounded distal subarticular tubercles on fingers; largest males with a fleshy white ridge on snout, no thumb asperities; no forearm fold; no prepollex; supratympanic fold weakly or barely developed; dorsal texture ranging from smooth to granular or tuberculate, usually granules or tubercles better developed posteriorly on back; belly smooth, seat patch area of under thighs areolate, rest of under sides of limbs smooth; toe lengths I<II<V<III<IV; toe tips barely to noticeably expanded into small, ungrooved disks, largest disks much smaller than tympanum; toes free, without fringes or webbing; inner metatarsal tubercle ovate, distinct, outer metatarsal tubercle distinct, rounded to ovate, 1/4 to same size as inner; heel smooth or with white-tipped tubercles; inner tarsal fold running about 7/8 length of tarsus with single row of white-tipped tubercles on crest; outer tarsal texture with a profusion of white-tipped tubercles; sole of foot with a profusion of white-tipped tubercles.

Dorsal pattern variable, including a central dorsal area of indistinctly mottled or indistinctly to distinctly spotted dark and light browns, with or without a light interorbital stripe, with or without a dark interorbital triangle, often a distinct pair of broad light dorsolateral stripes from back of eye to groin, bordered (or not) medially by a dark brown stripe, light mid-dorsal stripe from mid-body or sacrum to vent present or not, upper limbs banded in browns and tans; face mottled tans and brown, dark oblique bars from front (sometimes only this bar present) and back of eye to upper lip present or absent, lighter ill-defined stripe from below eye to shoulder present or absent, supratympanic fold usually dark outlined; flanks mottled; throat dotted with brown, belly cream or dotted with brown, under legs mottled; posterior surface of thigh mottled, sometimes a uniform brown area next to knee.

SVL 17.6-20.5, mean 19.3 mm (males), 17.6-22.9, mean 20.9 mm (females); mean head length 40% SVL (males), 38% SVL (females); mean head width 34% SVL (males), 32% SVL (females); mean thigh length 41% SVL; mean shank length 45% SVL (males), 44% SVL (females); mean foot length 51% SVL (males), 50% SVL (females).

Life Colors. — Iris bronze. Dorsum with tans and browns, light stripes orange, rusty orange, to salmon red, including heels and arms. Chin and throat gray, flecked with white, belly fleshy gray or yellow. Posterior surface of thigh mottled brown and black.

Larval Morphology. — Body pyriform in dorsal view, slightly wider than deep; snout narrowly rounded in profile; nostril nearer tip of snout than eye; distance between nares 74% interorbital width; nares rounded, dorsolateral and directed anterolaterally; eye dorsolateral, 11% body length; opening of the lateroventral spiracle directed laterally about 61% body length; anal tube short and median; tail height less than body height; dorsal fin origin on the body-tail juncture; dorsal and ventral fins slightly arched; tail musculature reaching the pointed tail tip; mouth anteroventral, width 35% body width; a single row of rounded oral papillae broadly interrupted anteriorly; teeth absent; beak not cornified.

Body dark gray on dorsum and sides of anterior half, rest cream; fins and tail musculature unpigmented; intestine full of yolk (Figure 30).

Larval Habitat. — The following field notes by Heyer are from 12-13 December 1976: "The foam nests are both behind moss and liverworts [moss bank on roadcut], where spherical chambers (about 30-40 mm diameter) have been formed and in big moss clumps themselves. The center of the nest, where the eggs, embryos, or larvae are found is gelatinous, covered all around by frothy, stiff foam. The foam is still fresh appearing in the nests with metamorphs. Two nests were found that just had foam. Apparently the froglets had metamorphosed out of them and the foam was still present." The seven occupied nests had clutch sizes ranging from 2-7 individuals.

Advertisement Call. — When actively calling, calls given in bursts of about 10-30 at a time at a

rate of 0.8-1.4 per s; calls consisting of single notes, call-note duration about 0.04-0.07 s; call begins abruptly, intensity maintained throughout most of the start of the call and then declines gradually towards the end; frequency rising rapidly within call; dominant (= fundamental) frequency 4500-5400 Hz; calls lacking harmonic or sideband structure (Figure 57).

Ecology. — Males commonly call on ground under vegetation in the late afternoons, frequently in association with showers. The call is commonly heard around the living quarters. This is one of the commonest frog species at Boracéia. The species is diurnal and occurs in the forest as well as in clearings. Individuals have been collected from August through May.

Ceratophrys aurita (Raddi)

Bufo auritus Raddi, 1823. Original description.
Ceratophrys aurita, Bokermann, 1965a. Recognition of *aurita* as a valid species of *Ceratophrys*.

Diagnosis. — Three Boracéia species of frogs have distinct eye horns (triangular flaps of skin extending over eye from upper eyelid): *Ceratophrys aurita, Proceratophrys boiei,* and *Proceratophrys melanopogon. Ceratophrys aurita* has an externally visible tympanum, whereas the two *Proceratophrys* have tympani covered by skin and not visible externally.

Adult Morphology (N = 1 female). — Snout rounded from above, strongly obtuse in profile; weak preocular, canthal, postocular, and pretympanic cranial crests; upper eyelid with prominent fleshy horn; tympanum large, distinct, about 5/6 eye diameter; vomerine teeth in small patches next to anteromedial borders of choanae (condition from other specimens, mouth firmly shut in specimen from Boracéia); finger lengths II<I≅IV<III; finger tips pointed; fingers free; basal finger subarticular tubercles better developed than distal finger subarticular tubercles; no forearm fold; no prepollex; no distinctive body glands or folds; dorsum with a bony shield extending almost to sacrum with posterolateral wings, rest of dorsum warty-tuberculate; throat and chest smooth, belly granular; toe lengths I<II<V<III<IV; toe tips pointed; toe webbing formula I trace II trace III 2 1/2-3 1/2 IV 4-2 1/2 V; inner metatarsal tubercle expanded, prominent, spade-like, no outer metatarsal tubercle; heel tuberculate, same texture as surrounding areas; inner tarsal fold extending from inner metartasal tubercle almost the full length of tarsus; outer tarsal texture and sole of foot smooth.

Head and dorsal shield tan with brown fields, light mid-dorsal stripe, rest of back dirty brownish-black, upper limbs banded tan and brown; face tan and brown, somewhat mottled; flanks a blending of dorsal and ventral patterns; throat cream with brown wash, rest of belly cream; posterior surface of thigh almost uniform brown.

SVL 149.0 mm (female); head length 47% SVL; head width 56% SVL; thigh length 39% SVL; shank length 37% SVL; foot length 39% SVL.

Life Colors. — Iris metallic gold to silver. Dorsum light brown with dark brown or black spots ringed with gray; central green dorsal stripe; legs banded green and brown above (life colors based on two specimens from nearby Casa Grande).

Larval Morphology. — Tadpoles not collected from Boracéia. Wassersug and Heyer (1988) give a brief description of the external morphology and a detailed description of the internal oral anatomy of specimens from Serra da Bocaina, São Paulo.

Advertisement Call. — Call not recorded at Boracéia.

Ecology. — The single specimen from Boracéia was collected in May 1965.

Crossodactylus dispar A. Lutz

Color Figure 29

Crossodactylus dispar A. Lutz, 1925a. Original description.

Nomenclatural Note. — Two species of *Crossodactylus* are represented in collections from Boracéia. The systematics of this genus is confused and it is not clear what names should be applied to the two forms. We are rather arbitrarily associating the name *dispar* with the species commonly represented at Boracéia by specimens and the name *gaudichaudii* to the single specimen representing the second species.

Diagnosis. — The only taxa at Boracéia that have dark, cornified spines on the thumb are *Crossodactylus dispar*, *C. gaudichaudii*, *Leptodactylus flavopictus*, *L. ocellatus*, and *Thoropa miliaris*. *Leptodactylus* and *Thoropa* have spines only on the males and lack dorsal scutes on the toe tips; the two *Crossodactylus* species have thumb spines in both sexes and have dorsal scutes on toe disks. *Crossodactylus dispar* has 3 spines per thumb; *C. gaudichaudii* has 2 spines per thumb.

Adult Morphology (N = 10 males, 10 females). — Snout outline from above rounded to almost semicircular, rounded to acute in profile; no cranial crests; no particular decoration on upper eyelid, texture same as surrounding dorsum; tympanum distinct to almost hidden, diameter just larger than 1/2 to 3/4 diameter of eye; no vocal sac in males; males usually lacking vocal slits, rarely small slits present; no vomerine teeth, sometimes a toothless ridge visible between anterior extent of choanae; finger lengths of I, II, IV variable, may be just shorter or longer than each other, finger III longest; finger tips rounded, not disked, upper surfaces lacking scutes or with weakly developed scutes; finger webbing absent, sides of fingers ridged; finger subarticular tubercles moderate, round, single; males and females with three spines per thumb, forearm hypertrophied in both sexes, in some large males, a row of small brown-tipped tubercles on the edge of the upper lip; two (rarely three) small white tubercles on outer forearm, one near wrist, other near elbow; no prepollex; weakly to modestly developed supratympanic fold; dorsal texture smooth to grandular, warty-grandular posteriorly; ventral texture smooth; toe lengths I<II<V<III<IV; toe tips expanded (or not much) into disks, larger than finger tips, much smaller than tympanum, dorsal surfaces of largest disks with distinct pair of scutes; toes ridged or fringed, ridging or fringing joined at base, no other web developed; inner metatarsal tubercle oval, outer round, protuberant, about 1/3 to 1/2 size of inner; single small white tubercle on dorsal aspect of heel; inner tarsal fold or fringe extending entire length of tarsus; outer tarsus with two small white tubercles offset from each other medially, one on outer edge nearer heel, second close to tarsal fold or fringe nearer toes, rest of outer tarsal texture smooth; sole of foot smooth.

Dorsum rarely uniform brown, usually with distinct symmetrical darker brown stripes including a Y from behind eyes to above shoulders, a pair of inwardly curving stripes on either side of Y, sometimes becoming parallel and interrupted to vent, may be an additional pair of dorsolateral stripes parallel to those, or a W-shaped pattern behind eyes, a continuous to interrupted light mid-dorsal pin stripe from snout to vent most distinct posteriorly present or absent, limbs striped; face with dark canthal stripe, sharply defined above, blending into rest of face color below to almost sharply defined below, loreal region and upper lip light to mottled or almost uniform, scattering of white dots under eye, on lip, and behind angle of jaw, supratympanic fold dark outlined; flanks with a bold mottle of dorsal and ventral colors low on flanks; throat and chest faintly to boldly mottled cream and tan, belly cream or with faint to distinct mottle of large proportions anteriorly; posterior surface of thigh almost uniform to indistinctly mottled brown and tan.

SVL 24.3-30.6, mean 28.2 mm (males), 25.8-30.9, mean 28.3 mm (females); mean head length 38% SVL (males), 37% SVL (females); mean head width 36% SVL; mean thigh length 44% SVL; mean shank length 44% SVL; mean foot length 48% SVL.

Life Colors. — Dorsum brown to orange brown; upper limbs brown, arms sometimes orange; fingers and toes sometimes with white spots; few white spots on side of head and shoulder. Throat cream and brown to white and flesh-color mottled, belly dirty white to gray. Under limbs translucent flesh colored. Groin pinkish.

Larval Morphology. — Tadpoles not collected from Boracéia.

Advertisement Call. — Call (if present) not recorded from Boracéia.

Ecology. — The species is diurnal, although a few were captured at night. Most individuals were found in the forests, associated with stream edges or seeps or puddles. The only other place where specimens were collected was at the quarry in shallow water among the rocks at night. Specimens were collected from September through April.

Crossodactylus gaudichaudii Duméril and Bibron

Crossodactylus gaudichaudii Duméril and Bibron, 1841. Original description.

Nomenclatural Note. — It is very possible that *gaudichaudii* is not the proper name for this single specimen collected from Boracéia. Also see note under *dispar*.

Diagnosis. — The only taxa at Boracéia that have dark, cornified spines on the thumb are *Crossodactylus dispar, C. gaudichaudii, Leptodactylus flavopictus, L. ocellatus,* and *Thoropa miliaris*. The two *Crossodactylus* species have thumb spines in both sexes and have dorsal scutes on the toe disks; the *Leptodactylus* and *Thoropa* species have spines only in the males and they lack dorsal scutes on the toe tips. *Crossodactylus gaudichaudii* has 2 spines per thumb; *C. dispar* has 3 spines per thumb.

Adult Morphology (N = 1 male). — Snout outline from above slightly truncate and nearly rounded, acute in profile; no cranial crests; upper eyelids lacking decoration, texture same as adjacent dorsal texture; tympanum present, distinguishable, diameter just greater than 1/2 eye diameter; no vocal sac; no vocal slits; no vomerine teeth, a pair of transverse toothless ridges lying between anterior extent of choanae; finger lengths I≅II≅IV<III; finger tips barely expanded, scutes not developed; fingers without webbing, sides of fingers slightly ridged; finger subarticular tubercles moderate, rounded, single; 2 spines on each thumb; 2 small white tubercles on outer forearm, one near wrist, other near elbow; no prepollex; moderate supratympanic fold; dorsal texture slightly glandular, warty-glandular posteriorly; ventral texture smooth; toe lengths I<II<V<III<IV; toe tips slightly expanded, just larger than finger tips, much smaller than tympanum, largest with a pair of well developed dorsal scutes; sides of toes ridged, ridging joined at base, no other toe web; inner and outer metatarsal tubercles pronounced, inner ovoid, outer rounded, about 1/3 size of inner; heel smooth; inner tarsal fold extending 7/8 length of tarsus; outer tarsus with indistinct pair of small white tubercles (as in *dispar*), otherwise smooth; sole of foot smooth.

Dorsum brown with an indistinct pair of broken darker dorsolateral stripes and other indistinct darker brown marks, mid-dorsal light pin stripe from tip of snout to vent, upper limbs mostly uniform brown; face with dark canthal stripe bordered below by light tan loreal stripe extending under eye; supratympanic fold dark outlined; flanks somewhat mottled low on sides; throat and belly cream with brown dotted wash; posterior surface of thigh mottled brown.

SVL 21.8 mm (male); head length 39% SVL; head width 35% SVL; thigh length 43% SVL; shank length 46% SVL; foot length 51% SVL.

Life Colors. — Not available for Boracéia specimen.

Larval Morphology. — Tadpoles not collected from Boracéia.

Advertisement Call. — Not available for Boracéia.

Ecology. — The single specimen was collected in September 1950.

Cycloramphus boraceiensis Heyer

Figure 10

Cycloramphus boraceiencis Heyer, 1983. Original description.

Cycloramphus dubius, Bokermann, 1951; Heyer and Mello, 1979; specimens cited from Boracéia.

Cycloramphus neglectus, Cochran, 1955. Cochran lists two specimens from Boracéia, MZUSP 2966 and USNM 129150. We have been able to locate only the USNM specimen, which is *C. boraceiensis*.

Diagnosis. — The only Boracéia frogs with a dorsal iris meniscus are *Cycloramphus boraceiensis, C. eleutherodactylus,* and *C. semipalmatus*. *Cycloramphus boraceiensis* has a warty skin and toe webbing; *C. eleutherodactylus* has a relatively smooth skin and lacks toe webbing. *Cycloramphus boraceiensis* is not as warty as *C. semipalmatus*. The warts of *C. boraceiensis* are relatively uniform in size; the warts of *C. semipalmatus* range from small to large and the large warts are often arranged in ridges. In addition, *C. boraceiensis* has more foot webbing (web obvious between toes I, II and III) than *C.*

semipalmatus (web almost non-existent between toes I, II, and III).

Adult Morphology (N = 8 males, 1 female). — Snout outline from above rounded to semicircular, rounded to rounded obtuse with flaring lip in profile; no cranial crests; no upper eyelid decoration; tympanum not visible; male vocal sac single, internal; vocal slits present in males; vomerine teeth in arched or straight transverse series lying between and posterior to choanae in medial contact or barely separated; finger lengths I<II<IV<III; finger tips slightly swollen, not disked; fingers without webbing, sides of fingers ridged; basal subarticular tubercles on fingers normal, rounded, single, distal subarticular tubercles indistinct; no asperities on thumb of male; no forearm fold; no prepollex; supratympanic fold moderately developed, males with large, ovoid-rounded, distinct lumbar gland; dorsal texture with shagreen and more or less uniform sized warts with or without white-tipped tubercles; venter granular; toe lengths I<II<III< or >V<IV; toe tips slightly swollen, not disked; modal toe webbing formula I 1-2 II 1^{+}-3^{-}III 1^{+}-3^{+}IV 3-1^{-} V; inner metatarsal tubercle oval, elongate, outer tubercle rounded or ovate, 1/4-1/2 size inner; heel tuberculate as surrounding area, without distinguishing features; weak inner tarsal fold extending 1/2 to 2/3 length of tarsus present or absent; outer surface of tarsus smooth to scattered with white tipped tubercles; sole of foot smooth or shagreened.

Dorsum with variegated browns with a light interorbital cross band, a central mid-body light spot present or absent, upper limbs faintly to boldly cross banded; face uniform brown with or without three light vertical stripes under front, middle, and back of eye and another stripe under nostril, supratympanic fold dark highlighted; flanks with meeting of dorsal and ventral patterns low on sides; venter tan or variegated tan and cream; posterior surface of thigh uniform brown, somewhat mottled, or with a few light dots on a brown field.

SVL 36.0-51.3, mean 43.4 mm (males), 53.9 mm (female); (rest of data for males, female values are matched by individual male values) mean head length 40% SVL; mean head width 43% SVL; mean thigh length 48% SVL; mean shank length 46% SVL; mean foot length 47% SVL.

Life Colors. — Iris copper. Dorsum brown, black, tan, area above vent sometimes orange-brown. Belly transparent pink or flesh mottled with white; sides, chest and throat flecked with white; chin also with brown.

Larval Morphology. — Body oval in dorsal view, wider than deep; snout rounded in profile; external nares absent; eye dorsolateral, 14% body length; opening of the lateral spiracle directed posteriorly about 61% body length; anal tube absent; tail height less than body height; dorsal and ventral fin origin on the posterior half of the tail musculature; dorsal and ventral fins almost straight; tail musculature reaching the pointed tail tip; mouth anteroventral, width 59% body width; a single row of oral papillae only on lateral portions; tooth row formula 2(2)/3; beak with chisel-like central cusp.

General aspect brown; fins unpigmented (Figure 31).

Larval Habitat. — Larvae were collected from the wet seeping rock walls of the quarry.

Advertisement Call. — Call of single note, given sporadically; call/note duration 0.04-0.06 s; call partially pulsed, 15-18 pulses per call/note, at a rate of about 400 pulses per s; call not notably frequency modulated; call beginning abruptly and loudly, then tapering off somewhat in intensity; fundamental frequency 1900-2000 Hz; dominant broadcast frequency band 600-2500 Hz; only first harmonic apparent; sidebands well developed due to partially pulsed nature of call (Figure 58).

Ecology. — This species was common on the wet rock face of the quarry at night. One individual was collected from under a rock at the quarry during the day. Another individual was collected from a 30 cm boulder in a 1 1/2 m forest stream at night. Specimens were collected in September through March, May and June.

Cycloramphus eleutherodactylus (Miranda-Ribeiro)

Color Figure 30

Iliodiscus eleutherodactylus Miranda-Ribeiro, 1920a. Original description.

Cyclorhamphus eleutherodactylus, Brazil and Vellard, 1926. Association with *Cyclorhamphus*, an emendation of Agassiz, 1847.

Cycloramphus eleutherodactylus, Bokermann, 1951. Return of *Cycloramphus* to original spelling and first association of *eleutherodactylus* with non- emended spelling.

Diagnosis. — The only species with a dorsal iris meniscus at Boracéia are *Cycloramphus boraceiensis, C. eleutherodactylus,* and *C. semipalmatus. Cycloramphus eleutherodactylus* lacks toe webbing; *C. boraceiensis* and *C. semipalmatus* have toe webbing (distinct at least between toes III, IV, and V).

Adult Morpology (N = 3 males, 3 females). — Snout outline from above almost semicircular, rounded in profile; no cranial crests; upper eyelid lacking distinctive features, with low warts or as surrounding dorsal area; tympanum not visible; no vocal sac or vocal slits in males; vomerine teeth in short transverse or obtuse series lying between posterior portion of choanae or posterior to choanae; finger lengths I≃ II<IV<III; finger tips slightly swollen, not disked; fingers without webbing, usually without ridging on sides of fingers; basal finger subarticular tubercles moderate, rounded, distal subarticular tubercles indistinct; no asperities on male thumb; no forearm fold; no prepollex; weak supratympanic fold; males with large, rounded lumbar gland; dorsal texture ranging from finely granular to having short folds forming symmetrical chevron or) (above shoulders and/or miscellaneus ridges and warts or tubercles; venter smooth; toe lengths I<II<V< or =III<IV; toe tips slightly swollen, not disked; no toe webbing, sides of toes lacking ridge or fringe; inner metatarsal tubercle oval, outer rounded, about 1/4-1/3 size of inner; no heel decoration; tarsus either lacking decoration or with very weak inner tarsal fold extending 3/4 length of tarsus; outer tarsal texture smooth; sole of foot smooth.

Dorsal pattern variable including variegated browns with indistinct small light blotches or dark brown with small distinct light spots or dots, or a light interorbital bar, upper surfaces of limbs distinctly or indistinctly cross banded with or without light stripes outlines of dark bands; face either dark with small light spots or mottled with 2-3 irregular oblique light stripes under eye; flanks with meeting of dorsal and ventral patterns low on sides; venter tan with indistinct light spots to dark with distinct light spots; posterior surface of thigh dark with distinct light spots.

SVL 36.2-38.0 mm (males), 34.8-42.4 mm (females); head length 38-42% SVL; head width 42-46% SVL; thigh length 46-51% SVL; shank length 48-55% SVL; foot length 49-57% SVL.

Life Colors. — Iris bronzy brown with several areas of pale blue-gray radiating down below pupil in a vague pattern. Dorsum black above with small light green spots on body and bands on limbs. Venter black with white dots, especially on throat and chest.

Larval Morphology. — Larvae unknown.

Advertisement Call. — Unknown from Boracéia.

Ecology. — Most individuals with data were collected in the forest at night on the ground or in tree stumps, never near water. Two specimens were found under stones and logs in the forest during the day. Specimens were collected from September through February.

Cycloramphus semipalmatus (Miranda-Ribeiro)

Color Figure 31

Iliodiscus semipalmatus Miranda-Ribeiro, 1920a. Original description.

Cycloramphus asper, Bokermann, 1951; Heyer and Mello, 1979; specimens cited from Boracéia.

Cycloramphus semipalmatus, Heyer, 1983. Association of *semipalmatus* with *Cycloramphus* and recognition of *semipalmatus* as a distinct species.

Diagnosis. — The only Boracéia frogs with a dorsal iris meniscus are *Cycloramphus boraceiensis, C. eleutherodactylus,* and *C. semipalmatus. Cycloramphus semipalmatus* has a warty skin and toe webbing; *C. eleutherodactylus* has a relatively smooth skin and lacks toe webbing. The warts of *C. semipalmatus* range from small to large and the large warts are often arranged in short rows; the warts of *C. boraceiensis* are relatively uniform in size. In addition, *C. semipalmatus* has less foot webbing (web almost nonexistent between toes I, II, and III) than *C. boraceiensis* (obvious web between toes I, II, and III).

Adult Morphology (N = 10 males, 10 females). — Snout outline from above rounded to semicircular, rounded to obtuse in profile, usually with flared lip; no cranial crests; upper eyelid lacking distinctive features, texture same as surrounding area; tympanum not visible; male vocal sac present (usually) or absent, internal; males with vocal slits (usually), rarely with vocal folds; vomerine teeth in short transverse or arched series lying between and posterior to choanae; finger lengths I< or = or >II<IV<III; finger tips rounded; fingers without webbing, sides of fingers weakly to moderately ridged; basal finger subarticular tubercles moderate, rounded, distal tubercles indistinct, small; no asperities on thumbs of males; no forearm fold; no prepollex; weak supratympanic fold, males with compact to large oval lumbar glands; dorsal texture very warty, with unequal sized warts, some of largest warts arranged in longitudinal straight or symmetrically sinuous rows or not, warts tipped with brown tubercles, shagreen in addition to warts and tubercles; venter smooth to somewhat granular; toe lengths I<II<V<III<IV; toe tips pointed or rounded, not expanded; modal toe webbing formula I trace II trace III 3-4 IV 3 1/2-2 V; inner metatarsal tubercle an elongate oval, outer rounded or indistinct, about 1/6-1/4 size inner; heels with warts as on dorsum, no other particular features; weak or indistinguishable inner tarsal fold extending 2/3 length of tarsus; outer tarsal texture warty tuberculate; sole of foot with small warts and/or tubercles on outer half, inner half smooth or shagreened.

Dorsal pattern variegated browns with or without a light interocular stripe and a central light spot in scapular region, upper limbs cross banded; face with variegated browns as on dorsum usually with alternating dark and light oblique lip bars; flanks with same pattern as back, meeting ventral pattern low on sides; venter lightly mottled browns and cream or chin speckled brown and white, belly cream; posterior surface of thigh almost uniform brown to indistinctly mottled brown.

SVL 38.8-43.8, mean 40.8 mm (males), 42.0-50.9, mean 47.8 mm (females); mean head length 41% SVL; mean head width 44% SVL (males), 43% SVL (females); mean thigh length 48% SVL (males), 46% SVL (females); mean shank length 46% SVL (males), 45% SVL (females); mean foot length 47% SVL (males), 45% SVL (females).

Life Colors. — Iris light brown to darker rust brown, lower part with vague rays of brown and tan or brown and silvery gray radiating from pupil. Dorsum brown and black, light marks on dorsum and side of head light brown. Belly pale gray, pinkish brown, or bluish. Posterior surface of thigh brown with white flecks.

Larval Morphology. — Tadpoles unknown.

Advertisement Call. — Call of single note, given sporadically, call/note duration 0.02-0.04 s; call weakly partially pulsed, pulse rate about 240 per s, 4-7 pulses per call; call of single, intense burst of energy; call not frequency modulated; fundamental frequency about 750-1000 Hz; dominant broadcast frequency band 400-2000 Hz; fundamental at about 800 Hz, second harmonic at about 1600 Hz; sidebands due to partially pulsed nature of call (Figure 59).

Ecology. — Males call at night from under or on top of rocks in or next to small forest streams. All specimens for which data are available were active at night in the same microhabitats males call from. A few individuals were collected during the day from under rocks in forest streams. Specimens were collected from September through April.

Eleutherodactylus Duméril and Bibron

Unidentified Specimens. — Three individual specimens of the genus *Eleutherodactylus* from Boracéia are unidentifiable. One, a juvenile (USNM 243675), was discussed previously as a problematical specimen (Heyer, 1985b). The other two individuals appear to represent an additinal two distinct species. One juvenile (AMNH 104048) is a member of the group that has at times been accorded generic status as *Basanitia*. The other adult male (AMNH 104049) has a suite of characteristics that are distinctive at the group level. Until collections from surrounding geographic areas are thoroughly examined for additional specimens of these species, it is premature to describe as new these taxa. These specimens are mentioned to point out that the frog fauna of Boracéia contains at least three additional *Eleutherodactylus* species.

Eleutherodactylus binotatus (Spix)

Color Figure 32

Rana binotata Spix, 1824. Original description.
Eleutherodactylus binotatus, Müller, 1927. First association of *binotatus* with *Eleutherodactylus*.

Diagnosis. — The Boracéia species having distinct toe disks with circumferential grooves and lacking toe webbing or fringes are *Eleutherodactylus binotatus*, *E. guentheri*, *E. hoehnei*, *E. nigriventris*, *E. parvus*, *E. randorum*, and *E. spanios*. Of these, *E. binotatus* is the only one with distinctive rows of almost parallel ridges on the dorsal surface of the body.

Adult Morphology (N = 10 males, 10 females). — Snout outline subelliptical to rounded from above, rounded in profile; no cranial crests; upper eyelids lacking distinctive features, but with extensions of dorsal ridges on the eyelids; tympanum distinct, diameter 1/3 to just less than 1/2 diameter of eye; no vocal sac or vocal slits in males; vomerine teeth in short transverse or arched series lying between and far posterior to choanae; finger lengths II<<I≅IV<III, II<IV<<III<I, or II≅IV<<III≅ or <I; fingers I (sometimes), III and IV with small grooved disks, disks on III and IV largest, disk on I sometimes as large as disks on III and IV, finger tip on II swollen, not disked, largest finger disks much smaller than tympanum; fingers usually free of ridges, fringe, or web, rarely the barest trace of basal webbing between fingers II and III; finger subarticular tubercles moderate to large in size, globose, single; no asperities on thumbs of males; outer forearm region smooth or usually with a row of low tuberculate warts or a broken ridge; no prepollex; moderately developed supratympanic fold, dorsum with series of ridges, somewhat oblique on back of head, more or less parallel on body; dorsal texture slightly to very granular; belly weakly glandular-granular or smooth; toe lengths I<II<V= or <III<IV; all toe tips disked and grooved, largest on toe IV, largest toe disks just larger than to 30% larger than largest finger disks; toes usually free of ridge, fringe, or web, rarely with trace of basal webbing between toes I, II, III, IV; inner metatarsal tubercle ovate, outer tubercle rounded to rounded-ovate, about 1/2 size to about same size of inner; heel usually with a single distinct tubercle (lacking in one individual examined), rest of heel with small warts; tarsus lacking fold, sometimes with an indistinct row of warty tubercles on the outer tarsus; outer tarsal texture smooth; sole of foot smooth with a few prominent fleshy rounded tubercles.

Dorsal pattern variable including snout light tan (distinct from rest of color on head) or not, with or without a narrow dark interorbital stripe, body uniform brown with a pair of faint to dark brown spots about mid-body or with or without a pair of brown spots just behind head, or with a pair of dark highlighted dorsolateral folds from behind eye or with light tan stripes from tip of snout above canthus to outer edge of upper eyelids to groin, upper limbs uniform to having distinct cross banding and a few scattered dark flecks, outer tarsus and sole of foot dark brown, contrasting with light tan/brown dorsal color; faint to distinct dark eye and supratympanic fold, loreal region tan or dark brown, upper lip light with or without dark oblique bars under eye; flank pattern same as dorsal pattern or with faint oblique bars; venter cream with a few brown dots on the chest; posterior surface of thigh uniform brown or almost so, faint dark triangular seat patch present or absent.

SVL 32.3-44.7, mean 38.8 mm (males), 46.4-63.8, mean 57.4 mm (females); mean head length 42% SVL (males), 41% SVL (females); mean head width 37% SVL (males), 39% SVL (females); mean thigh length 50% SVL; mean shank length 56% SVL; mean foot length 50% SVL (males), 49% SVL (females).

Life Colors. — Iris yellow, gold, or orange gold with or without black or rich red brown transverse band through pupil. Dorsal color brown, khaki, tan, rich red brown, rust orange or pale walnut brown; arms and heels often bright orange; faint orange red to red in groin, anterior surface of thigh, concealed portion of shank, and top of foot. Throat and belly white, translucent or opalescent; border of lower jaw mottled white and brown; under legs clear with orange laterally; undersides of heel and foot black. Posterior surface of thigh orange red to red.

Larval Morphology. — Members of the genus *Eleutherodactylus* have direct deve-

lopment. No egg clutches were found at Boracéia.

Advertisement Call. — The call has not been recorded from Boracéia.

Ecology. — For the specimens with ecological data, most individuals were collected from forest trails or leaf litter during the day. Several individuals were collected from leaves on low vegetation at night in the forest, as well as on the leaf litter at night. One individual was collected at the forest edge, 46 were collected in the forest proper. Specimens were collected from September through May.

Eleutherodactylus guentheri (Steindachner)

Color Figure 33

Hylodes guentheri Steindachner, 1864. Original description.

Eleutherodactylus guentheri, Lynn and B. Lutz, 1946. First association of *guentheri* with *Eleutherodactylus*.

Diagnosis. — The Boracéia species having distinct toe disks with circumferential grooves and lacking toe webbing or fringes are *Eleutherodactylus binotatus, E. guentheri, E. hoehnei, E. nigriventris, E. parvus, E. randorum,* and *E. spanios*. *Eleutherodactylus guentheri* does not have a series of more or less parallel ridges on the back of the body as does *E. binotatus*. In addition, the first finger is about the same length as the second in *E. guentheri;* the first finger is murch longer than the second in *E. binotatus*. Those individuals of *E. guentheri* with patterns approaching eye masks are not as distinctively eye masked as *E. hoehnei*. The canthal portion of the eye mask in *E. guentheri* is much narrower than the portion at the tympanum; in *E. hoehnei*, the canthal portion is about as broad as the portion including the tympanum. *Eleutherodactylus guentheri* lacks a distinctive boldly mottled pattern in the groin that is characteristic of *E. nigriventris*. The toe disks are ovate or indented in *E. guentheri*, pointed on at least some toes in *E. parvus*. *Eleutherodactylus guentheri* has vomerine teeth; *E. randorum* lacks vomerine teeth. The tympanum is distinct in *E. guentheri*, hidden in *E. spanios*.

Adult Morphology (N = 10 males, 10 females). — Snout outline subelliptical or subovoid from above, rounded in profile; no cranial crests; upper eyelid with pronounced warty tubercles to weakly tuberculate; tympanum present, usually distinct, sometimes uppermost portion hidden, lower portion always distinct, diameter about one half eye; vocal sac in males either weakly indicated or not indicated: vocal slits present in males; vomerine teeth in two small transverse series, narrowly separated, posterior to and between choanae; finger I just $<, \cong$, just $>II \cong IV < III$; fingers distinctly disked, ungual flap indented, disk width about one and one half times finger width just behind disk; fingers without webbing, sides of fingers free, weakly to noticeably ridged; finger subarticular tubercles moderate, not pointed; males with cream glandular appearing nuptial asperities on the inner base of the thumb; forearm fold usually absent, rarely very weakly indicated; no prepollex; body lacking glands or folds or sometimes with a single pair of narrow dorsolateral folds and/or a fold from the angle of the jaw to the shoulder, no supratympanic fold; dorsal texture smooth to profusely warty-tuberculate; belly smooth; first toe shortest, fifth toe longest, second, third and fifth toes about same length; toe disks similar to and just larger than finger disks; sides of toes with ridges or fringes, toes not webbed; outer metatarsal tubercle rounded, smaller than ovoid inner metatarsal tubercle; heel with tubercle, usually pronounced; tarsus lacking fold or tubercle; outer tarsus smooth; foot texture smooth or with 1-4 rounded fleshy tubercles.

Dorsal pattern extremely variable ranging from uniform dark or light to complexly variegated, to a symmetrical complex pattern involving dark markings in the scapular region or with wavy dark and light longitudinal lines; the dorsal aspect of the snout sometimes lighter than ground color; light broad or narrow mid-dorsal stripes present or absent; lateral aspect of face with dark and light vertical stripes or bars, dark canthal stripe present or absent; flank indistinctly mottled to distinctly patterned with a broad, dark transverse bar, dark supratympanic spot sometimes with posterior extension continuous or not with lateral transverse bar, dark sacral spot sometimes with anterior extension; throat

mottled brown and cream, belly mostly cream, or entire venter mostly light; posterior surface of the thigh almost uniform brown or indistinctly mottled, rarely with distinctive mottle along bottom of thigh, light pin stripe continuous with mid-dorsal pin stripe sometimes present, extending along lower thigh.

SVL 19.3-26.7, mean 25.0 mm (males), 26.4-40.0, mean 36.1 (females); head width 40% SVL (males), 39% SVL (females); head width 36% SVL; thigh length 59% SVL (males), 56% SVL (females); shank length 66% SVL (males), 64% SVL (females); foot length 63% SVL (males), 60% SVL (females).

Life Colors. — Iris ranging from green dorsally and gold elsewhere to green and copper or rarely yellow to copper without the dorsal green. Dorsum variously colored, always with darker brown to red-brown; other markings on back sometimes rust colored; lighter markings range from green, light brown to white; light stripes, if present, white; feet and hands red-brown or not. Belly and undersides of legs usually yellow, ranging from golden yellow to dirty translucent yellow; chin grey, mottled with white to transparent with fine black regular peppering and irregular silver blotches. Posterior surface of thigh brown; if light stripes present, pale tan. No flash colors.

Larval Morphology. — Members of the genus *Eleutherodactylus* have direct development. Egg clutches were not found at Boracéia.

Advertisement Call. — Call consisting of 7-10 notes; calls given sporadically; call duration 0.40-0.65 s; note duration 0.007-0.024 s; note rate 15-17 per s; notes of 1-2 pulses at about 80-100 per s; pulses weakly modulated at a rate of 300-500 Hz; calls notably frequency and intensity modulated, beginning low and quiet, rising in frequency and intensity to about mid-call, then maintaining relatively constant frequency and intensity; dominant (= fundamental) frequency range at beginning of call 2000-2500 Hz, dominant frequency range at end of call 2600-3650 Hz; side bands evident (Figure 60).

Ecology. — Males call from leaves or branches/twigs on low vegetation (20-60 cm). Calling often occurs in late afternoon through early night. In the afternoons, waves of calls pass through the forest, each individual giving 2-3 calls, then calling ceases for many minutes before another calling bout is initiated.

Individuals were collected both during day and night hours (08:20-22:00 h). Active individuals were collected from the very end of August through June.

Almost all individuals (161 of 164) for which data were taken were collected from within the forest. Of these, the specimens occurred on the forest floor both during the day and at night. The only specimens collected on low vegetation were males calling at night. Two of the three non-forest specimens came from second growth areas and were on the ground. The single specimen collected from a cleared area was on leaves on the ground.

Eleutherodactylus hoehnei B. Lutz

Eleutherodactylus hoehnei B. Lutz, 1958. Original description.

Diagnosis. — The Boracéia species having distinct toe disks with circumferential grooves and lacking toe webbing or fringes are *Eleutherodactylus binotatus, E. guentheri, E. hoehnei, E. nigriventris, E. parvus, E. randorum,* and *E. spanios.* Of these, *E. hoehnei* is the only one to have a broad, even, and dark eye mask extending from the tip of the snout through the tympanum and ending on the flank behind the arms. The other *Eleutherodactylus* with eye masks have irregular eye masks that are less pronounced and with the canthal portion much narrower than the portion associated with the tympanum.

Adult Morphology (N = 1 male, 1 female). — Snout outline subelliptical from above, rounded in profile; no cranial crests; upper eyelid with 2-3 tubercles; tympanum present, somewhat hidden, diameter about 1/3 eye diameter; no vocal sac in male; no vocal slits in male; vomerine teeth in two small patches lying between and posterior to choanae; finger lengths I≅II<IV<III; fingers with disks, circumferential grooves, and dorsal indentations, disk of finger I just <II<III≅IV, largest disks about same size as tympanum; fingers free of fringe, ridge, or webbing; finger subarticular tubercles moderate, rounded, single; no thumb asperities on male; weak low glandular ridge on outer forearm; no

prepollex; no body glands or folds; dorsal texture smooth; ventral texture smooth, under thigh with granular seat patch; toe lengths I<II<III= V<IV; toe disks large, largest equal to or just larger than largest finger disks; toes without webbing or with barest trace of basal webbing, sides of toes with slight ridges; inner metatarsal tubercle oval, outer rounded, somewhat protuberant, about 1/2 to 2/3 size of inner; no heel decoration; no tarsal decoration; outer surface of tarsus smooth; sole of foot smooth with 3-4 round fleshy tubercles.

Dorsal pattern tan with a few small brown spots or with a symmetrically sinuous mid-dorsal brown band with a pair of brown stripes from behind eye to groin, mid-dorsal light pin stripe from snout to vent, upper limbs faintly and obliquely cross striped, forearm fold white outlined, outer shank, tarsus and foot with longitudinal dark brown bands bordered above by light pin striping; sharply defined dark stripe from tip of snout including nares across canthus to eye and from back of eye through tympanum and fading out in mid-flank, loreal region tan, upper lip lighter; flanks with mottling of dorsal and ventral patterns low on sides in addition to dark stripe described above; venter cream with tan speckling, chin brown outlined; posterior surface of thigh weakly mottled, mostly cream with a few pinpoint melanophores.

SVL 22.0 mm (male), 29.4 mm (female); head length 39-44% SVL; head width 31-32% SVL; thigh length 51% SVL; shank length 61-64% SVL; foot length 57-58% SVL.

Life Colors. — Mostly pale and dark browns; upper eyelid and edge of pale brown area on snout reddish gold. Chin and throat dirty transparent yellow, belly opalescent cream, throat and belly with pale brown mottling; under thigh mottled with red, less so on under shank.

Larval Morphology. — Members of the genus *Eleutherodactylus* have direct development. Egg clutches were not found at Boracéia.

Advertisement Call. — Not recorded from Boracéia.

Ecology. — One specimen was collected on a forest trail during the day; one specimen was collected near a small forest stream at night 1 1/2 meters above the ground on a leaf. The specimens were collected in December and March.

Eleutherodactylus nigriventris (A. Lutz)

Hylaplesia nigriventris A. Lutz, 1925a. Original description.

Eleutherodactylus nigroventris (lapsus for *nigriventris*), Lynch, 1976. First association of *nigriventris* with *Eleutherodactylus*.

Diagnosis. — The Boracéia species having distinct toe disks with circumferential grooves and lacking toe webbing or fringes are *Eleutherodactylus binotatus, E. guentheri, E. hoehnei, E. nigriventris, E. parvus, E. randorum,* and *E. spanios. Eleutherodactylus nigriventris* has a boldly mottled pattern of dark and light in the groin and on the anterior surfaces of the thigh; the only other *Eleutherodactylus* likely to be confused with this species is *E. randorum. Eleutherodactylus nigriventris* has vomerine teeth; *E. randorum* lacks vomerine teeth.

Adult Morphology (N = 1 male). — Snout outline rounded from above and in profile; no cranial crests; upper eyelid with prominent tubercles; tympanum hidden, small, diameter about 1/4 eye diameter; male vocal sac single, expanded in chest region; male vocal slits present; vomerine teeth in two small patches lying between and posterior to choanae; finger lengths I<II<IV<III; fingers with truncate disks with dorsal indentations, disk smallest on finger I, large disks on II, III, IV, largest disk on III larger than tympanum; fingers free of webbing, fringes, or ridges; finger subarticular tubercles modest, round single; no asperities on thumb; row of 2-3 tubercles on outer forearm; no prepollex; pair of sinuous ridges from behind eye to just past shoulder region; dorsum tuberculate, largest tubercles on upper eyelids; venter strongly granular; toe lengths I<II<III<V<IV; toe disks truncate, large, largest just greater than largest finger disks; toes without webbing, sides of toes with weak ridges; inner metatarsal tubercle oval, outer rounded, about 1/3 size of inner; each heel granular with one large prominent tubercle; no tarsal decoration; outer tarsal texture smooth-glandular with row of 2-3 tubercles on outer portion; sole of foot nearly smooth.

Dorsal pattern of lichenous browns; dark spot in canthal region, two irregular dark oblique bars under eye to lip, dark mark above tympanum;

large bold light irregular spot in groin, rest of flanks as dorsum; underside with dark mottled browns; front of thigh and hidden portion of shank with bold light and dark brown mottle, posterior surface of thigh brown with oblong light longitudinally oriented oval next to knee, broken into two marks on right side.

SVL 19.0 mm (male); head length 40% SVL; head width 36% SVL; thigh length 47% SVL; shank length 48% SVL; foot length 47% SVL.

Life Colors. — Unavailable.

Larval Morphology. — Members of the genus *Eleutherodactylus* have direct development. Egg clutches were not found at Boracéia.

Advertisement Call. — Not recorded from Boracéia.

Ecology. — One individual was collected from the forest at night 1/2 meter above the ground on a leaf. Specimens were collected in March and April.

Eleutherodactylus parvus (Girard)

Color Figure 34

Hylodes parvus Girard, 1853. Original description.

Eleutherodactylus parvus, B. Lutz, 1944. First association of *parvus* with *Eleutherodactylus*.

Diagnosis. — The Boracéia species having distinct toe disks with circumferential grooves and lacking toe webbing or fringes are *Eleutherodactylus binotatus*, *E. guentheri*, *E. hoehnei*, *E. nigriventris*, *E. parvus*, *E. randorum*, and *E. spanios*. Of these, only *E. parvus* has pointed toe tips; the tips are ovate and/or indented in the others.

Adult Morphology (N = 10 males, 10 females). — Snout outline subovoid to nearly rounded from above, rounded in profile; no cranial crests; upper eyelids smooth or with scattered warty tubercles; tympanum hidden or not visible, diameter about same as or less than 1/2 diameter of eye; males with single, slightly expanded vocal sac; males with vocal slits; vomerine teeth in transverse or obtuse series, almost in medial contact, lying far posterior to choanae; finger lengths variable, finger I≃II≃IV<III; finger tips rounded and barely pointed to swollen and pointed, lacking circumferential grooves, tip of finger III largest; fingers free of webbing, fringing, or ridging; finger subarticular tubercles not well developed, large but not raised; base of thumb on males swollen or not, if swollen with light white pad; weak row of tubercles on outer forearm present or absent, no prepollex; weak supratympatic fold present or absent, weak symmetrical dorsal ridges present or absent, distinct pair of dorsolateral folds from behind eye to past sacrum present or absent; dorsal texture smooth or with scattered warts and small tubercles or slightly glandular; venter smooth, seat patch area of under thighs granular or not; toe lengths I<II<V≃ or <III<IV; toe tips expanded into pointed disks, grooved (toe I may lack grooves), much larger than finger tips, disk on toe IV largest; toes free of webbing, fringing, or ridging; inner metatarsal tubercle ovoid, moderate, outer rounded and small to moderate, about 1/6-1/2 size of inner; heel ranging from smooth to with a few tubercles to with a single pronounced tubercle; no tarsal decoration; outer tarsal texture smooth; sole of foot smooth with 1-2 round fleshy tubercles.

Dorsal pattern variable, including almost uniform brown with pair of small dark spots in shoulder region, or broad brown band covering head extending to vent on either side of which broad ill-defined tan bands, or symmetrical lichenous brown pattern with dark brown interorbital band, and/or bright white stripes from tip of snout across outer edge of upper eyelids to groin, or light dorsolateral folds, or pair of dark outlined light stripes between eyes extending to between sacrum and vent, or broad light area between dorsolateral folds with alternating, almost parallel, tan stripes, and/or mid-dorsal light pinstripe from tip of snout to vent, upper limbs faintly cross banded, outer tarsus and sole of foot dark brown contrasting with dorsal color; face pattern variable including a distinct dark canthal stripe (or not), upper lip with 1-3 broad, dark blotchy oblique or triangular bars, supratympanic fold area somewhat darker or not, snout region in front of eyes with much lighter ground color or not, upper lip sometimes mottled, sometimes with short light stripe from angle of jaw to shoulder; flanks with same pattern as dorsum with faint darker oblique band(s) on front half of flank and often with distinct dark spot in upper groin

area, venter mottled tan and cream, sides of belly sometimes with white dots or small white blotches; posterior surfaces of thigh with very dark brown and distinct seat patch, rest of thigh indistinctly to distinctly mottled browns, sometimes with light pin stripes from sacrum through vent and mid-ventral thighs crossed by stripe running across entire or middle half of thighs passing below vent.

SVL 12.9-15.2, mean 14.0 mm (males), 16.1-22.0, mean 19.7 mm (females); mean head length 42% SVL (males), 41% (females); mean head width 38% SVL; mean thigh length 46% SVL (males), 47% SVL (females); mean shank length 50% SVL (males), 47% SVL (females); mean foot length 43% SVL (males), 45% SVL (females).

Life Colors. — Iris metallic green or yellow above, copper or red on the sides and below. Dorsal colors include cream, tans, brown, black, rust, and orange; light stripes cream, orange, or white. Flanks pale orange. Venter mottled gray and clear, gray and white, red and white, yellow and black; chin and throat sometimes red or orange. Seat patch dark brown or black, rest of posterior surfaces of thighs brown.

Larval Morphology. — Members of the genus *Eleutherodactylus* have direct development. Egg clutches were not found at Boracéia.

Advertisement Call. — Call given sporadically; call consisting of 20-25 closely spaced notes; call duration 0.40-0.50 s; note duration 0.01-0.02 s, note rate 54-60 per s; each note pulsed usually with 2 major pulses at 110-120 per s; pulses amplitude modulated at a rate of about 440 Hz; call intensity modulated, beginning and ending of calls not as loud as middle, but call overall loud; call somewhat frequency modulated, frequency rising slowly throughout call; dominant (= fundamental) frequency range at beginning of call 2400-3300 Hz, at end of call 2600-3500 Hz; pulses with sideband structure, due to pulsatile nature of notes; calls without apparent harmonic structure (Figure 61).

Ecology. — All specimens with data were collected from the forests. Most specimens (96 of 102) were collected from the trails or on leaf litter during the day. A few individuals were collected on low vegetation or on the ground surface at night. Individuals have been heard calling from the forest floor in the late afternoon and at night. Specimens have been collected during every month of the year but June.

Eleutherodactylus randorum Heyer

Color Figure 35

Eleutherodactylus randorum Heyer, 1985b. Original description.

Diagnosis. — The Boracéia species having distinct toe disks with circumferential grooves and lacking toe webbing or fringes are *Eleutherodactylus binotatus, E. guentheri, E. hoehnei, E. nigriventris, E. parvus, E. randorum,* and *E. spanios. Eleutherodactylus randorum* is a small species (males 12-15 mm SVL, females 15-18 mm SVL) and is the only *Eleutherodactylus* at Boracéia that lacks vomerine teeth.

Adult Morphology (N = 8 males, 4 females). — Snout outline subovoid to nearly rounded from above, rounded in profile; no cranial crests; upper eyelids smooth to bearing several distinct tubercles; tympanum hidden or indistinct, diameter 1/4 to 1/2 eye diamenter; male vocal sac single, large, extending from under nostril level or under eye level extending onto belly behind level of arm insertion (smallest male examined, MZUSP 23665, without an externally expanded sac); males with vocal slits; no vomerine teeth; finger lengths I< or <<II≅ or <IV<III; tip of thumb swollen or not, finger II with large or small disk, large disks on fingers III and IV, largest disks about 1/3 diameter of eye; fingers free of webbing, fringing, or ridging; finger subarticular tubercles indistinct; males with microscopic white grandular asperities on base of thumb (absent in MZUSP 23666); no forearm fold; no prepollex; no body glands or folds; dorsum smooth or with scattered tubercles; chin and chest smooth, belly coarsely to finely granular; toe lengths I<II<III≅ or <V<<IV; toes with large disks, largest about same size as largest finger disks; toes free of webbing, fringing, and ridging; inner metatarsal tubercle bluntly ovoid to ovoid, outer tubercle round, small, distinct or not; heel smooth with a small indistinct to distinct tubercle; no tarsal decoration; outer surface of tarsus smooth; sole of foot smooth or with 2-3 low rounded white fleshy tubercles.

Dorsal pattern somewhat variable including uniform tan or brown with pair of small brown spots in middle of back, or mottled mid-dorsal area edged laterally by solid darker brown stripes with cream lateral band from upper lip to eye and top of eyelid to groin, or light brown mid-dorsally with dark central spot and a dark inter-orbital stripe with an indistinct mottle behind eyes or sides, and or a light mid-dorsal pin stripe from tip of snout to vent or only from sacrum to vent, upper limbs light brown with darker cross stripes to almost uniform; dark canthal stripe present or absent alternating darker and lighter brown or brown and cream bars from eye to upper lip, some individuals with a light snout; flanks either with lateral light band edged below by darker brown then blending into belly or no lateral light stripe and a bold to subtle black and white mottle in the groin or a light area in groin; venter dark speckled, center of belly lighter; anterior and posterior surfaces of thighs ranging from almost uniform light tan or brown to boldly mottled light and dark, dark seat patch distinct or indistinct.

SVL 11.8-15.0, mean 13.8 mm (males), 15.0-18.2 mm (females); mean head length 41% SVL (males), 39% SVL (females); mean head width 34% SVL; mean thigh length 45% SVL; mean shank length 50% SVL (males), 48% SVL (females); mean foot length 45% SVL (males), 41% SVL (females).

Life Colors. — Iris golden to lemon yellow with a narrow central transverse brown band. Dorsal colors on back variable, including rust red, orange tan, red brown; snout sometimes yellowish; legs dark and light brown, tops of forearms sometimes brassy, or greenish yellow with brown banding; mid-dorsal stripe golden; lateral band ivory white. Rich brown below eye and behind eye past ear, sometimes white line under eye. Flanks speckled dark brown and white, groin and anterior surface of thigh bright yellow edged with dark brown, orange, golden or with yellow wash. Chin and throat pale yellow or white; belly greenish gray, white, pearl, bronze, or cream with dark brown markings. Posterior surface of thigh mottled dirty white with brown-black or pale with dark markings.

Larval Morphology. — Members of the genus *Eleutherodactylus* have direct development. A single clutch was found at Boracéia (below) but the developmental series has not been described.

Advertisement Call. — Call consisting of 3-8 notes, call of about 2-5 s duration, call rate about 0.1-0.2 per s when actively calling; note duration 0.04-0.10 s; note rate 1.3-2.6 per s; notes strongly partially pulsed, each note with 4-10 discernible pulses of varying intensity, pulse rate about 280 per s, some pulses also weakly amplitude modulated at a rate of about 600 Hz; successive notes of equal loudness; calls not noticeably frequency modulated; dominant frequency range 3800-5200 Hz; no apparent harmonics (Figure 62).

Ecology. — Males have been heard calling from low vegetation in the forest at night. One complete clutch of 7 eggs was collected from a mossy bank on a road cut on 3 November; all but one egg hatched between 13-14 November (identifications based on hatchlings). No adult was observed attending the eggs, although the activity of separating moss may have frightened any adult away. Two other individuals were collected from the same moss banks, but all other individuals were collected at night from low vegetation, usually or leaves, in the forest. Specimens were collected from October through December and February through April.

Eleutherodactylus spanios Heyer

Eleutherodactylus spanios Heyer, 1985b. Original description.

Diagnosis. — The Boracéia species having distinct toe disks with circumferential grooves and lacking toe webbing or fringes are *Eleutherodactylus binotatus, E. guentheri, E. hoehnei, E. nigriventris, E. parvus, E. randorum,* and *E. spanios. Eleutherodactylus spanios* is a small species (male SVL 15 mm, female SVL 21 mm) with ovate, indented toe disks that is likely to be confused only with *E. randorum* at Boracéia. *Eleutherodactylus spanios* has vomerine teeth; *E. randorum* lacks vomerine teeth.

Adult Morphology (N = 1 male, 1 female). — Snout outline subovoid from above, rounded in profile; no cranial crests; upper eyelids with a few low tubercles; tympanum hidden or indistinct, diameter about 1/2 eye diameter; male with single, nom-expanded vocal sac; male with vocal

slits; vomerine teeth in two short transverse patches lying between and far posterior to choanae (vomerine teeth in male felt by probe, not visible under low magnification); finger lengths I<II<IV<III; tip of thumb swollen, disk on finger II moderate, disks on III and IV large, just smaller than tympanum; fingers free of webbing, fringes, or ridges; finger subarticular tubercles indistinct; no male thumb asperities; no forearm fold; no prepollex; no distinctive body folds or glands; dorsal texture smooth; belly smooth or weakly granular; toe lengths I<II<III≅V<IV; toe disks large, largest disks just smaller than largest finger disks; toes without webbing, fringes, or ridges; inner metatarsal tubercle oval, outer round, distinct; heel with a tubercle; no tarsal decoration; outer surface of tarsus and sole of foot smooth.

Dorsum with indistinct pattern of darker and lighter browns or almost uniform brown with 3 dark marks in the scapular region, upper limbs indistinctly cross banded; indistinct canthal stripe present or absent, ill-defined forwardly directed oblique bar under eye to upper lip, dark tympanic spot; flanks with extension of dorsal pattern, posterior portion light but no distinct pattern; throat almost uniformly brown, chest and front of belly mottled or with a few speckles; posterior surface of thigh light or mottled with a lighter area toward knee, dark seat patch, anterior surfaces of thigh not patterned.

SVL 14.7 mm (male), 21.4 mm (female); head length 37-40% SVL; head width 33-34% SVL; thigh length 43-44% SVL; shank length 44-52% SVL; foot length 41-44% SVL.

Life Colors. — Iris with blue dorsally. Dorsal colors brown, black, rust brown; fingers and toes orange or red. Loreal region greenish or brown. Throat and belly dark gray. Bright orange red or deep orange on concealed surfaces of arms and legs (including posterior surface of thigh) extending up onto belly where edges of red area become blotchy.

Larval Morphology. — Members of the genus *Eleutherodactylus* have direct development. Egg clutches were not found at Boracéia.

Advertisement Call. — Not recorded.

Ecology. — One individual was collected from a low dead roadside bush at the edge of the forest in the day by beating vegetation with a net. The other individual was collected at night from the forest sitting about a meter high on a leaf. Both were collected in February.

Holoaden luederwaldti Miranda-Ribeiro

Figure 11

Holoaden luederwaldti Miranda-Ribeiro, 1920c. Original description.

Diagnosis. — *Holoaden luederwaldti* is the only uniform brown frog at Boracéia with no toe disks, no toe webbing or fringe and with large, equal-sized bumps on its back.

Adult Morphology (N= 1 female). — Snout outline from above nearly rounded, rounded in profile; no cranial crests; upper eyelid with same warty-tuberculate texture as surrounding dorsum; tympanum not visible; vomerine teeth in two short transverse patches lying between and posterior to choanae; finger lengths I≅II≅IV<III; finger tips rounded, not expanded; fingers without webbing, fringes, or ridges; basal finger subarticular tubercles low and broad, distal tubercles indistinct; no forearm fold; no prepollex; no discernible body glands or folds; dorsal texture warty-tuberculate-glandular; venter smooth with a granular seat patch under the thighs; toe lengths I<II<V<III<IV; toe tips rounded, not expanded; toes without webbing, fringes, or ridges; inner and outer metartarsal tubercles ovate, large, about same size; no heel decoration; outer tarsal and sole of foot texture smooth.

Dorsum uniform brown; face brown; face brown with a lighter upper lip; flanks with a meeting of dorsal and ventral patterns low on sides; venter light tan-orange; posterior surface of thigh brown.

SVL 46.2 mm (female); head length 36% SVL; head width 38% SVL; thigh length 41% SVL; shank length 41% SVL; foot length 40% SVL.

Life Colors. — Dorsum dark brown (including limbs); no indication of pattern. Sides brown with gray brown granules. Ventral surfaces gray brown.

Larval Morphology. — The life history of this species is unknown; it is presumed to have direct development, like the other member of this genus.

Advertisement Call. — Not known. The single female collected, when handled, gave "a small peep of complaint."

Ecology. — The single specimen was taken from the ground on a forest trail at night in March, 1963.

Hylodes asperus (Müller)

Color Figure 36

Elosia aspera Müller, 1924b. Original description. - Cochran, 1955. Specimens cited from Boracéia.

Hylodes aspera, Myers, 1962. Transfer of *aspera* to *Hylodes*.

Diagnosis. — The Boracéia species having toes with distinct dorsal scutes and extensive fringing on the sides of the toes are *Crossodactylus dispar, C. gaudichaudii, Hylodes asperus, H. phyllodes,* and *Megaelosia goeldii. Hylodes asperus* lacks thumb spines; the two *Crossodactylus* species have thumb spines. The tympanum is distinct in *H. asperus,* hidden in *M. goeldii. Hylodes asperus* lacks a light lateral stripe; *H. phyllodes* has a light lateral stripe along the upper flank (distinct at least posteriorly).

Adult Morphology (N = 10 males, 10 females). — Snout outline subovoid from above, rounded-acute to acute in profile; no cranial crests; upper eyelids lacking distinctive features; tympanum distinct to somewhat indistinct, diameter about 1/2 eye diameter; male vocal sacs present, paired, externally expanded laterally; vomerine teeth in short obtuse or transverse series lying between posterior borders of choanae; finger lengths I<II<IV<III; finger disks large, disk on finger I smallest, disk on finger II next largest, followed by largest and approximately equal sized disks of III and IV, largest disks just smaller than tympanum; fingers without webbing, but sides of fingers fringed, fringing more extensive in males; finger subarticular tubercles moderately developed, single; no thumb asperities on males; no forearm fold; no prepollex; moderately developed supratympanic fold, dense field of small warts on sides of body extending to level behind center of eyelids on dorsum, weak longitudinal folds on upper shank and thigh present or absent; dorsal texture etched with small warts; ventral texture smooth; toe lengths I<II<V<III<IV; toe disks large; largest about same size as largest finger disks, dorsal surfaces with a pair of scutes; toes with a trace of basal webbing due to confluence of extensive fringing on sides of toes; inner metatarsal tubercle an elongate oval, outer rounded, about 1/4 to 1/3 size of inner; no heel decoration; extensive inner tarsal flap; texture on outer tarsus and sole of foot smooth.

Dorsum an indistinct dark brown mottle/blotch pattern or brown with small darker brown spots, upper limb surfaces indistinctly barred, upper leg surfaces sometimes with small whitish spots, row of white dots on outer ulnar region; face indistinctly mottled, pretty much like dorsum, sometimes with broken white mottling on upper lip; flanks almost uniform brown with light warts; venter whitish with brown wash, spotted or mottled, or mostly metallic white; posterior surface of thigh pattern brown with many small to fewer large light irregular spots or marks.

SVL 39.4-42.3, mean 40.5 mm (males), 43.2-50.2, mean 45.5 mm (females); mean head length 37% SVL (males), 36% SVL (females); mean head width 34% SVL (males), 33% SVL (females); mean thigh length 50% (males), 49% SVL (females); mean shank length 54% SVL (males); 55% SVL (females); mean foot length 50% SVL (males), 49% SVL (females).

Life Colors. — Dark dirty khaki brown above with heavy darker brown and black mottling. Granular pale yellow bumps in line along side from back of eye, brown band below this. Dark brown at snout, ear, and above shoulder. Sides pale orange. Gold at front and back of eye, and around bottom of ear. Loreal region between nares and edge of upper lip yellow gold. Legs and arms dark brown with pale orange (like sides) double bands. Top of inside toes and fingers bluish. Pale orange dumbbell mark at vent. Other specimens similar, but orange and yellow golden areas brighter or duller. Throat, belly, and under femur bright to dull bluish opalescent cast. Bottoms of feet and hands dark brown.

Larval Morphology. — Tadpoles not collected from Boracéia.

Advertisement Call. — Call not recorded from Boracéia. See below.

Ecology. — This species is active diurnally on rocks and low vegetation along larger forest streams and small forest rivers. A few inactive specimens were collected at night from leaves on low vegetation overhanging a stream or within a meter or two of a stream. Individuals were collected in September and December through May.

On four occasions Rand was able to watch an individual of this species calling from large boulders at the edge of a fast flowing, moderate-sized mountain stream. The call is a long, high-pitched whistled trill rising slightly in pitch towards the end and given at 1/2-1 minute intervals. The call is like that of the congeneric *Hylodes phyllodes*, but lower in pitch. *Hylodes phyllodes* lives in the same area, indeed along the same stream, as *H. asperus*, but in the more shaded areas and on the small tributaries. Both species seem to be active only by day.

One of the four males observed remained motionless while calling for 16 consecutives calls. The other three moved their hind feet synchronously with most of their calls (Table 1). Two types of movement were observed. In one, the frog, just after beginning its call, raised one hind leg and extended it slowly out and back in an arc to about 45° and then returned it to its side as it finished its call. As the leg was extended the toes were slightly curled so that the white upper surfaces of the expanded toe pads were very conspicuous. All three frogs gave this movement and all three used both legs at different times but with no regular alternation (or any other recognizable pattern). The second sort of movement was given by only one frog. During some of its calls this frog wiggled the toes of one or both hind feet slowly without otherwise moving the legs. Again, the white upper surfaces of the toe pads were conspicuous.

Many *Hylodes phyllodes* were watched calling. No movements of the hind legs were noticed, though the movements of the lateral vocal sacs during calling were conspicuous.

Hylodes phyllodes Heyer and Cocroft

Color Figure 37

Elosia lateristrigata, Cochran, 1955. Specimens cited from Boracéia.

Hylodes phyllodes Heyer and Cocroft, 1986. Original description.

Diagnosis. — The Boracéia species having toes with distinct dorsal scutes and extensive fringing on the sides of the toes are *Crossodactylus dispar*, *C. gaudichaudii*, *Hylodes asperus*, *H. phyllodes*, and *Megaelosia goeldii*. *Hylodes phyllodes* has vomerine teeth; *Crossodactylus dispar* and *gaudichaudii* lack vomerine teeth. The tympanum is distinct in *H. phyllodes*; the tympanum is hidden in *M. goeldii*. *Hylodes phyllodes* has a light lateral stripe along the upper flank (distinct at least posteriorly); *H. asperus* has no light lateral stripe.

Adult Morphology (N = 10 males, 10 females). — Snout outline truncately subelliptical to subovoid from above, protruding to rounded-protruding in profile; no cranial crests; upper eyelid same texture as rest of dorsum; tympanum distinct, diameter about 1/2 or just greater than 1/2 eye diameter; male vocal sacs expanded, paired, lateral; male vocal slits present, posterior; vomerine teeth in two short transverse patches, separated by about length of one patch, just posterior to choanae; finger lengths variable, third always longest, first, second, and fourth about equal length or second shorter than first and fourth or second and fourth subequal and shorter than first, or first and second subequal and shorter than fourth; finger disks distinct, much smaller than tympanum, disk on first finger smallest, disk on second finger intermediate, disks on third and fourth fingers largest, dorsal disk surfaces with a pair of scutes; fingers in males generally with more fringing than in females, base of fingers free or fringed, fingers of females barely fringed, ridged, or almost free; finger subarticular tubercles moderate, single or bifid under fourth finger; males with moderate to almost absent patch of small, whitish spines on inner surface of mid-first finger; no forearm fold; no prepollex; pair of weakly developed dorsolateral folds, upper leg with a series of longitudinal ridges; dorsal texture uniformly pitted-granulate in all specimens, a few warts scattered posteriorly, or short folds on posterior half of dorsum, or short ridges on body in some specimens; belly and chest smooth, under surface of thigh granular; toe lengths I<II<V<III<IV or III and V subequal;

Table 1. Display sequences for *Hylodes asperus*.

Call	Visual display
	Frog #1, 10 March 1963, late morning
1	none
2	right leg
3	toes on both feet
	(hopped a short distance to a new rock)
4	right leg
5	toes on both feet
6	left leg
7	right leg
8	toes on left foot
9	toes on left foot, then right leg
10	left leg
11	toes on left foots then right leg
12	right leg
13	toes on right foot
14	right leg
15-20	none
	Frog #2, 20 September 1963, ca. 1100
1	none
2	leg
3	leg
4	none
5	leg
6	leg
	Frog #3, 2 October 1963, 1130-1145
1	right leg
2	left leg
3	left leg
4	right leg, a quick thrust
5	right leg
6	left leg
7	none
8	left leg
9	none
10	none
	(jumped away)

Summary

frog	total	move	none	leg	toes	both	right	left	both
#1	20	13	7	7	4	2	6	3	4
#2	6	4	2	4	0	0			
#3	10	7	3	7	0	0	3	4	0

toe disks equal to or just smaller than finger disks, with dorsal scutes; toes of males strongly fringed, toes of females with less extensive fringing; inner metatarsal tubercle ovoid, outer rounded, pungent, about 1/3-2/3 size of inner; heel smooth, slightly granular-warty, or with a weak tubercle; tarsus with fold-flap extending 7/8 length of tarsus, continuous with fringe of first toe, extensively developed in males, less well developed in females; posterior surface of tarsus smooth to pitted granular; sole of foot smooth.

Dorsum brown to brassy brown (under microscope, made up of very fine mottling of bronze and gray) with various other markings, including an irregular mid-dorsal light stripe with almost regularly spaced small dark brown spots, or a series of short dark mid-dorsal dashes, or dorsum scattered with small dark brown spots, or series of mid-dorsal large light blotches, or big darker brown blotches on a lighter brown background, or almost uniform with a series of faint light mid-dorsal dots, pair of dark round or U-shaped spots, one on each side of vent, upper limbs distinctly to indistinctly crossbarred brown on tan; broad dark canthal stripe just below dorsal color from nostril to eye, narrower dark stripe from nostril to tip of snout, upper lip light, blending to enamel white just under eye continuous as a stripe under the tympanum to the arm, or upper lip to arm stripe just lighter than dorsal color; flank with dark brown (almost black) band behind eye across tympanum just to or above arm then fading to mottled brown and white to flank almost uniformly dark, light stripe from corner of eye bordering dark band to groin, more distinct on posterior half of flank; vocal sacs without white pigment, scattered with melanophores, dark stripe in mid-throat region between vocal sacs short to almost length of throat, throat and belly white with scattered to abundant distinct dark mottle, some females with almost entirely white bellies with a very faint throat stripe, under limbs lacking white pigment, mottled brown and pigmentless areas; posterior surface of thigh indistinctly to distinctly mottled brown and tan.

SVL 27.5-31.4, mean 29.2 mm (males), 29.0-35.5, mean 31.8 mm (females); mean head length 34% SVL (males), 35% SVL (females); mean head width 30% SVL; mean thigh length 45% SVL (males), 44% SVL (females); mean shank length 50% SVL (males), 52% SVL (females); mean foot length 47% SVL (males), 48% SVL (females).

Life Colors. — Iris copper, darker on sides forming a black band with pupil to metallic yellow. Dorsum olive to dark and light brown, light stripes cream, copper, yellow, yellow-gold, or gold, flanks dark brown, upper limbs dark and light brown with or without red cast, one juvenile with bright Chinese red front legs, yellow in groin or not. Throat and belly opalescent, bright opalescent yellow, or yellow to golden with distinct or less so brown spotting, brown throat stripe, under limbs colorless to dirty greenish yellow.

Larval Morphology. — Body oval in dorsal view, slightly wider than deep; snout broadly rounded in dorsal outline; nostril nearer eye than tip of snout; distance between nares 1.2 times interorbital width; nares rounded and dorsal; eyes dorsolateral, diameter almost 10% body length; opening of the sinistral spiracle directed posteriorly on the midline about 61% body length; anal tube short and dextral; tail higher than body; dorsal fin origin at body-tail juncture; dorsal and ventral fins slighty arched; tail musculature reaching the round tail tip; mouth anteroventral, width 55% body width; one row of oral papillae, broadly interrupted on the upper lip; tooth row formula 2(2)/3(1); beak strongly developed and serrated.

Body and tail musculature light cream with some brown flecks; tail fins transparent (Figure 32).

Larval Habitat. — Tadpoles were collected from the small forested stream that transects the road between the scientists' residence and the laboratory building.

Advertisement Call. — Calls given sporadically, call duration 1.05-2.10 s; 12-20 notes per call given at a rate of 9-11 per s; notes given at regular intervals at beginning of call, usually given in pairs at end of call; note duration 0.04-0.06 s; individual notes weakly and irregularly partially pulsed at a rate of 100-200 Hz; call at about the same loudness throughout; calls slightly frequency modulated, beginning higher, ending lower; notes strongly frequency modulated, rising 600-700 Hz in about 0.04 s; fundamental frequency about 1500-2200 Hz; dominant

frequency range at beginning of call 4300-5700 Hz, at end of call 4100-5300 Hz; call with harmonic structure (Figure 63).

Ecology. — Males call during the day next to or over small streams on roots, rocks, and leaves, although there is a single instance noted of a male calling on leaf litter after 19:20. Males call with either one or both vocal sacs inflated.

One female (MZUSP 23682) extruded about 30 cream colored eggs when seized.

Individuals are active during the day and can be collected from leaves of low vegetation (up to 2 m) at night. All specimens came from either the forest or overgrown streams in small clearings or secondary growth from smaller streams and less exposed sites than *H. asperus*. Males were found almost exclusively near streams. Females were also found in sample plots considerable distances from streams. One individual was collected under a small log 5 m from a dry stream bed during the day. When abundant, calling males are spaced more or less regularly at 1 to 2 m intervals. Individuals were collected from September through June.

Leptodactylus flavopictus A. Lutz

Leptodactylus flavopictus A. Lutz, 1926. Original description.

Diagnosis. — The Boracéia species that lack toe disks and webbing and have vomerine teeth are *Adenomera marmorata, Cycloramphus eleutherodactylus, Holoaden luederwaldti, Leptodactylus flavopictus, L. fuscus, L. ocellatus, Paratelmatobius gaigeae,* and *Thoropa miliaris. Leptodactylus flavopictus* has four dorsolateral folds (at least indicated by pattern in cases of indifferent preservation) and is a large species (SVL greater than 120 mm). Of this group, *L. fuscus* and *ocellatus* are the only other species with four or more dorsolateral folds. Both *L. fuscus* and *ocellatus* have at least six dorsolateral folds and both are smaller (SVL less than 105 mm) than *L. flavopictus*.

Adult Morphology (N = 2 males, 1 female). — snout outline subovoid, rounded, or nearly rounded from above, rounded or obtusely rounded in profile; no cranial crests; no distinctive upper eyelid decoration; tympanum distinct and large, diameter greater than 1/2 to 3/4 diameter of eye; males with single, internal vocal sac; males with vocal slits; vomerine teeth in long forwardly arched transverse series, almost abutting medially, abutting posteromedial edges of choanae laterally; finger lengths II≅IV<III just < or ≅I; finger tips rounded, not expanded; fingers without webbing, sides of fingers free or with very slight ridges; finger subarticular tubercles well developed, single; in smaller male, one large and one small spine on each thumb and two patches of small chest spines, in larger male, two large black spines on each thumb, 2 large chest spine patches, and the arms extensively hypertrophied; no forearm fold; second spine on thumb a prepollex, not really visible in female; one dorsolateral fold from posterior eye to mid-flank, a second dorsolateral fold (indicated by pattern) from eye to sacrum or groin, large gland in groin extending anteriorly just past mid-flank and posteriorly and dorsally to above and lateral to vent, small pair of glands lateral to vent, elongate gland in lower portion of posterior surface of thigh; dorsal texture smooth; ventral texture smooth or with a profusion of small tubercles; toe lengths I<II<V<III<IV; toe tips rounded, not expanded; toes without webbing, sides of toes free or with slight ridges; inner metatarsal tubercle ovoid, elongate, well developed, outer small and rounded; no heel decoration; inner tarsal fold extending 7/8 length of tarsus; texture of outer tarsus and sole of foot smooth.

Dorsal pattern dark brown with or without darker network, dorsolateral folds highlighted black, upper limbs broadly cross banded; distinct but incomplete black canthal stripe, light stripe from below eye extending under tympanum to posterior angle of jaw or to shoulder insertion, 1-2 narrow transverse light stripes on upper lip; flanks with light glandular stripe bordering above second dorsolateral fold extending to groin or flank gland blackish with central ill-defined light orange spot, below gland a transition to belly pattern; chin uniform brown to almost black, chest almost uniform brown with a few light distinct spots, belly mottled tan with irregular light spots; posterior surface of thigh black with large discrete round or elongate light orange or yellow spots.

SVL 121.9-134.9 mm (males), 131.6 mm (female); head length 37-40% SVL; head width 39-42% SVL; thigh length 43-45% SVL; shank length 44-47% SVL; foot length 43-47% SVL.

Life Colors. — Not available for Boracéia specimens.

Larval Morphology. — Tadpoles not collected at Boracéia. Bokermann (1957) described and illustrated the larvae from specimens collected from a shallow, 50 m^2, artificial pond at the edge of the forest at Paranapiacaba.

Advertisement Call. — Not recorded.

Ecology. — The few specimens with ecological notes have come from a broad array of habitats; one from the forest at night on the ground 7 m from a small stream, one at night from beside a forest stream, one at night from a meadow pond, and one in mid-afternoon from the road. Individuals were collected from October to December.

Leptodactylus fuscus (Schneider)

Color figure 38

Rana fusca Schneider, 1799. Original description.

Leptodactylus fuscus Heyer, 1968. Transfer of *fusca* to *Leptodactylus*.

Diagnosis. — The only Boracéia species that lack toe disks and have at least 6 distinct dorsolateral folds are *Leptodactylus fuscus* and *L. ocellatus*. The sides of the toes are slightly ridged in *L. fuscus* but are distinctly fringed in *L. ocellatus*. *Leptodactylus fuscus* is smaller (SVL less than 55 mm) than *L. ocellatus* (SVL greater than 90 mm).

Adult Morphology (N = 9 males). — Snout outline pointed to subellipticall from above, rounded to rounded-acute in profile; no cranial crests; no distinctive decoration on upper eyelids; tympanum distinct, large, diameter about 2/3 - 3/4 diameter of eye; male vocal sac single, expanded laterally; males with vocal slits; vomerine teeth in shallowly forwardly arched series, almost contacting medially, lying just posterior to chonae; finger lengths II< or ≅IV<I< or ≅ III; finger tips rounded or pointed, not expanded; fingers without webbing, sides of fingers ridged; basal finger subarticular tubercles distinct, distal tubercles not as distinct, single: no asperities on thumbs, male snout with rounded fleshy expansion extending as ridges on sides almost to level of eyes on upper lip; low glandular ridge on outer forearm area present to almost invisible; no prepollex; supratympanic fold distinct, distinct glandular fold at angle of jaw, 3 distinct plus 2 indistinct dorsolateral folds per side, flanks glandularly areolate; dorsal texture slightly glandular; venter smooth, seat patch under thighs granular; toe lengths I<II<V< or =III<IV; toe tips pointed; toes without webbing, sides of toes with weak ridges; inner and outer metatarsal tubercles oval, inner more distinct, outer about 1/2 - 2/3 size of inner; heel smooth or with indistinct whitish tubercles; tarsus with distinct inner fold extending 7/8 length of tarsus; outer tarsal texture smooth with a few poorly developed light tubercles; sole of foot smooth with a few to several indistinct light tubercles.

Dorsal pattern tan with dark outlined brown ocelli, with or without a broad light mid-dorsal stripe, second pair and/or most lateral pairs of dorsolateral folds whitish, upper limbs distinctly and regularly or irregularly cross banded; irregular dark canthal stripe, loreal region tan with or without dark spot(s), light stripe from tip of snout on top of upper lip under tympanum distinct or not, lower portion of upper lip mottled, angle of jaw gland whitish; flanks with a blending of dorsal and ventral patterns low on sides; lateral expansions of vocal sac blackened, rest of throat with a light gray wash, belly cream; posterior surface of thigh with a distinct transverse light stripe low on the thigh, above the stripe boldly mottled cream and brown.

SVL 41.9-48.9, mean 45.5 mm (males); mean head length 37% SVL; mean head width 35% SVL; mean thigh length 45% SVL; mean shank length 52% SVL; mean foot length 48% SVL.

Life Colors. — Iris bronze. Dorsum tan with brown spots; middle dorsolateral stripes same color as dorsal ground color, lateral dorsolateral stripe yellow. Lip stripe light tan. Belly white, vocal sac expansions black. Posterior surface of thigh mottled tan and brown, transverse stripe yellow, but not bright.

Larval Morphology. — Tadpoles have not been collected from Boracéia. Sazima (1975)

described and illustrated the tadpole from specimens collected from small, temporary to large, open-formation ponds at Campinas, São Paulo.

Advertisement Call. — Calls of single notes given frequently when actively calling; call (= note) duration 0.10-0.13 s; call strongly frequency modulated, a rising whistle; call beginning and ending more quiet than louder mid-portion; dominant (= fundamental) frequency beginning at about 900-1000 Hz, ending about 1500-1900 Hz; call lacking harmonics (Figure 64)

Ecology. Most specimens were collected at night while calling. Eight were taken from a marshy area in the pasture, three from a marshy area next to a pasture pond, and several from the quarry. Specimens were collected from October through January, all after 1971.

Leptodactylus ocellatus (Linnaeus)

Rana ocellata Linnaeus, 1758. Original description.

Leptodactylus ocellatus, Girard, 1853. First use of *ocellatus* with *Leptodactylus.*

Diagnosis. — The only Boracéia species that lack toe disks and have at least 6 distinct dorsolateral folds are *Leptodactylus fuscus* and *L. ocellatus.* The toes are fringed in *L. ocellatus;* only slightly ridged in *L. fuscus. Leptodactylus ocellatus* is also larger (SVL greater than 90 mm) than *L. fuscus* (SVL less than 55 mm).

Adult Morphology (N = 7 males, 5 females). — Snout outline subelliptical to subovoid from above, rounded, rounded-acute, or rounded-obtuse in profile, no cranial crests; no distinctive features on upper eyelid; tympanum distinct, large, diameter 2/3 to same size of eye diameter; males with internal single vocal sacs; males with vocal slits; vomerine teeth in elongate, forwardly arched series, approaching each other medially, lying between posteriormost portion of choanae or just posterior to choanae; finger lengths II just < or ≅IV<I just <III; no finger disks; fingers not webbed, sides of fingers ridged; moderate sized basal finger subarticular tubercles, distal tubercles moderately to weakly developed, single; male thumb with 2 black (or white) spines, male arm very hypertrophied in largest males; no forearm fold; no prepollex; distinct supratympanic fold, 8 dorsolateral folds, fold from angle of jaw to arm, rust colored diffuse gland on edges of belly present or absent; dorsolateral folds smooth, inter-fold spaces warty-tubercular; venter smooth with areolate seat patch under thighs; toe lengths I<II<V<III<IV; no toe disks; toes not webbed, sides of toes with extensive fringe, joined at base; inner metatarsal tubercle elongately ovoid, raised distally, outer small and round, 1/5 - 1/4 size of inner; no heel decoration; distinct inner tarsal fold extending 2/3 - 3/4 length of tarsus; outer tarsus with scattered to many brown-tipped tubercles; sole of foot with scattered to many small brown-tipped tubercles.

Dorsal pattern gray to dark brown with darker larger spots, all spots distinct or most distinct posteriorly or indistinct centrally, spots arranged in longitudinal rows or not obviously aligned; with or without two light stripes between first and second pair of folds and four pairs of folds light highlighted, upper limbs cross banded or partially banded and spotted; distinct dark canthal stripe, light lip stripe distinct or not, rest of loreal and lip area light tan with faint to distinct dark bars/blotches; flanks with meeting of dorsal and ventral patterns low on sides; venter mostly light or light brown with cream spots/mottling; posterior surface of thigh pattern variable, including indistinct light brown and tan mottle centrally with indistinct dark stripe ventrally along distal 2/3 of thigh under which almost distinct light stripe along distal 1/2 of thigh, or bold to indistinct dark and light mottle.

SVL 92.3-115.7, mean 104.5 mm (males), 91.8-101.3, mean 96.8 mm (females); mean head length 35% SVL; mean head width 34% SVL (males), 33% SVL (females); mean thigh length 47% SVL (males), 45% SVL (females); mean shank length 50% SVL (males), 48% SVL (females); mean foot length 55% SVL (males), 53% SVL (females).

Life Colors. — Dorsal colors include brown, bronze, olive green, and black. Chin dirty white; belly cream to pale yellow mottled with gray. Part of groin, anterior and posterior thigh surfaces heavily mottled with dark brown, dark green, or chartreuse.

Larval Morphology. — Tadpoles have not been collected from Boracéia. Cei (1980) illustrated larvae from Argentina.

Advertisement Call. — The call has not been recorded at Boracéia. Described by Rand as "whoosh."

Ecology. — This nocturnal species is occasionally seen in the daytime and characteristically occurs in clearings, usually near temporary or permanent ponds, streams, or marshes. Individuals were collected in September and December through March.

Megaelosia goeldii (Baumann)

Hylodes goeldii Baumann, 1912. Original description.

Megaelosia goeldii, A. Lutz, 1931. First use of *goeldii* with *Megaelosia*. - Cochran, 1955. Citation of specimen from Boracéia.

Nomenclatural Note. — The specimens from Boracéia are most likely not *M. goeldii*. Neither specimen (MZUSP 2347 [incorrectly cited as 2348 in Cochran, 1955], 22935) has a metatarsal flap as found in *M. goeldii*. Cochran's (1955) photograph of the type of *Elosia massarti* De Witte clearly shows a metatarsal flap, precluding application of *massarti* to the Boracéia species. Eugênio Izecksohn and Elio Gouvea are describing a new *Megaelosia* which may be the same as the Boracéia species. Resolution of the proper name will require a detailed comparison of all available specimens.

Diagnosis. — The Boracéia species with toe disks with distinct dorsal scutes and extensive fringing on the sides of the toes are *Crossodactylus dispar, C. gaudichaudii, Hylodes asperus, H. phyllodes,* and *Megaelosia goeldii*. Of these, *M. goeldii* is the largest (female 121 mm SVL, other species not exceeding 51 mm SVL) and is the only species with a hidden tympanum (distinct externally in the *Crossodactylus* and *Hylodes* species).

Adult Morphology (N = 1 female). — Snout outline rounded from above, rounded-acute in profile; no cranial crests; no upper eyelid decoration; tympanum hidden, diameter about 1/3 eye diameter; single fang-like vomerine tooth on each odontophore lying between choanae; finger lengths I<II≅IV<III; finger tips modestly expanded into small disks, upper surfaces with poorly defined scutes, largest disks smaller than tympanum; fingers without webbing, sides of fingers ridged/fringed; finger subarticular tubercles moderately developed, bifid under finger IV; no forearm fold; no prepollex; distinct supratympanic fold; dorsal texture of slightly granular shagreen; ventral texture smooth; toe lengths I<II<V<III<IV; toe disks just larger than finger disks, with distinct dorsal scutes; toes with trace of basal webbing, due to joining of well developed fringe on sides of toes; inner metatarsal tubercle elongate, outer rounded, small but distinct, about 1/5 - 1/4 size inner; no heel decoration; tarsus with extensive inner flap continuous with toe fringe on outside of toe I extending 7/8 length of tarsus; outer tarsal and sole of foot texture smooth.

Dorsum almost uniform brown with faint black mottling, limbs very faintly cross banded; face with continuation of dorsal pattern, but mottle more distinctive; flanks with a blending of the dorsal and ventral patterns low on sides; ventral pattern a bold dark brown and cream mottle; posterior surface of thigh almost uniform dark brown.

SVL 121.2 mm (female); head length 39% SVL; head width 39% SVL; thigh length 42% SVL; shank length 44% SVL; foot length 45% SVL.

Life Colors. — Not available.

Larval Morphology. — Body oval in dorsal view, slightly wider than deep; snout rounded in profile; nostril nearer eye than tip of snout; distance between nares 103% interorbital width; nares elliptical, dorsolateral, directed anterolaterally; eye dorsolateral, directed laterally, 9% body length; opening of the sinistral spiracle directed posterodorsally on the midline about 61% body length; anal tube short and dextral; Tail slightly higher than body; dorsal fin origin on body-tail juncture; dorsal and ventral fins arched; tail musculature reaching the rounded tail tip; mouth anteroventral, width 43% body width; a single row of oral papillae broadly interrupted anteriorly, a few scattered, bigger, inner papillae; tooth row formula 2(2)/3(1); beak very strong and serrated.

Body and tail musculature brown with some dark areas on sides of tail musculature; tail fins brown with few unpigmented areas (Figure 33).

Larval Habitat. — Both larvae with data were collected from under large rocks in a moderate-sized forest stream.

Advertisement Call. — Unknown.

Ecology. — The female was collected mid-December 1947; the juvenile, in February 1958.

Paratelmatobius gaigeae (Cochran)

Color Figures 39-40

Leptodactylus gaigeae Cochran, 1938. Original description.

Paratelmatobius gaigeae, Bokermann, 1966a. First use of *gaigeae* with *Paratelmatobius*.

Diagnosis. — *Paratelmatobius gaigeae* is a small species (SVL 16-20 mm) with vomerine teeth and no circumferential grooves on the toe tips. Of all Boracéia species, only *P. gaigeae* has flattened fingers and a bright ventral pattern of red (or white) and black in life (black and white in preservative).

Adult Morphology (N = 1 male, 3 females). — Snout outline semicircular from above, rounded to obtuse in profile; no cranial crests; edge of upper eyelid with a central single warty tubercle; tympanum hidden or not visible externally, large, diameter about 2/3 eye diameter; male vocal sac internal, single; male with vocal slits; vomerine teeth in short obtuse or transverse series lying between and just posterior to choanae; fingers flattened, thumb in some specimens about twice width of other fingers, finger lengths II<IV<I<III or I≅II<IV<III; tips of fingers rounded or pointed; fingers not webbed, sides of flattened fingers with slight ridges; basal finger subarticular tubercles low and rounded or indistinct, distal tubercles indistinct; male with large brown spinous pad covering most of inner and dorsal thumb surfaces; weakly developed continuous or interrupted glandular forearm ridge present or absent; no prepollex; weakly developed supratympanic fold present or absent, pair of dorsolateral folds from behind eye to groin present or absent; dorsal texture smooth; throat, chest and belly smooth or posterior portion of belly areolate same as seat patch area under thighs; toes flattened, toe lengths I<II<V<III<IV; toe tips expanded into tiny rounded ungrooved disks or not; toes not webbed, but sides of toes usually fringed, fringing joined at base; inner metatarsal tubercle oval, not pronounced, outer rounded, more distinctive than inner, about 1/2 to 2/3 size of inner; heel smooth or with 1-3 tubercles; tarsus with or without a very weakly developed inner tarsal fold extending about 1/2 length of tarsus; outer tarsal texture smooth or crenulate; sole of foot smooth.

Dorsal pattern uniform tan with indistinct broken dark outlined anteroposterior line between eyes and central brown spot interrupted medially in shoulder region or brown or gray with scattered small light spots, with or without a dark interorbital bar, with or without a dark outlined light pin stripe from tip of snout to vent, legs with dark brown cross stripes, arms with interrupted stripes, outer forearm ridge light highlighted; face tan with a dark oblique bar under eye to upper lip, with or without a couple of dark spots on lip between tip of snout and eye bar; flanks either with distinct dark stripe from behind eye under dorsolateral fold, remaining distinct dorsally along length of flank and becoming less well defined ventrally on lower flanks behind arm insertion or stripe distinct only past angle of jaw then becoming interrupted and indistinct, dorsolateral folds light highlighted or not, 1-2 small dark spots in upper groin region; ventral pattern variable, ranging from mostly light with a few brown spots to mostly brown black with a few irregular light spots on edge of belly and edge of chin; posterior surface of thigh tan with nondescript brown markings including pair of short dark stripes on either side of vent.

SVL 16.6 mm (male), 17.8-19.7 mm (females); head length 35-42% SVL; head width 33-38% SVL; thigh length 39-43% SVL; shank length 40-44% SVL; foot length 39-49% SVL.

Life Colors. — Iris silver gray or brown with a thin or broad vertical dark line through pupil. Dorsum dead leaf gray or brown with sparse speckling of silvery white, mid-dorsal stripe (when present) red brown or light green, concentration of silvery flecks above and along dorsolateral fold; flanks sometimes with broken white stripe; yellow dot just above vent or not. Chin and belly black with red or white spots or throat and venter light red with large white-rimmed black blotches. Arm brown above, red or purple below, hands with a pale yellow fringe or tinged

with orange or red above and below. Legs olive to brown above, purple or brown below. Back of thighs with contrasting black and red-orange with scattered white spots, or black with white spots. Back of shank black with white spots. Feet red.

Larval Morphology. — Tadpoles unknown.

Advertisement Call. — Call not recorded.

Ecology. — Individuals were taken at night in the forest either in the leaf litter or on the ground next to a 2 m diameter temporary pond. Three were collected at the forest edge from under rocks around a drain pipe. Individuals have been collected in November, January and February.

Physalaemus cuvieri Fitzinger

Color Figure 41

Physalaemus cuvieri Fitzinger, 1826. Original description.

Diagnosis. — *Physalaemus cuvieri* lacks toe disks, lacks toe web or fringe, has a hidden tympanum, and lacks vomerine teeth. This combination of states is shared with *Brachycephalus nodoterga, Physalaemus franciscae, P. maculiventris, P. olfersi,* and *Myersiella microps* at Boracéia. Of these species, *P. cuvieri* is the only one with a distinct tarsal tubercle.

Adult Morphology (N = 10 males, 1 female). — Snout subelliptical from above, rounded to rounded-acute in profile; no cranial crests; upper eyelid texture about same as surrounding area; tympanum not visible; male vocal sac single, externally expanded, large, including chest; males with vocal slits; no vomerine teeth, a few individuals with a slightly raised ridge between choanae; finger lengths I≅II≅IV<III; tips of fingers pointed-rounded; no finger webbing or fringes, sides of fingers slightly ridged; basal subarticular finger tubercles large and prominent, distal tubercles moderate, single; male thumb with a pair of brown nuptial pads, confluent or (usually) separated; no forearm fold; no prepollex; supratympanic fold moderately developed, weakly developed dorsolateral fold from behind eye to groin sometimes indicated only by pattern, small diffuse lumbar gland present or absent; dorsal texture smooth or finely granular, with or without a few short ridges; venter smooth with a granular seat patch under the thighs; toe lengths I<II<V< or ≅III<IV; tips of toes rounded-pointed; toes free of webbing or fringes, sides of toes smooth or with slight ridges; inner and outer metatarsal tubercles somewhat spade shaped, prominent, pungent, outer just smaller than or about same size as inner; heel lacking decoration; tarsus with prominent inner tubercle on distal half, with a distinct or indistinct fold from tubercle to foot; outer tarsal texture smooth or with 1-3 small white fleshy tubercles; sole of foot covered with small fleshy tubercles.

Dorsal pattern variable including almost uniform brown, or very complex symmetrically mosaic pattern of browns, tans and black, or series of dark and light parallel stripes to sacral region; two irregular dark spots in upper groin region on back, light mid-dorsal pin stripe from sacrum to vent; legs cross banded, arms weakly striped, outer edge of hand, forearm (or indistinct on forearm), and foot with light pin stripe or sharp contact of light dorsal and dark ventral colors; indistinct, irregular dark canthal stripe present or absent, rest of face nondescriptly patterned or with irregular white bars under eyes and irregular light stripe on posterior upper lip and angle of jaw; dark flank stripe distinct or not, including almost uniform gray under dorsolateral fold blending with ventral color as mottle of flank and belly patterns low on sides, or flank stripe black anteriorly, fading to gray, or brown stripe under dorsolateral fold with mottled below that; throat mostly gray, lightly mottled with cream, anterior belly (or most of belly) cream with large gray spots or cream and gray mottle, posterior belly cream; posterior surfaces of thigh with a few white spots on either side of midline below vent, rest of posterior thigh almost uniform brown.

SVL 25.9-29.5, mean 28.3 mm (males), 30.6 mm (female); (following proportional values for males; values for female fall within male ranges) mean head length 33% SVL; mean head width 30% SVL; mean thigh length 41% SVL; mean shank length 43% SVL; mean foot length 50% SVL.

Life Colors. — Iris bronze. Dorsal colors brown, black, ochre; edge mantle to up over eye gold ochre. Golden streaks from eye to lip; groin dirty orange, orange, or salmon pink. Hands and

feet gray. Belly white and gray. Posterior surface of thigh light salmon pink.

Larval Morphology. — Body oval in dorsal view, wider than deep; snout rounded in dorsal view; nostril midway from eye to the tip of snout; distance between nares 69% interorbital width; nares dorsal, round; eye dorsolateral, 13% body length; opening of the sinistral spiracle directed posterodorsally on the midline about 72% body length; anal tube dextral; tail higher than body; dorsal fin origin on body-tail juncture; dorsal fin arched and ventral straight; tail musculature reaching the almost rounded tail tip; mouth anteroventral, width 34% body width; a single row of oral papillae, absent on upper lip and with three interruptions on lower lip; tooth row formula 2(2)/3(1); beak moderately developed and finely serrated.

Dorsum of the body and tail brown; venter unpigmented. In life, body and tail musculature brown with scattered black spots; first half of venter unpigmented, second half black with silvery flecks; fins transparent with black flecks; iris with inner ring golden, outer ring black with golden spots (Figure 34).

Advertisement Call. — Calls given at a rate of 0.9-1.5 per s during active calling bouts; call duration 0.25-0.35 s; individual calls of single notes; three harmonically related frequencies containing most of the energy in both the audiospectrogram and wave form; the fundamental frequency at about 400 Hz in the beginning of the call falling to about 290 Hz by the end of the call (this frequency present and strongly expressed in the first half of the waveform but only hinted at in the audiospectrogram), second harmonic the dominant frequency in the sonogram and conspicuous throughout the wave form starting at about 800 Hz and falling to about 580 Hz, a third frequency (three times the fundamental) also visible in both the audiospectrogram and wave from, particularly in the first half of the call, a fourth frequency (4 times the fundamental) also visible throughout the call in the audiospectrogram but not in the wave form, higher harmonics also visible in some audiospectrograms but not in the wave form.

An equally plausible alternative call description: dominant frequency starting at about 800 Hz and falling to about 580 Hz and amplitude modulated (strongly partially pulsed) at half that frequency; this modulation strongly expressed in the wave form over the first half of the call and present in the last half of the call but very weakly expressed in the waveform; this modulation at half the carrier frequency expressed in the audiospectrogram as strong sidebands above the carrier at multiples of the modulation frequency (Figure 65).

Ecology. — Males have been observed calling at night from open situations, including from beneath rocks at the quarry, shallow water in grass at the quarry, and a water filled cow track in a pasture. Calling males are usually concealed in grass or other vegetation. All active specimens were taken at night from similar situations as calling males. A few specimens were collected during the day from beneath rocks at the quarry. Individuals were collected in October through March.

Physalaemus franciscae Heyer

Color Figure 42

Physalaemus signiferus, Cochran, 1955. The Boracéia specimens cited by Cochran are either this species or *maculiventris.*

Physalaemus franciscae Heyer, 1985b. Original description.

Diagnosis. — *Physalaemus franciscae* lacks toe disks, lacks toe webbing or fringes, has a hidden tympanum, and lacks vomerine teeth. This combination of states is shared with *Brachycephalus nodoterga, Physalaemus cuvieri, P. maculiventris, P. olfersi,* and *Myersiella microps* at Boracéia. *Physalaemus franciscae* has 5 toes; *B. nodoterga* has 3. *Physalaemus franciscae* has inner metatarsal tubercles; *M. microps* does not. *Physalaemus franciscae* lacks a tarsal tubercle; *P. cuvieri* has a tarsal tubercle. *Physalaemus franciscae* does not have a distinct light stripe from the eye to shoulder as does *P. olfersi. Physalaemus franciscae* has a broader snout than *P. maculiventris,* is larger (males 25-27 mm SVL, females 22-29 mm SVL) than *P. maculiventris* (males 19-23 mm SVL, females 19-25 mm SVL), and the sole of the foot has a few light fleshy tubercles in *franciscae* which are not found in *maculiventris.*

Adult Morphology (N = 10 males, 10 females). — From above, canthus and tip of snout pointed or broadly mucronate with upper lip rounded, snout rounded-acute in profile; no cranial crests; upper eyelid glandular or granular-tuberculate; tympanum hidden to almost distinct, vertical diameter just less than or about equal to 1/2 eye diameter; male vocal sac single, expanded externally from tip of chin through chest region or not; males with vocal slits; no vomerine teeth; finger lengths I<, =, or >II< or =IV<III; tips of fingers slightly swollen or not; fingers without webbing, fringes, or ridges; finger subarticular tubercles moderately large, globose, not pungent; male thumb with two brown nuptial pads, one at base of thumb, other extending for much of length of thumb on inner and dorsal surfaces, pads moderately separated to almost touching each other; no prepollex; supratympanic fold well developed to not visible, dorsolateral fold from eye to groin, lumbar gland present, visible or not externally; dorsum smooth or slightly grandular-warty, sometimes with scattered small warty tubercles; venter smooth or finely granular, granular seat patch under thighs; toe lengths I<II<V<III<IV; toe tips slightly swollen or not; toes without webbing or fringes, sides of toes smooth or sometimes with weak ridges; inner metatarsal tubercle ovoid, outer round, distinct, sometimes almost pungent, outer about 1/3 to same size as inner; no heel decoration; short distinct to indistinct fold on inner tarsus extending 1/4-1/3 length of tarsus, approaching or contacting inner metatarsal tubercle; texture of outer tarsus smooth; sole of foot smooth with a few white fleshy tubercles.

Snout light tan or cream or whole dorsal ground color cream, interorbital bar weakly developed or absent, back with large well-defined to faint irregularly shaped confluent chevrons, chevrons slightly darker brown than dorsal ground color with cream highlights on edges, chevrons with light tan central spots or not, rest of dorsum with other miscellaneous dark stripes or spots or not, 1-2 distinct light outlined black spots above groin region on each side, upper limbs with narrow cross bands; canthus with dark stripe sharply defined above, sharply defined below or blending into lighter brown of loreal region, upper lip mottled, mostly cream; flanks with distinct dark lateral band either entirely black for entire extent from back of eye to lower flank or leg or black in back of eye and brown for rest of extent, dark band bordered above and (sometimes) partly below by light pinstripe; chin almost black or with fine brown and cream mottle extending as far as mid-belly in some specimens, either entire venter, entire belly, or posterior half of belly and under surfaces of thighs with a bold or muted mottled pattern; black outlined (straight or curly) seat patch extending for most of length of posterior surface of thigh, above seat patch uniform brown, seat patch demarcation fuzzy distally, tending to mottle, under seat patch dark with light spots or mottled.

SVL 25.0-26.7, mean 26.1 mm (males), 22.7-28.2, mean 26.4 mm (females); mean head length 34% SVL (males), 33% SVL (females); mean head width 35% SVL (males), 33% SVL (females); mean thigh length 43% SVL; mean shank length 45 SVL (males), 44% SVL (females); mean foot length 45% SVL (males), 43% SVL (females).

Life Colors. — Iris bronze. Dorsal colors tan and brown. Groin and inner tibia salmon or orange cast. Throat gray or with salmon cast; belly cream or dirty white brown or black blotches. Posterior surface of thigh with tan, brown, and black coloration.

Larval Morphology. — Tadpoles not collected from Boracéia.

Advertisement Call. — Calls given frequently when calling; call duration 0.50-0.70 s; call of complex structure including harmonics and pulses, beginning and most of call with 22-28 notes, note duration 0.01-0.02 s; call ending with a short portion not developed into notes (or one long note of 0.04-0.05 s), note rate about 50 per s; notes partially pulsed, at about 250 per s; calls quiet, starting and ending with lower intensity; dominant frequency range 600-1600 Hz; several distinct sidebands (Figure 66).

Ecology. — Males have been observed calling at night from small temporary pools (even bootprints) in the forest under and on dead leaves near the water. Males of *P. franciscae* and *maculiventris* have been heard calling from the same trail ponds. Most individuals were collected from the forest, many of them from the trails during

the day. One individual was collected at night from a leaf of a low shrub. Only two specimens were collected outside the forest, one at night, one in the day, both on a road. Individuals were collected in August through March.

Physalaemus maculiventris (A. Lutz)

Color Figure 43

Eupemphix maculiventris A. Lutz, 1925a. Original description.

Physalaemus maculiventris, B. Lutz, 1951. First use of *maculiventris* with *Physalaemus*.

Remark. — USNM 243711, a 22.1 mm male, differs in some details of pattern from the rest of the specimens examined, most notably in having cream, unpatterned undersurfaces of the thighs (brick red in life). All other specimens examined have the same pattern on the thighs as on the belly. This specimen should be examined in any revisionary work involving *P. maculiventris*.

Diagnosis. — *Physalaemus maculiventris* lacks toe disks, lacks toe web or fringe, has a hidden tympanum, and lacks vomerine teeth. This combination of states is shared with *Brachycephalus nodoterga, Physalaemus cuvieri, P. franciscae, P. olfersi,* and *Myersiella microps* at Boracéia. *Physalaemus maculiventris* has 5 toes; *B. nodoterga* has 3. *Physalaemus maculiventris* has an inner metarsal tubercle; *M. microps* does not. *Physalaemus maculiventris* does not have a tarsal tubercle; *P. cuvieri* does. *Physalaemus maculiventris* lacks the distinct light stripe from the eye to shoulder of *P. olfersi*. *Physalaemus maculiventris* has a narrower, more pointed snout than *P. franciscae,* is smaller (males 19-23 mm SVL, females 19-25 mm SVL) than *P. franciscae* (males 25-27 mm SVL, females 22-29 mm SVL), and the sole of the foot is smooth in *maculiventris* (sole of foot with a few light fleshy tubercles in *franciscae*).

Adult Morphology (N = 10 males, 10 females). — Snout pointed or pointed-subelliptical from above, acute or rounded-acute in profile; no cranial crests; upper eyelid with extension of dorsolateral fold on outer rim; tympanum not visible; male vocal sac single, usually slightly to moderately expanded externally; males with vocal slits; no vomerine teeth; finger lengths I just < or ≅ II just < or ≅ IV<III; finger tips rounded to just slightly swollen; fingers without webbing, fringes, or ridges; finger subarticular tubercles moderately developed; single brown nuptial pad covering most of inner and dorsal surfaces of thumb in males, male forearms hypertrophied, thumb broad in male; very low ridge on outer forearm region or not; no prepollex; weakly developed supratympanic fold present or absent, fold from back corner of eye to midbody, then curving obliquely downward, large diffuse or discrete lumbar glands; dorsal texture smooth; ventral texture smooth with a granular seat patch under the thighs; toe lengths I<II<V< or ≅ III<IV; toe tips rounded, sometimes slightly swollen; toes without webbing or fringes, sides of toes smooth or slightly ridged; inner metatarsal tubercle ovoid, outer rounded, both pungent, outer about 1/2 to 3/4 size of inner; no heel decoration; tarsus with or without a very weakly developed inner tarsal fold extending about 1/5 length of tarsus; outer tarsal and sole of foot texture smooth.

Dorsal pattern tan with light outlined very distinct (rarely indistinct) dark marks including a broad interorbital bar and 2-3 broad chevrons plus many rounded/elongate spots, upper limbs cross banded, light pin stripe on outer forearm region present or absent; with or without a faint dark band from tip of snout across canthus to eye, upper lip with irregular dark marks, supratympanic fold rarely dark highlighted; flank variable, ranging from almost uniform brown to faint dark oblique bar from behind eye to past midbody below dorsolateral fold, discrete above, irregular below (sometimes defined below by light pin-stripe from eye to shoulder region), 1 large with or without 1-2 small intensely black spots in groin, at least large black spot on lumbar gland; dorsolateral fold cream, contrasting with surrounding patterns; throat and chest entirely dark gray or with large central mostly dark gray area surrounded by mostly creamy area, belly and limbs light cream with large black blotchy spots to mostly black; posterior surface of thigh with black seat patch with a discontinuous extension often breaking up into dark spots, other white outlined black round or elongate spots on thigh often extensions of dorsal bands.

SVL 19.0-22.3. mean 20.5 mm (males), 19.8-25.0, mean 23.3 mm (females); mean head length 32% SVL (males), 29% SVL (females); mean head width 32% SVL (males), 28% SVL (females); mean thigh length 46% SVL (males), 45% SVL (females); mean shank length 49% SVL (males), 47% SVL (females); mean foot length 53% SVL (males), 51% SVL (females).

Life Colors. — Iris bronze. Dorsum brown and tan with yellow outlining. Hands and feet with orange highlights. Chest with brick red; belly gray with blue cast; seat patch reddish.

Larval Morphology. — Tadpoles not collected from Boracéia. Bokermann (1963) described and illustrated the larvae based on specimens from forest ponds at Paranapiacaba, São Paulo.

Advertisement Call. — Calls given frequently when actively calling, at a rate of 0.5-1.4 per s; call duration about 0.20-0.75 s; calls pulsed, pulse rate about 130-170 per s; calls building in intensity through first half of call, loudest portion of call maintained for about 1/3 length of call, remainder of call gradually decreasing in intensity; calls not noticeably frequency modulated; dominant frequency range 700-3700 Hz, strongest frequencies between 1000-3000 Hz (range of all calls analysed, call spectrum of a typical individual call with strongest frequencies between 1600-2900 Hz, maximum at 2000 Hz), fundamental frequency included in the dominant range; calls apparently lacking harmonic structure; calls with strong sidebands due to pulsatile nature of call (Figure 67).

Ecology. — Males have been observed calling on the ground next to small temporary pools in the forest at night, sometimes in mixed choruses with *P. franciscae*. One foam nest contained 129 eggs. All specimens were collected from the forest at the same sites as calling males, and from forest trails during the day and at night. Individuals were collected from August through March.

Physalaemus olfersi (Lichtenstein and Martens)

Color Figure 44

Phryniscus olfersi Lichternstein and Martens, 1856. Original description.

Physalaemus olfersi, Parker, 1927. First use of *olfersi* with *Physalaemus*.

Diagnosis. — *Physalaemus olfersi* lacks toe disks, lacks toe web or fringe, has a hidden tympanum, and lacks vomerine teeth. This combination of states is shared with *Brachycephalus nodoterga*, *Physalaemus cuvieri*, *P. franciscae*, *P. maculiventris*, and *Myersiella microps* at Boracéia. *Physalaemus olfersi* has 5 toes; *B. nodoterga* has 3. *Physalaemus olfersi* has inner and outer metatarsal tubercles; *M. microps* lacks both. *Physalaemus olfersi* does not have a tarsal tubercle; *P. cuvieri* does. *Physalaemus olfersi* is larger (males at least 28 mm SVL, females at least 30 mm SVL) than *P. franciscae* and *maculiventris* (males smaller than 28 mm SVL, females smaller than 30 mm SVL) and has a distinct light pin-stripe from eye to shoulder lacking in *P. franciscae* and *maculiventris*.

Adult Morphology (N = 7 males, 2 females). — Snout outline pointed to subelliptical from above, acute in profile; no cranial crests; no upper eyelid decoration; tympanum hidden to not visible, diameter just over 1/3 eye diameter; male vocal sac single, external, moderately to greatly expanded; males with vocal slits; no vomerine teeth; finger lengths I≅IV just <II<III or I< or ≅II< or ≅IV<III; finger tips rounded-pointed; fingers without webbing or fringes, sides of fingers smooth or slightly ridged; finger subarticular tubercles moderately developed, single; males with two discrete brown nuptial pads on inner side of thumb, one associated with inner metacarpal tubercle, narrowly to moderately separated from one next to basal subarticular tubercle; no forearm fold; no prepollex; very weakly developed supratympanic fold, weak fold from posterior corner of eye to groin, lumbar gland distinct or somewhat diffuse (absent in one female); dorsal texture etched or smooth; ventral texture smooth with a granular seat patch under thighs; toe lengths I<II<V< or ≅III<IV; tips of toes pointed-rounded; toes without webbing or fringes, sides of toes smooth or slightly ridged; inner metatarsal tubercle ovoid, outer round to ovoid, both pungent, outer 1/2 to 2/3 size of inner; heel smooth or with 1 or a few small tubercles; very weak inner tarsal fold extending about 1/5 - 2/5 length of tarsus, single tubercle just above inner metartasal tubercle present or absent, with or without a row of scattered warts along outer tarsus; rest of outer tarsal texture

smooth; sole of foot mostly smooth with or without 1-2 small rounded fleshy tubercles.

Dorsal pattern moderately variable including brown back with darker interorbital triangle sometimes extending as an anastomosing ladder over back with a central light spot behind shoulder area or tan with scattered dark outlined light dots and dashes, light mid-dorsal pin stripe ranging from dark outlined and interrupted to distinct only from sacrum to vent, upper limbs brown with darker cross bands, row of light dots on outer forearm region and tarsus or not, outer forearm, tarsus, and sole of foot dark brown, contrasting with adjacent areas; distinct separation of lighter dorsal color from darker face and anterior flank color along tip of snout, canthus, and lateral fold from eye to groin, face light to dark brown with scattered small light spots or face darker below canthal stripe fading to tan on edge of upper lip, light stripe from back edge of eye to shoulder; flanks with broad dark oblique band, lumbar gland yellowish brown or undistinguished from dorsal color; ventral pattern somewhat variable, ranging from almost uniform dark brown with small light dots on throat, chest and front of belly, mid-belly mottled, posterior belly mostly cream, to throat and belly mottled cream and tan with white splotches; posterior surface of thigh mottled brown and white to almost uniform brown.

SVL 28.5-34.5, mean 32.0 mm (males), 30.9-31.9 mm (females); head length 31-34% SVL; head width 27-31% SVL; thigh length 38-43% SVL; shank length 40-46% SVL (males), 46-48% (females); foot length 46-52% SVL (males), 49-55% SVL (females).

Life Colors. — Iris bronze. Dorsum light brown with light green-bordered dark brown pattern. Eye-shoulder stripe yellow or white. Upper legs reddish. Belly gray around edge, white in center, entire belly with brick red network. Posterior surface of thigh brown-lavender.

Larval Morphology. — Tadpoles unknown.

Advertisement Call. — Calls given sporadically but frequently when actively calling; call duration 3.5-4.0 s; calls complexly partially pulsed, pulse rate 200-225 per s; calls with noticeable variable frequency modulation (warbling); either no noticeable intensity modulation or calls beginning quietly and gaining maximum intensity at 2/3 call duration and maintaining maximum intensity for remainder of call; fundamental frequency about 1700-2000 Hz; loudest broadcast frequency range 1000-2700 Hz; distinct sidebands due to pulsatile nature of call; calls with or without weak intermittent harmonic structure (Figure 68).

Ecology.— Males have been observed calling from open habitats at night, on the ground under or in vegetation including grass near marshy ponds at the edge of the forest. Most specimens were collected at night, from open habitats, secondary and primary forest habitats on the ground. Two individuals were taken during the day from the forest floor. Specimens were collected in August, November through January, and March.

Proceratophrys boiei (Wied)

Color Figure 45

Ceratophrys boiei Wied, 1824. Original description.

Proceratophrys boiei, Lynch, 1971. Transfer of *boiei* to *Proceratophrys*.

Diagnosis. — Three Boracéia species, *Ceratophrys aurita, Proceratophrys boiei* and *Proceratophrys melanopogon,* have distinct eye horns - triangular flaps of skin extending over eye from upper eyelid. In the two *Proceratophrys,* the tympanum is not visible externally; it is visible externally in *Ceratophrys aurita. Proceratophrys boiei* lacks a triangular fleshy appendage at the tip of the snout; *P. melanopogon* has such an appendage.

Adult Morphology (N = 1 male). — Snout outline rounded from above, obtuse with flaring lip in profile; distinct canthal and supraorbital cranial crests, parietal spur distinct; upper eyelid with an extensive triangular flap (or horn) with 3 complete folds and 1 broken fold extending to tip, upper eyelid and flap covered by shagreen and warts; tympanum not visible; male with single internal vocal sac; vocal slits present; vomerine teeth in two transverse series lying between posterior extent of choanae, separated by about 1/5 length of single vomerine tooth row; finger lengths IV<II<I≅III; no finger disks; no finger web, sides of fingers with distinct

ridges; larger, pronounced, moderately pungent subarticular finger tubercles; no male thumb asperities; no forearm fold; no external prepollex; symmetrical fold from tip of eye horns to sacrum and from horn to horn, folds initially narrowing to midbody, then ballooning in sacral region and converging over vent, series of 3 rows of warts from below and behind eye to shoulder and midbody; dorsum covered by warts and shagreen, on sides of body and on limbs, warts and shagreen or spinules on top of warts; venter granular and tuberculate; toe lengths I<II<V<III<IV; no toe disks; toe webbing formula I 2^{-}-2^{+} II 1 1/2-3^{+} III 1 1/2-4 IV 4^{+}-2 1/2 V; inner metatarsal tubercle very large, sickle shaped, outer metatarsal tubercle small, rounded, not much different from other warts in immediate area; no distinctive heel decoration; row of warts along inner side of inner tarsal tubercle extending along almost the entire length of tarsus; outer tarsus covered by warts, small tubercles and shagreen; sole of foot with large, light, rounded tubercles and small warts.

Dorsum with a complex symmetrical pattern of browns, creams, tans, dorsal fold complex cream; loreal region a mosaic pattern of tans and browns, one distinct dark brown suborbital bar anteriorly to upper lip, 2 additional oblique suborbital bars posteriorly not as distinct; flank pattern a continuation of dorsal pattern with a sharp transition to belly pattern ventrally; throat gray, belly and under limbs dirty cream with black irregular spotting; posterior surface of thighs undistinguished browns.

SVL 57.9 mm (male); head length 42% SVL; head width 45% SVL; thigh length 35% SVL; shank length 32% SVL; foot length 38% SVL.

Life Colors. — Iris bronze; mustard yellow stripe from eye horn to eye horn; rest of dorsum lighter and darker leaf browns; throat brown, chest and belly pinkish white with black spots; hands and feet with light pink tubercles; posterior surface of thigh brown, same as dorsal color.

Larval Morphology. — Tadpoles have not been collected from Boracéia. Larvae of this species have been described and figured by Izecksohn, Cruz, and Peixoto (1979), based on material from ponds at Teresópolis, Rio de Janeiro.

Advertisement Call. — Calls given sporadically; call duration about 0.70-0.80 s; 30-35 notes per call, note duration 0.008-0.01 s, note rate about 45 per s; each note with a simple wave form envelope; calls beginning quieter then quickly reaching maximum intensity, maintained for duration of call; dominant (= fundamental) frequency range 350-1350 Hz; lacking harmonic structure (Figure 69).

Ecology. — One male was calling at night from a densely overgrown swamp next to the road in an area of open secondary growth vegetation in December 1984.

Proceratophrys melanopogon (Miranda-Ribeiro)

Stombus melanopogon Miranda-Ribeiro, 1926. Original description.

Ceratophrys appendiculata, Cochran, 1955. Specimens cited from Boracéia.

Proceratophrys melanopogon, Lynch, 1971. First association of *melanopogon* (as a probable synonym) with *Proceratophrys.*

Nomenclatural Note. — Eugênio Izecksohn pointed out the specific distinctness of *melanopogon* to us and is resurrecting the name.

Diagnosis. — Three Boracéia species, *Ceratophrys aurita, Proceratophrys boiei* and *Proceratophrys melanopogon*, have distinct eye horns - triangular flaps of skin extending over eye from upper eyelid. In the two *Proceratophrys,* the tympanum is not visible externally; it is visible externally in *Ceratophrys aurita. Proceratophrys melanopogon* has a triangular fleshy appendage on the tip of the snout; *P. boiei* lacks such an appendage.

Adult Morphology (N = 6 males, 3 females). — Snout outline rounded to almost semicircular from above, obtuse in profile; moderately developed canthal and supraorbital crests, weakly developed pre- and post-orbital crests; upper eyelid with a very long fleshy triangle; no visible tympanum; male vocal sac single, essentially internal or external and somewhat expanded; males with vocal slits; vomerine teeth in two short transverse series lying between choanae; finger lengths I just < or ≅ II ≅ IV<III; tips of fingers pointed-rounded, not expanded; fingers

without webbing or with a trace of basal webbing, sides of fingers ridged, finger subarticular tubercles well developed, moderately pungent, single to slightly bifid; no asperities on thumb of male; row of elongate warts on outer forearm region; no prepollex; distinct ridges from edge of eye horn between eyes and extending as symmetrical, sinuous ridges from eye and joining above sacrum, tip of snout with triangular flap, ridge-like row of warts from under eye to angle of jaw, long tubercles at angle of jaw, oblique rows of warts on sides of body present or absent, patagium to elbow; dorsal texture of shagreen and warts; ventral texture of shagreen and granules; toe lengths I<II<V< or ≅ III<IV; toe tips rounded to pointed, not expanded; modal toe webbing formula I 1 1/2-2$^+$ II 1 1/2-3$^+$ III 2$^+$-4 IV 4-2$^+$ V; inner metatarsal tubercle ovate, pungent, almost spade-like, outer low, rounded, about 1/6-1/4 size inner; heel warty (same as dorsum), sometimes with one particularly well developed, pronounced warty tubercle; short warty inner tarsal fold extending 1/3-1/2 length of tarsus ending in large tubercle or not, row of triangular warts comprising outer tarsal fold; outer tarsal texture warty; sole of foot warty with large round fleshy tubercles.

Dorsal pattern variegated browns looking like dead leaves, upper limbs cross banded; face same pattern as dorsum with or without a dark oblique band under eye to lip; flanks rather uniform brown; throat and chest black or mottled black and brown, rest of venter tan with brown spots or mottled tan and black; posterior surface of thighs variegated browns to uniform tan with or without faint dark seat patch extending from above vent to bottom of posterior thigh about 1/3 distance on thigh.

SVL 33.4-45.2, mean 40.8 mm (males), 38.8-58.1, mean 50.7 mm (females); mean head length 45% SVL; mean head width 52% SVL (males), 53% SVL (females); mean thigh length 37% SVL; mean shank length 35% SVL (males), 36% SVL (females); mean foot length 39% SVL.

Life Colors. — Iris copper or red-bronze. Dorsal color browns, markings edged or not with green or white, feet and hands pale dirty orange, tips of fingers and toes bright orange, mid-back, sides, and elbows with pinkish cast; belly black, brown, or gray with or without orange cast.

Larval Morphology. — Tadpoles not collected from Boracéia.

Advertisement Call. — Call not recorded, nor have males been heard at Boracéia.

Ecology. — All specimens were collected in the forest on trails or leaf litter, usually during the day. Specimens were collected from September through May.

Thoropa miliaris (Spix)

Color Figure 46

Rana miliaris Spix, 1824. Original description.
Thoropa miliaris, Boulenger, 1882. First use of *miliaris* with *Thoropa*. — Wassersug and Heyer, 1983. Description of internal oral cavity anatomy of larvae from Boracéia.
Eupsophus miliaris, Cochran, 1955. Citation of specimens from Boracéia.

Diagnosis. — The Boracéia species that lack toe disks and webbing and have vomerine teeth are *Adenomera marmorata, Cycloramphus eleutherodactylus, Holoaden luederwaldti, Leptodactylus flavopictus, L. fuscus, L. ocellatus, Paratelmatobius gaigeae,* and *Thoropa miliaris.* The sole of the foot of *T. miliaris* is smooth; the sole of the foot of *A. marmorata* is covered with white-tipped tubercles. *Thoropa miliaris* lacks a dorsal iris meniscus; *Cycloramphus eleutherodactylus* has a meniscus. The dorsum of *Thoropa miliaris* is relatively smooth and has a pattern of 1-2 large blotches; the dorsum of *H. luederwaldti* has obvious large, rather uniform bumps and is uniform brown. *Thoropa miliaris* does not have distinct dorsolateral folds in addition to the supratympanic fold; all *L. flavopictus, fuscus, ocellatus* and some *P. gaigeae* have distinct dorsolateral folds. The belly of *T. miliaris* is not boldly patterned as is the belly of *P. gaigeae* and *T. miliaris* is much larger (54-81 mm SVL) than *P. gaigeae* (SVL 16-20 mm).

Adult Morphology (N = 10 males, 10 females). — Snout outline rounded to nearly rounded from above, rounded in profile; no cranial crests; no upper eyelid decoration; tympanum distinct, large, diameter 2/3-3/4 eye diameter; no vocal sac in males; no vocal slits in males; vomerine teeth in two short transverse series lying between or between and on a line

across posterior margins of choanae; finger lengths II<IV<<I<III or II<I=IV<III; tips of fingers slightly to noticeably swollen, not disked; fingers without webbing or fringes, sides of fingers smooth or with slight ridges; basal finger subarticular tubercles moderately well developed, distal tubercles less well developed, single; males with patches of nuptial spines on fingers, 3 patches on thumb in largest males, one patch on each joint (distal patch absent in small males), patch on top of second finger extending for most of length (just a few spines in small males), a few spines on top of finger III (absent in small males), forearms slightly hypertrophied (not in small males); outer forearm region smooth or with a very weak fold; no prepollex; well developed supratympanic fold, sides of body areolate with glandular warts; dorsal texture smooth or finely granular with scattered warty tubercles; ventral texture mostly smooth, posteriormost belly granular, extensive granular seat patch under thighs; toe lengths I<II<V< or ≅ III<IV; toe tips swollen, not disked; toes without webbing or fringes, sides of toes ridged; inner metatarsal tubercle ovoid, outer rounded or ovoid, outer 1/4-1/3 size of inner; heel smooth or with a few weak glandular warts; inner tarsal fold distinct (or not) in middle; extending about 2/3 length of tarsus; outer tarsal and sole of foot texture smooth.

Dorsal pattern tan and brown, ranging from two distinct oblong white outlined (or not) irregular dark blotches, one from between eyes to past shoulders, second just past sacrum to coalesced into one large oblong blotch, upper limbs faintly to distinctly cross banded; dark canthal stripe, rest of face light tan or with blotching on upper lip, tympanum dark outlined entirely or just by fold, supratympanic fold dark brown outlined; flanks with dark brown warts on tan background or mostly dark gray with whitish spots, groin with just a hint of anterior and posterior pattern; venter marbled tans or light brown with light marbling on throat; anterior and posterior surfaces of thighs usually with a bold dark and light mottle, rarely with reduced bold mottle and mostly indistinct mottle, bold mottle sometimes on hidden portion of shank and tarsus.

SVL 54.0-71.5, mean 60.7 mm (males), 64.6-81.0, mean 71.1 mm (females); mean head length 38% SVL (males), 37% SVL (females); mean head length 38% SVL (males), 37% SVL (females); mean head width 40% SVL; mean thigh length 50% SVL (males), 51% SVL (females); mean shank length 55% SVL; mean foot length 53% SVL (males), 52% SVL (females).

Life Colors. — Iris coppery red with black reticulations above, diffuse black with deeper red brown on sides, silver with black reticulations below or dull yellow with dark red at sides of pupil. Dorsal colors tan, brown, bronze. Groin dirty chrome yellow. Venter ranging from chin, throat and belly gray, belly more bluish, under legs purple to throat white to brown to clear. Anterior and posterior thigh dirty chrome yellow banded with dark brown.

Larval Morphology. — Tadpoles were collected from the wet quarry rock walls both night and day at Boracéia, but have been lost. Bokermann (1965b) described and figured the larvae based on specimens from Cubatão, São Paulo.

Advertisement Call. — Calls given sporadically, duration 0.20-0.30 s; 3-4 notes per call, note duration 0.05-0.06 s; note rate about 10-20 per s; notes pulsatile, pulse rate about 150-200 pulses per s; call not noticeably intensity modulated; entire call not notably frequency modulated; dominant frequency band (= fundamental?) at 400-800 Hz; sidebands strongly developed due to pulsatile nature of notes (Figure 70).

Ecology. — Males have been observed calling from the wet rock walls at the quarry at night. Most metamorphosed individuals were collected at night from open areas such as the quarry. Several individuals were collected from under rocks or grass during the daytine. The species was occasionally active at night in the clearings around the station buildings. One individual was taken from a forest trail during the day. Specimens were collected in all months of the year except June and July.

Family Microhylidae

Myersiella microps (Duméril and Bibron)

Figure 12

Engystoma microps Duméril and Bibron, 1841. Original description.

Myersiella microps, Nelson and Lescure, 1975. First association of *microps* with *Myersiella*.

Diagnosis. — This is the only small Boracéia frog (male 15 mm SVL) with no vomerine teeth or inner and outer metatarsal tubercles.

Adult Morphology (N = 1 male). — Snout outline pointed with a bulbous tip from above, rounded-acute in profile; no cranial crests; no upper eyelid decoration; tympanum not visible; no vocal sac in male; male without vocal slits; no vomerine teeth; finger lengths I<II<IV<<III; finger tips rounded; fingers without webbing, fringes, or ridges; finger subarticular tubercles indistinct; no nuptial asperities on thumb of male; no forearm fold; no prepollex; no body glands or folds; dorsal texture smooth; ventral texture smooth; toe lengths I<II<V<III<IV; tips of toes rounded; toes without webbing, fringes, or ridges; no visible inner or outer metatarsal tubercle; no heel decoration; no tarsal decoration; outer tarsal and sole of foot texture smooth.

Dorsal pattern brown, limbs marbled; face brown; flanks with meeting of dorsal and ventral patterns about midway down sides; ventral pattern a bold brown and cream mottle; posterior surface of thigh mottled.

SVL 15.0 mm (male); head length 32% SVL; head width 31% SVL; thigh length 41% SVL; shank length 41% SVL; foot length 41% SVL.

Life Colors. — Not available for Boracéia specimen.

Larval Morphology. — This species has direct development (Izecksohn et al., 1971). No clutches were found at Boracéia.

Advertisement Call. — Not recorded from Boracéia.

Ecology. — The single specimen from Boracéia was collected during the day on the ground under a rotten stick in September 1965, more than 1 km NE of the scientists' residence.

SPECIES DISTRIBUTIONS

Over Time

Boracéia is one of the few Neotropical localities for which data are available to evaluate changes in the herpetofauna over many years. There are many older tropical collections, but few are concentrated on a single small area and even fewer are from places where the habitat remains intact and has been resampled in the intervening years. In the late 1940s, when Vanzolini and Bokermann first collected at Boracéia, they found frogs abundant and diverse, as did the Rands in 1962-1964, Nelson and associates in 1969-1971, Heyer in 1975-1978, and Myers and Daly in 1979. However, when Peixoto and Cruz visited Boracéia in January 1982 they found that some species abundances had changed drastically.

Those changes described by Heyer et al. (1988) are summarized here. First, the abundances of some species were unchanged. For example, the pond breeders *Bufo crucifer, B. ictericus, Hyla faber, H. microps. H. minuta, H. pardalis, H. polytaenia, Ololygon crospedospila, O. hayii, Physalaemus cuvieri,* and *P. olfersi* and the forest species *Hyla albofrenata, H. astartea, H. hylax, H. leucopygia* and *Eleutherodactylus randorum* were about equally abundant in every collection from the 1940s to the present. Second, the abundances of those Boracéia species that are seasonal in appearance, rare or inconspicuous, or only occasionally encountered, cannot be evaluated. Third, at least one species has increased in numbers. *Hyla albopunctata* is now common and conspicuous in the same habitat where in 1963 we had found only the equally conspicuous but very different *Hyla prasina*, now rare or absent.

A number of species were common through mid-1979 and became rare or absent by 1982. *Fritziana ohausi* was common in association with large bamboos. Some time in the late 1970s these bamboos flowered and died. The first years after this must have provided superabundant breeding sites for *F. ohausi*, but thereafter, as the stems rotted, the prime beeding sites vanished. By 1982 these breeding sites were gone and no *Fritziana ohausi* were found. It probably still exists, breeding in tree holes, though much rarer than before. The reasons for the other changes are less obvious. *Centrolenella eurygnatha, Ololygon perpusilla, Adenomera marmorata, Eleutherodactylus guentheri, E. parvus,* and *Hylodes phyllodes* were all common and conspicuous frogs that were seen and/or heard daily. They

were all much less common after 1979. Some species seem to have disappeared completely: *Crossodactylus dispar, Cycloramphus boraceiensis, C. semipalmatus, Hylodes asperus* and *Thoropa miliaris*. All these were common and were always found when their microhabitats were examined. After 1979, they could not be found. The habitats appeared unchanged but the frogs were absent. There are no characteristics of phylogenetic relationship, size, reproductive mode, or habitat at any stage of the life cycle that completely unite the affected species and separate them from unchanged ones. Although all of the species with subaerial tadpoles have disappeared, they are not the only ones affected.

Detailed records exist only for Boracéia, but there are observations that suggest that frog populations crashed elsewhere in the Atlantic Forests. To the south in early 1982, Heyer could not find *Cycloranphus duseni* at its type locality in Paraná. To the north in late 1982, the once common *Cycloramphus granulosus* and *Hylodes glabrus* in the Serra da Mantiqueira and the previously abundant *Thoropa petropolitana* and *Phyllomedusa guttata* at Teresópolis could not be found. However, further north, Peixoto and Cruz collected at Santa Teresa in Espírito Santo before and after 1979 and saw no change in frog abundances.

At Boracéia these dramatic changes occurred between March 1979, when Myers collected there, and January 1982, when Peixoto and Cruz visited. More frequent sampling by Cruz and Peixoto at Teresópolis pinpoints the change there between early and late 1979. This timing is critical in evaluating possible causes. Two causes, not mutually exclusive, for the changes in frog populations seem likely: pollution or some unusual climatic event. Chronic pollution has had drastic local effects near the industrial plants at Santos, but this does not seen likely at Boracéia because the prevailing winds do not blow from Santos to Boracéia. Further, at Boracéia, three things argue against chronic pollution: (1) the plants, trees and epiphytes do not seem to be affected as they are around Santos; (2) the frogs affected are not all ecologically similar and frogs of similar ecology were not uniformly affected; and (3) there are hints of recovery in at least two species (*Hylodes phyllodes* and *Ololygon perpusilla*) between 1982 and 1984, though there has been no decrease in the output of industrial pollution in Brasil. These observations argue that the cause was a one-time event.

One possibility is a combination of pollution and an unusual climatic event, such as an unusual wind that carried the toxic effluents from Santos to Boracéia. Arguing against this is the evidence of at least roughly synchronous change over a very large area from the State of Rio de Janeiro to the State of Paraná. The most likely cause was the occurrence of unusually hard frosts in June and July of 1979. These unusual frosts were recorded at Casa Grande near Boracéia (Figure 2) and were more severe than the better known frost of 1975, called the worst in 100 years. The 1975 frost damaged coffee over much of southeastern Brasil and was much discussed because of its effect in increasing coffee prices around the world. The 1979 frost did not have as much economic impact and did not receive much attention because the coffee plants had not yet recovered from the 1975 disaster or because former coffee plantations were converted to cattle or soybean farming. That at least one species of frog, *Thoropa miliaris*, Which disappeared at Boracéia, survived in the lowlands on the nearby coast is concordant with the idea that low temperatures were the cause of mortality.

Even though frosts are infrequent, the frogs of southeastern Brasil must have experienced hard frost many times in the past. These infrequent climatic effects must have important evolutionary implications. Populations reduced to low levels are forced through a genetic bottleneck. Where the surviving populations are small and disjunct, this may result in genetic differentiation among the various populations as they again become more abundant. It is possible that the effects described here may be strong enough and the recovery slow enough to permit differentiation to the species level. It may not be coincidental that the genus *Cycloramphus*, with subaerial tadpoles, was among the gerena that disappeared at Boracéia and is a genus that shows high local differentiation in the Atlantic forest. The occurrence of unusual localized climatic events affecting population structure does not argue against the refugia hypothesis (Simpson and Haffer,

1978); major long term climatic changes with major shifts in habitat distribution must have had important offects on the distribution and differentiation of plants and animals in the Neotropics during the Pleistocene. But a short term, relatively minor climatic event such as the 1979 frost, even though it does not result in major habitat changes, may also have important evolutionary effects on some species.

Only further work at Boracéia will test the hypothesis that the abrupt populational changes seen in 1979 were due to the frost. If they were, the decimated frog populations should recover. If they do not recover, causes must be sought elsewhere, including changes due to human activity.

In Space

Any zoogeographic analysis of the frog faunal assemblages from the Atlantic Forests of Brasil will be only as good as the knowledge of the composition of the local assemblages. To use an analogy, we have a spapshot of the Boracéia fauna taken with a 30 year time exposure. In that snapshot, several species rarely encountered are visible, as well as records of species turnovers. The faunal picture at Boracéia is the best available for any local assemblage in the entire Atlantic Forest Morphoclimatic Domain. Most other snapshots have been taken at a much shorter exposure time and miss even the occurrence of relatively common species. The available snapshots allow but a coarse faunal comparison.

Data are available to examine general distributions of most Boracéia species. However, the confused systematics of a few species (*Hyla prasina, Ololygon brieni, Ololygon x-signata, Crossodactylus dispar, Crossodactylus gaudichaudii, Hylodes asperus, Megaelosia goeldii*), preclude knowledge of their geographic distributions, even at the coarse scale utilized. Most of the Boracéia species are shared with other Atlantic Forest assemblages, even though the distances among some of the Atlantic forest sites exceed the distance between Boracéia and the interior of the State of São Paulo (Figure 71). Within the Atlantic Forest region, there does seem to be a distance effect, with closer localities sharing the most species (Figure 71). With respect to habitat, of the 57 species of frogs at Boracéia whose species limits are reasonably well understood, six characteristically occur in both the forests and open habitats, 31 characteristically occur in the forests, and 17 characteristically occur in open habitats (no habitat occurrence data are available for three of the 57 species; available data reported in section on Resource Partitioning below). As expected, (1) there are more species that characteristically inhabit forests at Boracéia than occur in open habitats, and (2) the Boracéia species with the broadest geographic distributions are those that characteristically occur in open habitats (compare Figures 72 and 73).

The available data (as expressed in Figures 71-73) suggest that a large proportion of the Boracéia frog fauna has a very localized geographic distribution. In order to assess the magnitude of the endemic Boracéia fauna, detailed comparisons with the nearby area of Cubatão-Caminho do Mar-Paranapiacaba, about 50 km to the southwest of Boracéia (referred to hence simply as Cubatão for brevity), are necessary. The Boracéia and Cubatão faunas are the most similar of the available faunal samples. Although the combined frog sample from Cubatão is well represented in the MZUSP collections, it is still not as extensive as the Boracéia sample; certainly some of the differences between the two faunal lists are due to incomplete collections from Cubatão.

Seven species characteristically inhabiting open habitats at Boracéia are absent in the Cubatão sample: *Hyla microps, Hyla pardalis, Ololygon flavoguttata, Sphaenorhynchus orophilus, Hyla senicula, Cycloramphus boraceiensis,* and *Leptodactylus fuscus*. The first four species have been collected farther to the south than Cubatão within the Atlantic Forests and likely occur at Cubatão as well. Eleven species characteristically occur in forests at Boracéia but are absent in the Cubatão collection: *Centrolenella eurygnatha, Centrolenella uranoscopa, Hyla albofrenata, Ololygon flavoguttata, Phyllomedusa appendiculata* (although *P. appendiculata* is used for the Boracéia population, it is not the same species as *P. appendiculata* from Cubatão), *Proceratophrys boiei, Ololygon obtriangulata, Phyllomedusa cochranae, Eleutherodactylus randorum, Eleutherodactylus spanios,* and *Paratelmatobius gaigeae*. The first six species have

also been collected farther to the south than Cubatão within the Atlantic Forests and likely occurred at Cubatão as well. Thus, even assuming that these four open habitat and six forest associated species actually occur at Cubatão, some differences remain between these two frog faunas.

Six of the missing species from Cubatão (*Hyla senicula, Cycloramphus boraceiensis, Leptodactylus fuscus, Ololygon obtriangulata, Phyllomedusa cochranae,* and *Paratelmatobius gaigeae*) are all known from additional localities to the north and east of Boracéia within the Atlantic Forest Morphoclimatic Domain. As there is a latitudinal climatic cline along the Atlantic Forest corridor, the southern geographic limits of these species may not extend beyond Boracéia. *Eleutherodactylus randorum* and *E. spanios* are currently known only from Boracéia.

Six species of frogs from Cubatão are absent from Boracéia: *Phyllomedusa fimbriata, Cycloramphus dubius, Eleutherodactylus bolbodactylus, Hylodes mertensi, Leptodactylus furnarius,* and *Physalaemus bokermanni*. Both *P. fimbriata* and *C. dubius* have very closely related sister-species at Boracéia. The remaining four species are morphologically very distinctive, however. Also, *C. dubius, H. mertensi,* and *P. bokermanni* are known only from Cubatão or very nearby regions. Thus, although the nearby frog faunas of Boracéia and Cubatão are similar, they are not identical.

Based on the preceding information, but viewing distributions from a different perspective, five distribution patterns, falling into three major categories, exist for the 57 Boracéia species for which distributions are reasonably well known. In the classification following, numbers of species are included. These numbers are not meant to be exact, as they will be modified as further information becomes available on distributions. However, the categories and their relative representations will probably remain the same.

I. Boracéia regional endemics - 13 species.

The 13 species assigned to this pattern are known only from Boracéia or a very limited geographic area (about a 50 km radius) encompassing Boracéia. With one exception, all of these species characteristically occur in the forests. The exception, *Cycloramphus boraceiensis,* probably should be considered a forest associated, rather than an open habitat associated species — even though all but one of the specimens were collected from the walls of the quarry. The quarry is, however, a man-made open habitat surrounded by forest. One *C. boraceiensis* was collected along a forested stream. If the forests had been cleared at Boracéia; *C. boraceiensis* would likely have disappeared, and hence we conclude that all of the regional endemic pattern members should be considered dependent on the forests for their continued survival.

II. Widespread within the Atlantic Forest Morphoclimatic Domain - 37 species.

No sharp break in size of geographic ranges occurs between Pattern I and Pattern II species and most species assigned to Pattern II do not occur throughout the entire Atlantic Forest Domain. However, all species assigned to this pattern do have larger geographic ranges than species assigned to Pattern I. Three categories are discernible withn Pattern II (note that data are not available for habitat distributions for two species).

A. Characteristically occur in both forested and open habitats - 5 species.

Two of these, *Bufo crucifer* and *Bufo ictericus*, also occur in immediately adjacent morphoclimatic domains.

B. Characteristically occur only in forested habitats - 20 species.

C. Characteristically occur in open habitats - 10 species.

Three of these species also occur in geographic areas adjacent to the Atlantic Forest Morphoclimatic Domain.

III. Widespread (reaching Amazonia and/or Argentina) - 7 species.

The six species for which habitat occurrence data are available all characteristically occur in open habitats. The species for which Boracéia habitat occurrence data are lacking is *Osteocephalus langsdorffii.*

These distribution patterns suggest that: (1) most of the evolutionary history of any given assemblage of frogs along most of coastal Brasil is linked almost exclusively with the Atlantic Forest Morphoclimatic Domain; (2) regional endemics comprise a significant portion of frog assemblages within the Atlantic Forest Morphoclimatic Domain, and (3) in order to understand the frog species composition of any locality along coastal Brasil, individuals from both forest and open habitats must be collected.

Missing species?

Based on the above discussions and on our knowledge of the distributions of other genera, a few species are expected to occur at Boracéia but have not been collected there. Perhaps certain of these did occur at Boraceia in the past, but went locally extinct due to unusual conditions, as noted for several other species of frogs at Boraceia in 1979 (see above and Heyer et al., 1988).

Of the species present in the Cubatão region and absent from Boracéia, *Leptodactylus furnarius* is our top candidate for the species that should occur at Boracéia. In fact, it may have been present when cattle pastures were maintained and shortly thereafter in the earliest successional stages. Several species lists for Boracéia have been generated during the past two decades, and *Leptodactylus gracilis* has been included in some of them; *L. furnarius* is a relatively recently described species, related to *L. gracilis*. W.C.A. Bokermann (pers. comm.), when asked about this species at Boracéia, was not able to recollect with certainty whether the species calling in the pastures at Boracéia in the 1950's was *L. furnarius* or *fuscus*. No *L. furnarius* from Boracéia exist in the MZUSP frog collection, so that species is excluded from our list.

Two genera of hylid frogs, *Gastrotheca* and *Phrynohyas*, occur in the Atlantic Forests in the areas around Boracéia. As indicated in the discusssion on guilds, a large-bodied nocturnal sit-and-wait predator in the canopy appears to be missing at Boracéia. Some of the Atlantic Forest *Gastrotheca* would fall into this category. As also mentioned below, *Osteocephalus langsdorffii* has the correct body size, but its membership in a group of widespread species, all other members of which characteristically occur in open habitats, predicts that *O. langsdorffii* would occur in open habitats, not forests. At any rate, *Gastrotheca* or *Phrynohyas* species would be good candidates to colonize Boracéia.

Members of the *Bufo typhonius* species group occur only rarely throughout the Atlantic Forest (at least in our experience), although they are relatively common in other lowland forested portions of the Neotropics. Possibly the Atlantic Forests represent an ecologically marginal environment for members of this group. However, aside from this, there is no apparent reason for the absence of a *Bufo typhonius* group member at Boracéia.

Leptodactylus spixi occurs in the northern Atlantic Forests, and *L. notoaktites* occurs in the southern Atlantic Forests. Neither has been collected from the region around Boracéia (nor around Cubatão), but one or the other would be expected to occur at Boracéia. Thus, there are a few species that may have occurred at Boracéia before collections were started there in the late 1940's; may occur in low numbers; may be difficult to collect and thus far have eluded capture at Boracéia; or may be expected to colonize Boracéia at some time in the future. Despite the collecting efforts at Boracéia, surprises are still possible — both species known from elsewhere and even, perhaps in a microhabitat yet unexplored, species completely unknown. But the most exciting surprises probably will be discoveries about the biology of species we already know occur at Boracéia.

RELATIVE SPECIES ABUNDANCES

The collection of frogs from Boracéia was made in a biased manner. Not every frog observed was collected, nor were equal amounts of effort put into collecting all species in all habitats. For example, many more large *Bufo ictericus* were seen than collected. Also, when collecting within choruses of frogs, efforts were usually made to capture a few specimens of all species

calling, rather than to obtain a random sample of all frogs in the chorus. Collecting also was biased towards rare or unusual frogs. Thus, in terms of collecting effort, the rarely encountered frogs at Boracéia are represented in relatively unbiased numbers; i.,e., every effort was made to collect all individuals seen or heard of the species involved. Most collections of frogs from the Neotropics have been collected in the same fashion, including those primarily made for ecological anlysis (e.g., Crump, 1971; Duellman, 1978), with the exception of quadrat collections made by Toft (1981, 1985), Scott (1976), and Sexton et al. (1964).

The species abundance curve made from the Boracéia collections (Figure 74) should be reasonably accurate on the right and become less accurate and more biased downward on the left and central portions. Nonetheless, the species abundance curve of the metamorphosed frogs has one interesting feature. A considerable portion of the Boracéia frog fauna consists of species represented by very few specimens in collections. The only other intensive, single-site, frog collection with data available in numbers of individuals (Duellman, 1978 - Santa Cecilia, Ecuador) shows the same trend. The relative abundance of frogs from Santa Cecilia, Ecuador, with a larger number of species (81), also includes several species represented by few individuals in collections (Figure 74). Boracéia however, has proportionally more rare species than Santa Cecilia. Nine species at Boracéia (14% of the total known species) are represented by a single individual and 27 species (42% of total known species) are represented by 10 or fewer individuals. The data from Santa Cecilia show that there are 3 species (4%) known from a single individual and 20 (25%) known from 10 or fewer individuals. We predict that if a 30 year sampling period were possible at Santa Cecilia the proportion of rarer species in the Santa Cecilia frog fauna would approach that found in the Boracéia fauna.

Concordance of the only two data sets of Neotropical frog abundances allows us to conclude that any collection of frogs from a site-specific diverse species pool in the Neotropics will contain numerous rare species. Assuming this conclusion to be correct, the question arises: are rare species occurrences due to ineffective sampling, or to actual rarity in nature? Some species are indeed easier to collect than others. However, given 30 years of collecting at Boracéia, even species moderately difficult to collect should be represented by more than 10 individuals. Thus, the rarest species at Boracéia are rare in collections either because they are extremely difficult to collect or because their population densities are very low at Boracéia. The fifteen species from Boracéia represented by three or fewer individuals are: *Hyla albosignata, H. senicula, Ololygon x-signata, Osteocephalus langsdorffii, Phyllomedusa appendiculata, Ceratophrys aurita, Crossodactilys gaudichaudii, Eleutherodactylus hoehnei, E. nigriventris, E. spanios, Holoaden luederwaldti, Leptodactylus flavopictus, Megaelosia goeldii, Proceratophrys boiei,* and *Myersiella microps*. Some of these species, such as *Eleutherodactylus nigriventris, E. spanios,* and *Holoadon luederwaldti,* are known by few, if any specimens from other localities. For these species, the possibility exists that they occur in microhabitats difficult for humans to sample and that their actual density at Boracéia is greater than their rarity in collections suggests. However, rarity of other species from this list cannot be due to shortcomings of human collecting efforts. *Hyla albosignta* is known from one individual at Boracéia. Werner C.A. Bokermann, who did not collect any *H. albosignata* from Boracéia, collected seven other individuals throughout the species' range. It is likely that Bokermann, with the amount of time he spent at Boracéia, would have collected *H. albosignata* from there if it were even moderately rare. We have collected series of *Megaelosia goeldii* from Teresópolis. Even though the *Megaelosia* from Boracéia and Teresópolis are probably not conspecific, they likely have similar ecologies and we would have collected more from Boracéia if they were not rare. We have collected series of *Ololygon x-signata, Ceratophyris aurita,* and *Proceratophrys boiei* (which are almost unquestionably conspecific with the Boracéia populations) from other parts of the species' ranges. At least for these three species, and very likely for most of the other species rarely encountered from Boracéia, few specimens are in collections because the species occur at very low densities at Boracéia.

Assuming that several species are actually rare at Boracéia, what accounts for such low densities? And what impact do rare species have on the frog assemblage at Boracéia?

Extremely low densities at Boracéia could be due to several causes. Population densities may have been decimated by unusual climatic events and not recovered (see above discussion and Heyer, et al., 1988, for examples). Habitat critical for some aspect of the life cycle may support only a very low density of individuals of certain species at Boracéia. This is likely the case for *Fritziana ohausi*; it was common when large bamboos were common and is now rare or locally extinct after both species of large bamboo flowered, died and rotted at Boracéia (above discussion and Heyer, et al., 1988). Frogs are certainly capable of some dispersal through unfavorable habitat (as evidenced by the sudden arrival of *Hyla albopunctata* at Boracéia, Heyer et al., 1988); some of the rare individuals collected may have been dispersers, not residents. Unfortunately, data are not available to evaluate these explanations for the occurrence of several rare species of frogs at Boracéia.

From a zoogeographical perspective, one individual of a species has the same distributional information as a sample of 386 individuals. From an ecological perspective, the impact of very rare species is quite different from common species. It is hard to imagine that rare species have any meaningful effect on species interactions or would lead to habitat partitioning due to competition or to species isolating factors over evolutionary time. Therefore, in the following resource partitioning section, common or patchily occurring species interactions are emphasized. One object of our interest in the fauna at Boracéia is to understand the distribution of frogs relative to the Atlantic Forest Morphoclimatic Domain. In this regard, it is important to know the species that primarily live in the forests. In this case, even knowing that the single individual of *Holoaden luederwaldti* was taken from the forest provides some information. In the discussions following, we use such information, but cautiously.

RESOURCE PARTITIONING

In this section we examine resource partitioning of frogs at Boracéia; in the section following this we analyze Boracéia species guild structures and use them as a base to compare the frogs at Boracéia with those elsewhere.

In this section, we consider: (1) how the frog species are distributed in space; (2) how their activity is distributed in time; and (3) how differences in size and foraging behavior affect the kinds of prey eaten. We do not analyze larval ecologies, not because we think them unimportant, but because the Boracéia larval data are too limited. We stress similarities and differences among closely related species. Data of this sort cannot tell us the importance of competition among species in organizing the assemblage at Boracéia, but they are relevant in identifying species with similar ecologies where competition is at least possible and others in which it is unlikely.

As one of the organizing factors of this section involves examination of partitioning among related species pairs, it is necessary to outline phylogenetic relationships as currently recognized. Where two or more species of a genus occur at Boracéia, they are considered to be relatively closely related, at least for purposes of resource partitioning analysis. However, the intrageneric relationships differ in the Boracéia assemblage. For example, the two *Bufo, Hylodes*, and the three *Leptodactylus* species each belong to distinct species groups within their respective genera. The two *Centroenella* species relationships are not well understood with the context of the family; we do not know whether these two are each other's closest relative. Within hylids, there are several distinct species groups, some of which have more than one species. The green *Hyla, H. albofrenata, albosignata* and *leucopygia*, form a closely related group; within this group, *albosignata* and *leucopygia* are closest relatives. The *Hyla faber* group contains *H. astartea, circumdata, faber, hylax,* and *pardalis;* within this group, *astartea, hylax,* and *circum-*

data seem to form a closely related complex. *Hyla multilineata* and *polytaenia* form a closely related species-pair. *Ololygon crospedospila, hayii,* and *x-signata* appear to represent one species group, *O. brieni, flavoguttata,* and *obtriangulata* a second, and *O. perpusilla* either a third group or a member of the second. Within the leptodactylids, three genera need comment for our purposes. *Cycloramphus boraceiensis* and *semipalmatus* belong to one species group and *C. eleutherodactylus* belongs to another. The relationships among *Eleutherodactylus* are questionable; however, most of the common species (*E. binotatus, guentheri, parvus, randorum*) each appear to belong to different species groups. Within the genus *Physalaemus, P. franciscae* and *maculiventris* belong to one species group, *P. cuvieri* a second, and *P. olfersi* a third.

Time of Activity

Diel Patterns. — There is no clear separation among related species on the basis of time of activity. Most frogs are nocturnal, with a few exceptions such as the diurnal *Hylodes*. Activity times for the forest floor *Eleuthrodactylus* are not clear. For a tabulation and further discussion see the section on guilds below.

Seasonal Patterns. — The best data are from observations by Rand and Rand on a series of trips to Boracéia over about a two year period (Table 2). Most species were found on every visit (some of the gaps in the early part of the record were due to initial unfamiliarity with the fauna).

Frogs seem more conspicuous in terms of both calling and movement during warm, wet weather than during cold, dry weather. There has not been enough sampling in mid-winter to know if frog activity then stops completely. At least some activity occurs in all other times of the year. Although there seems to be a correlation of frog activity with the wetness of the forest, there is no evidence of any frog migration to stream valleys during drier periods. The dry periods at Boracéia are probably not long enough or severe enough to produce that kind of response.

Habitat

Macrohabitat Differences. — The distribution of the frogs collected at Boracéia can be considered in terms of macrohabitat categories (Table 3). Most of the Boracéia reserve is covered with forest. It is, therefore, no surprise that most of the Boracéia frog species occur in the forest. Within the forest some species are widely distributed, such as *Eleuthrodactylus parvus* and *guentheri*. Other species are associated with specific microhabitats, especially the various places where water accumulates, including bromeliads, puddles, streams, and rivers. In *Hylodes phyllodes*, males are always found close to water where breeding occurs, whereas females are sometimes encountered away from water in the forest. This pattern is also characteristic of *Bufo ictericus*. A few species were encountered in one or a few small areas in the forest that did not seem to differ in any significant way from nearby, unoccupied areas (e.g., *Brachycephalus* and *Dendrophryniscus)*. Some species have been found only inside the forest, whereas others also occur on the forest edges or in the clearings. Several forest species are found in the narrow grassy verges that occur along the road and in some other places such as along the aqueduct clearing and along the widest trails (e.g., *Adnomera marmorata, E. guentheri)*. Several species seem to be open habitat species that apparently have invaded along the man-made clearings. These include *Hyla albopunctata, Leptodactylus fuscus, L. ocellatus,* and *Physalaemus cuvieri*. Several species of hylids have non-breeding habitats that are hard to categorize. These species are found only when they breed in open vegetation at the edges of ponds or lakes. Of these, *Sphaenorhynchus* is probably always associated with the water, but others range into the forest when not breeding (e.g. *Hyla faber, H. microps, H. minuta, H. pardalis, H. polytaenia, Ololygon crospedospila* and *O. hayii)*.

There is no suggestion of resource partitioning on the basis of forest or open habitat preference (except possibly in *Cycloramphus,* but see below). Close relatives show identical or broadly overlapping macrohabitat distributions.

Microhabitat Distribution. — Considering closely related species, there are several in which

Table 2. Frogs of Boracéia observed on Rand and Rand visits, months from two years combined (+ found; c=calling; q= quarry; l=lago; rg=Rio Grande).

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
B. crucifer		c	c					+	c	+		c
B. ictericus		c	c						c	c	c	c
D. brevipollicatus										+		
C. eurygnatha		c	c	c				c		c	c	c
C. uranoscopa				c				c		c		
F. fissilis		+	+						+			
F. ohausi		+							+	c		
H. albofrenata				c					c	c		
H. astartea		c	c					c	c?	c	c	c
H. faber		cq	cq									
H. hylax		c	c					c	c?	c	c	c
H. leucopygia		c	c	c				c	c	c	c	c
H. microps								c				c
H. minuta		c	c					c		c	c	c
H. multilineata		c	c							c		c
H. pardalis								c	c	cq	c	c
H. polytaenia		c	c	c				c	c	c	c	c
H. prasina			c l									
O. brieni			+	c				c				c
O. crospedospila		cq										
O. flavoguttata									c	c		
O. hayii		c	c	+				c	+	c	c	c
O. perpusilla		c	c	+				c	c	c	c	c
P. cochranae		+						c				
A. marmorata		+	+						+	c?	+	c?
C. dispar		+	+	+					+	+	+	+
C. boraceiensis		cq	cq							cq		+q
C. eleutherodactylus										+		
C. semipalmatus		c	c	+					+	c	c	c
E. binotatus		+	+						+	+		+
E. guentheri		+	+	+				c	+	c	c	c
E. parvus		+	+					+	+	c	c	c
E. randorum		c	c	c				c	c	c	c	c
H. luederwaldti			+									
H. asperus		+rg	c					+	c	c		c
H. phyllodes		c	c					c	c	c	c	c
L. flavopictus										+		
L. ocellatus		c	+									c
P. cuvieri		c	cq									c
P. franciscae		c	+				+	c		+	+	c
P. maculiventris								c	+	+	+	
P. olfersi										c		c
P. melanopogon		+	+							+		
T. miliaris		+	+							+q		+

Table 3. Species occurrences within macrohabitats at Boracéia (c = common, p = patchy, r = rare;* 1 rock walls;* 2 lake;* 3 males in open, females largely in forest).

Species	Forest Only	Forest & Open	Forest = Open	Open & Forest	Open Only
B. nodoterga	p				
B. crucifer			c		
B. ictericus			c* 3		
D. brevipollicatus	p				
C. eurygnatha	c				
C. uranoscopa	p				
F. fissilis	p				
F. ohausi		c			
H. albofrenata	c				
H. albopunctata					p*2
H. albosignata	r				
H. astartea	c				
H. circumdata			c?		
H. faber				c	
H. hylax		c			
H. leucopygia	c				
H. microps					c
H. minuta					c
H. multilineata				c	
H. pardalis					c
H. polytaenia				c	
H. prasina					p
H. senicula					r
O. brieni			p		
O. crospedospila					p
O. flavoguttata			p		
O. hayii				c	
O. obtriangulata		p			
O. perpusilla		c			
O. x-signata	?	?	?	?	?
O. langsdorffii	?	?	?	?	?
P. appendiculata	p				
P. cochranae	p				
S. orophilus					c*2
A. marmorata			c		
C. aurita	?	?	?	?	?
C. dispar		c			
C. gaudichaudii	?	?	?	?	?
C. boraceiensis				c*1	
C. eleutherodactylus	p				
C. semipalmatus	c				
E. binotatus	c				
E. guentheri		c			
E. hoehnei	r				
E. nigrovittatus	r				
E. parvus	c				
E. randorum		c			
E. spanios			r		
H. luederwaldti	r				

Table 3. *(Continuation).*

Species	Forest Only	Forest & Open	Forest = Open	Open & Forest	Open Only
H. asperus	c				
H. phyllodes		c			
L. flavopictus			r		
L. fuscus					p
L. ocellatus					c
M. goeldii	r				
P. gaigeae	p				
P. cuvieri					c
P. franciscae		c			
P. maculiventris	c				
P. olfersi				c	
P. boiei			r		
P. melanopogon	c				
T. miliaris				c*1	
M. microps	?	?	?	?	?
				7	
Total	23	9	8		11

one is or both are too rare or poorly known to say anything about their ecology (e.g., *Centrolenella, Crossodactylus, Proceratophrys).* At least a few pairs of related species appear to differ in microhabitat: *Hylodes phyllodes* occurs along small streams, *H. asperus* along larger streams; *Cycloramphus semipalmatus* occurs along small streams, *C. boraceiensis* on larger wet rock exposures and the more distantly related *C. eleutherodactylus* on the forest floor away from streams; of the two *Fritziana* species, *F. ohausi* is restricted to bamboo and possibly tree holes, *F. fissilis* is not; *Hyla astartea* lives in bromeliads above the ground and *H. hylax* closer to the ground; all four *Physalaemus* species breed in small, shallow puddles — *P. cuvieri* in the open, *P. olfersi* usually on the forest edge, and the closely related *P. franciscae* and *maculiventris* in the forest itself. Further work will undoubtedly show diffrences among at least some of the other pairs. Microhabitat distribution is discussed further in the section on guilds.

Food

Because there is usually a correlation between a frog's size and the size of its prey (e.g., Toft, 1985), it is relevant to look for patterns of size differences among the Boracéia frogs. There are several species pairs with apparently similar spatial distributions where there is a major difference in size - the two *Bufo, Hyla polytaenia* and *multilineata, Leptodactylus ocellatus* and *fuscus, Hyla pardalis* and *faber.* In these pairs, the adult size differences are so pronounced that little overlap in prey size would be expected. Alternatively, the size differences between the species pairs *Centronella eurygnatha - uranoscopa* and *Physalaemus franciscae - maculiventris,* which have similar spatial distributions, would be expected to have broad overlap in the size of prey.

Undifferentiated Species Pairs

There are three species pairs for which no differences in time of activity, habitat, or size have been recognized — *Centrolenella eurygnatha - uranoscopa, Hyla albofrenata - leucopygia,* and *Physalaemus franciscae - maculiventris.* Within the genus *Eleutherodactylus* there are differences in size and in microhabitat among the species but there are also species pairs in which no differences are now recognized, perhaps due to small sample sizes (e.g., *E. randorum - spanios*).

Factors involved in Resource Partitioning

Toft (1985) argues that in amphibian and reptile assemblages resource partitioning may result from competition, predation and/or some physical/physiological factor or factors. She concludes that an assemblage is rarely structured by a single factor but usually by several interacting factors. Our review of the differences among the frogs at Boracéia (see Table 4) does not allow us to identify with certainty the factors that structure the assemblage and determine how resources are divided. However, based as much on perception as on data, we agree with her conclusion that a single factor explanation is probably inadequate.

The phenomena that we observe suggest that there is a pattern in the kinds of ecological changes that have occurred within species of similar morphologies that have resulted in resource partitioning. Among the species at Boracéia, close relatives frequently differ in microhabitat but seldom in gross habitat differences. Sometimes close relatives differ in size but seldom if ever in the time of day in which they are active. There is also a pattern in the ecological differences that seem to be evolutionarily conservative (e.g., retained by all members of a genus). Major habitat type seems evolutionarily conservative as does guild membership (see section following). Close relatives tend to live the same kinds of lives but do so in slightly different parts of the habitat so that they are spatially separated.

GUILD STRUCTURE

Studies focussing on ecologically similar species sets in frog assemblages, such as those of Toft (1981 and others cited therein), are not common, although there is a large literature dealing with guilds of birds and mammals (e.g., see entries under "guilds" in the subject index of Strong et al., 1984). Anuran studies have examined only portions of frog assemblages, either studying only the tadpoles (e.g., Morin, 1983), adults (e.g., Duellman's 1978 discussion), or a subset of the adult assemblage (e.g., Toft, 1981). Our attempt to group ecologically similar species is preliminary, because the available data are incomplete. However, even this preliminary attempt leads to some speculations that would not have been arrived at otherwise.

We have been unable to find a broad classification of adult frog guilds, although there is a largely complete classification of larval frog guilds (e.g., Wassersug and Heyer, 1988). Therefore, a classification of adult frog guilds is proposed and discussed in some detail.

Adult Guilds

The classification of adult guilds (Table 5) is based on the major kinds of frog interactions with their environment (on a worldwide basis), primarily where and how they secure food. For some of the guilds with no Boracéia representatives, examples give the best explanation. *Lepidobatrachus* adults are aquatic, sit-and-wait predators that lie motionless with their eyes just protruding above the water, waiting for prey (usually other frogs) to approach close enough so that a quick feeding motion will capture the prey (Cei, 1980, and WRH, pers. obs.). Many dendrobatids and members of the *Bufo typhonius* species group belong to the ground level, actively foraging, diurnal predator guild. *Dendrobates* cf *quinquevittatus,* a member of the understory, actively foraging, dirunal predator guild, is active in bamboo in the daytime in Peru (Cocroft, pers. comm.) *Dendrobates arboreus,* of Panamanian cloud forests, is a member of the canopy level, actively foraging, diurnal predator guild (Myers, et al., 1984). Some dendrobatids are active only along streams in the daytime; we assume that at least some of these species are active foragers, although the critical observational data are available only for *Colostethus inguinalis* (Wells, 1980). At least some *Phyllomedusa* species with opposable thumbs slowly search for prey at night in the forest understory (Cocroft, pers. comm.).

The proposed classification includes only what are believed to be actual interactions of organisms with the environment and does not

Table 4. Differences between related species. O = not different, X = different; (1) = possible difference, (2) = probable difference, ? = data unavailable.

Species	Time	Macrohabitat	Microhabitat	Size
B. crucifer *B. ictericus*	0	0	0	X
C. eurygnatha *C. uranoscopa*	0	0	X(1)	X
F. fissilis *F. ohausi*	0	0	X(2)	0
H. albofrenata *H. leucopygia*	0	0	0	0
H. faber *H. pardalis*	0	0	?	X
H. astartea *H. hylax*	0	0	X	X
H. multilineata *H. polytaenia*	0	0	0	X
O. crospedospila *O. hayii*	0	0	X	X
P. appendiculata *P. cochranae*	0	0	?	0
C. dispar *C. gaudichaudii*	0	0	?	X
C. boraceiensis *C. semipalmatus*	0	X(?)	X	0
E. binotatus *E. guentheri* *E. parvus* *E. randorum*	0	0	0 / X	0 / 0 / X
H. asperus *H. phyllodes*	0	0	X	X
L. fuscus *L. ocellatus*	0	0	X	X
P. franciscae *P. maculiventris*	0	0	0	0
P. boiei *P. melanopogon*	0	0	0	X

Table 5. Adult activity-habitat-feeding specializations with Boracéia representatives.

A. Aquatic, sit-and-wait predators.

B. Fossorial predators.
Myersiella microps

C. Ground level, actively foraging, diurnal predators.

D. Understory level, actively foraging, diurnal predators.

E. Canopy level, actively foraging, diurnal predators.

F. Ground level, sit-and-wait, diurnal predators.
Brachycephalus nodoterga?
Bufo crucifer?
Bufo ictericus?
Dendrophryniscus brevipollicatus
Adenomera marmorata
Eleutherodactylus binotatus?
Eleutherodactylus guentheri?
Eleutherodactylus parvus?
Physalaemus franciscae?
Physalaemus maculiventris?
Proceratophrys melanopogon?

G. Seep or streamside, sit-and-wait, diurnal predators.
Crossodactylus dispar
Crossodactylus gaudichaudii?
Hylodes asperus
Hylodes phyllodes
Magaelosia goeldii?

H. Seep or streamside, actively foraging, diurnal predators.

I. Pond or marshside, sit-and-wait, diurnal/nocturnal predators.
Sphaenorhynchus orophilus?
Leptodactylus ocellatus

J. Ground level, sit-and-wait, nocturnal predators.
Bufo crucifer?
Bufo ictericus?
Ceratophrys aurita
Cycloramphus eleutherodactylus
Eleutherodactylus binotatus?
Eleutherodactylus guentheri?
Eleutherodactylus parvus?
Leptodactylus flavopictus
Leptodactylus fuscus
Physalaemus cuvieri?
Physalaemus franciscae?
Physalaemus maculiventris?
Physalaemus olfersi?
Proceratophrys melanopogon?
Thoropa miliaris

K. Understory level, sit-and-wait, nocturnal predators.
Centrolenella eurygnatha?
Centrolenella uranoscopa?
Hyla albopunctata?
Hyla astartea?
Hyla hylax?
Hyla microps?
Hyla minuta?
Ololygon crospedospila?
Ololygon hayii
Ololygon obtriangulata
Ololygon perpusilla
Eleutherodactylus randorum?

L. Canopy level, sit-and-wait, nocturnal predators.
Fritziana fissilis?
Fritziana ohausi
Hyla albofrenata?
Hyla albosignata?
Hyla circumdata?
Hyla leucopuygia?
Phyllomedusa appendiculata?
Phyllomedusa cochranae?

Table 5. *(Continuation).*

M. Seep or streamside, sit-and-wait, nocturnal predators.
Cycloramphus boraceiensis *Cycloramphus semipalmatus*

N. Pond or marshside, sit-and-wait, nocturnal predators.
Sphaenorhynchus orophilus?

O. Understory level, actively foraging, nocturnal predators.

include possible or potential guilds. For example, we do not know of any ground level, actively foraging, nocturnal frogs.

The recognition of guilds is an artificial partitioning of a multidimensional continuum. Our frog guild classification is based largely on tropical forest experience — guilds characteristic of other environments have undoubtedly been overlooked. Species have been assigned to the guild that best matches their major activity pattern; some species overlap into other guilds.

Assigning the Boracéia frog fauna to guilds (Table 5) immediately calls attention to our lack of critical behavioral and diet data. For many species, the only collections were of reproductively active individuals (usually calling males) and there are no data on where, when, or what the species does during non-reproductive periods. Thus, we can not even make reasonable guesses as to which particular guild the following belong to: *Hyla faber, H. multilineata, H. pardalis, H. polytaenia, H. prasina, H. senicula, Ololygon brieni, O. flavoguttata, O. x-signata, Osteocephalus langsdorffii, Eleutherodactylus hoehnei, E. nigriventris, E. spanios, Holoaden luederwaldti, Paratelmatobius gaigeae, Proceratophrys boiei.* Even for many of the Boracéia species assigned to guilds, assignment is tentative due to lack of critical data (indicated by question marks in Table 5). The most common reasons for tentative assignments are lack of dietary knowledge and lack of behavioral observations to determine how and precisely when and where individuals are feeding. For example, species such as *Eleutherodactylus guentheri* are collected along trails during the daytime. We do not know whether the specimens collected were inactive or were foraging in a sit-and-wait mode when our approach disturbed them. We also lack the data to discern whether many arboreal, sit-and-wait, nocturnal predators are feeding in the understory or the canopy level.

There is a general correlation of snout-vent length of frogs with mouth width and with size of prey (Toft, 1985). In order to examine the likelihood of prey size partitioning by species within guilds, size distributions of species within guilds containing at least 5 species are compared to the size distributions of the entire frog fauna of Boracéia (Figure 75). In order to construct the figure, the adult size ranges were taken from the species accounts sections and the number of species occurring within 2 mm size classes were plotted. Two interpretations are suggested by this analysis: (1) the understory and canopy levels do not contain large species of frogs at Boracéia; and (2) the size distributions within guilds do not appear to be random subsets from the entire Boracéia fauna; rather, the size distributions appear flatter, indicating the possibility of food size partitioning within guilds. Because of the preliminary nature of guild assignment membership, stronger conclusions or further analyses are not warranted by the data. This kind of analysis does appear to be worth pursuing as anuran ecological interactions with the envirnoment are better understood at the local level.

It is worth noting that among closely related pairs of species, both members are in the same guild.

Larval Guilds

The larval guilds as defined by Wassersug and his colleagues (Lannoo, et al., 1987; Wassersug, 1980; Wassersug and Heyer, 1983, 1988) are used with minor adjustments (Table 6). The only guilds requiring comment are the separate guilds recognized for stream larvae that either have or lack some kind of ventral adhesive disk

Table 6. Larval habitat-feeding specialization categories with Boracéia representatives. * = larval assignment based on non-Boracéia data.

A. Typical suspension-feeding pond tadpoles
   a. Puddles
      Bufo crucifer
      Bufo ictericus
      Physalaemus cuvieri
      **Physalaemus franciscae*
      **Physalaemus maculiventris*
      **Physalaemus olfersi*

   b. Intermediate sized ponds
      * *Hyla faber*
      Hyla multilineata
      Hyla pardalis
      Hyla polytaenia
      Ololygon crospedospila
      Ololygon flavoguttata
      Ololygon hayii
      Ololygon obtriangulata
      **Leptodactylus fuscus*
      **Proceratophrys boiei*
   c. Permanent or almost permanent large ponds with abundant vegetation
      Hyla albopunctata
      **Leptodactylus ocellatus*
      Sphaenorhynchus orophilus

B. Non-feeding tadpoles
   **Brachycephalus nodoterga*
   **Fritziana fissilis*
   Fritziana ohausi
   Adenomera marmorata
   **Cycloramphus eleutherodactylus*
   **Eleutherodactylus - all 7 species*
   **Holoaden luederwaldti*

C. Stream or flowing water tadpoles; no ventral disk
   **Crossodactylus dispar*
   **Crossodactylus gaudichaudii*
   **Hylodes asperus*
   Hylodes phyllodes
   Megaelosia goeldii

D. Stream or flowing water tadpoles; ventral disk

E. Subaerial tadpoles
   Cycloramphus boraceiensis
   **Cycloramphus semipalmatus*
   Thoropa miliaris

F. Stream fossorial tadpoles
   **Centrolenella eurygnatha*
   **Centrolenella uranoscopa*

Table 6. *(Continuation).*

G. Macrophagous herbivores
Hyla microps
Hyla minuta?

H. Macrophagous carnivores
Ceratophrys aurita

I. Mid-water microphagous feeding tadpoles
Phyllomedusa appendiculata

J. Funnel-mouthed surface film feeding tadpoles
Phyllomedusa cochranae

K. Arboreal - Elongate, attenuate, macrophagous feeding tadpoles

L. Arboreal - Short, stout, macrophagous feeding tadpoles

M. Arboreal - Elongate, attenuate, microphagous feeding tadpoles

N. Incertae sedis
a. Pond type larvae living in ground bromeliads
**Dendrophryniscus brevipollicatus*
Ololygon perpusilla
b. Facultative carnivore
**Leptodactylus flavopictus*

(either oral or belly). The stream larvae lacking such disks live in the water column and feed like typical pond tadpoles. Such stream larvae differ from pond larvae in having reduced lungs and an elaboration of buccal papillae. Stream larvae with disks, in contrast, attach to rocks in fast flowing water and feed by rasping the biotic mats growing on the rocks.

Most tadpoles from Boracéia belong to the typical pond larval guild. The Boracéia pond tadpoles do not all occur in ponds of the same size. We have assigned larvae to three arbitrary size-classes of ponds, recognizing that there is considerable overlap of larval occurrence among these three classes (Table 6). However, we are not aware of any overlap in larval occurrence between the two extremes.

Comparison with Frog Fauna of Santa Cecilia, Ecuador

Duellman (1978) has provided the only data set that allows comparison with Boracéia guild memberships. The Santa Cecilia, Ecuador, data are not entirely comparable with the Boracéia data but are adequate to determine whether or not guilds are represented by the frogs at Santa Cecilia.

The following three adult guilds are represented at Santa Cecilia but not at Boracéia: aquatic, sit-and-wait predators; ground level, actively foraging, diurnal predators; and seep or streamside, actively foraging, diurnal predators (this is based on the assumption that *Colostethus sauli* is an active forager rather than a sit-and-wait predator and that the *Hylodes* species are not). Conversely, the following four adult guilds are represented at Boracéia but not at Santa Cecilia: fossorial predators; seep or streamside, sit-and-wait; diurnal predeators; pond or marshside, sit-and-wait, diurnal/nocturnal predators; and seep or streamside, sit-and-wait, nocturnal predators. All other adult guilds are represented at both Boracéia and Santa Cecilia, although they are represented by different numbers of species at each site. Duellman's (1978) data

suggest that there are many more nocturnal sit-and-wait predators in the understory than in the canopy level at Santa Cecilia. The Boracéia pattern would be similar if most of the hylids that were unassignable to guild did in fact belong to the understory, sit-and-wait nocturnal predator guild. Even assuming a similar relative representation of understory versus canopy level occupation at Boracéia and Santa Cecilia, there appears to be relatively larger representation of canopy level, sit-and-wait, nocturnal predators at Santa Cecilia than at Boracéia. Whereas (presumably) some species of *Fritziana, Hyla,* and *Phyllomedusa* represent this guild at Boracéia, some species of *Hyla, Nyctimantis, Osteocephalus, Phrynohyas,* and *Phyllomedusa* occupy this guild at Santa Cecilia. Another possible difference in guild membershipe between the two sites is a large number of *Eleutherodactylus* species at Santa Cecilia, for which Duellman (1978:97) uses the following characterization: "Data...reveal that this strictly forest-inhabiting frog is active on the forest floor by day and on low vegetation at night." If this statement is valid, this pattern would be worth separating out as a distinct guild. It is unclear from Duellman's statements whether activities were observed or whether frogs were collected from the forest floor during the day and from low vegetation at night. It is likely that Duellman did not have the critical observational data, just as we do not know whether the frogs we collected during the day from the forest floor were active or inactive. It is also possible that *Eleutherodactylus* attract females for mating from low vegetation at night, but feed on the forest floor during the day.

The three guilds of arboreal tadpoles are missing from both the Boracéia (although *Fritziana fissilis* may belong to one of these guilds and the ground bromeliad inhabiting tadpoles of *Dendrophyrniscus* and *Ololygon perpusill*a are assumed to belong to a separate guild) and Santa Cecilia (*Nyctimantis rugiceps* may belong to an arboreal tadpole guild) faunas, as well as the stream or flowing water tadpole with a ventral disk. Two tadpole guilds are represented at Boracéia that are not represented at Santa Cecilia: the subaerial tadpole guild and the funnel-mouthed surface film feeding tadpole guild. In contrast, all guilds represented at Santa Cecilia also occur at Boracéia. The two guilds with the largest memberships are the same at the two sites: the typical pond tadpole guild and the non-feeding tadpole guild. The stream or flowing water tadpole lacking ventral disk guild is represented by one species at Santa Cecilia (*Colostethys sauli)*, in contrast to the five species belonging to this guild at Boracéia.

Empty Guilds - Because of Ecology or History?

The above comparison of guild membership between the Boracéia and Santa Cecilia frog faunas invites speculation as to whether the observed differences, particularly involving empty guilds, are because of habitat constraints or historical factors.

One of the differences involving guild memberships certainly involves habitat differences between the two sites. Although small forest streams do occur at Santa Cecilia and in the surrounding Amazonian lowlands, they are not as numerous, rocky, or swiftly flowing as the streams at Boracéia and other Atlantic forest areas. Because of these habitat differences, it is not surprising that Santa Cecilia lacks (1) adult seep or streamside, sit-and-wait diurnal predators, (2) adult seep or streamside, sit-and-wait nocturnal predators, (3) stream or flowing water tadpoles with ventral disks, (4) subaerial tadpoles, and has (5) only one species of stream or flowing water tadpole lacking a ventral disk.

Moderate to large ponds that have water for extended periods of time but are dry often enough to prevent successful fish colonization are relatively rare at and around Boracéia, and those that occur are man-made. This perhaps accounts for the lack of members of the aquatic adult guild at Boracéia. Pseudids, a member of this guild, have a wide geographic distribution and would be expected to occur at Boracéia if suitable habitat were available. Lack of suitable habitat does not appear to account for the lack of pseudids at Santa Cecilia, however.

Lack of suitable habitat also does not appear to explain the other missing guilds; other explanations must be sought. Three caecilian species have been collected from Santa Cecilia, none from Boracéia. As non-aquatic caecilians feed

fossorially, their presence may preclude fossorially feeding frogs. As caecilians are usually difficult to collect, their local distribution patterns are not well understood, and any competitive interactions involving caecilians must be considered speculative. The environment at Boracéia does not seem to preclude representatives of the two diurnally active predator guilds. These guilds are represented in much of the Neotropics by dendrobatids and members of the *Bufo typhonius* group. A representative of the *Bufo typhonius* group occurs in the Atlantic forests in the general region around Boracéia, but has never been collected at Boracéia. Absence of this guild at Boracéia would seem to have some sort of historical explanation. One segment of an adult guild apparently missing at Boracéia is a large-bodied, canopy level, sit-and-wait nocturnal predator. This portion of the guild is filled at Santa Cecilia by the approximately 80-90 mm snout-vent length *Osteocephalus taurinus* and approximately 110-120 mm snout-vent length *Phyllomedusa tarsius*. *Osteocephalus langsdorffii* (male from Boracéia 75 mm snout-vent length) could be the apparently missing guild member at Boracéia. Arboreal bromeliads, suitable habitats for the three guilds of arboreal tadpoles, occur at Santa Cecilia and are abundant at Boracéia. The absence of any representative of these three guilds at either site is presently inexplicable (although *Fritziana fissilis* at Boracéia may belong to one of these guilds as may *Nyctimantis rugiceps* at Santa Cecilia). Answers may be found when the arboreal water-tank faunas are better understood both from sites that have and sites that lack members of the three arboreal tadpole guilds. Finally, the swiftly flowing, rocky streams of the southern Atlantic forests seem to be exactly the same habitat that supports the stream tadpole with a ventral disk in other parts of the world. The absence of this guild from Boracéia (and the southern Atlantic Forests) is surprising and must be due to historical (phylogenetic?) accident.

Guild Diversity

Before this exercise was undertaken, we had the impression that there were more larval than adult guilds recognizable for frogs. However, in this first attempt, almost the same number of larval and adult guilds are recognized. As the guilds recognized herein are refined further, more guilds undoubtedly will be recognized, but it is also likely that about as many new adult guilds will be recognized as new larval guilds. Without more comparative data, we do not know why only nine each of thirteen larval and fifteen adult guilds are present at Boracéia.

Membership in a particular larval guild does not predict the adult guild membership, and vice versa. For example, the three members of the subaerial larval guild at Boracéia belong to two different guilds as adults. The only noteworthy exception at Boracéia is that the members of the stream or flowing water tadpole without ventral disk guild are all in the diurnal streamside/flowing water sit-and-wait insectivore/predator guild as adults. In order to understand completely the ecological interactions of frogs with the environment, guilds must be studied at both the larval and adult levels.

BREEDING RESOURCES AND PREMATING REPRODUCTIVE ISOLATING MECHANISMS

Differences in where, when, and how sympatric frogs breed can be viewed as a system of partitioning breeding resources; differences can also, and as usefully, be viewed as ways in which frogs avoid breeding with heterospecifics. In frogs, the risk of mating with a heterospecific is particulary high because most species lack elaborate, multi-step courtships, fertilization is usually external, and the pair bond is ephemeral.

Commonly, sympatric species of frogs differ in time of breeding, place of breeding, and in breeding behavior. Of special importance is the advertisement call with which the male attracts a receptive female and often interacts with rival males.

Time

Diel Differences. — A few species call during the day, especially *Hylodes asperus* and *H. phyl-*

lodes. Most species call at night, particularly in the early evening. Some species, such as *Adenomera marmorata*, begin calling in late afternoon and continue into the evening. Sometimes calling activity continues almost to dawn but the choruses for most species on most nights are greatly reduced by 2100 or 2200 h and usually are quiet by midnight.

Seasonal Differences. — Temperate zone frog assemblages may show a regular progression of species breeding at different times of year. Such a seasonal progression is less conspicuous at Boracéia and perhaps in tropical assemblages generally. Many species call persistently every night, but we have no idea whether this represents a succession of individuals or the same individuals night after night. Our observations suggest that the conspicuous, diurnal and apparently territorial males of *Hylodes phyllodes* call every day from the same places whereas individual hylids that call from bushes at the edges of ponds spend a relatively short time at the calling sites.

Calling is more vigorous on warm, wet nights than on cold, dry nights, with more individuals calling, fewer pauses in the chorus, and calling continuing longer into the evening and resuming more quickly after disturbance. Indeed, calling is more active during the warmer, wetter months than during the cooler, drier ones (based on our personal observations; the summary data represented in Table 2, which record only presence or absence of calling, do not clearly reflect this pattern.

A few species are explosive breeders, such as the forest *Physalaemus* that call from puddles after heavy rains. The forest *Ololygon brieni* and *O. flavoguttata* breed in second-growth ponds or ponds in the open surrounded at least in part by bushes and are heard only in occasional, explosive choruses. These four species, although explosive breeders, have relatively quiet calls compared with the very loud calls of such explosive breeders as *Rhinophrynus* and *Scaphiopus* that breed in very open ponds in other parts of the world.

Some of the species for which we lack breeding information may be winter or very early spring breeders, e.g., *Ololygon obtriangulata*, the *Phyllomedusa* species, and *Proceratophrys melanopogon*.

Breeding Sites

There is great variety in anuran calling sites at Boracéia (Table 7). Variation exists in the selection of microhabitat (small stream versus pond) and in the calling site within the microhabitat (rock at the edge of the stream versus a leaf overhanging the stream).

Closely related species often differ in the breeding microhabitat (*Hylodes asperus* on larger streams, *H. phyllodes* on small streams) or in call site (*Hyla hylax* in holes or bromeliads close to the ground, *H. astartea* in bromeliads a meter or two above the ground). Even for species that generally differ with respect to microhabitat and call site, such as *Hyla astartea* and *hylax*, there is enough overlap that some individuals call from sites that are more typical of the other.

Species often seem clumped more than habitat irregularities can explain. Within an extensive marsh, groups of *Hyla minuta* are often segregated from other groups by areas that appear identical to the calling areas. Perhaps there are unrecognized habitat differences between sites, but these choruses may be true leks where males have gathered to display (call) and females come to select a mate.

Advertisement Displays

The most conspicuous displays given by the frogs of Boracéia are their advertisement calls. At least one species, *Hylodes asperus*, also has a visual display that appears to be used in an advertisement context. Efforts were made to record and collect representatives of all of the frogs heard calling; however, we still lack recordings of the calls for some of the species at Boracéia (results summarized in Table 8). Some rare species were encountered when not breeding or when no tape recorder was available. The *Crossodactylus* and *Megaelosia* species are suspected of being voiceless.

Though many frog species occur at Boracéia and there is little seasonal variation separating their breeding, they breed in a great variety of places so that only a few species call at any given place and time. It was common in an evening's walk around the Boracéia field station to hear 15-20 species calling. The maximum

Table 7. List of breeding habitats.

1. Forest, away from streams
   a. Leaf litter - *Brachycephalus nodoterga* (?), *Adenomera marmorata* (in holes), *Eleutherodactylus guentheri* (?), *E. parvus* (?), *E. binotatus* (?), *Cycloramphus eleutherodactylus* (?), *Holoaden luederwaldti* (?)
   b. Bromeliads - *Eleutherodactylus randorum* (eggs in moss), *Ololygon perpusilla*
   c. Bamboo - *Fritziana ohausi*
   d. Temporary puddles - *Physalaemus franciscae, P. masculiventris*
2. Forests, along streams
   a. Muddy seeps - *Crossodactylus gaudichaudii* (no call?)
   b. Water over rocks - *Cycloramphus semipalmatus*
   c. Small streams
      (1) banks under rocks, in holes - *Hyla hylax*
      (2) terrestrial bromeliads - *Hyla hylax*
      (3) bromeliads 1-2 m up - *Hyla astartea*
      (4) overhanging leaves - *Centrolenella eurygnatha, C. uranoscopa*
      (5) rocks and bank (smaller streams) - *Crossodactylus, Hylodes phyllodes*
      rocks and bank (larger streams) - *Hylodes asperus*
      (6) canopy above stream - *Hyla albofrenata, H. leucopygia*
   d. River
      (1) rocks - *Thoropa miliaris, Hylodes asperus, Megaelosia goeldii*
      (2) sand banks - *Bufo ictericus*
      (3) adjacent bushes - *Ololygon hayii*
3. Pasture pond, at forest edge
   a. Low bushes, emergent grass - *Hyla minuta, H. microps, H. polytaenia, H. multilineata*
   b. Larger bushes - *Ololygon hayii*
   c. On ground under vegetation - *Physalaemus olfersi*
4. Pasture stream
   a. On bank - *Leptodactylus ocellatus*
   b. Adjacent bushes - *Ololygon brieni, O. flavoguttata*
5. Pasture puddles - *Hyla pardalis*
6. Road puddles - *Bufo crucifer, B. ictericus, Physalaemus cuvieri*
7. Lago do Aterro
   a. Bushes - *Hyla faber, H. polytaenia, Ololygon crospedospila, O. hayii*
   b. Ground - *Bufo ictericus, Hyla faber, H. pardalis, Leptodactylus ocellatus*
   c. Emergent vegetation - *Hyla albopunctata, H. minuta, H. prasina*
   d. Floating vegetation - *Sphaenorhynchus orophilus*
8. Young second growth on ground under dense tall grass - *Proceratophrys boiei*
9. Quarry
   a. Ground - *Bufo ictericus, Leptodactylus fuscus*
   b. Puddles - *Hyla faber, H. pardalis, Physalaemus cuvieri*
   c. Bushes - *Ololygon crospedospila, O. hayii*
   d. Flooded grass - *Hyla polytaenia, H. minuta, H. prasina*(?)
   e. Wet rock walls - *Thoropa miliaris, Cycloramphus boraceiensis*
   f. Water, under vegetation - *Hyla pardalis, Physalaemus curvieri*
10. Unknown - *Dendrophryniscus brevipollitacus, Fritziana fissilis, Hyla circumdata, Paratelmatobius gaigeae, Proceratophrys melanopogon, Myersiella microps*

Table 8. Calls of Boracéia Frogs - Condensed Data

Species	Call duration (s)	Notes /call	Notes /sec	Pulses /note	Pulses /sec	Carrier Freq. (Hz)	FM	Male SVL (mm)
B. crucifer	4-7	60-150	11.5-15.5	4-7	130-170	1.2-1.4	no	68
B. ictericus	4-20	40-180	8.5-9	1-3	65-85	0.5-0.7	up	128
C. eurygnatha	0.12-0.4	1-3	8.0-12.0	3-12	25-70	4.5-4.7	up	20
C. uranoscopa	0.04-0.1	1-5	0.9-3.2	2-3	80-100	4.4-4.6	var	21
F. ohausi	0.65-0.9	5-6	5.0-6.0	5-7	150-200	2.4-2.6	up	28
H. albofrenata	0.04-0.06	1	0.7-1.7	2-3	40-60	2.3-2.5	dn	39
H. albopunctata-A	0.4-0.7	1	-	4-6	100-200	0.9-1.1	no	58
-B	0.4-0.7	6-20	16.5-28.0	50-60	100-200	0.9-1.1	no	
H. astartea	0.35-0.95	4-9	9.1-16.7	1-20	100-350	1.4-1.7	var	40
H. faber	0.1-0.12	1	1.0-1.6	2-3	70-115	0.2-0.4	dn	99
H. hylax	0.5-1.00	5-10	~10	1-12	100-175	1.1-1.4	no	58
H. leucopygia	0.08-0.15	1	1.0-3.0	-	-	2.2-2.4	var	41
H. microps-A-1	0.3-1.3	1	-	40-60	70-90	4.8-5.2	no	23
-2	-	0-3	1.8-1.9	4-8	70-140	4.8-5.2	no	
-B	0.5-0.6	25-30	44-45	25-35	45-55	4.8-5.2	no	
H. minuta-A-1	0.3-1.0	1	-	20-25	160-180	5.8-6.0	var	20
-2	-	0-2	2-3	6-8	160-180	5.8-6.0	no	
H. multilineata-A	0.07-0.45	1-2	3-4	8-11	100-200	1.4-1.6	no	43
-B-1	0.7-1.05	1	-	6-10	200-250	1.4-1.6	no	
-2	-	9-14	16-33	1	-	1.4-1.6	no	
H. pardalis-A	0.15-0.35	1	-	10-20	55-170	0.6-1.0	no	64
H. polytaenia-A-1	1.0-1.5	1-4	3-5	5-15	150-250	5.2-6.2	var	30
-2	-	4-13	6-20	1	-	5.2-6.2	var	
O. crospedospila	0.25-0.32	5-7	22-33	7-16	425-470	1.2-1.4	no	31
O.hayii-A	0.2-0.26	15-20	60-70	3-4	350-380	1.2-1.4	up	42
-B	0.05-0.18	1-2	10-12	3-5	300-500	1.2-1.4	var	
O. perpusilla	0.25-0.4	4-5	11-15	4-10	180-290	4.7-5.0	no	17
S. orophilus-A	0.3-1.8	2-10	4-7	2-4	~200	2.3-2.6	no	30
-B	0.25	20-25	130-150	20-25	130-154	2.3-2.6	no	
A. marmorata	0.04-0.07	1	0.8-1.4	1	-	4.6-4.8	up	19
C. boraceiensis	0.04-0.06	1	-	15-18	400-400	1.8-2.0	no	43
C. semipalmatus	0.02-0.04	1	-	4-7	~240	0.8-0.9	no	41
E. guentheri	0.4-0.65	7-10	15-17	1-2	80-100	2.5-3.0	up	25
E. parvus	0.4-0.5	20-25	54-60	2	110-120	2.8-3.0	up	14
E. randorum	2-5	3-8	1.3-2.6	3-8	280-280	4.2-4.4	no	14
H. phyllodes	1.05-2.1	12-20	9-11	2-6	200-250	4.8-5.2	up	29
L. fuscus	0.1-0.13	1	-	1	-	1.3-1.5	up	45
P. cuvieri	0.25-0.35	1	-	1	-	0.6-0.7	dn	28
P. franciscae	0.5-0.7	22-28	~50	2-4	~250	1.1-1.2	wrbl	26
P. maculiventris	0.2-0.75	1	0.5-1.4	25-30	135-200	1.7-2.1	no	20
P. olfersi	3.5-4.0	1	-	700-900	200-225	1.7-2.0	wrbl	32
P. boiei	0.7-0.8	30-35	~45	-	-	1.5-1.7	up	58
T. miliaris	0.2-0.3	3-4	10-20	6-10	150-200	0.5-0.6	no	61

diversity encountered was at the small ponds at the forest edge, and even here it was rare for more than 6-8 species to be calling together (Table 9). However, from one of these ponds it was often possible to hear several other species calling inside the forest and perhaps one or two more from more open sites. The largest breeding site studied was the "Lago do Aterro", which had one of the largest complements of calling species. Even there, different species tended to concentrate in different parts of the interconnected pond system. The other locality with a large number of species concentrated in a small area was the quarry, probably because of the proximity of quite different microhabitats. Despite the spatial separations among species at Boracéia, different habitats are juxtaposed so that most species must at least occasionally be able to hear the calls of most of the other species.

Table 9. Frogs of Boracéia heard calling synchronously.

	Nov 1983		Boracéia Field Station - Dec 1962			
Species	Lago	Quarry	Edge Pond	Forest Stream	Forest	Open Habitat
B. crucifer		X				X
B. ictericus		X				X
C. eurygnatha				X		
C. uranoscopa				X		
F. ohausi					X?	
H. albofrenata					X	
H. albopunctata	X					
H. astartea				X		
H. faber	X					
H. hylax				X		
H. leucopygia					X	
H. microps			X			
H. minuta	X	X	X			
H. multilineata			X			
H. pardalis	X	X				
H. polytaenia	X	X	X			
O. crospedospila	X	X				
O. hayii	X	X	X			
O. perpusilla					X	
S. orophilus	X					
A. marmorata					X	X
C. boraceiensis		X				
C. semipalmatus				X		
E. binotatus					X?	
E. guentheri					X	
E. parvus					X	
E. randorum					X	
L. fuscus		X				
L. ocellatus	X					X
P. cuvieri	X	X				X
P. franciscae					X	
P. maculiventris					X	
P. olfersi		X	X			
P. boiei	X					

Differences Between Species. — No species at Boracéia have calls that are identical or even similar enough to be confused even when only one is heard, with the possible exception of *Cycloramphus boraceiensis* and *C. semipalmatus* (see also Table 10). Based on available data, there are no species pairs that can be separated on morphology but not on call. Additional data may provide a possible exception to this general rule. *Hyla circumdata* has been collected several times but no call has been recorded. It is possible that its call is being confused with that of the closely related *H. hylax*.

Several call features may enable females to select conspecific mates, including: (1) the time when calling occurs; (2) the calling site of the male, both in terms of gross habitat and precise location (Table 7); and (3) the physical characteristics of the call. As discussed below, many species possess differences between call sites and habitats, but these features overlap among several species. In contrast, there is no ambiguity in identifying calls to species on characteristics that conspecific female frogs should be able to hear, based on hearing and call discrimination in other frogs (Gerhardt, 1987). Females should be

Table 10. Diagnostic comparison of calls emphasizing closely related Boracéia frogs.

Bufo crucifer and *ictericus*

Similarities - very long, regular trill; internote intervals > notes; notes regularly partially pulsed; dominant = fundamental.

Differences -	dominant frequency	note rate	pulse rate
crucifer	960-1750	11.5-15.5	130-170
ictericus	320-850	8.5-9.0	65-85

All differences higher in smaller *B. crucifer*, but not proportionally; duration subequal such that *crucifer* has relatively more pulses per note and therefore more sidebands.

Centrolenella eurygnatha and *uranoscopa*

Similarities - high pitched, short to very short calls, note shape complex with at least two frequencies of amplitude modulation and very short rise and fall times.

Differences -	note rate	pulse rate
eurygnatha	8-12	25-70
uranoscopa	0.9-3.2	80-100

Fritziana ohausi

Short series of regular, widely spaced notes; notes pulsed, pulses short but neither start nor stop abruptly.

Hyla albofrenata and *leucopygia*

Similarities - call a single unpulsed note; several well separated, well tuned harmonics; first three harmonics with considerable energy.

Differences -	call/note length	rise time
albofrenata	0.04-0.06	abrupt
leucopygia	0.8-.15	gradual

Hyla albopunctata

Two calls; both harsh, regularly pulsed; one broken into notes and the other not; energy in first two harmonics.

Hyla astartea and *hylax*

Similarities - harsh calls; calls composed of short pulses irregularly combined into notes.

Differences -	note rate	pulse rate
astartea	9.1-16.7	100-350
hylax	~10	100-175

Though these overlap the extremes reached in every call differ so there is no ambiguity.

Table 10. *(Continuation)*

Hyla faber

Low pitched thumps, regular short notes pulsed at start with clear harmonics.

Hyla pardalis

Occasionally given short harsh call, strongly pulsed.

Hyla microps and *minuta*

Not closely related but small and with high pitched calls with primary and secondary notes (diphasic); *H. microps* also has a monophasic call.

Similarities - diphasic calls with long first notes; short secondary notes; high dominant frequency; calls/notes pulsed; both strongly amplitude modulated at a relatively low frequency.

Differences -

	note duration		pulse rate	dominant
	primary	secondary		
microps	.2-.35	.09-.1	70-140	first harmonic
minuta	.13-.16	.05-.05	160-180	second harmonic

Hyla multilineata and *H. polytaenia*

Similarities - two kinds of calls, one harsh and pulsed and the other a trill of a series of notes; length and number of notes; length of calls; decreasing pulse rate in the harsh note.

Differences -	dominant frequency	shape of pulses
multilineata	1100-2200	rise time more abrupt
polytaenia	4500-6700	rise time more gradual

Ololygon crospedospila, O. hayii and *O. perpusilla*

Similarities - calls with complex amplitude modulation (at harmonically related intervals in *hayii* and *crospedospila*); calls given at regular intervals.

Differences - *hayii* has two kinds of calls and a more complex note organization, the others only one call and simple notes.

	dominant	pulse rate	maximum call rate
crospedospila	1200-1500	425-470	1.4
hayii	1200-2800	350-380(A)	3
perpusilla	3500-5900	180-290	.3-.4

Sphaenorhynhus orophilus

Diphasic call with a long introductory note and a following series of very short clicks.

Adenomera marmorata

Call a single short unpulsed note with an abrupt start and a rising frequency, given in regular series.

Cycloramphus boraceiensis and *C. semipalmatus*

Similarities - short, single note call; infrequently given; modulated at less than 50% at a rate that is not a harmonic of the carrier, but close, about 4 times in both species, producing distinct sidebands; call begins noisily because of abrupt start.

Differences -	call duration	pulse rate
C. boraceiensis	.04-.06	400
C. semipalmatus	.02-.04	240

Eleuthrodactylus guentheri, parvus and *randorum*

Similarities - calls a series of short notes; complexly amplitude modulated at two harmonically related (or very nearly) such that successive note envelopes of complex but not identical shapes.

Table 10. *(Continuation)*

Differences -	note rate	pulse rate	tertiary rate	dominant frequency
E. guentheri	15-17 5x	80-100 5x	300-500	2000-3650
E. parvus	54-60 2x	110-120 4x	450	2400-3500
E. randorum	1.3-2.6	280	600	3800-5200

Hylodes phyllodes

A long series of similar notes evenly spaced at the start and in pairs at the end; each note high pitched and rising sharply.

Leptodactylus fuscus

Single note calls with rising frequency.

Physalaemus cuvieri, franciscae, maculiventris and *olfersi*

Similarities - all four calls with the energy concentrated in several distinct, narrowly tuned bands, harmonics or sidebands

Differences -	frequency modulation	call duration	pulse rate (harmonic)
cuvieri	strong	.25-.35	400-500
franciscae	weak warble	.5-.7	250
maculiventris	weak warble	.2-.75	135-200
olfersi	weak warble	3.5-4.0	200-225

Proceratophrys boiei

A short trill of a regular series of separated notes each of a single pulse with only four cycles of the carrier frequency.

Thoropa miliaris

A short, low pitched, noisy call given infrequently, of several complexly pulsed notes.

able to discriminate calls on the basis of the temporal characteristics of call length, note rate, pulse rate, carrier frequency, and frequency modulation (Boracéia characteristics summarized in Tables 8 and 10). Even for the *Cycloramphus boraceiensis* and *semipalmatus* pair, the acoustic partitioning is such that female frogs likely differentiate between them (Tables 8 and 10). A female of any species must be able to distinguish a call of a conspecific male not only from that of a male of a closely related species, but also from calls of all heterospecific males at Boracéia. The four call characteristics of call duration, note rate, pulse rate, and carrier frequency are compared for all species pairs to see if the ranges are completey separated, abut, or overlap. The resultant matrix indicates that most pairs are completely separate in at least one of these acoustic characteristics (Table 11). Of the 326 possible species pair comparisons, only four have abutting or overlapping characteristics in all four call parameters: *Hyla astartea - Hyla hylax, Hyla astartea - Hyla multilineata, Fritziana ohausi - Sphaenorhynchus orophilus,* and *Hyla polytaenia - Hylodes phyllodes.* Macro- and microhabitats of calling and breeding sites of the species involved in the latter three pairs are very different (Tables 3, 7), so that even if a female of one species were confused by a call of another species, she would be unlikely to hear it when and where she was searching for a male. When the summary matrix is produced for overlapping call characteriestics only, only one of these species pairs still overlaps in all four parameters analyzed: *Hyla astartea* and *Hyla multilineata,* whose calls are very different in fine structure. As there are no such comparable matrices available for other diverse frog assemblages, the generality of the level of acoustic partitioning of the Boracéia assemblage is unknown.

The degree of acoustic partitioning observed invites two observations. First, acoustic contact may cross habitat boundaries. The calls of most species are quite loud and very different calling habitats may be juxtaposed. Thus the green hylas and other forest hylids (e.g., *Hyla hylax)* could

Table 11. Number of overlapping and abutting call parameters (call duration, note rate, pulse rate, carrier frequency) for frogs of Boracéia whose calls were recorded.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
1	*B. crucifer*	0	1	1	0	1	0	1	3	0	2	0	0	1	1	1	2	1	1	1	0	0	0	0	1	0	1	0	1	0	1	1	1	0	2
2	*B. ictericus*		0	2	1	0	0	0	0	1	0	0	1	0	0	2	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	1	0	1
3	*C. eurygnatha*			0	1	0	1	1	2	2	1	1	2	1	0	2	1	1	1	3	1	1	0	0	1	1	0	1	1	1	0	1	0	1	2
4	*C. uranoscopa*				0	0	2	1	1	3	1	2	2	1	0	1	0	0	0	0	0	3	1	1	1	0	2	0	1	0	0	1	0	0	0
5	*F. ohausi*					0	1	2	2	0	2	1	1	2	2	1	1	0	0	1	4	0	0	0	2	0	0	1	0	0	1	2	1	1	1
6	*H. albofrenata*						0	0	0	1	0	2	0	0	0	1	0	0	0	0	1	2	1	1	1	0	1	0	0	0	0	1	0	1	0
7	*H. albopunctata*							0	3	1	3	0	1	2	3	2	2	1	0	2	2	0	0	1	3	2	0	1	0	0	2	2	1	1	2
8	*H. astartea*								0	1	4	0	1	2	4	2	2	1	2	3	2	0	0	1	3	2	1	2	1	1	2	3	2	2	2
9	*H. faber*									0	1	2	1	0	0	1	0	0	0	0	0	1	0	0	1	1	1	0	1	0	0	1	0	0	0
10	*H. hylax*										0	0	1	2	2	1	3	1	1	0	1	0	0	0	2	2	0	1	1	0	2	2	0	1	2
11	*H. leucopygia*											0	1	1	0	1	0	0	0	0	1	2	0	0	0	0	1	0	1	0	0	1	0	0	0
12	*H. microps*												0	1	1	2	2	1	0	2	1	1	0	0	2	1	1	2	0	1	1	1	0	1	1
13	*H. minuta*													0	1	2	3	1	0	2	1	0	0	0	1	1	1	0	0	1	1	2	0	1	2
14	*H. multilineata*														0	0	3	2	1	1	2	0	0	1	1	0	0	2	1	0	2	2	1	2	2
15	*H. pardalis*															0	1	1	1	1	1	0	1	2	1	1	0	0	1	3	0	3	1	0	3
16	*H. polytaenia*																0	1	0	2	2	0	0	1	1	0	0	4	0	0	1	1	1	0	2
17	*O. crospedospila*																	0	2	1	1	0	0	0	0	0	0	0	1	1	1	1	0	0	1
18	*O. hayii*																		0	1	0	0	0	0	0	1	0	0	1	1	1	1	0	0	1
19	*O. perpusilla*																			0	2	1	0	1	2	1	1	3	0	1	1	2	1	0	3
20	*S. orophilus*																				0	0	0	0	2	1	0	2	0	1	1	2	1	1	2
21	*A. marmorata*																					0	1	1	0	0	1	1	0	0	0	1	0	0	0
22	*C. boraceiensis*																						0	2	0	0	0	0	1	1	0	2	2	0	0
23	*C. semipalmatus*																							0	0	0	0	1	1	1	0	1	1	0	0
24	*E. guentheri*																								0	2	0	0	0	0	1	1	0	0	1
25	*E. parvus*																									0	0	0	0	0	1	1	0	0	0
26	*E. randorum*																										0	1	0	0	0	1	1	0	0
27	*H. phyllodes*																											0	0	0	1	1	1	0	2
28	*L. fuscus*																												0	2	0	1	1	1	0
29	*P. cuvieri*																													0	0	2	1	0	2
30	*P. franciscae*																														0	1	0	1	0
31	*P. maculiventris*																															0	3	2	2
32	*P. olfersi*																																0	1	1
33	*P. boiei*																																	0	0
34	*T. miliaris*																																		0

be in the same acoustic environment not only with conspecific males and males of other forest hylas but also with such forest edge breeders as *Hyla minuta, Hyla microps, Ololygon hayii,* and *Physalaemus olfersi*. However, at the other extreme, *Fritziana ohausi* calling from forest bamboo likely never hears *Sphaenorhynchus orophilus* calling from the water at Lago do Aterro. A second observation derives in part from the first. One might expect calls of sympatric, closely related species to differ to minimize the risk of mating with a heterospecific. However, the degree of acoustic partitioning evidenced by the Boracéia assemblage suggests that there may be evolutionary divergence of call parameters in response to the total sound environment, including all other frogs in acoustic contact.

We have been discussing calls from the point of view of species discrimination. There seems little question that this is important but other factors also infuence the kind of calls that frogs may make. These factors, which are discussed in turn, include size of the caller, characteristics of the physical environment, interference of other calling species, and social factors.

Size and Call. — A widely reported generalization concerning anuran vocalization is that bigger frogs generally have lower pitched calls (e.g., Duellman and Pyles, 1983). In the frogs of Boracéia, this is seen as a linear relationship if the logs of dominant frequency and SVL are compared (Figure 76). However, there are several species that do not fall as close to the line as the others. As Ryan (1985) pointed out, *Physalaemus* have lower pitched calls than would be expected for their small size, and this is true for 3 of the 4 Boracéia *Physalaemus*. Ryan (1985) has shown that in *Physalaemus pustulosus*, females prefer males with low pitched calls. He suggests that this may be widespread in the genus and that the sexual selection generated by female choice may explain the low frequency calls in *Physalaemus* generally.

One can suggest ad hoc explanations why *Hylodes phyllodes* and *Hyla polytaenia* should have high pitched calls; the former lives along fast flowing streams (see below) and the latter is sympatric with a larger, closely related species form which its call differs primarily in higher dominant frequency. We have no suggestion as to why the two small *Eleutherodactylus* have lower calls than expected.

The general relationship between male size and dominant frequency presumably is a result of the general physical relationship between these two physical parameters. Other aspects of calls may be related to size as well. Of those tested there is a weak positive relationship between size and call length ($r^2 = .36$); but no significant relation of size to note rate or pulse rate.

Interspecific Interference. — Though many frogs that call together differ in dominant frequencies, there are several cases in which the dominant frequencies overlap. There is no simple separation of species by different frequency bands. We do not have the data to determine whether or not species with similar dominant frequencies calling in the same area tend to call while the others are not calling, as Straughan (1973) has suggested for Queensland and Costa Rica assemblages and Schwartz and Wells (1983) have shown for two species of small *Hyla* in Panama. If this sort of temporal partitioning does occur, it is on a short time scale, in terms of seconds or minutes rather than hours or days.

Physical Environment. — Several authors have reviewed species calling assemblages looking for correlations between call characteristics and physical aspects of the calling environment. Duellman and Trueb (1986) offer the generalization that frogs in forest habitats tend to have softer, higher pitched and more discontinuous calls than do open habitat species. In some ways the frogs at Boracéia conform to these expectations, but in others they do not. Certainly all of the open pond breeders (whether permanent or temporary ponds) have loud voices and tend to call continuously, but some are high pitched. Some forest species such as the temporary pond breeders *Physalaemus fransiscae* and *P. maculiventris* have soft voices but they call persistently and have low frequencies for their size. On the other hand other forest species such as the three *Eleutherodactylus* species call occasionally but have loud calls. Perhaps significantly the species with quiet calls are those that breed in spatially fixed (predictable) spots that are restricted in size, like forest floor pools, seeps, and open or forest habitat rock outcrops (the *Crosso-*

dactylus that lives in these situations may be voiceless). Louder calls tend to be from larger breeding sites such as stream edges or more widely distributed forest understory bormeliads, and perhaps spatially unpredictable temporary pools in the open.

Schiøtz (1967) noted that in West Africa "A number of species occurring in pools of stagnant water in high forest have a very characteristic voice, consisting of a few soft and quiet clicks followed by a soft buzzing." As noted above, the forest puddle and rock face species have soft calls and include both buzzes and clicks, but lack the temporal pattern observed in West Africa.

Zimmerman (1983) pointed out that, at least for the Amazonian species she studied, the forest species are more likely to have a tonal call. At Boracéia there are few tonal calls, and these occur in both forest and open habitats.

Zimmerman (1983) also found that species calling in floating meadows had lower pulse rates than either forest or open species, and suggested that this was because the vegetation in floating meadows is denser than in either of the other habitats. Heyer (1971), in analyzing a frog fauna in Thailand, suggested that for microhylids there was a positive correlation between the density of the vegetation in which a species called (so that the caller was harder to find), and the dominant frequency of its call. Heyer also suggested that higher pitch made the call easier to localize. He also noted that species in which males were attracting females to a chorus had low dominant frequencies of narrow bands, whereas those in which males were attracting females to individuals had higher frequencies and wider bands. Though there are certainly differences in density of vegetation and of chorus concentrations, only in *Bufo* do we have direct observations that males actively pursue the females after they reach the chorus; their calls, as predicted, are low and narrow-banded. It is likely that in the hylids and most of the leptodactylids, females are attracted to an individual male, although perhaps initially to a chorus.

Dubois and Martens (1984) argue that the calls of the torrent species in the genus *Rana (Paa)* in Nepal have calls that are adapted to be heard above the background noise. The calls are composed of short sequences of notes separated by long periods of silence; the notes are pure, short, and have a narrow frequency band; and the notes are rhythmically separated with the sequences. The call of *Hylodes phyllodes* shows most of these characteristics, although the notes are strongly frequency swept and thus have a wide frequency band overall.

Duellman and Trueb (1986) noted that species that live along torrential streams usually have calls that are "short, impulsive, high-pitched" or are voiceless. The *Hylodes* at Boracéia fit this characterization in having high pitched calls, whereas their larger relative *Megaelosia* is probably voiceless. Further, the *Hylodes* living along the larger and noisier streams adds a conspicuous visual display to its call as do certain ranids in Southeast Asia.

The similarities of adult behavior between stream frogs from Borneo and Boracéia could be due to convergence. Foot displays have been described for two species of ranid frogs from Borneo (*Staurois parvus (= tuberilinguis)* (Harding, 1982) and *S. latopalmatus* (Davison, 1984)). Like *Hylodes asperus*, these ranids live along tropical mountain streams and display during the day. Unlike *H. asperus,* they call at night as well. Like *H. asperus,* the display involves an extension of a hind leg and a display of a distinctive color that makes the animal very conspicuous. Unlike *H. asperus,* the foot display is not given synchronously with the call and the conspicuous color is on the webbing between the toes (light blue in *S. parvus* or whitish to light grey in *S. latopalmatus)* rather than on the toe pads.

The independent evolution of visual displays in two distantly related frog lineages living at the edges of rocky mountain streams suggests that the display may be an adaptation to that habitat. Mountain streamside habitats are unusual among frog calling sites in at least two ways. First, the rushing water creates a noisy environment in which a vocal signal might be less easily heard than in most habitats. Second, a frog perched on the edge of a mountain stream has a refuge in the water into which it can easily escape from a predator attracted by its display. Visual displays are thus relatively more valuable and less risky for frogs living along mountain torrents than for frogs living in most other habitats. It would be

interesting to know if frogs living in similar habitats in other parts of the world also have similar displays.

We are struck by the overall similarity in morphology of *Hylodes asperus* from Boracéia and *Litoria nannotis* from Australia, especially the same light digit tips (see figures in S. and K. Breeden, 1982). It is not known whether *L. nannotis* uses the digit tips in a visual display.

Menzies and Tyler (1977) have shown that in Papua New Guinea, subterranean species have calls that differ from other sympatric frogs in being narrow band, below 1000 hz, and with one or more short notes of constant amplitude. There are no truly fossorial species at Boracéia except *Myersiella,* whose call is unknown to us. The only species at Boracéia known to call from below the surface is *Adenomera marmorata*, which may call from subsurface chambers. *Adenomera* has a call that is short but high pitched and strongly frequency swept from 4500 to 5400 Hz

Repertoir Complexity and Social Behavior. — One of the aspects of the calls not discussed earlier is the complexity of the calls and of the calls repertoires. Call complexity ranges from the relatively simple call of *Adenomera marmorata*, consisting of a single note repeated regularly, to the call of *Hyla polytaenia,* with two very different notes. Other *Hyla*, such as *H. microps*, have two very different calls that are both heard frequently. These differences undoubtedly relate to the ways in which the calls are used by the different species, particularly the ways in which males interact competitively. We have noted in the species accounts where this sort of complexity has been recorded.

Though the small *Hyla* (and perhaps others) probably use sound to space themselves out in a chorus, acoustic advertisement of a permanent territory is more likely in *Hylodes* and the *Eleutherodactylus* (especially *guentheri*). Other species probably defend a limited resource needed for breeding, such as *Adenomera* defending the breeding chamber, *Ololygon perpusilla* and *E. randorum* defending bromeliads, and *Fritziana ohausi* defending bamboo holes. More information on the social behavior of these species and the role calls play is needed badly.

BIOLOGICAL LACUNAE

We have attempted to provide the information needed to identify specimens collected from Boracéia. The names used herein will doubtless change and future researchers need to stay abreast of these changes. The number of recognized Boracéia frogs has increased from 50 or so species listed by Rand and Rand in the 1960's and Nelson and colleagues in the 1970's to the currently recognized 64 species, several of which were described as new in preparation for this summary. We also recognize that at least three unnamed *Eleutherodactylus* occur at Boracéia. About 25% of the names used in earlier lists have changed because of new understanding of species limits and distributions. For some species, we have used a conveniently available name; with further study, different names may well be applied to the Boracéia populations (particularly *Hyla albofrenata, H. multilineata, H. prasina, Ololygon brieni, O. perpusilla, Phyllomedusa appendiculata, Crossodactylus dispar, C. gaudichaudii, Hylodes asperus*, and *Megaelosia goeldii).* Workers also should be aware that because of the dynamic nature of the frog assemblage at Boracéia and the large number of apparently rare species, the chances are good that species not reported herein will be collected at Boracéia in the future.

Although we know a great deal about the frogs of Boracéia, there is also a great deal that we do not know. We have repeatedly noted this in the species accounts and in the discussion. Some of the aspects about which we are conspicuously ignorant are: clutch parameters (how many eggs are laid, how big they are and how they vary with female size); diets (what frogs actually eat and how they catch it); life history details and demography (e.g., how long it takes tadpoles to grow to metamorphosis, survival rates of larvae and adults, how long adults live and how often they breed); winter activity

(whether all frog species become inactive in the winter or whether there are some winter breeders); movement and dispersal patterns (how far individuals move to and from breeding sites); social behavior (how spatial patterns are maintained, how much agression there is, whether males defend calling sites and/or females and/or oviposition sites, whether either sex defends a feeding area, if there is any parenteral care); complete call repertoires (what calls are given in addition to the familiar advertisement calls, under what conditions, and with what results); and antipredator behavior (use of toxins, use of flash colors, death feigning, etc.).

In providing descriptions of the external morphologies of the frogs at Boracéia and notes on their natural histories, this monograph is intended as a base from which further work can be done — a tool to facilitate the studies which we have not had the time or the wit to complete. If our work serves this purpose, its doing will have been worthwhile.

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LIST OF SPECIMENS EXAMINED

AMNH = American Museum of Natural History, New York; MZUSP = Museu de Zoologia da Universidade de São Paulo; USNM = National Museum of Natural History, Smithsonian Institution, Washington, DC.

Brachycephalus nodoterga

MZUSP 30625-26, 30653, 57673; USNM 208682, 266187-190

Bufo crucifer

MZUSP 4161-62, 4588-92, 9928-29, 10510-14, 27397-405, 27407-16, 27814, 28779-83, 30523, 30549, 37725-26, 37768, 54424-25; USNM 208683-94, 243546-47

Bufo ictericus

MZUSP 3093, 3099, 3104-05, 3114-15, 3123, 3950, 4142, 4160, 4163-68, 4593-605, 9388-93, 9936-61, 10476-509, 16192-96, 16334-42, 21023-58, 22624-38, 28447-541, 28565-653, 30526-28, 30550-52, 54534-40, 54688-704; USNM 208695-701, 243548-49

Dendrophryniscus brevipollicatus

MZUSP 4059-60, 30562, 37786; USNM 208703-11

Centrolenella eurygnatha

MZUSP 30788-809, 37588-94, 37769-70, 37775-82; USNM 200561-63, 208712-33, 243550

Centrolenella uranoscopa
MZUSP 2952-53, 34636, 30814-17, 49647; USNM 232354

Fritziana fissilis
AMNH 103958; MZUSP 2199, 3921, 32052-62; USNM 243551-52

Fritziana ohausi
MZUSP 26522, 26525-26; 31216-46, 34582-84, 34606-11, 34616-17, 34634, 34637, 36585 (larvae); USNM 217710-21, 243553

Hyla albofrenata
MZUSP 2232, 30824, 60565-66; USNM 208734-41, 243554

Hyla albopunctata
USNM 243555-62

Hyla albosignata
MZUSP 30839

Hyla astartea
MZUSP 2452, 2820-21, 3856, 4029, 22511, 34585-87, 34592-93, 34602, 37738, 54385; USNM 208775, 208778, 243563-66

Hyla circumdata
MZUSP 2543, 2546, 3871-95, 5378, 14717, 14720, 14722-23, 30895, 30900, 30904, 31010, 34570, 34574-75, 34605, 37799-800, 54430; USNM 208745, 208748, 208750-53, 208755-56, 208758-63, 208772-74, 208783

Hyla faber
MZUSP 2341, 3371, 9963, 31007-09, 31011-17, 32100, 37724; USNM 208784-91, 243567-68

Hyla hylax
MZUSP 2357, 2535-41, 4030-31, 30875-78, 30892-94, 30901-03, 34571, 34576-80; 34588-91, 34594-601, 34603-04, 37795, 37801-03, 54499-501, 59937; USNM 208744, 208746-47, 208749, 208754, 208757, 208764-71, 208776-77, 208779-82, 243466-70, 243471-74

Hyla leucopygia
MZUSP 30834-38; USNM 208742-43

Hyla microps
MZUSP 3088, 31143-48; USNM 208792-834, 234569-75

Hyla minuta
MZUSP 2946-48, 4076-83, 10903, 26548-60, 31151-65, 34581, 37624, 37751-54, 54375; USNM 208835-52

Hyla multilineata
MZUSP 3999, 31190-92, 37718-20, 37722, 37737, 37740, 37746-47, 37774, 37792-94; USNM 208853-58

Hyla pardalis
MZUSP 1611-13, 4571, 5376, 10375, 31247-67, 37659, 54476; USNM 208859-66, 243592-600

H*yla polytaenia*
MZUSP 2225-28, 2815-16, 3437-38, 3446, 4073-74, 4574, 31397-424, 36876, 37554, 37598-609, 37629-44, 37723, 37739, 37771-73, 54494-95; USNM 208867-979, 243601-20

Hyla prasina
MZUSP 3857, 26562, 31556-60

Hyla senicula
USNM 208980

Ololygon brieni
MZUSP 451, 2828, 3515, 3926, 4021, 30846-47, 30849-63, 30848, 30864-69, 37610-15, 54427-29, 54486, 54488, 54492, 54987-91; USNM 129105, 208037, 208981-9002

Ololygon crospedospila
MZUSP 30906-07; 37670-77; 37762; USNM 209003-18, 243621-44

Ololygon flavoguttata
MZUSP 2229, 3515, 32000, 36566 (larvae); USNM 209019, 247846

Ololygon hayii
MZUSP 2179-81, 2183, 2613-24, 2627-32, 2635, 2637, 3416, 3816, 3986-89, 3991-97, 4581-86, 5377, 9930-34, 10515-17, 16197-98, 22967-71, 31046-74, 34572-73, 34612-14,

34629, 34631-32, 34638-39, 37553, 37595-97, 37645, 37756-61, 37763, 38855-56, 54376, 54378-81, 54383; USNM 209020-49, 243645-56.

Ololygon obtriangulata
MZUSP 36572 (larvae); USNM 129104, 243657-61

Ololygon perpusilla
MZUSP 474, 3090, 3121, 3125-26, 3596, 4072, 4576, 31272-81, 31396, 34630, 34633, 37796, 49646; USNM 209050-76, 243663-66

Ololygon x-signata
MZUSP 54382

Osteocephalus langsdorffii
MZUSP 10568

Phyllomedusa appendiculata
MZUSP 3998, 9387, 36559 (larvae), 37669

Phyllomedusa cochranae
MZUSP 3609, 32071-76, 36541 (larvae), 36544, 36569 (larvae); USNM field 3828, 4524

Sphaenorhynchus orophilus
MZUSP 37668; USNM 243667-72

Adenomera marmorata
MZUSP 2730-31, 2733, 2745-46, 3373, 3375, 3945, 3948, 4061-62, 4580, 10518, 24142-45, 24147, 24293-313, 26860, 36866; USNM 129175, 209077-120, 209363-69 (eggs, embryos, and larvae), 243673-74

Ceratophrys aurita
MZUSP 31374

Crossodactylus dispar
AMNH 103751-55; MZUSP 2728, 3949, 4064, 4066-69, 4141, 6474, 10905, 23571-96, 37570-72, 37791; USNM field 3841-42, 4003-04, 4334, 4374-75, 4402-08, 4477-81, 4483-87, 4652, 4667-68, 4670

Crossodactylus gaudichaudii
MZUSP 4579

Cycloramphus boraceiensis
MZUSP 2287, 3050, 3426, 3430, 3433-34, 3439-41, 3443, 3866, 3923, 3934, 4048, 4541, 16199, 23037-38, 23784-92, 37652-58; USNM 129150, 217933 (larvae), 217936-66.

Cycloramphus eleutherodactylus
AMNH 103957; MZUSP 3428-29, 3432, 22642, 22997, 23793, 36875, 37564; USNM 217897

Cycloramphus semipalmatus
AMNH 103803-08, 103799-800; MZUSP 1575, 3060, 3424-25, 3436, 23394-95, 23398-99, 23766-68, 23773-83, 37563, 37766; USNM 217918-28

Eleutherodactylus binotatus
MZUSP 2503, 3506, 3509, 3939-41, 4044, 4046-47, 22979, 22988, 22990, 23137, 23597, 23600, 23602-34, 23748, 37805, 49645, 54458-60; USNM 209121-40, 243676-77

Eleutherodactylus guentheri
MZUSP 2286, 2726-27, 4056-58, 4578, 22981, 22984-85, 22987, 22989, 23698-703, 23705-44, 23746-47, 23749-54, 34657, 37806; USNM 235630-98

Eleutherodactylus hoehnei
MZUSP 23704; USNM 209141

Eleutherodactylus nigriventris
MZUSP 23677, 37787

Eleutherodactylus parvus
MZUSP 457, 460, 4045, 4050, 4052-54, 9935, 22978, 22982, 23635-63, 23745, 25785, 25857, 37788-90, 38876; USNM 209142-214, 243681-83

Eleutherodactylus randorum
MZUSP 23665-70, 23672-76, 34635, 36865, 37555, 49644, 59936; USNM 243475-79, 244635, 247860-61

Eleutherodactylus spanios
MZUSP 23664, 23671

Holoaden leuderwaldti
MZUSP 23794

Hylodes asperus
MZUSP 1752-53, 1755, 1757, 1759, 1761, 1763-4, 1766-68, 1783-88, 1790-94, 1796-97, 1800, 1802-03, 1806-10, 1812, 1814-15, 4032-39, 23048-49, 23544, 23562-64, 23755-64, 27983, 37586-87, 37661-66, 37710-11, 37764-65, 37767, 56498; USNM 245916-17

Hylodes phyllodes
MZUSP 1700-02, 1704-06, 1708-11, 1714, 1716-21, 3308, 3527, 3529, 4040-43, 4143, 23050-53, 23561, 23678-97, 36874, 37573-85, 37678-87, 37701-03, 37712-17, 38854, 56497, 59934; USNM 129156-58, 24241 (larvae), 243480-506

Leptodactylus flavopictus
MZUSP 21240, 24098; USNM 209215

Leptodactylus fuscus
USNM 209216-22, 243684-85

Leptodactylus ocellatus
MZUSP 2084, 4496, 4569, 24513-16; USNM 209223-31

Megaelosia goeldii
MZUSP 2289 (larva), 2347, 22935, 36545 (larva), 36554 (larva)

Paratelmatobius gaigeae
AMNH 103980; MZUSP 4063, 37700; USNM 209232, USNM field 8428

Physalaemus cuvieri
MZUSP 25809-18, 25871, 36867; USNM 209233-53, 243686-710

Physalaemus franciscae
MZUSP 3947, 4084, 4114, 25831, 25853, 25856-70, 25872-82, 26036-37, 37565-68, 59935; USNM 243507-45

Physalaemus maculiventris
MZUSP 3819, 3942, 4088, 4092, 4094-95, 4097, 4100-02, 4104-05, 4107, 4111, 25825-40, 36868-73, 37569, 54384, 56808; USNM 209254-99, 241242, 243711

Physalaemus olfersi
MZUSP 3946, 25843-48; USNM 209300-03, 243712

Proceratophrys boiei
MZUSP 60670

Proceratophrys melanopogon
MZUSP 950, 3508, 3922, 4000, 9386, 23385, 23958, 31339-48, 31352, 31358, 37695-99, 37721, 57580; USNM 128147-49, 209304-17, 243713-15

Thoropa miliaris
MZUSP 2295-98, 2499-502, 2838, 2852, 3019, 3096-98, 3100-01, 3120-22, 3376, 3379-414, 3421, 3486-89, 3492, 3496, 3502-03, 3505, 3532, 4537-38, 10519, 27218-19, 27254-65, 27268-99, 37557-62, 37648-51, 37704-09, 37727-35, 49648, 54377, 56896; USNM 129163-73, 209318-58

Myersiella microps
MZUSP 36404

GLOSSARY

ADVERTISEMENT CALL. The most commonly heard call, given spontaneously by a male that is ready to breed and serving to advertise his position to females that are in serach of a mate and to other males that are potential rivals.

AMPLITUDE MODULATION. Changes in intensity or amplitude of a sound over time. If the sound is completely interrupted it is said to be 100% modulated. Frog calls are often amplitude modulated at several different levels. The levels used here, listed in order from largest to the smallest, are: call group, call, note, and pulse. These categories are arbitrary and to some extent artificial and arbitrary decisions were made as to whether the amplitude modulation in a particular call produced, for instance, pulses or notes. When the

amplitude changes over time are not simple this is seen in the wave form as pulses or notes that have complex shapes.

AUDIOSPECTROGRAM. A visual representation of a call displaying the frequency of the sound over time (also called a sonagram in the acoustic literature; sonagram is also a term used in the medical literature for something entirely different).

BANDPASS FILTER. An electronic filter which decreases the intensity of a sound above and below a specified band of frequencies.

BANDSTOP FILTER. An electronic filter which decreases the intensity of a sound within a specified band of frequencies.

BELLY. The ventral portion of the adult frog behind the chest and in front of the thighs (Figure 77).

CALCAR. A pronounced fleshy appendage on the heel.

CALL. An acoustic unit of a frog vocalization, may be broken into either identical or different notes; separated from other calls by a period longer than call; can function alone as an independent vocalization; often not temporally organized into larger units.

CALL GROUP. Calls may be organized into groups which are separated by long periods of silence; spacing of calls within a group is regular, usually uniform or changing in a predictable pattern. Call groups are usually longer than a few seconds and therefore not immediately evident in the field and too long to be seen on an audiospectrogram. They are probably more common than generally recognized.

CARRIER FREQUENCY. By analogy to the terminology used to describe radio transmission, the sound a frog produces may be considered to have a carrier frequency, usually the dominant frequency, which may be frequency or amplitude modulated.

CHEST. The area of the ventral portion of the adult frog between the arms and in back of the throat and in front of the belly (Figure 77).

DOMINANT FREQUENCY. The frequency at which most sound energy in a call is concentrated.

FINGERS. Digits of the hand (Figure 78).

FOOT LENGTH. Measured by calipers as the distance from the posteriormost portion of the inner metatarsal tubercle to the tip of the fourth toe (Figure 77).

FREQUENCY MODULATION. Changes in frequency of a sound over time.

HARMONIC. Many sounds have their energy concentrated in several separated, evenly spaced frequencies called harmonics. These frequencies are multiples of the lowest or first harmonic which is also called the fundamental.

HEAD LENGTH. Measured by calipers as the distance from the tip of the snout to the angle of the jaw (Figure 77).

HEAD WIDTH. Measured by calipers as the widest distance of the head at or anterior to the angles of the jaws.

HIGHPASS FILTER. An electronic filter which decreases the intensity of a sound above a specified frequency.

LOWPASS FILTER. An electronic filter which decreases the intensity of a sound below a specified frequency.

NOISY CALL. The sound energy is distributed across a broad band of frequencies.

NOTE. Calls are often broken into smaller subunits by 100% amplitude modulation with only short intervals between them relative to the length of the note. A call which is amplitude modulated to 100% is said to be made up of notes; one which is modulated at less than 100% is said to be pulsed.

PREPOLLEX. A vestigial digit on the inner side of the first digit of the hand. Usually the prepollex is barely indicated externally. Some species, however, have enlarged external spines, most pronounced in males, arising from the prepollex.

PULSE. The smallest named subunit of a call, produced by amplitude modulation which may be 100% but often less. A note which is modulated, to whatever depth, is said to be pulsed. A call in which the primary modulation is not 100% is said to have only one note which is pulsed.

SHANK LENGTH. Measured by calipers as the distance from one end of the tibia and covering tissues to the other. (Figure 78).

SIDEBANDS. If a call is amplitude modulated at a rate too fast for the sonagraph to resolve in the time domain, sidebands appear on either side of the central frequency separated from it by the frequency of the modulation.

SNOUT OUTLINE (DORSAL VIEW, ADULTS). The shape of the dorsal outline of the snout as compared to the standards illustrated in Figure 79. The standards originally came from the laboratory of Jay M. Savage.

SNOUT PROFILE (ADULTS). The shape of the lateral outline of the snout as compared to the standards illustrated in Figure 80. The standards originally came from the laboratory of Jay M. Savage.

SVL (SNOUT-VENT LENGTH). Distance between the tip of the snout and the vent (Figure 78).

THIGH LENGTH. Measured by calipers as the distance from mid-vent to the distal end of the femur (Figure 78).

THROAT. The ventral portion of the adult frog between the lower jaws and in front of the chest (Figure 77).

TOES. Digits of the foot (Figure 78).

TOOTH ROW FORMULA (LARVAE, FIGURE 81). The fractional system proposed by Altig (1970:181-182) is used: "A fraction designates the number and position of the rows of labial teeth; the numerator indicates the number of rows on the anterior labium, and the denominator indicates the rows on the posterior labium. ... The fraction is written in line with the rows with median gaps in parentheses. A range in the number of rows is hyphenated, and variability in the presence of a median gap is indicated by brackets."

TUNED CALL. The sound energy is concentrated in one or a few frequencies.

UNGUAL FLAP. The dorsal portion of the distal part of well developed toe disks above the circumferential groove (Figure 82).

VOCAL SACS. Vocal sacs are defined by the presence of vocal slits (openings) in the floor of the mouth of male frogs. Vocal sacs can be permanently expanded and thin walled (external) or not appearing any different from the surrounding throat or chest region (internal).

WAVEFORM. A visual representation of a call displaying the amplitude of the sound as it changes over time.

WEBBING FORMULA. The original formula proposed by Savage and Heyer (1967), modified by Myers and Duellman (1982) is used. Roman numerals represent fingers or toes (Figure 82) and arabic numerals represent the number of phalanges (and metacarpals or metatarsals, if appropriate) completely or partially free of webbing. A 0 indicates the webbing extends to the very tip of the digit, 1 indicates the disk or entire terminal segment is free of web.

Figure 1. Typical epiphyte load on forest tree at Boracéia.

Figure 2. Forest trail at Boracéia.

Figure 3. Fallen tree trunk across forest trail at Boracéia.

Figure 4. Small forest stream at Boracéia.

Figure 5. Water supply pond at edge of forest.

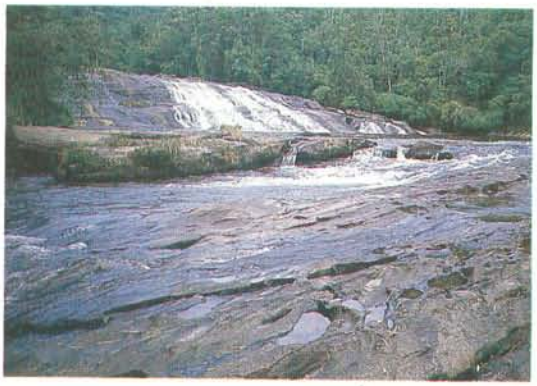

Figure 6. Rio Claro at Boracéia.

Figure 7. *Brachycephalus nodoterga*. Photograph courtesy of J.P. Bogart, University of Guelph.

Figure 8. *Centrolenella uranoscopa*. This is one of two members of the genus *Centrolenella* at Boracéia. Photograph courtesy of J. P. Bogart, University of Guelph.

Figure 9. *Fritziana fissilis*. Photograph courtesy of C. W. Myers, American Museum of Natural History.

Figure 10. *Fritziana ohausi*. Photograph courtesy of J. P. Bogart, University of Guelph.

Figure 11. *Hyla albofrenata*.

Figure 12. *Hyla albopunctata*.

Figure 13. *Hyla circumdata*. Photograph courtesy of J. P. Bogart, University of Guelph.

Figure 14. *Hyla faber*.

Figure 15. *Hyla hylax*.

Figure 16. *Hyla leucopygia*. Photograph courtesy of J. P. Bog art, University of Guelph.

Figure 17. *Hyla microps*.

Figure 18. *Hyla minuta*. Photograph courtesy of C.W. Myers, American Museum of Natural History.

Figure 19. *Hyla multilineata*. Photograph courtesy of J. P. Bogart, University of Guelph.

Figure 20. *Hyla pardalis*.

Figure 21. *Hyla polytaenia*. Photograph courtesy of J. P. Bogart, University of Guelph.

Figure 22. *Ololygon brieni*. Photograph courtesy of J. P. Bogart, University of Guelph.

Figure 23. *Ololygon crospedospila*. Photograph courtesy of J. P. Bogart, University of Guelph.

Figure 24. *Ololygon flavoguttata*.

Figure 25. *Ololygon hayii*.

Figure 26. *Phyllomedusa cochranae*. This is one of two species of *Phyllomedusa* at Boracéia that are green in life.

Figure 27. *Sphaenorhynchus orophilus*.

Figure 28. *Adenomera marmorata*. Photograph courtesy of C. W. Myers, American Museum of Natural History

Figure 29. *Crossodactylus dispar*. Photograph courtesy of C. W. Myers, American Museum of Natural History

Figure 30. *Cycloramphus eleutherodactylus*. Photograph courtesy of C. W. Myers, American Museum of Natural History

Figure 31. *Cycloramphus semipalmatus*. Photograph courtesy of C. W. Myers, American Museum of Natural History

Figure 32. *Eleutherodactylus binotatus*. Photograph courtesy of C. W. Myers, American Museum of Natural History

Figure 33. *Eleutherodactylus guentheri*. Photograph courtesy of C. W. Myers, American Museum of Natural History

Figure 34. *Eleutherodactylus parvus*. Photograph courtesy of C. W. Myers, American Museum of Natural History

Figure 35. *Eleutherodactylus randorum*.

Figure 36. *Hylodes asperus*. Photograph courtesy of C. W. Myers, American Museum of Natural History

Figure 37. *Hylodes phyllodes*. Photograph courtesy of C. W. Myers, American Museum of Natural History

Figure 38. *Leptodactylus fuscus*.

Figure 39. *Paratelmatobius gaigeae*, dorsal view. Photograph courtesy of C. W. Myers, American Museum of Natural History

Figure 40. *Paratelmatobius gaigeae*, ventral view. Photograph courtesy of C. W. Myers, American Museum of Natural History.

Figure 41. *Physalaemus cuvieri*.

Figure 42. *Physalaemus franciscae*. Photograph courtesy of J. P. Bogart, University of Guelph.

Figure 43. *Physalaemus maculiventris*.

Figure 44. *Physalaemus olfersi*. Photograph courtesy of J. P. Bogart, University of Guelph

Figure 45. *Proceratophrys boiei*. The other species of *Proceratophrys* at Boracéia, *P. melanopogon*, is superficially similar to *P. boiei*.

Figure 46. *Thoropa miliaris*.

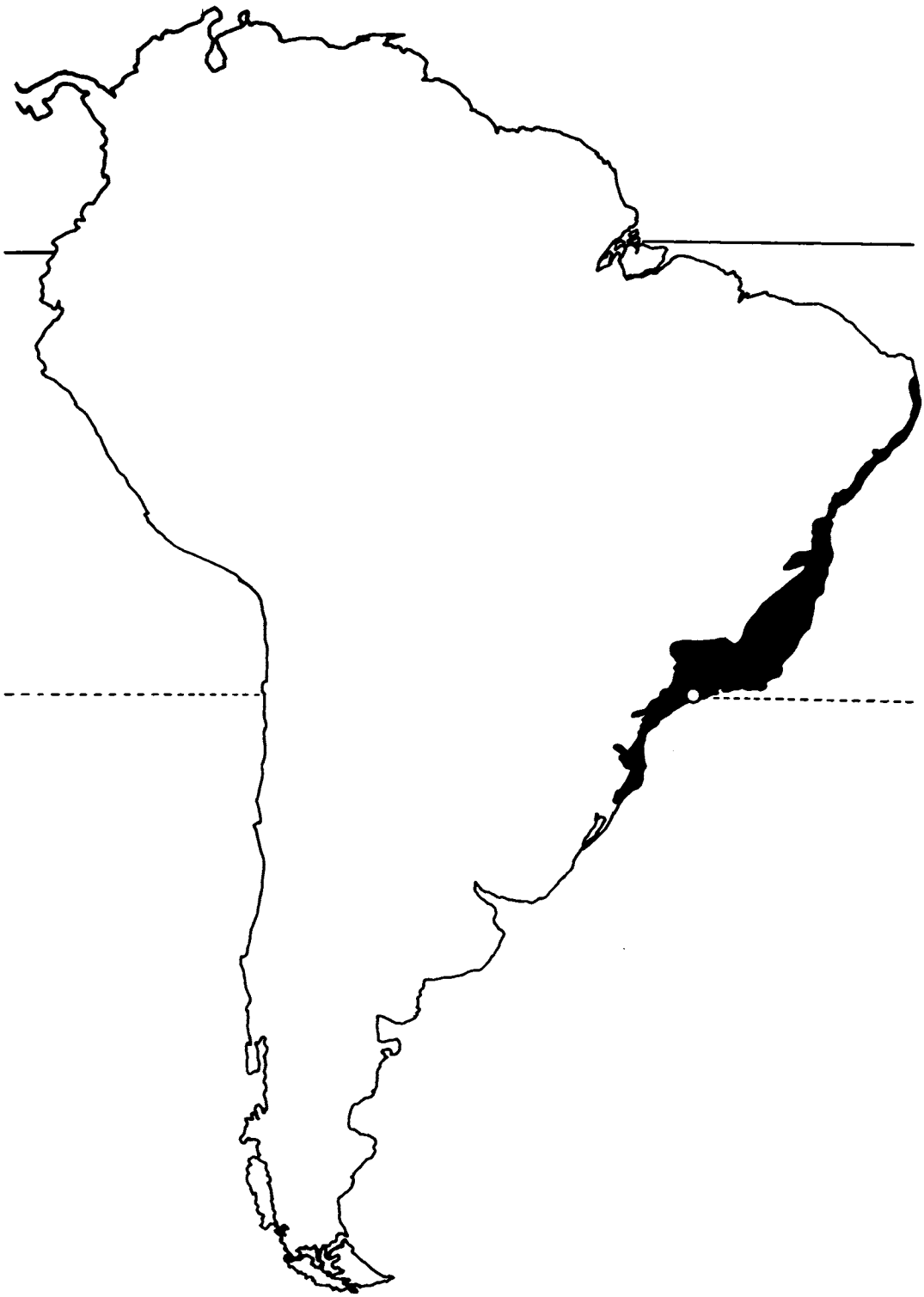

Figure 1. Map of South America, showing extent of Atlantic Forest Morphoclimatic Domain (in black) (Ab'Sáber, 1977) and the site of Boracéia (circle).

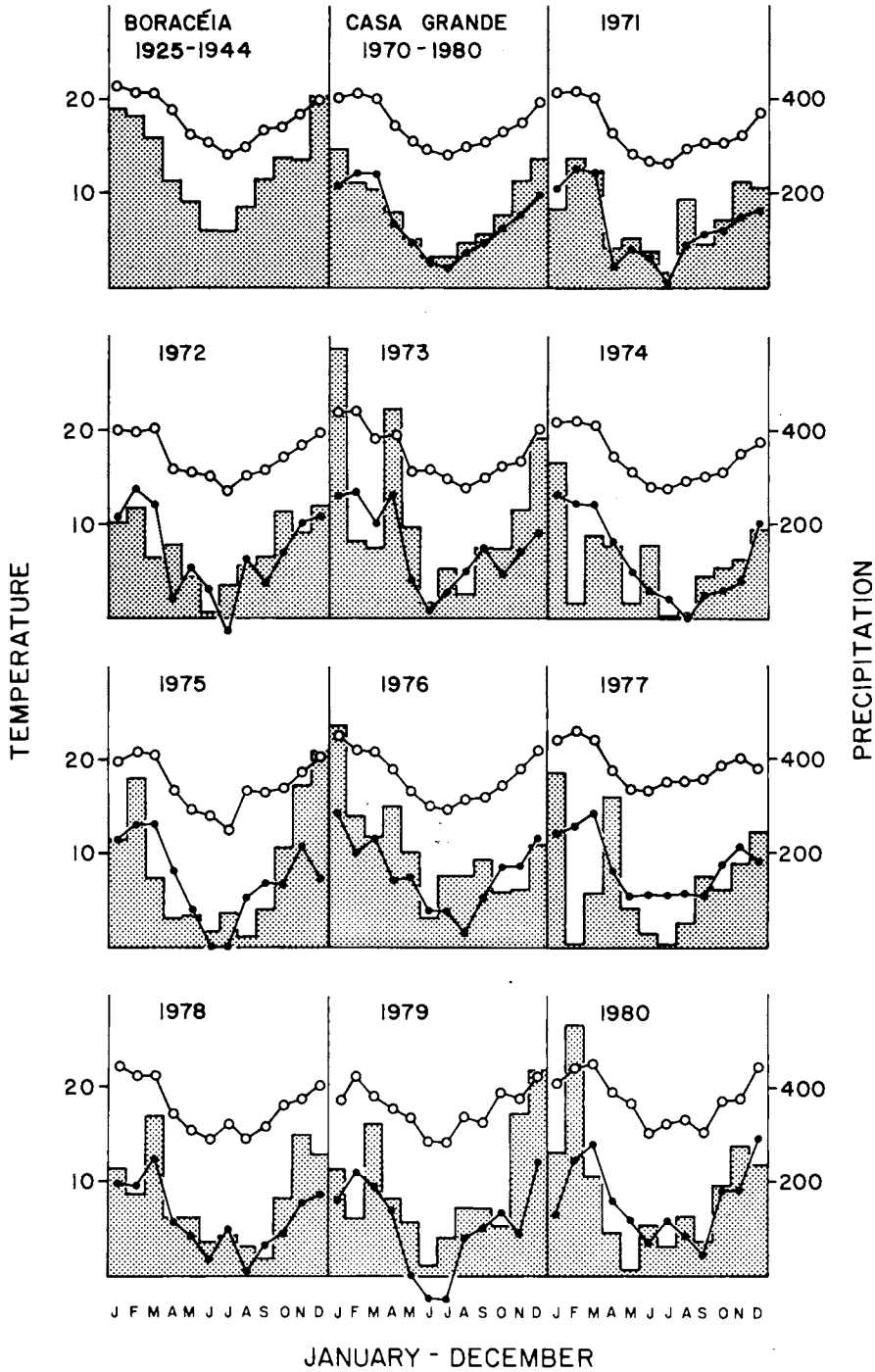

Figure 2. Climatic summaries for Boracéia and nearby Casa Grande. Average monthly temperatures indicated by connected circles. Minimum temperature within months indicated by connected dots. Monthly rainfall indicated by bar graphs. Upper left figure represents monthly averages at Boracéia for the time period 1925-1930 for temperature and 1925-1944 for rainfall (Setzer, 1946). The upper center figure is the average values at Casa Grande for 1970-1980. Note that the average temperatures of Boracéia and Casa Grande are very similar, but Boracéia gets noticeably more rainfall than Casa Grande. All other figures represent single year summaries at Casa Grande (Anonymous, 1970-1980).

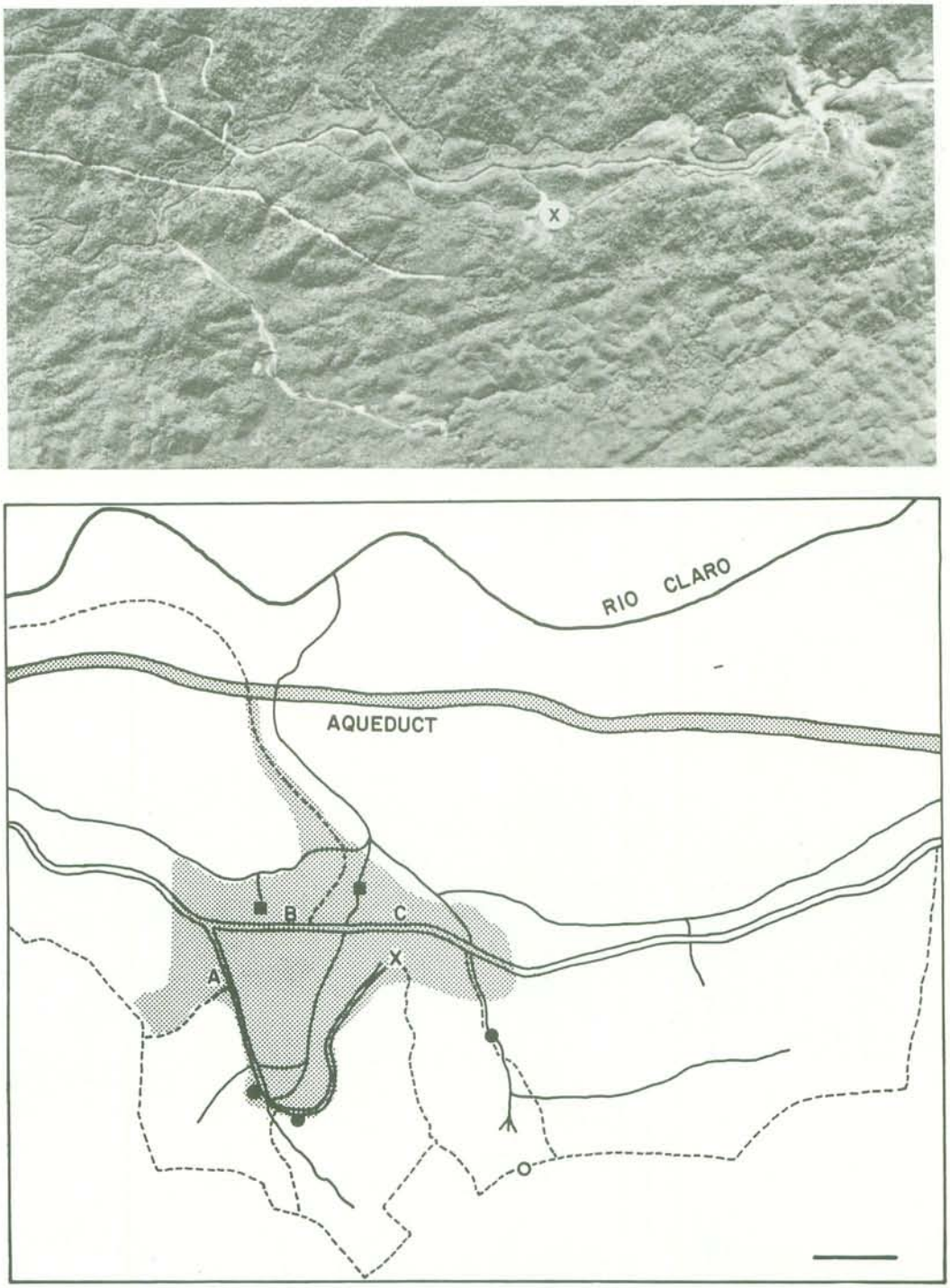

Figure 3. Aerial photograph taken in 1977 (above) and diagrammatic features (below) of Boracéia in the immediate vicinity of the scientist's house. In lower figure, rivers and streams shown as solid lines; roads shown as parallel lines; trails shown as dashed lines; extensive clearings shown by stippling; more permanent ponds (at least during wet season) shown as dots; former pond sites shown as squares; intermittent pond system shown as circle; scale (lower right corner) approximately 100 m; A and C are caretakers' houses; B is a stable, now unused. In both figures, X indicates site of scientists' house.

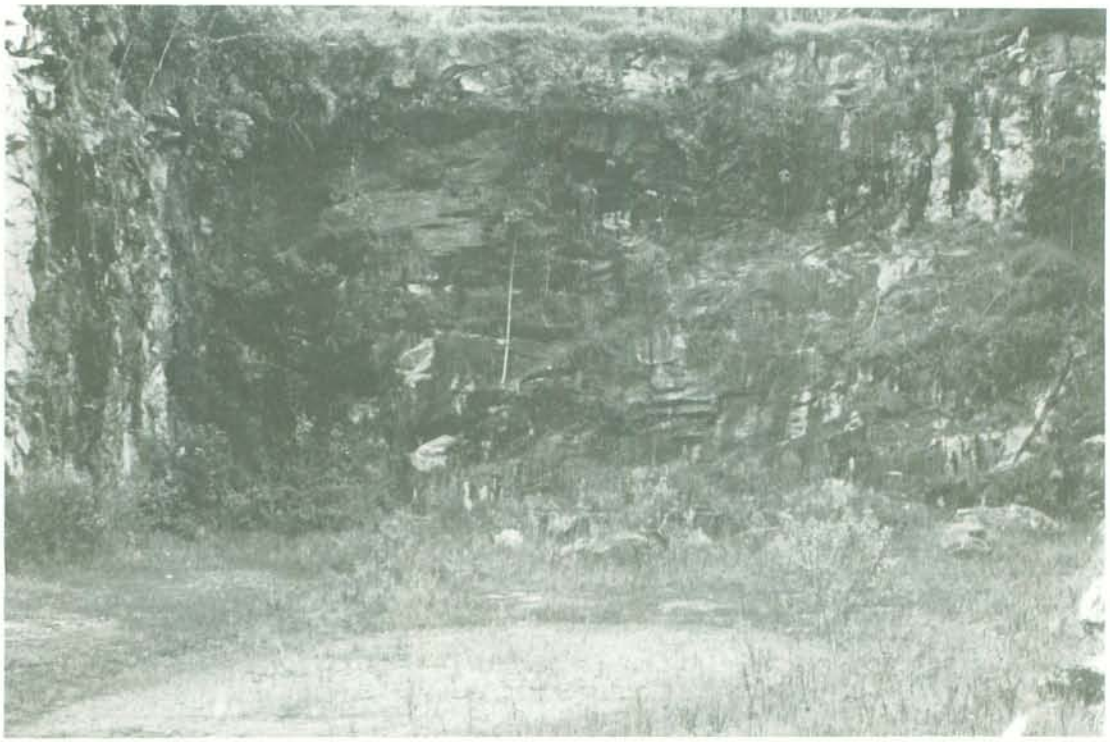

Figure 4. Photograph of quarry wall and floor. *Cycloramphus boraceiensis* and *Thoropa miliaris* adults and larvae were collected from the wall; several species of hylids and *Physalaemus* were collected from the quarry floor. The floor has streams and temporary pools.

Figure 5. Lago do Aterro. *Hyla albopunctata* and *Hyla prasina* were collected at this site.

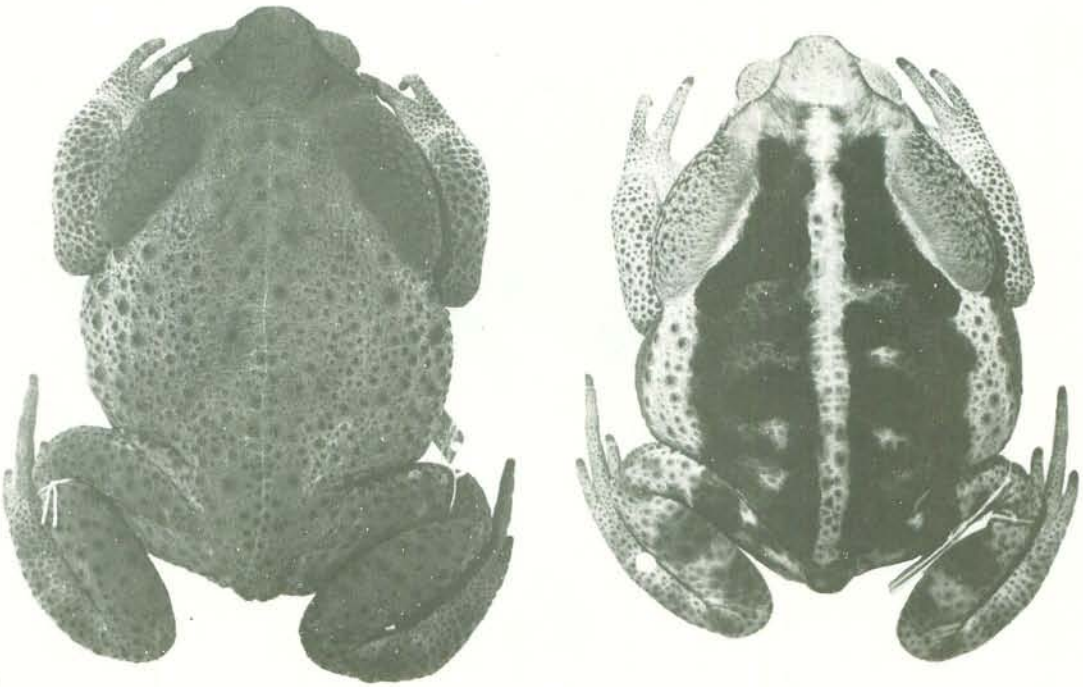

Figure 6. Male (left) and female (right) *Bufo ictericus*.

Figure 7. *Dendrophryniscus brevipollicatus*.

Figure 8. *Ololygon brieni* (left), *flavoguttata* (center), and *obtriangulata* (right); scale bars all equal 5.0 mm.

Figure 9. *Ololygon perpusilla*.

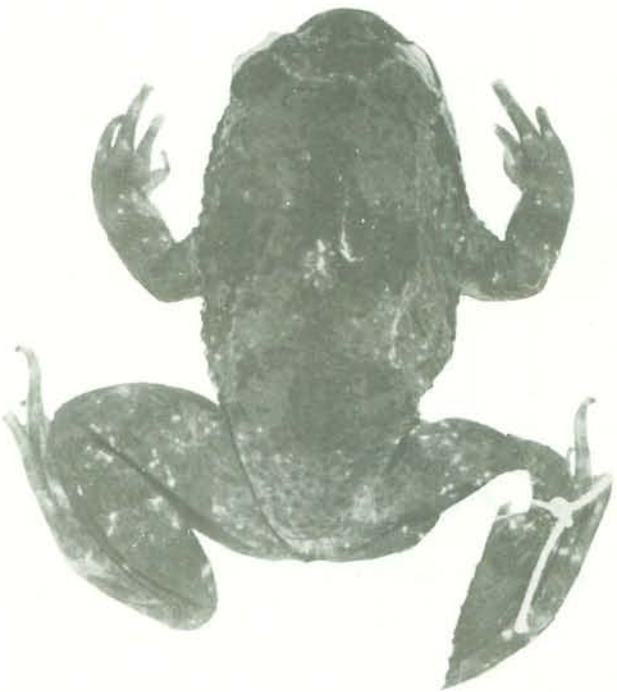

Figure 10. *Cycloramphus boraceiensis*

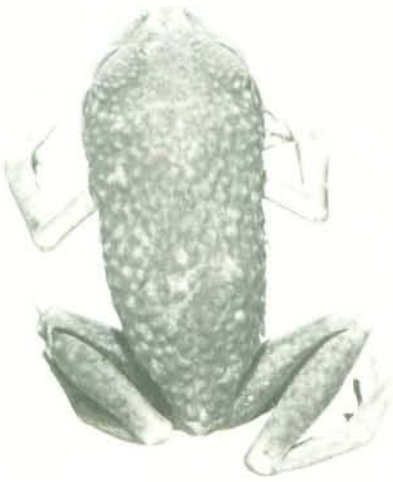

Figure 11. *Holoaden luederwaldti*.

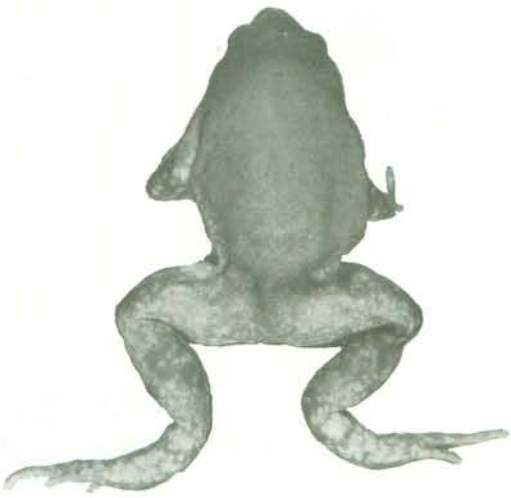

Figure 12. *Myersiella microps*.

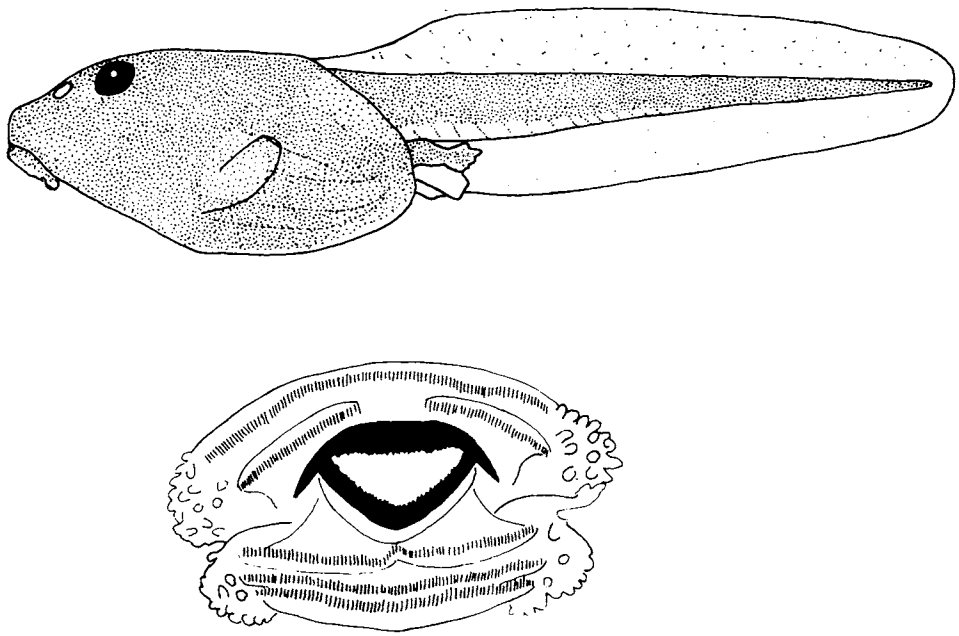

Figure 13. Larval *Bufo crucifer*, stage 35; lateral view total length 20.5 mm, mouthpart width 2.5 mm.

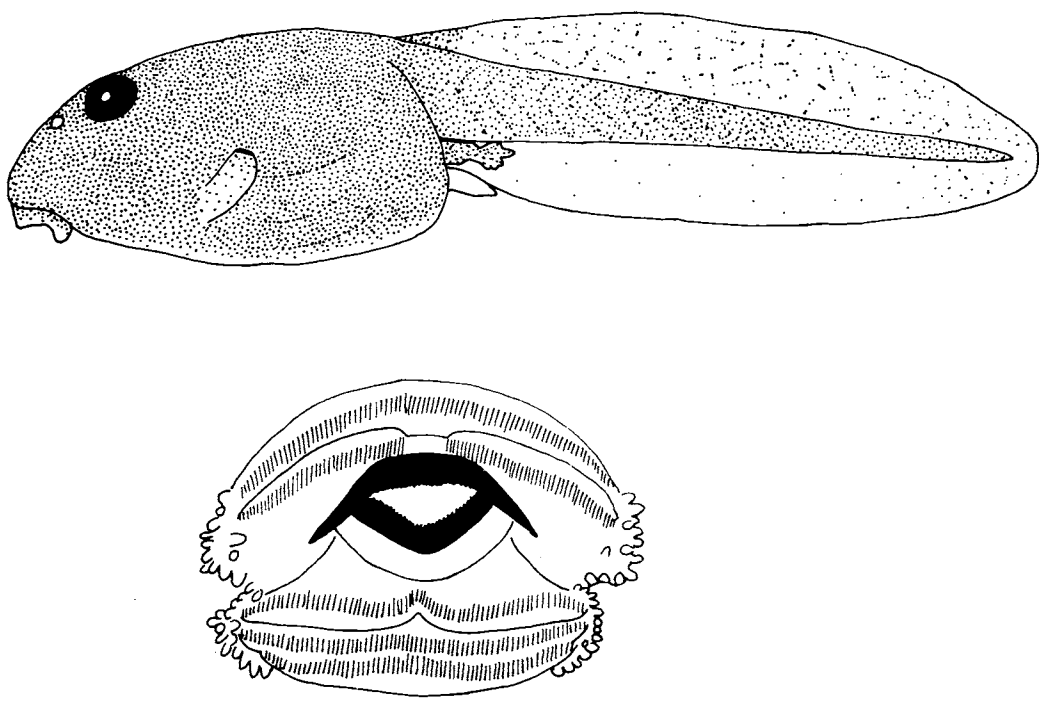

Figure 14. Larval *Bufo ictericus*, stage 36; lateral view total length 22 mm, mouthpart width 2.5 mm.

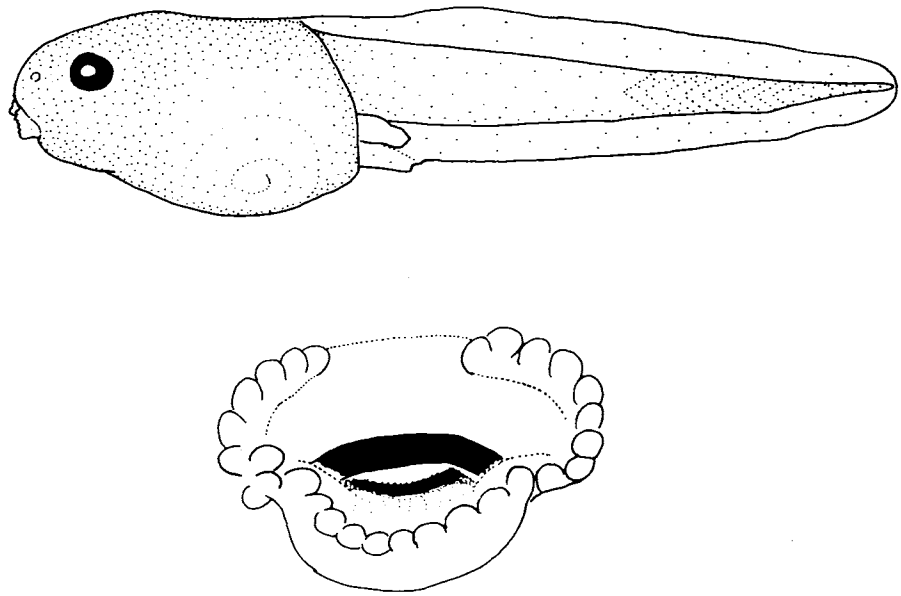

Figure 15. Larval *Fritziana ohausi*, about stage 31; lateral view total length 18.5 mm, mouthpart width 1.0 mm.

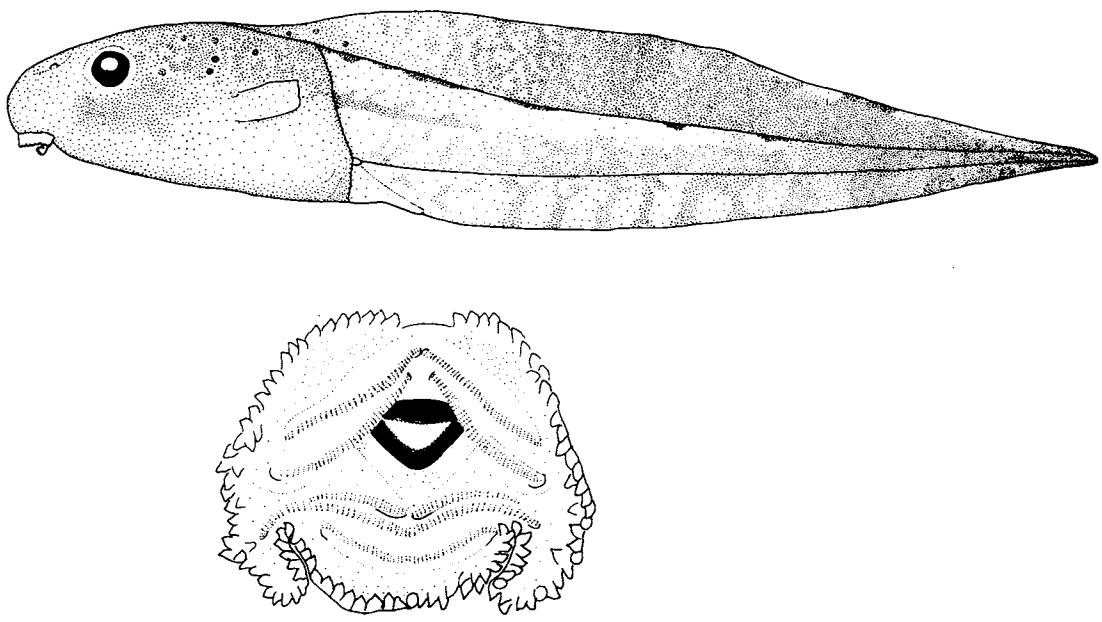

Figure 16. Larval *Hyla albopunctata*, stage 27; lateral view total length 36.3 mm, mouthpart width 1.7 mm.

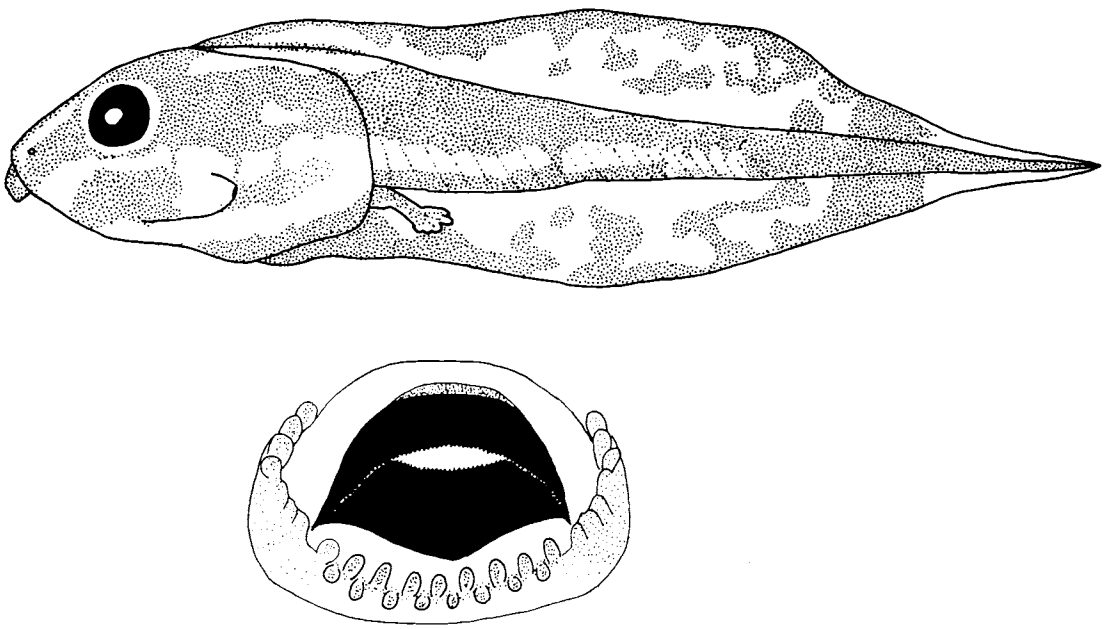

Figure 17. Larval *Hyla microps* stage 36; lateral view total length 27.5 mm, mouthpart width 1.2 mm.

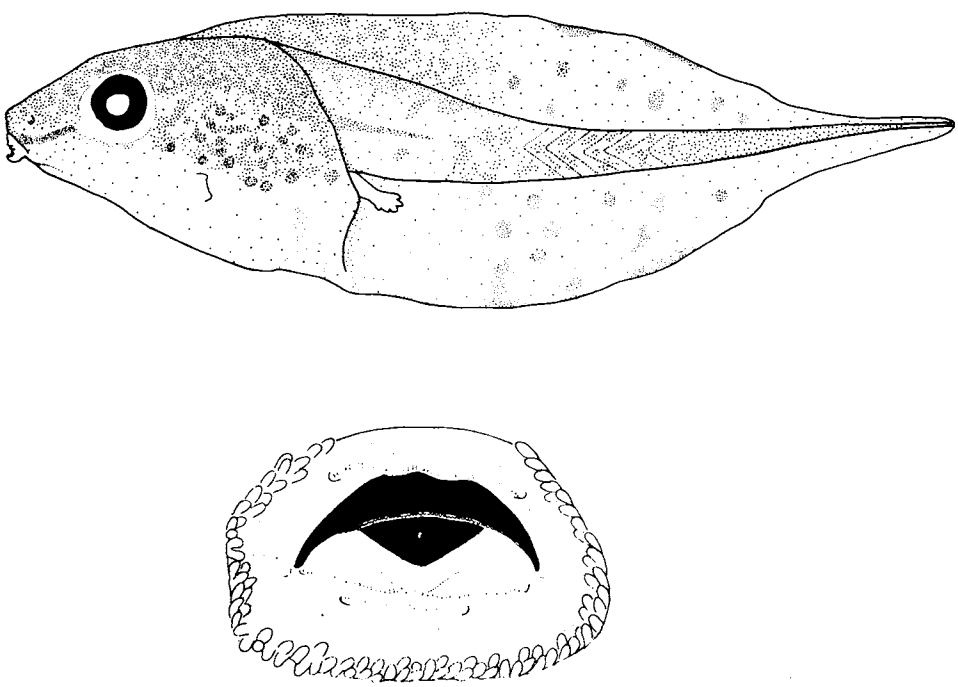

Figure 18. Larval *Hyla minuta*, stage 35; lateral view total length 26.2 mm, mouthpart width 1.4 mm.

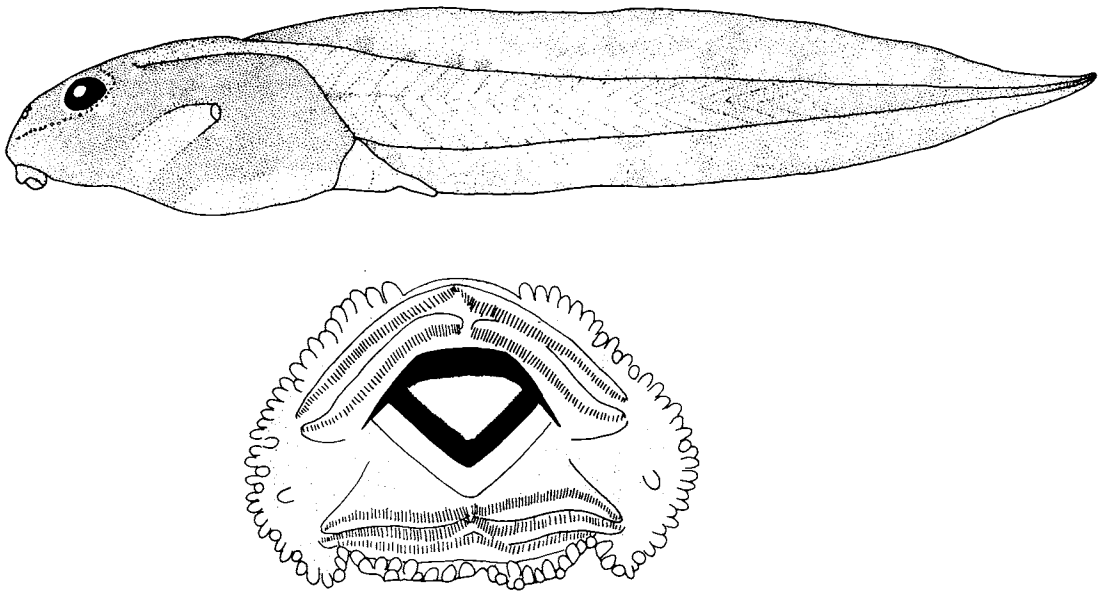

Figure 19. Larval *Hyla multilineata*, stage 26; lateral view total length 41.0 mm, mouthpart width 2.5 mm.

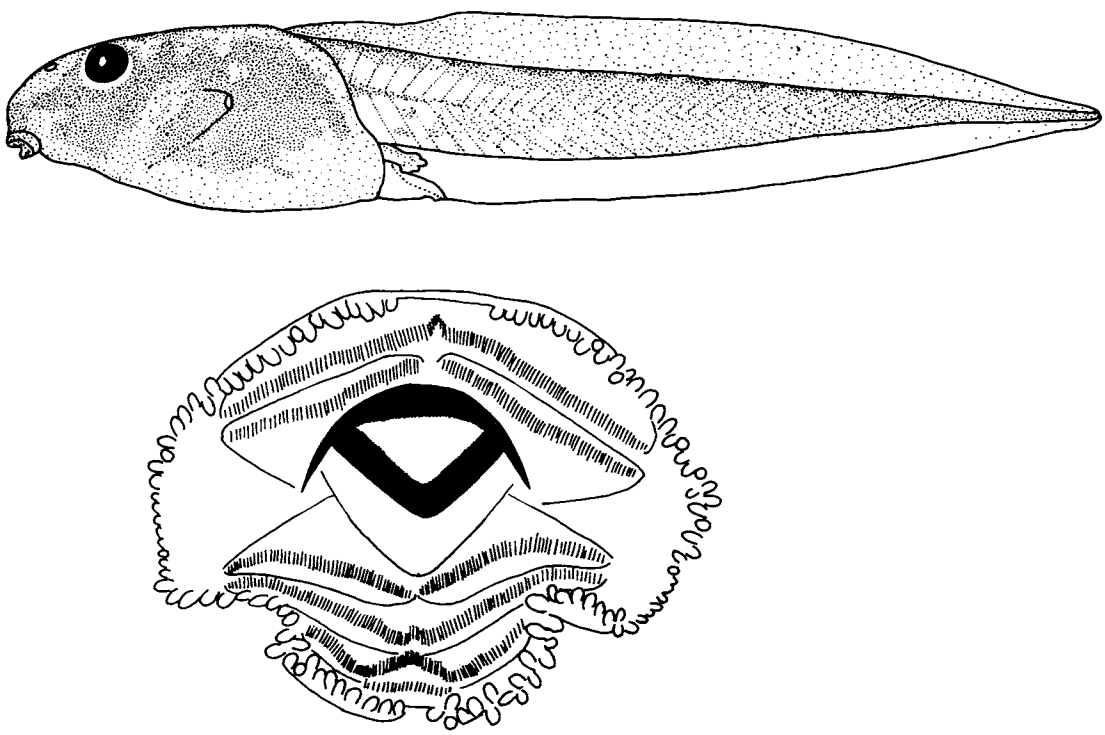

Figure 20. Larval *Hyla pardalis*, stage 35; lateral view total length 39.2 mm, mouthpart width 2.6 mm.

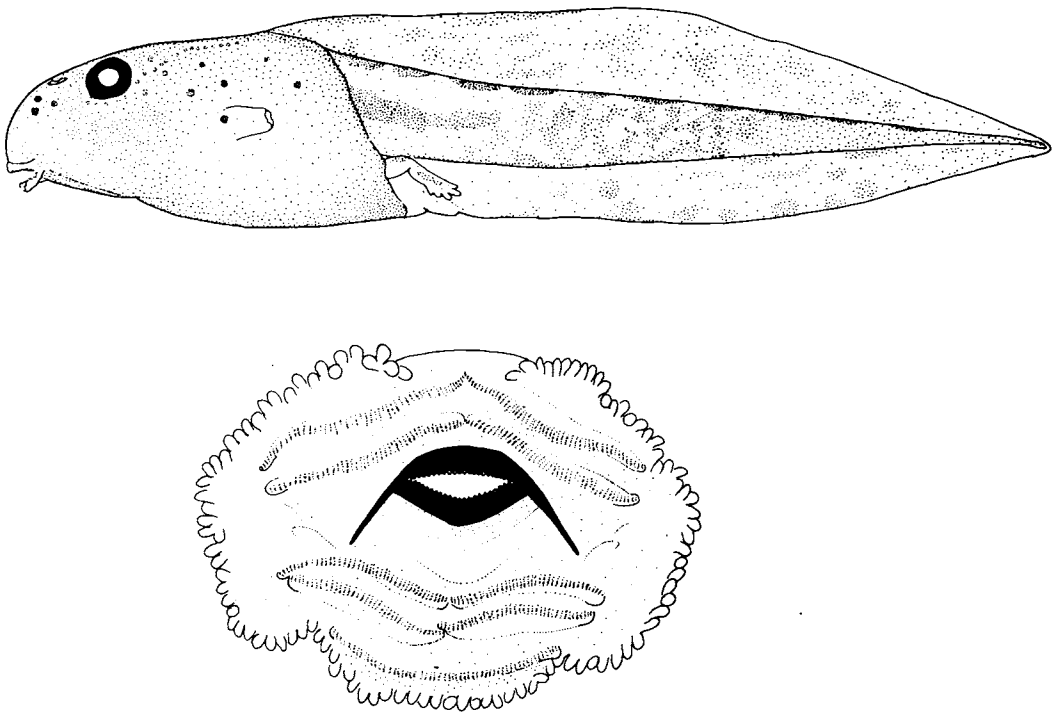

Figure 21. Larval *Hyla polytaenia*, stage 37; lateral view total length 38.0 mm, mouthpart width 2.6 mm.

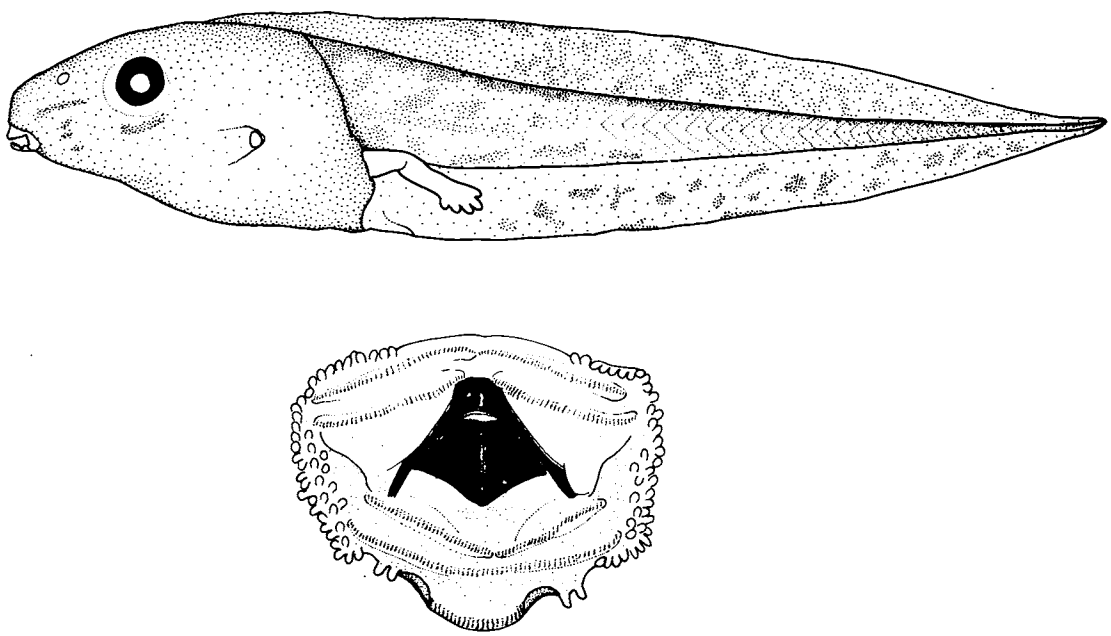

Figure 22. Larval *Ololygon crospedospila*, about stage 37; lateral view total length 33.0 mm, mouthpart width 2.0 mm.

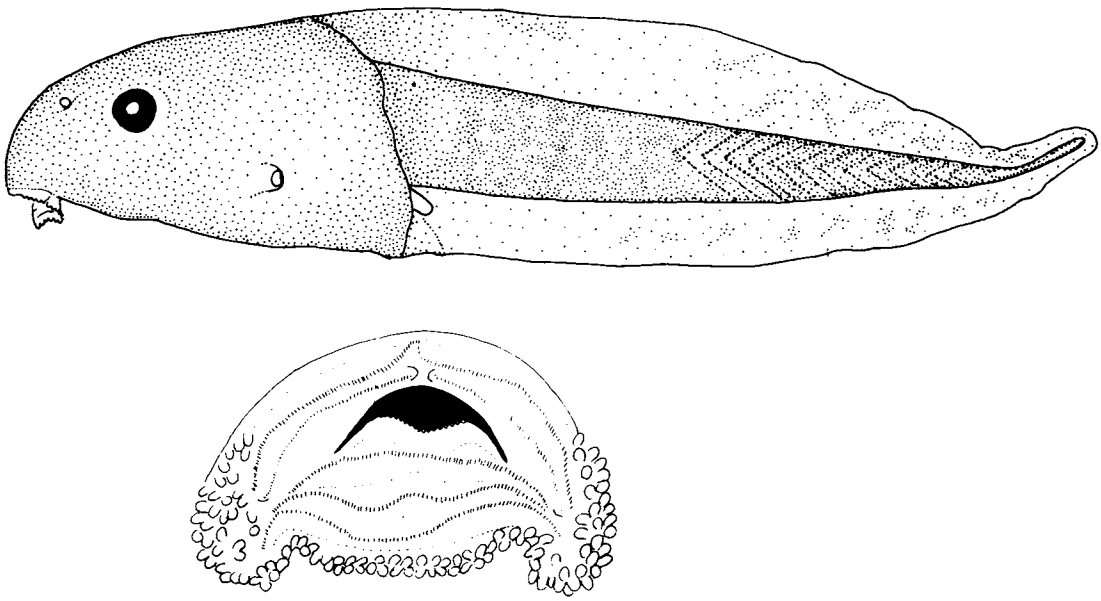

Figure 23. Larval *Ololygon flavoguttata*, about stage 28: lateral view total length 23.1 mm, mouthpart width 1.9 mm.

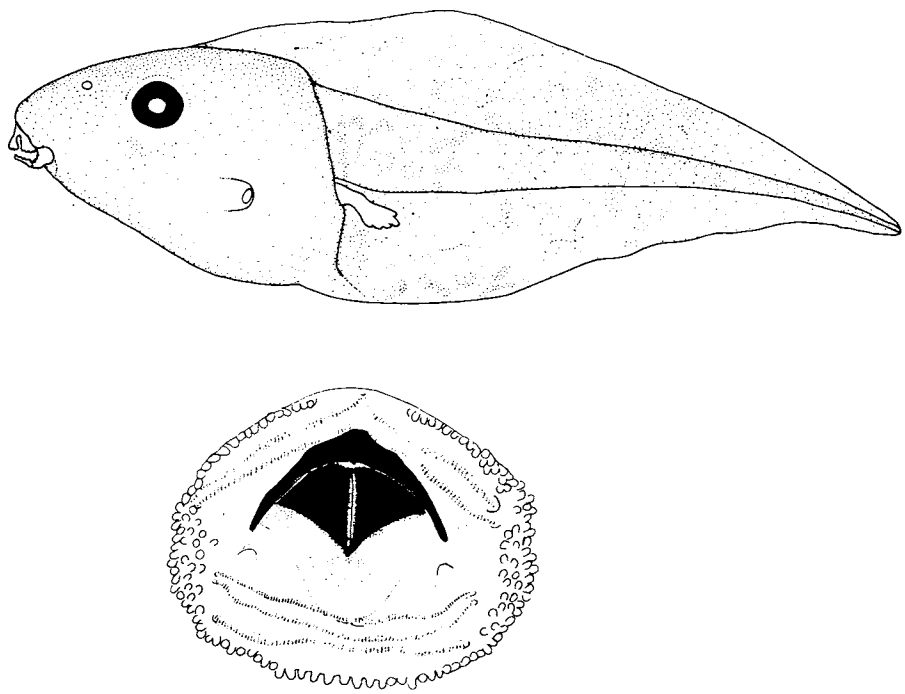

Figure 24. Larval *Ololygon hayii*, stage 36; lateral view total length 28.8 mm, mouthpart width 2.6 mm.

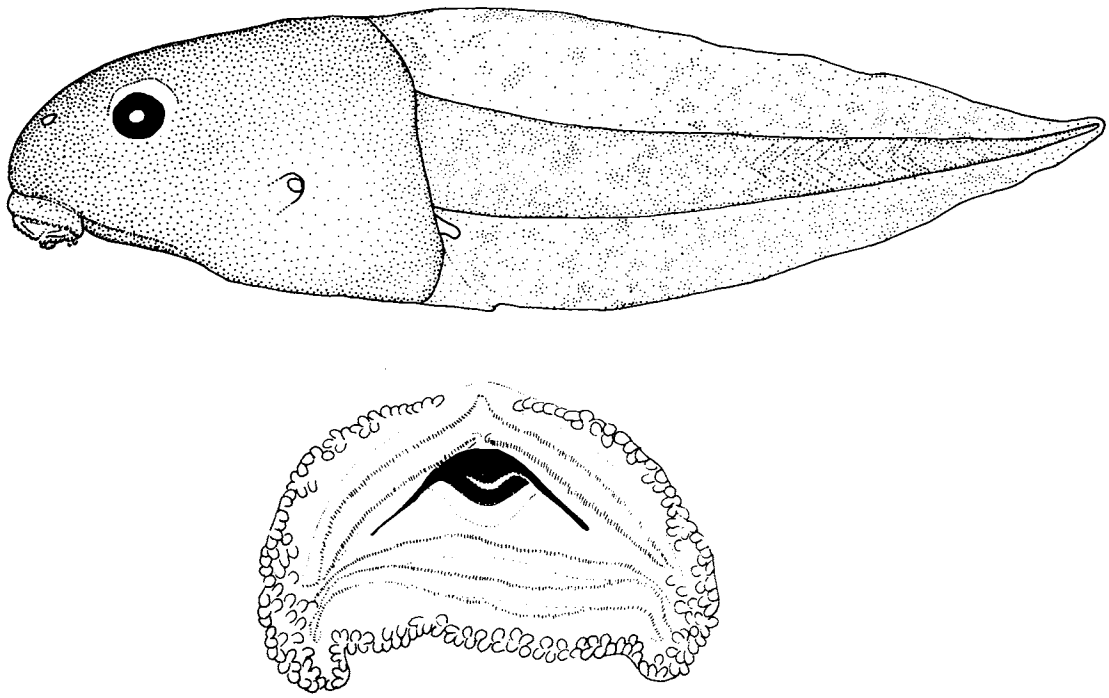

Figure 25. Larval *Ololygon obtriangulata*, stage 30; lateral view total length 27.3 mm, mouthpart width 2.9 mm.

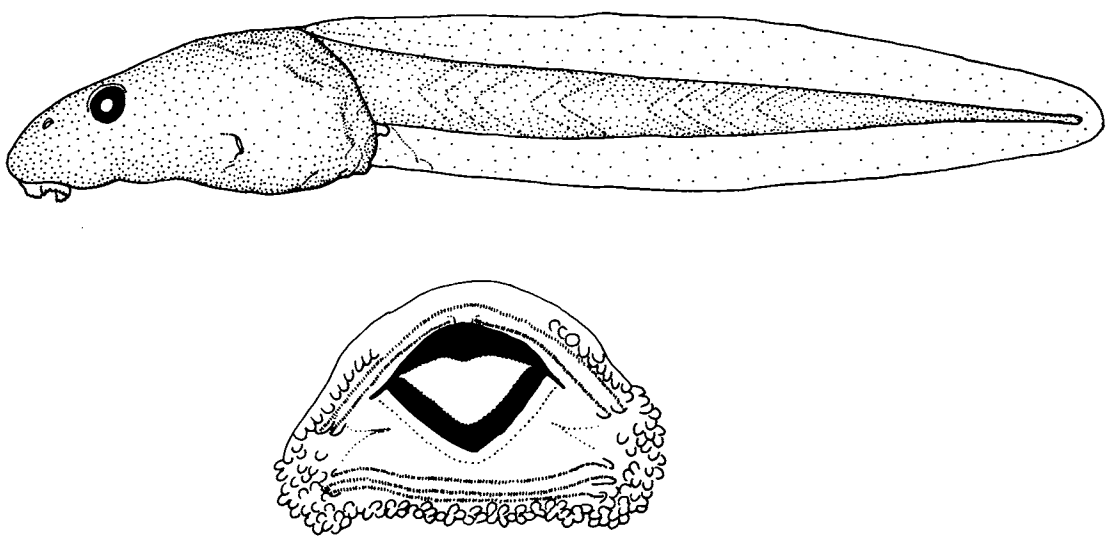

Figure 26. Larval *Ololygon perpusilla*, about stage 28; lateral view total length 19.5 mm, mouthpart width 1.7 mm.

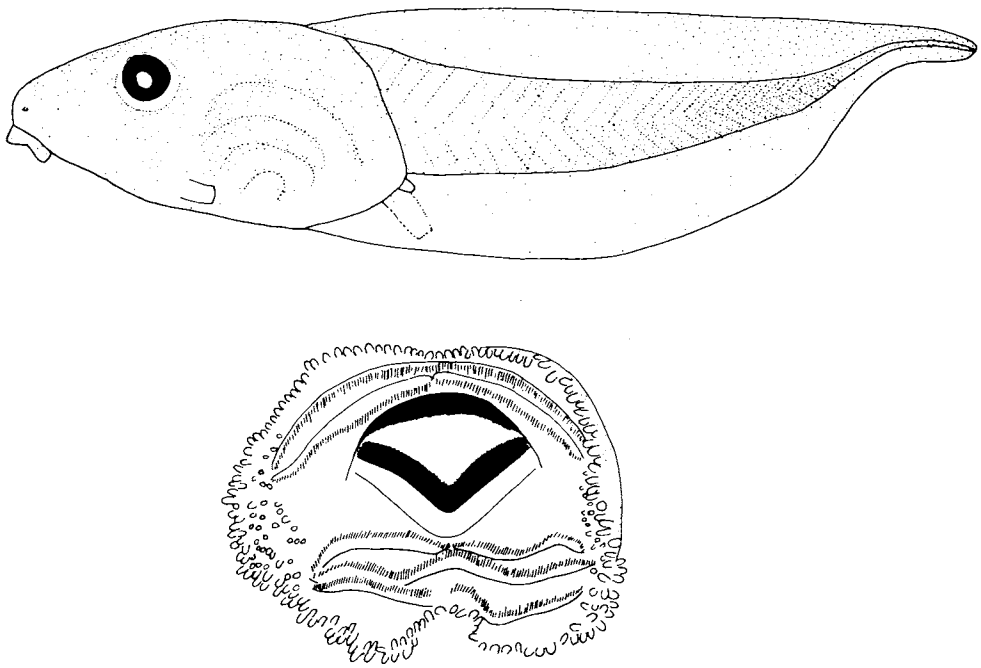

Figure 27. Larval *Phyllomedusa appendiculata*, about stage 28; lateral view total length 38.0 mm, mouthpart width 3.5 mm.

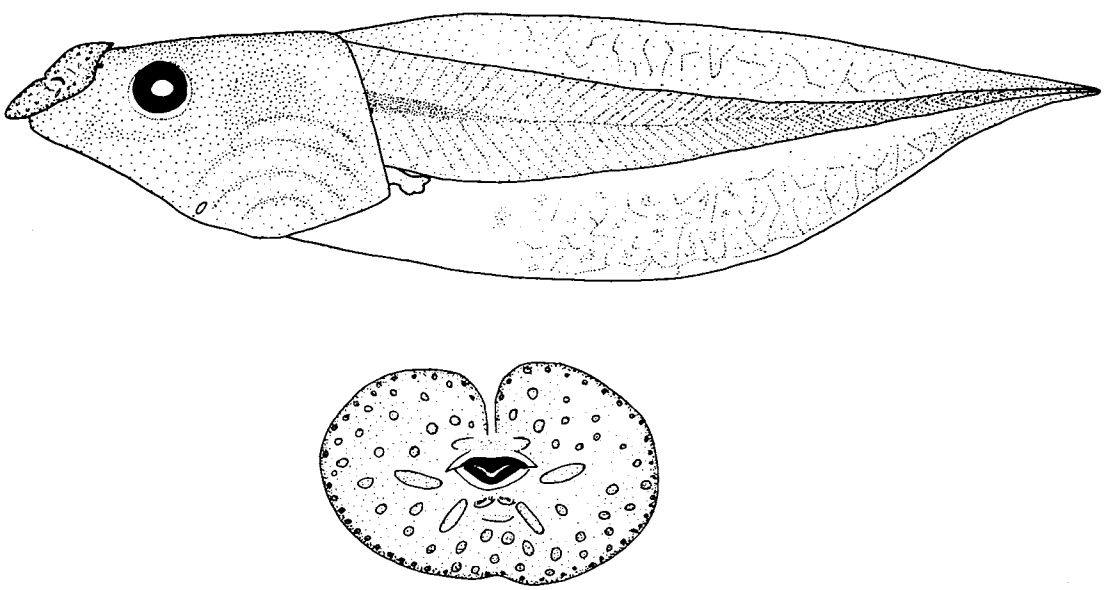

Figure 28. Larval *Phyllomedusa cochranae*, about stage 34; lateral view total length 48.5 mm, mouthpart width 7.7 mm.

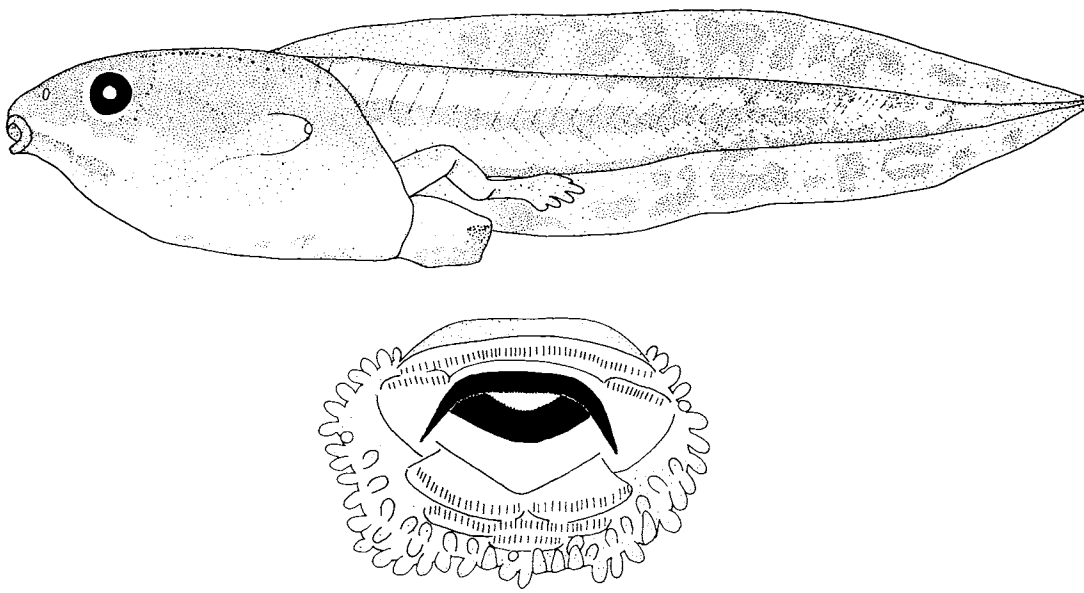

Figure 29. Larval *Sphaenorhynchus orophilus*, stage 39; lateral view total length 47.0 mm, mouthpart width 2.0 mm.

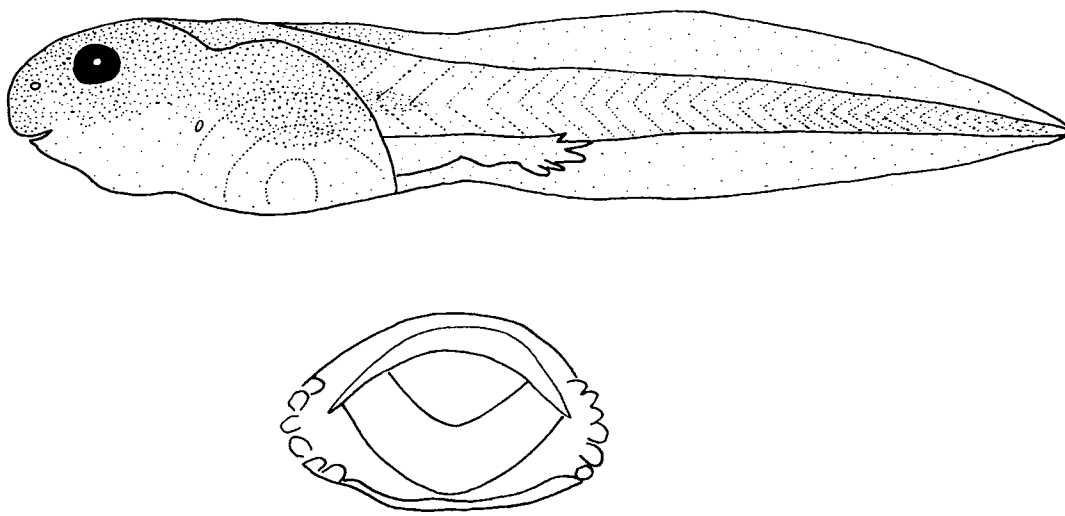

Figure 30. Larval *Adenomera marmorata*, about stage 40; lateral view total length 15.0 mm, mouthpart width 1.1 mm.

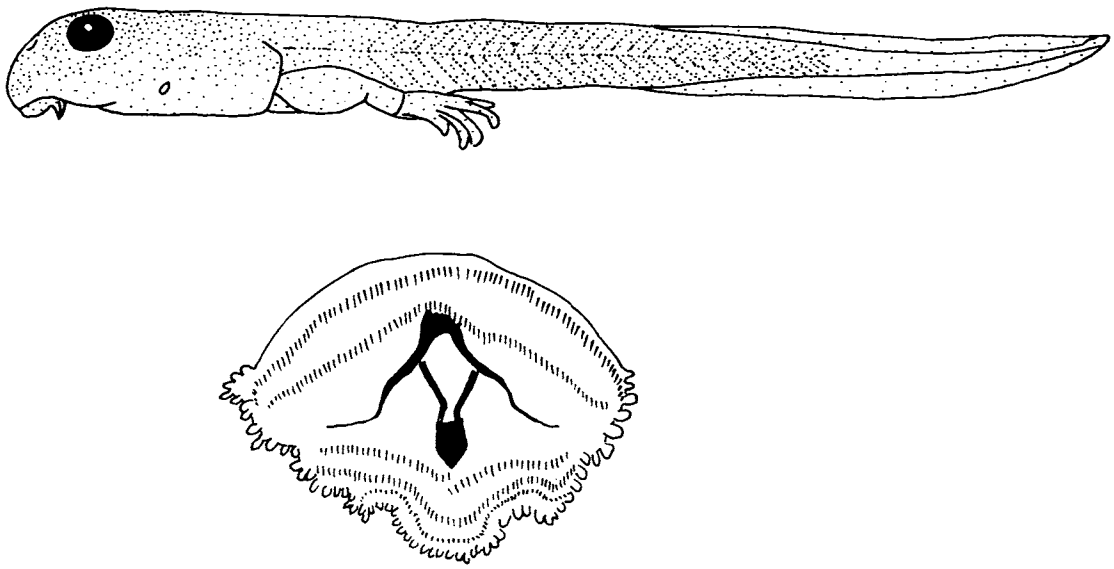

Figure 31. Larval *Cycloramphus boraceiensis*, about stage 40; lateral view total length 26.5 mm, mouthpart width 2.3 mm.

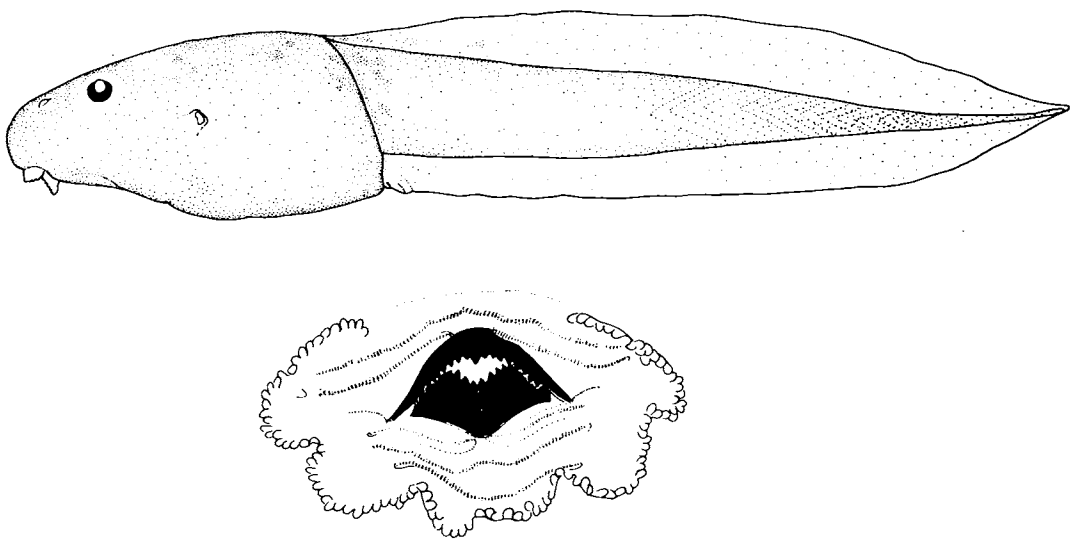

Figure 32. Larval *Hylodes phyllodes*, about stage 25; lateral view total length 36.3 mm, mouthpart width 4.4 mm.

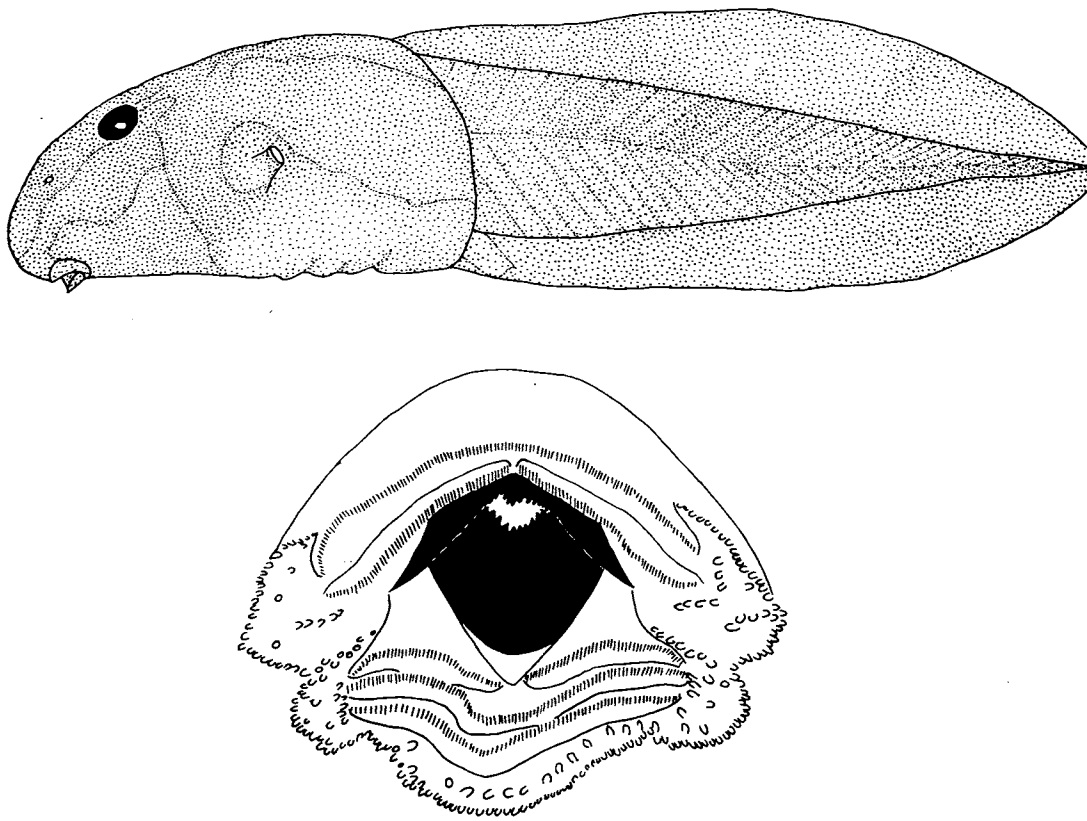

Figure 33. Larval *Megaelosia goeldii*, about stage 25; lateral view total length 76.0 mm, mouthpart width 9.0 mm.

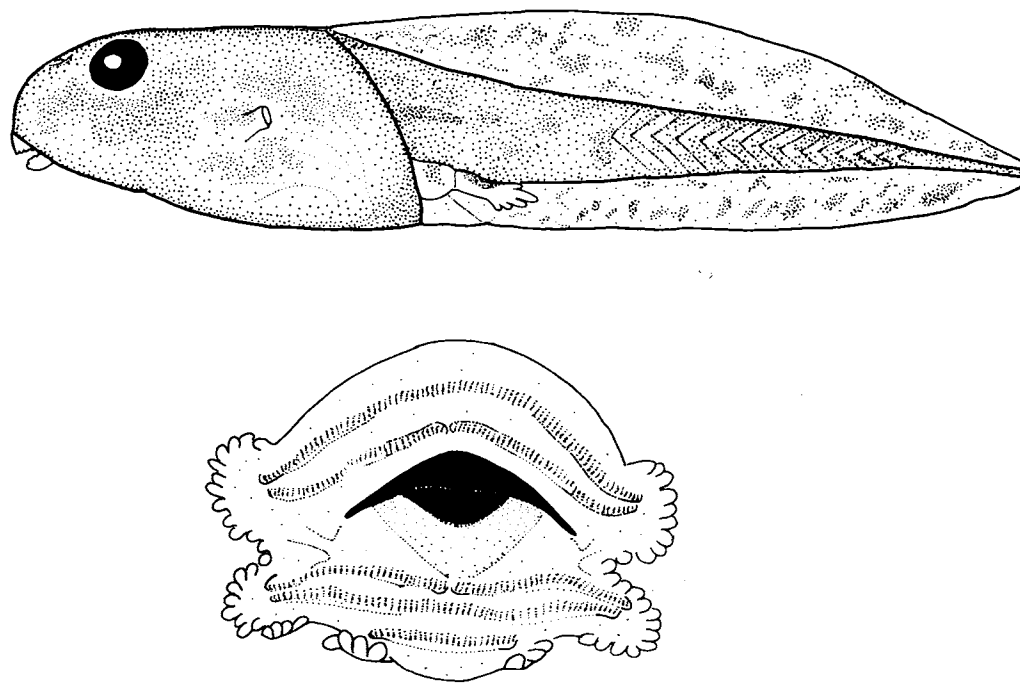

Figure 34. Larval *Physalaemus cuvieri*, stage 34; lateral view total length 23.3 mm, mouthpart width 1.8 mm.

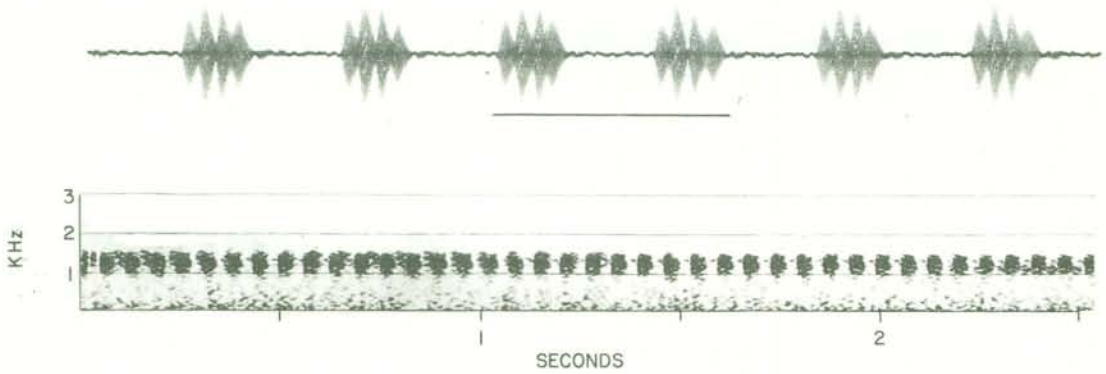

Figure 35. Advertisement call of *Bufo crucifer*, portion of call shown (all audiospectrograms were produced using the narrow [45 Hz] filter). Wave form 1/3 octave bandpass filtered at 1250 Hz; scale line 0.1 s. Voucher specimen USNM 243547, recorded 2 November 1983, about 19° C air temperature.

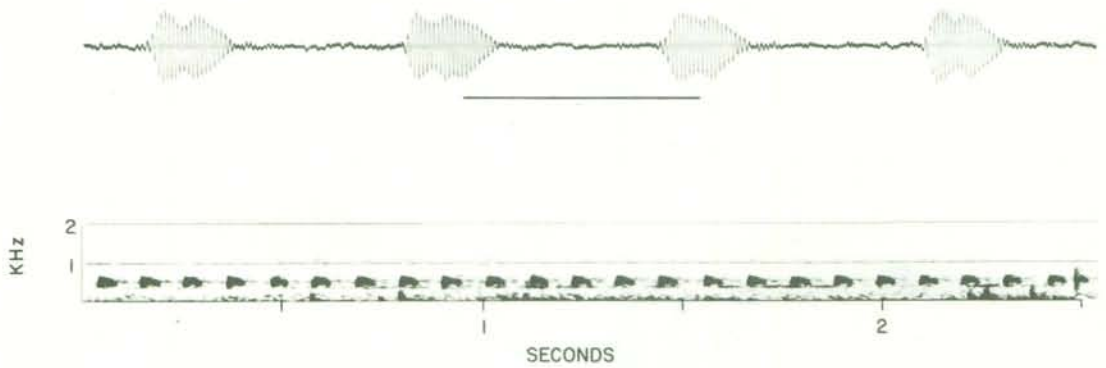

Figure 36. Advertisement call of *Bufo ictericus*, portion of call shown. Wave form scale line 0.1 s. Voucher specimen USNM 243548 recorded 19:25 h, 4 November 1983, 17.5° air temperature.

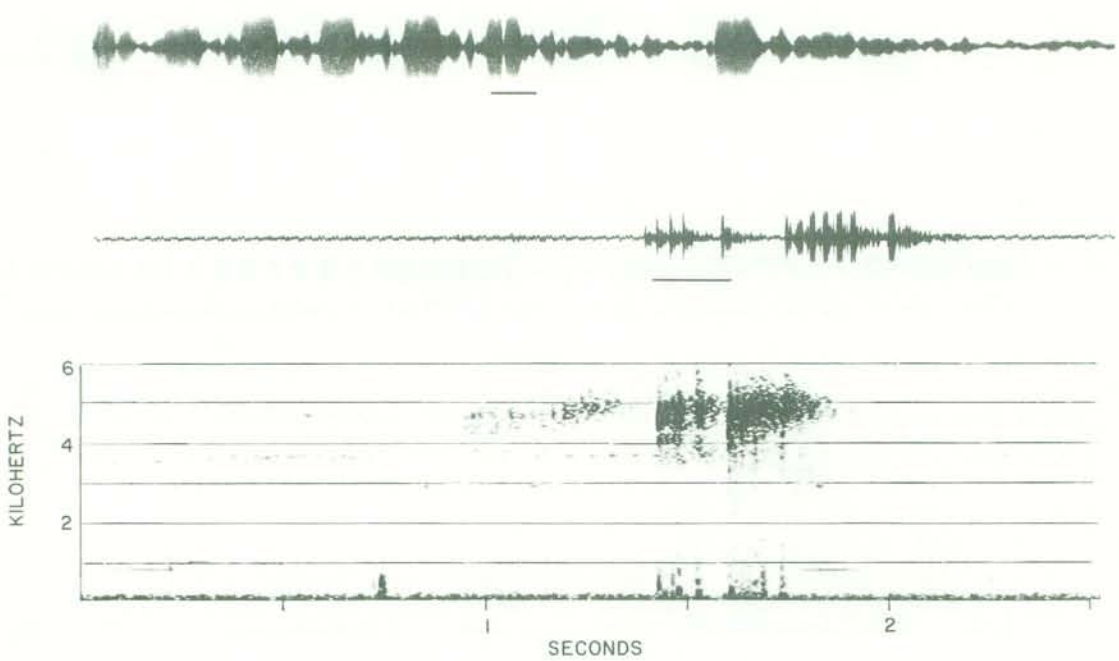

Figure 37. Advertisement call of *Centrolenella eurygnatha*. Single complex note shown; notes sometimes consist of first portion (5 pulses) only. Lower wave form showing entire note, scale line 0.1 s; upper wave form showing second portion of note, scale line 0.01 s. Specimen USNM 208728 recorded 19:35 h, 3 December 1976, 18.6° C air temperature.

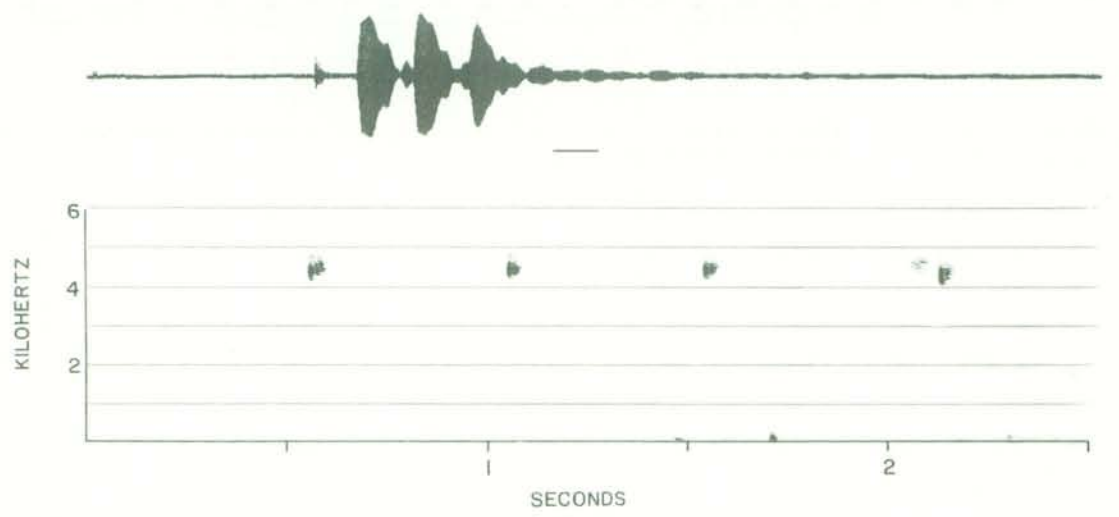

Figure 38. Advertisement call of *Centrolenella uranoscopa*. Four note call illustrated. Wave form of fourth note shown on audiospectrogram; scale bar 0.1 s. Specimen recorded 23 November 1971, 15-15.5° air temperature.

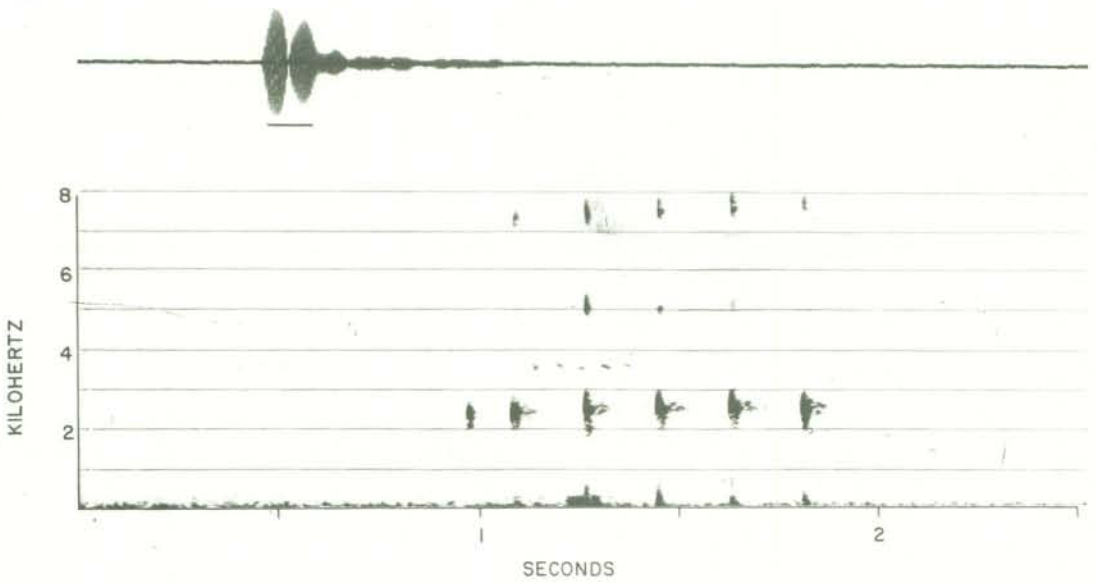

Figure 39. Advertisement call of *Fritziana ohausi*. Wave form of final note shown in audiospectrogram; wave form scale line 0.01 s; signal highpass filtered at 500 Hz. Audiospectrogram unfiltered. Voucher specimen USNM 217716, recorded 19:25 h on 11 December 1976, 18.5° C air temperature.

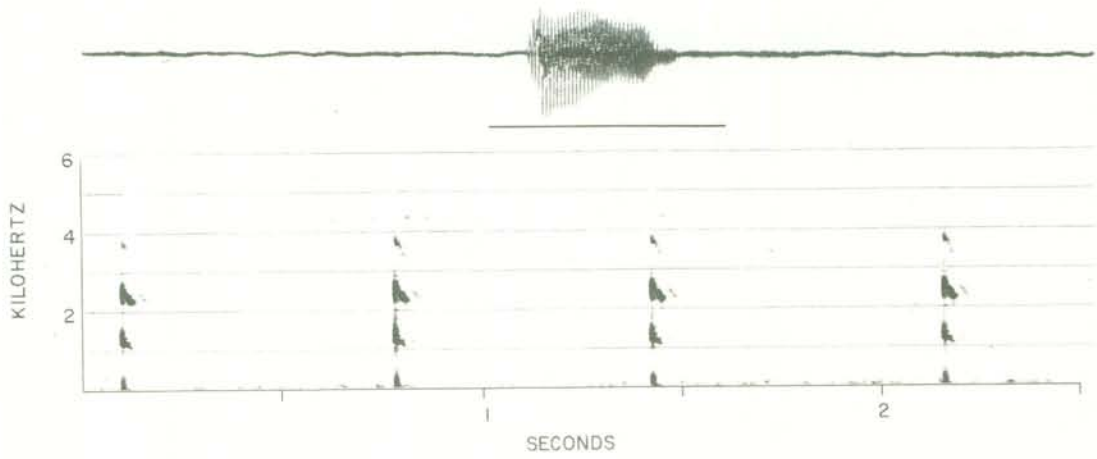

Figure 40. Advertisement call of *Hyla albofrenata*. Wave form of first call shown at left on audiospectrogram, scale line 0.1 s. Voucher specimen USNM 208736, recorded 7 December 1976, 21.8° C air temperature.

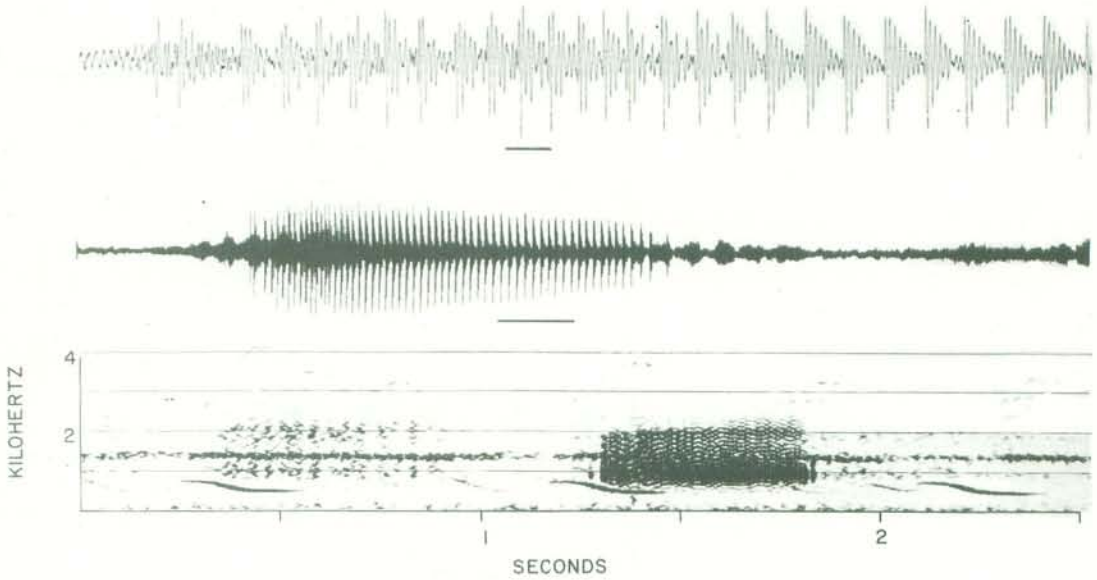

Figure 41. One type of advertisement call of *Hyla albopunctata*. Lower wave form showing entire call, scale line 0.1 s. Upper waveform showing beginning of call, scale line 0.01 s. Specimen not captured, recorded 6 November 1983, air temperature 17-18° C.

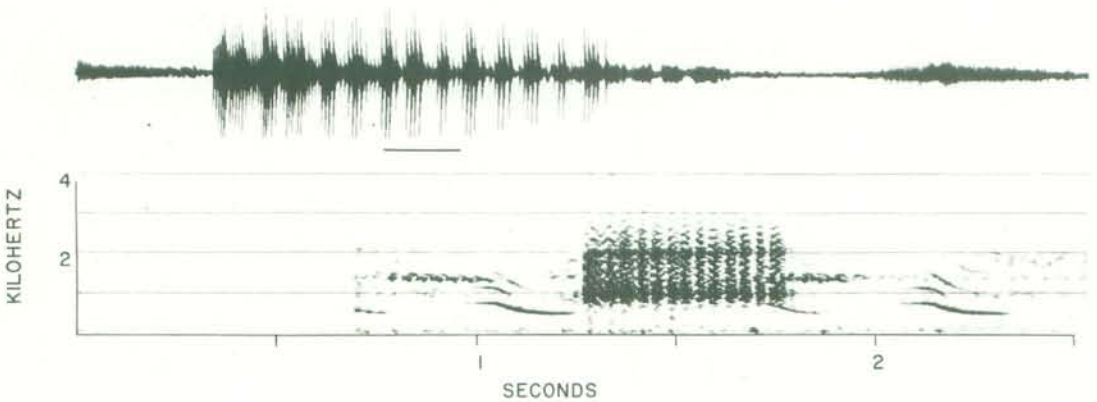

Figure 42. Second type of advertisement call of *Hyla albopunctata*. Wave form showing entire call, scale line 0.1 s. Specimen not captured, recorded 6 November 1983, air temperature 17-18° C.

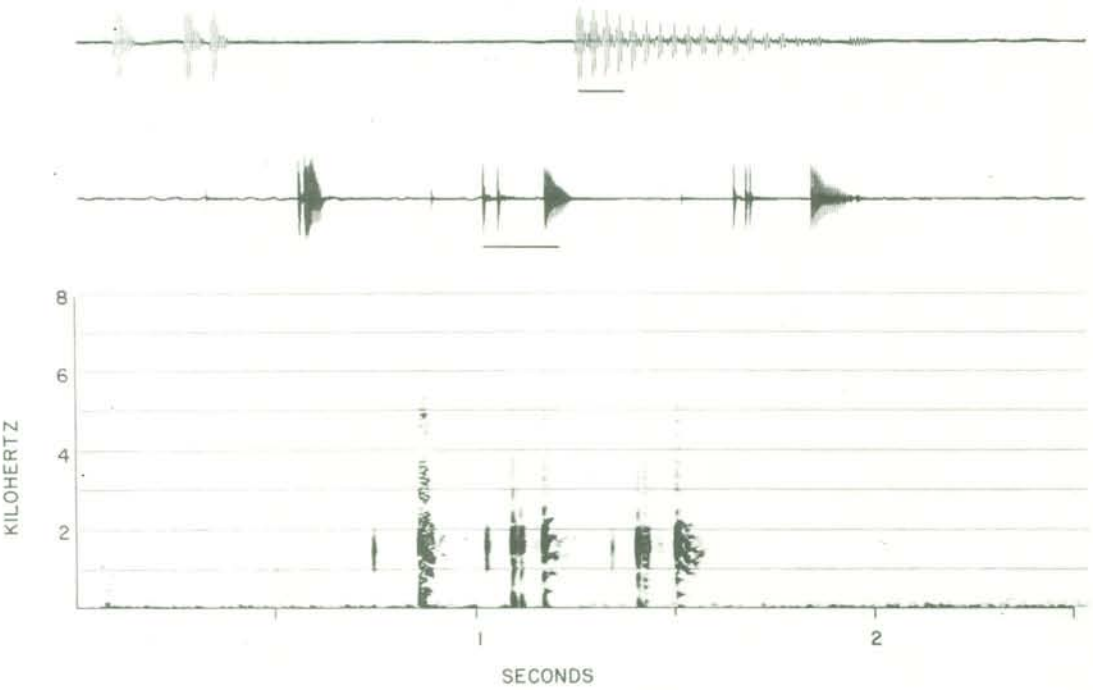

Figure 43. Advertisement call of *Hyla astartea*. Lower wave form showing entire call scale line 0.1 s. Upper wave form showing final note group, scale line 0.01 s. Voucher specimen USNM 243565 recorded 8 November 1983, 16.6° C air temperature.

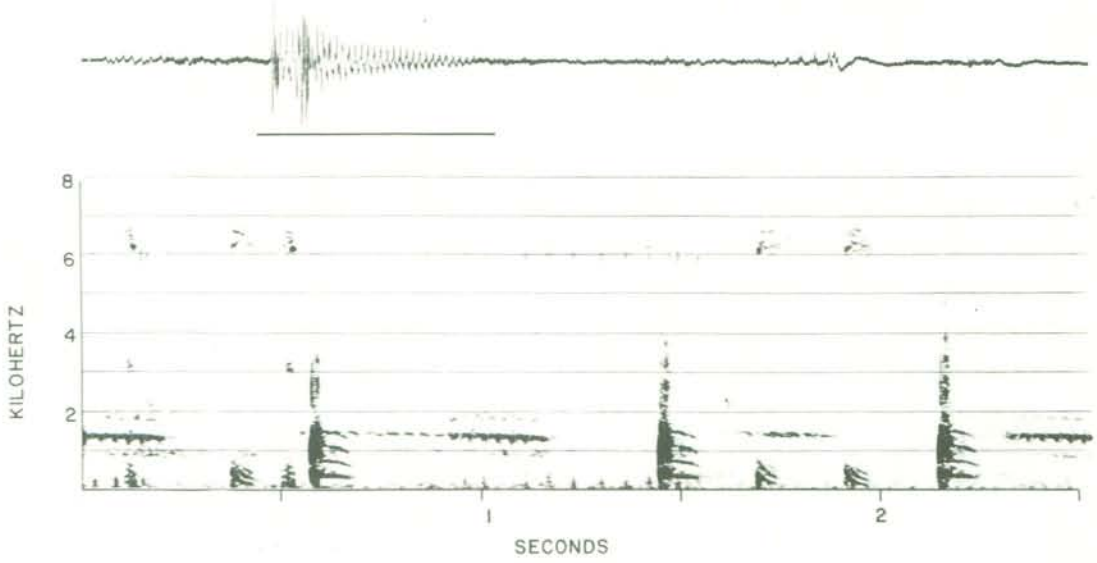

Figure 44. Advertisement call of *Hyla faber*. Wave form of a call from same indicidual, but not same calls as shown on audiospectrogram, scale line 0.1 s. Voucher specimen USNM 243567 recorded 21:20 h on 5 November 1983, 17-18° C air temperature.

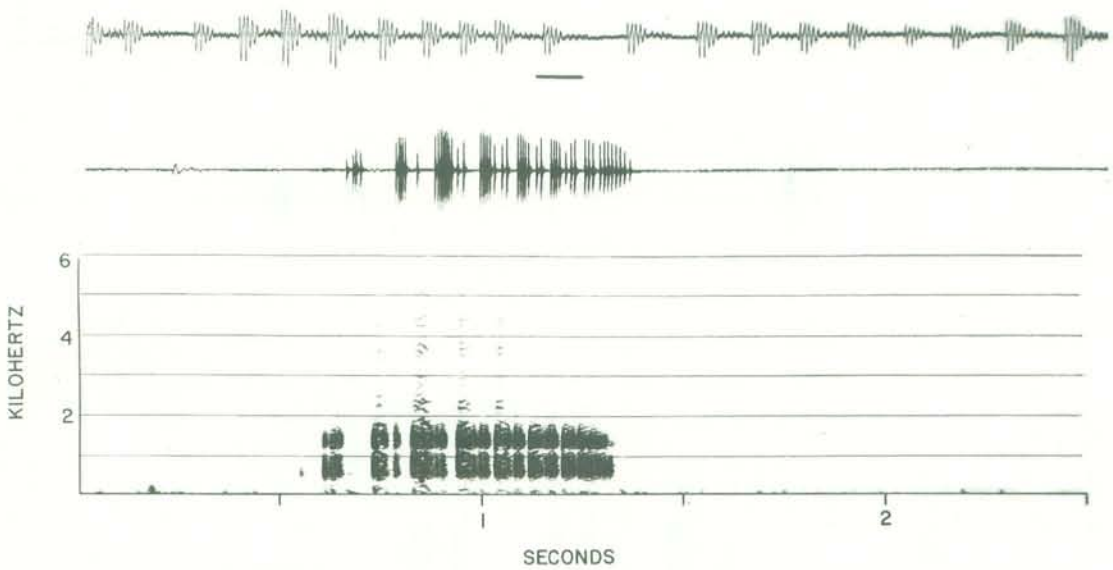

Figure 45. Advertisment call of *Hyla hylax*. Upper wave form showing portion of call recorded from USNM 243470, 19:58 h, 4 November 1983, air temperature 17.5° C, scale line 0.01 s. Lower waveform showing entire call, same call and time scale as audiospectrogram, specimen not captured, recorded 9 November 1983, air temperature 19° C.

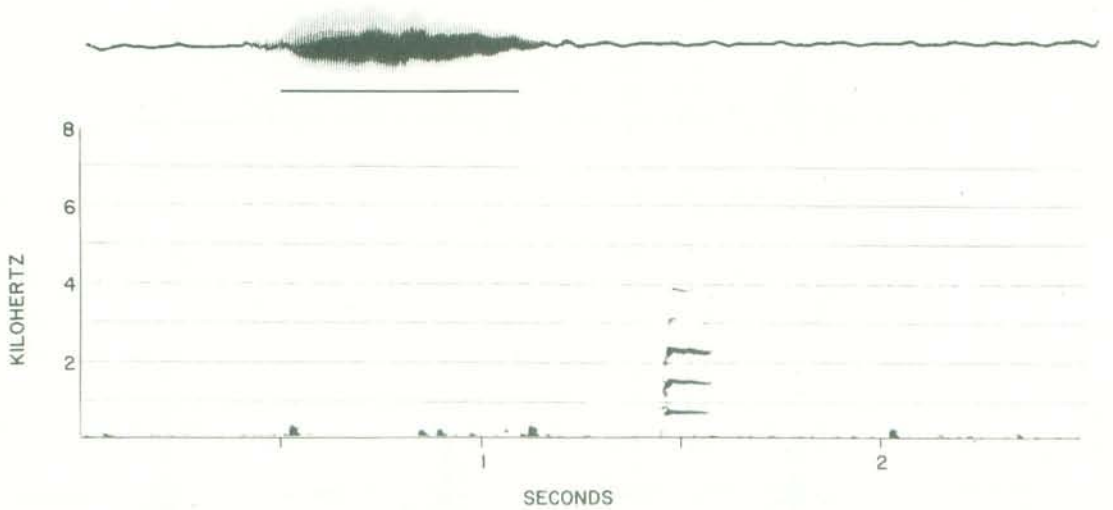

Figure 46. Advertisement call of *Hyla leucopygia*. Wave form of note shown in audiospectrogram, scale line 0.1 s. Voucher specimen USNM 208742 recorded about 20:00 h, 3 December 1976, air temperature 18.6° C.

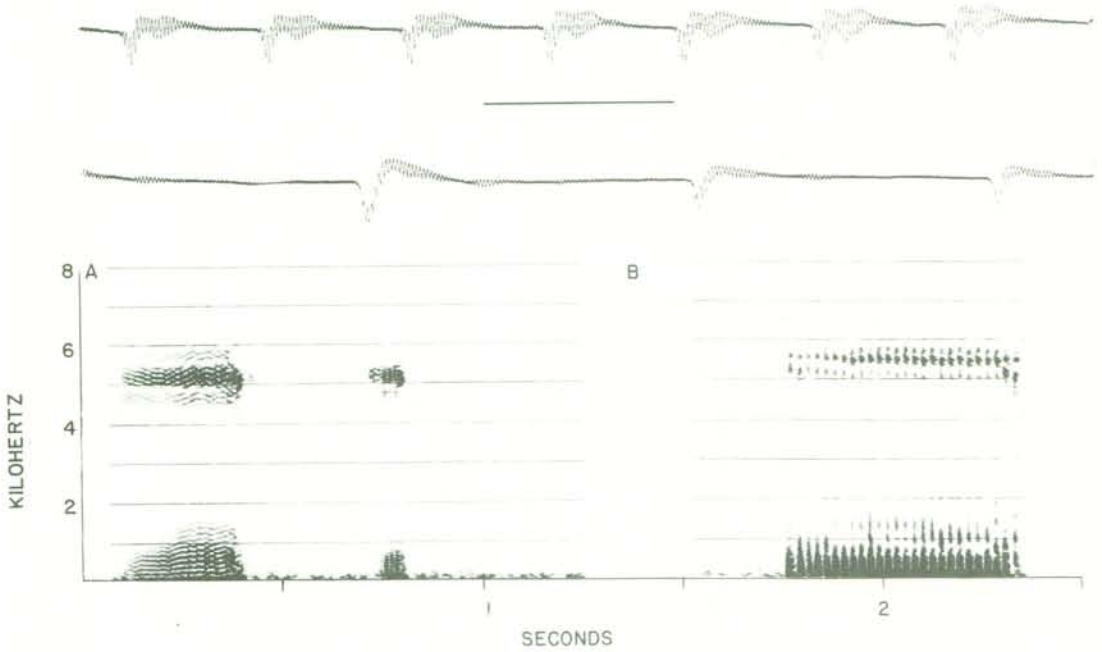

Figure 47. Advertisement calls of *Hyla microps*. Scale lines 0.01 s for both wave forms. Upper wave form of portion of call shown in audiospectrogram A, voucher specimen USNM 243574, recorded 20:12 h, 8 November 1983, 18° C air temperature. Lower wave form of portion of call shown in audiospectrogram B, voucher specimen USNM 243573, recorded 19:45 h, 8 November 1983, 18° C air temperature.

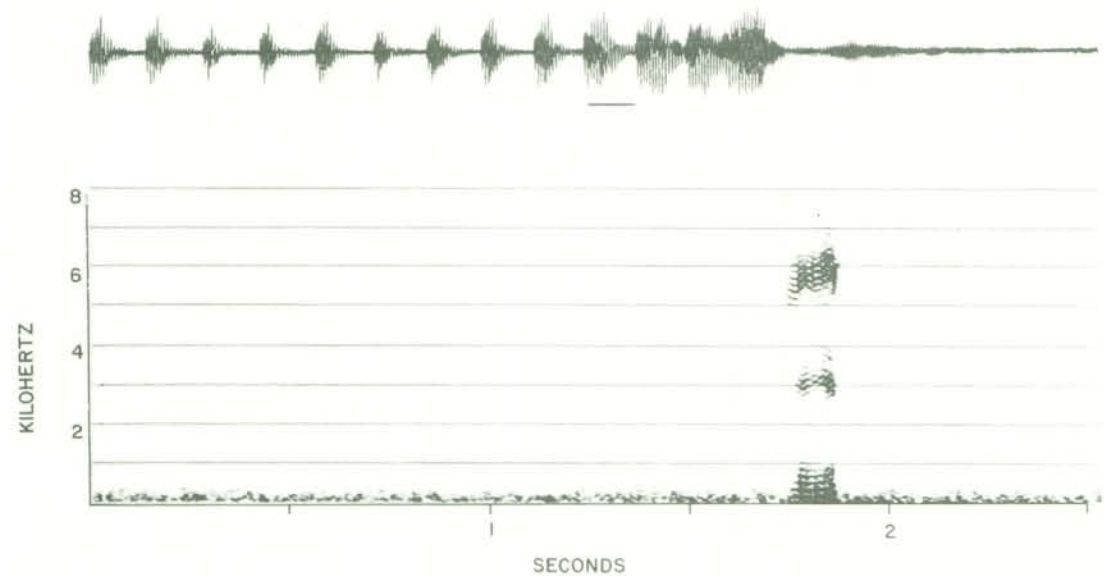

Figure 48. Advertisement call of *Hyla minuta*. Wave form scale line 0.01 s, signal highpass filtered at 1000 Hz. Audiospectrogram of unfiltered signal. Voucher specimen USNM 243591, recorded 22:21 h, 9 November 1983, 18° C air temperature. Note that the call often includes secondary notes (not figured).

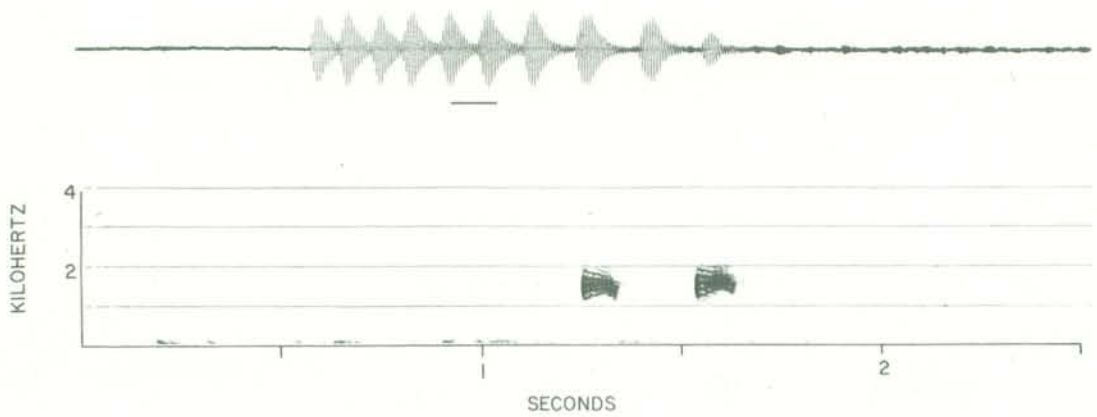

Figure 49. Type 1 advertisement call of *Hyla multilineata*. Wave form of first note shown in audiospectrogram; wave form scale line 0.01 s; signal highpass filtered at 500 Hz. Voucher specimen not captured, recorded 11 November 1971, 15° C air temperature.

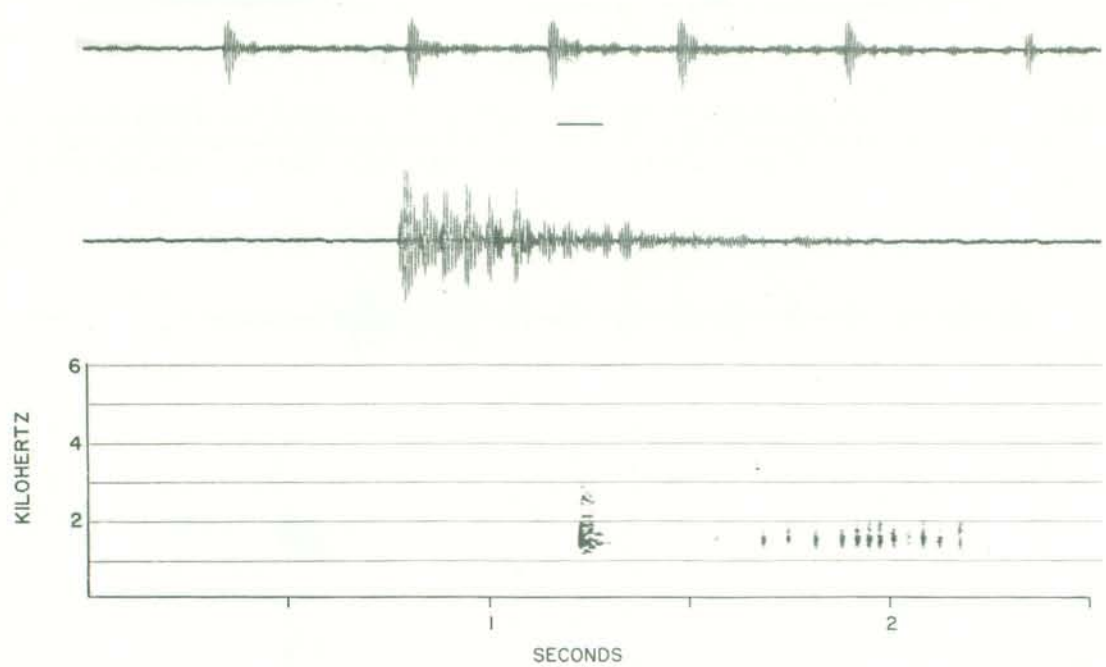

Figure 50. Type 2 advertisement call of *Hyla multilineata*. Upper wave form of 6 middle notes in second portion of call shown on audiospectrogram; lower wave form of initial note on audiospectrogram; signal highpass filtered at 500 Hz; scale line 0.01 s. Voucher specimen not captured, recorded 15 March 1963, temperature not recorded.

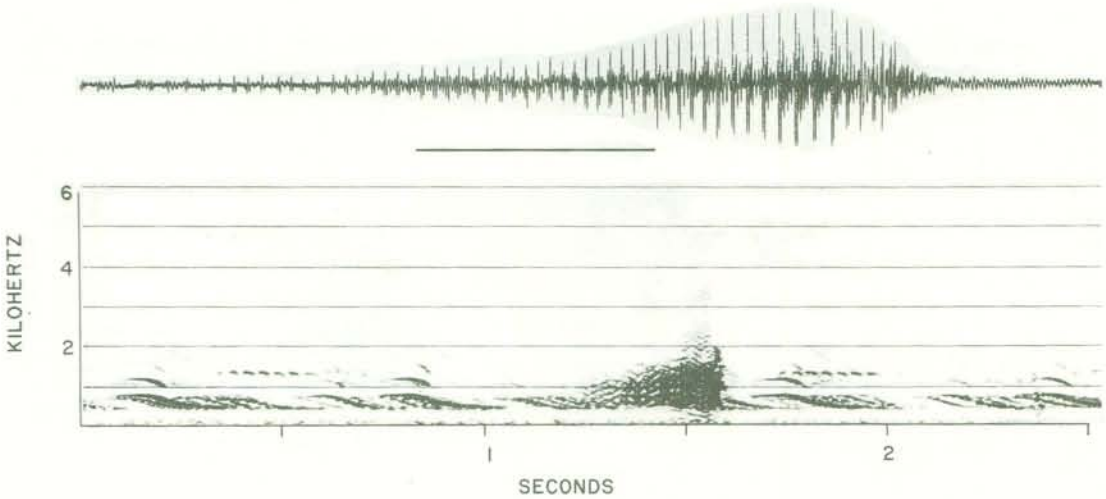

Figure 51. Advertisement call of *Hyla pardalis* in a chorus of *Physalaemus cuvieri*. Wave form scale line 0.1 s. Voucher specimen USNM 243593 recorded 19:50 h, 3 November 1983, 19-20° C air temperature.

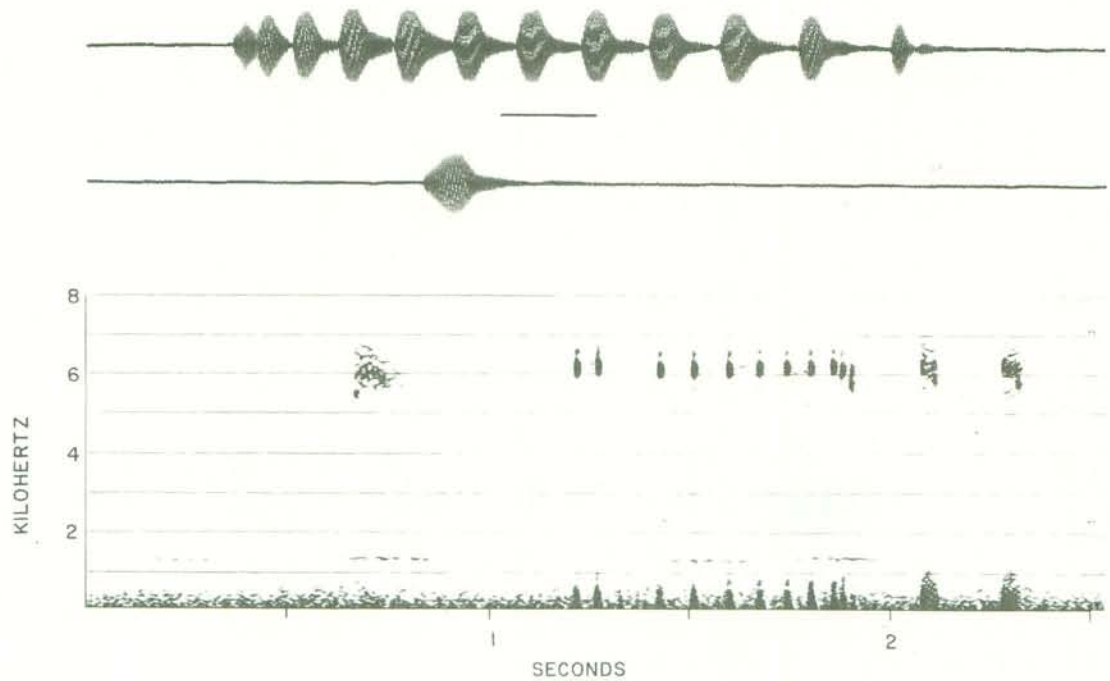

Figure 52. Advertisement call of *Hyla polytaenia*. Upper and lower wave form scale line 0.01 s, both signals highpass filtered at 2200 Hz; upper wave form of harsh call, lower of a trill note; wave forms of recording from voucher specimen USNM 208874, 12 December 1976, 17° C air temperature. Audiospectrogram of harsh note followed by trilled notes followed by harsh notes, recorded from specimen USNM 243618, 21:45 h, 3 November 1983, 19-20° air temperature.

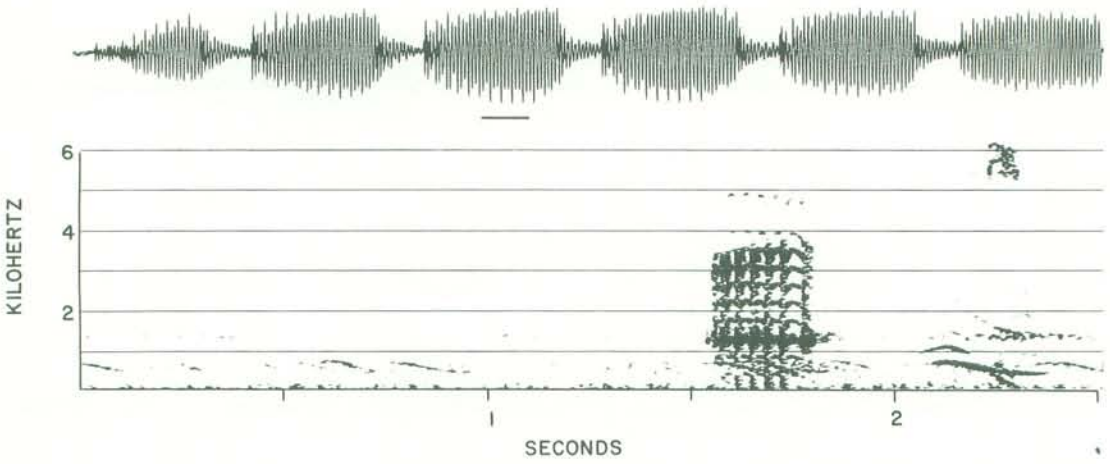

Figure 53. Advertisement call of *Ololygon crospedospila*. Wave form showing all but last portion of final note of call, scale line 0.01 s. Voucher specimen USNM 243623 recorded 20:06 h, 3 November 1983, 19-20° C air temperature.

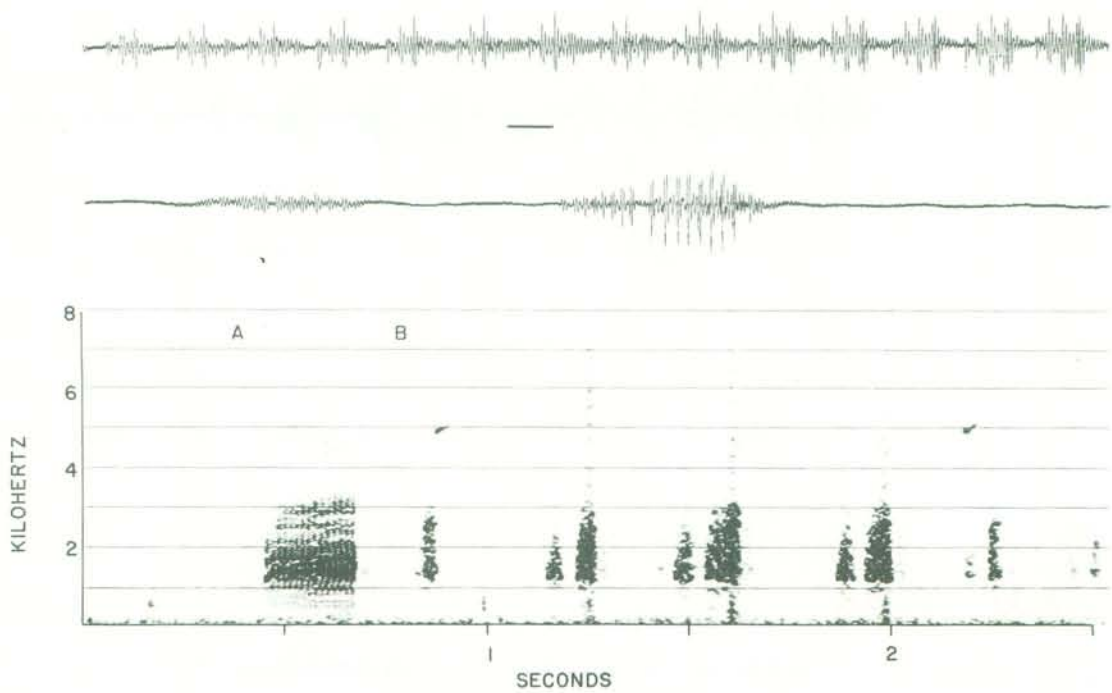

Figure 54. Advertisement calls of *Ololygon hayii*. Upper wave form showing initial portion of advertisement call (audiospectrogram A). Lower waveform showing first double noted occasional call (audiospectrogram B). Upper and lower wave form scale line 0.01 s. Audiospectrograms: A, advertisement call; B, occasional call. Voucher specimen USNM 243654 recorded 10 November 1983, 19:45 h, 19-20° C air temperature.

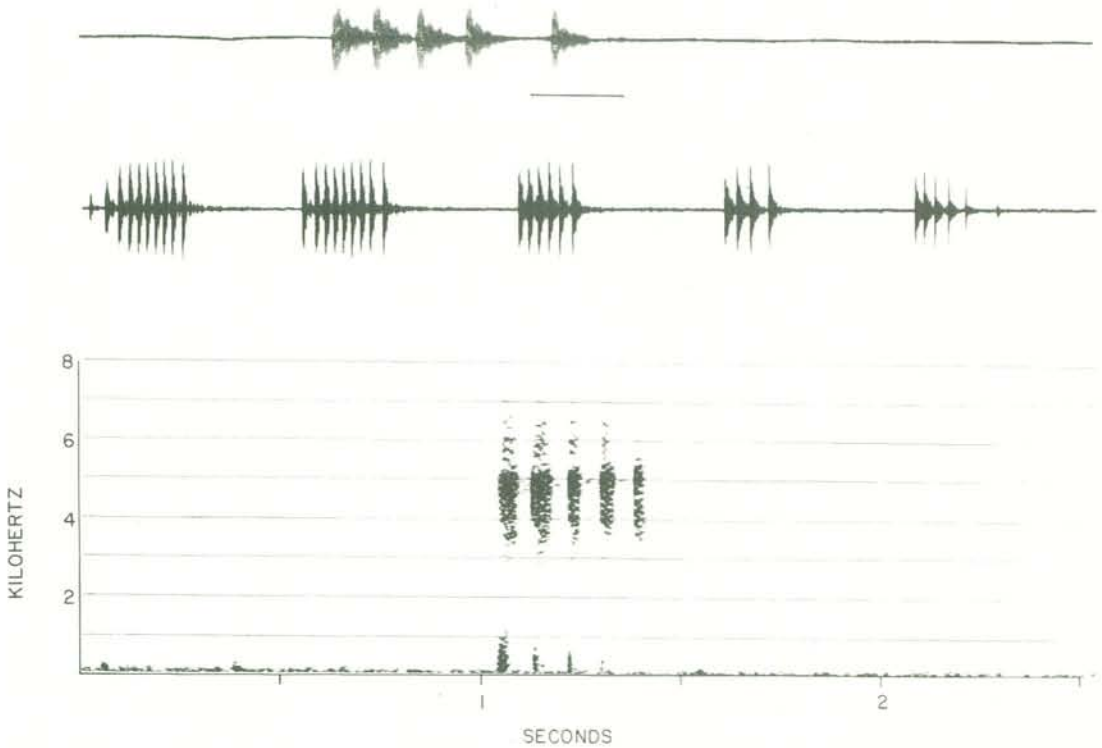

Figure 55. Advertisement call of *Ololygon perpusilla*. Lower wave form signal highpass filtered at 1000 Hz, scale line 0.1 s. Upper wave form of last note shown on audiospectrogram. Audiospectrogram unfiltered. Voucher specimen USNM 209058 recorded 21:30 h, 3 December 1976, 18° C air temperature.

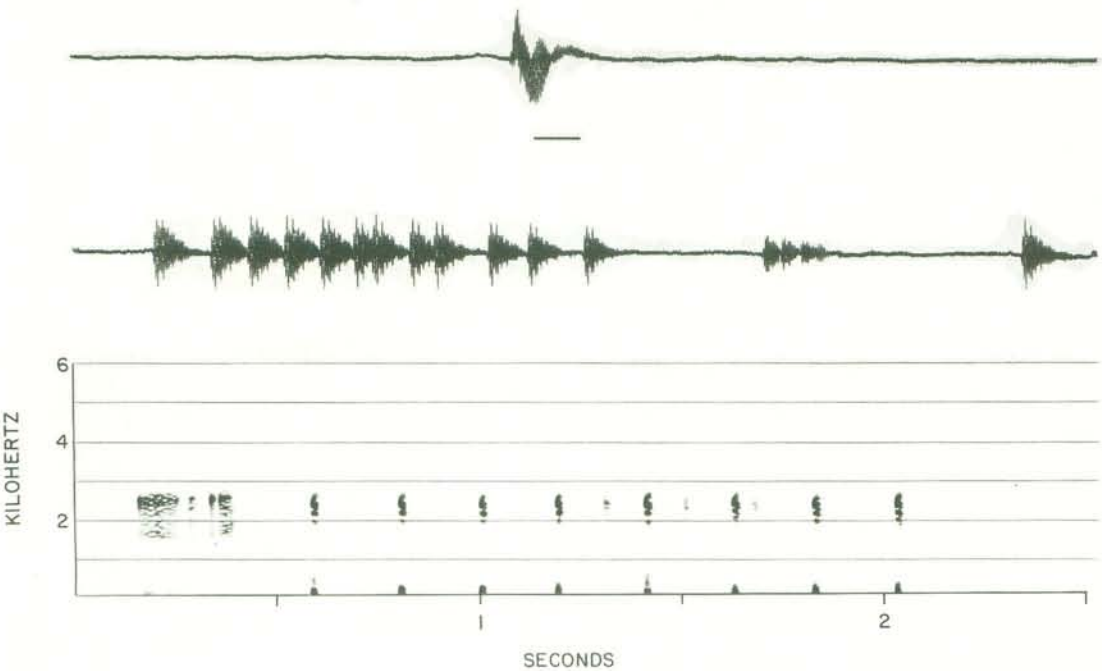

Figure 56. Advertisement calls of *Sphaenorhynchus orophilus*. In audiospectrogram, less common type precedes more commonly heard call type. Lower wave form of less common call on audiospectrogram, upper wave form of first note of more common call on audiospectrogram, scale line 0.01 s. All analyses figured bandstop filtered at 3% at 1300 Hz to remove strong frequency band of other frog species. Voucher specimen USNM 243668, recorded 21:15 h, 5 November 1983, 17-18° C air temperature.

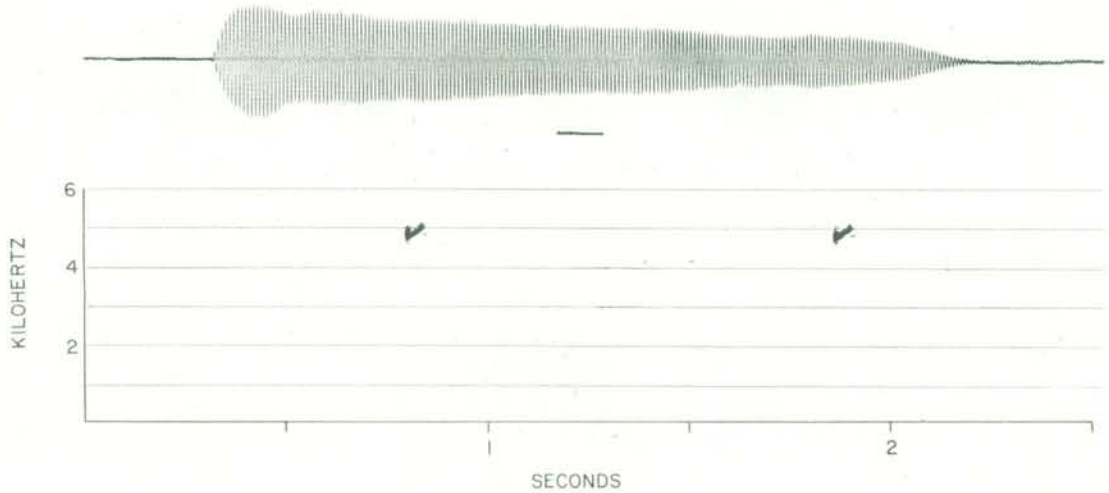

Figure 57. Advertisement call of *Adenomera marmorata*. Wave form of second call shown on audiospectrogram; signal high pass filtered at 1000 Hz; scale line 0.01 s. Audiospectrogram unfiltered. Recorded 12 December 1976, air temperature 18° C. Specimen not captured.

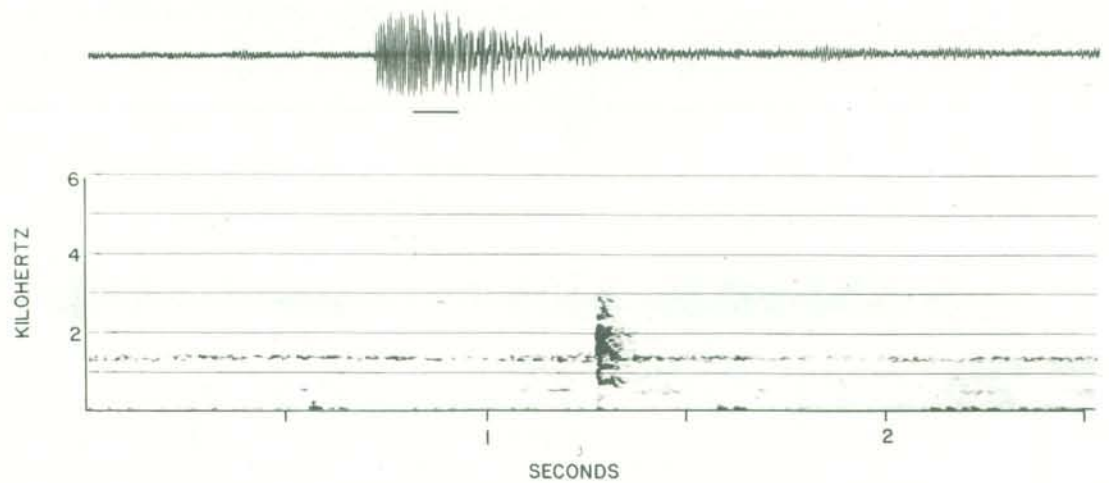

Figure 58. Advertisement call of *Cycloramphus boraceiensis*. Wave form signal highpass filtered at 500 Hz, scale line 0.01 s. Audiospectrogram unfiltered. Voucher specimen USNM 217937, recorded 15 December 1976, 19° C air temperature.

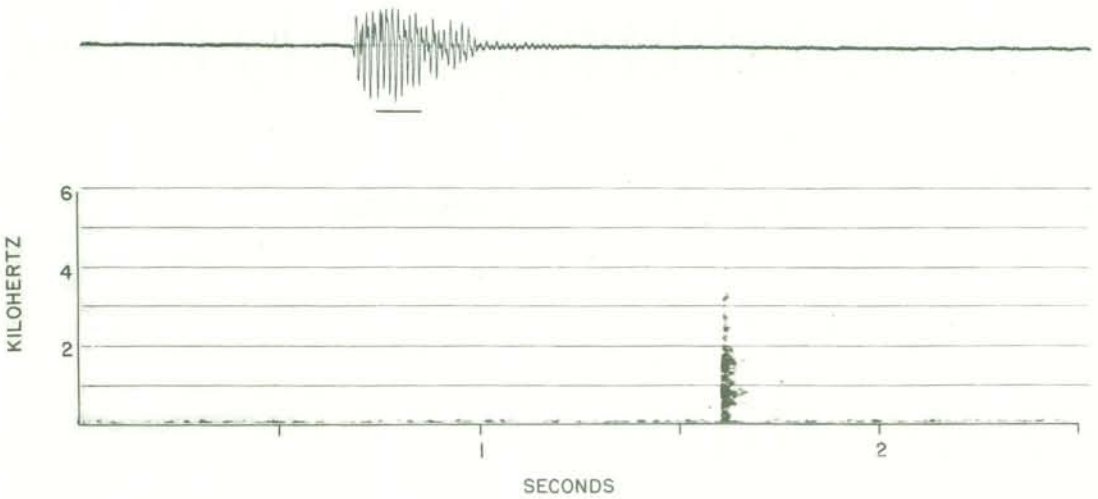

Figure 59. Advertisement call of *Cycloramphus semipalmatus*. Wave form signal highpass filtered at 100 Hz, scale line 0.01 s. Voucher specimen USNM 217923, recorded 7 December 1976, 21.8o C air temperature.

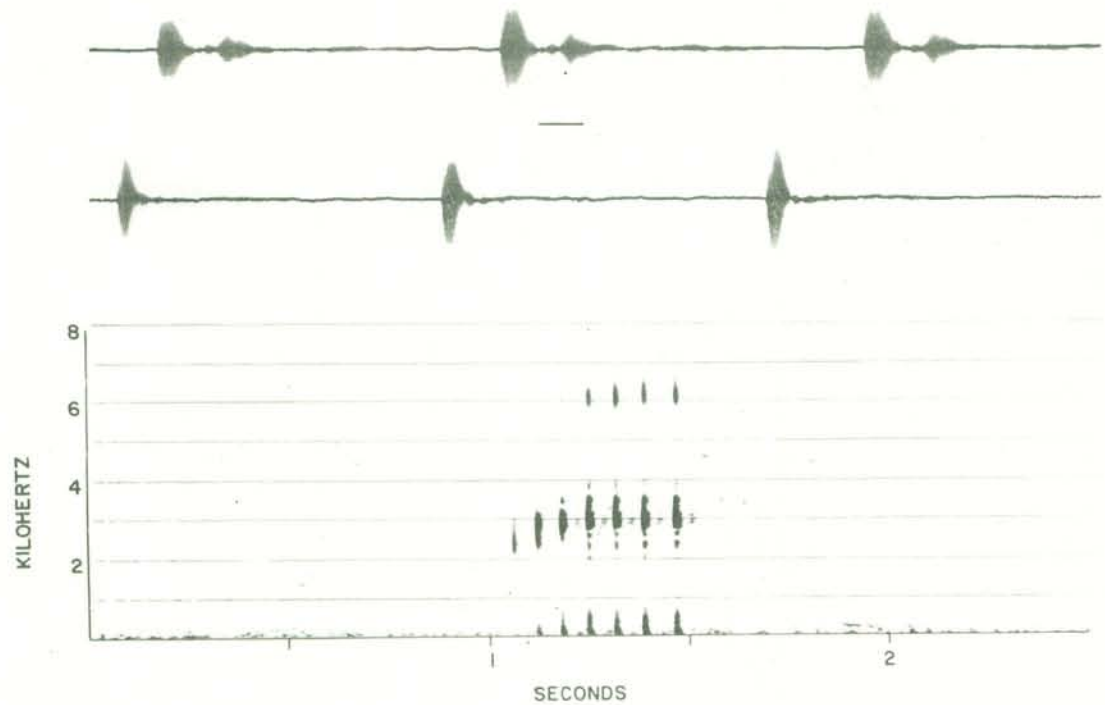

Figure 60. Advertisement call of *Eleutherodactylus guentheri*. Upper and lower wave form scale line 0.01 s; upper wave form showing three two-pulsed notes; lower wave form showing 3 single-pulsed notes of audiospectrogram call. Calling individual not captured, recorded at about 19:20 h, December 1984, air temperature 19.2° C.

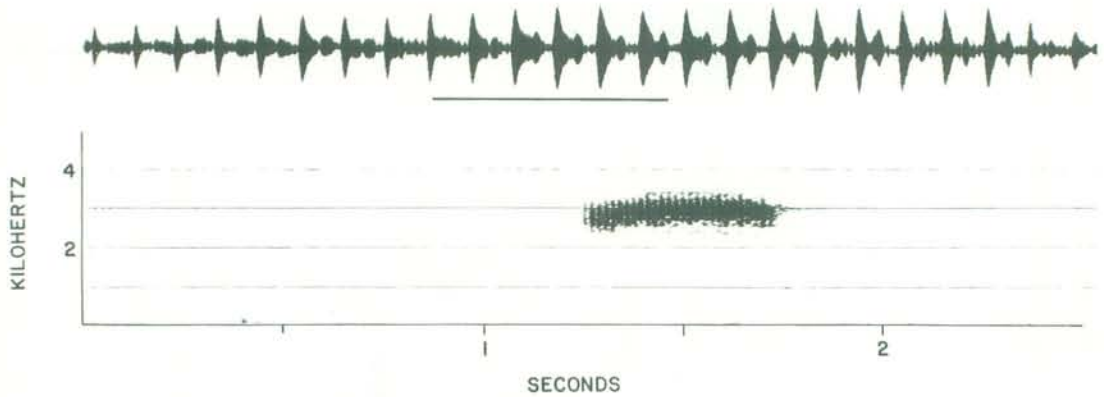

Figure 61. Advertisement call of *Eleutherodactylus parvus*. Wave form of portion of call shown in audiospectrogram, scale line 0.1 s. Specimen not captured, recorded at 20:47 h, 10 November 1983, air temperature 19.2° C.

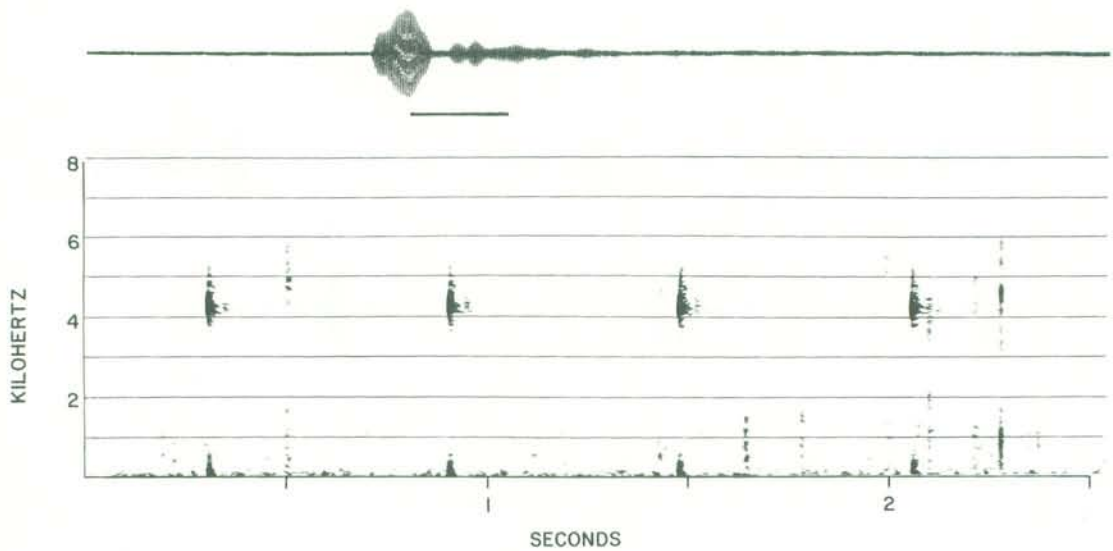

Figure 62. Advertisement call of *Eleutherodactylus randorum*. Wave form of a note highpass filtered at 3000 Hz, scale line 0.01 s. Voucher specimen MZUSP 59936, recorded 2 November 1983, about 19° C air temperature.

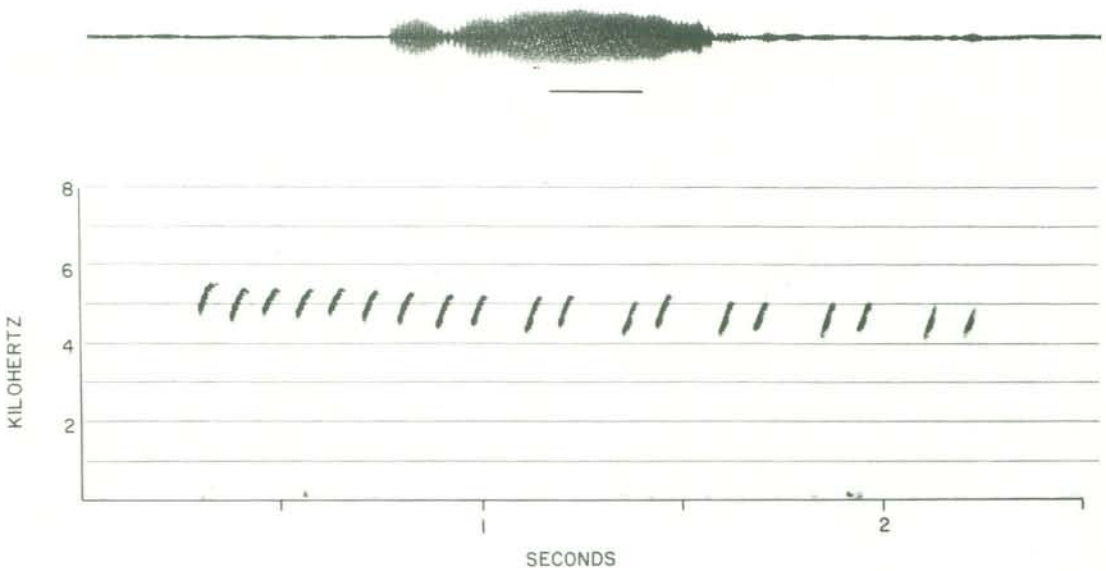

Figure 63. Advertisement call of *Hylodes phyllodes*. Wave form showing one note, scale line 0.01 s. Voucher specimen MZUSP 59934, recorded 15:30 h, 6 December 1976.

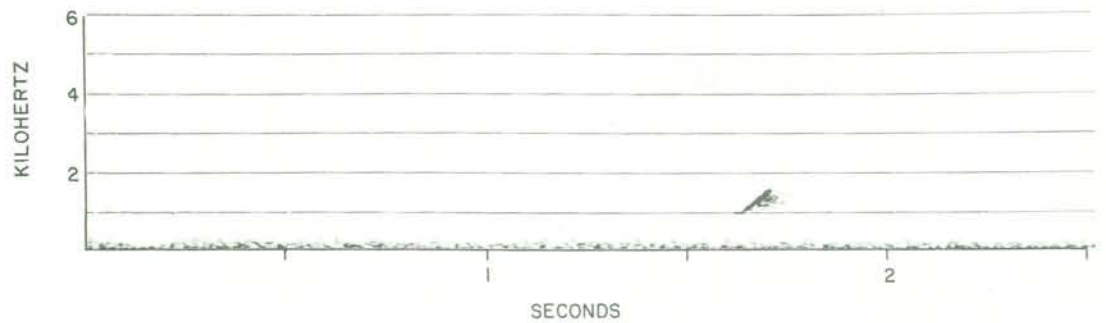

Figure 64. Advertisement call of *Leptodactylus fuscus*. Voucher specimen USNM 243685, recorded in laboratory at 19:15 h on 6 November 1983, 20-21° C air temperature.

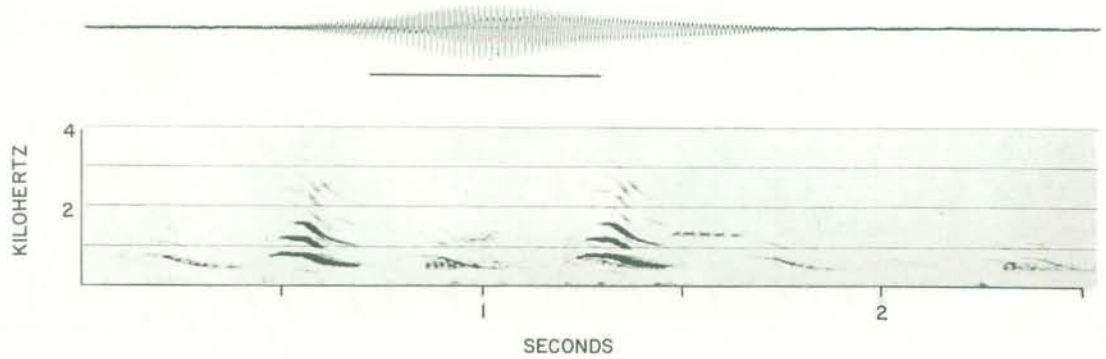

Figure 65. Advertisement call of *Physalaemus cuvieri*. Wave form scale line 0.1 s. Voucher specimen USNM 243710, recorded 6 November 1983, 19:50 h, 18.4° C air temperature.

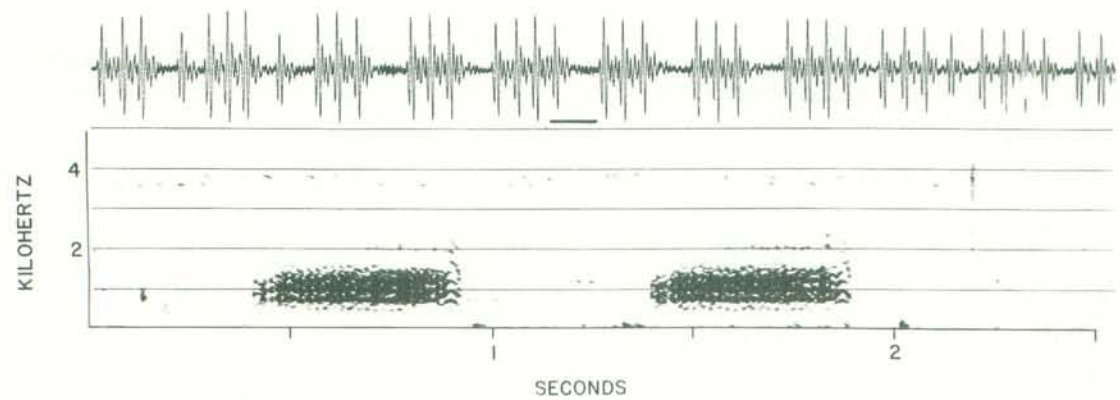

Figure 66. Advertisement call of *Physalaemus franciscae*. Wave form showing portion of call on left of audiospectrogram, scale line 0.01 s. Voucher specimen MZUSP 59935, recorded 8 December 1976, 21.5° C air temperature.

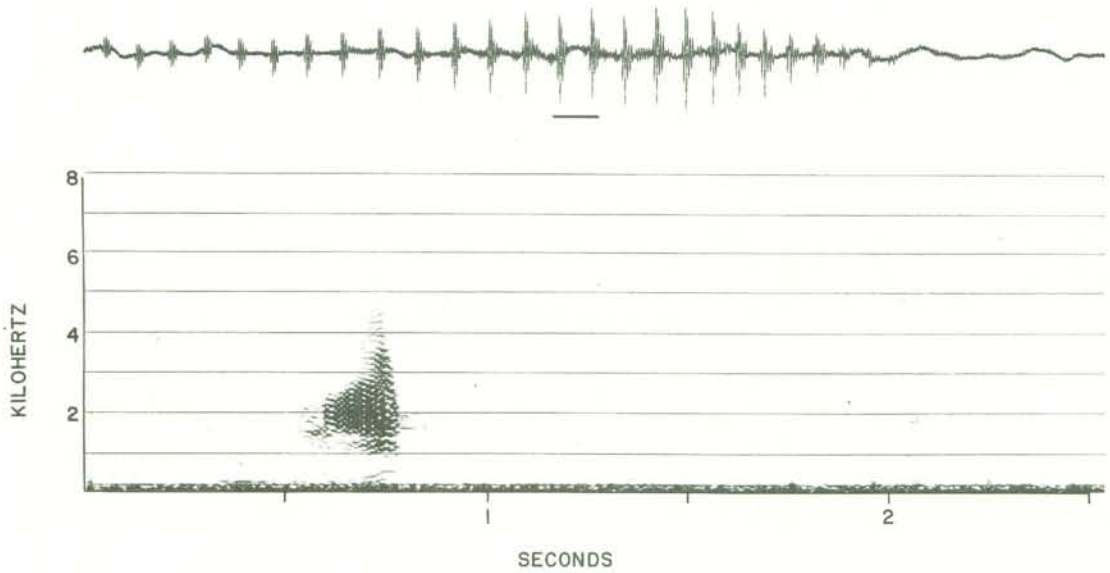

Figure 67. Advertisement call of *Physalaemus maculiventris*. Wave form scale line 0.01 s. Voucher specimen USNM 209262, recorded 8 December 1976, 21.5° C air temperature.

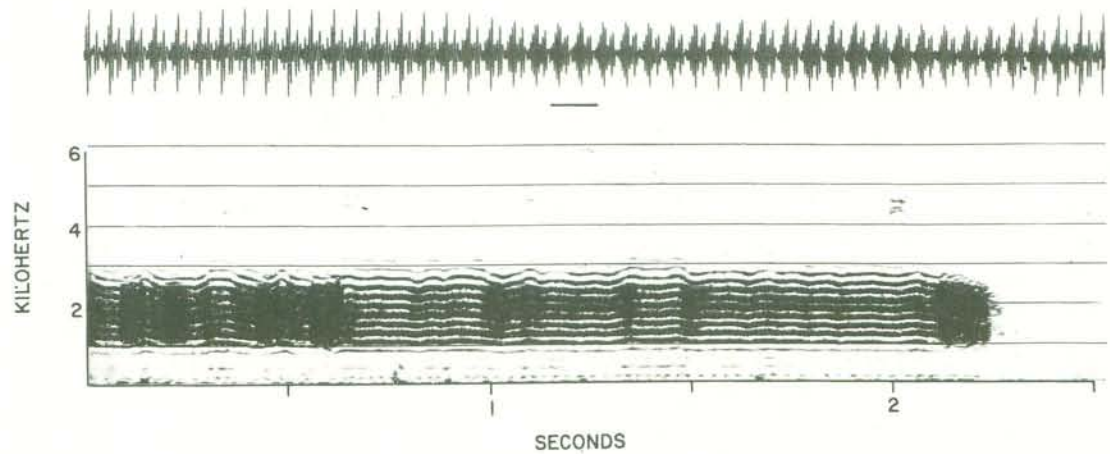

Figure 68. Advertisement call of *Physalaemus olfersi*. Wave form showing portion of call, scale line 0.01 s. Audiospectrogram of end of call. Call recorded 9 November 1971, 20.0° C air temperature, specimen not captured.

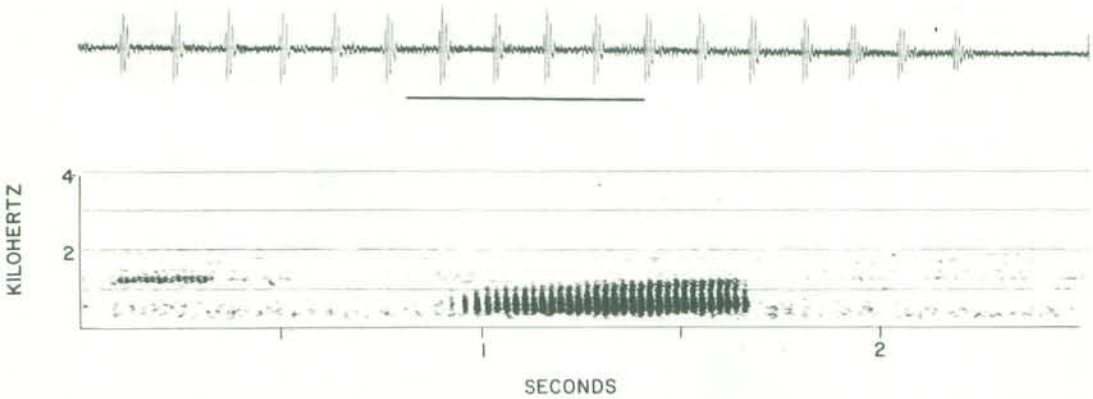

Figure 69. Advertisement call of *Proceratophrys boiei*. Wave form showing portion of call displayed below on audiospectrogram, scale line 0.1 s. Both displays of signals filtered by bandpass of 200-1250 Hz. Voucher specimen MZUSP 60670. Recorded 21:00 h, 4 December 1984, air temperature 19.4° C.

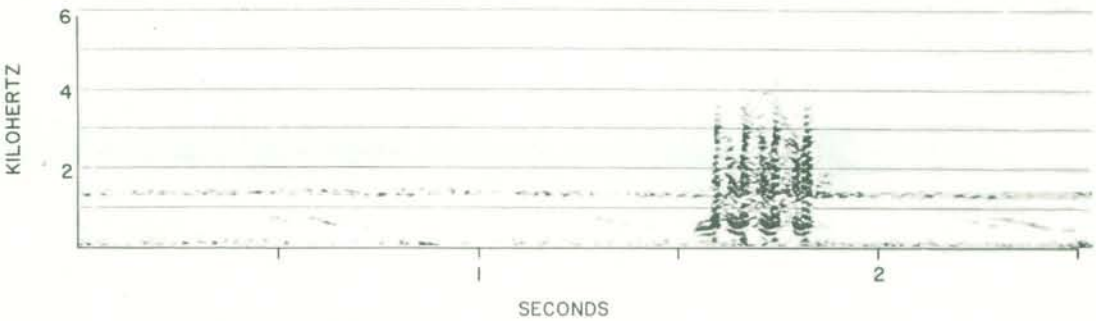

Figure 70. Advertisement call of *Thoropa miliaris*. Voucher specimen USNM 209326, recorded 15 December 1976, 19° C air temperature.

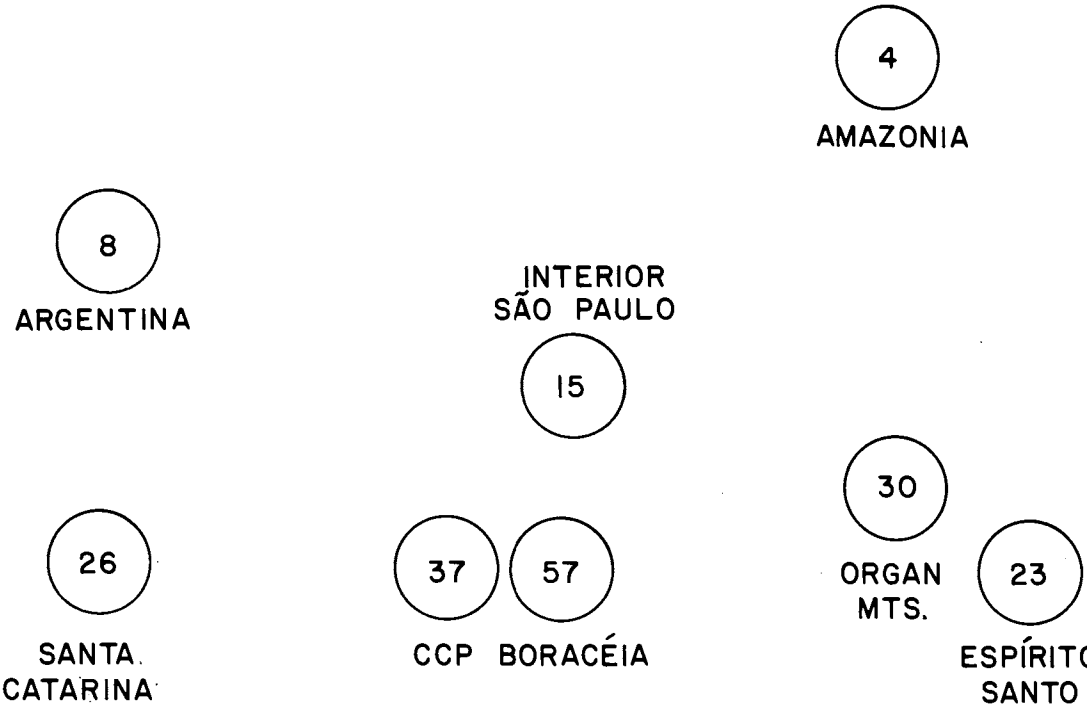

Figure 71. Representation of Boracéia species with adequate distributional data at other selected localities. CCP = Cubatão-Caminho do Mar-Paranapiacaba region, Espírito Santo and Santa Catarina = records for the respective states.

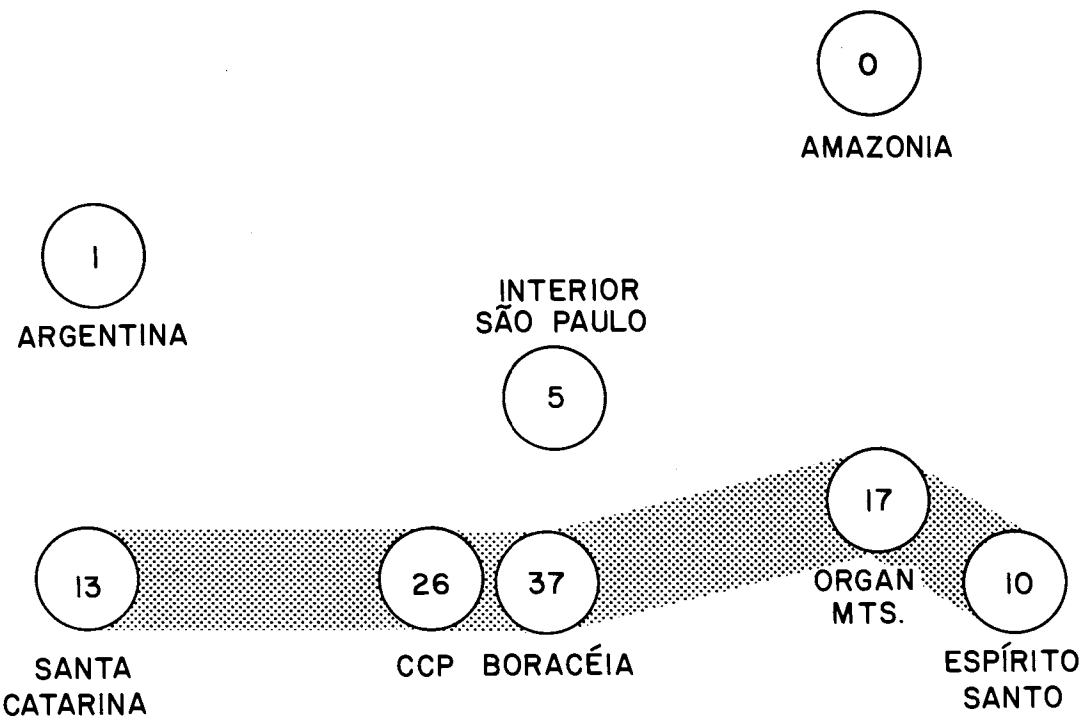

Figure 72. Representation of Boracéia species that characteristically occur in forests at other selected localities. CCP = Cubatão-Caminho do Mar-Paranapiacaba region, Espírito Santo and Santa Catarina = records for the respective states. Stippling connects localities within the Atlantic Forest Morphoclimatic Domain.

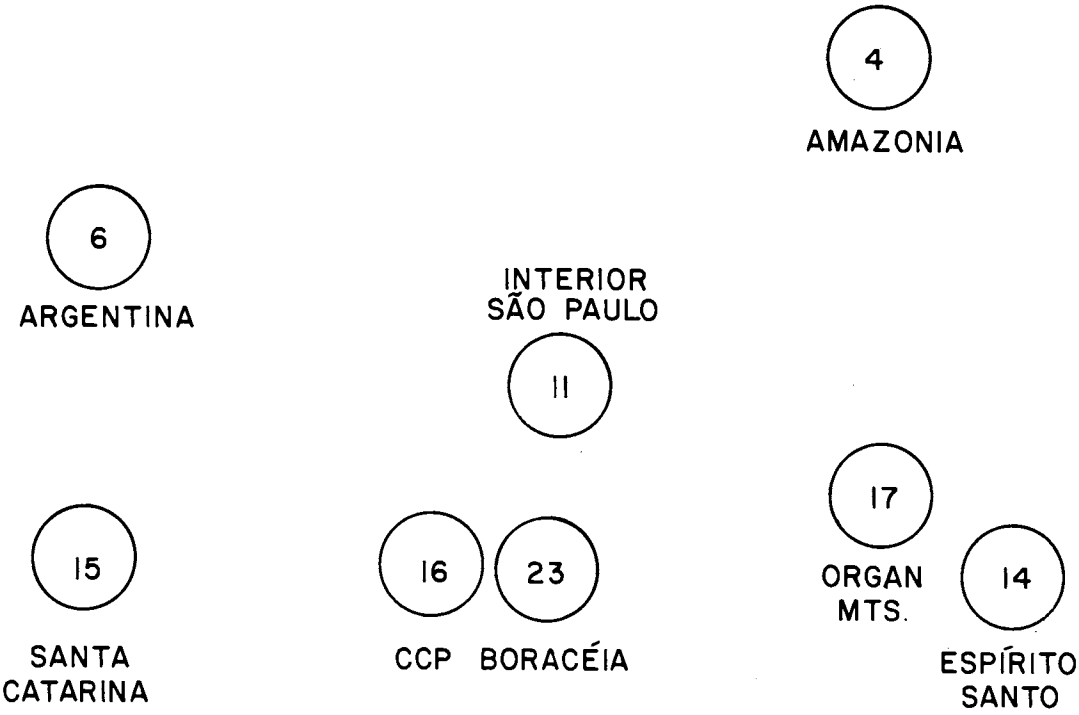

Figure 73. Representation of Boracéia species that characteristically occur in open formations at other selected localities. CCP = Cubatão-Caminho do Mar-Paranapiacaba region, Espírito Santo and Santa Catarina = records for the respective states.

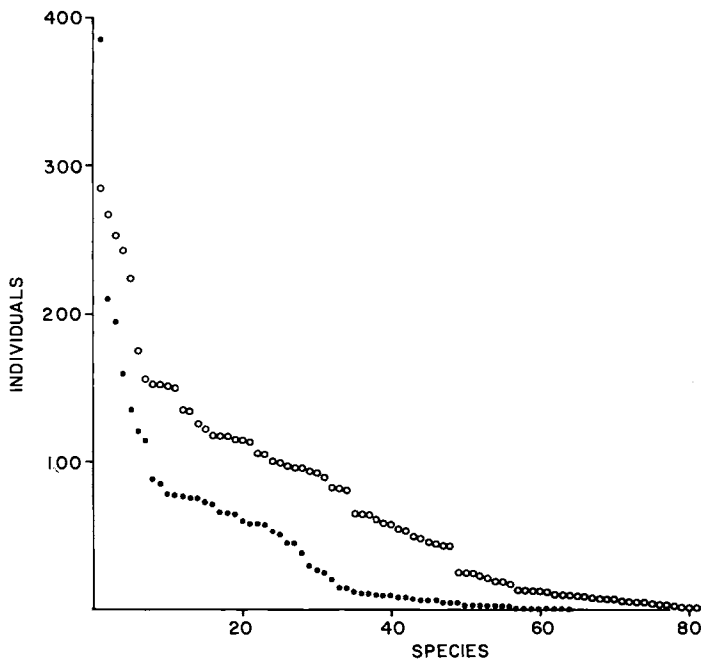

Figure 74. Number of individuals per species, ranked from most common in collections to most rare in collections. Dots = Boracéia data, circles = Santa Cecilia data.

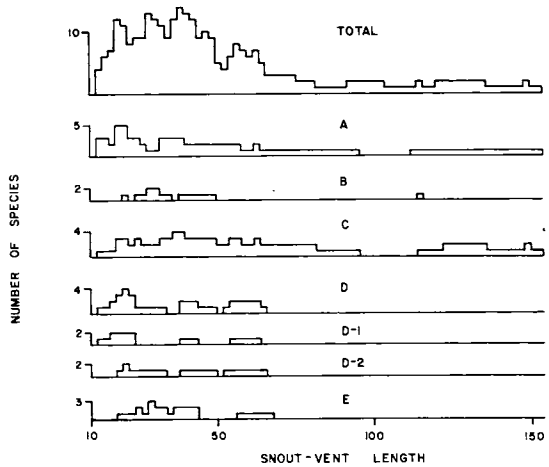

Figure 75. Snout-vent length distributions for all Boracéia adult frogs (total) and adult guilds represented by 5 or more species. A = ground level, sit-and-wait, diurnal predator guild; B = seep or streamside, sit-and-wait, diurnal predator guild; C = ground level, sit-and-wait, nocturnal predator guild; D = understory level, sit-and-wait, nocturnal predator guild, D-1 = forest species of the understory level, sit-and-wait, nocturnal predator guild, D-2 = open formation species of the understory level, sit-and-wait, nocturnal predator guild; E = canopy level, sit-and-wait, nocturnal predator guild.

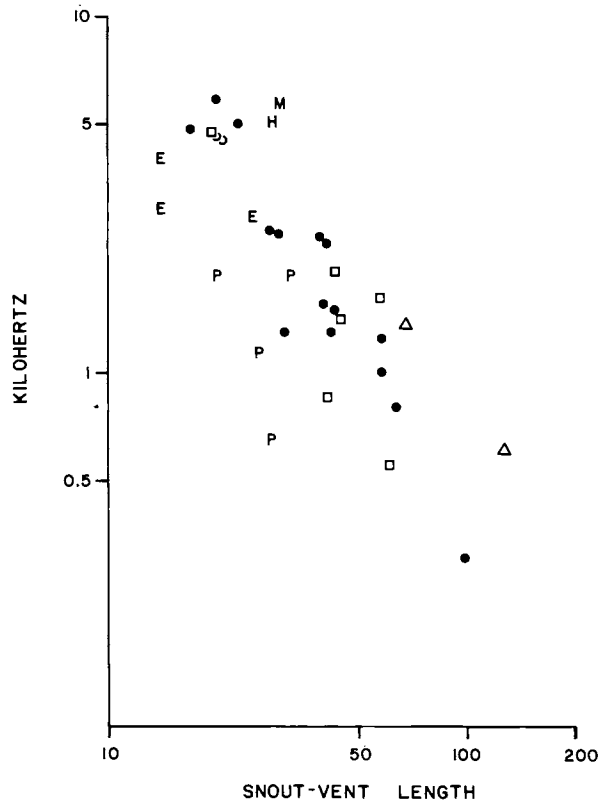

Figure 76. Log-log plot of mean carrier frequency versus snout-vent length for frogs of Boracéia for which calls were analyzed. Dots = hylids, circles = centrolenids, squares = leptodactylids, triangles = bufonids; M = *Hyla polytaenia*, H = *Hylodes phyllodes*, E = *Eleutherodactylus* species, P = *Physalaemus* species.

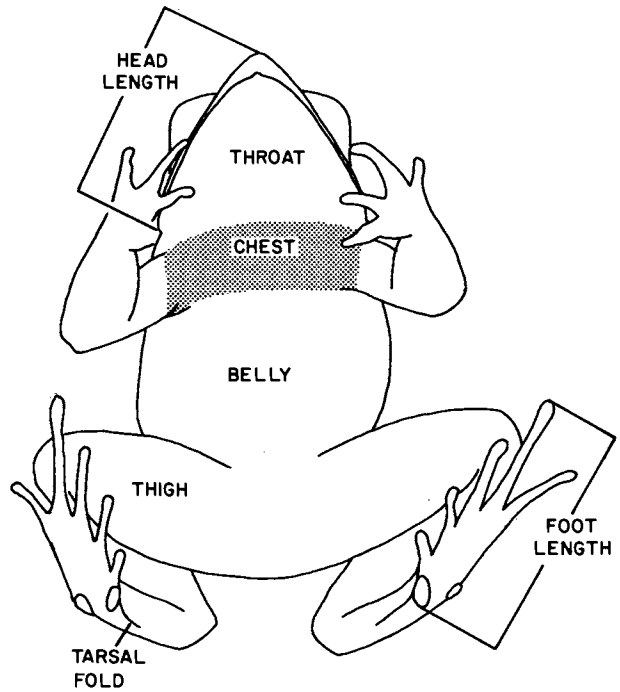

Figure 77. Ventral view of diagrammatic frog showing some terms used in text. Chest region indicated by stippling.

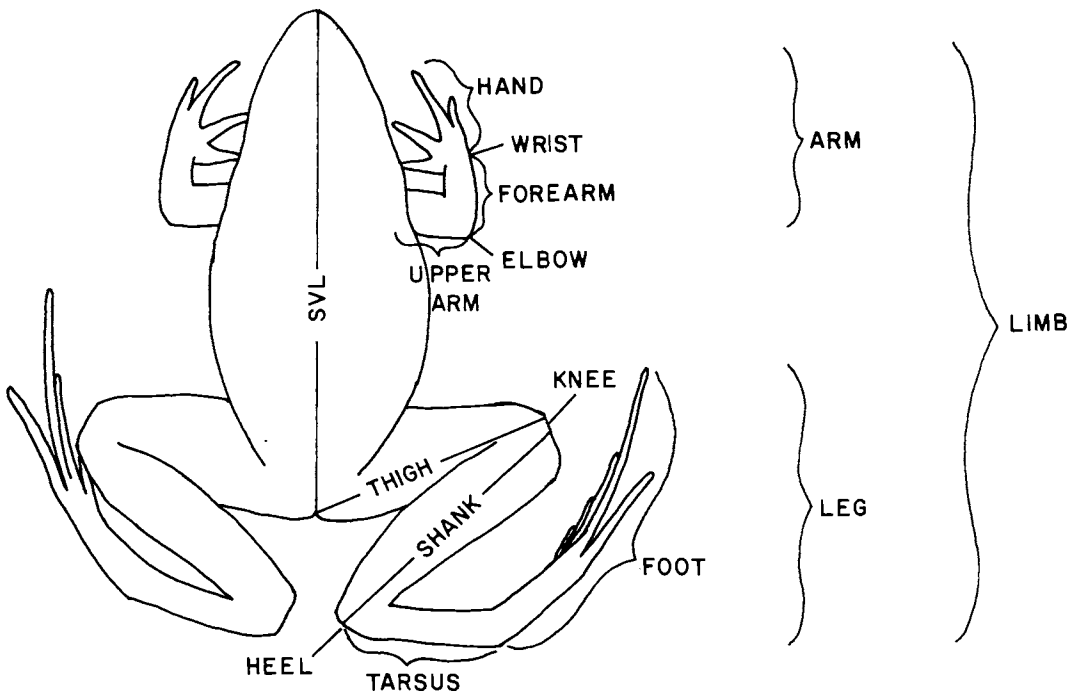

Figure 78. Dorsal outline of diagrammatic frog showing some terms used in text. SVL = snout-vent length.

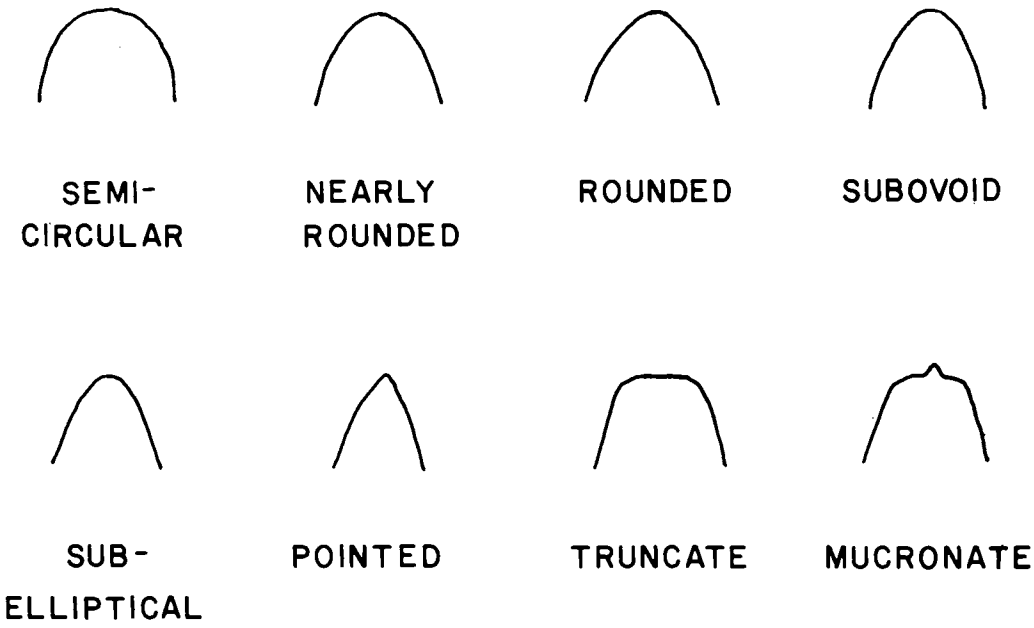

Figure 79. Dorsal outline of snout standards as used in text.

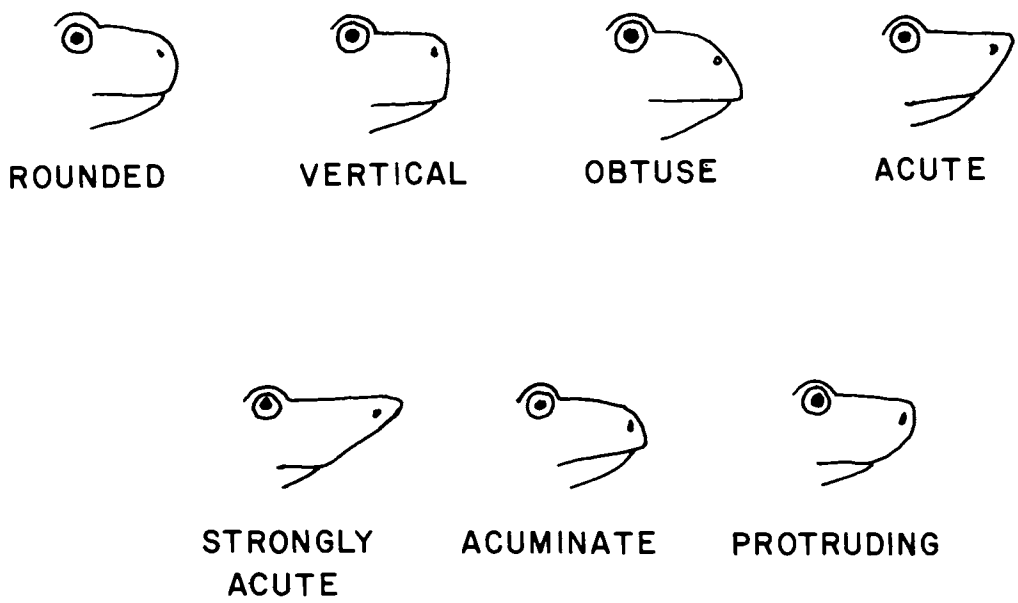

Figure 80. Snout profile standards as used in text.

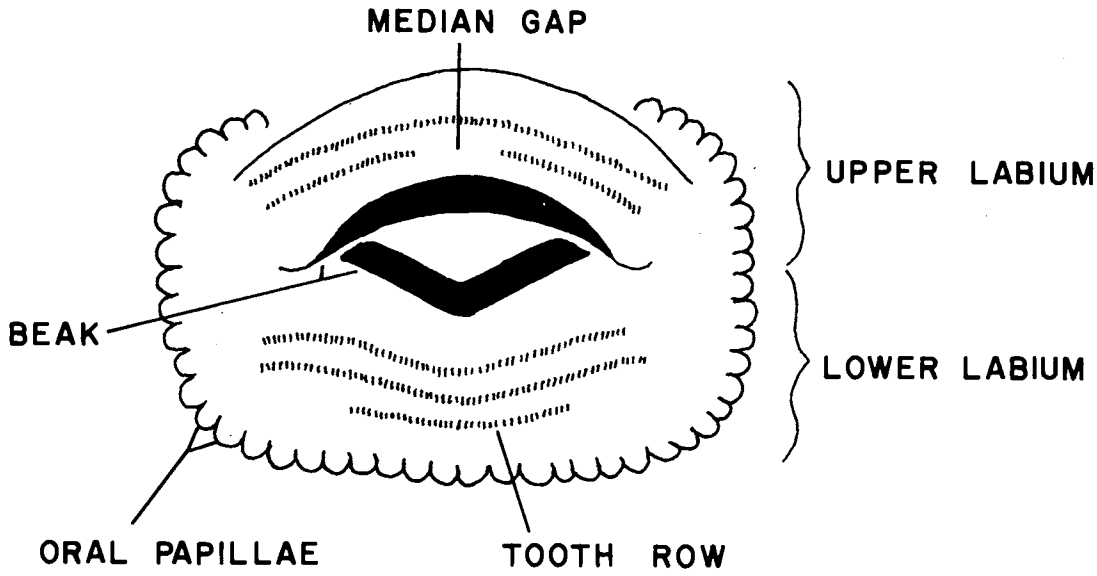

Figure 81. Diagrammatic figure of larval mouthparts showing some terms used in text.

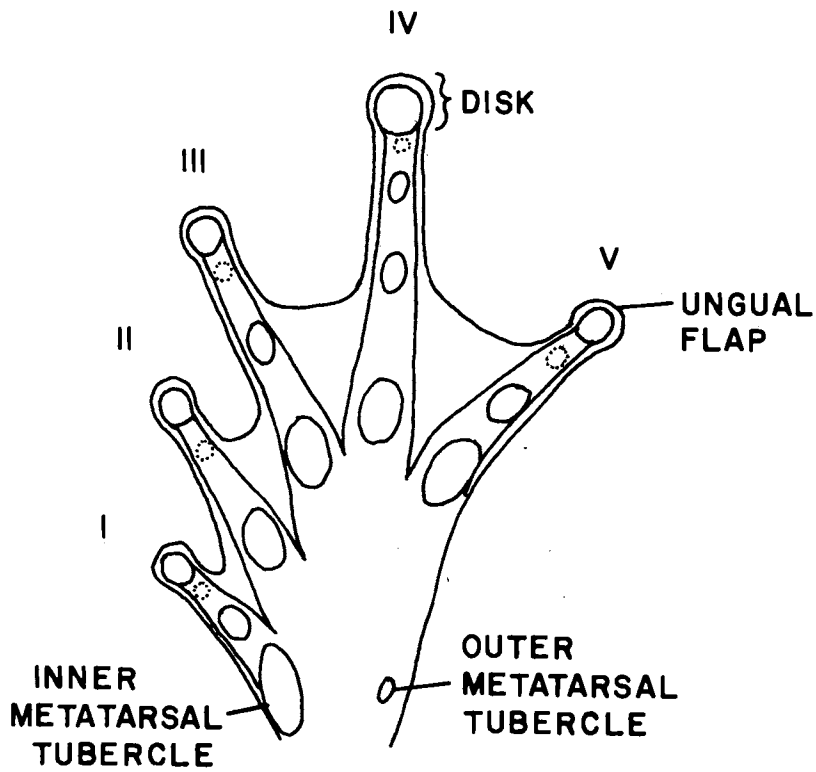

Figure 82. Diagrammatic figure of ventral view of left foot showing some terms as used in text. Toes numbered by Roman numerals. The webbing formula shown is I 1-2 II 1-2 1/2 III 1 1/2-3+ IV 3-1 V.